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Nowhere to run: semi-permeable barriers affect pronghorn space use

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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. Pronghorn (*Antilocapra americana*) habitat in western North America has been fragmented by roads, railways, and fences. Although pronghorn are sensitive to barriers, neither the relative permeability of different barriers to crossing nor their influence on space use have been quantified. We used a large global positioning system (GPS)-collar dataset of pronghorn ($n = 1{,}010$ animal-years) in Wyoming, USA, to first quantify the likelihood that pronghorn cross each of 5 different anthropogenic barriers, including fences, county roads, railroads, state highways, and interstate highways (i.e., interstates). Next, we assessed how each barrier influenced pronghorn space use during the winter as indexed by the area occupied, and daily displacement relative to the density of barriers on an individual's winter range. The semi-permeability of the 5 barriers varied substantially, with the interstate being the most severe barrier to pronghorn movement. Pronghorn were >300 times less likely to cross interstates compared to state highways. Although pronghorn space use was rarely influenced by barriers within individual core winter ranges, pronghorn space use was constrained by barriers on the buffered periphery of individual winter ranges. Despite their different permeability to movement, the density of fences and combined interstates and railroads had similarly negative effects on pronghorn space use. Our results illustrate that the degree to which pronghorn

avoid crossing barriers may scale up to affect access to habitat. Additionally, our results indicate that the effects of barriers on habitat access are not proportional to their permeability. Our results add to a growing consensus that effective management of mobile species depends on understanding how different kinds of semi-permeable barriers influence access and use of habitats.

Anthropogenic habitat fragmentation is one of the greatest threats to biodiversity and ecosystem function (Haddad et al. 2015, Crooks et al. 2017). Nonetheless, independent of habitat loss, the ecological consequences of fragmentation 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 based on their movement capacity (Wiens 1989, Ricketts 2001). Behavior and 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 accounting for movement behavior, the patchiness of habitats does not necessarily imply habitat fragmentation. Meanwhile, the growing subdiscipline of movement ecology has contributed to the understanding of the interaction between an animal's movement and the landscape (Nathan et al. 2008, Cagnacci et al. 2010). Merging the methods of movement ecology with fragmentation research can help quantify the ecological consequences of human development.

Anthropogenic linear features (e.g., roads, railways, fences) have become a ubiquitous disturbance for many wildlife species (Forman and Alexander 1998). For example, in the western United States all landlocked locations are within 35 km of a road (Watts et al. 2007) and within 48 km of a fence (McInturff et al. 2020). 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 and manage grazing intensity (Li et al. 2017, Løvschal et al. 2017, McInturff et al. 2020). Linear features can directly affect wildlife populations through vehicle collisions or fence entanglement (Jaeger et al. 2005). When linear features restrain animal movement, they can pose a pervasive indirect threat to populations (Forman and Alexander 1998, Jaeger et al. 2005). Specifically, by limiting movement and fragmenting habitat, linear features 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 that rarely cross barriers will underuse otherwise available habitat (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 the animal's movement behavior and the structure of the barrier, which together influence permeability. Less permeable barriers are crossed less frequently than more permeable barriers, which creates a gradient of access to bordering habitat as a consequence of infrequent crossings (Dyer et al. 2002, Beyer et al. 2016). Barriers impermeable to crossing cause bordering habitat to be inaccessible; however, when barriers are semi-permeable, their effects on habitat access are less clear (Kozakiewicz 1993, Beyer et al. 2016). For instance, changes to the permeability of patch boundaries in metapopulations have nonlinear effects on emigration, gene flow, and population dynamics (Stamps et al. 1987, Ries et al. 2004). Along barriers, differences in permeability may similarly have a nonlinear effect on larger scale

processes such as emigration (Frair et al. 2008), yet this expectation has rarely been tested. Advances in wildlife tracking data and movement ecology (Kranstauber et al. 2012, Thurfjell et al. 2014) can provide tools to directly quantify the species-specific permeability of barriers, and their effects on space use.

Pronghorn (*Antilocapra americana*) habitats in western North America are intersected by linear networks of roads and fences (Knick and Rotenberry 1997, Davies et al. 2011, Jones et al. 2019). Pronghorn rarely jump over fences and often will either cross under the fence if the bottom wire is high enough from the ground, or forgo crossing and quickly move away from the fence (Byers 1997, O'Gara and Yoakum 2004, Harrington and Conover 2006, Jones et al. 2020, Xu et al. 2021). At northern latitudes and when free to move, pronghorn are facultative migrants, where the distance and direction of movement is conditional on winter severity (Bruns 1977, O'Gara and Yoakum 2004, Jakes et al. 2018*a*). Barriers that inhibit the movements of pronghorn have contributed to population crashes by limiting access to available habitat (Martinka 1967, Oakley and Riddle 1974, Barrett 1982, Ryder et al. 1984). For example, in 1983 a winter storm in south-central Wyoming, USA, 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 space use, which ultimately will promote access to surrounding habitat, but the degree to which semi-permeability of barriers impedes space use remains unclear. Quantifying the relationship between barrier permeability and pronghorn space use will help managers assess the ecological consequences of barriers and prioritize which barriers to mitigate.

The objectives of our study were to quantify the permeability of anthropogenic linear features (i.e., fences, county roads, state highways, railroads, and interstate highways) and then assess how permeability influenced space use of pronghorn across southern Wyoming. We used space use as an indicator of habitat access, where more constrained use of space implies limited access to habitat. We reasoned that pronghorn near less permeable barriers should have more constrained space use than pronghorn near more permeable barriers. Thus, we expected that space use as measured by individual areas of winter range and daily displacements should increase as nearby barriers become more permeable.

STUDY AREA

We used a global positioning system (GPS) dataset of movement data from 7 pronghorn populations in southern Wyoming: Red Desert, Bitter Creek, Sublette, Medicine Bow, Baggs, Uinta-Cedar, and Carter Lease populations between 2002 to 2020 (~80,000 km^2; Figure 1). Across populations, climate was generally characterized by cold winters (Dec–Mar) and dry summers (Jun–Sep) with relatively cold springs (Mar–Jun) and autumns (Sep–Dec). Across populations, 30-year average annual precipitation ranged from 25 cm/year to 52 cm/year. The average minimum temperature in January ranged from −15°C to −11°C, and the average maximum temperature in July ranged from 25°C to 29°C (PRISM Climate Group 2014). The average elevation was 2,200 m. The Medicine Bow and Baggs populations were in south-central Wyoming, an arid to semiarid sagebrush (*Artemisia* spp.)-steppe with Wyoming big sagebrush (*A. tridentata wyomingensis*) as the predominant vegetation cover, with mountains to the west characterized by stands of alderleaf mountain mahogany (*Cercocarpus montanus*), aspen (*Populus tremuloides*), and limber pine (*Pinus flexilis*; Taylor et al. 2016). We included pronghorn in eastern Platte Valley with the Baggs population to maintain equivalent sample sizes across populations. The Bitter Creek, Sublette, Uinta-Cedar, Red Desert, and Carter Lease populations 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. t. vaseyana*), mixed shrubland, and aspen (Reinking et al. 2018). Land use in this area included livestock grazing, hunting, and oil and natural gas extraction.
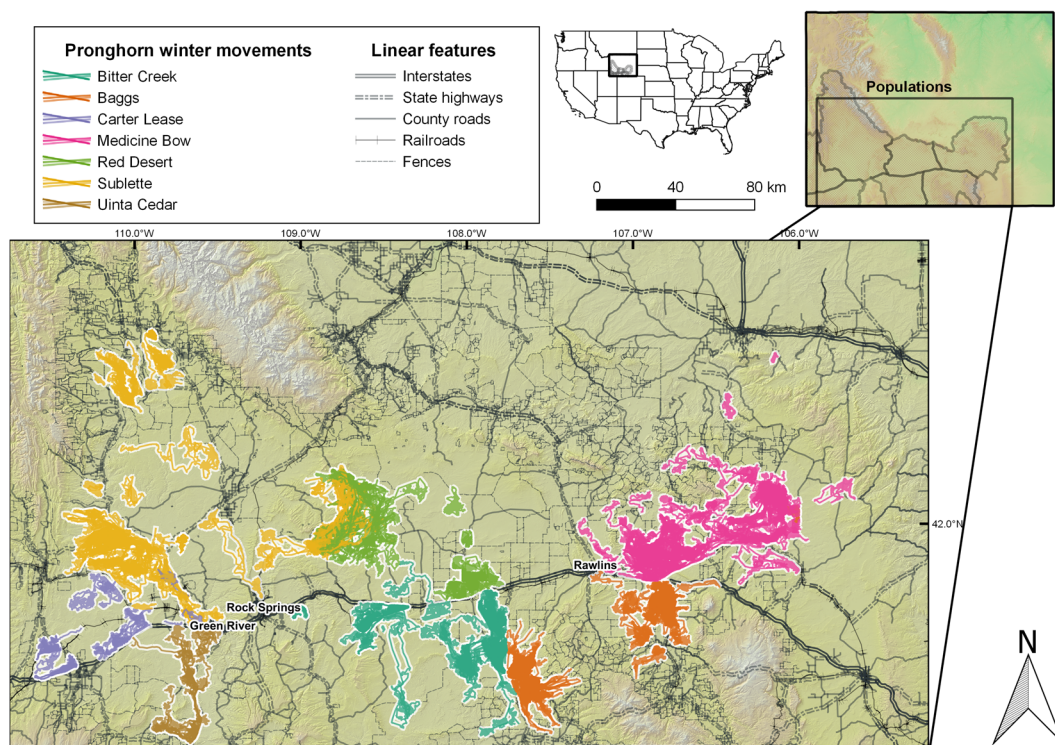
FIGURE 1 Pronghorn movements during winter from the 7 different populations in Wyoming, USA, 2002–2020.

METHODS

Across study sites, we equipped pronghorn with GPS-collars that collected locations at programmed fix rates of 1–2 hours (if tracked after 2012), 4 hours (Sublette 2009–2011), or 7–8 hours (all other populations tracked before 2012). Years of pronghorn tracking varied by population; the Medicine Bow population was tracked in 2010–2012 and 2018–2020; the Baggs population was tracked in 2010–2015; the Bitter Creek population was tracked in 2013–2020; the Sublette population was tracked in 2002–2003, 2009–2011, 2013–2015, and 2017–2020; the Uinta-Cedar population was tracked in 2017–2020; the Red Desert population was tracked in 2013–2016; and the Carter Lease population was tracked in 2002–2003 and 2017–2020. We used GPS-collars from Advanced Telemetry Systems (Isanti, MN, USA; models G2110D and G2110B), Telonics (Mesa, AZ, USA; models TGW-3400 and RECON-4560-4 Globalstar), and Lotek Wireless (Newmarket, ON, Canada; models GlobalstarTrack Pro L and Litetrack Iridium-420). Of the original GPS data, only 2 groups of collars had a fix success <95%, which were the collars within the Sublette and Carter Lease populations between 2002–2003 (accuracy = 81.6%), and the Medicine Bow pronghorn between 2018–2020 (accuracy = 88.9%). Thus, the majority of collars had a fix rate success greater than 95%.

Step-selection function

To calculate permeability to anthropogenic features, we used a step-selection function framework to quantify the relative odds of crossing linear features. A step-selection function estimates the odds an animal will move to a

location, given what is available to the animal. Thus, the beta coefficients in our step-selection function measured semi-permeability as the odds an animal will cross a linear feature when available. When no linear feature is available, then the given step does not contribute to the beta coefficient of each linear feature. Our quantification of semi-permeability is only interpretable up to the odds ratio of 1. Because of the sensitivity of step-selection functions to different intervals in time between points (Thurfjell et al. 2014), we subsampled the dataset to 7- or 8-hour fix rates (a 29.6% reduction in the original dataset). Pronghorn in the Medicine Bow and Uinta-Cedar populations had 7-hour fix rates; all others had 8-hour fixes. To reduce pseudoreplication, we randomly sampled 1 step/day for every animal-year. Additionally, we removed any animal-years that had <90 GPS fixes to ensure convergence (loss of 14 animal-years out of 1,028).

In the step-selection function framework, barrier types were separated into 5 layers: fences, county roads, state highways, interstates, and railroads. We combined fence datasets from Sweetwater and Uinta counties (E. De Groot, Wyoming Cooperative Fish and Wildlife Research Unit, unpublished data) with fence data from the Bureau of Land Management (BLM) Rawlins Field Office (compiled by BLM) and Casper Field Office (R. H. Mathis and D. C. Burger, BLM, unpublished data). To merge the datasets and avoid duplication, we removed all fences from the Rawlins BLM Field Office that overlapped with a convex polygon of the fence dataset in Sweetwater and Uinta counties, then we removed all fences from the Casper Field Office within a convex polygon of the merged Sweetwater and Uinta County–Rawlins Field Office fence data. Although there have likely been some changes as to fence presence since these data were compiled, we were comfortable with the assumption that overall, these fence data accurately represented fence locations throughout our study period. Moreover, in our study area there have not been substantial changes in land ownership, which is a strong correlate to fence presence (Poor et al. 2014).

Road and railroad data were available from the Wyoming Department of Transportation (WYDOT 2018). We categorized road layers as either county roads, state highways, or interstates. We classified county roads as all roads with county administration that were 2-lane paved roads. We classified state highways as 2- or 4-lane state highways usually with right-of-way fences (fences along major highways). Interstates consisted of Interstate 80 and Interstate 25, 4-lane roads with right-of-way fences or game-proof fences. Interstates had the highest daily traffic volume, followed by state highways, with county roads having the lowest daily traffic volume (WYDOT 2020). Railroads consisted of the 2 major railroads in Wyoming. Any barrier effect by state highways and the interstate included the barrier effects of state mandated right-of-way fencing (often woven-wire; WY-DOT, unpublished data) and occasional game-proof fencing. In our analyses, we could not differentiate the degree to which the roads or their associated right-of-way fencing caused a barrier effect. Thus, highways and interstates instead estimated the combined linear feature of the road and the nearby fencing. To avoid conflating interior pasture fences with right-of-way fences, we removed any fences within 250 m of state highways and the interstate. Otherwise, pronghorn crossings of state highways and interstates would have been correlated with crossings of fences. Thus, by removing right-of-way fences neighboring highways from our geographic information system, our covariates of state highways and interstate measured the collective semi-permeability of the road and neighboring right-of-way fence. Only 40% of our fence dataset included attributes for the type of fencing. Nonetheless, where we had attributes for types of fences, the interstate was predominantly fenced with woven-wire along the right-of-way (434 km). Four-wire strand was the predominant type of fencing along state highway right-of-ways (962 km). These estimates confirmed our expectations that interstates were fenced with woven-wire, and state highways were fenced with woven-wire or 4–5-strand fences (R. S. Gamo, WYDOT, personal communication). Interstates also had 80 km of game-proof fencing, and state highways had 75 km (B. S. Robb, University of Wyoming, unpublished data). Four-wire strand was also the predominant fence type along county road right-of-ways (577 km); however, these fences were often along frontage roads parallel to a highway, or were highly fragmented and were more likely interior pasture fences than right-of-way fencing. Moreover, county roads were primarily located within just 1 grazing allotment, which confirmed our expectation that these roads were characterized by open range with minimal fencing along the right-of-way (BLM and U.S. Forest Service, unpublished data). We separated railroads and interstates in the step-selection function, but we summed

the densities of each for all further analysis because railroads often paralleled interstates so their densities were collinear (variance inflation factor > 2; Zuur et al. 2009).

To quantify the permeability of different barriers, we used a step-selection function, with 10 random steps for every observed step (the straight-line distance between consecutive GPS fixes; Fortin et al. 2005, Thurfjell et al. 2014). We drew random steps simultaneously with replacement from the observed distribution of step lengths and angles across the dataset, with a maximum length of 4,896 m (the 99th percentile of empirical pronghorn step lengths for every 7–8 hr between GPS fixes). Covariates were binary variables indicating whether a given barrier was crossed during a step. We included step length to reduce bias in estimated step-selection function coefficients (making it an integrated step-selection function; Avgar et al. 2016). We fit step-selection functions with a mixed effects conditional Poisson model with a large, fixed variance of 10^3 to avoid shrinkage of the intercepts towards the overall mean (Muff et al. 2020). We included random slopes for each of the 5 linear features relative to each animal-year, nested by their population to account for the hierarchical structure of our dataset. Additionally, including random slopes for each of the 5 linear feature covariates provided the opportunity to assess whether there were differences in barrier permeability among individuals. Our final sample size for the step-selection function analysis was 1,010 animal-years and 176,304 used steps. Of the animal-years, 364 animals were tracked for >1 year.

Area analysis

To assess the effects of barriers on space use, we regressed the area pronghorn occupied in the winter as a metric of space use relative to barrier densities within those winter ranges. Because previous studies illustrate comparable dates of migration across populations (Robb 2020), we defined pronghorn as on winter range between 3 January and 14 March, which were the respective 75th percentile of when autumn migrations ended and 25th percentile of when spring migrations began (visualized through net-squared displacement; Bunnefeld et al. 2011). Movement barriers can circumscribe the outer bounds of pronghorn home ranges (Sheldon 2005), and thus are often overlooked with typical delineations of individual winter range. Therefore, we ran separate analyses incorporating barriers within core individual winter range and within a buffered winter range, which gave insight to the differences between interior barriers and barriers at the periphery of each animal's individual winter range for a given year. We defined core winter ranges of individuals as the 95% contour of the utilization distribution from a dynamic Brownian bridge (Kranstauber et al. 2012). We defined buffered winter range as the core winter range buffered by half the average weekly distance pronghorn moved, 11.4 km. To assess whether our results were sensitive to this buffer distance, we reran this analysis with a buffer distance of 1 km, 5 km, 15 km, and 20 km. Only the effects of county road density and state highway density were sensitive to buffer distance (Table A1). We calculated winter ranges only for animals tracked for ≥7 days in a given year (loss of 38 animal-years) and had >31 GPS points (loss of 2 animal-years).

To test whether space use as measured by winter range area should increase as nearby barriers become more permeable, we used a generalized linear regression to compare the area that pronghorn occupied relative to the densities of each barrier within individual core and buffered winter ranges. We estimated barrier densities as the density (km/km^2) of each barrier within each animal core or buffered winter range for each year; the response variable was the area (km^2) of the 95% contour of the utilization distribution. We fit a generalized linear mixed effects model with a gamma distribution, log link, and population as a random intercept to the core and buffered winter range models. In the winter range analysis, sample size was 682 animal-years.

Displacement analysis

To further assess the effects of barriers on space use, we regressed the mean daily displacement (km) of pronghorn in the winter relative to the density of barriers within core and buffered 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. We included only animal-years that had an estimated individual winter range in the mean daily displacement analysis (loss of 40 animal-years). To assess whether our results were sensitive to buffer distances, we reran this analysis with a buffer distance of 1 km, 5 km, 15 km, and 20 km. We observed no changes in direction or significance of the effects of barrier densities on mean daily displacement (Table A2).

To test whether space use as measured by daily displacement should increase as nearby barriers become more permeable, we used a generalized linear regression to compare the average daily displacements (km) of pronghorn relative to the densities of each barrier within individual core and buffered winter ranges. We fit a generalized linear mixed effects model with a gamma distribution and log link to predict the mean displacement, given the barrier density from the core or buffered winter ranges. Each model had population as a random intercept. In this analysis, sample size was 682 animal-years.

For the area analysis and displacement analysis, 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 2 Akaike's Information Criterion (AIC) of the null model then we considered the model not explanatory (Burnham and Anderson 2004). We used R version 3.6.2 (R Core Team 2016) for all statistics and analyses; we used glmmTMB for the mixed effects conditional Poisson regression (Brooks et al. 2017), and lme4 for generalized linear mixed effects models (Bates et al. 2015).

RESULTS

All 5 linear features were barriers to pronghorn movement, as demonstrated by negative coefficients from the step-selection function with 95% confidence intervals that did not overlap zero (Table 1). Yet we observed high variability in the degree to which each barrier was permeable to pronghorn movement. When each respective barrier was available, the interstate was the least permeable to pronghorn movement (Figure 2). When in the vicinity of a road (i.e., within an available step length, on average 0.916 km), pronghorn were >300 times less likely to cross the interstate than state highways, the second least permeable barrier (Table 1). When in the vicinity of a state highway or a railroad, pronghorn were 4 times less likely to cross state highways than railroads, the third least permeable barrier. When in the vicinity of a railroad or a fence, pronghorn were 2 times less likely to cross railroads than fences. Finally, when in the vicinity of a fence or a county road, pronghorn were almost 2 times less likely to cross a fence than county roads.

TABLE 1 Beta coefficients from a step-selection function and exponentiated odds ratios for pronghorn to cross each movement barrier in Wyoming, USA, 2002–2020. We included step length (km) as a predictor to correct for movement constraints on selection coefficients. Beta coefficients for each linear feature are the calculated semi-permeability for crossing each linear feature when encountered by an animal. None of the confidence intervals of the beta coefficient overlapped zero. We included population and animal-year as nested random intercepts with each barrier as a random slope. Odds ratios are the exponentiated beta coefficients, where <1 indicates a lower likelihood of crossing.

|	Coefficient	95% CI	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 highway	−3.260	−4.265, −2.255	0.038
Interstate	−9.205	−12.185, −6.225	<0.001
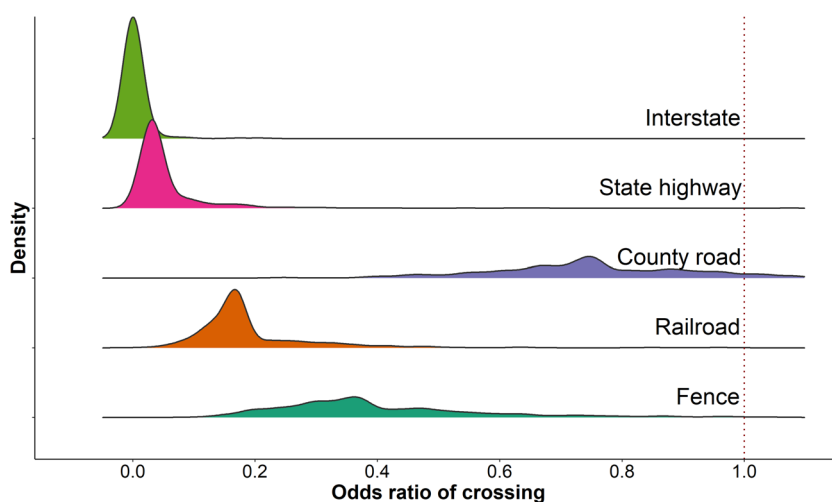
FIGURE 2 Distribution of odds ratios for individual pronghorn to crossing each anthropogenic linear feature, where the farther from 1 (no effect) suggests stronger avoidance to crossing the barrier type. Because we fit the step-selection function using random slopes for each animal-year, we estimated the distribution of odds ratios by exponentiating each beta coefficient for each barrier (semi-permeability) from the random slopes of the 1,010 animal-years in Wyoming, USA, 2002–2020.

When pronghorn were in the vicinity of each respective barrier, pronghorn on average crossed county roads 15.8% of the time, fences 13.7% of the time, railroads 8.2% of the time, state highways 5.3% of the time, and the interstate 0.2% of the time over the course of 7–8 hours. Although the interstate was the most severe barrier, only a quarter of the sampled pronghorn ever encountered the barrier (i.e., individuals with ≥1 point within a step length of the interstate; Table B1). Using the predicted odds of crossing from the step-selection function (Table 1), we ran a *post hoc* simulation 1,000 times to quantify how many time steps (7 hr) it would require for a simulated pronghorn to cross when in the vicinity of each respective barrier. The median time was 14 hours to cross a county road (2 time steps), 21 hours to cross a fence, 35 hours to cross a railroad, 147 hours to cross a state highway, and 49,462 hours (5 yr) to cross the interstate.

Pronghorn occupied a smaller area when there was a higher density of fences within individual core winter range (Figure 3; ΔAIC = 4.00 less than null model). The area pronghorn occupied was 10% smaller for every $1 \, km/km^2$ increase in fence density (Table 2). The effects of barriers on the area pronghorn occupied were stronger within buffered winter range than core winter range. Pronghorn with a higher density of fences, state highways, and interstates and railroads within their buffered winter range occupied less area (Figure 3; ΔAIC = 76.54 less than null model). The area pronghorn occupied was 17% smaller for every $1 \, km/km^2$ increase in fence density within buffered winter range, 7% smaller for every $1 \, km/km^2$ increase in state highway density, and 22% smaller for every $1 \, km/km^2$ increase in interstate and railroad density (Table 2). The area pronghorn occupied was 7% larger for every $1 \, km/km^2$ increase in county road density within buffered winter range.

Pronghorn moved less when there was a higher density of fences and state highways within individual core winter range (Figure 4; ΔAIC = 44.81 less than null model). The daily distance pronghorn moved was 6% shorter for every $1 \, km/km^2$ increase in fence density and 3% shorter for every $1 \, km/km^2$ in state highway density within individual core winter range (Table 3). Within buffered winter range, the daily distance pronghorn moved was 8% shorter for every $1 \, km/km^2$ increase in fence density, 5% shorter for every $1 \, km/km^2$ in state highway density, and 6% shorter for every $1 \, km/km^2$ in interstate and railroad density (Table 3; ΔAIC = 100.41 less than null model).
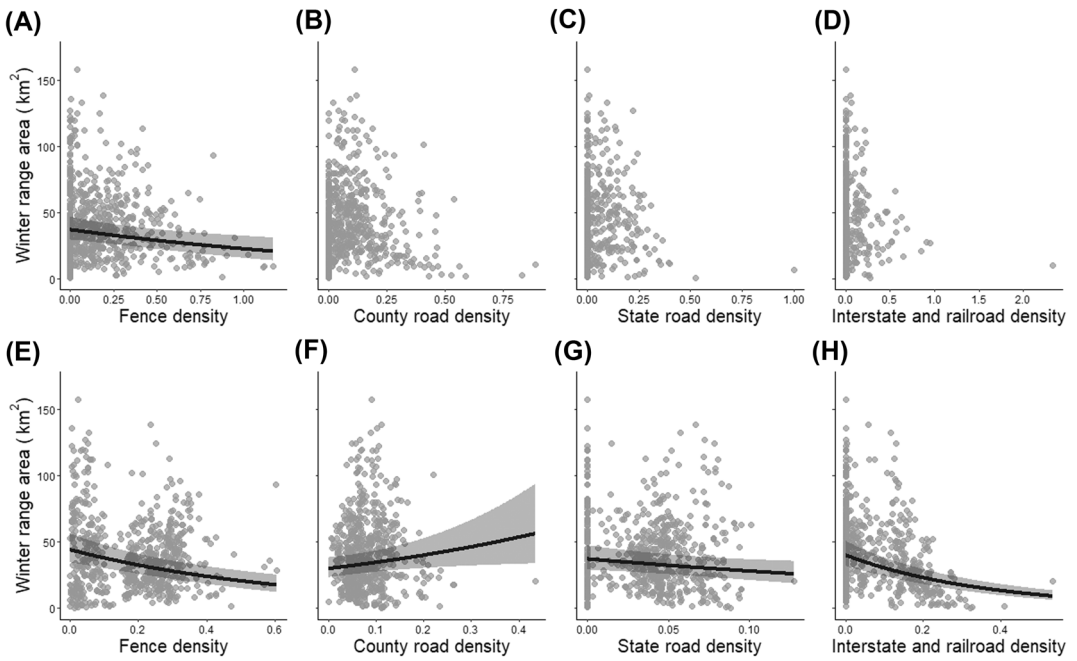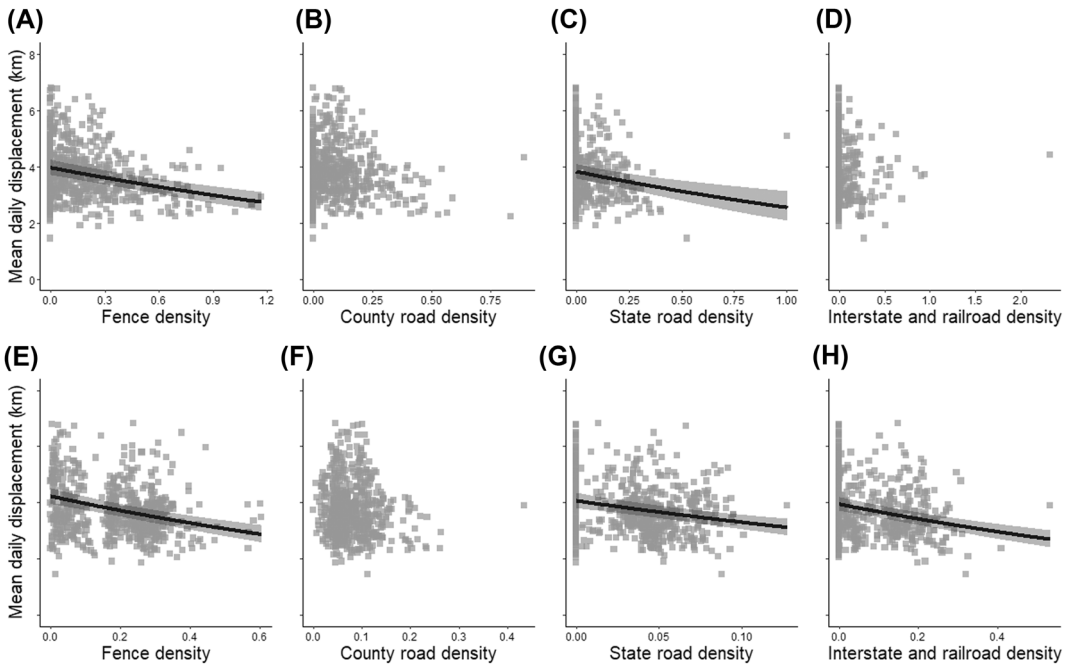
FIGURE 3 The effects of barriers on pronghorn winter range in Wyoming, USA, 2002–2020. Within core winter range, an increasing density of fences (A) decreased winter range area, but we did not observe an effect for county roads (B), state highways (C), and interstates and railroads (D). Within buffered winter range, increasing density of fences (E), state highways (G), and interstates and railroads (H) decreased pronghorn winter range area, but county roads (F) increased pronghorn winter range area (n = 682). Trend lines are included for barriers with 95% confidence intervals that did not overlap with zero. Trend lines show the predicted effect of the given barrier (black line) with 95% confidence interval (shading) from a generalized linear mixed effect model with a gamma distribution and log link, where all other variables were held at the mean for visualization. Density of barriers are in km/km^2.

TABLE 2 Coefficients with 95% confidence intervals of the effect of barrier density on winter range area of pronghorn within core and buffered winter range in Wyoming, USA, 2002–2020. Coefficients are from a generalized linear mixed effects model with a gamma distribution and log link function with population as a random intercept. Coefficients with an asterisk (*) have 95% confidence intervals that do not overlap zero.

Barrier (km/km^2)	Core winter range		Buffered winter range	
	Coefficient	95% CI	Coefficient	95% CI
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 highway	−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*

DISCUSSION

Pronghorn showed a wide range of avoidance behavior to 5 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 loss of available habitat (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 space

FIGURE 4 The effects of barriers on pronghorn daily displacement while on winter range in Wyoming, USA, 2002–2020. Within core winter range, increasing density of fences (A) and state highways (C) lowered mean displacement, but the density of county roads (B) and interstates and railroads (D) did not have an effect on mean displacement. Within buffered winter range, an increasing density of fences (E), state highways (G), and interstates and railroads (H) lowered mean displacement. Density of county roads (F) did not have an effect ($n = 682$). Trend lines are included for barriers with 95% confidence intervals that did not overlap with zero. Trend lines show the predicted effect of the given barrier (black line) with 95% confidence interval (gray shading) from a generalized linear mixed effect model with a gamma distribution and log link, where all other variables were held at the mean for visualization. Density of barriers are in km/km^2.

TABLE 3 Coefficients with 95% confidence intervals of the effect of barrier density on mean daily displacements of pronghorn within core and buffered winter range in Wyoming, USA, 2002–2020. Coefficients are from a generalized linear mixed effects model with a gamma distribution and log link function with population as a random intercept. Coefficients with an asterisk (*) have 95% confidence intervals that do not overlap zero.

Barrier (km/km^2)	Core winter range		Buffered winter range	
	Coefficient	95% CI	Coefficient	95% CI
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 highway	−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*

use was constrained by movement barriers, indicating that pronghorn surrounded by a higher density of barriers had less access to habitat. The larger-scale barrier effects on space use were not proportional to permeability. In particular, the interstate's influence on pronghorn winter range size and displacement was no greater than fences and had no effect at the core winter range. Overall, our results indicate that pronghorn space use was severely constrained by barriers, with cascading (but noisy) effects on access to habitat.

Pronghorn rarely crossed interstates and state highways because each had combined barrier effects caused by traffic and associated right-of-way fences. Interstates have woven-wire or game-proof fences along the right-of-way, both of which are nearly impermeable to pronghorn movement (Gates et al. 2012). Woven-wire fences along the interstate certainly contributed to its low permeability for pronghorn. In comparison, state highways predominantly had 4–5 strand right-of-way fences, with some limited sections of game-proof or woven-wire fences. Yet state highways still had a substantially lower permeability than other interior fences, indicating that fences alone do not explain the barrier effect of highways. Thus, it seems reasonable to infer that traffic loads on the interstate and state highways contributed to their severe barrier effects. In contrast, county roads were relatively permeable to pronghorn movement; these roads rarely had fenced right-of-ways and were likely located in open range.

Although high traffic is conflated with parallel right-of-way fences, our results indicate barrier effects caused by traffic were likely additive to existing barrier effects created by fences. Through auditory and visual disturbances, traffic can expand the influence roads have on wildlife beyond the paved surface (Forman and Alexander 1998). Species such as pronghorn can perceive the disturbances of road traffic as a predation risk, particularly when fawns are present (Frid and Dill 2002, Gavin and Komers 2006). Such disturbances likely strengthen the barrier effects of roads and create memory effects that reinforce impermeability (Bracis and Mueller 2017). In northern Arizona, USA, pronghorn rarely crossed Interstate 40 and were more likely to cross another state highway, even when a section of the fenced right-of-way was temporarily removed (Hart et al. 2001). Thus, even when a road's permeability is improved (e.g., removing fencing or creating wildlife crossing structures), managers should expect a time-lag before pronghorn successfully cross roads with high traffic loads (Seidler et al. 2018).

Pronghorn avoided crossing the interstate and its associated right-of-way fences more than other barriers, 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 combined interstates and railroads. Despite increased vigilance along roads (Gavin and Komers 2006), pronghorn can move parallel to major highways for up to 10.5 km (Dodd et al. 2011, Gates et al. 2012). Without ever crossing, pronghorn can partially cope with the barrier effects of roads by elongating their winter range along the barrier (Dodd et al. 2011). In contrast, pronghorn may be boxed in by the higher density of fences, despite such barriers being easier to cross. Pronghorn from one of our study populations will encounter fences on average 250 times/year, and when not crossing, pronghorn behaviorally respond to fence barriers by turning around rather than moving parallel (Xu et al. 2021). By causing pronghorn to backtrack, this behavioral response to fences could further constrain space use if fence density is high enough to counteract their relative permeability.

Within the rural United States, the linear extent of fences can be up to 16 times greater than paved roads (Jakes et al. 2018b). Some of the variability in permeability to fences was likely caused by different types of fences, data for which were unavailable for our study. Indeed, the variable permeabilities of fences in our study emphasize the importance of high-quality fence data. Even barriers that are relatively permeable to animal movement can be a threat to habitat access if they occur at high density. In a study similar to ours, Jones et al. (2019) reported that doubling the abundance of fences can cause pronghorn to lose access to up to 11% of relative high-quality habitat. Wildlife have been hypothesized to lose access to habitat at a nonlinear rate, as thresholds in disturbance disrupt connectivity (With and Crist 1995). Although we did not directly assess this possibility, our results suggest that the degree to which pronghorn can access habitat is likely influenced by both the semi-permeability of barriers and the abundance of barriers.

As expected, pronghorn space use was more obstructed by barriers that occur within their buffered 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 space use and barrier density at the larger grain of the buffered winter range. Within core winter range, pronghorn are likely capable of adjusting their behavior to minimize exposure to barriers; however, at the peripheral edges of winter range, pronghorn were more likely restricted by barriers. Peripheral barriers likely inhibit pronghorn movements to nearby habitat. Wildlife will

often need to adjust their core home ranges when environmental conditions change (Börger et al. 2006, Van Beest et al. 2011). Notably, for species such as pronghorn, exploratory movement from core areas to alternative habitat is fundamental to their survival when environmental conditions fluctuate (Barrett 1982, Christie et al. 2015, Reinking et al. 2018). Such examples highlight the importance of connectivity so that pronghorn can access ephemeral winter habitat.

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 Asiatic wild ass (*Equus hemionus*), which were more exploratory and able to relocate to alternative habitat (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 habitat, fragmentation created by barriers can lower carrying capacity for populations dependent on movement (Boone and Hobbs 2004). The causal link we have identified between movement barriers and space use suggests that movement barriers fundamentally influence pronghorn movement and the degree to which the surrounding habitat is accessible.

Analytical tools such as those used in our study can benefit managers interested in improving habitat connectivity. For example, our step-selection function estimates individual values of barrier permeability for each animal. Using these estimates of permeability, managers can locate where animals are most impeded by barriers (i.e., which animals have a lower propensity to cross a barrier). A limitation of our step-selection function analysis was that it assumed the permeability of barriers was independent of variation in habitat quality (Beyer et al. 2016). Because of our large sample size and spatial coverage, we doubt underlying habitat conditions biased our metrics of permeability. Moreover, even without metrics for habitat quality, our permeability estimates can be used to locate where permeability is higher than expected, which could indicate increased movement to high-quality habitat. Additionally, our regression framework of space use relative to barrier density can be incorporated into management plans. By setting a minimum area to sustain healthy populations, researchers can identify locations where wildlife access to habitat may be lower than the desired threshold. Such areas can be prioritized for habitat restoration efforts. Finally, our analysis of space use can be merged with a behavioral analysis of wildlife response to barriers (Xu et al. 2021). By incorporating the behavioral effects of barriers within our framework of space use, researchers can map the barrier locations likely to have the greatest consequence on wildlife habitat and target them for removal or modification.

Pronghorn are highly mobile ungulates that depend on the ability to move long distances, and our results demonstrate that barriers of different permeability and prevalence constrict winter range size and limit movement. Anthropogenic linear features are expanding globally (Dulac 2013, Ibisch et al. 2016), and our findings illustrate how semi-permeable barriers scale up to constrain space use and access to habitat. By reducing availability of habitat, barriers may 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 (McDonald and St. Clair 2004, Clevenger and Waltho 2005, Xia et al. 2007, Gagnon et al. 2011, Seidler et al. 2018), fence modifications (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 access to fragmented habitats.

MANAGEMENT IMPLICATIONS

Because it is infeasible and, in some cases, counterproductive to entirely remove barriers, barrier mitigation often occurs by identifying locations where permeability could be improved. Yet the site-specific decision of where to mitigate barriers remains a substantial management challenge. Our research illustrates that barriers on the

periphery of core winter ranges can be productive candidates to improve habitat access, given the strong effect peripheral barriers had on pronghorn space use. By mapping pronghorn movement, the peripheral barriers at the edge of core ranges are important candidates to improve pronghorn access to habitat. For mobile species such as pronghorn that depend on long-distance movements, even locations infrequently visited could be important to connectivity and habitat use when unpredictable weather pushes pronghorn to novel habitats. Managers of pronghorn habitat should be aware of the importance of collecting movement data across a range of years and weather conditions to create a comprehensive understanding of pronghorn habitat use, which in turn can be used to identify barriers that can be altered to assist pronghorn movement.

CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

ETHICS STATEMENT

All pronghorn captures followed protocols in accordance with guidelines from the American Society of Mammalogists (Sikes 2016), Wyoming Game and Fish Department (Chapter 33-1104, Chapter 33-1162, Chapter 33-923, and Chapter 33-742 permits), and University of Wyoming Institutional Animal Care and Use Committee (protocols 20170227MK00231-01, 20180306MK00297-03, 20131028JB00037, and 01012010).

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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APPENDIX A: COMPARISON OF BUFFER DISTANCES

TABLE A1 Coefficients with 95% confidence intervals of the effect of barrier density on winter range area of pronghorn within 1-km, 5-km, 15-km, and 20-km buffer distances in Wyoming, USA, 2002–2020. Coefficients are from a generalized linear mixed effects model with population as a random intercept. Coefficients with an asterisk (*) have 95% confidence intervals that do not overlap zero. Coefficients are in km/km².

	1-km buffer		5-km buffer		15-km buffer		20-km buffer	
	Coefficient	95% CI	Coefficient	95% CI	Coefficient	95% CI	Coefficient	95% CI
Fence	-0.195*	-0.259, -0.131*	-0.145*	-0.211, -0.078*	-0.193*	-0.271, -0.115*	-0.175*	-0.257, -0.094*
County road	-0.014	-0.074, 0.047	-0.009	-0.066, 0.047	0.063*	0.008, 0.119*	0.041	-0.016, 0.097
State highway	-0.097*	-0.159, -0.034*	-0.050	-0.111, 0.010	-0.064	-0.130, 0.003	-0.044	-0.114, 0.026
Interstate and railroad	-0.248*	-0.309, -0.187*	-0.246*	-0.306, -0.187*	-0.234*	-0.294, -0.174*	-0.215*	-0.275, -0.155*

TABLE A2 Coefficients with 95% confidence intervals of the effect of barrier density on mean daily displacements of pronghorn within 1-km, 5-km, 15-km, and 20-km buffer distances in Wyoming, USA, 2002–2020. Coefficients are from a generalized linear mixed effects model with population as a random intercept. Coefficients with an asterisk (*) have 95% confidence intervals that do not overlap zero. Coefficients are in km/km².

	1-km buffer		5-km buffer		15-km buffer		20-km buffer	
	Coefficient	95% CI	Coefficient	95% CI	Coefficient	95% CI	Coefficient	95% CI
Fence	-0.082*	-0.101, -0.062*	-0.068*	-0.089, -0.047*	-0.078*	-0.102, -0.054*	-0.073*	-0.098, -0.048*
County road	0.005	-0.013, 0.023	-0.001	-0.019, 0.018	0.012	-0.006, 0.030	0.004	-0.014, 0.022
State highway	-0.054*	-0.073, -0.036*	-0.057*	-0.076, -0.038*	-0.058*	-0.080, -0.036*	-0.055*	-0.078, -0.032*
Interstate and railroad	-0.039*	-0.057, -0.021*	-0.057*	-0.074, -0.039*	-0.067*	-0.086, -0.049*	-0.071*	-0.089, -0.052*

APPENDIX B: INDIVIDUAL EFFECT SIZES FROM STEP-SELECTION FUNCTION

TABLE B1 Individual pronghorn random slopes separated by year relative to each movement barrier in Wyoming, USA, 2002–2020. 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 highway	0.004	1.073	629
Interstate	<0.001	0.209	227