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Reintroductions of extirpated species are an important global conservation tool, yet can be challenging for wide-ranging species. Fences that help anchor reintroduced species to a target area may have deleterious effects on other wildlife. Here we assessed the wildlife-permeability of six bison drift fence designs at three spatial scales during the reintroduction of a wild herd of plains bison *Bison bison* to a 1200 km² wilderness area in Banff National Park, Canada. First, we used an array of remote cameras along fences to capture wildlife interactions for 12 species, and modelled crossing success, preferred crossing methods and age–sex class tendencies. Second, we investigated fence barrier effects on wildlife movement at the local scale using cameras that were in place before and after fence construction. Finally, we tested for changes in movement rates of migratory elk and resident wolves at the landscape scale using GPS collar telemetry. Our results point to a single fence design that maximizes permeability for several species with diverse crossing strategies, and can be adjusted to contain bison. Wildlife detections increased independently of fence construction in our broader study area. Fence construction did not affect wolf or elk movements and migration at a landscape scale even when fences were deployed to obstruct bison. Our study highlights the important role of wildlife permeable fences in the reintroduction of large mammals such as bison.

Keywords: barrier, bison, connectivity, fence, reintroduction, wildlife movement

Reintroductions of threatened species are frequently used to re-establish extirpated wildlife populations within their historical ranges (Armstrong and Seddon 2008, Soorae 2011, Ripple and Beschta 2012, Corlett 2016). The prevalence of reintroductions has increased as rates of biodiversity and habitat loss escalate (Sarrazin and Barbault 1996, Seddon et al. 2014, Ceballos et al. 2017). Metrics of reintroduction success often focus on both population viability and the long term adoption of the reintroduction zone. Success rates are increased by building on the achievements and failures of previous reintroductions (Malone et al. 2018, Abáigar et al. 2019). This in part has evolved into the applied science of reintroduction biology, which works to provide knowledge to facilitate decisions about the appropriate management strategies used for reintroductions (Taylor et al. 2017). These strategies consider ecological, genetic, bureaucratic factors and an array of reintroduction techniques and tools (Reading et al. 2002). Fences are one such tool that can encourage

newly reintroduced species to explore and ultimately anchor to a target landscape (Hayward and Somers 2012).

The use of fences in conservation can be controversial as they introduce artificial barriers that can constrain natural behaviour (Demarais et al. 2002, Hayward and Kerley 2009, Bull et al. 2018), which may lead to unintended impacts on sympatric wildlife movement, migration and broader ecological dynamics (Harrington and Conover 2006, Jones 2014, Jakes et al. 2018). Yet, fences may be required to prevent excursions of reintroduced species into areas where they are unprotected or not permitted (Morrisette 2000). Moreover, fences can help anchor reintroduced animals to their new range. Drift fences, which are finite sections of wire or wood-rail fence strategically placed to influence animal movement, could be applied to reintroduction projects. Rangeland managers use drift fences to contain cattle and often build drift fences between natural barriers such as steep cliffs and heavy timber (Skovlin 1965). Yet, questions remain about optimal designs of drift and other fences in terms of fence height, bottom wire height (Jones et al. 2018) and type of material (wood versus wire), especially when the objective is to build a fence that is permeable to some but not all species. More generally, little is known about the positive and negative effects of fences (VerCauteren et al. 2007,

Beyer et al. 2016, Jones et al. 2020), especially at the broad scale (Jakes et al. 2018).

After nearly 150 years of extirpation and 18 months on site in a soft-release pasture, 31 wild plains bison *Bison bison* were reintroduced to the backcountry of Banff National Park, Alberta, Canada in July 2018. One objective of this pilot project is to restore the ecological role of this large grazer since many of the park's endemic species have co-evolved with plains bison over millennia and have intimately tied life-histories (Freese et al. 2007, Polak and Saltz 2011, Hale and Koprowski 2018). Evidence of this long term occupation within the front ranges of the rugged Rocky Mountains is widespread, including the archaeological remains of plains bison, their ancient dust wallows, and the oral history of the region's Indigenous peoples (Langemann 2004). The return of these keystone species to the landscape is a globally significant example of using reintroduction to restore ecosystems (Polak and Saltz 2011) and the associated social and cultural benefits encompassed in the undertaking (Weiss et al. 2007).

Bison reintroductions can be challenging due to the animals' propensity for long-range dispersal after release (Simon and Fortin 2019). For example, in 1978 a herd of 28 wood bison *Bison bison athabascae* were reintroduced to Jasper National Park, Canada, but after only two weeks all but one of the animals travelled 300 km beyond the park and had to be recaptured, bringing the project to an end (Davidson and Norcross 1978). Another reintroduction in 1988 saw three yearling wood bison bulls move over 375 km immediately after release in Yukon Territory, Canada (Jung and Larter 2018). Such dispersal movements can be discouraged and site-fidelity increased by holding animals for an extended conditioning period prior to release (Schmitz et al. 2015), by using fire to enhance habitat quality (Shaw and Carter 1990), by herding animals when required (McCann 2015), and through the strategic use of drift fences (Morrisette 2000, Ryckman et al. 2010). Managers in Banff National Park applied all of these techniques: we held animals in a soft-release pasture and conditioned them to an electric fence for 18 months, we enhanced habitat quality in the reintroduction zone with prescribed fire, we herded the bison 15 times in the first year since their release, and we installed eight sections of drift fencing in strategic locations (Heuer 2017).

Fence systems capable of deterring bison are typically robust in rangeland settings (Minard 2003) but can disrupt the free movement of resident and migratory wildlife (Meagher 1989, Jakes et al. 2018). Knowing these challenges, Gates (2006) developed guidelines for a wildlife-friendly bison-fence intended for ranchers grazing domesticated bison on public lands. The Banff reintroduction provided an experimental opportunity to evaluate the permeability of Gates' design and several modified versions using a broad assemblage of wildlife species in a remote wilderness setting. Many of these species had likely never encountered fences before, which offered an ideal assessment of their preference for fence configurations, crossing strategies, and of the impact of fences on their movements. We also evaluated the impact of these same fences on broader ecosystem processes including wildlife movement rates and barrier effects. Given the known and unknown impacts of fences on ecosystem function, Jakes et al. (2018) state that there is an urgent need to assess alternate fence designs and their effect on wildlife.

Our objective was to test the permeability of several fence designs on sympatric wildlife species including a configuration specifically to deflect bison. The analysis was carried out at three scales: 1) site-specific (at fences) using an array of remote cameras to determine permeability of different fence designs, 2) locally around the fences with off-fence cameras and a before–after–control–impact (BACI) design to assess for barrier effects of fences in two configurations: wildlife-permeable and bison-deflection and 3) at a landscape-scale with data from GPS-collared migratory elk, resident wolves and reintroduced bison to assess the effect of fences on species' movements. We hypothesize that (a) crossing rates for the majority of species will be highest at fence designs with the smallest dimensions, and (b) the appearance of fences on the landscape will create some restriction of wildlife movement regardless of permeability.

Material and methods

Study area

The bison reintroduction area extends over 1200 km² across the remote backcountry of Banff National Park, Canada (51.5°N, 115.9°W). The Park is characterized by extremely mountainous terrain, separated by large valleys (Steenweg et al. 2016). The region is typified by alpine and sub-alpine herbaceous meadows, closed Engelmann spruce *Picea engelmannii* and lodgepole pine *Pinus contorta* forests, open expanses of willow *Salix* spp. and birch *Betula* spp. shrubland, and patches of grassland meadow *Festuca* spp. along low southern aspects and valley bottoms. The reintroduction zone encompasses some of the best bison habitat within the park with ample summer and winter forage (Steenweg et al. 2016). The high ridges of the Rocky Mountains naturally contain most of the reintroduction zone and drift fencing was only required in eight locations, collectively spanning 5.6 km and ranging from 98 m to 2.6 km long, around the zone's 145 km perimeter. We used data from the three longest fences along the eastern boundary (Dormer, Panther and Red Deer valleys) as well as from two additional fences constructed specifically for this study which have since been removed (Tyrrell drainage and Ya Ha Tinda ranch). Fence designs varied within each location.

Fence designs

We examined six fence designs of both wire and wooden rail construction (Fig. 1), of which two were recommended by Gates (2006); the other four were modified versions of the Gates design. Gates (2006) recommended using either a 5-wire or a 3-rail fence to contain ranched bison on public rangeland in the province of Alberta. These two designs, which were our tallest, had approximate top wire/rail heights of 150 cm and 140 cm, respectively, and a bottom distance of 50 cm off the ground. We tested four additional designs: 4-wire with either extra height on the bottom or a lower height on top, 2-wire and 2-rail. Wires were spaced 25–30 cm apart, and rails 30–50 cm apart. Such ground-to-bottom-wire height, as
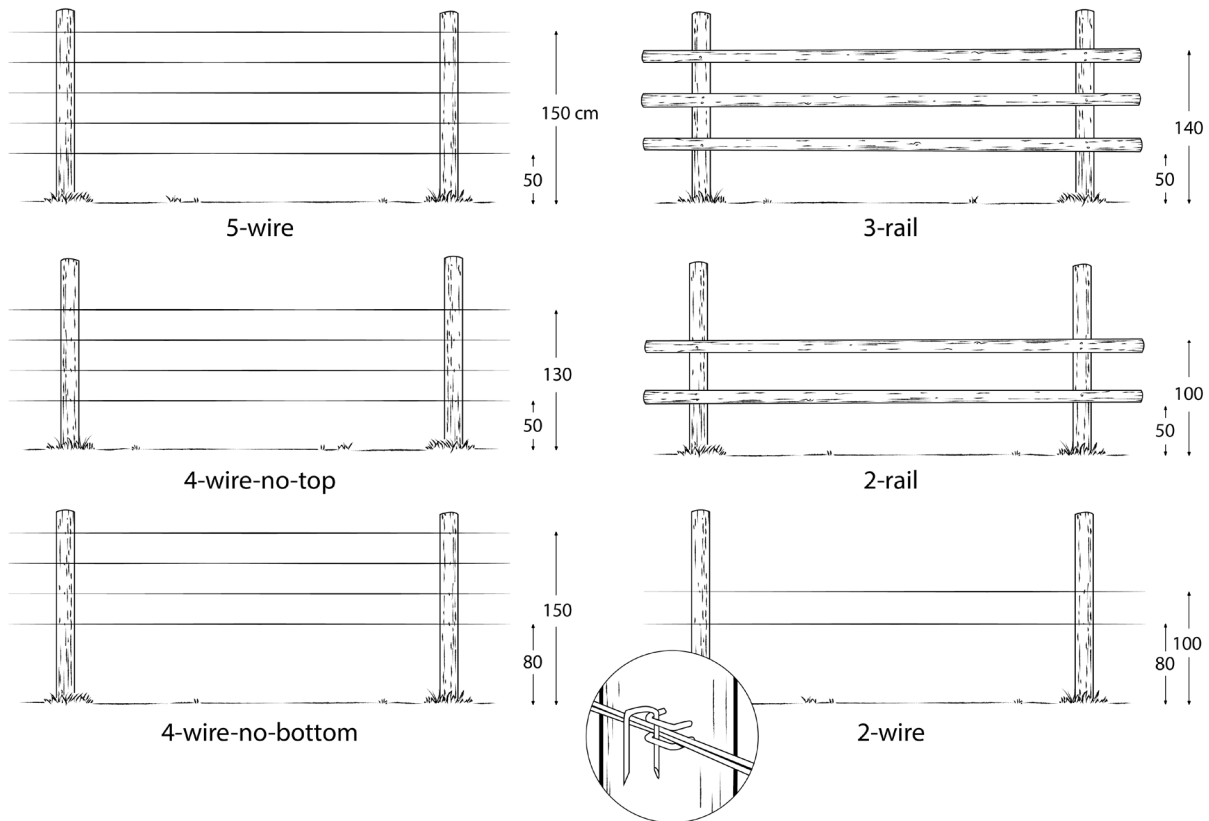
Figure 1. The six fence designs, clockwise from top left: 5-wire, 3-rail, 2-rail, 2-wire, 4-wire-no-bottom, 4-wire-no-top. Height in cm. Inset is of the staple latch system that holds multiple wires depending on the fence configuration (figure adapted from Paige 2008).

well as distance between wires, has been shown to be optimal to reduce ungulate entanglement (Burkholder et al. 2018, Jones et al. 2020). The 2-wire design is a dynamic modification of the 5-wire fence where the top three wires, and bottom two wires, are pinched together (staple latch method in Paige 2015). Logistics surrounding remote backcountry fence locations dictated that post materials were a combination of wood, metal t-posts and live trees. While post spacing was based on Gates (2006) of no more than 4 m apart, both spacing and material ultimately varied based on terrain, ground substrate and tree availability.

Fenceline configurations

Each fenceline contained several fence designs that varied over space and time. We termed these broader fence setups as configurations. We considered three configurations: no fence (pre-construction), wildlife-permeable and bison-deflection. Fences in wildlife-permeable configuration consisted of 2-wire or 2-rail designs that typically occurred at game trails and along distinct wildlife movement routes, and open gates across human use trails. Bison-deflection configuration used 5-wire and 3-rail designs (except for short sections of 2-wire fencing in bighorn sheep habitat high on talus slopes where bison did not travel) and closed gates. We used the 4-wire-no-top configuration on steep slopes where the effective fence height increased with steep terrain (Paige 2008). The switching of configurations between wildlife-permeable and bison-deflection was infrequent (Supplementary material Appendix 1 Table A1).

Site-specific: fence crossing rates and behaviour

We monitored wildlife behaviour at four study fences (Panther, Red Deer, Tyrrell and Ya Ha Tinda) from June 2015 to November 2018 using 34 remote trail cameras (Reconyx, Holmen, WI, USA and UWAY, Lethbridge, AB, Canada). Cameras captured still images, with the exception of 11 cameras which collected video data during the first six months of the study period (comprising 13% of the final dataset). We set still image cameras at high sensitivity to capture five rapid fire images per trigger with no delay between triggers, and video cameras at medium sensitivity to collect 20 s clips. We placed cameras along fences built across pre-existing game trails within our study area. The number of cameras per fence design was as follows: 5-wire: 17 cameras; 4-wire-no-top: 18 cameras; 2-wire: 20 cameras; 3-rail: 12 cameras; 2-rail: 15 cameras; 4-wire-no-bottom: 3 cameras. As fences were switched to different configurations a single camera could monitor more than one fence design over the course of the study. Additional details of the site-specific camera-fence design pairings and observation effort (including adjustments for days-not-working) are located in Supplementary material Appendix 1 Table A2.

We classified images using Timelapse image analysis system (Greenberg et al. 2019). Detections of an individual or group of individuals of the same age–sex classifications separated by more than 10 min, or at different fence designs, were classified as separate events. For example, a group of five animals crossing the fence would count as five events. For each event, we recorded whether an animal crossed the fence,

and if so, whether it was under, over or through the fence. Following classification, we deleted duplicate records from overlapping camera fields of view and pooled data from all four study fences to maximize sample size, similar to other studies (Jones et al. 2020). We analysed the effect of fence design on bighorn sheep *Ovis canadensis*, elk *Cervus canadensis*, mule deer *Odocoileus hemionus*, white-tailed deer *Odocoileus virginianus* and carnivores. We pooled carnivore data due to the low number of detections. Carnivores included black bear *Ursus americanus*, bobcat *Lynx rufus*, cougar *Puma concolor*, coyote *Canis latrans*, grizzly bear *Ursus arctos*, lynx *Lynx canadensis*, red fox *Vulpes vulpes* and wolf *Canis lupus*.

We assessed wildlife behaviour at the fences three ways: we modelled overall crossing success (cross/not-cross), crossing method (over versus under/through) and crossing success based on age–sex effects of ungulates using generalized linear mixed effects models with a logit link (i.e. logistic regression). We included random effects for camera location to account for repeated measures at individual locations. We selected the top model for each dataset by comparing covariate combinations using Akaike's information criterion (AIC) (Burnham and Anderson 2002). We analysed our data here and below using R ver. 3.5.1 (<www.r-project.org>) and the glmmTMB package (Brooks et al. 2017).

To assess the probability of crossing success, we used the number of animals that crossed/did not cross a fence as the response variable, which was akin to the proportion of animals that crossed weighted by the number of animals detected. Explanatory variables were fence design, species/guild and their interaction. We omitted the 4-wire-no-bottom design from crossing success models due to a small sample size and associated convergence issues, and removed two interaction terms (elk:3-rail and bighorn sheep:3-rail) because of low sample sizes (n = 0 and 4 respectively) and convergence issues.

We assessed the effects of fence design on how animals crossed the fence. Our response variable was the number of animals that crossed over versus under/through a fence. Explanatory variables were species, fence material (wire or rail), and fence height (full height [5-wire, 4-wire-no-bottom, 3-rail], reduced height [4-wire-no-top, 2-wire, 2-rail]), and probable two-way interactions between covariates including: Fence material × Guild, and Fence height × Guild (Supplementary material Appendix 1 Table A4). We excluded carnivores from the crossing method models based on their physiological and behavioural predisposition to cross fences at ground-level.

We evaluated the effects of age and sex on crossing success for antlered species by running separate candidate model groups for elk, mule deer and white-tailed deer. Explanatory variables were fence material, fence height and three age–sex classes: adult female, juvenile (yearlings and young of year) and antlered male. We defined an antlered male as any adult male outside of the following pedicled periods: 15 March–15 May for elk, 15 February–15 April for mule deer and 1 February–15 March for white-tailed deer (Metz et al. 2018). We excluded the antlered male: full height category from the analysis because it had zero crossings.

Local scale: probability of detection

We used a BACI design (Stewart-Oaten and Bence 2001, De Palma et al. 2018, Christie et al. 2019) to investigate whether drift fences affected wildlife detection probability at an intermediate spatial scale. We used 19 pre-existing remote trail cameras (exclusive of those used for the site-specific scale analyses) that were part of Parks Canada's broader wildlife remote camera network (Steenweg et al. 2017, Whittington et al. 2019). Of these cameras, 16 were located adjacent to study fences (Dormer, Panther, Red Deer and Tyrrell) at distances ranging from 8.9 m to 416.5 m. Three control cameras were located at much greater distances from the fences (10.6–13.4 km), but within the same drainage and habitat. Depending on the camera, data collection began between June 2010 and December 2015 and ended between September 2018 and October 2019.

To maximize sample size, we merged camera data from the four study fences and grouped species into the following guilds: canid (coyote, red fox, wolf), felid (cougar, lynx), ungulate (bighorn sheep, elk, moose *Alces alces*, mule deer, white-tailed deer) and ursid (black bear, grizzly bear). We omitted sampling days when the associated fence for any camera was in an incomplete phase of construction. Fence construction finished in the spring of 2018, except for the Panther which was finished in spring 2016. For this scale of analysis, the cumulative camera monitoring effort for each configuration was 18 605 days for no fence (pre-construction), 5066 days for wildlife-permeable and 2407 days for bison-deflection.

We selected candidate models to test whether the presence/configuration of fences or the distance of cameras from fences affected detection probability. Again, we analysed the data using generalized linear mixed effects models. We ranked candidate models by AIC following methodology outlined in Whittington et al. (2019), with some updates for this investigation. We defined our response variable as the proportion of active camera sample days on which an animal was detected, weighted by the total number of sample days. Explanatory variables were 'fence configuration' (no fence, wildlife-permeable, bison-deflection; categorical), 'guild' (canid, felid, ungulate, ursid; categorical), 'associated fence' (physical location; categorical), 'fence distance class' (adjacent-to-fence cameras; continuous, off-fence control cameras; categorical), 'distance to fence' (meters; continuous), 'fence presence' (pre-construction, post construction; categorical), 'slope' (degrees; continuous) and 'elevation' (meters; continuous). We included a random effect for camera location in each candidate model.

Landscape scale: crossing speed and crossing rates with GPS data

Our intent was to keep drift fences in wildlife-permeable configuration for most of the time once bison were released, but the unpredictable nature and speed of bison movements combined with limited monitoring capabilities resulted in two of the eight drift fences (in the Panther and Red Deer valleys) being deployed in bison-deflection configuration continuously for 18 months. Although unplanned, this allowed us to retroactively compare the effects of no fence, wildlife-perme-

able and bison-deflection fences on wildlife movements at a landscape scale. We developed a custom analysis for detecting barrier-effects on the broad-scale wildlife movement through these migration corridors using a comprehensive, long-term GPS-collar telemetry archive for migratory elk (Dec 2001–Jan 2020; n = 184; fixes = 889 089), resident wolves (Dec 2002–Jan 2020; n = 34; fixes = 112 028) and the reintroduced bison (31 July 2018–Jan 2020; n = 16; fixes = 55 973). We first tested for changes in movement rates of animals passing by the drift-fences and then changes in crossing rates. We removed erroneous GPS fixes and used fix intervals ranging between one and 12 h in our analysis. Using the associated time stamps, we calculated animal speed from steps occurring within 12 h of a fence crossing (crossing event = two temporally subsequent steps on either side of a fence). We analysed the data using generalized linear mixed models with a Gaussian link and used AIC to test for significant changes in travel speed during wildlife-permeable and bison-deflection configurations from speed through the area preceding fence installation. Finally, we assessed fence crossing rates by creating a 1 km spatial buffer around each fence location to detect occurrences where animals approached a fence (entered the buffer) and either crossed the fence or turned back without crossing. Here we also used generalized linear mixed models to assess the effects of fence configuration on crossing rates, used AIC to rank candidate models, and ANOVA to determine significant differences between them. The explanatory variables used to predict these effects were fence location, fence configuration, and the interaction between the two.

Results

Site-specific

We recorded 6104 wildlife-fence events involving 2272 elk, 2015 white-tailed deer, 764 mule deer, 644 bighorn sheep and 409 carnivores. Most events occurred at 2-wire fences (n= 1876), followed by 2-rail (n = 1500), 4-wire-no-top (n = 1452), 5-wire (n = 906), 3-rail (n = 316) and lastly 4-wire-no-bottom (n = 54). We recorded 340 bison–fence interactions in 23 discrete events with only one direct crossing.

Crossing success
Predictors of crossing probability in the top-ranked model were species, fence design and their interaction (Table 1). Model ranks for site-specific scale analyses are available in the online appendix (Supplementary material Appendix 1 Table A3–A7). We used 5-wire and mule deer as reference variables. Generally, wildlife were less likely to cross 4-wire-no-top and 3-rail designs, and were more likely to cross 2-wire fences. We identified 11 species-fence design interactions for which there was evidence of an increased probability of successful crossing compared to the reference. Bighorn sheep and elk were less likely to cross any fence compared to mule deer. Of 51 elk interactions with 3-rail fences, none resulted in a successful crossing. Predicted crossing probabilities ranged from 0.51 (mule deer:4-wire-no-top, 95% CI = 0.50–0.52) to 0.69 (white-tailed deer:2-wire, 95% CI = 0.67–0.70) (Fig. 2). Two-wire fences were the design with the highest crossing probability for elk (0.60, 95% CI = 0.57–0.63), mule deer (0.63, 95% CI = 0.60–0.66) and white-tailed

Table 1. Results from top logistic regression models for crossing success (cross: not cross) and crossing method (over: under/through). We report the beta coefficient estimate (β), standard error (SE), z-statistic (z) and p-value (p). Reference variables were 5-wire (design) and mule deer (species) for crossing success; wire (material) and elk (species) for crossing method.

Parameter		β	SE	z	p
Crossing success	Intercept	−0.61	0.33	−1.83	0.067
	4-wire (no top)	−2.72	0.80	−3.42	< 0.001*
	3-rail	−1.74	0.51	−3.40	< 0.001*
	2-rail	−0.46	0.39	−1.19	0.233
	2-wire	0.70	0.28	2.50	0.013*
	Bighorn sheep**	−1.15	0.46	−2.49	0.013*
	4-wire (no top)	2.76	0.89	3.10	0.002*
	2-rail	1.31	0.55	2.39	0.017*
	2-wire	−0.12	0.45	−0.27	0.787
	Carnivore	−0.15	0.58	−0.25	0.801
	4-wire (no top)	2.97	1.09	2.71	0.007*
	3-rail	3.53	0.87	4.04	< 0.001*
	2-rail	2.17	0.67	3.25	< 0.001*
	2-wire	0.35	0.62	0.57	0.572
	Elk**	−1.78	0.36	−4.91	< 0.001*
	4-wire (no top)	3.34	0.81	4.11	< 0.001
	2-rail	0.49	0.44	1.11	0.269
	2-wire	1.37	0.41	3.34	< 0.001*
	White-tailed deer	0.04	0.28	0.15	0.878
	4-wire (no top)	1.60	0.83	1.93	0.054
	3-rail	1.62	0.59	2.75	0.006*
	2-rail	1.51	0.41	3.67	< 0.001*
	2-wire	1.21	0.32	3.85	< 0.001*
Crossing method	Intercept	1.04	0.59	1.76	0.078
	Material – rail	3.29	0.69	4.79	< 0.001*
	Bighorn sheep	−7.83	0.99	−7.93	< 0.001*
	Mule deer	−7.92	1.00	−7.88	< 0.001*
	White-tailed deer	−7.52	0.84	−8.94	< 0.001*

* Indicates significance at α = 0.05.
** Excludes 3-rail:elk (0 successful crossings, n = 51) and 3-rail:bighorn sheep (n = 4).

deer (0.69, 95% CI = 0.67–0.70), and were second and third highest (and within the confidence intervals) for bighorn sheep and carnivores, respectively. Five-wire fences had the lowest crossing probability for bighorn sheep (0.54, 95% CI = 0.51–0.56), carnivores (0.58, 95% CI = 0.52–0.64) and elk (0.52, 95% CI = 0.51–0.53). The lowest crossing probabilities for both mule and white-tailed deer occurred at 4-wire-no-top fences (0.51, 95% CI = 0.50–0.52, and 0.54, 95% CI = 0.52–0.56, respectively). We were concerned with low crossing rates for bighorn sheep regardless of fence design and have since installed an in-line t-gate structure at a known sheep trail and continued monitoring efforts. It consists of a 3.4 m long section of wire fence bisecting the regular fence line perpendicularly, with a mean gap of 74 cm on either side. Results are promising so far: of 94 bighorn sheep, 82 crossed successfully (87%), as did all 7 cougars.

Crossing method
We examined how fence design affected wildlife decisions to cross over versus under/through fences. Of 452 successful elk fence crossings, 339 (75%) occurred by jumping over the top (Fig. 3). In contrast, 132 of 242 bighorn sheep (55%), 146 of 168 mule deer (87%) and 810 of 881 white-tailed
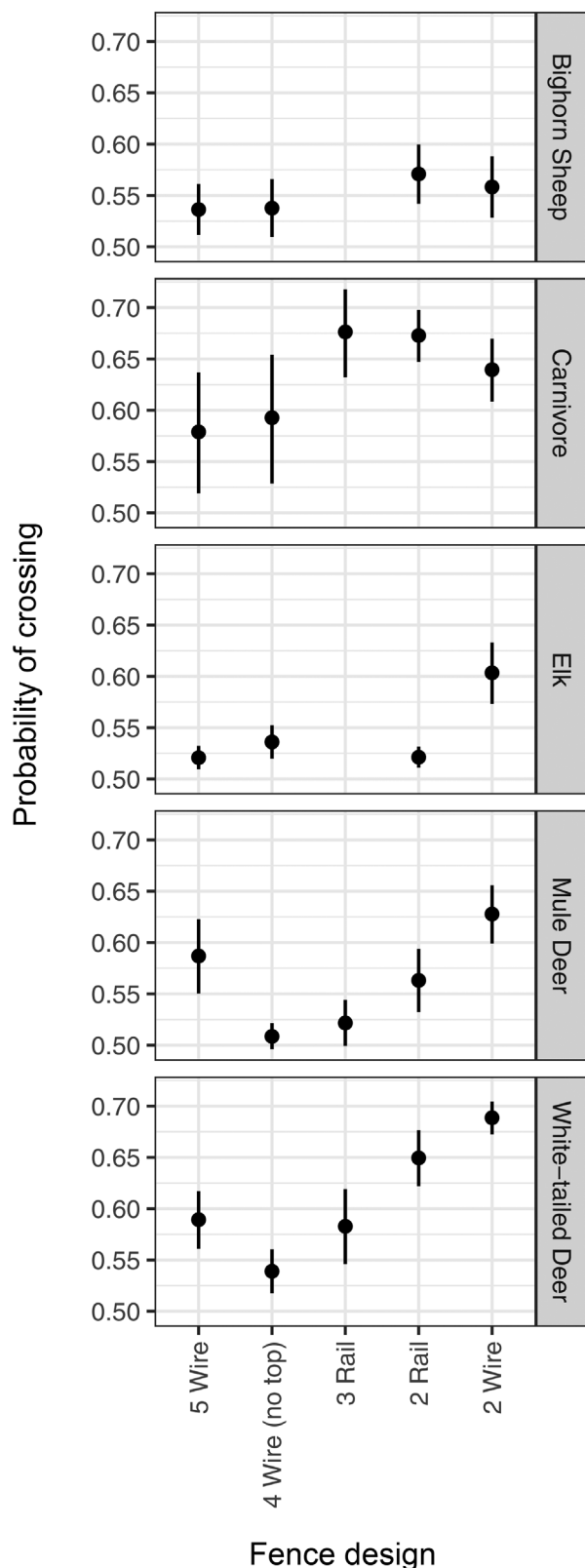
Figure 2. Predictions of fence crossing probability from the top-ranked crossing success model. Bars represent confidence intervals for each variable. The highest crossing probabilities for elk, mule deer and white-tailed deer occur at 2-wire fences, while the lowest probabilities for bighorn sheep, carnivores and elk occur at 5-wire fences.

deer (92%) crossed underneath the fences. The top model for crossing method contained fixed effects for species and fence material, with the reference variables being elk and wire (Table 1). Bighorn sheep, mule deer and white-tailed deer were each less likely to cross over fences (versus under or through) compared to elk, while wildlife were more likely to jump over rail fences than wire fences (Fig. 4). Fence height occurred in the third ranked model ($\Delta AIC = 21.24$), which also contained an interaction between height and species.

Age–sex classes

We found that fence height and fence material were predictors in the top age–sex models for each antlered species, but only found evidence of an effect of these variables on crossing success for elk and white-tailed deer (Supplementary material Appendix 1 Table A8). Reference variables were adult female, reduced height and rail. Model results for elk showed a higher probability of crossing for antlered males compared to adult females. The antlered male:wire and juvenile:full height interactions resulted in reduced crossing probabilities, and zero of 16 antlered male elk interactions with full height fences resulted in successful crossings. Top model results for mule deer showed no evidence of an effect of age–sex on crossing success, while for white-tailed deer the juvenile:full height interaction increased crossing likelihood.

Local scale

Cameras adjacent to fences collected data for a total of 20 342 sampling days while control cameras operated for 5736 sampling days. We detected ungulates on 1708 days, canids on 1125, ursids on 472, and felids on 312 days. The top model contained the interaction between fence configuration and guild as well as fence location (Table 2). Here detection probabilities increased when fences were in either wildlife-permeable or bison-deflection configuration, compared to when there was no fence ($p < 0.001$, $\beta = 0.37$, 0.32, SE = 0.07, 0.08). Detection probabilities predicted by the top model were inconsistent among guilds. Specifically, compared to the reference variables of ungulate and no fence, there was increased detection probability for felid:bison-deflection, felid:wildlife-permeable and ursid:wildlife-permeable, and decreased probability for canid:wildlife-permeable. The top-model intercept of -3.79 indicates that ungulate detection was low in general even before the fences were constructed (Supplementary material Appendix 1 Table A9).

Distance from fence, when used as either a continuous or categorical (adjacent/control) variable, was a poor predictor of detection probability. The model containing the interaction between fence configuration and distance performed poorly compared with the top model ($\Delta AIC > 1500$, $w_i = 0.0$). Distance from fence variables (i.e. control–impact) did not have a significant effect in the model containing the interaction between fence configuration and distance, performed worse than the null, were not significant predictors at $\alpha = 0.05$ when used in univariate models, and were not covariates in the top ranked model.

Landscape scale

We assessed the effects of fence presence and configuration on the movement and crossing rates of wolves and elk.
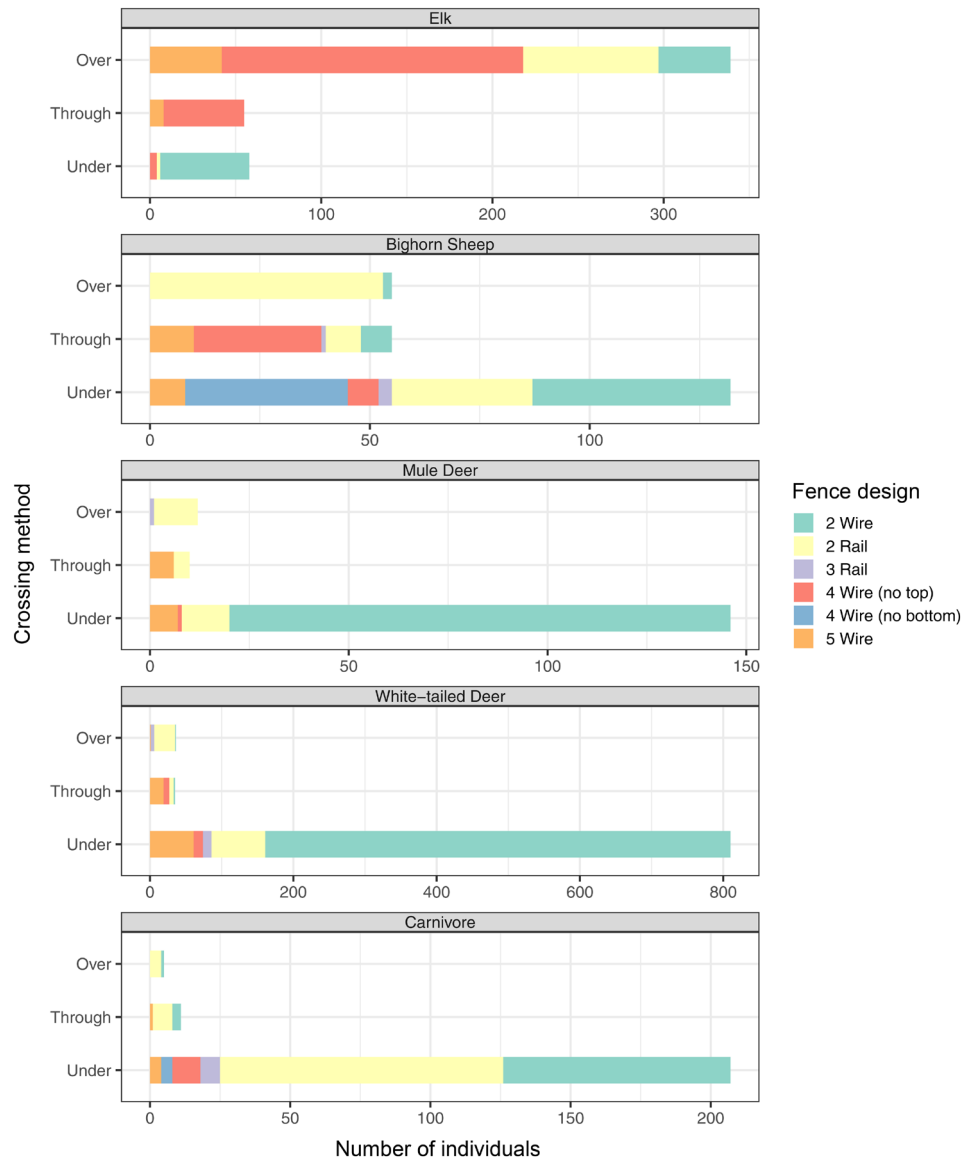
Figure 3. Crossing methods (over, through or under fences) for elk, bighorn sheep, mule deer, white-tailed deer and carnivores. Observations are pooled from 34 remote cameras that recorded 6104 wildlife-fence interactions.

We found no significant change in movement rates for GPS collared wolves when they encountered fences in bison-deflection configuration, however their speeds significantly increased when passing by the Red Deer fence when in wildlife-permeable configuration; this was approximately 400 m h^{-1} faster than when no fence was present (Fig. 5). Elk showed no significant slowing when the Panther fence was permeable, but increased their speed when it was in bison-deflection configuration. At the Red Deer location elk were slowed by approximately 200 m h^{-1} when encountering fences in both wildlife-permeable and bison-deflection configurations. Although subtle, this was a significant decrease in speed as compared to when no fence was present at the red deer (Supplementary material Appendix 1 Table A10).

The rate at which elk approached, but turned back from fence locations did not significantly change after fences were constructed (Fig. 6). There was nearly a significant difference in crossing proportions when the fences were deployed in

bison-deflection configuration (ANOVA p = 0.06), and no change in crossing rates of wildlife-permeable fences (Supplementary material Appendix 1 Table A11). The proportion of elk crossings when the fences were permeable is not any different than no fence being there. Fence location had no bearing on crossing proportion for elk. For wolves, significantly more crossings occurred when a fence was permeable compared to having no fence (Fig. 6). However, there was a significant drop in crossing proportion when the fence was deployed in bison-deflection configuration. Movement past the fences in bison-deflection configuration for both species is shown in Fig. 7. Fences in bison-deflection configuration were very effective at preventing bison from leaving the reintroduction zone with a few notable exceptions: one dispersing bull jumped the red deer fence, another scrambled around the fence terminus; and a cow with two offspring ducked a net spanning the river at the panther fence only to return and jump back over the fence the following day.
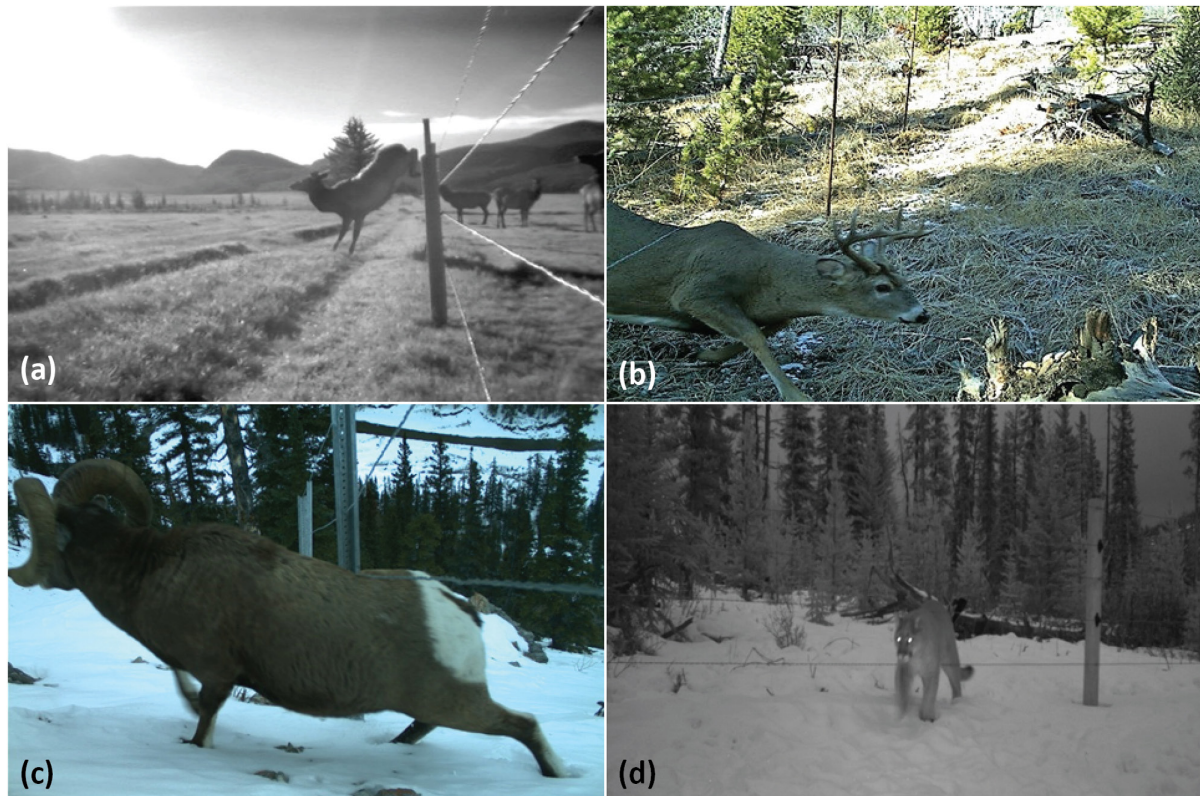
Figure 4. Remote camera images of wildlife crossing study fences in Banff National Park. Female elk over (a), male antlered white-tailed deer under (b), male bighorn sheep under (c) and cougar through (d).

Discussion

Our results pointed to a single fence design that maximized permeability for species with diverse crossing strategies and can be adjusted to effectively obstruct bison when they are in the area. We tested six fence designs and found that the minimal 2-wire, 100 cm high fences were the most permeable to wildlife. When switched to the 5-wire design, we found it to be comparatively impermeable to bison after withstanding hundreds of direct interactions. For that reason, the optimal drift fence design is a dynamic configuration that is manually switched from 2-wire to 5-wire depending on the proximity of bison. Irrespective of permeability, it was hypothesized that the appearance of fences on the landscape would alter wildlife movement in some way. However, our local-scale analysis examined barrier-effects in the proximity of the fences and found no significant changes in the relative abundance of wildlife detections in the area after the fences were constructed. Impedance of broader scale movements through these valleys was assessed in our landscape-scale analysis, and found negligible aversion or slowing of wildlife moving past the fences compared to before they were constructed.

Table 2. Model selection results for detection probability. For each model, we report the degrees of freedom (df), Akaike's information criteria (AIC), AIC difference from top model (ΔAIC) and AIC weight or probability that the model is the best model in the set of candidate models (w_i). Explanatory variables were fence configuration (no fence, wildlife-permeable, bison-deflection), guild (ungulate, canid, felid, ursid), associated fence (Dormer, Panther, Red Deer, Tyrrell), fence distance class (adjacent, control), fence presence (no fence, fence), distance to fence, slope and elevation. All candidate models contained a random effect for camera location.

Model	df	AIC	ΔAIC	w_i
Fence configuration × Guild + Associated fence	16	2415.7	0	0.84
Fence configuration × Guild + Associated fence + Slope + Elevation	18	2419.3	3.5	0.15
Fence configuration × Guild	13	2424.6	8.9	0.01
Fence configuration × Guild + Distance to fence	14	2426.0	10.2	0.01
Fence presence × Guild + Associated fence	12	2440.8	25.1	0.0
Guild	5	2601.7	186.0	0.0
Fence configuration × Fence distance class + Associated fence	10	3959.6	1543.8	0.0
Fence configuration × Fence distance class	7	3968.6	1552.9	0.0
Fence configuration	4	3980.3	1564.6	0.0
Associated fence	5	4061.4	1645.7	0.0
Null	2	4071.8	1656.0	0.0
Distance to fence	3	4073.3	1657.5	0.0
Fence distance class	3	4073.5	1657.8	0.0

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Travel speed versus Fence configuration
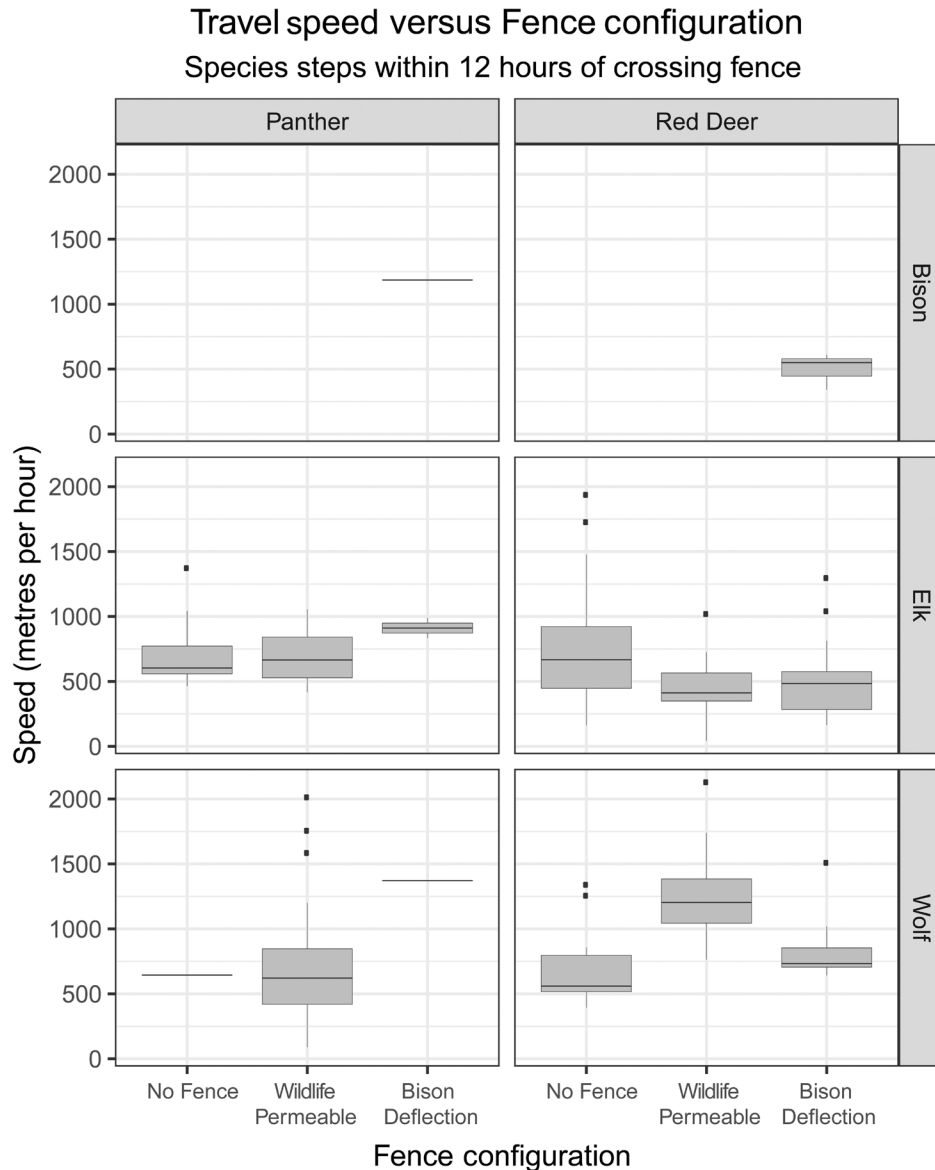### Species steps within 12 hours of crossing fence

Figure 5. Boxplot of wildlife movement rates before and after two drift fence installations in separate valleys in Banff National Park. Average travel speed (m h⁻¹) derived from GPS telemetry steps within 12 h of animals approaching and departing fences in wildlife-permeable and bison-deflection configurations. No before or wildlife-permeable data for bison since they were not on the landscape prior to fence construction and only interacted with fences in bison-deflection configuration.

Our site-specific fence design assessment found, as one might expect, permeability to decrease for all ungulate species except bighorn sheep as more wires or rails were added to the above design. Fencing materials mattered more than height for several species and species varied in their preferences for going over or under specific fence designs. For example, elk primarily went over wire fences and preferred four-wire-no-top and 5-wire over the wooden 2-rail despite the latter being significantly lower (by 25 and 46 cm respectively). Not a single elk was observed crossing over the 3-rail fence. Knight et al. (1997) found that when top wires were replaced with sections of wood railing or poly-vinyl chloride (PVC) pipe at popular crossings, elk chose to cross at the end of the railing. Scott (1992) also found that elk had little success crossing rail fences in Yellowstone. Meanwhile, we found deer preferred to pass under fences

(as did Burkholder et al. 2018 and Jones et al. 2020) but, like elk, were more likely to cross wire than rail fences. Burkholder et al. (2018) noted a similar aversion of mule and white-tailed deer to PVC pipe added to bottom wires to ease passage of pronghorns *Antilocapra americana*. Perhaps the rigidity of rails/pipe makes passing under fences more difficult than flexible smooth wire for cervids, especially for those possessing antlers. The increased visual mass of such fences may also be perceived as a greater physical barrier (Jones et al. 2018). Finally, sheep and carnivores were quantifiably indifferent to construction material but preferred to pass under fences. Gates (2006) describes that both rail and wire fences are capable of containing bison, and recommends the use of rail sections as a targeted wildlife crossing structure at known crossing sites. Our results suggest that including rail sections was not a worthwhile wildlife perme-

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Crossing rates versus Fence configuration

Proportion of crossings versus approaches within 1 km of fence
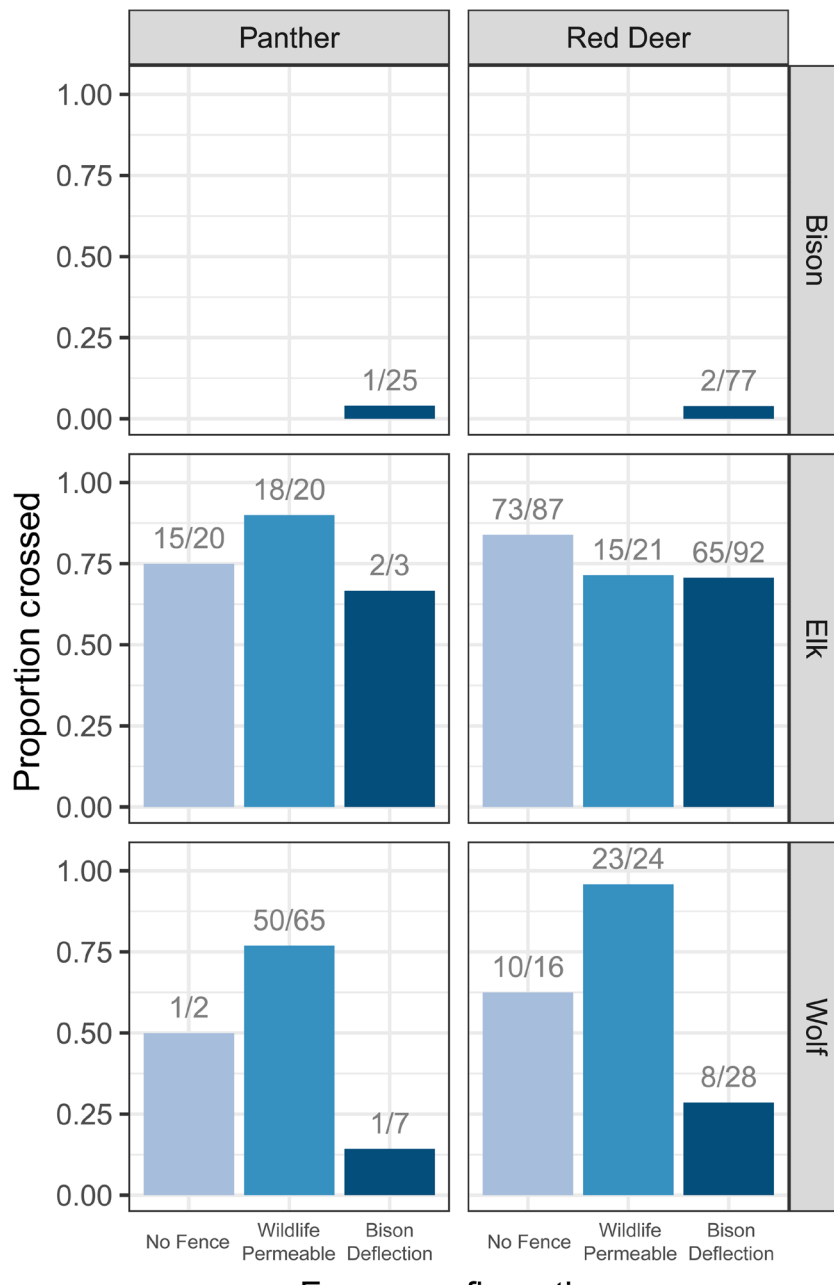
Figure 6. Crossing rates at two fence locations for wolves, elk and bison. A non-crossing event occurred when an animal came within 1 km of a fence but did not cross. There was no significant difference in crossing rates after the fences were installed (Supplementary material Appendix 1 Table A9). Histogram labels indicate the number of crossings/non-crossings for each configuration (bison-deflection and wildlife-permeable). Analysis at two fence locations in separate valleys near the eastern boundary of Banff National Park (Panther and Red Deer).

ability strategy for our project and the simpler, more cost-effective approach of constructing fences completely with wire is preferable.

Significant age–sex effects were few and inconsistent, suggesting fences did not exert a disproportionate influence on antlered male ungulates compared to their conspecific counterparts. These results differ from studies elsewhere in western North America which found reduced crossing success for adult males compared with adult females in mule and white-tailed deer (Burkholder et al. 2018, Jones et al. 2020). We did record a slightly reduced crossing likelihood of antlered male elk compared to adult females of the full height (5-wire and 3-rail) fences.

Our remote cameras likely underestimated individual-based fence crossing rates because some individuals that appeared on a camera may have paralleled the fence and
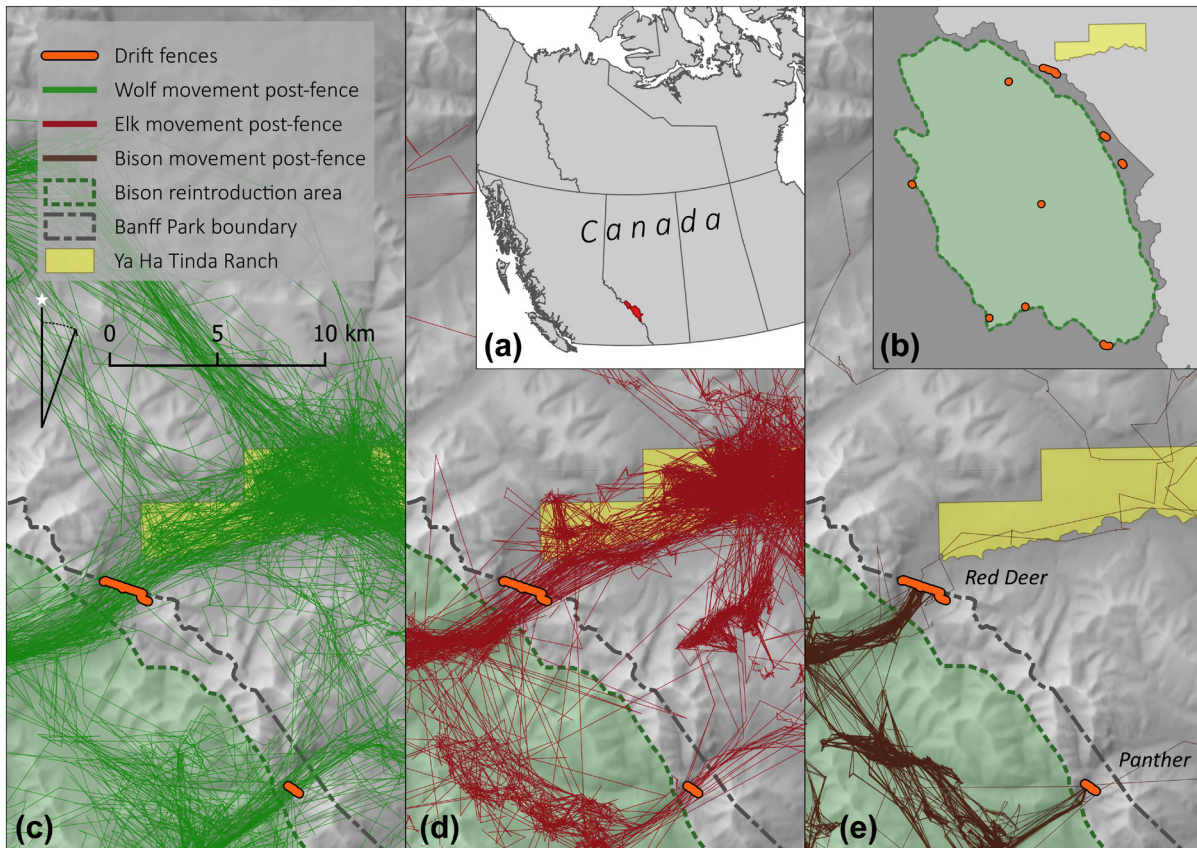
Figure 7. GPS telemetry paths of wolves (c), elk (d) and bison (e) subsequent to drift fence construction along the eastern boundary of the bison reintroduction area (b) in Banff National Park, Canada (a).

crossed outside the camera field of view. However, our study estimated the relative permeability of multiple fence designs. We analysed the remote camera data with a random effect for location and changing fence designs within a location increased our ability to compare the permeability of each design. Conversely, spatial and temporal correlation among camera locations along a fence could result in negatively biased estimates of precision. The fences were strategically placed to prevent bison excursions rather than randomly on the landscape, therefore camera locations along the fence line were correlated in both space and time. Additional fence-effects studies are required to strengthen the inference about how fence designs affect wildlife. We strengthened inference in our study by using a before–after–control–impact study design and by assessing the effects of fences on multiple species using both remote camera and GPS tracking data.

We found a slight but significant increase in nearby wildlife detections after the fences were constructed. Unlike altering the fence configuration to physically increase permeability, mitigating proximity effects is more challenging since the risk-perception of wildlife is so multifaceted (Beyer et al. 2016). Taken alone, this metric is difficult to interpret and presents a counterintuitive result (are animals doubling-back or looking for alternate routes?). However, the distance of cameras from fences (our control–impact variable) was not a significant predictor of detection probability. Therefore, we found no evidence of a fence effect on wildlife detection at this scale. This suggests that the increase was likely not attributable to the presence of fences, instead alluding to

some broader correlative factor such as a general change in species abundance over time.

GPS collared migratory elk did not change direction of movement after fences were constructed and there was no difference between wildlife-permeable and bison-deflection configurations. This differs from our findings at the site-specific scale where remote cameras showed elk crossings were significantly lower for the 5-wire over the 2-wire design. This discrepancy is likely due to animals paralleling fences and passing multiple cameras before actually crossing a fence at preferred crossing locations, a bias we could not avoid due to our inability to differentiate individuals in photos. The fact that such paralleling effects did not register at the landscape level suggests even 5-wire fences were not significant barriers to elk movement when considered at a more meaningful migratory scale. It also highlights the importance of evaluating fence effects at multiple scales.

Wolves did not slow when passing fences in any configuration and crossing rates did not change when fences were in wildlife-permeable configuration. However, wolves often turned back when fences were in bison-deflection configuration. This result was unanticipated given the presumed ease by which a wolf can pass under a smooth wire fence. It might be due to a wariness of wire from wolves being killed with wire snares by fur trappers just outside of the park boundary. Wariness to such snares has been reported elsewhere (Cluff and Murray 1995) and may explain why wolves were willing to cross under a fence where the wire is 80 cm above the ground (wildlife-permeable configuration) but not one

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that is only 50 cm high (bison-deflection). It is likely that additional factors such as changes in territorial boundaries from turnover in pack composition affected movement through these areas rather-than solely the presence of fences. The cumulative effects of other biotic and abiotic variables on the landscape could be further examined to isolate how they impede or facilitate movement at this scale (Spear et al. 2010, Bartzke et al. 2015, Seidler et al. 2015). Moreover, as wildlife continue to interact with the fences they will grow conditioned to their presence and learn to negotiate them more easily on subsequent encounters (Jones et al. 2018, 2020). Additional research is required to quantify this rate of 'learning' following fence installation. On the contrary, some wary individuals of species not included in our landscape-scale analysis may have come to perceive the Panther and Red Deer fences as greater impediments to movement since these locations have remained in bison-deflection configuration for nearly two years. This could impact future crossing behaviour as these individuals may have grown spatially conditioned to the increased barrier-effect at these locations despite being switched to wildlife-permeable configuration. This type of boundary conditioning is favorable for reintroduced species, but there is the undesirable possibility that some wildlife may be conditioned as well.

Fences in bison-deflection configuration effectively redirected bison back into the reintroduction zone on most occasions. There were a few exceptions when highly motivated bulls dispersed far outside the reintroduction zone, despite multiple efforts to herd them back (see also Jung and Larter 2018). We did not test more-permeable fence designs on bison because it was deemed too risky to the overall project. We did, however, observe dispersing bulls respecting 105 cm-high 2 and 3-wire ranch fences outside of the park before they were recaptured. This is likely due to the initial cohort of bison having an inherent respect for wire, learned from the national park from which they were translocated (which has a 245 cm-high perimeter fence of woven wire) and the electrified 5-wire fence we conditioned them to in the backcountry soft-release pasture. Our study identified an optimal fence design that effectively obstructed bison but remained permeable to wildlife. This is a dynamic fence that is manually adjusted between two states: 5-wire if the likelihood of bison interaction is high, otherwise it remains as 2-wire. This design was found to have the highest permeability for the twelve wildlife species observed interacting with the fences. Generally, carnivores passed fences more easily than ungulates, however all species were able to negotiate the fences regardless of their design or configuration. Improved drift-fence designs are essential for large mammal reintroductions, helping to move beyond short-term species relocations and towards maintaining deep-rooted, ecologically effective populations.

Conclusion

Species reintroductions are a burgeoning and progressive ecosystem restoration technique (Polak and Saltz 2011) with an increasing number involving bison (Schmitz et al. 2015). One of the primary challenges of such projects is for the reintroduced animals to develop site fidelity to a target reintroduction zone (Jung and Larter 2018). This is especially important where surrounding jurisdictions have policies and land uses that are incompatible with reintroduced animal survival. Short, strategically positioned sections of drift fencing were a critical tool to overcome this challenge in Banff National Park and allowed us to establish a free-roaming herd of plains bison within a backcountry wilderness area. Doing so was contingent on developing a fence that not only deflects bison back into the reintroduction zone but also allows for the free passage of resident and migratory wildlife species. Through adjustability and prior bison-fence conditioning, we developed a fence system that meets these seemingly contradictory objectives, highlighting the significant role fences can play in the complex experiment of species reintroductions (Lorimer and Driessen 2014). These fences are being used as an interim tool and may be removed in the future as the initial generation of bison become conditioned to these boundaries while subsequent generations reside in their established home range.

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Supplementary material (available online as Appendix wlb-00751 at <www.wildlifebiology.org/appendix/wlb-00751>). Appendix 1.