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# Species and demographic responses to wildlife-friendly fencing on ungulate crossing success and behavior

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**Abstract**

Fencing is a ubiquitous part of the landscape across the Great Plains of North America. This can fragment habitats and reduce the ability of wildlife to move between patches. A relatively novel conservation tool aimed at mitigating these impacts is the use of wildlife-friendly fencing. However, there is still an incomplete understanding as to how this tool affects ungulate movement and whether it increases habitat connectivity across barriers. Using camera trap data from three properties across the American Prairie Reserve, Montana, we investigated the effects of fencing on four ungulate species. Averaged across species and demographics, this wildlife-friendly fencing design increased the probability that ungulates successfully crossed a fence by 33% and reduced the time taken to cross by 54%, but has limited effects on species' crossing behavior. Responses to the wildlife-friendly fencing differed between species, sex, and age class. The greatest improvement in permeability was detected for mule deer, females, and juvenile groups. Yet, permeability remained lowest for elk, juveniles, and males overall at both fence types. Understanding these differences between groups is important when improving or selecting fence designs, and we highlight vulnerable groups that may require further study when implementing this conservation tool.

**KEYWORDS**

elk, fence ecology, great plains, habitat permeability, mule deer, pronghorn, white-tail deer

## 1 | INTRODUCTION

Habitat fragmentation resulting from human actions is widely considered the greatest threat to the migration and daily movement patterns of global wildlife (Harris, Thirgood, Hopcraft, Cromsigt, & Berger, 2009; Tucker et al., 2018). The recent global decline in abundance and distribution of migratory ungulates is attributable, in part, to linear anthropogenic features bisecting seasonal ranges and routes (Dobson, Borner, & Sinclair, 2010; Tucker et al., 2018). An important driver of fragmentation

is the increasing use of fencing, the effects of which on wild, migratory animals or those with large ranges has been highlighted as a major, emerging issue for global biological diversity (Sutherland et al., 2016), and has been understudied in comparison to other forms of linear infrastructure (Jakes, Jones, Paige, Seidler, & Huijser, 2018). At its most severe, fencing has led to mass-mortality events of migratory ungulates during severe exogenous events, blocking them from accessing essential resources such as waterholes (Mbaiwa & Mbaiwa, 2006; Williamson & Williamson, 1984; Yoakum, 2004). Gavin

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and Komers (2006) also found that anthropogenic impediments can lead to negative behavioral changes, such as directing essential time away from finding high-quality forage to avoiding fences and roads (Seidler, Long, Berger, Bergen, & Beckmann, 2015). Additionally, barriers may have severe long-term ecological consequences, including genetic isolation. This may increase rates of inbreeding and mortality, and reduce species' ability to adapt to environmental change (Dodd, Gagnon, Sprague, Boe, & Schweinsburg, 2011). This is particularly worrying considering recent climate change, potentially amplifying the effects of barriers in the future (Opdam & Wascher, 2004; Post & Forchhammer, 2008). While the negative impact of fences on ungulates was recognized early in the scientific literature (e.g., Canton, 1877), fence ecology remains a fledgling discipline, with recent calls to better understand the scale and directionality of these effects on wildlife and society (Jakes, Jones, et al., 2018).

Fencing is now a ubiquitous part of the landscape across the prairie ecosystem of the Great Plains of North America (Poor, Jakes, Loucks, & Suitor, 2014), having first been introduced by homesteaders in the 19th century to delineate agricultural and private land (Hayward & Kerley, 2009). Fences in these areas are free-standing structures primarily designed to restrict or prevent movement of livestock across demarcated boundaries; while this can sometimes be beneficial, such as to reduce numbers of animal-vehicle collisions along roads, their structures can also negatively affect the movement of wild ungulates (Jakes, Jones, et al., 2018; McCollister & Van Manen, 2010). The widespread use of fencing has contributed to the increasing isolation of habitat patches and contributed to the loss of between 76 and 82% of mixed grassland, a key habitat for most prairie wildlife (Samson & Knopf, 1994). Many of the species affected undertake long-distance migrations, widely considered an increasingly rare phenomenon, with migratory ungulates seen to play an important role both as key drivers of ecosystem processes and economically with their hunting tags funding many conservation initiatives within the United States (U.S. Department of the Interior, 2011; Sawyer et al., 2012). Conservative estimates suggest that roughly 75% of migration routes for ungulates have been lost on average in or adjacent to the Greater Yellowstone region, an area of low human density, and the remaining corridors along which they continue to pass through are increasingly narrow (Berger, 2004).

Barbed- or woven-wire fences can also cause high levels of ungulate mortality, as well as an elevated risk of injury and reduced fitness (Visscher, MacLeod, Janzen, Visser, & Lekas, 2016). For example, Harrington and Conover (2006) estimated that along road-fence lines there was a mortality rate of 0.25 ungulates/km/annum. A primary cause of this mortality rate is entanglement when ungulates attempt to jump over barbed-wire fencing (Harrington & Conover, 2006). Additionally, from a management perspective, unsuccessful wildlife crossings result in damage to the fences themselves and subsequent costs to landowners (Andrews & Rowley, 1998).

In light of these risks to wildlife and landowners, it is important that mitigation measures are investigated and implemented to maintain and restore connectivity of key habitat. While there are a variety of crossing structures designed to assist wildlife movement, such as wildlife bridges and underpasses, one measure that has gained recent attention is the replacement of traditional barbed-wire fencing with wildlife-friendly fencing. One of the key design changes to standard fencing to make it wildlife-friendlier is the use of a raised, smooth bottom wire; this is based on accumulated evidence that this design change improves the permeability of the barrier, with lower aversion and increased crossing rates compared to barbed-wire fencing (Figure 1) (Jones et al., 2020; Karhu & Anderson, 2003). Other modifications include visible markers,

(a) Barbed Wire Fencing    (b) Wildlife Friendly Fencing



LEGEND:
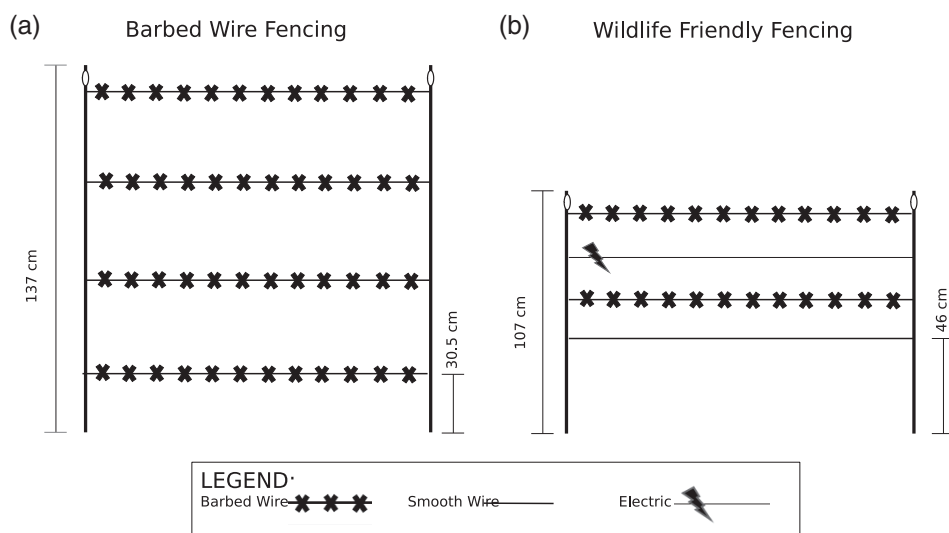Barbed Wire ✕✕✕    Smooth Wire ——    Electric ⚡

**FIGURE 1** A schematic showing the design of the barbed wire fence and the wildlife-friendly fence types that were used in the study

reducing the height of the top wire and using seasonal electric fencing (Paige, 2012). However, it is expensive and time-consuming for conservation initiatives and land-owners to switch fencing. Furthermore, while there is some data on ungulate-fence mortality, there is little evidence about behavioral changes along fence lines (Jakes, Jones, et al., 2018; Jones et al. 2020). Therefore, understanding the effects that wildlife-friendly fencing has on ungulate movement and habitat connectivity at patch-scale is critical to establishing whether limited conservation resources should be invested into this tool.

Within this study, we investigate whether wildlife-friendly fencing can provide conservation benefits to ungulates, by improving movement and connectivity across property boundaries in the Great Plains, in comparison to traditional barbed-wire fencing. The four species of study were elk (*Cervus canadensis*), pronghorn (*Antilocapra americana*), white-tail deer (*Odocoileus virginianus*), and mule deer (*Odocoileus hemionus*). These are among the most abundant wild ungulates in the region and are often cited as being negatively affected by

fencing (Hayward & Kerley, 2009). Furthermore, as wildlife-friendly fence designs are often made with adult ungulates in mind, we also investigated whether species, sex, or age-stages are differently affected by the change in fence treatment. In doing so, we are able to understand which species and demographics are most at risk from such barriers and shed light on how wildlife-friendly fencing might be improved as a conservation tool in the future.

## 2 | METHODOLOGY

### 2.1 | Area description

The American Prairie Reserve (APR) is a privately funded Non-Governmental Organisation located in the mixed-grass prairie ecosystem of Phillips and Fergus County in North-eastern Montana (lat 47° 45′48″N, long 107° 41′43″W; Figure 2). This landscape contains large areas of relatively intact grassland habitat (Forrest et al., 2004).
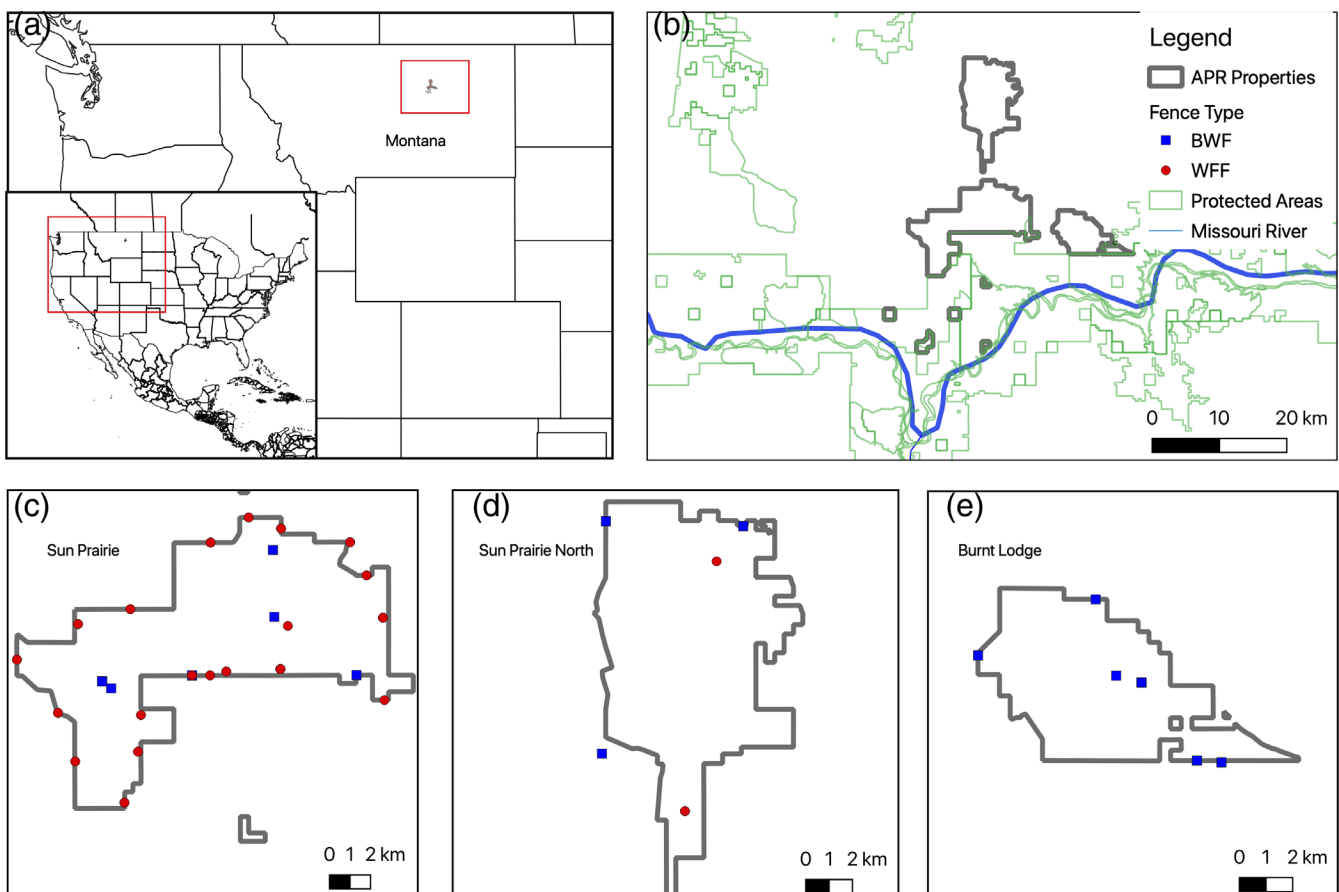


**FIGURE 2** Maps of the study site, showing: (a) the location of the American Prairie Reserve (APR) within Montana, (b) the location of the three focal APR properties in relation to the Missouri River and other protected areas, and the placement of the cameras from which data were collected for this study within (c) Sun Prairie, (d) Sun Prairie North, and (e) Burnt Lodge. In (c–e), red circles indicate cameras that were placed on wildlife-friendly fences (WFF) and blue squares indicate cameras that were placed on barbed-wire fences (BWF)

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Dominant plant species on the APR are representative of a sagebrush steppe system with sedges, cacti, and forb species also common in the area. The climate is semiarid with yearly precipitation ranging from 25.4–27.9 cm and a mean annual temperature of 6.6°C, ranging from 8.5°C in January to 20.9°C in July. APR comprises a collection of noncontiguous private and public properties, previously used for intensive agriculture and livestock. APR is restoring native species including bison, which are currently classed as livestock in Montana and must be fenced. APR selected this type of wildlife-friendly fence based on experimentation and recommendations in the literature in a bid to improve fence permeability and connectivity, while retaining bison (Paige, 2012).

## 2.2 | Study design

Fences on three of these properties, Sun Prairie, Sun Prairie North, and Burnt Lodge, were evaluated during the study (Figure 2). Each property currently borders private or public agricultural land and they are replacing barbed-wire fencing with wildlife-friendly fencing. Since December 2013, the APR have been recording the effects the change in fencing had on the resident wildlife using camera traps set along the fence lines. Analyzing data from a treatment/control study design implemented by the APR, we were able to quantify differences in ungulate movement and behavior that result from the two fence types.

This study used data collected from 39 camera trap positions between the years 2013–2016. Fence types remained constant during the study period, with 15 barbed-wire fencing and 24 wildlife-friendly fencing sites (Figure 2). The wildlife-friendly fencing in this study was a high voltage (3,000–9,000 V) solar-powered electric fence, intended to contain livestock and bison, while allowing other ungulates to cross. It was, on average, 107 cm tall, contained a raised, 46 cm, smooth bottom wire, two barbed-wires, and one electric middle wire (Figure 1). Barbed-wire fencing was nonrandomly replaced with this wildlife-friendly design on the three properties. Bushnell Trophy Cam traps were established on both fence types across the three properties (Figure 2). Camera trap locations were guided using GIS maps of the sites and placed in areas identified with suitable ungulate habitat and distributed across grassland, sagebrush, and riparian zones. The methodology and set up of the camera traps were guided by the lead scientist of the organization at the time, as well as volunteer crews, who could use their knowledge of the local area to inform the final decision of the camera placement. Cameras were placed on vertical fence posts above the top rung of the fence at an average of 90 cm above the ground. Cameras were set to record videos of 60 s in length and 5 s intervals to reduce the risk of missing observations.

Video observation criteria were determined in advance to distinguish between a successful or failed crossing attempt, as well as the time taken to cross by each individual.

A fence crossing attempt was based on the following criteria:

1. The ungulate sticks their head under, through and/or over the fence either more than once in the 60 s clip or for longer than 15 s of the clip. The ungulate must be seen to touch at least the tip of its nose to the wire.
2. The ungulate approaches the fence more than once within the 60 s clip, without browsing. An approach is defined by rotating the body 90° toward the fence and moving toward it.
3. An independent crossing event/attempt is either when each video is separated by 30 min; the ungulates are clearly different based on sex, obvious markers, and/or demographic signs.
4. Interactions must be along the fence and not with the camera.

A successful crossing attempt was defined by the following criteria:

1. The ungulate manages to get its full body across the wire by jumping over, crawling under, or moving through the wire. The point at which the crossing terminates is when the ungulate has resumed a full standing position on the other side of the fence.
2. The ungulate is not visibly injured.
3. If an ungulate manages to cross within the limits of a dependent video (i.e., >1 of visibly the same ungulate within 30 min is found), then this is defined as one crossing event.

The time taken to cross was measured from the point where an ungulate begins to interact with the fence, to the time of a fully successful crossing or the video ends and there is no other video of the ungulate within 30 min of the initial attempt. Each individual within a video was identified as an independent data point. This was based on the assumption that the ability for an individual to cross the fence is not impacted by other individuals crossing. Furthermore, it was assumed that age-stage and sex would respond differently to fence types and this could be measured more easily if they were treated independently.

Full video observation criteria and methodology were adapted from methodology used by the APR

(Appendix S1). Metadata pertaining to each video was also recorded (Appendix S2).

## 2.3 | Data analysis

To estimate the effect of wildlife-friendly fencing on ungulate behavior we analyzed the camera-trap data using Bayesian multilevel models. We fitted separate models for the three measured outcome variables: (a) the probability an observed individual successfully crossed the fence and, for successful crossings; (b) the time taken to cross (in seconds, log10 transformed to reduce skew then centered and scaled by dividing by 2 $SD$ (Gelman, 2008)); and (c) the probability that the crossing is made by going under rather than over the fence, subsequently referred to as "positive" crossing behavior. We also visually examined crossing locations by all species to determine if there were crossing "hotspots" (i.e., favored areas determined by high concentrations of crossing attempts and areas of higher crossing success) (Figure S1).

To model the grouping structure within the data, in which multiple observations were recorded from the same camera trap, and camera traps were placed along different sections of the same fence, all models estimated varying intercepts for camera trap ID and fence ID. These batches of intercept terms were each given independent hierarchical Normal priors centered on zero. Each of the three models also included two predictor variables—a dummy variable indicating the type of fencing observed (wildlife-friendly = 1; barbed wire = 0) and a three level factor indicating the demographic group (adult female, adult male; juvenile)—and their interaction, and all of these effects were allowed to vary by species (a four level factor: elk, pronghorn, white-tailed deer and, mule deer). The parameters corresponding to the average effects were given Normal priors (mean = 0, $SD$ = 1) which were chosen to be weakly informative. The overall intercept was given an uninformative diffuse Normal prior (mean = 0, $SD$ = 10).

All models were fitted using the stan_glmer or stan_lmer functions from the rstanarm package in R (Goodrich, Gabry, Ali, & Brilleman, 2018). For each model, four Markov chains each containing 2,000 samples were drawn from the posterior, with the first 1,000 discarded as warmup. Convergence was assessed by consulting Gelman–Rubin statistics for each parameter (with values <1.01 taken to indicate adequate convergence) and visually inspecting trace-plots. The adequacy with which the models fit the data was examined using graphical posterior predictive checks.

Using the fitted models, we generated predictions on the scale of the linear predictor for each response variable and for every combination of fencing-type, species, and demographic group. To examine marginal effects (i.e., the effect of fencing type for a given species, averaging across demographic groups) we calculated estimated marginal means following Searle, Speed, and Milliken (1980). All predictions were then back-transformed so that effect sizes are presented on the scale of the original data (probability for crossing success and mode of crossing; seconds for the time taken to make a crossing) accompanied by their associated 95% credible intervals (CI). In describing the results, we consider there to be good evidence for an effect when its associated 95% CI does not overlap zero, and weaker evidence when zero lies within the 95% CI but outside of the 80% CI.

## 3 | RESULTS

Prior to analysis, observations containing missing values for any variables used in modeling were excluded ($N$ = 48), leaving 929 observations for analysis across the three properties. These observations came from 39 camera traps, across 28 fence lines with 4 species observed per fence type. There were 533 observations across wildlife-friendly fencing sites and 376 observations across barbed wire sites. For demographic groups, we recorded 559 observations for adult females, 252 for adult males, and 118 for juvenile. For species, we recorded 220 observations for elk, 71 for pronghorn, 122 for white-tailed deer, and 516 for mule deer. This was recorded over an average of 908 camera trap days for barbed-wire fencing and 819 days for wildlife-friendly fencing. When averaged across species and demographics, this wildlife-friendly fencing design increased the probability that ungulates successfully crossed a fence by 33% and reduced the time taken to cross by 54%, but had limited effects on species' crossing behavior. We did not determine any spatial preferences in crossing attempts or success across species for this study.

## 3.1 | Crossing success

Across all species, the marginal probability of a successful fence crossing was 0.739 (95% CI: 0.648, 0.831). Pronghorn were most likely to make a successful crossing (0.877, 95% CI: 0.755, 0.982), followed closely by white-tailed deer (0.806, 95% CI: 0.686, 0.921) and mule deer (0.798, 95% CI: 0.733, 0.859). The rate of successful crossings was substantially lower for elk (0.325, 95% CI: 0.181, 0.462). There was some evidence for differences associated with demographics, with adult females only slightly more likely to make a successful crossing (0.795, 95% CI:

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0.720, 0.863) than adult males (0.750, 95% CI: 0.664, 0.845) but somewhat more than juveniles (0.658, 95% CI: 0.459, 0.843).

Across species and demographics there was, however, clear evidence that the probability of successful crossings at wildlife-friendly fences (0.828, 95% CI: 0.743, 0.917) was higher than the probability of successful crossings at barbed-wire fencing (0.622, 95% CI: 0.494, 0.751). The size of this effect is broadly consistent across species and demographic groups (Figure 3a), with the largest effects observed for white-tailed deer (difference = 0.190, 95% CI: 0.014, 0.391) and mule deer (difference = 0.182, 95% CI: 0.064, 0.304), and slightly smaller effects for elk (difference = 0.157, 95% CI: −0.061, 0.382) and pronghorn (difference = 0.128, 95% CI: −0.002, 0.302). Averaging

across species, adult females and males were both more likely to cross successfully at wildlife-friendly fences (females: difference = 0.197, 95% CI: 0.078, 0.322; males: difference = 0.193, 95% CI: 0.025, 0.359), but the evidence for juveniles was less clear (difference = 0.210, 95% CI: −0.038, 0.469).

## 3.2 | Behavior during successful crossings

Similar patterns were observed in our analysis of crossing behavior. Across all species and demographics, the marginal probability of a successful, positive crossing was 0.784 (95% CI: 0.627, 0.930). However, we observed
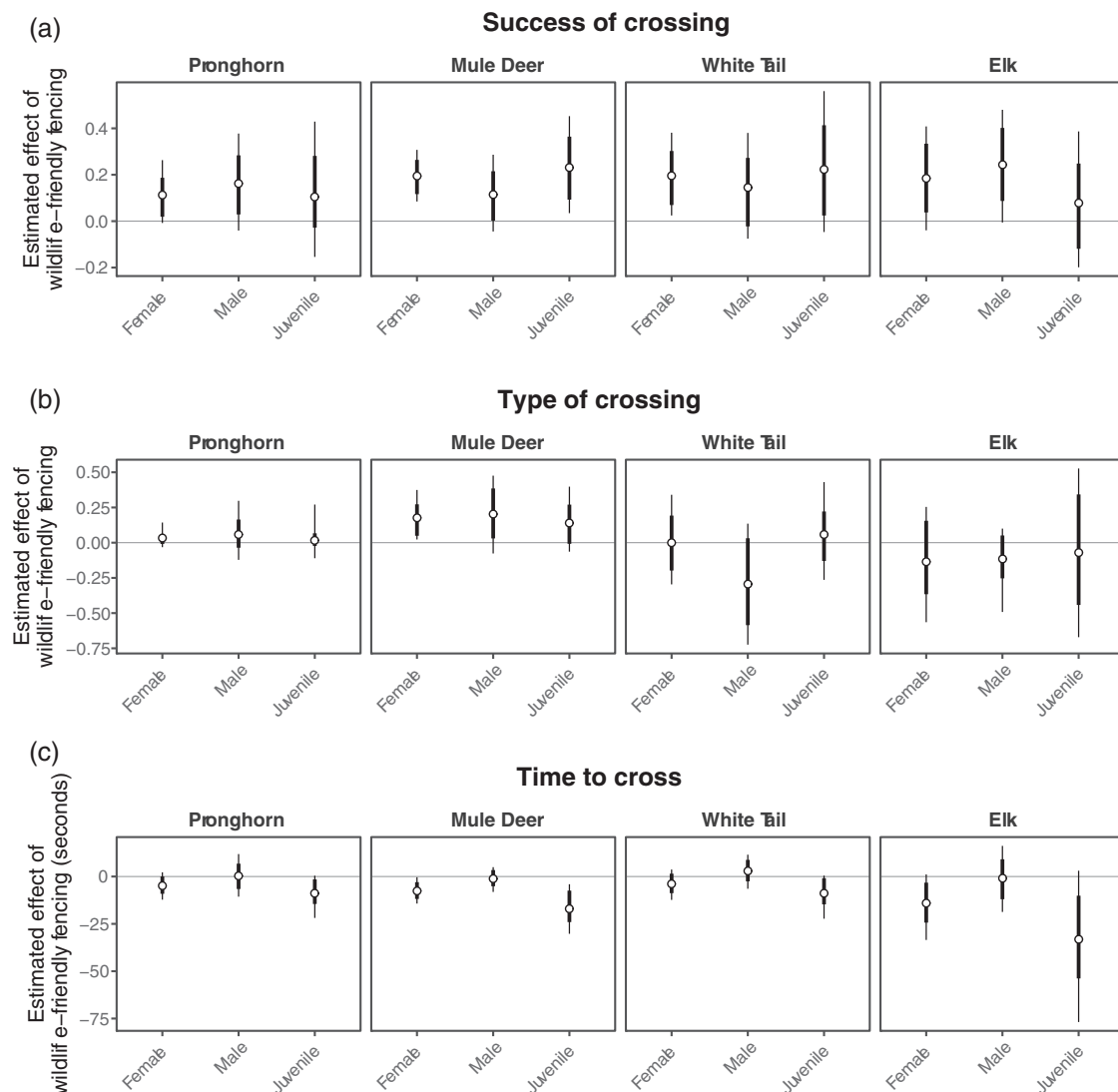


**FIGURE 3** The estimated effect of wildlife-friendly fencing on the study species. Panel (a) presents the probability of an observed individual successfully crossing, Panel (b) presents the probability that the individual crossed using positive behavior (crawling under the fence line as opposed to jumping over), and Panel (c) presents the seconds for the time taken to make a crossing. Thin lines and thick lines indicate 95 and 80% CI, respectively

substantial differences in the crossing behaviors of different species. Pronghorn used positive crossing behaviors in almost all successful crossings (0.979, 95% CI: 0.930, 1.000). The probability of positive crossing behavior was significantly lower amongst mule deer (0.761, 95% CI: 0.620, 0.885) and white-tailed deer (0.740, 95% CI: 0.497, 0.950), while the lowest probability was observed for elk (0.225, 95% CI: 0.025, 0.467). There were also differences associated with demographics, with adult females (0.850, 95% CI: 0.727, 0.953) and juveniles (0.900, 95% CI: 0.758, 0.995) significantly more likely to use positive crossing behaviors than adult males across all species (0.456, 95% CI: 0.227, 0.712).

Mule deer were the only species that saw a clear change in their crossing behavior between fencing types, with adult females significantly more likely to use positive crossing behaviors at wildlife-friendly fences (difference = 0.176, 95% CI: 0.023, 0.374; Figure 3b). There was weaker evidence for a similar positive effect of wildlife-friendly fencing among adult males (difference = 0.202, 95% CI: −0.077, 0.476) and juvenile mule deer (difference = 0.140, 95% CI: −0.064, 0.398). There was no clear difference in crossing behavior between fence types for any other species we observed.

## 3.3 | Time taken for successful crossings

On average, the marginal time taken for a successful fence crossing was 13.3 s (95% CI: 10.0, 16.5), but we found that time taken to cross was highly differentiated by species and demographics. White-tailed deer (9.9 s, 95% CI: 5.7, 14.2) and pronghorn (10.3 s, 95% CI: 5.7, 14.6) made the quickest crossings, followed by mule deer (13.2 s, 95% CI: 10.5, 16.1). The expected crossing time for elk was approximately twice as long (24.5 s, 95% CI: 14.4, 35.8). Demographic differences in expected crossing times were smaller overall, with adult females (14.6 s, 95% CI: 11.6, 17.9) and adult males (14.4 s, 95% CI: 10.9, 18.2) taking slightly longer to cross than juveniles (11.3 s, 95% CI: 6.4, 16.6).

On average, successful fence crossings were quicker for wildlife-friendly fencing than for barbed-wire fencing (difference = −7.0 s, 95% CI: −13.9, −0.7; Figure 3c). The largest expected reduction in crossing time was observed for elk (difference = −14.7 s, 95% CI: −34.2, 2.8), although the clearest evidence of an effect of fencing was obtained for mule deer where the difference was smaller (difference = −8.1 s, 95% CI: −14.8, −1.9). There was also weaker evidence for a smaller reduction in crossing time for pronghorn (difference = −5.4 s, 95% CI: −12.6, 1.7). Comparing demographic groups, the clearest reductions in crossing time at wildlife-friendly fences were observed

for juveniles (difference = −14.0 s, 95% CI: −25.9, −3.4) and there was weaker evidence for a smaller reduction in crossing time for adult females (difference = −6.5 s, 95% CI: −13.9, 0.4). There was no effect of wildlife-friendly fencing on the time taken for successful crossings by adult males (difference = 0.6 s, 95% CI: −6.8, 7.8).

## 4 | DISCUSSION

This study adds to the growing body of evidence that wildlife-friendly fencing can improve the overall rate of successful crossing, increase the proportion of crossings that are made by crawling under the fence line, and reduce the average time taken to make a fence crossing. However, we also show that the benefits are not uniformly realized across species and demographic groups, suggesting that such factors should be taken into account when improving both the design and implementation of wildlife-friendly fencing in the future.

### 4.1 | Crossing success at fence types

We found that wildlife-friendly fencing increases the probability of a crossing attempt being successful across species and demographics by 33%. This finding is broadly reflected in previous studies investigating fencing design improvements for ungulate species. Jones et al. (2020) found that the use of a smooth bottom wire in conjunction with a raised height of 46 cm was the most effective fence modification in comparison to control fence types for pronghorn, increasing crossing rates by 0.35 crosses/day. Burkholder, Jakes, Jones, Hebblewhite, and Bishop (2018) and Jones et al. (2020) similarly found improvements in the rate of crossing success for white-tailed deer, mule deer, and pronghorn with modifications of increased bottom and smooth wire.

These findings further complement previous studies which have demonstrated that traditional barbed-wire fencing forms a substantive barrier to daily movement and migration (Hanophy, 2009; Harrington & Conover, 2006). Barbed-wire fencing is known to discourage ungulates from using migration paths, whereas this effect was not found in areas with wildlife fencing (Sheldon, 2005). Therefore, an improvement of one third in crossing rate may have positive implications for both the short- and long-term fitness of wild ungulates in heavily fenced areas.

However, although the estimated benefits of wildlife-friendly fencing were fairly consistent across three of the species observed, elk remained heavily disadvantaged. They were only able to cross successfully one third of the

time, and were less likely to succeed at wildlife-friendly fencing than other species are at barbed-wire fences. The other three species, conversely, exhibited a near 100% success in crossing at wildlife-friendly fencing. Elk are commonly found to have the most difficulty crossing fences, cross most often and cause the most economic damage to fencing (Hanophy, 2009; Harrington & Conover, 2006; Visscher et al., 2016). Previous studies have shown that by raising the bottom wire further to 53 cm and lowering the top wire to 96.5 cm (in comparison to the 46 and 107 cm studied here), elk can be encouraged to cross (Visscher et al., 2016). Therefore, changing the wire heights used in the type of wildlife-friendly fences studied here may help improve elk crossing success rate.

## 4.2 | Crossing behavior among fence types

Mule deer were the only species that exhibited a clear change in crossing behavior among the fence types. Mule deer are thought to be particularly vulnerable to traditional fencing, only jumping over fence lines when forced (Burkholder et al., 2018). Most ungulates (66% of juveniles and 77% of adults) that die along fence crossings get entangled while jumping over (Harrington & Conover, 2006), which may discourage them from doing so. We found that even at barbed-wire fencing, whitetails, pronghorn, and mule deer all preferred to crawl under than to jump. However, at barbed-wire fencing, crossing under can pose significant indirect health risks. Pronghorn are often seen with lateral dorsal scars and hair loss hypothesized to be the result of cutting themselves as they pass under barbed wire (Jones, 2014). The loss of hair due to tick infestations is associated with higher levels of hypothermia and lower body fat levels in moose (Glines & Samuel, 1989; Samuel, 1991). Although this risk has not been determined for the species studied here, the effect of losing hair due to barbed wire may be similar (Jones, 2014). Where the smooth bottom wire at wildlife-friendly fencing does not contribute to these risks, it may encourage ungulates to crawl under and, resultantly, reduce direct mortality risks via entanglement.

We found that pronghorn almost always crossed either fence type by crawling under the fence line. Pronghorn have light, fragile bone structures and are endemic to prairie landscapes with low ground cover, which makes them poorly adapted for jumping (Yoakum, 2004). Even more so than mule deer, they are unlikely to choose to jump over a fence, even when the height is lowered, as observed in Jones et al. (2020). Pronghorn are also the

species most likely to suffer from injury and mortality during fence crossings (Harrington & Conover, 2006). Therefore, the 13.6% improvement in crossing success for pronghorn, while relatively small, may considerably reduce the raw number of injuries and fatalities along fence lines in this region.

As with crossing success, elk were the species most disadvantaged by both fence designs. Visscher et al. (2016) showed that elk significantly preferred crossing under fences when the modification of the bottom wire was 8 cm higher than the design we investigated here, suggesting that the smaller gap may be insufficient. Elk can be 75–150 cm in height, while their antlers can add another 120 cm. Pronghorn, in comparison, are only 81–104 cm in height. Elks' relatively large bodies may mean that the reduction in the height of the top wire, as well as the increased tautness of the top two wires is more important for improved crossing. However, given the low rate of success for elk crossing at either fence type, further investigation is likely required into fence designs to ensure that elk can improve their crossing rates overall.

## 4.3 | Time taken to cross

Wildlife-friendly fencing significantly reduced the time that the four species of study took to cross compared to barbed-wire fencing. On average, ungulates crossed 54% faster, a reduction of 7 s per fence crossing. This reduction should be viewed within the context of fence density in the area of study, a mean of 2.4 km/km$^2$ (Poor et al., 2014). Elk have home ranges of 45 km$^2$ (Edge, Marcum, & Olson, 1985) and pronghorn migrate up to 550 km across state boundaries (Berger, 2004; Jakes, Gates, et al., 2018). Given that ungulates likely encounter several fence lines a day, accumulated savings may contribute to several beneficial fitness impacts. The vast majority (95%) of the migratory season is normally spent in stopover sites to exploit quality forage, track phenological gradients of vegetation, and to rest (Sawyer & Kauffman, 2011; Sawyer et al., 2012). Given the high percentage of time dedicated not to movement, but to resource exploitation, any additional time spent trying to cross barriers may cumulatively reduce ungulates' fitness (Sawyer et al., 2012). Second, there is potentially an increased predation risk along fence lines, as predators may learn to deliberately trap prey along fence lines, although this requires further study (Harrington & Conover, 2006). In areas with predation risk, ungulates may be better able to escape predators quickly across land parcels separated with wildlife fencing.

## 4.4 | Demographic responses among fence type

We found that juveniles were able to cross a wildlife friendly fence 14 s faster than at barbed-wire fencing, more than twice the reduction achieved by adults. Juveniles were also more likely to exhibit positive crossing behavior at wildlife-friendly fencing relative to adults. However, despite this increased improvement for juveniles, adults were still 20% more likely to cross successfully. Juveniles across species are widely regarded as the demographic most at risk from fence crossings, as they are eight times more likely to die in fences than adults. Of ungulate carcasses found near fences in a multiyear study, 90% were fawns who had become separated from their mothers during crossing events (Harrington & Conover, 2006). The same study also showed that juvenile mortality along fence lines is highest in August, during the weaning season. This may be because they can no longer rely on adults to show them safe crossing routes and methods (VerCauteren, Lavelle, & Hygnstrom, 2006). From this, we hypothesize that the experience adults accrue over numerous fence crossings is a more important factor in crossing successfully than the physiological advantage that juveniles have by virtue of their smaller size.

We found that across species, male and female ungulates respond very differently to barriers, as the average increase in permeability among fence types is primarily realized by females. Although the crossing success rate was largely the same, females were more likely to exhibit positive crossing behaviors and cross faster at both fence types. The size of effect was also larger for females at wildlife-friendly fencing for both metrics. This sex-specific response may be explained by the sexual dimorphism exhibited in ungulate species (Pérez-Barbería, Gordon, & Pagel, 2002). Females are smaller, on average, and do not grow antlers seasonally as males do, which may impede ease of movement. Therefore, the purported benefit of the raised bottom wire may benefit females more than males. However, males are more likely to disperse and move among subpopulations than females, so it is important that fence design can accommodate this movement (Shaw, Lancia, Conner, & Rosenberry, 2006). Considering that male ungulates are also more likely to jump over fences, it may be important to focus attention on the lowering the height of the top wire to 101 cm and increasing the space between the top two wires to 30.5 cm as suggested by Paige (2012) to better accommodate their crossing behaviors and reduce the risk of injury or entanglement.

Our study adds to the growing body of evidence that wildlife-friendly fencing improves the permeability of fencing barriers for the ungulate species of study. We were able to demonstrate a clear improvement on average crossing time and success when species and demographics were grouped. When we examined specific models, we found that there was a larger change in permeability for juveniles, females and mule deer; however, both fence types remain most permeable to adults, females, mule deer, and pronghorn overall. One of the leading hypotheses to explain the remaining disparity is the difference in morphology and levels of experience among these groups. It is likely that the change in fence design along wildlife-friendly fencing is still too marginal for elk and males to attain higher levels of permeability, while juveniles may still lack the level of experience required to cross as effectively as adults. Therefore, while it provides a substantive improvement in habitat connectivity at a patch-level, future designs may work to accommodate those groups that still have below acceptable levels of success. Furthermore, while we did not detect a clear pattern of crossing behavior across our study sites, future studies may also take into account migratory routes of species when determining where and when species are most at risk from fencing, as well as how this could affect fence-crossing behavior across seasons. However, it is important to recognize that for all groups, wildlife-friendly fencing remains only semipermeable. Where fencing may be avoided entirely, which requires taking into account other factors such as road presence and the potential risk of animal-vehicle collisions, we recommend that this may confer substantive improvements to ungulates, as well as other affected species.

Across the Great Plains, there are both increasing barriers to wildlife movement, as well as opportunities to use modern technologies to mitigate for them. As humans further encroach on wilderness areas, it is essential that we ensure the continued coexistence with other species that use the same habitat. Such simple measures as an improved fence design may play a large role in reducing human-wildlife conflict, as well as establishing corridors along which ungulates can safely roam. In doing so, we help to ensure a prairie landscape that continues to benefit wildlife as much as it does us.

## CONFLICT OF INTEREST

## AUTHOR CONTRIBUTIONS
**Josiane Segar**: conceptualization; research design; analysis; writing. **Aidan Keane**: supporting conceptualization; supporting research design; analysis; writing.

## DATA AVAILABILITY STATEMENT
The data used in this research have been included as Supplementary Material S2.

## ETHICS STATEMENT
This research was conducted in accordance with the University of Edinburgh School of GeoSciences Policy on Research Ethics and Integrity.

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## SUPPORTING INFORMATION

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