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Original Article

Evaluating Responses by Sympatric Ungulates to Fence Modifications Across the Northern Great Plains

PAUL F. JONES,[1] *Alberta Conservation Association, 817 4th Avenue S #400, Lethbridge, AB T1J 0P3, Canada*
ANDREW F. JAKES,[2] *Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, W.A. Franke College of Forestry and Conservation, University of Montana, 32 Campus Drive, Missoula, MT 59812, USA*
AMANDA M. MacDONALD, *Alberta Conservation Association, 817 4th Avenue S #400, Lethbridge, AB T1J 0P3, Canada*
JASON A. HANLON, *The Nature Conservancy, Matador Ranch 4883 Ranch Road, Dodson, MT 59524, USA*
DANIEL R. EACKER,[3] *Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, W.A. Franke College of Forestry and Conservation, University of Montana, 32 Campus Drive, Missoula, MT 59812, USA*
BRIAN H. MARTIN, *The Nature Conservancy, 32 S Ewing, Suite 215, Helena, MT 59601, USA*
MARK HEBBLEWHITE, *Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, W.A. Franke College of Forestry and Conservation, University of Montana, 32 Campus Drive, Missoula, MT 59812, USA*

ABSTRACT Across North America, incentive programs have assisted landholders with the construction of fences, often considered "wildlife friendly," to assist in grazing management, which has resulted in a proliferation of fencing on the landscape. Many suggested "wildlife-friendly" fence modifications have not been evaluated for their effectiveness on the targeted species or evaluated to assess consequences for nontarget species. We evaluated the effects of 2 modifications aimed to increase fence visibility (sage-grouse [SAGR] reflectors and white polyvinyl chloride [PVC]) on the fence-crossing behavior of 3 sympatric ungulates in the Northern Great Plains. We used trail cameras from 2016 to 2018 to capture images of pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*) at sites before and after fence sections were modified and compared crossing success by the 3 ungulates with that achieved at unchanged control sites. We used generalized linear modeling and a time-to-event approach to test the effect of fence modifications on ungulate crossing behavior. Our results showed that both SAGR reflectors and white PVC pipe did not impede fence-crossing behaviors for either pronghorn or deer, nor was there a time lag in use of sites observed after modifications were deployed. Though we did not alter the height of the bottom wire, there was enough variability in bottom wire height between sites that our results indicate a greater probability of successful crossing by all 3 ungulates as bottom wire height increased. We recommend implementation of both SAGR reflectors and white PVC pipe because our results demonstrate no substantial unintended consequences on the crossing behavior of pronghorn and deer. © 2020 The Authors. *Wildlife Society Bulletin* published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

KEY WORDS *Antilocapra americana*, fence modification, mule deer, Northern Great Plains, *Odocoileus hemionus*, *Odocoileus virginianus*, pronghorn, PVC pipe, sage grouse reflectors, white-tailed deer.

Across the globe there has been a proliferation of fences constructed to assist landholders in management of their pastures (Toombs and Roberts 2009). For example, between 2004 and 2007, 10,000 km of fencing was erected across 17 western states in the United States (Knight et al. 2011). Though fences are expensive and time-consuming to erect and maintain (Knight et al. 2011), there are incentive programs that lessen the burden (e.g., U.S. Department of Agriculture Natural Resources Conservation Service's [NRCS] Environmental Quality Incentives Program). Such incentive programs are intended to allow safe passage for wildlife, increase fence visibility, and improve wildlife habitat (NRCS 2011). These fences are promoted by

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[1] *E-mail: paul.jones@ab-conservation.com*
[2] *Current affiliation: National Wildlife Federation, Northern Rockies, Prairies & Pacific Region, 240 North Higgins Avenue, Suite 2, Missoula, MT 59802, USA*
[3] *Current affiliation: Alaska Department of Fish and Game, Division of Wildlife Conservation, P.O. Box 110024, 802 Third Street, Douglas, AK 99824, USA*

conservation agencies as a tool to assist landholders in increasing vegetation heterogeneity (Teague et al. 2013); improve habitat for grassland birds, including greater sage-grouse (*Centrocercus urophasianus;* hereafter, SAGR); and encourage the use of "wildlife-friendly" designs for any new fences erected.

Each jurisdiction has their own guidelines as to what constitutes "wildlife-friendly" fencing (e.g., Paige 2012, 2015). Within the guidelines for landholders, there are recommendations to make fences friendly for wildlife by increasing the visibility of the fence wires. Two common approaches for increasing the visibility of fences include placing SAGR reflectors on the top and third wires or white polyvinyl chloride (PVC) pipe on the top wire of a barbed wire fence (Paige 2012, 2015). The placement of SAGR reflectors and PVC pipe on the fence is intended to reduce mortality for grouse (and other birds) and assist deer in crossing over the fence, respectively (Paige 2012, 2015). It has been demonstrated that reflectors reduce SAGR mortalities as a result of striking fences during flight (Stevens et al. 2012, Van Lanen et al. 2017). However, neither study evaluated whether the fence markers acted as "visual barriers" and affected the crossing ability of ungulates.

Most recommendations found within landholder guides are species-specific or based on anecdotal accounts with few empirical studies assessing specific fence designs or their effects on more than just the targeted species (Jakes et al. 2018). Recently, Jones et al. (2018) and Burkholder et al. (2018) evaluated the effectiveness of 3 fence modifications at allowing easier passage by pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*). Both studies concluded that there was a negative response to one of the modifications tested—the white goat-bar (PVC pipe used to clip the bottom 2 wires together). If all 3 ungulates also react negatively to SAGR reflectors and white PVC pipe that are often used to increase visibility, then a once permeable fence may become a barrier to movement. How pronghorn and deer react to the SAGR reflectors or white PVC pipe along fence lines is unknown and warrants evaluation.

We used a before–after–control–impact (BACI) design to evaluate pronghorn and deer behavioral interactions with fences modified to increase the visibility of the fence (Underwood 1994). Specifically, we evaluated 1 behavioral interaction for pronghorn and 2 for deer. For pronghorn, we evaluated whether pronghorn were successful at crossing a fence (hereafter, crossing success) because pronghorn predominately cross under a fence and very rarely jump over (Jones et al. 2018). For deer, in addition to evaluating crossing success, we also evaluated whether the successful cross occurred by the deer crawling under the bottom wire or jumping over the top wire (hereafter, crossing decision). The 2 modifications evaluated were SAGR reflectors on the top and third wires or white PVC pipe on the top wire at fence panels located at known crossing locations. We assessed the following covariates in our models: treatment–period interaction, bottom wire height, area, snow coverage, group composition, and group size. First, we predicted that if all 3 ungulates reacted to the modifications in a similar fashion as they did to the white goat-bars on the bottom wires (Burkholder et al. 2018, Jones et al. 2018), then the probability of successfully crossing a fence would decrease at sites following installation of modifications and remain stable or increase at the unchanged sites. Secondly, we predicted that pronghorn crossing success would be positively correlated with bottom wire height, with success increasing as bottom wire height increased. Deer can crawl under or jump over a fence, so we predicted that none of the covariates assessed would affect crossing success. However, we predicted that deer crossing decisions (i.e., to crawl under or jump over) would be affected by demographic factors, with females and fawns having a greater probability of crossing under than males (Burkholder et al. 2018). Lastly, all 3 ungulates have a learned predisposition to cross at certain fence panels along fence lines that allow easier passage to the other side (Burkholder et al. 2018, Jones et al. 2018). Both modifications were placed on fence panels at known crossing locations; therefore, we predicted that pronghorn and deer would gradually habituate to these fence modifications because of their propensity to cross at these specific fence panels (Jones et al. 2018).

STUDY AREA

We studied pronghorn and deer crossing behavior at 2 study areas in the Northern Great Plains. The study areas included Canadian Forces Base (CFB) Suffield (50°15′N, −111°10′W) in Alberta, Canada, and The Nature Conservancy's Matador Ranch (47°55′N, −108°19′W) in Montana, USA. Both study areas were semiarid, native sagebrush steppe habitats. Commercial livestock grazing was the predominant human-land-use activity in both areas, with additional land uses including agricultural crop production, transportation networks, energy development (oil, gas, and wind), rural residential development, and urban expansion. The study area on CFB Suffield occurred on the National Wildlife Area, which was outside of the active military training area that occurred on the base. Each study area had fences used to control the distribution of large livestock (cattle; *Bos taurus*), with 4- and 3- or 5-strand fences being used predominately in Alberta and Montana, respectively. The 3-strand "wildlife-friendly" fences in Montana consisted of double-stranded smooth wire at approximately 46 cm above ground on the bottom and 2 strands of barbed wire above. All other fence designs consisted of barbed wire strands. Details on fence panels (e.g., bottom wire heights) are provided in Supporting Information, Table S1. Cattle were sporadically present in both study areas from June through October as they were rotated between pastures. Additional information on the study area can be found in Jones et al. (2018).

METHODS

Experimental Design

Our study used a BACI design at fence panels with known crossing locations to assess behavioral interactions between pronghorn and deer to proposed modifications designed to improve fence visibility of livestock pasture fences

(Underwood 1994). We used photos captured on remote trail cameras placed at fence panels with known crossing locations (hereafter, camera site; Supporting Information, Fig. S1) to assess fence-crossing success and crossing decision behaviors of pronghorn and deer. We identified crossing locations through ground surveys that identified fence sections with abundant fecal pellets, hair strands observed on fencing, and where the ground on both sides of the fence had been continuously trampled by pronghorn and deer. In addition, most crossing locations contained a distinct trail in the grass leading to and away from the fence. We initially monitored all fence camera sites without any modifications installed (hereafter, before period); then, following approximately 80 days ($\bar{x} = 80.8$ days, standard error [SE] = 2.6) of monitoring, we installed the modifications (hereafter, after period) and continued to monitor for approximately 400 days ($\bar{x} = 409.1$ days, SE = 5.7). During the after period, we installed white PVC pipe on the top wire at one-third of our camera sites, SAGR reflectors on the top and third from the top wires at one-third of our camera sites, while the remaining one-third of our camera sites were left unchanged and served as our control camera sites. For clarification, the general term "camera site(s)" refers to all camera locations while we used the term "modified sites" to refer to those camera sites that will or had a modification (i.e., either PVC pipe or SAGR reflectors) at them (i.e., does not include the camera sites used as controls). The PVC pipe was approximately 3 m in length and placed directly above the crossing location. In Alberta, for the approximately 12–15-m fence sections ($n = 18$), 6 and 4 reflectors were evenly spaced on the top and third wires, respectively, while for the 3–4-m fence sections ($n = 4$), 3 and 2 reflectors were evenly spaced on the top and third wires, respectively. In Montana, 4 and 3 reflectors were evenly spaced on the top and third wires, respectively, at all modified sites.

Camera Set-up and Photo Classification

We measured the response of pronghorn and deer interacting with fences using digital images captured by remote trail cameras (Reconyx© PC650, PC800 or PC900; Reconyx, Holmen, WI, USA). Dates for camera deployment, take down, and number of days for the before and after period are provided in Supporting Information, Table S1. In summary, for Alberta, we deployed 31 cameras on 25 and 26 October 2016, while in Montana, we deployed 26 cameras on 30 November 2016 and 1 December 2016 with an additional 4 cameras being deployed on 24 January 2017. We set cameras to only capture photos to maximize battery and digital (SD) card life and minimize the potential of missing observations as a result of the longer file upload times of videos. We deployed single cameras at each fence panel with a crossing location (Supporting Information, Fig. S1). We set cameras to rapid-fire to take 3–5 images/trigger with no delay between triggers. We set camera sensitivity to high except during the summer when we lowered the sensitivity to reduce false triggers. All cameras used in our study had a motion sensor activation between 15 and 18 m; therefore, there should not be significant differences in image capture capability between study areas related to width of fence panels. We mounted cameras to wooden fence posts in Alberta and either wooden fence posts or on custom-built brackets attached to T-bar posts in Montana at a mean height of 74.69 cm ± 2.32 (SE).

We used a 2-step procedure to process images of pronghorn and deer behavior captured by the trail cameras. We only processed behaviors for pronghorn and deer that were within 2–3 m on either side of the fence panel following Jones et al. (2018). First, we classified photos into either pronghorn, mule deer, or white-tailed deer and placed observations into events. We defined an event as ≥1 animal captured in an image and all subsequent images until there was ≥15 minutes between the last image with the animal in it and the next photo with an animal in it. We then categorized observations into 2 distinct behaviors: 1) failed attempt, or 2) successful attempt as per Burkholder et al. (2018) and Jones et al. (2018). An attempt was when an individual animal (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 (on the same side that it approached the fence), orientated its body more parallel to the fence than perpendicular (failed attempt), or successfully crossed to the other side (successful attempt). In addition, for deer we included as part of an attempt when the deer positioned its mass on its legs as if to jump the fence. For successful attempts, we recorded the number of instances where an individual "crossed under," "crossed over," or "crossed through" (i.e., between the wires) the fence. We estimated pronghorn group size and when possible, identified groups as being all male, all female, or mixed. We consider our estimate of group size for pronghorn as an approximation because of the difficulty in enumerating large group sizes (Moeller 2017). For all pronghorn events, we could not assign crossing behavior (failed or successful attempt) to an individual when group size >1; therefore, we allowed the event to be classified into multiple behaviors and recorded the number of instances of each behavior. For example, if a group of 10 female pronghorn approached a fence and only 3 successfully crossed to the other side on their first attempt, and the remaining 7 pronghorn attempted to cross as a group 12 times, we would classify the event as Successful Attempt = 3, Failed Attempt = 12, Group Size = 10, and Group Composition = All Female. Deer groups were smaller and their decision to cross more pronounced, so we broke events with >1 deer into individual deer events and determined whether the individual's attempt was successful or not. We classified each individual deer as either an adult male, adult female, or an unknown fawn. Unless otherwise stated, we pooled data across study areas for all analyses because results were similar when the analysis was completed separately for each area. We completed our analysis separately for pronghorn, mule deer, and white-tailed deer.

Statistical Analysis

Factors affecting crossing events.—We used generalized linear models with a logit link function (i.e., logistic regression) to evaluate pronghorn group crossing success (Hosmer and Lemeshow 2000). For pronghorn, 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 area (AB or MT), group size, group composition (i.e., all male, all female, or mixed), bottom wire height, and treatment-period (control-before, control-after, PVC pipe-before, PVC pipe-after, SAGR reflector-before, or SAGR reflector-after) as explanatory covariates in our models. We used the covariate treatment-period as a surrogate for the interaction of treatment and period because it is easier to interpret the results than the interaction term, does not affect the results of the logistic regression, and provides an easy way to deal with missing combinations of treatment and period. 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 first screened for collinearity and eliminated one if there was high correlation (i.e., $|r| \geq 0.7$) between 2 covariates. Then we explored our data by comparing the single covariate model with the null model and eliminated the covariate from further modelling efforts if $P \geq 0.05$ to reduce global model complexity (Zuur et al. 2010). 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 possible combinations of covariates from the global model using a best-subsets regression approach (Grueber et al. 2011) achieved with the dredge function in Program R version 3.5.1 (R Core Team 2018) package MuMIn (Barton 2018). We used $\Delta\mathrm{AIC}_c < 2.0$ as the initial cut-off to compare competing top models, then examined the covariates in each top model to determine if including them improved model performance (Arnold 2010). If we determined that >1 model was competitive, we report the full model-averaged β coefficients (Grueber et al. 2011). We calculated the odds ratio values and 95% confidence intervals (CI) using the unstandardized covariates and where there was >1 top model, we report the odds ratios for the unstandardized model-averaged β coefficients and associated 95% CI. We evaluated model fit using Receiver Operator Curves (ROC) and used the scores to classify model fit as excellent (>0.9), good (0.8–0.9), adequate (0.7–0.79), satisfactory (0.6–0.69), or poor (<0.6; Hosmer and Lemeshow 2000).

We used a similar approach to assess factors influencing deer crossing behavior except for 2 major differences. First, we evaluated the crossing behavior of an individual mule deer and white-tailed deer, as opposed to the group crossing success by pronghorn as noted above. Both mule deer and white-tailed deer groups were relatively small compared with pronghorn, so we were able to keep track of individual deer and classify their behavior as to whether they successfully crossed or failed to cross. In instances where we had a deer cross a fence and then turn around and cross back, we recorded the event as one successful crossing. Secondly, in addition to evaluating crossing success, we also evaluated crossing decision (see fig. 1 in Burkholder et al. 2018). We evaluated crossing decision by individual deer by subsampling our data for successful crossings, then determined whether the deer crossed the fence by crawling under (coded 1) or jumped over (coded 0). We removed any instances where a deer went through the fence from our decision analysis. We used the same covariates as for the pronghorn analysis except group composition was replaced with the covariate age–sex (adult male, adult female, or fawn unknown), and we included the covariate snow coverage (none, partial ground coverage, or full ground coverage at fence panel) for which there was no evidence of an effect for pronghorn but there was for deer (P.F. Jones, unpublished data). We used a categorical covariate for snow, as opposed to actual snow depth, because we did not have snow measurements for each camera site throughout the winter seasons. We analyzed mule deer and white-tailed deer separately. We conducted all analyses in Program R 3.5.1 (R Core Team 2018).

Multiple comparison analysis.—In logistic regression when categorical covariates are included in the top model, the beta coefficient (direction and size) for each level of the categorical covariate are only in relation to the reference category and do not provide an indication of how the other levels compare with each other. Therefore, for categorical covariates included in the logistic regression top model, we used a Tukey-like comparison to account for the proper alpha level when comparing proportions (and not means as used in the standard Tukey comparison) to estimate pairwise-effect sizes among levels of the categorical covariate using the emmeans package on the probability scale (Lenth 2018). Estimates of the probability (for success or decision) were obtained for each categorical covariate separately, if they were contained in the top model(s) of the logistic regression. Likelihood methods generate an estimate and SE on the logit scale, with the 95% CI calculated on the logit-scale by taking the estimate ±1.96 SE. We then estimated the probability of success or decision as the anti-logit of the logit value and the 95% CI bounds and report these values. We were particularly interested in how each modified camera site compared prior to and after installation of the modification, so we only report those results. We provide results for the other categorical covariates in the top model(s) in the online supplemental material (Supporting Information, Fig. S2 [pronghorn], Fig. S3 [mule deer], and Fig. S4 [white-tailed deer]).

Time to event analysis.—We used a time-to-event approach with multiple events to estimate daily crossing rates for pronghorn and deer among fence panel types during the before and after periods (Hosmer et al. 2008, Jones et al. 2018). We used days since camera deployment and modification as the origin for all cameras for the before and after periods, respectively, and interval-censored cameras when they were not operable as a result of insufficient battery power or other issues. We pooled data across all years and study areas to summarize crossing rates. We estimated cumulative daily crossing rates for the 3 fence panel types (control, PVC pipe, SAGR reflector) 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 crossing events. We restricted crossing rates to a maximum of 1 event/day at each fence panel to eliminate 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 (Rebora et al. 2018) to estimate smoothed daily treatment-specific crossing rates with 95% CI. We conducted the time-to-event analyses in Program R 3.5.1 (R Core Team 2018).

RESULTS

Combining data for Alberta and Montana, we recorded 7,665 and 1,787 successful crossing attempts for pronghorn and mule deer, respectively (Table 1). We recorded 341 successful crossing attempts for white-tailed deer in Alberta only (Table 1). We did not record any successful or failed fence-crossing attempts for white-tailed deer in Montana. Pronghorn successfully crossed a fence 49% of the time and did so predominately by crossing under (99.9%). Mule deer successfully crossed the fence 75% of the time and did so predominately by going under (83%) as opposed to over. White-tailed deer crossed the fence 65% of the time and did so predominately by going under (60%). In Montana, we captured images during the before and after periods of pronghorn and mule deer crossing at fence sections 2–12 m from the fence panel where the camera was located (Supporting Information, Table S2). We did not include these images in our analysis.

Factors Affecting Crossing Success

For our analysis, the 15,771 crossing attempts (successful and failed) by pronghorn represented 2,394 events, of which 1,520 (63.5%) of the events had >50% of the group successfully cross and were considered successful (coded 1) for our logistic regression analysis. We removed group composition from our model selection because it was correlated with maximum group size. We selected one model that included 4 covariates with a model weight of 100%; the next best model had a $\Delta AIC_c = 34.58$ and was not considered as a competing model (Table 2; Supporting Information, Table S3). The covariate treatment-period was retained in the final model for pronghorn crossing success. Bottom wire height was retained in the selected model, with the odds of a pronghorn successfully crossing the fence greater for every 1-cm increase in bottom wire height (unstandardized odds ratio = 1.08, 95% CI = 1.07–1.10). In addition, group size was retained in the model, with the odds of a pronghorn successfully crossing the fence greater for every additional individual in the group (unstandardized odds ratio = 1.06, 95% CI = 1.05–1.08). Lastly, pronghorn had a greater probability of successfully crossing a fence in Montana (unstandardized odds ratio = 2.15, 95% CI = 1.67–2.79). The model performed adequately with a ROC score of 0.73.

For mule deer we recorded 2,397 individual deer attempting to cross (successful and failed) with a 75% crossing success rate (1,787/2,397). We selected one model for mule deer crossing success that contained 4 covariates with a model weight of 100%; the next ranked model had a $\Delta AIC_c = 15.43$ and was not considered as a competing model (Table 2; Supporting Information, Table S3). All covariates in the selected model had a negative relationship except for bottom wire height (Table 2). The covariate treatment-period was retained in the final top-ranked model for mule deer crossing success. Odds of a mule deer successfully crossing the fence were greater for every 1-cm increase in bottom wire height (unstandardized odds ratio = 1.05, 95% CI = 1.04–1.06). Mule deer had a lower probability of successfully crossing a fence in Montana (unstandardized odds ratio = 0.41, 95% CI = 0.32–0.52). Lastly, mule deer adult males and unknown fawns had a lower probability of successfully crossing (male-adult: unstandardized odds ratio = 0.46, 95% CI = 0.38–0.57; fawns-unknown: unstandardized odds ratio = 0.64, 95% CI = 0.47–0.87) compared with females. The model performed satisfactorily with a ROC score of 0.68.

For white-tailed deer in Alberta, we recorded 525 individual deer attempting to cross (successful and failed) with a 65% crossing success rate (341/525). There were only 8 individual fawns detected during our study, so we removed

Table 1. Number of successful and failed fence-crossing attempts made by pronghorn, mule deer, and white-tailed deer in Alberta, Canada, and Montana, USA, 2016–2018. Crossing attempts were determined from photos captured using trail cameras at fence sections with a crossing site. Note that the attempts by pronghorn are the total number and may include repeated attempts by an individual during the same event on account of the difficulty keeping track of individuals in groups, whereas attempts by mule deer and white-tail deer are for individuals because group sizes tended to be smaller and we could keep track of individuals.

Species	No. under	No. over	No. through	Total successful attempts	Total failed attempts	Total attempts
Pronghorn	7,656	1	8	7,665	8,106	15,771
Mule deer	1,482	298	7	1,787	610	2,397
White-tailed deer	205	135	1	341	184	525

Table 2. Standardized parameter estimates for the covariates in the top model(s) for crossing success and crossing decision by pronghorn, mule deer, and white-tailed deer in the Northern Great Plains region of Alberta, Canada, and Montana, USA, 2016–2018. We defined crossing success as going from one side of the fence to the other by any means (under, over, or through) while crossing decision was defined as successfully crossing under a fence as opposed to over. We considered the following as explanatory covariates for crossing success and crossing decision in our models: 1) treatment-period (control-before, control-after, polyvinyl chloride [PVC] pipe-before, PVC pipe-after, sage-grouse [SAGR] reflectors-before, and SAGR reflectors-after); 2) area (AB or MT); 3) group size; 4) group composition (for deer [adult female, adult male, unknown-fawn]); 5) snow (for deer [none, patch, full coverage]); and 6) bottom wire height (cm). For pronghorn, we classified successful crossing events where >50% of the group successfully crossed, whereas for both deer species we considered crossing success and decision at the individual level. n/a, not applicable.

		Success						Decision			
		Pronghorn		Mule deer		White-tailed deer		Mule deer[b]		White-tailed deer[c]	
Covariate[a]	Subcategory	β coeff.	SE	β coeff.	SE	β coeff.	SE	β coeff.	SE	β coeff.	SE
Intercept		−0.98	0.21	2.47	0.27	1.22	0.46	2.14	0.40	0.01	0.56
Treatment-period	Control-after	1.18	0.22	−0.62	0.27	0.11	0.48	0.42	0.39	0.26	0.63
	PVC pipe-before	0.59	0.25	−1.24	0.36	−0.30	0.61	0.50	0.56	1.28	0.78
	PVC pipe-after	1.13	0.22	−0.75	0.27	−0.44	0.47	1.47	0.40	1.84	0.64
	SAGR reflectors-before	−0.13	0.26	−1.15	0.34	0.71	0.67	−0.18	0.56	0.48	0.72
	SAGR reflectors-after	1.10	0.22	−0.38	0.27	−0.76	0.50	1.82	0.41	1.66	0.68
Group size[d]	Maximum	1.09	0.15	n/a		n/a		−0.03	0.12	−0.35	0.35
Wire height[d]	Bottom	1.05	0.10	0.88	0.12	0.70	0.22	2.91	0.25	2.39	0.36
Area	Montana	0.77	0.13	−0.94	0.12	n/a		−0.27	0.24	n/a	
Group composition	Fawn—unknown	n/a		−0.47	0.16	n/a		1.01	0.42	n/a	
	Male—adult	n/a		−0.76	0.11	−0.81	0.19	−2.40	0.18	−1.61	0.30
Snow coverage	Full	n/a		n/a		0.27	0.38	n/a		n/a	
	Patchy	n/a		n/a		1.67	0.77	n/a		n/a	

[a] Reference categories for fence modification type (control-before), area (AB), age-sex (adult female), and snow coverage (none).

[b] For mule deer crossing decision, the beta coefficients are averaged across the top 3 models that had a $\Delta AIC_c < 2.00$.

[c] For white-tailed deer crossing decision, the beta coefficients are averaged across the top 2 models that had a $\Delta AIC_c < 2.00$.

[d] β coefficients standardized by subtracting the mean and dividing by 2 standard deviations.

them and the associated females during those events from further analysis, resulting in our age–sex composition being either adult female or adult male. We removed events with fawns from the analysis because the small number created model instability. For our crossing success analysis, we selected one model containing 4 covariates with a total cumulative model weight of 74%; the next-ranked model had a $\Delta AIC_c = 2.99$ and was not considered as a competing model (Table 2; Supporting Information, Table S3). The covariate treatment-period was retained in the final top model for white-tailed deer crossing success. Odds of a white-tailed deer successfully crossing a fence increased for every 1-cm increase in bottom wire height (unstandardized odds ratio = 1.05, 95% CI = 1.02–1.08), while the odds decreased if the individual was an adult male (unstandardized odds ratio = 0.44, 95% CI = 0.30–0.65) than if it was an adult female. Odds of successfully crossing a fence increased if the snow coverage was patchy (unstandardized odds ratio = 5.31, 95% CI = 1.45–34.33) or full (unstandardized odds ratio = 1.31, 95% CI = 0.63–2.88) compared with no snow coverage. The top model performed satisfactorily with a ROC score of 0.68.

Factors Affecting Crossing Decision

We recorded 1,482 individual mule deer deciding to cross under a fence, resulting in 83% (1,482/1,780) of the individual deer deciding to cross under as opposed to jumping over. We removed the 7 individual instances of a deer crossing between the wires for the decision analysis. For our crossing decision analysis, we selected 3 models that had $\Delta AIC_c < 2.0$ with a total cumulative model weight of 88% (Table 2; Supporting Information, Table S3). The next-ranked model had a $\Delta AIC_c = 2.56$ and was not considered as a competing model. The covariate treatment-period was retained in the final top model for mule deer crossing decision. We model-averaged the beta coefficients and determined that bottom wire height, group composition, area, and group size were important covariates in the top model (Table 2). Odds of a mule deer successfully crossing under a fence increased for every 1-cm increase in bottom wire height (unstandardized odds ratio = 1.16, 95% CI = 1.13–1.19). Odds of a mule deer crossing under a fence increased if the individual was an unknown fawn (unstandardized odds ratio = 2.74, 95% CI = 1.20–6.27) and decreased if the individual was an adult male (unstandardized odds ratio = 0.09, 95% CI = 0.06–0.13) than if it was an adult female. Lastly, the odds of a mule deer crossing under a fence decreased for every additional individual in the group (unstandardized odds ratio = 0.97, 95% CI = 0.89–1.05) and decreased if the individual was in Montana (unstandardized odds ratio = 0.69, 95% CI = 0.46–1.03) when compared with Alberta. The top model performed good with a ROC score of 0.90.

We recorded 205 individual white-tailed deer deciding to cross under a fence, resulting in 60% (205/340) of the individual deer deciding to cross under as opposed to jumping over. We removed the one instance of an individual deer going between the wires from the decision analysis. We selected 2 ranked models that had $\Delta AIC_c < 2.0$ with a total cumulative model weight of 100% (Table 2; Supporting Information, Table S3). The next-ranked model had a $\Delta AIC_c = 15.31$ and was not considered as a competing model. The covariate treatment-period was retained in the final top model for white-tailed deer crossing decision. Our selected models contained the covariates bottom wire height, adult males, and group size (Table 2). Odds of a white-tailed deer successfully crossing under a fence increased for every 1-cm increase in bottom wire height (unstandardized odds ratio = 1.17, 95% CI = 1.12–1.23), while the odds decreased if the individual was an adult male (unstandardized odds ratio = 0.20, 95% CI = 0.11–0.36) than if it was an adult female, and decreased for every additional member of the group the individual was in (unstandardized odds ratio = 0.83, 95% CI = 0.68–1.01). The top model performed good with a ROC score of 0.85.

Multiple Comparison Analysis

Crossing success.—The categorical covariate treatment-period was included in the top model for crossing success for all 3 species. Presented beta coefficients are in comparison with the reference category (i.e., control-before; Table 2); therefore, we fit our Tukey-like multiple comparisons to compare each level of the covariate with the other levels. We found a trend, though not significant, of a greater probability of successful crossing by pronghorn during the after period at all camera sites compared with the corresponding camera sites during the before period (Fig. 1). We found the probability of successfully crossing by mule deer changed between the before and after periods for each camera site type (Fig. 2). Mule deer had a greater probability of successfully crossing at each modified camera site following installation of modifications in respect to the same camera sites during the before period. The exception was for the control camera sites where the probability was lower during the after period than the before period (Fig. 2).

We found none of the levels (e.g., control-after) influenced the probability of successfully crossing a fence by white-tailed deer than any of the other levels (Fig. 2). However, though not significant, there was a trend of increased probability of successfully crossing a fence at the modified camera sites during the before period compared with the same camera sites during the after period (Fig. 2). The exception was at control camera sites where crossing success remained relatively the same between periods (Fig. 2).

Crossing decision.—The categorical covariate treatment-period was included in the top model for crossing decision by both deer species in reference to the category (control-before; Table 2). We found mule deer had a greater probability of crossing under the bottom wire at the SAGR reflectors and PVC-pipe camera sites following installation compared with the same camera sites before we installed the modifications (Fig. 2). There was a lower probability of crossing under at the control camera sites during the after period compared with the before period (Fig. 2). We found a weaker, but similar pattern of a greater probability of crossing under a fence at the modified camera sites by white-tailed deer once the modifications were installed (Fig. 2). There was a consistent probability of crossing under at the control camera sites between the before and after periods (Fig. 2).

Time-to-Event Analysis

Our pooled analysis for pronghorn included 4,850 camera-days during the before period and 24,548 camera-days during the after period. We detected 247 and 1,034 pronghorn daily crossing events during the before (days 0–105) and after (days 0–456) periods, respectively. Most daily pronghorn crossing events during the before period occurred at the PVC-pipe camera sites, which reached a cumulative rate of 5.20 (95% CI = 3.91–6.48) daily crossings/fence panel by 105 days since camera deployment (Table 3; Fig. 3). By day 105 during the after period, all treatments had reached their respective before-period cumulative crossing rate, indicating no effect of the fence modifications (Fig. 3). The cumulative rate of daily crossings per fence continued to increase at all camera sites during the after period (Table 3; Fig. 3), with the greatest increase observed at the SAGR-reflector camera sites (after

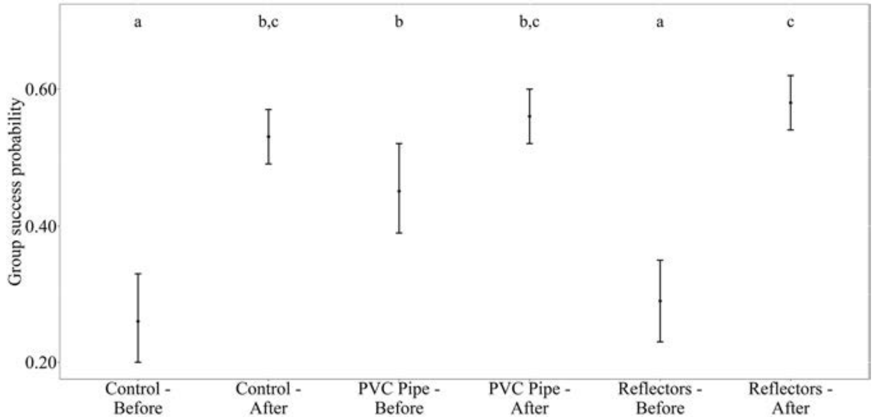

Figure 1. Mean probability and 95% confidence limits for the covariate treatment-period for group crossing success by pronghorn in Alberta, Canada, and Montana, USA, 2016–2018. For pronghorn, we classified successful crossing events where >50% of the group successfully crossed from one side of the fence to the other by any means (under, over, through). Similar letters above points indicate no difference between probabilities based on Tukey-like multiple pair-wise comparisons. We completed the multiple comparisons using a Tukey-like comparison to account for the proper alpha level when comparing proportions (and not means as used in the standard Tukey comparison) to estimate pairwise-effect sizes among levels of the categorical covariate on the probability scale using just the covariate separately and not in conjunction with the other covariates in the top model.

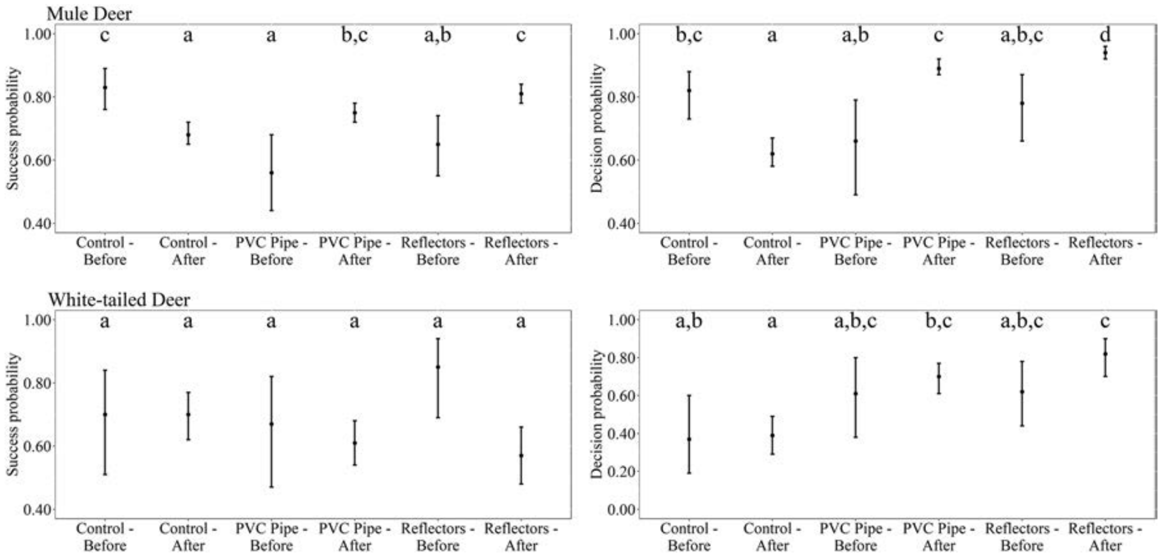

Figure 2. Mean probability and 95% confidence limits for the covariate treatment-period for individual crossing success (left column) and crossing decision (right column) by mule deer (top row) and white-tailed deer (bottom row) in Alberta, Canada, and Montana, USA, 2016–2018. Crossing success was defined as crossing from one side of the fence to the other by any means (e.g., under, over, or through), while crossing decision was defined as the probability of crossing under. Similar letters above points indicate no difference between probabilities based on Tukey-like multiple pair-wise comparisons. We completed the multiple comparisons using a Tukey-like comparison to account for the proper alpha level when comparing proportions (and not means as used in the standard Tukey comparison) to estimate pairwise-effect sizes among levels of the categorical covariate on the probability scale using just the covariate separately and not in conjunction with the other covariates in the top model.

CIF = 22.18, 95% CI = 7.36–37.05) followed by the PVC-pipe camera sites (after CIF = 20.48, 95% CI = 7.77–33.23).

Our pooled analysis for mule deer included 4,850 camera-days during the before period and 24,548 camera-days during the after period. We detected 76 and 779 mule deer daily crossing events during the before (days 0–105) and after (days 0–456) periods, respectively. Most daily mule deer crossing events during the before period occurred at the control camera sites, which reached a cumulative rate of 1.57 (95% CI = 1.33–1.82) daily crossings/fence panel by 105 days since camera deployment (Table 3; Fig. 3). At all camera sites there was a leveling off for daily crossing rates occurring around day 30 of the before period. By day 105 during the after period, all treatments had reached or slightly exceeded their respective before-period cumulative crossing rate, indicating no effect of the fence modifications (Fig. 3). The cumulative rate of daily crossings per fence continued to increase at all camera sites during the after period until approximately day 250 where the rates leveled off (Table 3; Fig. 3). By day 456 all the treatment types exceeded their before crossing rates, with the greatest increase observed at the PVC-pipe camera sites (after CIF = 13.85, 95% CI = 6.43–21.26) followed by the SAGR-reflector camera sites (after CIF = 12.89, 95% CI = 6.91–18.88).

Our pooled analysis for white-tailed deer in Alberta included 2,498 camera-days during the before period and 13,579 camera-days during the after period. We detected 67 and 251 white-tailed deer daily crossing events during the

Table 3. Cumulative incidence functions (CIF) with 95% confidence intervals (CI) and total number of events (*n*) for 3 fence panel types during before and after fence-modification periods for pronghorn, mule deer, and white-tailed deer in Alberta, Canada, and Montana, USA, 2016–2018. Treatments included control, polyvinyl chloride (PVC) pipe on top wire, and sage grouse (SAGR) reflectors on top and middle wires. For white-tailed deer, data are from Alberta only, with $t = 85$ days before. Although multiple crossing events occurred within a day at a fence, we restricted crossing rates to a maximum of 1 event/day/fence panel to eliminate multiple crossings of the same individual at a fence.

		Before ($t = 105$ days[a])				**After ($t = 456$ days)**			
Species	**Treatment**	***n***	**CIF**	**95% CI lower**	**95% CI upper**	***n***	**CIF**	**95% CI lower**	**95% CI upper**
Pronghorn	Control	69	4.29	3.08	5.51	311	19.12	6.23	32.24
	PVC pipe	93	5.20	3.91	6.48	347	20.48	7.77	33.23
	SAGR reflectors	85	5.14	3.65	6.63	376	22.18	7.36	37.05
Mule deer	Control	26	1.57	1.33	1.82	248	12.40	6.22	18.58
	PVC pipe	22	1.12	0.96	1.28	274	13.85	6.43	21.26
	SAGR reflectors	28	1.49	1.34	1.65	257	12.89	6.91	18.88
White-tailed deer	Control	19	1.90	1.40	2.40	91	9.11	4.12	14.11
	PVC pipe	19	1.90	1.38	2.41	92	8.45	3.88	13.02
	SAGR reflectors	29	3.13	2.25	4.02	68	6.81	3.13	10.49

[a] For white-tailed deer the before period was 85 days and data were from Alberta only.

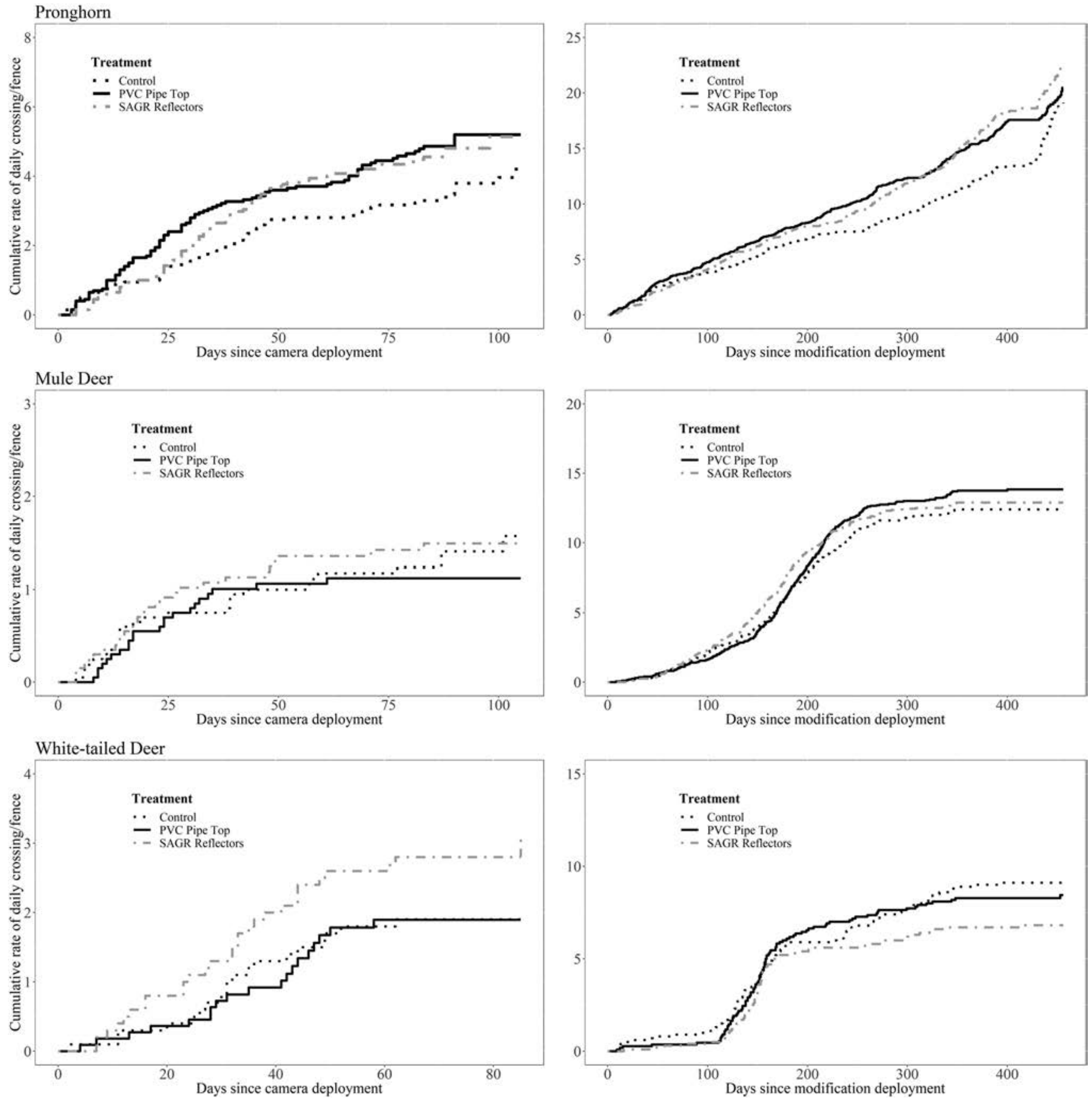

Figure 3. Cumulative incidence functions for fence modification treatments during before ($t = 0$–105, left column) and after ($t = 0$–456, right column) periods for pronghorn (top), mule deer (middle), and white-tailed deer (bottom) in Alberta, Canada, and Montana, USA, 2016–2018. Treatments included control, polyvinyl chloride (PVC) pipe, and sage grouse (SAGR) reflectors. White-tailed deer had a before period of 85 days because data were from Alberta only. Although multiple crossing events occurred within a day at a fence, we restricted crossing rates to a maximum of 1 event/day/fence panel to eliminate multiple crossings of the same individual at a fence.

before (days 0–85) and after (days 0–456) periods, respectively. Most daily white-tailed deer crossing events during the before period occurred at the SAGR-reflector camera sites, which reached a cumulative rate of 3.13 (95% CI = 2.25–4.02) daily crossings/fence panel by 85 days since camera deployment (Table 3; Fig. 3). By day 85 during the after period, all treatments had cumulative crossing rates slightly below their respective before period; but by day 100 cumulative crossing rate increased and by day 456 rates exceeded those observed during the before period (Fig. 3). Overall the greatest increase in cumulative crossing rates were at control camera sites (after CIF = 9.11, 95% CI = 4.12–14.11) followed by the PVC-pipe camera sites (after CIF = 8.45, 95% CI = 3.88–13.02).

DISCUSSION

Our results showed that both SAGR reflectors on the top and third wire and the white PVC pipe on the top wire did not impede fence-crossing success for pronghorn, mule deer, or white-tailed deer. Thus, our initial predictions that the modifications would have a negative effect were not supported by our data (see Jones et al. 2018). Certainly, not having the white PVC pipe on the bottom wire, but instead on the top wire, did not impede pronghorn movement (Jones et al. 2018). There was variability in bottom wire height within our sample of camera sites, which resulted in a greater probability of successfully crossing the fence by all 3 species at the sites that had higher bottom wires. Lastly, based on crossing sample sizes for each species, our results suggest that these crossing locations are not just used by pronghorn, as we originally thought; they are instead communal in nature, receiving significant use by all 3 species, further indicating their importance to daily and seasonal movements.

Our objective was to examine how pronghorn and deer react to potential visual barriers placed at fence panels with crossing locations. This assessment was initiated because pronghorn react negatively to goat-bars (white PVC) placed on the bottom 2 wires (Jones et al. 2018). In the case of the goat-bar, pronghorn tended not to cross directly underneath the PVC pipe itself but instead crossed at the side where the fence wires were raised. In addition, Burkholder et al. (2018) found both mule and white-tailed deer showed minimal use of goat-bar fence-crossing sites and attributed this to the white color of the goat-bar, which acted as a "visual barrier" and deterred use by deer. Both studies postulated that the negative reaction to goat-bars may be in response to the white color acting as a repellent, similar to the defensive behavior of flaring their white rump patch or raising and waving their tail, a warning signal exhibited by pronghorn (O'Gara 2004) and white-tailed deer (Stelfox 1993), respectively. Riginos et al. (2018) also found that white, in their case canvas, was more effective at reducing mule deer–vehicle collisions along highways than the standard road-side reflectors or the 2 nonreflective treatments (black canvas and removing reflectors). Our results indicate that both modifications did not lower the probability of successfully crossing a fence by pronghorn or deer, and we did not see a time lag in use of the modified camera sites following the installation of the reflectors and PVC pipe. Therefore, we would recommend continuing the use of these modifications to achieve their intended purpose of increasing fence visibility for grouse and ungulates (Jakes et al. 2018).

Our results indicate that the 2 modifications evaluated may serve their purpose of making fence lines more visible (Paige 2012, 2015). When an ungulate approaches a fence to cross, 3 basic decisions are made: 1) which specific fence panel along the fence line to approach (broad-scale choice), 2) whether to cross (fine-scale interaction), and 3) whether to cross by going under or over (fine-scale decision; see fig. 1 in Burkholder et al. 2018). When we look closely at the logistic regression results, and specifically the multiple comparisons for the treatment-period covariate, there appears to be a positive trend (though not significant in all cases) for the modified fence panel sites. It appears that the modified fence panel sites tend to have greater probability of successful crossings by pronghorn and mule deer once the modifications were in place compared with when they were absent, with the opposite occurring for white-tailed deer. This increase in probability of successfully crossing may be a result of pronghorn and mule deer making decisions at the broad-scale and approaching the modified fence panel sites as a result of the increased visibility provided by the white PVC pipe and SAGR reflectors. The white of the PVC pipe and to a lesser degree the SAGR reflectors, which are smaller in size but move in the wind, can be seen from a distance, act as visual stimuli, and may attract both species to those specific fence panels to investigate. Once at these modified sites they continue on their way and cross the fence, as seen by an increase in crossing probability at modified sites following our installation of the PVC pipe and reflectors. If modifications do attract ungulates at broad scales to the fence panel they are installed on, then further investigation is required to determine if these modifications can be used to attract ungulates to "wildlife-friendly" enhanced fence panels or road crossing structures to facilitate easier crossing (Paige 2012, 2015; Seidler et al. 2018). Consequently, substantial savings in terms of funds and time could be realized by landholders and conservation groups because entire fence lines may not need to be made "wildlife friendly" (i.e., double-stranded smooth wire on the bottom at 46 cm). Instead modifications could be applied to only certain fence panels (e.g., at crossing locations, along identified migration routes, fences adjacent to watering holes, etc.) along the fence line. Modifications should include either the white PVC pipe or SAGR reflectors on the top wires to create a broad-scale visual stimulation and fine-scale safe passage.

A simplistic view of deer–fence interactions is that deer predominantly jump fences. Burkholder et al. (2018) provided evidence that deer were as likely to crawl under the bottom wire as opposed to jumping over (when not under stress). Our results provide additional support that deer prefer to crawl under fences, with mule and white-tailed deer crawling 85% and 60% of the time, respectively, under the bottom wire. These results differ from those of Harrington and Conover (2006) who found mule deer predominately jumped over fences in Colorado and Utah, USA. The preference for crawling under is likely 2-fold; to reduce energy associated with jumping over (Burkholder et al. 2018) and also reduce potential mortality risk from getting a leg caught between the top 2 wires (Harrington and Conover 2006). For our study, the PVC pipe on the top wire was not designed to create easier passage over the fence (i.e., lower the top wire) by deer but instead to create a more visible fence. Alternatively, deer may prefer to jump fences but were forced to crawl under the fence because the top wire was too high to facilitate easy passage over. To test which method of crossing (under vs. over) is preferred, an evaluation of crossing behavior by deer at fence panels with crossing locations with a high bottom wire (i.e., ≥46 cm) and a modified top wire height (lowered to 102–107 cm) could be performed. Lowering the top wire height could be achieved by clipping (e.g., using PVC pipe or carabiners) the top wire to the wire below, effectively lowering the overall height of the fence.

Evaluating the 2 modifications at the same time would also allow one to assess whether the PVC pipe provides the added benefit of decreasing injuries by enclosing the barbs on the top wire and reducing the potential of deer snagging their legs on the barbs when jumping over.

Our study used a BACI study design with slight differences between Alberta and Montana study areas. We had anticipated differences in the ability of each species to cross based on study area because 70% of the camera sites in Montana consisted of "wildlife-friendly" fence designs (3-wire fence design with bottom wire being double-stranded smooth). We would expect both pronghorn and mule deer to have a greater probability of successfully crossing at the Montana camera sites, but this was not the case. Results of our logistic regression analysis indicate that the probability of successfully crossing for pronghorn was higher in Montana with the opposite occurring for mule deer. In the Montana study area, 70% of the sampled fences were converted to a "wildlife-friendly" design in 2013 and 2014. This is ample time for both pronghorn and mule deer to learn that the entire fence line is permeable and that they do not need to cross at the specific fence panels with crossing locations, though further research is required to assess how long after a fence is modified do ungulates habituate to crossing at any section and not just the previously known crossing site(s). The idea that ample time has passed for both species to acclimatize to crossing anywhere along the fence line is supported by the number of crossing events by both pronghorn and mule deer recorded in Montana. During the before and after periods we recorded images of both species successfully crossing at fence panels next to the panels with cameras (Supporting Information, Table S2). However, as previously noted, when we completed the analysis for each area separately, the results were similar and provided justification for reporting only combined results.

Our results show that both reflectors and PVC pipe do not create a visual barrier and do not impede the movement of pronghorn and deer. We recommend the implementation of both SAGR reflectors and white PVC pipe on the top to increase fence visibility for grouse and ungulates. Our results contribute to assessing the effectiveness of "wildlife-friendly" fencing recommendations, but there is still much work to be done. Further research is required to assess combinations of fence modifications to ascertain which design is truly the most effective for the intended species (while not affecting other species), the length of time required for species to habituate to fence modifications (especially those installed along an entire fence section and not just at panels with crossing locations), and lastly the influence of the color white on ungulate fence-crossing behavior (and whether other colors are more appropriate). In addition, an evaluation of the effectiveness of modifying entire fence lines versus important sections (i.e., at fence-crossing locations, along identified migration routes, adjacent to important resources [e.g., watering holes]) in creating fence-crossing opportunities would provide landholders with insight into whether modifications should be installed along the entire fence line or at specific locations. That is, the question "Do ungulates continue to cross at panels with crossing locations regardless of whether the entire fence line has been modified?" needs to be answered.

MANAGEMENT IMPLICATIONS

There is becoming an increasing awareness of the effects of fences on wildlife and the need for mitigation (Jakes et al. 2018). There are numerous documents available to landholders and conservationists that outline various fence designs aimed at facilitating wildlife movement and reducing mortality (Paige 2012, 2015). Most of these designs are species- or guild- (e.g., ungulate) specific and have not been rigorously tested to ensure they achieve their intended outcome or assessed how they potentially affect other non-target species. Our results give credence to the idea that converting an entire fence, where economically feasible, will create more opportunities for ungulates to cross, resulting in reduced energetic costs of having to travel along a fence to reach a panel with a crossing location (Jones et al. 2012). Therefore landholders have options for making fences ungulate friendly: 1) where economically feasible, convert the entire fence line and use a double-stranded smooth wire at 46 cm on the bottom to facilitate more opportunities to cross under; or 2) where it is not economically feasible, use clips to raise the bottom wire to 46 cm (Burkholder et al. 2018, Jones et al. 2018) and use SAGR reflectors or white PVC pipe on the top wire to potentially attract ungulates to the "wildlife-friendly" fence panel. We feel the latter is a good combination to make fences more "wildlife friendly" based on our results, though an assessment of the effectiveness of various combinations is required.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

Table S1. Camera site information for Alberta (AB), Canada, and Montana (MT), USA, 2016–2018.

Table S2. Number of instances of pronghorn and mule deer crossing at fence sections 2–12 m from the camera site at the Montana, USA, study area, 2016–2018.

Table S3. Competing top model(s) for pronghorn, mule deer, and white-tailed deer crossing success and crossing decision for Alberta, Canada, and Montana, USA, 2016–2018.

Figure S1. Depiction of the experimental study design used to evaluate the effects of fence modifications on pronghorn, mule deer, and white-tailed deer fence-interaction behaviors in Alberta, Canada, and Montana, USA, 2016–2018.

Figure S2. Mean probability and 95% confidence limits for the covariate area for group crossing success by pronghorn in Alberta, Canada, and Montana, USA, 2016–2018.

Figure S3. Mean probability and 95% confidence limits for significant covariates for crossing success (top row) and crossing decision (bottom row) by individual mule deer in Alberta, Canada, and Montana, USA, 2016–2018.

Figure S4. Mean probability and 95% confidence limits for significant covariates for crossing success (top row) and crossing decision (bottom row) by individual white-tailed deer in Alberta, Canada, and Montana, USA, 2016–2018.