Original Article

Evaluating Responses by Pronghorn to Fence Modifications Across the Northern Great Plains

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ABSTRACT Pronghorn (*Antilocapra americana*) is an endemic North American ungulate susceptible to negative effects of fences, especially given the vast amount of barbed-wire fencing currently on the landscape. Despite multiple nongovernmental organizations, and state and provincial wildlife agencies publishing guidelines for creating wildlife-friendly fencing, there are no published studies that evaluate and compare evidence of the effectiveness of endorsed practices. We analyzed pronghorn crossing success in Alberta, Canada, and Montana, USA, between 2012 and 2016 in response to fence-modification treatments to understand 1) differences between bottom wire height at selected versus available fence sites, 2) the change in crossing rates before and after fence modification treatments, 3) the effect of a suite of fence, environmental, and demographic characteristics on group crossing success, and 4) the time lag until pronghorn became habituated to different fence modifications after initiation of treatments. Use of either smooth wire or clips with a bottom wire height of approximately 46 cm were most effective at allowing passage by pronghorn, while the commonly proposed goat-bar was ineffective and created a negative behavioral response by pronghorn. Though smooth wire and clips were effective at allowing passage, we observed a time lag as pronghorn switched use from their strong fidelity at known-crossing sites to using modified sites. Pronghorn-group crossing success was greatest during summer, for all-male groups, and increased with larger group sizes. We advocate not using goat-bars as modifications to fences, and instead, recommend using smooth wire and clips at a minimum bottom-wire height of 46 cm to allow movement by pronghorn. Our study provides guidance for wildlife-friendly fencing techniques to wildlife managers and private landholders as a means to improve permeability for pronghorn and additionally, can be used as a model to evaluate fence modifications for pronghorn and other target species that may be sensitive to fence interactions.

KEY WORDS *Antilocapra americana*, clip, fence modification, goat-bar, Northern Sagebrush Steppe, pronghorn, smooth wire.

Grasslands of North America are one of the most threatened ecosystems in the world (Gauthier et al. 2003, Forrest et al. 2004). Grasslands are under threat from conversion to agricultural crops, infrastructure (roads, cities, urban sprawl, etc.), and energy development (Gauthier et al. 2003, Forrest et al. 2004, Pool et al. 2014). These threats continue to result in habitat loss and fragmentation for the suite of species reliant upon grasslands. This is especially true for migratory ungulates that require the ability to move long distances between seasonal ranges or escape extreme climatic conditions (Berger 2004, Sawyer et al. 2005, Harris et al. 2009). Thus, a primary conservation focus in grasslands is to reduce habitat fragmentation to maintain daily and seasonal long-distance movements and overall habitat connectivity (Berger 2004, Hilty et al. 2006, Taylor et al. 2006). Often overlooked are disrupting effects that linear anthropogenic

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features such as fences have on daily movement patterns, long-distance migration, and landscape connectivity for ungulates.

Barbed-wire fencing was erected across large portions of western North America during the homesteading era to mark property boundaries and control the distribution of livestock, with additional fences being erected during the subsequent sod-busting era to keep livestock out of crops (O'Gara and McCabe 2004). By 1885, 40 tons of barbed-wire was strung across the plains of North America, up from the 5 tons produced just 6 years earlier (Yoakum 2004). The escalation in production of barbed-wire continued and by 1945 it was approximately 234,000 tons (Leftwich and Simpson 1978). Consequences of the proliferation of fences across western North America were predominately negative for wide-ranging wildlife including entanglement and death, sustained injuries, habitat fragmentation, and barriers to movement (Mackie 1981, Kie et al. 1996, Kindschy 1996, Harrington and Conover 2006). These effects were particularly detrimental to free-ranging ungulates that complete annual migrations between seasonal ranges (Berger 2004, Harris et al. 2009, Seidler et al. 2015).

Pronghorn (*Antilocapra americana*) is an endemic North American ungulate highly susceptible to negative effects of fences (Yoakum 2004, Gates et al. 2012, Jones 2014). Pronghorn evolved over millennia on the open plains without vertical barriers that inhibited movement, and they lack the ability to jump fences like deer (*Odocoileus* spp.; Yoakum 2004). During the proliferation of fences across the plains, pronghorn adapted their behavior by crawling under fences and have developed cognitive maps of known fence-crossing locations (Yoakum 2004, Jones et al. 2012). These cognitive maps guide the movement patterns of pronghorn that have become habituated to crossing fences at specific locations (Jones et al. 2012). However, where the bottom wire of a fence is too close to the ground due to fence design, or when accumulation of snow or vegetation blocks otherwise passable fences, the fence can become a barrier and restrict daily and seasonal movements of pronghorn (Yoakum 2004). This restriction in movement has resulted in major mortality events of pronghorn, especially on the northern extent of their range where animals become trapped by fences in severe winter conditions (Martinka 1967, Barrett 1982, Yoakum 2004). Where the bottom wire is high enough to allow passage by pronghorn, direct negative effects can still occur from crawling under barbed-wire fences, such as hair loss, scarring, and open wounds on the neck, back, and rump of pronghorn (Jones 2014). In response to the negative effects of fences on pronghorn, multiple nongovernmental organizations (NGOs), state, and provincial wildlife agencies have published guidelines for creating wildlife-friendly fencing that include fence modifications (e.g., goat-bar) as well as setting the bottom wire height between 38–49 cm (Ticer et al. 2002; Paige 2012, 2015; Yoakum et al. 2014). For example, the goat-bar is a modification recommended for pronghorn and aptly named after the "speed goat" as an informal name for pronghorn. Despite these guidelines, no published studies have evaluated and compared the effectiveness of these recommended fence modifications or bottom wire heights. Thus, an empirical assessment of pronghorn fence-crossing behavior in relation to proposed fence modifications will assist resource managers and landholders in maintaining landscape connectivity for pronghorn.

We used a Before-After-Control-Impact (BACI) study design to evaluate the use of fence modifications by pronghorn (Underwood 1994). Specifically, we used trail cameras to capture images of pronghorn crossing behavior at fence sites before and after they were modified (i.e., promote movement at modification sites and discourage movement at known-crossing sites) and compared them with control sites that remained unchanged. We used 4 metrics to measure the crossing behavior and efficacy of fence modifications for pronghorn: 1) an analysis of variance (ANOVA) approach to compare the bottom wire height at selected versus available fence panel sites, 2) an ANOVA approach to evaluate crossing rates at fence panels before and after the installation of fence modifications, 3) a logistic regression approach to compare the effects of fence modifications, season, snow, group size, and group composition on group crossing success during the after period, and 4) a time-to-event approach to evaluate pronghorn habituation to each modified fence type. First, we predicted that pronghorn would select to cross at fence panels where the bottom wire was higher than at available neighboring fence panels and pronghorn would have greater crossing success at fence panels where the bottom wire was 38–49 cm from the ground (Ticer et al. 2002; Paige 2012, 2015; Yoakum et al. 2014). Secondly, we expected that pronghorn crossing success rates would increase at fence modification sites during the after period following installation of modifications because they were designed to increase the bottom wire height. Currently, the goat-bar modification is promoted by many agencies and NGOs because, along with increasing the bottom wire height, this modification is considered to have the secondary benefits of protecting animals that crawl under from getting scratched and losing hair, and increasing visibility from a distance for animals searching for a place to cross (Jones 2014). Therefore, we predicted that goat-bars would perform the best out of the 3 modifications tested. Thirdly, we predicted that group size would not affect crossing success because the decision to cross a fence is an individual pronghorn decision and not a group decision, and all-male groups would have lower group crossing success than all-female groups because the significantly taller horns of males may make it more difficult to cross compared with the shorter horns of females (O'Gara 2004*a*). In addition, we predicted that the migratory season would positively influence crossing success because pronghorn may have greater crossing rates during this time period of long-distance travel. During the after period, the known-crossing sites, at which pronghorn were habituated to cross at (Jones et al. 2012), were blocked to discourage crossing. We predicted that pronghorn would gradually habituate to fence modifications during the after period as they discovered the modified sites placed in proximity to the known-crossing sites and begin to use them with regularity.

STUDY AREA

We studied pronghorn crossing behavior in the Northern Great Plains of southeastern Alberta (AB), Canada, and northcentral Montana (MT), USA, within the region referred to as the Northern Sagebrush Steppe. These study areas included Canadian Forces Base (CFB) Suffield (50°15′N, −111°10′W) in AB and The Nature Conservancy's Matador Ranch (47°55′N, −108°19′W) in MT. Both study areas were characterized by rolling hills with flat open plains created as a result of glaciation recession and deposits (Mitchell 1980). Badlands and deep coulees exposed and created by rivers and other waterways are also common features of this area (Mitchell 1980). Both study areas were semiarid, native sagebrush steppe habitats characterized by blue grama (*Bouteloua gracilis*), needle-and-thread (*Hesperostipa comata*), western wheatgrass (*Pascopyrum smithii*), June grass (*Koeleria macrantha*), silver sagebrush (*Artemisia cana*), Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis*), western snowberry (*Symphoricarpos occidentalis*), cactus (*Opuntia polyacantha*), and rose (*Rosa* spp.; Jakes 2015). The study area received on average 24.4 cm and 88.2 cm annually of rain and snow, respectively, based on measurements taken at Medicine Hat, AB (Environment Canada 2010). Commercial livestock grazing was the predominant human-land-use activity in the area, with additional land uses including agricultural crop production, transportation network, energy development (oil, gas, and wind), rural residential development, and urban expansion. Fences for livestock management, as well as for property ownership delineation, are a common feature on the landscape. For example, in Montana's Hi-Line area, there was estimated to be an average density of 2.4 km of fencing/km^2 (Poor et al. 2014), while in the grasslands of Alberta, the density was estimated to be 1.14 km of fencing/km^2 (Seward et al. 2012). Each study area had fences used to control the distribution of cattle (*Bos taurus*), with 4- and 5-strand barbed-wire being used predominately in AB and MT, respectively. Cattle were sporadically present in the pastures with cameras on the Matador from June through October as they were rotated between pastures, whereas no cattle were present during the after period in AB.

METHODS

Experimental Design

Our study used a Before-After-Control-Impact (BACI) design from 2012 to 2016 to assess the effectiveness of 3 proposed fence modifications to improve passage by pronghorn across barbed-wire fences used to control livestock distribution (Underwood 1994). Specifically, our BACI design used remote trail cameras to detect and compare pronghorn fence-crossing rates both before and after fence modifications were installed. We identified known-crossing sites through ground surveys by identifying pronghorn crossing locations from fecal pellets, hair strands observed on fencing, and where the ground had been continuously trampled. As part of our experimental design, we lowered the bottom wire at the known-crossing sites during the after period to deter pronghorn from using the sites while providing adjacent modified and control crossing sites. During the after period, the 3 fence modifications installed were goat-bar (i.e., white polyvinyl chloride [PVC] pipe; Supporting Information, Fig. S1), quick-link or carabiner (hereafter, "clip"; Supporting Information Fig. S2), and smooth wire (Supporting Information, Fig. S3). We standardized the bottom wire to the height of 46 cm at modified fence panels to allow comparisons between the different modifications (Paige 2012, 2015). The goat-bar created a crossing site for pronghorn that was 305 cm wide, whereas clips raised the bottom wire and created a crossing site that averaged between 75 cm (AB) and 104 cm (MT) wide, and did not offer to pronghorn the added protection from the barbs that the goat-bar did. We used this spacing for the clips, as opposed to the full fence panel, to simulate the width pronghorn used at known-crossing sites. The smooth wire spanned the entire fence panel and replaced the bottom wire, removing the threat of hair loss and scaring, but was not as visible as the goat-bar. The control sites remained unchanged between the before and after period.

Camera Set-up and Photo Classification

We measured the response of pronghorn and cattle interacting with fences using digital images captured by remote trail cameras (Reconyx PC650, PC800 or PC900, Reconyx, Holmen, WI, USA; Bushnell Trophy Camera, Bushnell Corporation, Overland Park, KS, USA, and U-way Trail Camera-VH200HD, UWAY Outdoors Canada, Lethbridge, AB, Canada). We used photos as opposed to video to maximize battery and secure digital (SD) card life, and minimize the potential of missing observations due to the longer file upload times of video compared with photo. We deployed cameras in sets of 3 (hereafter referred to as a "set") with a control, modification, and a centrally located known-crossing fence panel (Fig. 1). We set cameras to rapid-fire to capture 3–5 images/trigger with no (AB) or

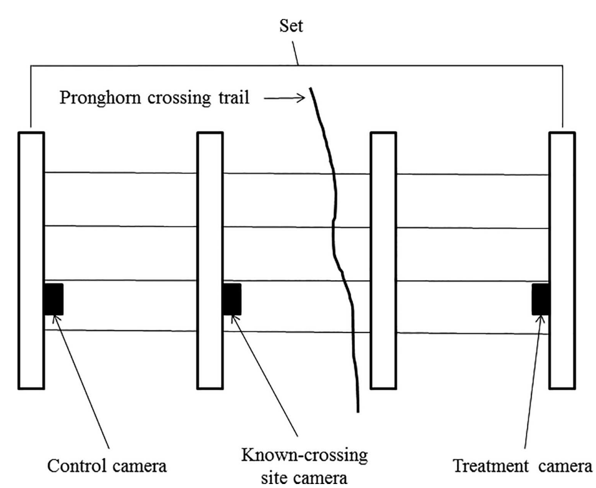

Figure 1. Depiction of the experimental design used to test effects of fence treatments on pronghorn crossing behavior in Alberta, Canada, and Montana, USA, 2012–2016. Depicted are the placement of cameras indicating a central known-crossing site and randomized control and modification camera placement to either side of the known-crossing site.

1-second (MT) delay between triggers to ensure as best as possible that the complete set of images for an event was captured. We set camera sensitivity at high except during the summer when we lowered the sensitivity to reduce false triggers. Additionally, we cut the grass at MT sites to further reduce false triggers from grass blowing in the wind and SD cards filling up quickly during summer. All makes and models of cameras used in our study had a motion sensor activation between 15 m and 18 m; therefore, there should not be significant differences in image capture capability between study areas related to width of fence panels (see below for differences in width between fence posts in the 2 study areas).

The study began in AB and was expanded into MT; therefore, there were slight differences in study design between the 2 areas. Mainly, the number of cameras and length of time for the before and after periods varied between years and study sites (Supporting Information, Table S1). We used the CFB Suffield study site to assess fence modifications for pronghorn, with cameras deployed September through April–May; and we tested only 1 modification type at a time; goat-bar (2012–2013), clip (2013–2014), and smooth wire (2015–2016). We mounted all cameras to a wooden fence post with an average distance between posts of approximately 14 m. We initially deployed cameras at the Matador Ranch in MT in March 2015; we installed all 3 modifications on 23 or 25 June 2015; and cameras remained active until 13 August 2016. There were 16 camera sets (48 cameras in total) at the Matador Ranch. We either mounted cameras to wooden fence posts or on custom-built brackets for metal T-bar posts (Supporting Information, Fig. S2). The average distance between posts at the Matador study site was 4 m.

We used a 2-step procedure to process images of pronghorn behavior captured by the trail cameras. We only processed behaviors for pronghorn that were within 2–3 m on either side of the fence panel. First, we grouped photos of pronghorn into events based on time. An event consisted of any set of images of at least a single pronghorn captured by a camera and contained any number of photos, lasted any length of time (seconds to hours), involved any number of pronghorn and ended when there was a minimum of 15 min between the last image of a group of photos and the next set of images captured by the same camera. We then categorized the set of photos for each event into 2 distinct behaviors: 1) failed attempt or 2) successful attempt. We defined an attempt as when an individual pronghorn (either by itself or as part of a group) approached a fence, orientated its body perpendicular to the fence, approached within 2 body lengths of the fence, and had its head lowered and either attempted to make or made contact with the fence or put its head under the bottom wire of the fence and then pulled it back. The attempt ended when the individual moved away from the fence, orientated its body more parallel to the fence than perpendicular (failed attempt), or successfully crossed to the other side (successful attempt). For successful attempts, we recorded the number of instances where the individual "crossed under," "crossed over," or "crossed through" (i.e., between the wires) the fence. We estimated group size and identified individuals as either being male or female (when possible). We consider our estimate of group size as an approximation because of the difficulty of keeping track of individuals (especially as group size and length of time of the event increased) as they moved in and out of the camera's field of view (Moeller 2017).

Pronghorn are gregarious in nature and do not show matrilineal lines, but instead regularly switch groups (Kitchen 1974, Byers 1997, White et al. 2012). This suggests that individuals generally make independent decisions rather than strictly adhering to group behavior. We considered the decision to approach a fence as a group decision, but considered an attempted crossing event at a fence as an individual decision. For all events, we allowed the event to be classified into multiple behaviors, and recorded the number of instances of each behavioral category. We recorded total instances and not total instances per individual because of difficulties keeping track of all individuals from one photo to the next, resulting from individuals moving out of the camera's field of view (Moeller 2017). Unless otherwise stated, we pooled data for all analyses across study areas because both areas had similar habitats and pronghorn were interconnected within the 2 areas (Jakes 2015).

Statistical Analysis

Bottom-wire height.—We compared the bottom-wire height at the pronghorn known-crossing sites (selected) to the bottom-wire height at the neighboring (or adjacent) fence panels (available) to test optimal bottom-wire height selected by pronghorn to cross fences. We used an ANOVA to compare the bottom-wire height between selected and available fence panels, where the response variable was bottom-wire height (cm) and the explanatory variables were type (selected and available), study area (AB or MT), and the interaction term of type $\times$ study area. We used bottom-wire heights during the before period (unaltered bottom-wire height) at control and modification sites to represent available sites in the analysis. To avoid pseudoreplication with the AB data, we randomly selected 1 year of data for known-crossing (and companion) sites for those sites that were used over multiple years, whereas we used all of the sites for MT in the analysis. If an effect was detected for the type $\times$ study area explanatory variable, we used the Tukey honest significant difference (HSD) test to conduct multiple comparisons (Zar 1984).

Crossing success.—We used a mixed-effect ANOVA to compare pronghorn crossing success between the before and after period at each fence panel with modifications, where the response variable was mean actual success and explanatory variables were treatment type (modification type [goat-bar, clip, or smooth wire], control, or known-crossing), study area (AB or MT), the interaction term of treatment $\times$ study area, and the random term of set (name assigned to each group of 3 cameras). We used instances of successful crossing as the response variable because we felt it allowed evaluation of overall change in crossing success and provided insight into the use and differences between treatment types and periods. The before and after periods included a maximum of 106 and 419 days of camera monitoring, respectively. The before period included fewer camera monitoring days than the after period because it was intended to establish baseline rates of crossing before installation of fence-modification treatment. The before and after periods differed in terms of number of days, so we first calculated the mean number of successful crossing instances per day for each camera and then calculated the mean number of successful crossing instances per period (before or after) per camera. We then calculated the actual success as the difference between the mean number of successful crossing instances per day after installation and mean number of successful crossing instances per day before installation. We removed those days from the initial calculation for instances where the camera did not record photos because of the SD card being full, batteries dying, or camera failure. If we detected an effect for any explanatory variable, we used the Tukey HSD test to conduct multiple comparisons (Zar 1984). During the processing of the images associated with the goat-bar sites, we noted some pronghorn not crossing underneath the goat-bar but instead crossing off to the side where the bottom wire was still raised and there was no protection from hair loss and scaring. We classified these instances where pronghorn did not cross directly under the goat-bar as a failed attempt for all analyses because pronghorn appeared to specifically avoid the goat bar. We performed the ANOVA analyses in JMP v13.1.0 (SAS Institute, Inc., Cary, NC, USA).

Factors affecting crossing events.—We used generalized linear models with a logit link function to control for seasonal and demographic factors and estimate the effect of fence modification treatments on pronghorn-group crossing success (Hosmer and Lemeshow 2000). Specifically, we considered season (i.e., winter, summer, or migratory; see Jakes 2015), group size, group composition (i.e., male, female, or mixed), snow presence (i.e., none, partial ground coverage, or full ground coverage at fence panel), and fence modification treatments (i.e., control, clip, smooth, goat-bar, and known-crossing) as explanatory variables. We classified crossing events where >50% of the group successfully crossed as successful (coded as 1) and the remaining events as failed attempts (coded as 0) for our response variable. We considered the >50% group success rate was an acceptable threshold because it produced similar results to >75% and >90% group success rate analysis (P.F. Jones, unpublished data). We standardized continuous variables by subtracting the mean and dividing by 2 SDs, allowing their effect sizes to be comparable to categorical variables (Gelman 2008). We used the antilogit transform and unstandardized coefficient estimates to make predictions on the probability scale. We used Akaike's Information Criteria for small sample sizes (AIC_c) to evaluate the support among models (Burnham and Anderson 2002). We compared all nested models using the dredge function in Program R version 3.3.2 (R Core Team 2016) package MuMIn (Barton 2016). We used $\Delta AIC_c < 2.0$ as a cut-off to compare competing top models. Finally, we evaluated model goodness-of-fit using a likelihood ratio test, but did not report this result unless we found evidence of lack of fit.

Time to event analysis.—We used a time-to-event approach with multiple events to estimate daily crossing rates for pronghorn among fence panel types during the before and after periods (Hosmer et al. 2008). We used days since camera deployment and modification for before and after periods, respectively, as the origin for all camera sets, and we interval-censored cameras when they were not available to detect pronghorn crossing a fence (e.g., insufficient battery power). We explored using a recurrent calendar date as the origin, but found no qualitative differences in our results (P.F. Jones, unpublished data). We pooled data across all years and study areas to summarize crossing rates. We estimated cumulative daily crossing rates for the 5 fence panel types (known-crossing, control, goat-bar, clip, and smooth) and 2 periods (before and after) using nonparametric cumulative incidence functions (CIFs; Heisey and Patterson 2006). When competing risks of an event are involved, the incidence of event type k occurring at time t is generally defined as the hazard of event k at time $t[h_k(t)]$ multiplied by the overall probability of survival at $t-1$ just before event k occurs (Kleinbaum and Klein 2012). However, we assumed a survival probability at $t-1$ of 1.0 because cameras did not fail (or die) when they detected pronghorn fence-crossings. Although multiple crossing events could occur within a day at a single fence panel, we restricted crossing rates to a maximum of 1 event/day at each fence panel to eliminate bias due to multiple crossings of the same individual. We modified the R code provided in Eacker et al. (2016) to estimate CIFs and used the R package survival (Therneau 2015). We used the R package bshazard to estimate smoothed daily treatment-specific crossing rates, and conducted all statistical analyses in Program R 3.4.0 (R Core Team 2016).

RESULTS

In AB, we captured images of pronghorn in 1,584 events in 2012–2013, 808 events in 2013–2014, and 2,217 events in 2015–2016; whereas, we captured images of pronghorn in 3,460 events from 2015 to 2016 in MT. Events can represent multiple individuals as well as multiple behaviors; therefore, events in the AB study area included 14,978 instances of paralleling the fence, 5,738 instances of lingering, 3,368 instances of successfully crossing under the fence, and 8,247 instances of failing to cross. We recorded 3 instances of pronghorn jumping over the fence and 4 going through in AB. In MT, events included 1,968 instances of paralleling the fence, 1,024 instances of lingering, 2,148 instances of successfully crossing under the fence, and 3,563 instances of failing to cross. We recorded 1 instance of a pronghorn jumping over the fence and 1 instance of a pronghorn going through the fence in MT. All instances of pronghorn going over or through a fence were considered failed attempts. Of the 123 instances of pronghorn using the goat-bar sites at CFB Suffield, there was only 1 instance of a pronghorn actually going under the goat-bar, but 122 instances where they crossed to the side and under barbed-wire. In MT, there were 9 instances of pronghorn crossing at goat-bar sites with only 5 going under the goat-bar. We recorded 1 cattle (calf) going through the fence at a goat-bar panel and no successful crossings by cattle at a clip or smooth wire site during the after period in MT; there were no cattle present in the after period in AB. Mean percent crossing success for pronghorn groups ($n \geq 2$) was 65.58% (SE = 1.19, range = 2–100%), which supported our conjecture that crossing a fence was an individual-based decision.

Bottom Wire Height

There was an effect of type ($F_{1,1} = 108.59$, $P < 0.001$), study area ($F_{1,1} = 23.07$, $P < 0.001$), and the interaction between type and study area ($F_{1,1} = 6.20$, $P = 0.01$) on the mean bottom-wire heights between those selected and those available to pronghorn to cross at. The mean bottom-wire height at known-crossing sites ($\bar{x} = 46.75$ cm, SE = 1.51) was 1.7 times greater than at the available sites ($\bar{x} = 27.44$ cm, SE = 1.07), whereas the overall mean bottom-wire height in AB ($\bar{x} = 41.55$ cm, SE = 1.29) was 1.3 times greater than in MT ($\bar{x} = 32.64$ cm, SE = 1.33). The results of the Tukey HSD test revealed that the mean bottom-wire height at known-crossing sites in AB and MT were not different, but both the known-crossing sites in AB and MT were different than the available sites in AB and in MT (Fig. 2).

Crossing Success

There was an effect of treatment ($F_{4,133} = 17.63$, $P < 0.001$), but not study area ($F_{1,89} = 0.04$, $P = 0.84$) or an interaction between study area and treatment ($F_{4,133} = 0.61$, $P = 0.66$), on the mean daily actual rate of success crossing by pronghorn. The mean actual rates of success crossing at the known-crossing sites differed from the 3 modifications and control sites (Fig. 3a). The mean actual rate of success crossing at the known-crossing sites was negative, indicating a decrease in successful crossings during the after period, whereas the mean for the 3 treatments were positive. This result highlighted that lowering the bottom wire at the known-crossing fence panels influenced our results, suggestive of the importance of known-crossing sites to pronghorn. Therefore, we redid the analysis removing the known-crossing fence data to allow for interpretation of the effectiveness of the 3 modifications. There was an effect of treatment ($F_{3,85} = 7.08$, $P < 0.001$), but not study area ($F_{1,76} = 0.65$, $P = 0.42$) or an interaction between study area and treatment ($F_{3,85} = 2.44$, $P = 0.07$), on the mean daily actual rate of success crossing when we analyzed the 3 modifications and the control data separately. Smooth wire sites were similar to clips sites, and clip sites, goat-bar sites, and control sites were similar (Fig. 3b). Smooth wire increased average crossing success by 0.35 crosses/day (or ~1 additional cross every 3 days), clips increased the average crossing success by 0.14 crosses/day (or ~1 additional cross every 7 days), whereas goat-bars decreased the average crossing success by −0.002 crosses/day (or ~1 fewer cross every 500 days).

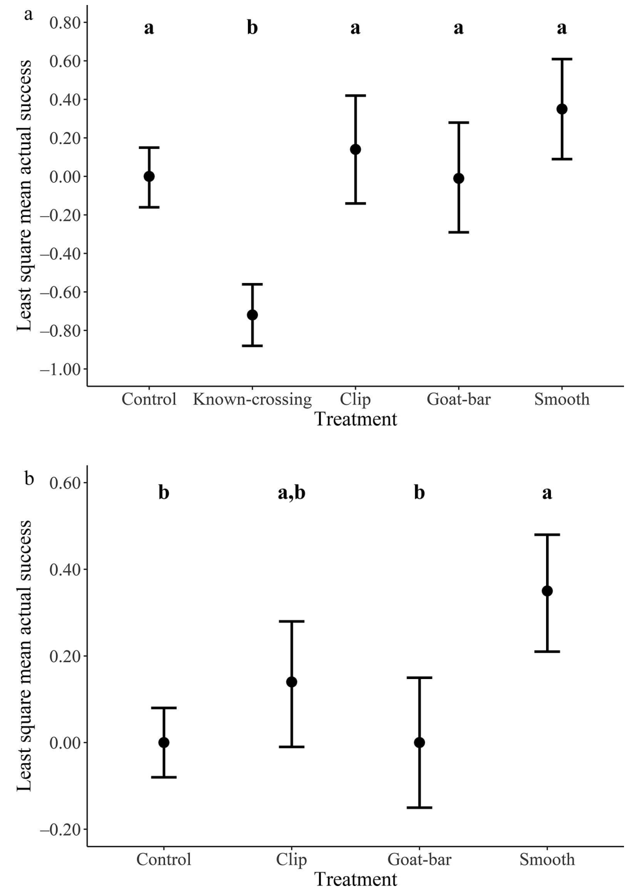

Figure 3. Least squared mean and 95% confidence limits for actual successful crossing rate for the 5 fence panel types (a) and 4 fence panel types (b) by pronghorn in Alberta, Canada, (2012–2016) and Montana, USA (2015–2016). Actual successful crossing rate was calculated as the difference between the mean number of successful crossing instances per day after the modification was installed and the mean number of successful crossing instances per day before the modification was installed. Similar letters above points indicate no differences between means.

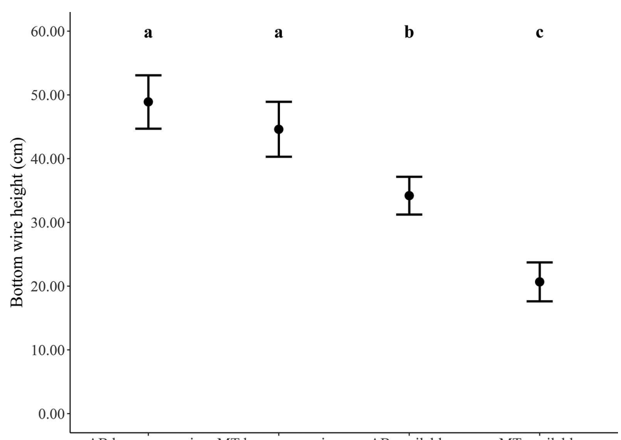

Figure 2. Least squared mean and 95% confidence limits for bottom-wire height (cm) at fence panels selected and available to cross at by pronghorn in Alberta (AB), Canada, during 2012–2016, and Montana (MT), USA, during 2015–2016. Similar letters above points indicate no differences between means.

Factors Affecting Crossing Success

We recorded 2,684 events of pronghorn attempting to cross during the after period (Supporting Information, Table S2).

We selected a single top model that had 92.5% of the AIC_c model weight and included the full suite of candidate variables, with the next closest model having a ΔAIC_c of 5.03 and one less parameter (Table 1). The top model was highly supported over a null model (LRT: $\chi^2_9 = 1{,}265.1$, $P < 0.001$). We found that the clip ($\hat{\beta} = 5.44$, SE = 0.73, $P < 0.001$) and smooth-wire ($\hat{\beta} = 4.72$, SE = 0.72, $P < 0.001$) fence modifications had greater relative importance for pronghorn-group crossing success than any environmental or demographic parameter, and had greater group crossing success probability compared with the control group (Table 1; Fig 4a). In contrast to our predictions, we found strong evidence that all-male groups had greater crossing success than all-female groups ($\hat{\beta} = 0.75$, SE = 0.17, $P < 0.001$), but there was no difference between all-female and mixed-group composition ($P = 0.98$). Although the effect size was relatively weak, group crossing success was greater in summer ($\hat{\beta} = 0.95$, SE = 0.30, $P = 0.002$) and lower in winter ($\hat{\beta} = -1.10$, SE = 0.31, $P < 0.001$) compared with the migratory season (i.e., spring and autumn; Fig 4b). After controlling for season, fence treatment, and group composition, we estimated that the odds of a group successfully crossing increased by 1.02 for every additional individual that was in a group (Fig. 4), but this effect was marginal—the 95% CI nearly overlapped 1.0 (95% CI = 1.004–1.03, $P = 0.01$).

Time-to-Event Analysis

Our pooled analysis included 9,912 camera-days during the before period and 35,138 camera-days during the after period. We detected 733 and 653 daily crossing events during the before (days 0–106) and after (days 0–419) periods, respectively. Most daily crossing events occurred at the known-crossing sites during the before period, which reached a cumulative rate of 33.76 (95% CI = 21.41–56.96) daily crossings/fence by 106 days since the onset of camera deployment (Table 2; Fig. 5a). Thus, if there were 100 known-crossing sites in the study area, we would expect 3,376 crossing events to have occurred after 106 days (not accounting for multiple crossings events/day/fence). Although none of the treatment groups reached the before crossing rate of known-crossing sites, both clipped (CIF = 29.66, 95% CI = 20.48–44.96) and smooth (CIF = 29.99, 95% CI = 20.37–46.39) wire modifications were of similar effectiveness, and reached comparable rates as before known-crossing sites during the after period by 419 days (Table 2; Fig. 5b). However, the steady increase in crossing rates observed around day 270 (see Fig. 5; Supporting Information, Fig. S4) was driven solely by the MT data because the maximum right-censoring day for AB data was day 157. Thus, although clipped and smooth wire modifications appeared as effective as known-crossing sites, this result should be interpreted with caution because the number of cameras was relatively small for the clipped ($n = 5$) and smooth ($n = 6$) wire treatments during days 159–419 in the after period. The control sites had the lowest crossing event rates during the after period (CIF = 0.39, 95% CI = 0.27–0.51), followed by the goat-bar sites (CIF = 1.66, 95% CI = 3.61–4.78), which appeared to be ineffective as a fence modification.

DISCUSSION

Our results showed that the 3 modifications tested did not perform equally. Of the 3 modifications tested, smooth wire and clips are effective at allowing pronghorn to cross under fences. Though smooth wire and clips were effective at allowing passage, there was a lag time in use by pronghorn as they become accustomed to using modifications when compared with known-crossing sites. Our results also showed the commonly proposed goat-bar was not effective and instead did not increase crossing success rates by pronghorn. We found that pronghorn show high site fidelity for known-crossing sites at fences and the recommended height of bottom wire of 46 cm from the ground to allow passage was well-supported.

To our knowledge, this is the first study to have explicitly tested and shown that the smooth wire and clip fence modifications are effective to allow passage by pronghorn. These 2 modifications are not visually obvious and appear similar to regular barbed-wire fences with which pronghorn are accustomed to interacting. Though both are effective, there are trade-offs associated with their use. Although smooth wire is typically strung out along the entire fence

Table 1. Logistic regression results from the top model of group crossing success (>50%) for pronghorn in the northern sagebrush steppe region of Alberta, Canada, and Montana, USA, during the after period, 2012–2016. For all model parameters, we report the coefficient estimate ($\hat{\beta}$), standard errors (SE), 95% confidence intervals, and *P* values. We considered season (migratory, summer, winter), fence modification type (control, clip, goat-bar, smooth, and known-crossing), group composition (all female, all male, or mixed) and group size as explanatory variables for group crossing success. The reference group (i.e., intercept) was female group composition and the control fence modification during the migratory season. We standardized group size by 2 standard deviations to compare relative effect sizes among categorical factors and continuous covariates.

Parameter	$\hat{\beta}$	SE	Lower 95%	Upper 95%	*P*
Intercept	−4.618	0.78	−6.500	−3.305	<0.001
Season: summer	0.946	0.30	0.371	1.548	0.002
Season: winter	−1.100	0.31	−1.704	−0.481	<0.001
Fence: known-crossing	1.860	0.72	0.690	3.673	0.010
Fence: clip	5.439	0.73	4.239	7.265	<0.001
Fence: goat-bar	1.282	0.89	−0.392	3.286	0.15
Fence: smooth	4.719	0.72	3.545	6.533	<0.001
Group: all male	0.749	0.17	0.425	1.079	<0.001
Group: mixed	0.004	0.22	−0.425	0.435	0.98
Group size	0.324	0.13	0.082	0.593	0.01

line to create numerous crossing opportunities, it is time-consuming to install and costlier than clips (US$82.80/roll vs. $4.58/clip). Typically, smooth wire can be installed during new fence construction or when an existing fence is being rebuilt. Comparatively, clips are a cost-effective alternative to smooth wire, quick and simple to install, and provide landholders the ability to adjust the bottom wire height when preferred (e.g., lowered when calves are in a pasture adjoining a highway). In addition, clips would need to be placed either at known-crossing sites to further enhance them or randomly selected fence panels and not the entire fence length. Both techniques should be promoted as effective modifications to enhance pronghorn movement, with the decision left to landholders as to which one to install based on their needs, goals, and financial resources.

As expected, there was a lag time in use of the 2 modifications as pronghorn located and became accustomed to crossing at smooth wire and clip sites. Patience must be exercised when installing modifications because it will take time before pronghorn begin to use the modifications. It is expected that as females learn to use and become comfortable with crossing at the modification sites that these modification locations will be passed on to fawns and over time pronghorn will show similar fidelity to modified fence sections as they do to naturally occurring known-crossing sites.

Goat-bars were the least-used fence modification—pronghorn only crossed directly under 6 times. Our results contradicted those of Ticer et al. (2002), who found pronghorn used goat-bars in northern Arizona, USA, when they were installed along a fence that had been identified as a complete barrier with no known-crossing sites and where the fence formed the boundary of pronghorn home ranges. Results provided by Ticer et al. (2002) may be an artifact of pronghorn being able to access once unreachable resources (e.g., forage, water), which overwhelmed a pronghorn's natural reluctance to use goat-bars. Instead, we suggest the reluctance to use goat-bars by pronghorn is due to 3 factors. First, pronghorn may be deterred by the white color of the PVC pipe. Initially, we hypothesized that the white PVC pipe would serve as an attractant for pronghorn and aid in identifying potential crossing sites from a distance. This originated in the idea that during the breeding season hunters lure males into shooting range with the use of white-colored objects (O'Gara 2004*b*, Brown and Ockenfels 2007). However, during most times of the year, pronghorn will flare their white rump patch as a warning signal to other members of the herd and confuse attacking predators (Kitchen 1974, O'Gara 2004*a*). Therefore, the white color of the PVC pipe may in fact serve as a repellant or be visually intrusive to pronghorn and not an attractant. Second, pronghorn may not be accustomed to the anthropogenic appearance and texture of the PVC pipe and therefore, are reluctant to cross directly under. Third, we noticed that wind blew through the PVC pipe, creating noise that may have deterred pronghorn from crossing under it. Further research into the use of different-colored goat-bars by pronghorn as well as the effects that other white proposed fence modifications (e.g., sage grouse [*Centrocercus urophasianus*] reflectors, white PVC pipe on the top wire for deer and elk [*Cervus canadensis*]) have on pronghorn is required. If a similar negative behavioral response by pronghorn to other white fence modifications is attained, then deleterious consequences to pronghorn daily and seasonal movements may occur. In addition, our study design centered on known-crossing sites and did not allow us to test whether the goat-bar served to attract pronghorn to fences. A multiscale evaluation of whether white goat-bars serve as an attractant to a fence panel (broad-scale decision) and whether pronghorn will use goat-bar fence panels to cross (fine-scale decision) in areas where fences are complete barriers to pronghorn is required.

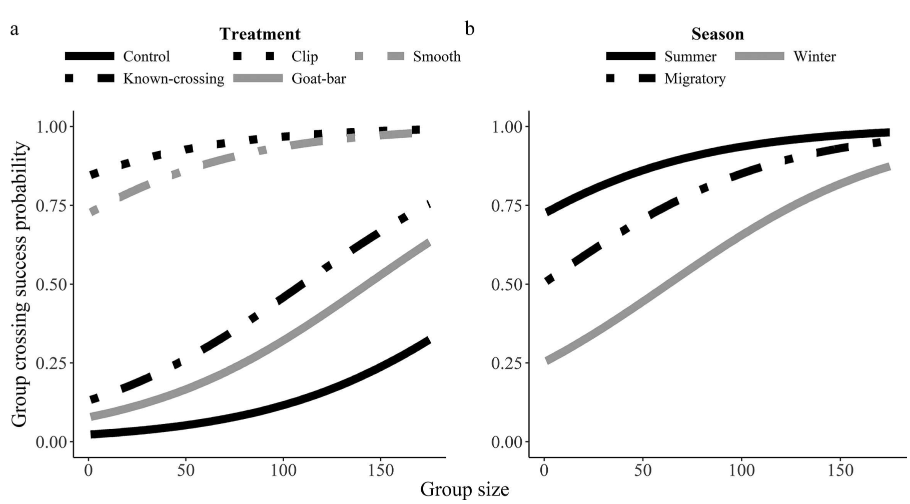

Figure 4. Predicted group-crossing success probability from the top logistic regression model for fence modification treatments (a) and seasons (b) over the range of observed group sizes ($n = 1$–175) for pronghorn in Alberta, Canada, during 2012–2016, and Montana, USA, during 2015–2016. We classified crossing events where >50% of the group successfully crossed as successful (i.e., event = 1). We based our predictions for fence modification treatments (a) on all-female group composition during summer and seasons (b) on all-female group composition and the smooth fence modification treatment.

Table 2. Cumulative incidence functions (CIF) with 95% confidence intervals (CI) and total number of events (n) for 5 fence panel types during before and after fence-modification periods for pronghorn in Alberta, Canada (2012–2016), and Montana, USA (2015–2016). Treatments included clip, control, goat-bar, known-crossing, and smooth wire. Although multiple crossing events occurred within a day at a fence, we restricted crossing rates to a maximum of 1 event/day/fence to eliminate bias due to multiple crossings of the same individual at a fence.

	Before ($t = 106$ days)				After ($t = 419$ days)			
Treatment	***n***	**CIF**	**95% CI lower**	**95% CI upper**	***n***	**CIF**	**95% CI lower**	**95% CI upper**
Clip	6	0.37	0.27	0.47	181	29.66	20.48	44.96
Control	9	0.18	0.081	0.31	17	0.39	0.27	0.51
Goat-bar	1	0.08	0.03	0.14	9	1.66	1.271	2.98
Known-crossing	710	33.76	21.41	56.96	169	4.12	3.61	4.78
Smooth	7	0.40	0.26	0.52	277	29.99	20.37	46.39

Pronghorn are believed to have cognitive maps of locations along fence lines where they can easily cross, which we called known-crossing sites (Jones et al. 2012). We consider our results as clear evidence that pronghorn have fidelity to the known-crossing sites and specifically travel to these locations when selecting to cross as proposed by Jones et al. (2012). Our regression results supported the notion of fidelity to known-crossing sites—even after we lowered the bottom wire at these sites, the known-crossing sites still outperformed the control sites as animals attempted and occasionally succeeded at crossing. We infer that pronghorn walking down fence lines are not necessarily looking for a place to cross, but rather, traveling to a known crossing location, effectively using a cognitive map of crossing locations (Jones et al. 2012, Bracis and Mueller 2017). There is likely a learned behavior component to the fidelity of known-crossing sites, with females teaching young the spatial location of sites and how to navigate the bottom wire (Bracis and Mueller 2017). Known-crossing sites tended to be at locations along a fence line where the bottom wire is higher than bottom wires at other fence panels due to depressions in the ground, the fence slopes due to topography, or broken bottom wires. Yoakum (2004) reported similar attributes for pronghorn fence-crossing sites across their range. In our same study areas, mule deer (*O. hemionus*) and white-tailed deer (*O. virginianus*) selectively used identified known-crossing sites to cross fences and switched to crossing at clip sites once fence modifications were installed (E. Burkholder, University of Montana, unpublished data). This suggests that identified known-crossing sites are not only used by pronghorn, but serve as communal crossing sites for a suite of ungulates. Though these known-crossing sites are critical in facilitating movement by pronghorn and other ungulates, multiple challenges arise for conservation and management. First, mapping these locations across pronghorn range would be extremely time consuming and expensive, though new technology such as drones may make mapping more feasible. Second, natural depressions and topography indicate that many known-crossing sites may be unusable if snow drifts to a level that reduces the distance to the bottom wire. Third, broken barbed-wire fences eventually will be repaired, which will prevent continued passage at these locations. As an initial step, we need to inform landholders of the value of known-crossing sites for pronghorn (and other ungulates) and how to identify them when preforming regular fence maintenance. Only then can protection and enhancement of existing known-crossing sites be achieved, especially when we provide landholders with a tool box of tested and effective enhancement techniques.

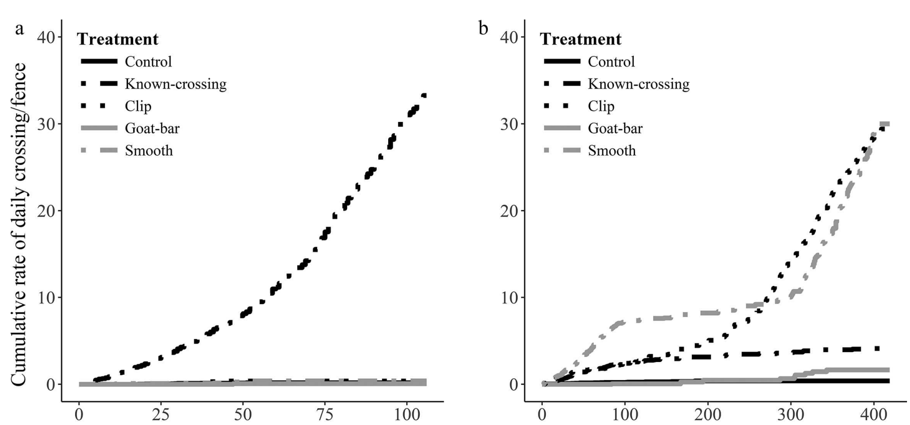

Figure 5. Cumulative incidence functions (CIF) for fence modification treatments during (a) before ($t = 0$–106) and (b) after ($t = 0$–419) periods for pronghorn in Alberta, Canada (2012–2016), and Montana, USA (2015–2016). Treatments included control, known-crossing, goat-bar, clip, and smooth wire. Although multiple crossing events occurred within a day at a fence, we restricted crossing rates to a maximum of 1 event/day/fence to eliminate potential bias due to multiple crossings of the same individual at a fence.

Proper bottom-wire height for sustaining wildlife movement has always been a debated issue. If the bottom wire is installed too low to the ground, it becomes a barrier to pronghorn and other wildlife. However, if the wire is installed too high, landholders contend that it enables cattle to escape. Current recommendations for the bottom wire height suggest 38–49 cm to allow pronghorn to cross under fences (Yoakum 2004; Paige 2012, 2015). However, we are unaware of any formal studies that form the basis for these recommendations and, when managers are provided a range in bottom wire height, the typical default becomes the lower height. Our results clearly show that pronghorn have selected sites with a mean bottom-wire height of 46.75 cm as known-crossing sites compared with those available. These sites used by pronghorn are at the upper end of the range previously recommended. Therefore, we recommend a height of 46 cm as the minimum bottom-wire height for both standard fences and those with modifications (e.g., clips). This height will ensure easy passage by pronghorn.

Our study used a BACI design with only slight differences between study areas. In AB, we tested modifications from September–October to April with 1 modification tested each year; whereas in Montana, we tested all 3 modifications simultaneously over a longer time period and across seasons. Additionally, in AB, some of the known-crossing sites were used across years. Although these differences could potentially have affected our results, we consider this effect minimal. We observed similar results in use of the different modifications between animals in AB and MT, which suggests that there was not a learned effect of animals in AB immediately searching for crossing sites on fence panels adjacent to the known-crossing site in each subsequent year of testing. In addition, there was a 6–7-month period where the fence was in its original state before the next subsequent modification was installed. Lastly, we used an unbalanced design with the number of cameras and length of time cameras were active varying between the 2 study areas and pooled data to increase sample size to strengthen inferences from our results. We caution the interpretation of the logistic regression results related to seasonality because of the potential for confounding effects based on differences in the number of camera-trap days between seasons. Ideally we would have preferred to evaluate whether there were seasonal variations associated with the use of modified fence sites; however, our primary objective was to evaluate the use of modifications and assess how long it took pronghorn to habituate to using modified fences. The only approach to accomplish this was to have cameras and modifications span across seasons to achieve sufficient sample sizes.

We evaluated snow presence during the screening process for our logistic regression analysis, as a surrogate for the multifaceted effects of snow (i.e., presence, depth, moisture content, etc.) on pronghorn crossing success. Results indicated that snow presence was not influential on crossing and therefore, not included in our logistic regression analysis. However, this result may be misleading in understanding the effects of snow on pronghorn movement. Pronghorn have the lowest mean chest height and highest foot-loading index of any North American ungulate, making them highly sensitive to snow accumulation (Telfer and Kelsall 1984). Consequently, pronghorn search for areas with lower snow depths for foraging opportunities during winter, especially under severe conditions (Bruns 1977, Jakes 2015). Ideally, snow depth would be measured daily to account for microvariation in snow accumulation at each camera site. However, we were unable to complete daily snow-depth measurements throughout the course of our study and, as a result, its influence on crossing success may not be adequately reflected.

The concept of wildlife-friendly fencing can serve as both a management tool and form of education and outreach directed toward landholders. Wildlife-friendly fencing can improve permeability for wildlife while continuing livestock confinement. To be accepted by landholders, assurances that proposed modifications will confine cattle are warranted. Our results show that the 3 modifications evaluated will contain cattle in intended pastures. We would caution against the use of goat-bars because we observed a significant amount of time being spent at these sites by cattle, who engaged in rubbing and chewing on the goat-bar and may put added pressure on the fence wires. Our results showed little to no cattle escaping at modified sites with standardized bottom-wire heights of 46 cm. Further uptake of wildlife-friendly fencing standards by landholders is urgently needed.

MANAGEMENT IMPLICATIONS

To increase landscape connectivity and allow pronghorn to move freely across the landscape, reduce instances of mass die-offs (Martinka 1967, Barrett 1982, Yoakum 2004), and maintain population viability, landholders and agencies should implement and adopt tested modifications for fences that are actually pronghorn and wildlife friendly. Although improving fence design by individual landholders is appreciated, landscape connectivity will only be achieved when there is significant participation among private and public landholders. To achieve success, we recommend that landholders and resource managers adopt a standard of 46 cm as the minimum for bottom-wire height and, where possible (time and financially feasible), use double-stranded smooth wire on the bottom or clips (as the alternative) to raise existing wires to meet the minimum height. We do not recommend the use of white goat-bars until further study is completed to determine whether they will serve as an attractant to bring pronghorn to sites that are not known-crossing locations, whether they function in areas where fences are a complete barrier to movement in their current form, or if alternative colors would increase the functionality of goat-bars. Our study provides guidance for wildlife-friendly fencing techniques to wildlife managers and private landholders as a means to improve permeability for pronghorn and additionally, can be used as a model to evaluate fence modifications for pronghorn and other target species that may be sensitive to fence interactions.

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LITERATURE CITED

Barrett, M. W. 1982. Distribution, behavior and mortality of pronghorns during a severe winter in Alberta. Journal of Wildlife Management 46:991–1002.

Barton, K. 2016. MuMIn: Multi-Model Inference. R package version 1.15.6. https://CRAN.R-project.org/package=MuMIn. Accessed 21 Dec 2016.

Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. Conservation Biology 18:320–331.

Bracis, C., and T. Mueller. 2017. Memory, not just perception, plays an important role in terrestrial mammalian migration. Proceedings of the Royal Society B 284:20170449.

Brown, D. E., and R. A. Ockenfels. 2007. Arizona's pronghorn antelope. A conservation legacy. Arizona Antelope Foundation, Phoenix, USA.

Bruns, E. H. 1977. Winter behavior of pronghorns in relation to habitat. Journal of Wildlife Management 41:560–571.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Byers, J. A. 1997. American pronghorn: social adaptations and the ghosts of predators past. University of Chicago Press, Illinois, USA.

Eacker, D. R., M. Hebblewhite, K. M. Proffitt, B. S. Jimenez, M. S. Mitchell, and H. S. Robinson. 2016. Annual elk calf survival in a multiple carnivore system. Journal of Wildlife Management 80:1345–1359.

Environment Canada. 2010. Yearly and long-term (1981–2010) climatic conditions. http://www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html. Accessed 1 Dec 2017.

Forrest, S. C., H. Strand, W. H. Haskins, C. Freese, J. Proctor, and E. Dinerstein. 2004. Oceans of grass: a conservation assessment for the northern Great Plains. Northern Plains Conservation Network and Northern Great Plains Ecoregion, World Wildlife Fund-US, Bozeman, Montana, USA.

Gates, C. C., P. Jones, M. Suitor, A. Jakes, M. S. Boyce, K. Kunkel, and K. Wilson. 2012. The influence of land use and fences on habitat effectiveness, movements and distribution of pronghorn in the grasslands of North America. Pages 277–294 *in* M. J. Somers and M. Hayward, editors. Fencing for conservation: restrictions of evolutionary potential or a riposte to threatening processed? Springer-US, New York, New York, USA.

Gauthier, D. A., A. Lafon, T. P. Toombs, J. Hoth, and E. Wiken. 2003. Grasslands: toward a North American conservation strategy. Canadian Plains Research Center, University of Regina, Regina, Saskatchewan, and Commission for Environmental Cooperation, Montreal, Quebec, Canada.

Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine 27:2865–2873.

Harrington, J. L., and M. R. Conover. 2006. Characteristics of ungulate behavior and mortality associated with wire fences. Wildlife Society Bulletin 34:1295–1305.

Harris, G., S. Thirgood, J. G. C. Hopcraft, J. P. G. M. Cromsigt, and J. Berger. 2009. Global decline in aggregated migrations of large terrestrial mammals. Endangered Species Research 7:55–76.

Heisey, D. M., and B. R. Patterson. 2006. Review of methods to estimate cause-specific mortality in the presence of competing risks. Journal of Wildlife Management 70:1544–1555.

Hilty, J. A., W. Z. Lidicker, Jr., and A. M. Merenlender. 2006. Corridor ecology: the science and practice of linking landscapes for biodiversity conservation. Island Press, Washington, D.C., USA.

Hosmer, D. W., and S. Lemeshow, editors. 2000. Applied logistic regression. John Wiley and Sons, New York, New York, USA.

Hosmer, D. W., S. Lemeshow, and S. May. 2008. Applied survival analysis: regression modeling of time-to-event data. Second edition. John Wiley & Sons, Hoboken, New Jersey, USA.

Jakes, A. F. 2015. Factors influencing seasonal migration of pronghorn across the northern sagebrush steppe. Dissertation, University of Calgary, Alberta, Canada.

Jones, P. F. 2014. Scarred for life; the other side of the fence debate. Human-Wildlife Interactions 8:150–154.

Jones, P. F., B. Seward, L. Seward, and H. Dorchak. 2012. Opening up the prairies: evaluating the use of goat-bars by pronghorn. Proceedings of Pronghorn Workshop 25:52–58.

Kie, J. G., V. C. Bleich, A. L. Medina, J. D. Yoakum, and J. W. Thomas. 1996. Managing rangelands for wildlife. Pages 663–688 *in* T. A. Bookout, editor. Research and management techniques for wildlife and habitats. Fifth edition. The Wildlife Society, Bethesda, Maryland, USA.

Kindschy, R. R. 1996. Fences, waterholes, and other range improvements. Pages 369–381 *in* P. R. Krausman, editor. Rangeland wildlife. Society for Range Management, Denver, Colorado, USA.

Kitchen, D. W. 1974. Social behavior and ecology of the pronghorn. Wildlife Monographs 38.

Kleinbaum, D. G., and M. Klein. 2012. Survival analysis: a self-learning text. Third edition. Statistics for Biology and Health, Springer Science and Business Media, LLC, Atlanta, Georgia, USA.

Leftwich, T. J., and C. D. Simpson. 1978. The impact of domestic livestock and farming on Texas pronghorn. Proceedings of Pronghorn Antelope Workshop 8:307–320.

Mackie, R. J. 1981. Interspecific relationships. Pages 487–507 *in* O. C. Walmo, editor. Mule and black-tailed deer of North America. University of Nebraska, Lincoln, USA.

Martinka, C. 1967. Mortality of northern Montana pronghorn in a severe winter. Journal of Wildlife Management 31:159–164.

Mitchell, G. J. 1980. The pronghorn antelope in Alberta. University of Regina, Saskatchewan, Canada.

Moeller, A. K. 2017. New methods to estimate abundance from unmarked populations using remote camera trap data. Thesis, University of Montana, Missoula, USA.

O'Gara, B. W. 2004*a*. Physical characteristics. Pages 109–143 *in* B. W. O'Gara and J. D. Yoakum, editors. Pronghorn: ecology and management. Wildlife Management Institute, University Press of Colorado, Boulder, USA.

O'Gara, B. W. 2004*b*. Hunting. Pages 765–805 *in* B. W. O'Gara and J. D. Yoakum, editors. Pronghorn: ecology and management. University Press of Colorado, Boulder, USA.

O'Gara, B. W., and R. E. McCabe. 2004. From exploitation to conservation. Pages 41–73 *in* B. W. O'Gara and J. D. Yoakum, editors. Pronghorn: ecology and management. University Press of Colorado, Boulder, USA.

Paige, C. 2012. A landowner's guide to wildlife friendly fences. Second edition. Private Land Technical Assistance Program, Montana Fish, Wildlife & Parks, Helena, USA.

Paige, C. 2015. A Wyoming landowner's handbook to fences and wildlife: practical tips for fencing with wildlife in mind. Second edition. Wyoming Community Foundation, Laramie, USA.

Pool, D. B., A. O. Panjabi, A. Macias-Duarte, and D. M. Solhjem. 2014. Rapid expansion of cropland in Chihuahua, Mexico threatens declining

North American grassland bird species. Biological Conservation 170: 274–281
Poor, E., A. Jakes, C. Loucks, and M. Suitor. 2014. Modeling fence location and density at a regional scale for use in wildlife management. PLoS ONE 9(1):e83912.
R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/. Accessed 21 Dec 2016.
Sawyer, H., F. Lindzey, and D. McWhirter. 2005. Mule deer and pronghorn migration in western Wyoming. Wildlife Society Bulletin 33:1266–1273.
Seidler, R. G., R. A. Long, J. Berger, S. Bergen, and J. P. Beckmann. 2015. Identifying impediments to long-distance mammal migrations. Conservation Biology 29:99–109.
Seward, B., P. F. Jones, and A. T. Hurley. 2012. Where are all the fences: mapping fences from satellite imagery. Proceeding of the Pronghorn Workshop 25:92–98.
Taylor, P. D., L. Fahrig, and K. A. With. 2006. Landscape connectivity: a return to the basics. Pages 29–43 *in* K. R. Crooks and M. Sanjayan, editors. Connectivity conservation. Cambridge University Press, New York, New York, USA.
Telfer, E. S., and J. P. Kelsall. 1984. Adaptation of some large North American mammals for survival in snow. Ecology 65:1828–1834.
Therneau, T. 2015. A package for survival analysis in S. R package, version 2.38. http://CRAN.R-project.org/package=survival. Accessed 18 Apr 2017.
Ticer, C. L., J. C. DeVos, Jr., and R. A. Ockenfels. 2002. Pronghorn use of modified fences in northern Arizona. Proceedings of Pronghorn Workshop 20:153–159.
Underwood, A. J. 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. Ecological Applications 4:3–15.
White, P. J., C. N. Gower, T. L. Davis, J. W. Sheldon, and J. R. White. 2012. Group dynamics of Yellowstone pronghorn. Journal of Mammalogy 93:1129–1138.
Yoakum, J. D. 2004. Habitat conservation. Pages 571–630 *in* B. W. O'Gara and J. D. Yoakum, editors. Pronghorn: ecology and management. University Press of Colorado, Boulder, USA.
Yoakum, J. D., P. F. Jones, J. Cancino, R. J. Guenzel, R. Seidler, A. Munguia-Vega, I. Cassaigne, and M. Culver. 2014. Pronghorn management guides. Fifth edition. Western Association of Fish and Wildlife Agencies' Pronghorn Workshop and New Mexico Department of Game and Fish, Santa Ana Pueblo, USA.
Zar, J. H. 1984. Biostatistical analysis. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1. Photo of a goat-bar site from Alberta, Canada.

Figure S2. Photo of a clip site from Montana, USA. Notice the camera mounted to the special bracket to the side of the metal fence post.

Figure S3. Photo of a smooth wire site from Montana, USA.

Figure S4. Smoothed daily fence panel type-specific crossing rates (i.e., crossing rate/day) for 5 fence-modification treatments during before and after periods for pronghorn in Alberta, Canada (2012–2016) and Montana, USA (2015–2016).

Table S1. Mean (SE) number of days and fence bottom-wire height (cm) before and after modifications were installed at trail camera sites evaluating the use of modifications by pronghorn on Canadian Forces Base Suffield, Alberta, Canada, and Matador Ranch, Montana, USA, 2012–2016.

Table S2. Frequency of attempts made by pronghorn and their crossing success during the posttreatment period at 5 fence panel types in Alberta, Canada (2012–2016), and Montana, USA (2015–2016).