




Original Article

To Jump or Not to Jump: Mule Deer and White-Tailed Deer Fence Crossing Decisions

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ABSTRACT Modified fencing structures have been recommended with the intention of enhancing ungulate movement. Ungulates such as mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) typically negotiate fences by jumping over them. We examined 2 fine-scale fence crossing decisions to determine factors influencing 1) crossing success and 2) the mode of crossing by 2 sympatric deer species. From 2010 to 2016, we used remote cameras along fence lines in 2 study areas—Canadian Forces Base Suffield in southeastern Alberta, Canada, and The Nature Conservancy’s Matador Ranch in north-central Montana, USA—that captured images of deer–fence interactions before and after fence modifications were installed. We used logistic regression to model the probability of deer successfully crossing a fence and mode of crossing (jumping over vs. crawling under) based on fence characteristics and demographic factors. We documented 486 crossing attempts, of which 313 were successful (64.4%), indicating that pasture fences acted as a semipermeable barrier to deer. Of these 313 successful attempts, 152 crawled under the fence (48.6%) as opposed to jumping over it. We documented behavioral differences in mode of crossing between species when successfully crossing a fence. Results indicate that deer are selecting known crossing sites at broad scales as places to negotiate fences, and when assessing finer scale decisions at these sites, white-tailed deer seemed to acclimate better than mule deer to our imposed changes (switched from crawling under to jumping over the fence). Though sample size was low in terms of use at modified fence sites, we recommend visually inconspicuous modifications (such as clips to increase the bottom wire height as opposed to goat-bars) when implementing pasture fencing that was friendlier for deer. We also recommend modifications be implemented strategically; placement of modifications may be just as important to consider as the modification type. © 2018 The Wildlife Society.

KEY WORDS barrier, fence, modification, mule deer, *Odocoileus hemionus*, *Odocoileus virginianus*, white-tailed deer.

Wildlife need to move, whether daily or seasonally, to locate food and other resources. If movement is hindered, overall fitness can be affected directly and indirectly (Harrington and Conover 2006, Sawyer et al. 2013). Anthropogenic, biotic, and abiotic conditions can hinder movement by acting as complete or semipermeable barriers (Crooks and Sanjayan 2006). Consequently, there is growing appreciation for the benefits of enhancing connectivity for wildlife across

anthropogenic barriers, such as roads, railways, cities, and fences (Crooks and Sanjayan 2006, Beckmann et al. 2010, Sawyer et al. 2013).

Fences can represent complete or semipermeable barriers to wildlife movement. For example, 8-foot (2.4-m) page-wire fences are used as complete physical obstructions to large wildlife, such as deer (*Odocoileus* spp.) and elk (*Cervus canadensis*); such fences prevent animals from crossing over, through, or under them, thus forcing animals to cross elsewhere (Huijser et al. 2009, Sawyer et al. 2013). Alternatively, common barbed-wire fences associated with roads and pastures managed for livestock are often semipermeable. They allow some form of negotiation yet make movement more difficult, but not impossible, by fragmenting the landscape (Harrington and Conover 2006, VerCauteren et al. 2006, Sawyer et al. 2013).

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Both impassable and semipermeable fences can have direct (i.e., mortality and injuries) and indirect (obstacles to resources, alter responses to variable conditions) effects on wildlife. Harrington and Conover (2006) reported 0.14 mortalities/km of fencing per year in mule deer (*Odocoileus hemionus*; 60.5% of mortalities), pronghorn (*Antilocapra americana*; 23.7%), and elk (15.8%). In their study, mortalities were most often caused when an individual's leg(s) became caught between the top 2 wires. In addition, juveniles were more likely to get caught and die in fences than adults. Jones (2014) demonstrated significant hair loss and resulting scarring on the neck, back, and rump of pronghorn crossing under fences and postulated the potential negative ramifications of such injuries. Fences indirectly affect an animal's fitness by limiting daily and seasonal movements, thereby preventing access to additional resources. For example, Seidler et al. (2015) found a length of nonwildlife-friendly fencing (woven-wire sheep fencing) that completely impeded 89% of radiocollared migrating pronghorn from crossing a fence-road complex in Wyoming, USA. The other 11% were able to migrate across this fence-road complex only after extensive searching and locating a stretch of wildlife-friendlier fencing.

Despite the previous focus on effects of fencing on wildlife along transportation corridors, there is a growing interest in the effects of pasture fencing on ungulates and other wildlife, given their widespread nature (Poor et al. 2014). Deer movement in these increasingly converted and fragmented landscapes depends on decisions made when encountering and negotiating fences and can be influenced by various fence characteristics and demographic factors. Physical characteristics associated with fences, such as bottom and top wire heights on barbed-wire fencing, could alter ungulate crossing decisions (mode of crossing hereafter). VerCauteren et al. (2010) found a positive, linear relationship between fence height and white-tailed deer (*O. virginianus*) deterrence of jumping over fencing until it reached 100% deterrence at 2.4 m. Harrington and Conover (2006), however, observed mule deer mortalities on fences that were just over 1 m tall.

To decrease both wildlife mortality and fence repair costs by landholders, multiple agencies have proposed various fence-modification techniques to allow for easier passage by wildlife, including deer (Paige 2012, 2015). These modifications include replacing the bottom barbed wire with smooth wire, using polyvinyl chloride pipe (hereafter, goat-bars) to raise the height of the bottom wire or lower the height of the top wire, using seasonal electrical fencing, installing visible markers, and raising the bottom wire to the same level as the second wire from the ground (Paige 2012, 2015). In this paper, we refer to any fencing that has specific modifications implemented with the goal to allow permeability to wildlife as wildlife-friendlier fencing. This includes any modifications that alters the top or bottom wires to allow greater permeability for wildlife. Demographic factors such as species, age, and sex may also influence how an individual animal interacts with fencing. For example, a juvenile's ability to navigate fences may differ from adults as a result of their smaller body size and lack of experience (Riley and

Dood 1984, VerCauteren et al. 2006), or they may not be physically capable of jumping fences at heights comparable to adults. In addition, we may observe a difference in fence interactions between males and females due to different body sizes and the presence or absence of antlers. We are unaware of any studies that have assessed how deer interact with various fence modifications and their influence on crossing success and mode of crossing.

Here, we examine fence characteristics and demographic variables that influence mule and white-tailed deer-fence interactions. As part of a study examining the effectiveness of fence modifications at enhancing fence permeability for pronghorn (Jones et al. 2018), sufficient data were collected to examine fine-scale fence interactions (crossing success and mode of crossing) made by these sympatric deer species (Fig. 1). First, we tested whether individuals from both deer species were successful or unsuccessful at negotiating barbed-wire fences (fine-scale interaction) and, if successful, the individual's mode of crossing the fence (fine-scale decision). We hypothesized that as deer approached a fence they would successfully cross the fence 100% of the time and would predominantly do so by jumping over as opposed to crawling under it. We hypothesized that there would be no crossing failures because the top wire on the fence sections within our study sites did not exceed 2.4 m, which is the maximum height a deer can jump (VerCauteren et al. 2010). Secondly, we expected crossing success and mode of crossing to not be influenced by intrinsic and extrinsic factors because, as previously stated, we expected both species of deer to jump over the fence. We predicted fence modifications would not influence crossing successes and mode of crossing because modifications were installed specifically to facilitate pronghorn movement (i.e., alterations to the bottom wire[s]). We expected deer to jump over the fence at the fence panel they successfully cross regardless of the height and modifications present on the bottom wires. Regarding demographic factors, we expected only age, not species, to influence crossing success and mode of crossing. We expected fawns, as opposed to adult males or adult females, to have a more difficult time successfully crossing fences because of their body size; and, when successful at crossing, they would do so by crawling under the bottom wire (Harrington and Conover 2006). Understanding fence crossing behaviors of deer will help inform decisions on the construction of truly wildlife-friendlier fencing guidelines, while also reducing cost and time requirements for repairing fences from deer damage.

STUDY AREA

We studied mule deer and white-tailed deer-fence interactions at 2 different sites in a transboundary region of southeastern Alberta, Canada (AB), and north-central Montana, USA (MT); part of the area referred to as the Northern Sagebrush Steppe (NSS). The 2 study sites included Canadian Forces Base Suffield (CFBS) in AB (50°15'N, -111°10'W) and The Nature Conservancy's Matador Ranch in MT (47°55'N, -108°19'W). The NSS was characterized by flat open plains and rolling hills as a result of glaciation recession and deposits with fluctuating

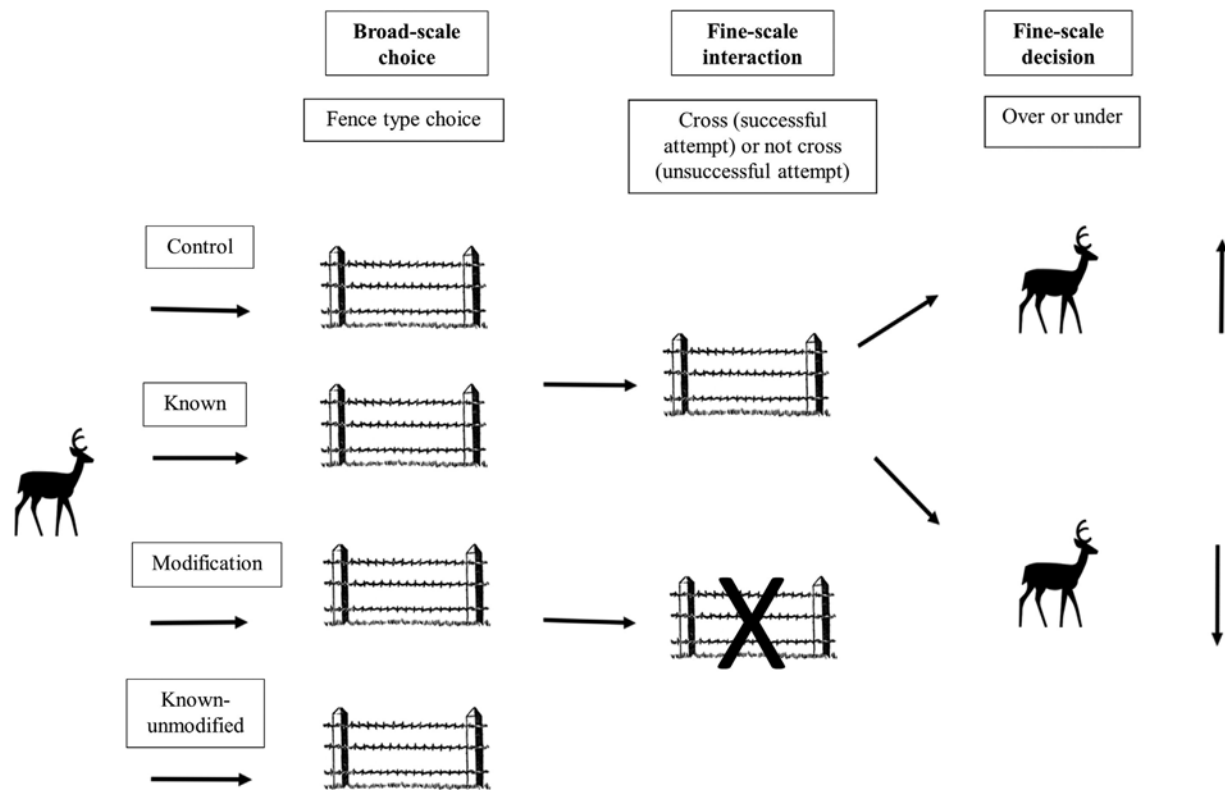


Figure 1. Scale-dependent decisions that deer make when approaching a fence. The broadest-scale choice is which fence section to approach. Finer scale interactions include to 1) cross or not at the selected fence section, and 2) whether to jump over or crawl under a fence section.

annual temperatures (Mitchell 1980). This region was made up of badlands (steep slopes and sparse vegetation) and deep coulees (valley or drainage zone), exposed and created by rivers and other waterways (Mitchell 1980). The NSS was considered semiarid, receiving on average 327 mm of precipitation annually, as measured by the agricultural Canada research substation in southern AB, 1940–1970 (Barrett 1984). During the 2010–2016 study period in southeastern AB, daily snow depth ranged from 0 to 30 cm. (Environment Canada 2018). During the 2015–2016 study period in north-central MT, daily snow depth ranged from 0 to 12.7 cm. (National Oceanic and Atmospheric Administration [NOAA] 2018). Both study sites were native sagebrush steppe habitats characterized by species such as western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*), needle-and-thread (*Hesperostipa comata*), June grass (*Koeleria pyramidata*), silver sagebrush (*Artemisia cana*), big sagebrush (*A. tridentata*), western snowberry (*Symphoricarpos occidentalis*), cactus (*Opuntia polyacantha*), and rose (*Rosa* spp.; Barrett 1984, Poor et al. 2012).

METHODS

Experimental Design

We used photos of deer, captured by trail cameras during a study to assess fence modification effects on pronghorn movement, to evaluate fence crossing success and mode of crossing by deer from 2010 to 2016. We placed remote trail cameras (predominately Reconyx© PC650, PC800 or PC900;

Reconyx, Holmen, WI, USA) along fence lines and mounted to wooden fence posts or custom-built stands for metal T-bar posts. Camera heights were variable at the Matador Ranch and positioned to most efficiently capture wildlife–fence interactions along the fence panel of interest. CFB Suffield had 53 cameras during the 2015–2016 year, which we set with a mean height of 78.06 cm and standard error of 1.40 cm. The mean distance between posts was $14.08 \text{ m} \pm 0.31 \text{ m}$ and $4.84 \text{ m} \pm 0.19 \text{ m}$ at CFBS and Matador, respectively. Most fences in our study site were 3 or 4 strands and did not exceed 1.28 m in height. 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 sections (i.e., the portion of fence between 2 fence posts). We set cameras in AB to rapid fire, capturing 3 images/trigger with no delay between triggers. In MT, we set cameras to rapid fire, capturing 5 images/trigger with a 1-second delay. We set sensitivity at high but adjusted it at different times of the year to reduce false triggers (e.g., from moving grass during the summer).

We used the study design already in place for the pronghorn project, which entailed a Before-After-Control-Impact (BACI) experimental design (Underwood 1997). During the first 2 winters (2010–2011 and 2011–2012) at CFBS, we employed a complete randomized BACI design, where we placed cameras along randomly selected fence sections, of which we randomly selected 50% to have a modification installed. We monitored all cameras initially for

a period of time with no modifications to the fence section (premodification period) and measured the bottom and top wire heights. Height of bottom wire ranged from 43.18 cm to 62.23 cm with a mean of 49 cm. After this period, we installed modifications at half the sites at a height of 46 cm and monitored all cameras for a period of time (postmodification period). When it appeared that pronghorn were not selecting the modified fences, but instead crossed at well-used and established trails, we changed the study design in the winter of 2012–2013 at CFBS henceforth and implemented the new design at the Matador Ranch through the remainder of the study (Jones et al. 2012).

As the basis for the new design, we deployed cameras at and next to these well-used and established wildlife-crossing fence sections (Jones et al. 2018). Pre-camera-deployment surveys were used to determine established wildlife crossing locations, identified through a combination of fecal pellets, hair strands observed on fencing, and trampled ground. We termed these locations as a known crossing site and the entire panel as a known fence section. The 2 adjacent sections to a known fence section were included as part of the experiment (see Jones et al. 2018 for depiction of camera placement). One of the adjacent fence sections was left unaltered and acted as the control (hereafter, control fence section). We modified the other adjacent fence section with 1 of the 3 fence modifications (hereafter, modification fence section). We termed this grouping of the known, control, and modification fence sections as a set. We deployed a camera at each fence section, so that each set had 3 cameras associated with it. We first monitored all cameras with fence sections unaltered and no modifications, and we measured the bottom and top wire heights (premodification period). Bottom wire heights at CFBS for modification fence sections ranged from 17.78 cm to 57.15 cm with a mean of 32.87 cm. At the Matador, bottom wire heights at modification fence sections ranged from 10.16 cm to 39.37 cm with a mean of 15.29 cm. After a certain length of time, we lowered the bottom wire at these known fence sections so that pronghorn (and other wildlife) could not easily cross under them, while at the modification fence sections, we installed a modification to a height of approximately 46 cm (see Table S1 in Supporting Information [online] for no. of days monitored during the pre- and postmodification period). We termed the time period after the fences were altered or the modification was added as the postmodification period. We did not change the control fence sections during the postmodification period.

Lastly, only during the winters of 2013–2014 and 2014–2015 at CFBS, we placed additional single cameras at known fence sections that acted as a second type of “control” (which will now be referred to as the known-unmodified fence section to differentiate from the known fence sections that were altered during the postmodification period) because these sections were left unaltered during the postmodification period. The known-unmodified fence sections were stand-alone sections and not a part of a set (known, control, and modification fence sections). Slight variations between each study site and between years at each site regarding length of camera deployment, modifications

used, camera numbers, and length of time during premodification and postmodification periods are described in Supporting Material, available online.

Photo Processing Protocol and Database Development

We followed standardized protocols on deer–fence behaviors and interactions captured from trail cameras to populate subsequent databases using a photo classification protocol developed by Alberta Conservation Association (Jones et al. 2018). We identified a potential fence–interaction zone within the camera view at each fence section, which extended from the camera to adjacent post and 2–3 m on each side of the fence line. We did not record deer–fence interactions if an animal crossed outside of this identified zone, even if the deer was successful. Within the interaction zone, at a given fence section, we recorded the number of failed attempts per individual (coded as 0) and successful crosses (coded as 1), which defined the response variable for subsequent crossing success analyses. For successful crosses, we recorded whether an individual jumped over the fence (0) or crawled under the bottom wire (1). This mode of crossing defined the response variable for subsequent crossing decision analyses.

We defined an event as a set of images with ≥ 1 animals interacting with the fence. An event may involve an individual or group of animals, contain any number of photos, and last any length of time (seconds to minutes), but ends when 15 minutes has passed between an individual or group fence interaction and the next individual or group fence interaction at the same camera. An attempt occurred when an individual approached a fence, oriented its body perpendicular to the fence, approached within 2 body lengths of the fence, and lowered its head to attempt to cross or positioned its weight on its legs as if to jump the fence. The attempt ended when the individual moved away from the fence, oriented its body more parallel to the fence than perpendicular (failed attempt), or successfully crossed to the other side (successful cross). If the attempt was successful, we further categorized each successful cross as jumping over, crawling under, or going through the fence (only one animal crossed through the fence and it was left out of analysis). If we could not determine the mode of crossing, we did not record the interaction (10 unknown events). Group sizes for deer were relatively small (ranged from 1 to 5 with a mean group size of 1.3) and allowed us to keep track of individuals during each event. In addition to recording response variables for crossing rates and mode of crossing, we recorded fence characteristics and demographic factors for each event. Variables used in analyses included a term for the interaction of fence section type and time period (i.e., control premodification, control postmodification, known premodification, known postmodification, etc.), the bottom wire and top wire height (cm), species (mule deer or white-tailed deer), sex–age class (adult female, adult male, and fawn unknown sex), and number of crossing attempts for each individual.

Data Analysis

We aimed to assess 2 behavioral responses (crossing success and mode of crossing) by deer when interacting with fences

and not to evaluate the effectiveness of the modifications (designed for pronghorn) at facilitating movement across fences by mule and white-tailed deer. For that reason, we used logistic regression to evaluate crossing success and mode of crossing separately from both the premodification and postmodification period data sets (Hosmer and Lemeshow 2000). To maximize sample size and reduce the probability of a Type I or II error, we pooled data across both study sites. We first screened the aforementioned continuous variables for collinearity using Pearson's product-moment correlation index with $r > |0.6|$ as the threshold cut-off value. We further screened variables by conducting univariate analysis on retained variables following recommendations by Hosmer and Lemeshow (2000). Variables with $P > 0.05$ were deemed insignificant and discarded for further analysis. We modeled the effects of retained variables on our 2 response variables using generalized linear models with a logit link (i.e., logistic regression). We used Akaike's Information Criteria (AIC) to evaluate model support in predicting crossing success and mode of crossing (Burnham and Anderson 2002). We ranked models using the stepAIC function in the Program R library MASS. We report only the top-ranked logistic regression model for both crossing success and mode of crossing. For significant categorical variables with >2 levels (e.g., fence section type–period interactive term) we used the lsmeans package to correct for multiple comparisons (Tukey test). We evaluated model goodness of fit using Receiver Operator Curves (ROC) where scores >0.9 indicate excellent model fit, 0.8–0.9 good model fit, 0.7–0.8 adequate model fit, 0.6–0.7 satisfactory model fit, and 0.5–0.6 indicate a model that barely explains more than random chance in binomial outcomes (Hosmer and Lemeshow 2000). Finally, we report odds ratios, for crossing success and mode of crossing, indicating the successful crossing rates and crossing

under rates. We also include in this table the percent change between pre- and postmodification periods. We conducted all analyses using Program R 3.4.1 (R Core Team 2013).

RESULTS

We recorded 486 occurrences (we had 10 unknown events where we could not determine mode of crossing and so left them out of analysis because they had little influence on crossing success rate) of individual mule deer and white-tailed deer–fence interactions across AB and MT, which included 305 adult females, 141 adult males, and 40 fawns. Of those, 313 individuals crossed the fence successfully (64%), where 152 chose to cross underneath (49%), and 161 chose to jump over (51%). Of these individuals, 295 were mule deer (61%) and 191 (39%) were white-tailed deer, with the majority of white-tailed deer primarily in the AB study area. The majority of our deer–fence interactions occurred at known fence sections during both the pre- and postmodification time period (58%), followed by control fence sections (16%), known-unmodified (11%), clips (7%), smooth wire (7%), and goat-bar sites (2%).

Crossing Success

Bottom wire height and the top wire height coefficients were correlated ($r = 0.51$), but not strongly enough to prevent inclusion in our models. Otherwise, the remaining variables were uncorrelated. All covariates were deemed significant ($P < 0.05$) in influencing crossing success of deer through our univariate analysis. The top ranked model included the interaction variable of fence section type and pre- or postmodification time period, bottom wire height, species, sex–age class, and number of attempts (Table 1). The final model provides insight into predicting rates of success of deer crossing fences based on fence characteristics and

Table 1. Logistic regression results from the top model of crossing success for (1 = cross, 0 = failed to cross) mule deer and white-tailed deer (WTD) in the Northern Sagebrush Steppe region of Montana, USA, and Alberta, Canada, 2010–2016. For each variable, the beta (β) coefficient estimate, standard error (SE), z , P , the odds ratio (e^β), and percent difference are reported. The reference variables are as follows: mule deer, female, and control fence section. “NA” is not applicable.

Variables	β	SE	z	P	e^β	% difference ^a
Intercept	−0.07	0.62	−0.11	0.91	0.94	NA
Species—WTD	0.98	0.29	3.44	<0.01	2.66	166
Sex—Age—Adult male	−0.86	0.25	−3.44	<0.01	0.42	−58
Sex—Age—Fawn	0.65	0.47	1.38	0.17	1.92	92
No. of attempts	−1.01	0.16	−6.34	<0.01	0.36	−64
Bottom wire height	0.02	0.01	1.51	0.13	1.02	2
Premodification						
Known	0.44	0.49	0.90	0.37	1.56	56
Known-unmodified	0.67	0.60	1.11	0.27	1.94	94
Smooth wire	0.91	0.69	1.33	0.19	2.48	148
Clip	0.84	1.24	0.68	0.50	2.31	131
Goat-bar	−0.45	1.51	−0.30	0.76	0.64	−36
Postmodification						
Control	0.58	0.57	1.01	0.31	1.78	78
Known	−0.24	0.50	−0.48	0.64	0.79	−21
Known-unmodified	15.44	691.07	0.02	0.98	5,080,905	5,080,904
Smooth wire	−0.53	0.71	−0.75	0.45	0.59	−41
Clip	2.06	0.89	2.31	0.02	7.83	683
Goat-bar	−2.89	1.25	−2.31	0.02	0.06	−94

^a The percent difference was calculated as $1 - e^\beta$ converted to percentage in comparison to the reference variable.

demographic factors. As bottom wire height increased, deer were 2% more likely to cross successfully for every 1-cm increase in height, though this was not statistically significant ($P=0.13$). Overall, we found that white-tailed deer were 166% more likely to cross successfully than mule deer ($P < 0.001$) and that males were 58% times less likely to cross successfully compared with females ($P < 0.001$). We found that as the number of attempts increased, the likelihood of deer crossing successfully decreased by 64% ($P < 0.001$; Table 1). The multiple comparison of the variable fence-section type by time period revealed no significant differences between any of the categories and all were placed in the same group (Table S2 in Supporting Information available online). The top model had a ROC score of 0.81, confirming good model fit and discrimination between successful and unsuccessful crosses. Relationships among height of bottom

wire and probability of crossing successfully varied among age and sex classes and by species (Fig. 2a and b).

Deer crossing-success frequencies varied by experimental period (pre- or postmodification), fence section classification, and species (Table 2). We observed a slight change in use of the various fence panel types during the postmodification period (Fig. 3). Sixty-seven percent of all successful events during the premodification period were observed at known fence sections (Table 2). During the postmodification period, only 49 deer out of 131 (37%) crossed at known fence sections (Table 2). We observed a change in crossing success at the modification fence sections after installation of the 3 modifications. At fence sections where clips were installed on the bottom wires, deer crossing success increased 33%. At fence sections where goat-bars were installed, deer were 94% less likely to cross successfully

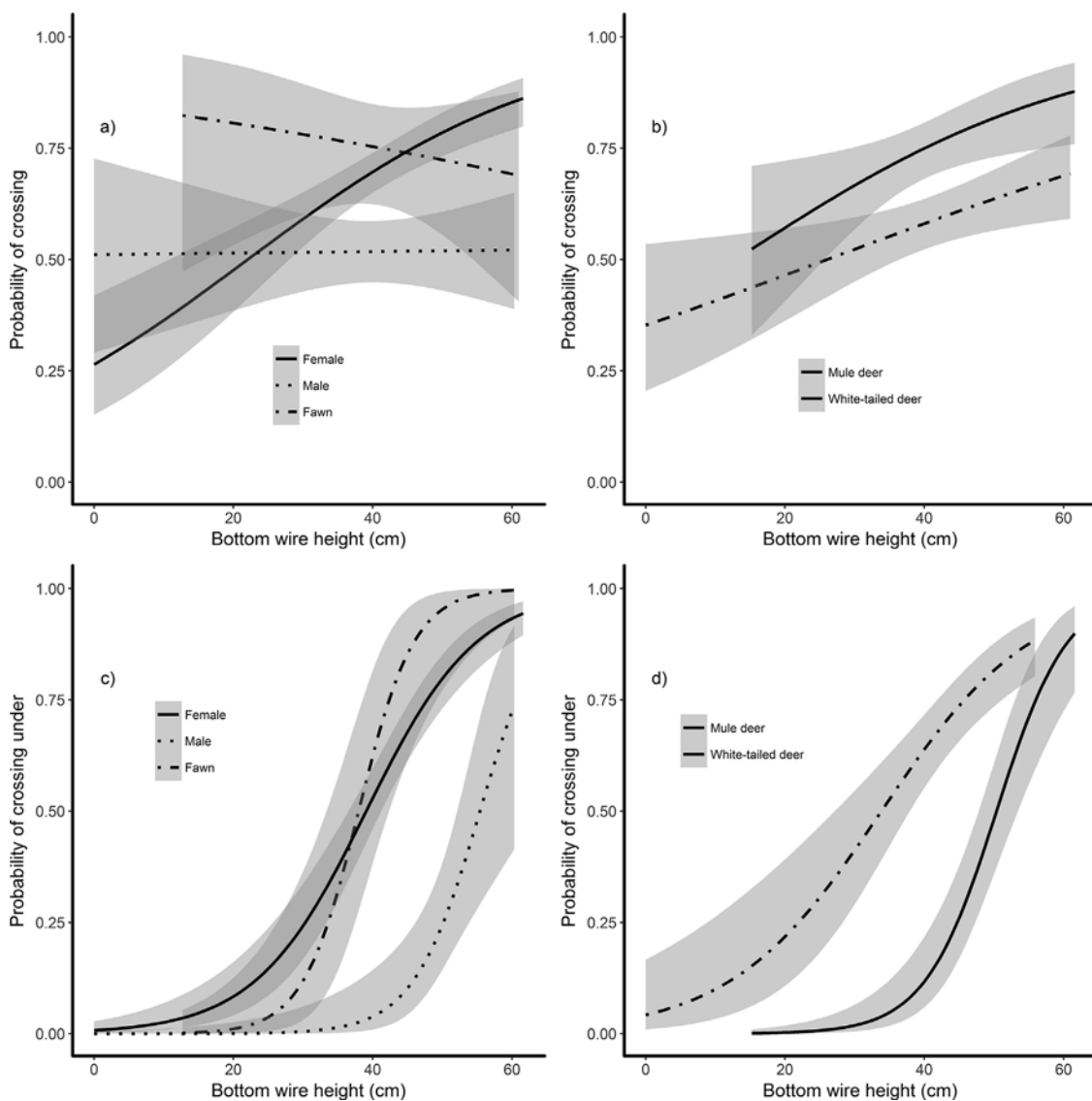


Figure 2. Probability of crossing success and mode of crossing for mule deer and white-tailed deer across the Northern Sagebrush Steppe, Alberta, Canada, and Montana, USA, 2010–2016. As the bottom wire height increases, the probability of crossing a fence successfully neither increases nor decreases for males, increases for females, and slightly decreases for fawns (panel a). The probability of crossing success increases for both white-tailed deer and mule deer as the bottom wire height increases (panel b). As the bottom wire height increases, the probability of crossing under a fence increases for males, females, and fawns (panel c). The probability of crossing under also increases for white-tailed deer and mule deer as the bottom wire height increases (panel d).

Table 2. Odds ratio results for crossing success for mule deer and white-tailed deer in the Northern Sagebrush Steppe region of Montana, USA, and Alberta, Canada, 2010–2016. The pre- and postmodification period data for each variable are shown. Data are separated by total events, unsuccessful attempt (US), successful attempt (S), probability of crossing successfully, change in probability between pre- and postmodification period, and the odds of crossing successfully. “NA” is not applicable.

Variables	Total pre	Total post	No. US ^a pre	No. US post	No. S ^b pre	No. S post	<i>P</i> (cross) pre	<i>P</i> (cross) post	% change	Odds pre	Odds post
Control	31	48	16	11	15	37	0.48	0.77	29	0.93	3.36
Known	189	91	67	42	122	49	0.65	0.54	-11	1.82	1.17
Known-unmodified	41	11	14	0	27	11	0.66	1.00	34	1.93	NA
Smooth	19	14	5	8	14	6	0.74	0.43	-31	2.8	0.75
Clips	5	29	2	2	3	27	0.60	0.93	33	1.5	13.5
Goat bar	2	6	1	5	1	1	0.50	0.17	-33	1	0.2
Total	287	199	105	68	182	131	0.63	0.66	3	1.73	1.93

^a US—Unsuccessful attempt.

^b S—Successful attempt.

and their probability of successfully crossing decreased 33%. The probability of deer successfully crossing decreased 31% when smooth wire was added (Table 2). However, our sample size at fence sections that received a modification was small in terms of use (Table 2).

Crossing Decision

Univariate analysis determined that the number of crossing attempts had an insignificant ($P > 0.05$) effect on mode of crossing by deer and removed it from further analysis. The top model included bottom wire height, top wire height, species, and sex–age class, and provided insight into predicting the mode of crossing by deer based on these factors (Table 3). As the height of the bottom and top wire increased, deer were found to be 14% ($P < 0.001$) and 5% ($P = 0.005$), respectively, more likely to cross under a fence for each 1-cm increase. We also found that white-tailed deer were 95% less likely to go under compared with mule deer ($P < 0.001$) and that males for both species were 96% less likely to cross under compared with females ($P < 0.001$). The

multiple comparison for sex–age class mode of crossing revealed that females and fawns were placed in the same group separate from males, indicating that fawns behaved similarly to, and males behaved differently from, females (Table S3 in Supporting Information available online). The top model had a high ROC score of 0.92, indicating excellent model fit and discrimination between a deer crawling under or jumping over a fence. The probability of crawling underneath relative to the height of bottom wire varied by demographic factors (Fig. 2c and d).

The probability of deer crawling under at known fence sections declined from 72% during the premodification period to 25% during the postmodification period (Table 4). After exploring these data, we observed a difference in mode of crossing by species, which indicates that during the postmodification period, mule deer were 68% more likely to crawl under fencing while white-tailed deer were 85% more likely to jump over fencing (Table 4). When we separated mule deer and white-tailed deer, we observed a difference in behavior between the 2 species at known fence sections. The probability of white-tailed deer crawling under a fence decreased from 66% to 18% at known fence sections (Table 4). White-tailed deer were still attempting to cross at known fence sections during the postmodification period (35 events premodification and 39 events postmodification); however, their crossing behavior switched from crawling under to jumping over (Table 4). Mule deer, on the other hand, did not appear to alter their behavior as consistently as did white-tailed deer. At known crossing sections, mule deer use declined by 38% from 87 out of 134 (65%) successful crosses during the premodification period to 10 out of 37 events (27%) successful crosses during the postmodification period (Table 4). Mule deer, instead of switching their behavior to jump over the fence, either attempted to cross at another fence section or did not attempt to cross at any of our monitored fence sections. Clips received the most use by mule deer out of all monitored fence sections during the postmodification period with 16 out of 37 (43%) successful crossing events where 81% chose to crawl under (Table 4). Mule deer were more likely to crawl under at clip fence sections during the postmodification period than they were at known fence sections during the premodification period (Table 4).

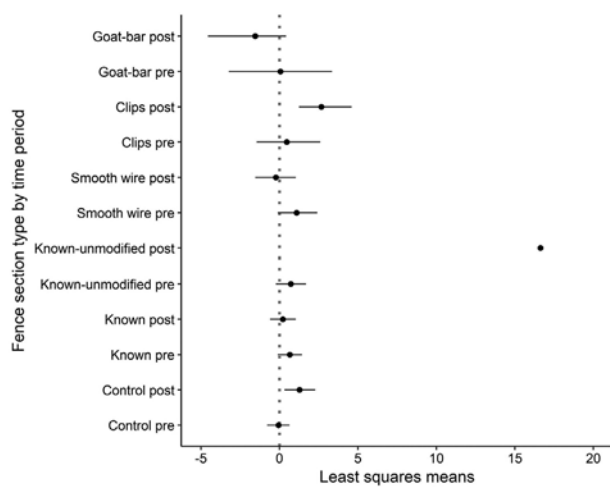


Figure 3. Mule deer and white-tailed deer use of fence section type during the pre- and postmodification periods in the Northern Sagebrush Steppe, Alberta, Canada, and Montana, USA, 2010–2016. The x-axis depicts the least squares means and horizontal lines indicate confidence limits for each variable. Results indicate that goat bars, smooth wire, and known fence sections show a decline in crossing success, whereas clips, known-unmodified, and control fence sections show an increase in crossing success.

Table 3. Logistic regression results from the top model for model of crossing (1 = under, 0 = over) for mule deer and white-tailed deer (WTD) in the Northern Sagebrush Steppe region of Montana, USA, and Alberta, Canada, 2010–2016. For each variable, the beta coefficient estimate (β), standard error (SE), z , P , the odds ratio (e^β), and percent difference are reported. The reference variables are as followed: mule deer, female, and the control fence section.

Variables	β	SE	z	P	e^β	% difference ^a
Intercept	-6.56	1.85	-3.54	<0.01	<0.01	<-99
Species—WTD	-2.92	0.42	-6.91	<0.01	0.05	-95
Sex—Age—Adult male	-3.24	0.51	-6.36	<0.01	0.04	-96
Sex—Age—Fawn unknown	-0.18	0.64	-0.28	0.78	0.84	-16
Bottom wire height	0.13	0.02	6.42	<0.01	1.14	14
Top wire height	0.05	0.02	2.79	0.01	1.05	5

^a The percent difference was calculated as $1 - e^\beta$ converted to percentage in comparison to the reference variable.

DISCUSSION

When a deer approached a fence, we expected a 2-fold decision process would occur at the fine scale—an interaction (either successful or unsuccessful crossing attempt) followed by a decision as to the mode of crossing (either crawling under or jumping over). We expected that an individual's intent was to cross the fence by jumping over and as a result they would be successful each time. Our findings demonstrate that this is a simplistic view of how deer negotiate fences. Our lower than anticipated crossing success rates indicate that pasture fencing across the landscape can be considered a semipermeable barrier to deer movement. In addition, we found that almost half of the successful crosses occurred by deer crawling under the bottom wire. The divergence from the simplistic view of deer–fence interactions (i.e., deer walk up to a random fence section and jump over) occurred because of unexpected decisions made by deer, not only at the 2 fine scales examined, but first at a broader scale, and then secondly, with unanticipated behavioral decisions at the species level as to mode of crossing a fence.

We did not expect deer to select where to cross a fence (broad-scale choice), but instead expected deer to approach

the closest fence section and then make a decision at finer scales. Our results indicate that deer, similar to pronghorn, are using known crossing sites as places to negotiate fences, indicating that deer are also making choices at the broad-scale similar to pronghorn (Jones et al. 2018). The known crossing sites have bottom wires that are significantly higher than adjacent fence panels, which facilitated movement under the fence as opposed to over (Jones et al. 2018). The bottom wire height at these sites explained why we observed a high percentage of successful crossings by crawling under. In addition, the use of known crossing sites is an intriguing result because these sites were originally identified as pronghorn crossing locations and not deer. Therefore, it appears that these crossing sites are used by multiple species and essentially form communal crossing sites.

We expected mule deer and white-tailed deer would display congruent behaviors regarding their interactions with fences and therefore have similar crossing success rates and similar choices in mode of crossing. However, our results illustrate a divergence in fence interactions between the 2 species. White-tailed deer had greater overall successful crossing rates compared with mule deer. This was especially evident

Table 4. Odds ratio results for mode of crossing for mule deer and white-tailed deer in the Northern Sagebrush Steppe region of Montana, USA, and Alberta, Canada, 2010–2016. The pre- and postmodification period data for each variable are shown. Data are separated by total events, jumping over, crawling under, probability of crawling under, change in probability between pre- and postmodification period, and the odds of crawling under. “NA” is not applicable.

Species	Fence type	Total pre	Total post	No. over pre	No. over post	No. under pre	No. under post	P (under) pre	P (under) post	% change	Odds pre	Odds post
Combined	Control	15	37	13	35	2	2	0.13	0.05	-8	0.15	0.06
	Known	122	49	34	37	88	12	0.72	0.25	-47	2.59	0.32
	Known-unmodified	27	11	7	5	20	6	0.74	0.55	-19	2.86	1.20
	Smooth wire	14	6	11	2	3	4	0.21	0.67	46	0.27	2.00
	Clips	3	27	3	13	0	14	0.00	0.52	52	0.00	1.08
	Goat bar	1	1	1	0	0	1	0.00	1.00	100	0.00	NA
	Total	182	131	69	92	113	39	0.62	0.30	-32	0.57	0.42
Mule deer	Control	10	4	9	3	1	1	0.10	0.25	15	0.111	0.333
	Known	87	10	22	5	65	5	0.75	0.50	-25	2.955	1.000
	Known-unmodified	26	2	7	0	19	2	0.73	1.00	27	2.714	NA
	Smooth wire	10	5	7	1	3	4	0.30	0.80	50	0.429	4.000
	Clips	0	16	0	3	0	13	NA	0.81	NA	NA	4.333
	Goat bar	1	0	1	0	0	0	0.00	NA	NA	0.000	NA
	Total	134	37	46	12	88	25	0.66	0.68	2	1.913	2.083
White-tailed deer	Control	5	33	4	32	1	1	0.20	0.03	-17	0.250	0.031
	Known	35	39	12	32	23	7	0.66	0.18	-48	1.917	0.219
	Known-unmodified	1	9	0	5	1	4	1.00	0.44	-56	NA	0.800
	Smooth wire	4	1	4	1	0	0	0.00	0.00	0	0.000	0.000
	Clips	3	11	3	10	0	1	0.00	0.09	9	0.000	0.100
	Goat bar	0	1	0	0	0	1	NA	1.00	NA	NA	NA
	Total	48	94	23	80	25	14	0.52	0.15	-37	1.087	0.175

during the postmodification period, where we observed an increase in successful crossing by white-tailed deer while mule deer experienced a decline in crossing success between the 2 periods. We attribute this difference to behavioral flexibility observed in white-tailed deer and not in mule deer when making crossing decisions (i.e., whether to go under or over). During the premodification period, white-tailed deer were equally likely to jump over versus crawl under a fence, while mule deer were more likely to crawl under the fence. Interestingly, we observed a behavioral switch for white-tailed deer during the postmodification period (when we lowered the bottom barbed wire at known fence sections), with approximately 85% of white-tailed deer jumping over the fence, mostly at control and known crossing sections. We did not observe this behavioral switch in mule deer. Results suggest mule deer prefer to crawl underneath, and only jump when forced to (i.e., because bottom wire is too low, larger size of individual, presence of antlers, when facing predation, stress, etc.; Wallmo 1981). We hypothesize 3 reasons for the divergence in behavior. First, mule deer may choose to crawl under a fence to save energy. Although there is little difference in energetic costs between crawling under one fence versus jumping over it, fine-scale daily energetic costs add up over time and could significantly affect deer fitness even when resources are high (Hanley et al. 1989). Secondly, mule deer may crawl under fences as a means of reducing mortality risk. Harrington and Conover (2006) reported that mule deer mortalities were most often caused when an individual's leg(s) became caught between the top 2 wires when attempting to jump over a fence. Crawling under the bottom wire alleviates the potential of getting caught in the top 2 wires when attempting to jump. Lastly, the flexibility white-tailed deer showed when negotiating a fence could be attributed to general habitat-selection differences in prairie systems between 2 species. White-tailed deer are commonly found in, and are adapted to, riparian areas, which are often composed of dense underbrush and downed trees that often facilitate the need to jump. On the other hand, mule deer are primarily located in grassland and sagebrush vegetation types that tend to be open and do not often require the need to jump. Additional research is needed to quantify which of our proposed hypotheses (if any) is the reason that mule deer prefer to crawl under fences and the resulting behavioral differences between the 2 species of deer.

As predicted, we could not distinguish any influence of the 3 modification types on crossing decision, mainly because of the lack of interactions at modified fence sections. Out of 131 successful crosses during the postmodification period, only 34 (26%) occurred between the 3 modification fence sections. However, we did identify interesting trends worth discussing. Once fences were modified, mule deer in particular attempted to cross at fence sections modified with clips and did so by crawling under 80% of the time. We infer that the increased mule deer use at clip sections is due to the raised bottom wire height and the inconspicuousness of the clips themselves. Conversely, visually conspicuous goat-bars were used minimally by deer. Goat-bars have been promoted to provide visibility for wildlife to avoid fence-collisions (Paige

2015). With only 6 fence interactions, goat-bars may be acting as a “visual barrier” deterring deer from attempting to cross. Deer can observe these modifications on the landscape from a distance (i.e., broad-scale) because of the unnatural, anthropogenic quality of the goat-bar. Once deer approach these modified fence sections, however, the goat-bar stimulates a negative response at this finer scale and deter deer before they attempt to cross. Our results indicate that goat-bars do not provide benefits to crossing fences for deer, which also holds true for pronghorn (Jones et al. 2018). We recommend that further research is needed to investigate the time required for deer habituation to varying modifications over time.

MANAGEMENT IMPLICATIONS

Effective wildlife-friendlier fencing is important to consider for both landowners and wildlife because of the cost and time associated with repairing destroyed and damaged fences from wildlife conflicts and implications to sustaining wildlife populations. Before implementing effective wildlife-friendlier fencing, certain factors should be taken into account including target species and the location of wildlife-friendlier fencing. Elk and pronghorn typically are the primary species targeted when designing wildlife-friendlier fences because pasture fences are assumed to be permeable to deer movement due to their ability to jump over these structures. As we have shown, both mule deer and white-tailed deer can benefit from the implementation of wildlife-friendlier fencing recommendations. We recommend the use of clips for wildlife-friendlier fencing and urge against the use of goat-bars. In addition to modification types, the placement of modifications may be just as important as the modification type itself. Multiple species cross fences at known crossing sections, which animals have been shown to habitually use. Individuals learn to repeatedly cross at locations where they have been previously successful. We anticipate that as modifications to fencing continue to be deployed on the landscape to improve connectivity for wildlife that individuals will learn to cross at these passible locations as well, especially when opportunities to cross at known crossing sites may be thwarted.

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SUPPORTING INFORMATION

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

Table S1. Camera deployment information for CFB Suffield and Matador.

Table S2. Multiple comparison table for Fence Section by Time Period for crossing success.

Table S3. Multiple comparison table for mode of crossing by sex-classes.