

ARTICLE

Fence types influence pronghorn movement responses

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Abstract

Impediments that constrain animal movements across spatiotemporally heterogeneous landscapes can result in reduced or complete loss of access to critical resources. Across their range in North America, pronghorn (*Antilocapra americana*) are exposed to fences that can affect their ability to permeate the landscape, access critical resources, and respond to climatic variations. Understanding pronghorn movement responses to fences is essential for improving landscape permeability; however, prior studies provide only limited insight due to lack of information on fence characteristics and small sample sizes. Our study used hourly collar locations from adult female pronghorn in six herds in Montana, USA, and identified encounters with mapped fences to evaluate three movement responses (i.e., probability of an unaltered initial response, probability of crossing following an altered initial response, and passage time following an altered initial response) as a function of fence and landscape attributes. Based on 5581 encounters identified from movement pathways of 265 collared pronghorn and 979 km of mapped fences, we found that variability in pronghorn fence response was correlated with fence type. Woven wire fences substantially reduced unaltered initial and crossing responses and increased passage times as compared with low (i.e., average lowest wire height <41 cm) or high (i.e., average lowest wire height ≥41 cm) strand fences. Both low and high strand fences elicited similar responses of being relatively permeable at the initial encounter with reduced permeability thereafter. Fence crossing probabilities following altered initial responses increased through time modestly for strand fences but only negligibly for woven wire fences, with passage times averaging approximately 14 h. Pronghorn knowledge of and fidelity to specific permeable locations along fences, which may be due to inconsistent fence and landscape characteristics along the fence stretch, likely allow some woven wire fences and most strand fences, regardless of the average lowest wire height, to be permeable. Improving landscape permeability for pronghorn should focus on removing woven wire fences, replacing woven wire fences with strand fences, and incorporating variation in the lowest wire heights into new fence designs or modifications of existing fences.

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KEYWORDS

Antilocapra americana, crossing, fences, fence encounters, Montana, movement barriers, movement behaviors, movement responses, permeability, pronghorn, wildlife friendly, woven wire

INTRODUCTION

Animal movements across spatially and temporally heterogeneous and often fragmented landscapes are necessary to improve individuals' fitness by accessing resources (e.g., forage, mates; Dingle & Drake, 2007; Fryxell et al., 1988; Hebblewhite et al., 2008), reducing predation risk (Gaynor et al., 2019; Hebblewhite & Merrill, 2009), and reducing density-dependent competition (Berg et al., 2019; Taylor & Norris, 2007). In temperate climates, where the availability of nutritional resources can vary dramatically depending on the timing and amount of winter snow accumulation and spring regrowth, animals employ various movement strategies ranging from year-round residency to seasonally migratory, even within the same population (i.e., partially migratory populations; Chapman et al., 2011; Dingle & Drake, 2007; Rolandsen et al., 2017). Individually and in aggregate, these movement strategies can have important effects on the maintenance of populations, communities, and ecosystems (Schindler et al., 2015; Van Moorter et al., 2020), particularly under a changing climate (Cross et al., 2012; Morelli et al., 2017).

Anthropogenic barriers (henceforth, "barriers," e.g., fences, reservoirs, and roads), coinciding with land-use, development, and management practices, are ubiquitous and increasing worldwide, posing threats to animal movements and their ability to access resources (Jakes et al., 2018; McInturff et al., 2020; Van Moorter et al., 2020). Barriers that are impossible or difficult to cross can result in additional energy expenditure, injury, or direct mortality (e.g., drownings, fence entanglements, and vehicle collisions; Caldwell & Klip, 2021; Harrington & Conover, 2006; Rautenstrauch & Krausman, 1989; Rey et al., 2012). These effects can be exacerbated during times of abnormally severe environmental conditions, such as heavy snowfall or drought (Van Moorter et al., 2020). Given the substantial impacts movement barriers may have on individual- and population-level fitness (Holderegger & Di Giulio, 2010; Tewksbury et al., 2002; Trombulak & Frissell, 2000; Van Moorter et al., 2020), an understanding of how animals respond to barriers is critical for resource managers to conserve and improve landscape permeability, remediate barriers, and develop land-use and conservation plans to benefit animal populations (Jakes et al., 2018;

McInturff et al., 2020). For migratory ungulates in particular, identifying barriers within seasonal ranges and migratory corridors is an important priority for state and federal agencies (U.S. Department of the Interior, 2018; National Fish and Wildlife Foundation, 2021) and has been recognized as critical for maintaining migratory populations (Berger, 2004; Bolger et al., 2008) and ecosystem processes (Cozzi et al., 2013; Van Moorter et al., 2020).

Barriers can strongly influence the daily and seasonal movements of pronghorn (*Antilocapra americana*), a medium-sized ungulate endemic to the plains, montane valleys, and sagebrush (*Artemisia* spp.) steppe regions of western North America that often require large, permeable landscapes to access resources (Berger, 2004; Jones et al., 2020; Kolar et al., 2011; Van Moorter et al., 2020; White et al., 2007; Xu et al., 2021). Livestock fences are often ubiquitous features in pronghorn habitat (O'Gara & McCabe, 2004; Yoakum, 2004) and can act as barriers that pose a particular challenge because pronghorn infrequently jump fences like other ungulates, such as deer (*Odocoileus* spp.) and elk (*Cervus canadensis*), and typically must pass under the lowest wire of the fence (Yoakum, 2004). If the lowest wire is too low or the wires are woven near the ground, or snow or vegetation have accumulated against otherwise permeable fences, pronghorn movements can be fully obstructed (Barrett, 1982; Martinka, 1967; Yoakum, 2004). Furthermore, attempts by pronghorn to cross less permeable fences can result in substantial hair loss, injury, or death due to entanglement, entrapment, or vehicle or train collisions (Harrington & Conover, 2006; Jones, 2014; O'Gara, 2004). These consequences may be exacerbated during winter when pronghorn face increased thermoregulatory and locomotive costs equating to net energy loss and declining body condition (Jones, 2014; O'Gara, 2004).

Fence constructions designed to increase permeability to wildlife without sacrificing the functional utility of the fence, commonly termed "wildlife friendly," can be used to improve the passage of pronghorn by converting the lowest wire from barbed to smooth and raising the height of the lowest wire (Jones et al., 2018). Guidelines developed from anecdotal observations of pronghorn fence crossings generally recommend a minimum lowest wire height of 41 cm to improve pronghorn passage and have been widely adopted by resource agencies (Hanophy, 2009; Paige, 2012, 2015; Yoakum et al., 2014).

More recent studies based on camera traps at known-crossing sites recommend a minimum lowest wire height of 46 cm (Jones et al., 2018, 2020); however, empirical studies that evaluate the effect of traditional and wildlife friendly fence designs on pronghorn movement behavior are needed for mitigation and conservation planning (Durant et al., 2015; Jakes et al., 2018). Although previous studies have evaluated pronghorn behavioral responses to fences (Jones et al., 2018, 2020; Xu et al., 2021), these are limited due to lack of information available on fence characteristics, smaller sample sizes from single populations or at isolated, known-crossing sites, and/or inability to track individuals across time as they encounter fences.

To help resource managers develop strategies for improving landscape permeability for pronghorn, our observational study sought to understand how variable characteristics of fences influence pronghorn movement behavior and crossing success across a broad landscape ranging from montane valley and prairie environments. Specifically, we asked three questions regarding the effect of different fence types: (1) When a fence is encountered, what is the probability that the pronghorn movement response remains unaltered? (2) When a fence alters a movement response, what is the probability that the pronghorn will cross the fence? and (3) When a fence alters a movement response, how does the probability of a pronghorn crossing the fence vary through time? We addressed these by using fine spatiotemporal locations from a sample of radio-collared female pronghorn and mapped fences in six study areas in southwest, central, and southeast Montana, USA, to identify pronghorn fence encounters and develop models representing movement responses as a function of fence characteristics and other landscape attributes. The movement responses included initial response (unaltered or altered), crossing response following an altered initial response, and passage time following an altered initial response.

We tested three primary hypotheses with each model: (1) fences, regardless of design characteristics, do not substantially affect pronghorn movement responses; (2) woven wire and low strand fences result in reduced probabilities of unaltered initial and crossing responses and increased passage times of pronghorn as compared with high strand fences; and (3) woven wire fences are more likely to result in reduced probabilities of unaltered initial and crossing responses and increased passage times of pronghorn as compared to low and high strand fences. We predicted that woven wire and low strand fences would have reduced probabilities of unaltered initial and crossing responses and increased passage time, as compared with high strand fences, with woven wire fences having a stronger effect as compared with low strand fences.

STUDY AREA

We conducted our study from January 2019 to June 2021 in one montane valley area in southwest Montana (Madison study area; 1143 km²; mean elevation 1783 m) and five prairie areas in central and southeast Montana: Fergus-Petroleum (2580 km²; mean elevation 952 m), Garfield-Rosebud (6783 km²; mean elevation 902 m), Musselshell (2090 km²; mean elevation 1186 m), Powder River-Carter (6208 km²; mean elevation 1045 m), and South Philips (4184 km²; mean elevation 822 m) study areas (Figure 1). The study areas represent the annual ranges of pronghorn herds defined by 95% kernel density estimate of all GPS locations for each herd and were selected for sampling to span a gradient of ecological and environmental conditions. These areas typify the open and relatively flat environments occupied by pronghorn across the majority of their range. The prairie of the central and southeast study areas was dominated by sagebrush (*Artemisia* spp.) steppe and mixed grass prairie (i.e., thickspike wheatgrass [*Elymus lanceolatus*], green needlegrass [*Nassella viridula*], blue grama [*Bouteloua gracilis*], and needle and thread grass [*Hesperostipa comata*]). The southwest study area was dominated by valley grasslands (i.e., bluebunch wheatgrass [*Pseudoroegneria spicata*], Idaho fescue [*Festuca idahoensis*], and western wheatgrass [*Pascopyrum smithii*]) interspersed with an understory of herbaceous forb species. Cultivated croplands also occur (range = 7%–20% of the total land cover) in each study area and consist mostly of common wheat and leguminous forbs (e.g., field peas, lentils, and alfalfa).

The study areas experienced strong seasonal variation in annual climate typical of temperate latitudes, with winters characterized by cold temperatures and moisture occurring as snow and summers characterized by relatively warm temperatures. Climate varied among the study areas with average annual precipitation ranging from 446 to 670 mm and mean temperatures for July ranging from 17.2 to 21.9°C and for January ranging from –7.1 to –3.6°C (PRISM Climate Group, 2016). Ownership varied among the study areas but was dominated by private (range = 56%–88%), federal (range = 5%–36%), and state of Montana (range = 6%–8%) lands. In the central and southeast study areas, federal lands were primarily managed by Bureau of Land Management (BLM), while in the southwest study area, federal lands were managed by both US Forest Service (6%) and BLM (4%). Levels of anthropogenic development (i.e., roads, urban areas, and fencing infrastructure) varied across study areas. Livestock grazing, cultivated crops, recreation, and big game hunting were predominant land uses. Pronghorn herd sizes varied across the

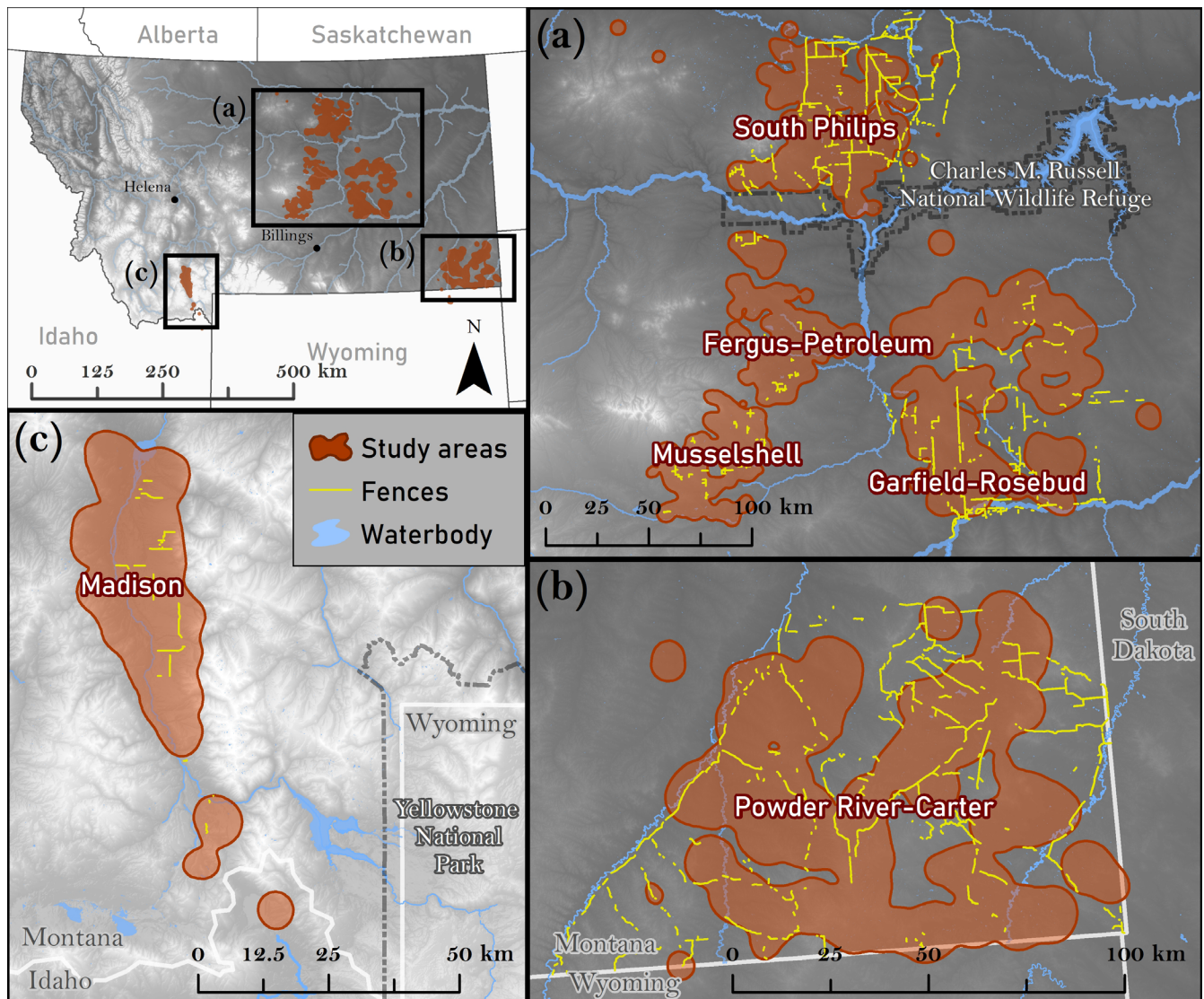


FIGURE 1 The six study herds (red polygons) used to evaluate female pronghorn movement responses to fence encounters in prairie (panels (a) and (b)) and montane valley (panel (c)) regions of Montana, USA, 2019–2021. The study areas were defined using a 95% kernel density estimate of all GPS locations for each herd. Mapped fences (yellow lines) were verified and characterized in the field. Elevation is represented by the dark gray (low) to light gray (high) gradient. Note differences in panel scales.

study areas from an estimated low of 1567 animals in the Madison to 15,983 in Powder River in 2019–2020. Within each study area, migratory patterns of individuals varied across a continuum that ranged from year-round residency to large, seasonal movements between summer and winter ranges; however, resident individuals dominated all study areas and comprised approximately 65%–94% of the total collared individuals each year. Pronghorn in all study areas were hunted during a five-week fall archery season and a five-week rifle season that begins in mid-October. The number of hunting licenses allocated per herd varied widely, from 475 in Fergus-Petroleum to 10,000 shared across a broad region that both Powder River-Carter and Garfield-Rosebud were a part of. Mule deer (*Odocoileus hemionus*),

white-tailed deer (*Odocoileus virginianus*), and elk were sympatric with pronghorn in the study areas. Potential predators of pronghorn varied by study area and included mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), gray wolf (*Canis lupis*), coyote (*Canis latrans*), American black bear (*Ursus americanus*), grizzly bear (*Ursus arctos*), and golden eagle (*Aquila chrysaetos*).

METHODS

Data collection

We captured and radio-collared 473 adult (>1.5 years old) female pronghorn across all study areas during

winters 2019–2021. Of these animals, we collared 82 in the Madison (40, 20, and 22 in 2019, 2020, and 2021, respectively) and 76–82 in each of the remaining study areas (60 per study area in 2020 and 16–22 per study area in 2021). We captured individuals using helicopter net gunning in accordance with animal welfare protocols (Institutional Animal Care and Use Committee Project Number: FWP12-2018 and FWP10-2019). We instrumented individuals with a GPS collar (Lotek LiteTrack Iridium 420, Lotek Wireless, Newmarket, ON, Canada) programmed to collect locations every hour, excepting collars deployed: (1) in 2019 programmed with location fix intervals that varied from 30 min to 4 h depending on the time of year and (2) during July in the Musselshell study area programmed with location fix intervals of 30 min. After downloading the location data, we removed locations with low spatial precision (positional dilution of precision values >10 ; D'eon & Delparte, 2005). After censoring, fix success rate of individual pronghorn was $0.99 \pm 0.001\%$ (mean \pm SD). We removed data with >1 -h fix intervals and rarefied the 30-min fix interval data to create a dataset with 1-h fix intervals that we used for analysis. To evaluate the ability of 1-h fix interval data to produce similar results as the 30-min fix interval data and to provide guidance in selecting adequate fix intervals for future studies, we used and rarefied data from individuals with 30-min fix intervals and compared the ability of 30-min, 1-h, 2-h, and 4-h fix interval datasets to detect pronghorn encounters and responses to fences (Appendix S1: Figure S1).

We mapped the spatial position of fences in each of the study areas using two methods: (1) using field tablets (Apple iPad Model A1566, Apple Inc., Cupertino, CA, USA) to record GPS tracks of driving and walking routes paralleling segments of fence, spatial locations of gates, and characteristics of each fence segment, and (2) locating and drawing fence segments based on aerial imagery base maps in ArcGIS Online (ESRI, 2021a). We visited fence segments drawn from aerial imagery to verify spatial positioning and record fence characteristics and spatial locations of gates. Each fence segment represented a stretch of fence sharing the same overall characteristics and often started and ended at junctions with other fences or at angle changes in the overall fence. Fence characteristics included wire type (e.g., barbed wire, smooth wire, woven wire, post-and-rail, etc.), number of strands (i.e., 3–7), lowest wire height (in centimeters), and highest wire height (in centimeters). Lowest and highest wire heights represented average height values of five different locations along the fence segment, with each location measured at the midpoint of adjoining fence posts and at least three fence posts away from other measurement locations. For fences recorded from driving

or walking routes, we repositioned the GPS tracks to more spatially accurate positions based on the distance of the road to the fence attribute, if recorded, and/or on visual examination of results with aerial imagery base maps in ArcGIS 10.7 (ESRI, 2021b). For this study, we included only fences with barbed, smooth, or woven wire, and grouped barbed and smooth wire together as “strand” wire given a low sample size of smooth wire in our study and an assumption that wire height is likely more influential to pronghorn passage than whether the wire is smooth or barbed. Additionally, because pronghorn have been found to alter behaviors and avoid areas near roads with higher traffic volume (Gates et al., 2012; Gavin & Komers, 2006; Kolar, 2009) and to reduce the potential confounding effect that vehicle traffic on roads adjacent to fences may have on pronghorn movements, we constrained the fence data to exclude those that occurred adjacent (i.e., within 50 m) to roads with estimated average traffic volumes of ≥ 200 vehicles/day (Gavin & Komers, 2006; Montana Department of Transportation, 2019).

Identifying encounters and movement responses

Using the collar data and mapped fences, we estimated three response variables representing pronghorn movement responses to fence encounters within a 48-h time period (henceforth, “encounter periods”) beginning at the location of the initial encounter: initial response, crossing response following an altered initial response, and passage time following an altered initial response. To estimate these variables, we first identified all encounters and crossing events of collared pronghorn with mapped fences. We used the Barrier Behavior Analysis (BaBA) package (Xu et al., 2021) in the R environment for statistical computing (R Core Team, 2019) to identify the majority of encounters and crossing events. The BaBA method defines encounters and crossings based on collar locations that occur within a user-specified buffer from fences. We specified this buffer as 50 m, which we considered to represent a distance that pronghorn may perceive and interact with a fence. A 110-m buffer has been determined to be optimal for 2-h fix interval data (Xu et al., 2021); however, given our finer fix interval data and the limited ability of BaBA to capture quick fence crossings for lower buffer values (e.g., collar locations of quick cross movements are less likely to occur within smaller buffers and therefore less likely to be identified as an encounter), we considered 50 m adequate. To account for quick fence crossings not captured by BaBA, we intersected each animal’s movement path with the

fence data, identified crossing events where intersections occurred but were not identified by BaBA, and added the results to the encounter data. We classified initial responses to each fence encounter into two categories: unaltered or altered. Unaltered responses represented movements where the animal crossed the fence or did not change its movement pattern notably (i.e., an “average” movement as identified by BaBA). Altered responses represented movements where the animal moved away from (i.e., bounced), back and forth adjacent to, or along the fence (i.e., traced), or was constantly located near the fence (i.e., trapped). We used the movement response at the beginning of each encounter period as our first response variable, initial response.

Next, for each encounter period with an altered initial response, we identified the number of hours from the initial encounter (i.e., first location within 50 m of the fence) to a crossing event. If no crossing was detected within 48 h, we considered the outcome of the encounter as a non-crossing. For encounter periods with a crossing outcome, we retained only those in which the initial encounter and the crossing occurred at the same fence segment. We used the presence or absence of a crossing event in each encounter period as our crossing response variable. Finally, we used the total hours elapsed from the altered initial encounter to the crossing event or the end of the encounter period at 48 h as our third response variable, passage time.

Analysis of movement responses

Our analysis approach consisted of the development of three separate models describing the effects of fence and landscape characteristics on the probability of an unaltered initial response, the probability of a crossing

following an altered initial response, and passage time following an altered initial response. To model the probability of an unaltered initial response, we used mixed-effects logistic regression with the response variable classified as 1 for unaltered responses and 0 for altered responses. To model the probability of a crossing following an altered initial response, we used mixed-effects logistic regression with the response variable classified as 1 for encounters resulting in a crossing and 0 for encounters not resulting in a crossing within 48 h after the initial encounter. To model passage time, we used a Cox proportional hazards model with the total elapsed hours from the altered initial encounter until crossing or the end of the 48-h period. To account for individual variation in the rates individuals encountered mapped fences and their behavioral responses to encounters, we specified a random intercept for individual in the initial and crossing response models and a cluster term for individual in the passage time model.

To develop each model, we evaluated competing models representing the influence of noncollinear (Pearson correlation coefficient $|r| < 0.6$; Appendix S2: Figure S1) combinations of fence and landscape covariates on each response variable (Table 1). We used fence type based on fence characteristics and classified the covariate into woven wire, low strand (i.e., any strand fence with an average lowest wire height < 41 cm), and high strand (i.e., any strand fence with an average lowest wire height ≥ 41 cm). Although highest wire height may influence permeability of some fences for pronghorn, the rare observations of pronghorn jumping fences suggest this behavior is atypical (Yoakum, 2004), and therefore we did not incorporate this variable into our models here. We aggregated four landscape covariates based on a review of published studies and hypotheses of fence effects on pronghorn movements, which included terrain

TABLE 1 Covariate descriptions, functional form, and hypothesized direction of relationship for covariates used in modeling pronghorn movement responses to fence encounters in six study areas in southwest, central, and southeast Montana, USA, 2019–2021.

Covariate	Description	Form (hypothesis)
Fence type	Woven wire, low strand, high strand	(–), (–), (+)
Ruggedness	Vector ruggedness measure	Li, Ln (+)
Shrub land cover	Binary (1 = shrub-dominated, 0 = non-shrub-dominated)	Shrub-dominated (–)
Shrub canopy cover	Percent shrub canopy cover	Li, Ln (–)
Snow depth	Modeled snow depth (cm)	Li, Ln (–)
Seasonal movement indicator	Binary indicating period of typical seasonal directional movements (1 = spring [20 Mar–30 Apr] and fall [15 Sep–31 Oct], 0 = otherwise)	(+)

Note: Positive (+) relationships are hypothesized to be less modified (i.e., initial responses more likely to be unaltered movements, higher probability of crossing a fence, and decreased passage time) and negative (–) relationships are hypothesized to be more modified (i.e., initial responses less likely to be unaltered movements, lower probability of crossing a fence, and increased passage time).

Abbreviations: Li, linear; Ln, natural log.

ruggedness, shrub land cover type, percent shrub canopy cover, and snow depth. We hypothesized that areas with more topographic variation result in variable lowest wire heights and therefore predicted that more rugged areas provide pronghorn with more fence crossing opportunities (Jones et al., 2018; Yoakum, 2004). We used the `spatialEco` package (Evans, 2020) in Program R to calculate an index of topographic ruggedness ranging from 0 (e.g., flat) to 1 (e.g., most rugged) based on the variation in the three-dimensional orientation of a 3×3 neighborhood of 30-m resolution elevation raster pixels (Sappington et al., 2007). The amount of live vegetation and snow accumulation at fences may limit permeability by altering the relationship between movement behaviors and bottom wire heights (Yoakum, 2004). We hypothesized that fences in shrub-dominated cover types or in areas with more shrub cover would be more likely to accumulate live or dead vegetative material than other cover types, such as herbaceous-dominated grassland or agriculture, or in areas with less shrub cover. We used the 2021 Montana land cover dataset (Montana State Library, 2021) and reclassified land cover classes into a binary indicator of shrub land cover (i.e., shrub-dominated) or non-shrub land cover. We used mean percent shrub canopy cover derived from the annual vegetation cover dataset in the Rangeland Analysis Platform (RAP, 2021) and averaged across the five years (2015–2020) previous to the study as a competing covariate. We used the snow depth dataset from the Snow Data Assimilation System (National Operational Hydrologic Remote Sensing Center, 2021) to assign daily snow depth to each fence encounter based on the date of the initial encounter. All landscape covariate datasets were represented by 30-m resolution rasters, excepting the snow depth dataset, which was represented by 1-km resolution rasters. We were not able to feasibly acquire a finer resolution snow depth dataset; therefore, the snow depth covariate only broadly represents seasonal effects of average predicted snow depth on movement responses.

To associate fence type with fence encounters, we spatially joined the nearest fence feature to the initial location of each encounter and, for quick crosses, to the location intersecting the fence along the movement path. To associate landscape covariates to fence encounters, we extracted the mean covariate value of a 50-m buffered area around the initial encounter location of each encounter and, for quick crosses, around the location 25 m from the fence along the movement path intersecting the fence in the direction of the first location. For the land cover covariate, we extracted the dominant vegetation cover type within the buffered area. We used the buffered area to better capture the covariate conditions along the fence given uncertainties associated with

the spatial accuracy in the raster datasets and the precise location of where quick crosses occurred along the fence. Additionally, to account for responses that may be associated with within seasonal range movements as opposed to directional migratory movements, we evaluated a seasonal movement covariate indicating whether the response occurred within time windows during which spring (20 March–30 April) and fall (15 September–31 October) migratory movements typically occur within our study herds.

We considered linear and natural log functional forms of each continuous covariate to allow flexibility in the hypothesized relationships that may better describe the data (Franklin et al., 2000). To aid in model convergence and covariate comparisons, all continuous covariates considered for linear functional forms were mean-centered and divided by their SDs. For each response variable analysis, we included fence type in all models with high strand fence as the reference level and conducted model selection in a tiered approach to evaluate competing landscape covariates and select a best-supported model. We ranked and selected models in each tier based on corrected Akaike information criterion (AIC_c; Burnham & Anderson, 2002). We used the first and second tiers to perform simple model comparisons for determining a best-supported, representative functional form of each continuous covariate (Franklin et al., 2000) and type of covariate measuring similar landscape attributes (i.e., shrub land cover and shrub canopy cover), respectively (Table 1). In the third tier, we fit and competed multivariate models that included a null model, a model with fence type only, and additive models containing all combinations of covariates and functional forms selected in the first and second tiers and the seasonal movement indicator. From this final suite, noncompetitive models that were similar to well-supported models but containing uninformative parameters were discarded (Arnold, 2010; Burnham & Anderson, 2002). To account for model selection uncertainty, we model averaged the unconditional coefficient mean and error estimates of the top performing models $<4 \Delta AIC_c$, using the `MuMIn` package (Bartoń, 2022). Based on the model-averaged estimates, we calculated 95% confidence intervals (CIs) and inferred support for relationships where CIs did not overlap zero. We performed data processing and analysis tasks primarily using the `sf` (Pebesma, 2020), `raster` (Hijmans, 2020), `tidyverse` (Wickham, 2020), `lme4` (Bates et al., 2020), and `survival` (Therneau, 2021) packages in the R environment for statistical computing.

To evaluate the predictive performance of the final models for the initial and crossing responses, we used a k -fold cross-validation, where k indexed each individual

rather than a random data fold. Within an iterative process, we withheld the encounter periods for each individual, 1 through k , fit the final model with the individuals that were retained, and then predicted the fitted values for the observations that were withheld. We classified the predicted log-odds values to 0 or 1 for values <0 or ≥ 0 , respectively, calculated proportion of predicted values that equaled observed values, and averaged the proportions across individuals. Lastly, we tested whether the final passage time model met the assumption of proportional hazards for Cox regression models by evaluating plots and p values associated with the correlation of Schoenfeld residuals for each covariate over time (Grambsch & Therneau, 1994).

RESULTS

Across all study areas, we mapped and recorded the characteristics of 1554 fence segments (range = 49–529 segments/study area) that totaled 1672.8 km (range = 67.4–591.9 km/study area) and had 2276 gates (range = 23–1181 gates/study area) or approximately 1.4 gates/km of fence. From the 473 adult female pronghorn collared in our study, we obtained 3,923,164 GPS locations or an average of 8455 (range = 22–21,426) locations/individual. Of these pronghorn, 265 (range = 25–58 individuals/study area) encountered mapped fences during the period spanning January 2019–June 2021 (Appendix S3: Figures S1 and S2). We recorded 5581 encounter periods, averaging 21.1

(SD = 21.6, range = 1–126) encounter periods/individual. Encounters occurred at 708 unique fence segments that totaled 978.7 km and included 663.1 (66.6%), 225.9 (23.1%), and 89.8 (9.1%) km characterized as low strand, high strand, and woven wire, respectively. The lowest and highest wire heights of encountered fence segments of all strand fences averaged 34.7 cm (range = 0–71.1 cm) and 106.2 cm (range = 50.8–132.1 cm), respectively. The highest wire height of encountered fence segments characterized as woven wire averaged 103.3 cm (range = 88.9–127.0 cm).

Of the total encounter periods, we identified 4567 (81.8%) unaltered and 1014 (18.2%) altered initial responses, averaging 18.3 (SD = 19.0, range = 1–110) unaltered and 4.9 (SD = 4.2, range = 1–20) altered responses/individual. Altered responses comprised 16.6%, 15.6%, and 42.3% of the total encounters with low strand ($n = 3764$), high strand ($n = 1425$), and woven wire ($n = 392$) fences. The average proportion of altered initial responses across individuals was similar for low strand (0.18, SD = 0.23) and high strand (0.17, SD = 0.25) and higher for woven wire (0.44, SD = 0.42) fence types (Figure 2a). Of the encounter periods classified as altered initial responses, we identified 398 (39.3%) crossing and 616 (60.7%) non-crossing responses, averaging 2.7 (SD = 2.7, range = 1–17) crossings/individual. Non-crossing responses comprised 54.9%, 57.0%, and 88.0% of the total encounters with low strand ($n = 625$), high strand ($n = 223$), and woven wire ($n = 166$) fences. The average proportion of crossing events following an

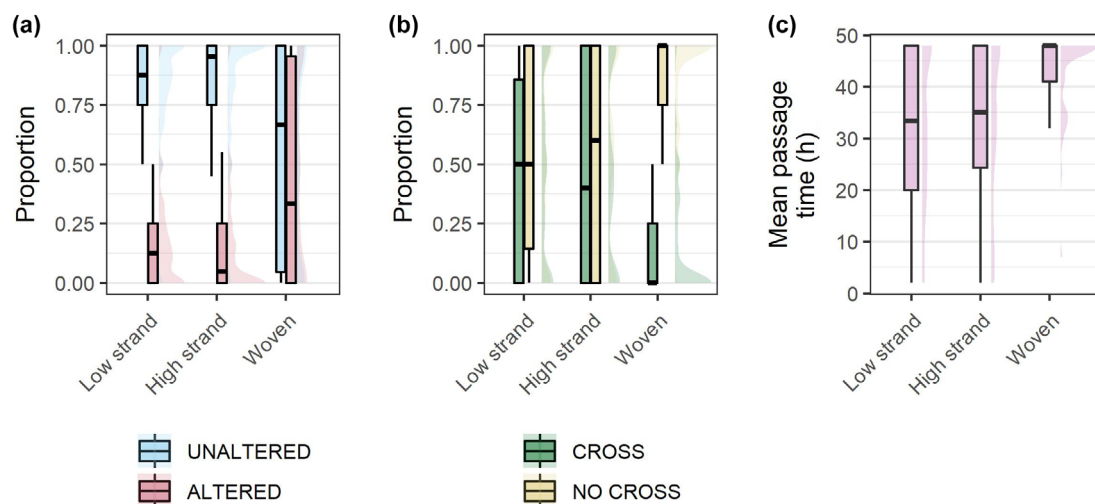


FIGURE 2 Proportion of encounters resulting in initial responses (panel (a)) and in crossing responses following an altered initial response (panel (b)) and mean passage time following an altered initial response (panel (c)) of female pronghorn for different fence types in six study areas in southwest, central, and southeast Montana, USA, 2019–2021. Distributions are based on proportions and means calculated for each individual. Low and high strand fences are defined as wire fences with lowest wire height <41 and ≥ 41 cm, respectively. Horizontal lines through boxes represent median values, the length of the box represents the interquartile range (i.e., the middle 50% of observations), and vertical lines represent values within 1.5 times the interquartile range.

altered initial response across individuals was modestly higher for low strand (0.50, SD = 0.39) than high strand (0.43, SD = 0.41) and lowest for woven wire (0.14, SD = 0.24) fence types (Figure 2b). Average passage time of crossing events following an altered initial response across individuals was 14.1 (SD = 12.1) h and was similar for low strand (14.2 h, SD = 12.2), high strand (13.8 h, SD = 11.9), and woven wire fence (13.8 h, SD = 11.1). Overall average passage time (i.e., including encounter periods with no crossing response through 48 h) following an altered initial response was similar for low strand (32.8 h, SD = 18.7) and high strand (33.3 h, SD = 18.7) and markedly higher for woven wire (43.9 h, SD = 11.8) fence types (Figure 2c).

For all strand fence types, the average lowest wire height of unaltered (35.5 cm, SD = 10.4) and altered (34.3 cm, SD = 11.1) initial responses and of crossing (35.3 cm, SD = 10.0) and non-crossing (33.5 cm, SD = 11.8) responses was similar. For all fence types, the average highest wire height of unaltered (106.1 cm, SD = 15.1) and altered (103.9 cm, SD = 20.8) initial responses and of crossing events (105.0 cm, SD = 16.9) and non-crossing events (102.0 cm, SD = 23.4) was similar. Passage times varied widely across lowest and highest wire heights (Appendix S4: Figure S2).

In the first model tiers, the top-ranked functional forms included natural log ruggedness, natural log shrub canopy cover and linear snow depth for the initial response analysis, and linear ruggedness, natural log shrub canopy cover, and natural log snow depth for the crossing response and passage time analyses (Table 2). In the second model tiers, shrub land cover outranked linear shrub canopy cover for the initial response analysis, and natural log canopy cover outranked shrub land cover for the crossing response and passage time analysis. In the third model tiers, we competed 18 models in each analysis. After models with uninformative parameters and $\geq 4 \Delta AIC_c$ were removed from each model selection set, only three models remained in the initial and crossing response analyses and one model remained in the passage time analysis. The top-ranked models varied across each analysis, with the top model for the initial response analysis including fence type, snow depth, and shrub land cover; for the crossing response analysis including fence type and ruggedness; and for the passage time analysis including fence type and shrub canopy cover. These models outranked the model containing only fence type and the null model by 21.6 and 91.3 ΔAIC_c in the initial response analysis, by 3.3 and 38.8 ΔAIC_c in the crossing response analysis, and by 6.6 and 73.0 ΔAIC_c in the passage time analysis. Second- and third-ranked models differed from the top model for the initial response only by the addition of the seasonal

movement indicator and the substitution of shrub land cover with ruggedness, respectively, and for the crossing response by the substitution of shrub land cover with ruggedness and the exclusion of ruggedness, respectively. The k-fold cross-validations indicated reasonable model performance, with an average accuracy of 0.78 (SD = 0.24) and 0.60 (SD = 0.35) for the initial and crossing response models. All covariates examined within our final passage time model met the proportional hazards assumption (p value for fence type = 0.69, natural log canopy cover = 0.63, and the global model = 0.78). The coefficients for the random intercept or cluster term on individual for the top-ranked models in each analysis indicated that a continuum of estimated responses existed across individuals (Appendix S5: Figure S2).

Based on model-averaged coefficient estimates for the initial response analysis (Appendix S5: Figure S1 and Table S1), the probability of an unaltered initial response in non-shrub-dominated, snow-free, and relatively flat areas during non-migratory periods was greatest and similar for low strand (0.86, 95% CI = 0.84–0.88) and high strand (0.87, 95% CI = 0.84–0.89) fences, and significantly less for woven wire fences (0.57, 95% CI = 0.49–0.65; Figure 3a). Although shrub land cover type was supported in model selection and indicated a reduced probability of an unaltered initial response in shrub-dominated areas, as compared with non-shrub-dominated areas, the probabilities for all fence types were similar (i.e., in shrub-dominated areas: 0.84 [95% CI = 0.81–0.87] for low strand, 0.85 [95% CI = 0.81–0.88] for high strand, and 0.53 [95% CI = 0.44–0.62] for woven wire fences). Similarly, probabilities for all fence types were identical during seasonal migratory periods as compared with non-migratory periods (i.e., 0.86 [95% CI = 0.84–0.88] for low strand, 0.87 [95% CI = 0.84–0.89] for high strand, and 0.57 [95% CI = 0.49–0.65] for woven wire fences). The probability of an unaltered initial response decreased with increasing snow depth; in non-shrub-dominated and relatively flat areas, probabilities declined to 0.77 (95% CI = 0.69–0.83) at 20 cm and to 0.61 (95% CI = 0.44–0.77) at 40 cm of snow for high strand fences, and to 0.40 (95% CI = 0.29–0.52) at 20 cm and to 0.26 (95% CI = 0.13–0.42) at 40 cm of snow for woven wire fences. The probability of an unaltered initial response decreased modestly with increasing ruggedness; in areas with the highest ruggedness values, probabilities declined to 0.84 (95% CI = 0.79–0.88) for high strand fences and 0.52 (95% CI = 0.41–0.62) for woven wire fences.

Based on model-averaged coefficient estimates for the crossing response analysis, the probability of a crossing response following an altered initial response to a fence encounter in relatively flat areas with no shrub canopy cover was greatest and similar for low strand (0.10, 95% CI = 0.001–0.63) and high strand

TABLE 2 Tiered model selection results evaluating three pronghorn movement responses to fence encounters in southwest, central, and southeast Montana, USA, 2019–2021.

Response	Model tier	Model ^a	K	AIC _c	ΔAIC _c	w _i
Initial	Tier 1	Ruggedness ^{Ln}	5	4984.60	0	0.51
		Ruggedness	5	4984.70	0.10	0.49
		Shrub canopy cover ^{Ln}	5	4989.95	0	0.52
		Shrub canopy cover	5	4990.09	0.14	0.48
		Snow depth	5	4979.52	0	0.99
		Snow depth ^{Ln}	5	4989.96	10.44	0.01
	Tier 2	Shrub land cover	5	4980.75	0	0.99
		Shrub canopy cover ^{Ln}	5	4989.95	9.20	0.01
	Tier 3 ^b	Snow depth + shrub land cover	6	4969.59	0	0.64
		Snow depth + shrub land cover + SMI	7	4971.59	2.01	0.23
Snow depth + ruggedness ^{Ln}		6	4972.89	3.30	0.12	
Crossing	Tier 1	Ruggedness	5	1251.46	0	0.66
		Ruggedness ^{Ln}	5	1251.82	1.36	0.34
		Shrub canopy cover ^{Ln}	5	1253.56	0	0.63
		Shrub canopy cover	5	1254.58	1.03	0.37
		Snow depth ^{Ln}	5	1256.22	0	0.53
		Snow depth	5	1256.50	0.27	0.47
	Tier 2	Shrub canopy cover ^{Ln}	5	1253.56	0	0.60
		Shrub land cover	5	1254.58	0.78	0.40
	Tier 3 ^c	Ruggedness	5	1251.46	0	0.61
		Shrub canopy cover ^{Ln}	5	1253.56	2.10	0.21
		Null fence type model	4	1254.81	3.36	0.11
	Passage time	Tier 1	Ruggedness	3	5259.63	0
Ruggedness ^{Ln}			3	5260.65	1.01	0.38
Shrub canopy cover ^{Ln}			3	5255.16	0	0.55
Shrub canopy cover			3	5255.56	0.40	0.45
Snow depth ^{Ln}			3	5263.64	0	0.51
Snow depth			3	5263.76	0.12	0.49
Tier 2		Shrub canopy cover ^{Ln}	3	5255.16	0	0.87
		Shrub land cover	3	5258.92	3.76	0.13
Tier 3 ^d		Shrub canopy cover ^{Ln}	3	5255.16	0	1.00

Note: The crossing and passage time responses are defined as responses occurring following an altered initial response. Each model contains a random intercept or cluster term for individual and a fixed effect for fence type additive to covariates presented. The top two models and models within 4 ΔAIC of the top-ranked model for each tier are presented, along with their respective number of parameters (*K*) and AIC_c weight (*w_i*).

Abbreviations: AIC_c, corrected Akaike information criterion; SMI, seasonal movement indicator.

^aSuperscripts indicate functional form (Ln = natural log, [none] = linear).

^bThe null and fence type only model had AIC_c = 5060.87 and 4991.22, respectively.

^cThe null and fence type only model had AIC_c = 1290.23 and 1254.77, respectively.

^dThe null and fence type only model had AIC_c = 5328.18 and 5261.75, respectively.

(0.09, 95% CI = 0.001–0.60) fences, and less for woven wire fences (0.03, 95% CI = 0.001–0.21; Figure 3b). Crossing probabilities for all fence types increased with higher ruggedness and shrub cover values. In relatively rugged areas with no shrub cover, crossing probabilities

were 0.19 (95% CI = 0.001–0.87) for low strand, 0.18 (95% CI = 0.001–0.85) for high strand, and 0.07 (95% CI = 0.001–0.52) for woven wire fences. In relatively flat areas with 20% shrub cover, crossing probabilities were 0.50 (95% CI = 0.38–0.63) for low

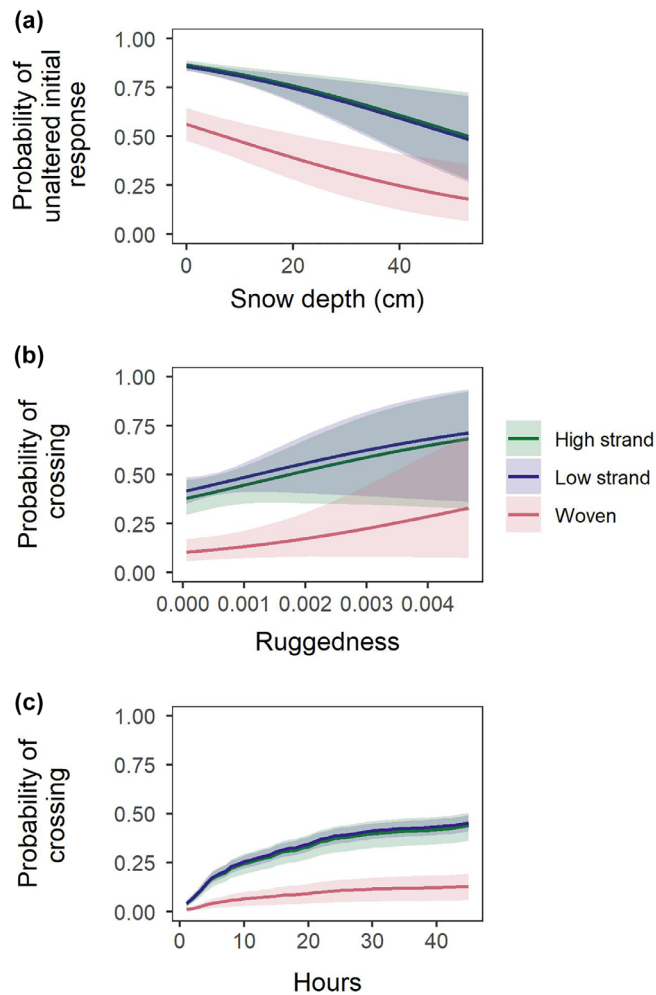


FIGURE 3 Predicted relationships of the probability ($\pm 95\%$ CI) of unaltered initial response (panel (a)), probability of crossing following an altered initial response (panel (b)), and passage time (i.e., probability of crossing through time) following an altered initial response (panel (c)) of pronghorn fence encounters for different fence types in six study areas in southwest, central, and southeast Montana, USA, 2019–2021. Displayed relationships are based on averaged top models from each respective analysis and contain the range of the observed covariate values while keeping all other covariates constant at their mean value. Low and high strand fences are defined as wire fences with the lowest wire height < 41 and ≥ 41 cm, respectively.

strand, 0.46 (95% CI = 0.33–0.60) for high strand, and 0.14 (95% CI = 0.07–0.25) for woven wire fences.

Based on hazard ratios from the top model in the passage time analysis, pronghorn were as likely (1.02 times, 95% CI = 0.94–1.11) to cross a high strand fence as a low strand fence and more than two times as likely (2.24 times, 95% CI = 1.45–3.44) to cross a high strand than a woven wire fence following an altered initial response to a fence encounter. Crossing response (i.e., hazard ratios) increased by 1.2% (95% CI = 1.0%–1.4%) for approximately every

10% increase in percent shrub cover. Holding shrub cover at its mean observed value, the predicted crossing probability during the first hour after the encounter was highest and similar for low strand (0.04, 95% CI = 0.03–0.06) and high strand (0.04, 95% CI = 0.03–0.05) fences, and lowest for woven wire fences (0.01, 95% CI = 0.003–0.02; Figure 3c). At the 10th hour after the encounter, the predicted probabilities of crossing increased, respectively, to 0.26 (95% CI = 0.22–0.29), 0.25 (95% CI = 0.19–0.29), and 0.07 (95% CI = 0.03–0.10). By the 40th hour after the encounter, the predicted probabilities of crossing modestly increased to 0.43 (95% CI = 0.39–0.47), 0.42 (95% CI = 0.34–0.48), and 0.12 (95% CI = 0.05–0.18), respectively.

DISCUSSION

Our study found no support for the hypothesis that fence design does not substantially affect pronghorn movement responses. All fence designs evaluated in our study, including low strand (i.e., average lowest wire height < 41 cm), high strand (i.e., average lowest wire height ≥ 41 cm; commonly characterized as “wildlife friendly” with respect to pronghorn; Hanophy, 2009; Jones et al., 2018; Paige, 2012, 2015), and woven wire fences, negatively influenced pronghorn movement responses. Fence designs differed, however, by the magnitude of their effect on movement responses (Figure 3), with our results supporting the hypothesis that woven wire fences, in comparison with low and high strand fences, are substantially more likely to result in reduced probabilities of unaltered initial responses (e.g., movements that do not “bounce” away or parallel the fence) and crossing responses and in increased passage times. In addition, crossing probabilities through time increased moderately for strand fences but only minimally for woven wire fences. Together, these results are consistent with observations and studies that pronghorn are characteristically prone to alter their movement patterns when encountering fences constructed of wire strands at or near ground level (Xu et al., 2021; Yoakum, 2004); however, we found that low and high strand fences were associated with nearly identical responses. These results run counter to our hypothesis and prediction that low strand fences would reduce response probabilities in comparison to high strand fences, as well as to popular paradigms and recommendations for improving permeability of fences to pronghorn by raising the height of the lowest strand (Hanophy, 2009; Jones et al., 2018; Paige, 2012, 2015).

The fact that pronghorn permeated strand fences regardless of whether the lowest strand height met standards for pronghorn-friendly fencing does not necessarily

indicate that high strand fences lack effectiveness. Rather, the relatively high estimated probabilities of unaltered initial responses for both strand fence types indicate that low strand fence constructions are likely still often permeable to pronghorn. The similarity in movement responses between these strand fence types may be due to variation in lowest wire heights from inconsistent construction, deterioration, or uneven terrain along fence segments that is not captured in our field measurements (e.g., the average height value from five measurements along the fence), in addition to strong fidelity of pronghorn to known-crossing sites (i.e., regardless of strand type, pronghorn regularly return to the same site to cross; Jones et al., 2018). Additional research using finer scale GPS fix interval and fence data could help elucidate this possibility; however, further evidence of the importance of known-crossing sites may be indicated by our results that the probability of crossing through time following an altered initial response increased only minimally for all fence types (Figure 3c). In other words, if a pronghorn crosses a fence, the crossing is likely to occur relatively quickly (i.e., at the initial encounter) and not thereafter, suggesting the pronghorn know where crossing sites are located. However, it remains unclear if, following an altered initial response, pronghorn continued to seek passage but were barred from doing so or if pronghorn were never seeking to cross the fence at all.

Although woven wire fences substantially impacted pronghorn responses relative to strand fences, our results demonstrate that all fence types evaluated in our study influence pronghorn movements to some degree. Given the ubiquity of fences that often occur across pronghorn ranges, the cumulative effect of these movement responses may be important, particularly for pronghorn with altered initial encounters. For example, if the approximate 14-h average crossing rate following an altered initial encounter that we found in our study represents individuals attempting to permeate fences, the time required to permeate each additional fence encounter could accumulate substantially. Such quantities of time required to permeate fences may be particularly important when relatively quick passage may be needed to access resources. While the seasonal movement indicator covariate was supported in one model of our crossing response analysis, the CIs for the predicted effect spanned zero, indicating that pronghorn spend similar amounts of time negotiating fences in nonmigratory and migratory seasons. If a relatively quick passage is needed due to rapid seasonal changes, such as deep snow during fall migration, the quantities of time required to permeate multiple fences may be particularly impactful. These cumulative effects may therefore markedly compromise the ability of individuals to access resources necessary

for survival, reproductive needs, such as pregnancy, gestation, and lactation, and to facilitate gene flow, and consequently negatively impact individual- and population-level fitness (Beyer et al., 2016; LaCava et al., 2020). In combination with temporal and spatial changes in resources due to climate change, these consequences may be even greater (Van Moorter et al., 2020; Zeller et al., 2021). More research is needed, however, to evaluate the link between individual movement responses to fences and consequences to population vital rates.

Consistent with our predictions, we found evidence that pronghorn were more likely to have an altered initial response if the encounter occurred in an area dominated by shrubs or with greater snow depth, suggesting that the effective lowest wire height at particular sites or along the entire fence is reduced by accumulation of shrub growth and snow along fences. Conversely, in the crossing and passage time analyses, percent shrub cover was positively associated with crossing and passage time probabilities. Only in the passage time analysis, however, was the effect of the shrub covariate important, with 95% CIs excluding zero. The interpretation of this positive relationship remains unclear, but it may be possible that shrub growth adds variation to the lowest wire height. The effect of terrain ruggedness in our initial and crossing response models was consistent with our predictions that pronghorn were more likely to cross a fence in more rugged areas; however, the predicted effect was minimal, with 95% CIs overlapping zero. We caution that uncertainties may exist in our results associated with the snow depth variable due to disparities in spatial scale of the snow depth raster and collar location data (i.e., 1-km resolution vs. highly precise; Brennan et al., 2013) and in timing of field measurements of fences (i.e., during snow-free summer periods) relative to when pronghorn encounters during winter occurred.

Our study provides the first empirical evaluation of the influence of fence and landscape characteristics on pronghorn movement responses to fence encounters using fine spatiotemporal collar data and mapped fences. The framework we developed for identifying and quantifying movement responses to fence encounters could be adapted to be used with a wide variety of terrestrial animals. Our three movement response metrics (i.e., initial response, crossing following an altered initial response, and passage time following an altered initial response) provide straightforward indices to monitor animal responses to fences and evaluate effects of fence remediation on movement behaviors. This information is critical for monitoring and improving the effectiveness of fence remediation efforts, enhancing landscape permeability, and developing land-use and conservation plans that benefit wildlife populations.

Overall, our results indicate that efforts to remediate fences and facilitate landscape permeability for pronghorn should prioritize the removal of woven wire, the replacement of woven wire fences with strand fences, and the possible incorporation of variation in lowest wire height along strand fences (e.g., by attaching carabiner clips to raise the lowest wire at various points along the fence). The latter is a substantially more cost- and labor-effective alternative to fence replacement (Jones et al., 2018), which may be particularly important in areas prone to snow accumulation. Further, given that low and high strand fences shared similar permeabilities, we emphasize that definitions of pronghorn-friendly fences should be dependent on site-specific characteristics and environmental conditions, not based strictly on a lowest wire height value. Alternatively, to limit permeability and exclude pronghorn from areas (e.g., roadways, crops), we recommend woven wire fences. Fence designs should be carefully tailored to both meet their intended purpose (e.g., keeping livestock in or animals out, identifying property boundaries) and address their effects on pronghorn and other species that occupy similar habitats, such as deer species, elk, and sage grouse. Deliberate monitoring and adjustments are necessary to ensure projects have minimal adverse effects.

The presence and ubiquity of gates across our study areas likely also influenced fence permeability by contributing additional variation in lowest wire heights or by being open. Although we did not measure gate attributes and could not record when gates were open relative to pronghorn movements, we recorded a high number of gates in our study areas, approximately 1.4 gates/km of fence. We suspect that closed gates along woven wire fences were built to be similarly impermeable, whereas closed gates along strand fences contained more irregularities in construction, contributing to our results that strand fences were more permeable than woven wire fences. No studies exist on the effects of gates on pronghorn movement; however, several sources promote leaving gates open when livestock are not present to improve fence permeability for pronghorn (Gates et al., 2012; Yoakum et al., 2014), and this approach may present a more cost-effective approach to increasing permeability of fences as compared with remediation of entire stretches of fence to meet pronghorn-friendly standards. Further, replacing or modifying gate construction to permit pronghorn passage is an alternative strategy to managing gate closures that does not require return trips to the field and may be equally effective.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are not publicly available due to the sensitivity of precise location data occurring on private and indigenous lands and occurring during the hunting seasons for this harvested species. Data can be obtained by submitting a data request to Montana Fish, Wildlife and Parks.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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