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Original Article

Road Mitigation Is a Demographic Filter for Grizzly Bears

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ABSTRACT Crossing structures (i.e., underpasses and overpasses) are becoming a widespread approach to promote movement of wildlife across roads. Studies have shown that species select for different crossing structure designs, yet little is known about intraspecific variation (i.e., differences among demographic classes) in crossing structure preference. Using data on grizzly bear (*Ursus arctos*) movement in Banff National Park (AB, Canada), we focused on selection by family groups (adult females travelling with young) and singleton (adult male or female) bears for 5 crossing structure designs distributed among 44 sites. Using data from the world's longest running monitoring program (1997–2014) on wildlife crossing structure use, we created an economic model to estimate demographic-specific cost-effectiveness for each crossing structure design. We found that all grizzly bears selected larger and more open structures (overpasses and open-span bridges). Use of these structures has generally increased with time at a rate that exceeds estimates of population growth. Family groups were more selective than singletons and strongly selected overpasses. In spite of singletons' selection for overpasses and open-span bridges, box culverts were comparable in cost-effectiveness. Our results suggest that structure designs targeting the selection of grizzly bear family groups are effective at restoring population connectivity, but a systematic approach to designing highway mitigation also would consider the role of lesser used structures in reducing intraspecific predation and multispecies connectivity targets. © 2017 The Wildlife Society.

KEY WORDS connectivity, ecopassage, fragmentation, highway, mitigation, movement, overpass, underpass, *Ursus arctos*.

Large carnivores are hypothesized to drive critical ecological processes, including fire, erosion, disease outbreaks, and forest regeneration (Estes et al. 2011, Ford et al. 2014, Ripple et al. 2014*b*). These processes are being altered in human-dominated landscapes as populations of large carnivores decline (Woodroffe 2000, Estes et al. 2011, Ripple et al. 2014*b*) or recover (Woodroffe 2011, Larue et al. 2012, Chapron et al. 2014). Whether carnivores will continue to exert influence on ecosystems in human-dominated landscapes will depend, in part, on the effect of infrastructure on animal movement, behavior, and population growth.

Infrastructure can have positive (McLoughlin et al. 2003; Latham et al. 2011, 2013) or negative (Woodroffe and Ginsberg 1998, Woodroffe 2000) effects on carnivores. Specifically, roads may form a barrier to movement (Riley et al. 2006; Proctor et al. 2012, 2015) or contribute to direct mortality from collisions with vehicles (Collins and Kays 2011). To counter these negative effects, exclusion fencing and wildlife overpasses and underpasses (hereafter referred to collectively as crossing structures) have been used to facilitate the safe movement of animals across roads (Corlatti et al. 2008, Beckmann et al. 2012). Crossing structures reduce mortality from wildlife–vehicle collisions and frequently are used by several species of large mammal (Clevenger et al. 2001, Clevenger and Waltho 2005, Ford et al. 2009, Barrueto et al. 2014). Crossing structures also increase costs of highway construction and maintenance (McGuire and Morrall 2000, Huijser et al. 2009), so it is important to quantify their value to conservation and evaluate the effectiveness of different designs.

Research assessing the effectiveness of highway mitigation has largely focused on environmental factors (e.g., topography, land cover, or shape of crossing structure) that are correlated with animal passage rates (Clevenger and Waltho 2005, Corlatti et al. 2008, Rytwinski et al. 2015). Until now, these correlations were assessed at the species level and have, with few exceptions, overlooked variation among demographic classes that may have important consequences for population viability. Riley et al. (2006) is an exception, and they found that young bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) crossed a major highway in southern

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California, USA, but did not successfully reproduce after dispersal. Instead, only dominant, territorial individuals reproduced; and these individuals did not cross the highway. Information on the status of breeding individuals and types of demographic classes (age, sex) crossing highways remains largely unknown for almost all large carnivore species.

The Rocky Mountains of western Canada hosts one of the most diverse (9 species >10 kg) assemblages of large, terrestrial carnivores in North America (Weaver et al. 1996). Of the large carnivores that occur in the Rocky Mountains, few species can rival the management profile of the grizzly bear (*Ursus arctos*). The conservation of North American grizzly bears ties directly to issues of human–wildlife conflict (Northrup et al. 2012), human safety (Craighead and Craighead 1971), population fragmentation (Chruszcz et al. 2003, Apps et al. 2004, Proctor et al. 2012), and mortality (McLellan et al. 1999, Gibeau et al. 2002, Nielsen et al. 2004, Lamb et al. 2017). Grizzly bears are linked to vital ecosystem processes (Ripple et al. 2014*a*), often used as an 'umbrella species' in conservation planning (Noss et al. 1996), and listed as Threatened under the 1973 Endangered Species Act (as amended) in the conterminous United States and a Special Concern in Canada (COSEWIC 2012). Currently, U.S. federal agencies are considering restoring grizzly bears to the North Cascades Ecosystem in Washington, USA—an area bisected by major highways. Recent genetic analyses have shown that the viability of grizzly bear populations depends on the survival and dispersal of adult females across highways (Proctor et al. 2012, Hauer et al. 2016). Thus, understanding how roads in general, and highway mitigation specifically, filter the demographic connectivity of grizzly bears is an urgent priority for the conservation of this species.

We examine how crossing structure design affected movement of grizzly bears across a major highway, the Trans-Canada Highway. The Trans-Canada Highway bisects 2 national parks and a UNESCO World Heritage Site in the Canadian Rocky Mountains. During 1980–2014, 90 km of exclusion fencing and >44 crossing structures were built along the Trans-Canada Highway with the dual goals of reducing vehicle collisions and restoring connectivity for wildlife populations (Ford et al. 2009*b*). These crossing structures have been monitored continuously since 1996 (Ford et al. 2009*a*, Barrueto et al. 2014), putting this study system in a unique position to assess long-term changes in crossing structures use by grizzly bears. Indeed, quantifying use of crossing structures over the long term (>5 yr) is key to measuring the effectiveness of mitigation for slow-reproducing species such as grizzly bears (Rytwinski et al. 2015). Our goals were to quantify the long-term response of grizzly bears to different crossing structure designs, compare crossing structures selection by family groups (i.e., adult females with cubs) with singletons (nonbreeding females or adult males), and evaluate costs of different crossing structure designs relative to their efficacy in facilitating the movement of grizzly bears.

STUDY AREA

Our study occurred in Banff National Park, Alberta, Canada. Elevation ranged from 1,300 m to 3,400 m and the valley floor transected by the Trans-Canada Highway was approximately 2–5 km wide. Vegetation was characterized by montane, subalpine, and alpine ecoregions. Montane cover types were found in low-elevation valley bottoms and characterized by Douglas fir (*Pseudotsuga menziesii*), white spruce (*Picea glauca*), lodgepole pine (*Pinus contorta*), aspen (*Populus tremuloides*), and natural grasslands. Subalpine and alpine ecoregions primarily consisted of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forests interspersed with riparian shrub communities, subalpine grasslands, and avalanche terrain, giving way to open shrub–forb meadows in the alpine ecoregion. Banff National Park was bisected by 90 km of the Trans-Canada Highway, a 4-lane highway with traffic of 17,000–30,000 vehicles/day (Clevenger et al. 2014).

METHODS

In 1996, we initiated monitoring of wildlife movement at 23 crossing structures along the Trans-Canada Highway, and increased our monitoring effort as new crossing structures were built in subsequent years. Between 1996 and 2006, we used track-pads to quantify the number of passages by individual grizzly bears at crossing structures. Track-pads were approximately 2 m wide, consisted of sandy-loam soil, and enabled us to record the impression of animals' feet as they passed through the crossing structure. We visited track-pads every 2–4 days. In some cases, differences in the foot size of grizzly bears at track-pads indicated that adult females were travelling with young; however, large juvenile tracks can be mistakenly identified as adults with this method. As such, track-pads by themselves are not reliable for quantifying group composition of grizzly bears. Starting in 2006, we installed remote cameras (ReconyxTM LLP, Holmen, WI, USA) at some crossing structures, and at all crossing structures by 2008. Further details of monitoring methods are described in Ford et al. (2009*a*). We monitored grizzly bear movement among crossing structures consisting of 5 designs: overpasses, open-span bridges, large metal culverts, small concrete culverts, and small metal culverts. Details of crossing structure designs are available in the online supporting information file (see online supporting information Fig. S1).

To assess the temporal dynamics of crossing structure use by grizzly bears, we pooled both track-pad and camera-based monitoring (1997–2014). We used generalized additive mixed models to quantify the effect of crossing structure design on the number of grizzly bear passages detected at each crossing structure on an annual basis, with a nonparametric smoother fit to year to address temporal dependence of residuals. We used a negative binomial distribution to model the response variable (passages/yr).

To assess the effect of crossing structure design on demographic filtering, we used camera-based monitoring (2006–2014) and examined group composition of grizzly bear passages on an annual basis. We classified each passage as a family group (adult female with cubs) or singleton. A family group counted as a single passage, irrespective of the number of young that were associated with the adult female. We then used a generalized least-square analysis with the number of passages per crossing structure per year (hereafter referred to as passage rate) as the response variable, a structured correlation term for year, and crossing structure design as the predictor. We performed a Tukey's *post hoc* comparison of passage rates at overpasses with the 4 other designs. Additionally, we compared the diversity of crossing structures used by family groups and singletons, calculating the Simpson's index of diversity (D') for each of the 8 years of monitoring (2006–2014). We compared the Simpson's index of diversity (response variable) using an analysis of variance and group composition (family groups vs. singletons) as the predictor.

Local variation in topography or vegetation cover near crossing structures is spatially correlated with crossing structure design (Clevenger and Waltho 2005). This variation could change the functional availability of crossing structures to grizzly bears. For example, if underpasses tend to be located near a specific type of cover and this type was avoided, it would appear that bears were avoiding underpasses when they actually were avoiding cover types adjacent to the underpass. This covariation might confound the response to crossing structure design with the functional (i.e., topography or vegetation cover-mediated) availability of crossing structures. We therefore examined a subset of crossing structure designs—4 pairs of sites, each consisting of an overpass with an underpass <600 m apart. Each pair of sites was unique and did not include crossing structures paired with other sites in this subsetted analysis. Relative to the expansive home ranges ($\sim$350 km^2) and movement rates (600 m/hr at peak travel times) of grizzly bears (Graham and Stenhouse 2014), the proximity of these paired sites means that animals are effectively choosing between 2 equally available options to cross the highway. Differences in use of crossing structures at paired sites thus more directly measures the effect of design and avoids confounding variation linked to topography or cover type.

Depending on their location or design, crossing structures vary greatly in their construction costs, with underpasses generally being less expensive than overpasses (McGuire and Morrall 2000). In our study area, costs of building and installing the 5 crossing structure designs varied from US $2,800–119,300/m, equivalent to US$800,000–1,700,000/structure. Analogous to the Single Large or Several Small debate over optimal reserve design (Simberloff and Abele 1976), we considered that it may be more effective to build several small, inexpensive crossing structures that perform better in aggregate than a single, large, and expensive crossing structure. To quantify the cost-effectiveness (rather than total cost) of crossing structure designs, we calculated the mean number of passages per year for each crossing structure design, aggregated over 8 years (2006–2014), and divided these means by the cost of building each structure (standardized to US$1,000,000). This value (passages/yr/US $1,000,000) provides the cost-effectiveness of each crossing structure design. To simplify the presentation of these values, we show the expected number of passages by grizzly bears for $n \times$ crossing structures that could be built with an arbitrary budget of US$5,000,000 (see online supporting information, Table S1). We note that this economic model assumes 1) density of crossing structures along a given section of highway has no bearing on the probability of use by grizzly bears; 2) level of use is determined only by crossing structure design (i.e., it does not account for the placement of the crossing structure with respect to local topography or vegetation cover, human use at crossing structures, or grizzly bear population size); and 3) that the cost of crossing structure construction are for new structures, rather than upgrades of existing structures such as drainage culverts or bridges. We obtained the cost of each crossing structures design from Parks Canada's Highway Service Centre (Clevenger et al. 2014).

RESULTS

Between 1996 and 2014, we observed 1,745 individual grizzly bears crossing the Trans-Canada Highway at 39 crossing structures (see online supporting information, Table S2). Use of crossing structures increased from 0.3 passages/year/crossing structure (1997) to a high of 7.6 passages/year/crossing structure (2008), and increasing at a mean $\pm$ standard error of 0.6 ± 0.4 passages/year/crossing structure. Approximately 42% of these passages occurred at open-span bridges and 39% at overpasses (Fig. 1); however,

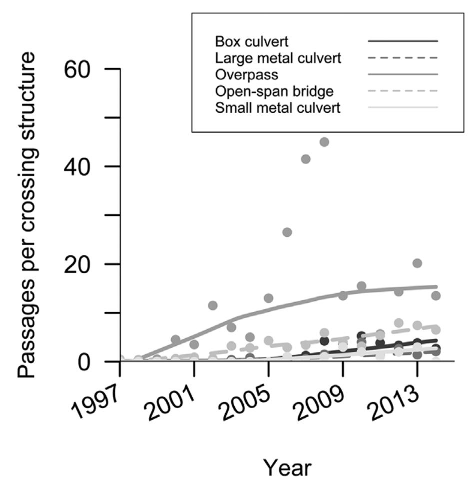

Figure 1. Distribution of grizzly bear passages among 5 designs of crossing structures ($n = 39$) along the Trans-Canada Highway in Banff National Park, Alberta, Canada, between 1997 and 2014. Box culverts, large metal culverts, open-span bridges, and small metal culverts were underpasses built below the road surface, while overpasses were built above the road surface. Grizzly bears used overpasses more often than underpasses; year had a significant effect ($P < 0.001$) on passage rates for all crossing structure designs, except for small metal culverts ($P = 0.63$). These values show the amalgamated (male, female, and family groups) response of grizzly bears. Lines of fit are derived from LOESS smoothers. Details on crossing structure design and cost are described in the online supporting information file.

when accounting for the availability of each crossing structure design, there were 97% more passages at overpasses (241 passages/crossing structure) than the rest of the sites combined (122 passages/crossing structure). At the species level, grizzly bears overwhelmingly selected overpasses rather than underpasses.

Between 2006 and 2014, we recorded passages by 82 family groups ($n = 233$ individuals) and 1,078 singletons (Fig. 2). Of these 82 family groups, 40 were observed at overpasses, 35 at open-span bridges, and 7 at the remaining structure types. When accounting for the availability of crossing structures, there were approximately 5 times as many passages at overpasses (1.4 family group passages/yr/crossing structure) than at underpasses (range = 0.0–0.29 family group passages/yr/crossing structure). Of the 1,078 passages made by singletons, 388 were at overpasses and 435 were at open-span bridges, while the remaining passages were at other structure types. When accounting for the availability of crossing structures, singletons used overpasses (12 passages/yr/crossing structure) at least 3 times more often than underpasses (range = 0.9–4.4 passages/yr/crossing structure). Crossing structure design was a significant predictor of passages for family groups ($F_{4,36} = 2.94$, $P = 0.03$), with overpasses having greater use (Tukey's *post hoc* analysis, $P = 0.02$–0.03) compared with other designs, except open-span bridges (Tukey's *post hoc* analysis, $P = 0.07$). Crossing structure design was a significant predictor of passages for singletons ($F_{4,36} = 21.82$, $P < 0.001$), with overpasses having greater use than other crossing structure designs (Tukey's *post hoc* analysis, $P < 0.001$). Singletons used a greater

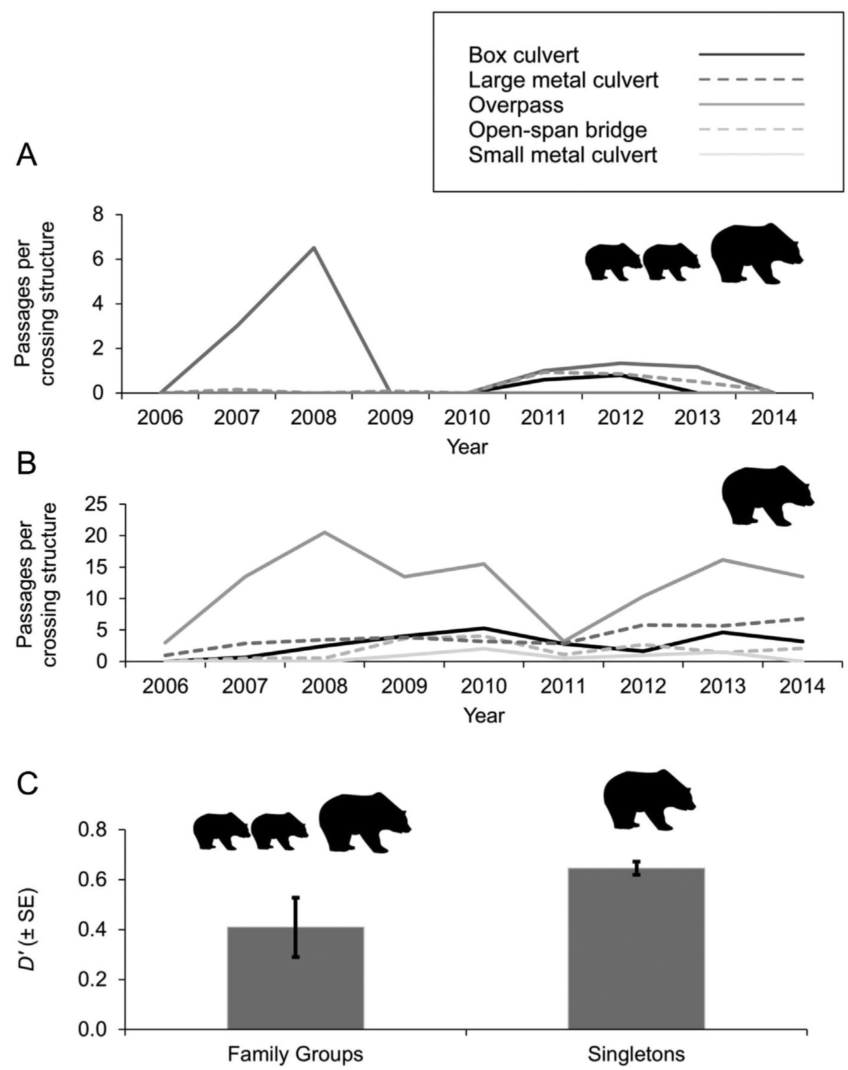

Figure 2. Demographic filtering of road crossing by grizzly bears at crossing structures. (A) Number of passages by family groups per crossing structure—by design—between 2006 and 2014 in Banff National Park, Alberta, Canada. (B) Number of passages by singleton grizzly bears per crossing structure—by design—between 2006 and 2014 in Banff National Park. Based on a 2006–2008 field study (Sawaya et al. 2014), approximately 55% of these singletons are male. (C) Singletons used a greater diversity (D' = Simpson's index of diversity) of the 5 crossing structure designs available than did family groups (i.e., ad F with cubs). Details on crossing structure design and cost are described in the online supporting information file.

diversity of crossing structures ($D' = 0.65 \pm 0.03$) than family groups ($D' = 0.41 \pm 0.12$; $F_{1,12} = 6.52$; $P = 0.03$; Fig. 2).

For the subset of paired overpasses and adjacent underpasses, there were 41 passages by family groups, of which 95% occurred at overpasses. This translates to 0.64 passages/year/crossing structure for overpasses, and 0.03 passages/year/crossing structure for the adjacent underpasses. For singletons, there were 353 passages in total, of which 82% were at overpasses. This translates to 8.5 passages/year/crossing structure for overpasses, and 2.4 passages/year/crossing structure for the adjacent underpasses. Thus, when controlling for local topography or cover type, use of overpasses—especially for family groups—was much greater than adjacent underpasses.

Only 3 crossing structure designs were used by family groups (box culverts, overpasses, and open-span bridges). Of these, box culverts and overpasses were the most cost-effective (0.86 passages/yr/US\$1,000,000 and 0.82 passages/yr/US\$1,000,000, respectively) and open-span bridges were least effective (0.34 passages/yr/US\$1,000,000; Fig. 3). The most cost-effective crossing structure design for singleton grizzly bears was box culverts (15.20 passages/yr/US \$1,000,000), while the least cost-effective crossing structure design was open-span bridges (5.56 passages/yr/US \$1,000,000).

DISCUSSION

Grizzly bears—both family groups and singletons—selected overpasses and open-span bridges, which are crossing structure designs characterized by wide openings, ample light, high visibility, and high construction cost. However, singleton bears were more tolerant of the smaller and more constricted box culverts than were family groups, at least enough to make this design comparable with overpasses for the most cost-effective designs we tested.

Our results have important implications for grizzly bear conservation and management. First, crossing structure designs targeted at selection by family groups might be one of the most effective means to enhance the viability of populations in human-modified landscapes. The safe movement of adults and young across highways can be critical for the per capita population growth rate (Proctor et al. 2005, 2015; Hauer et al. 2016). Of 76 known grizzly bear mortalities in our study area occurring during 1990–

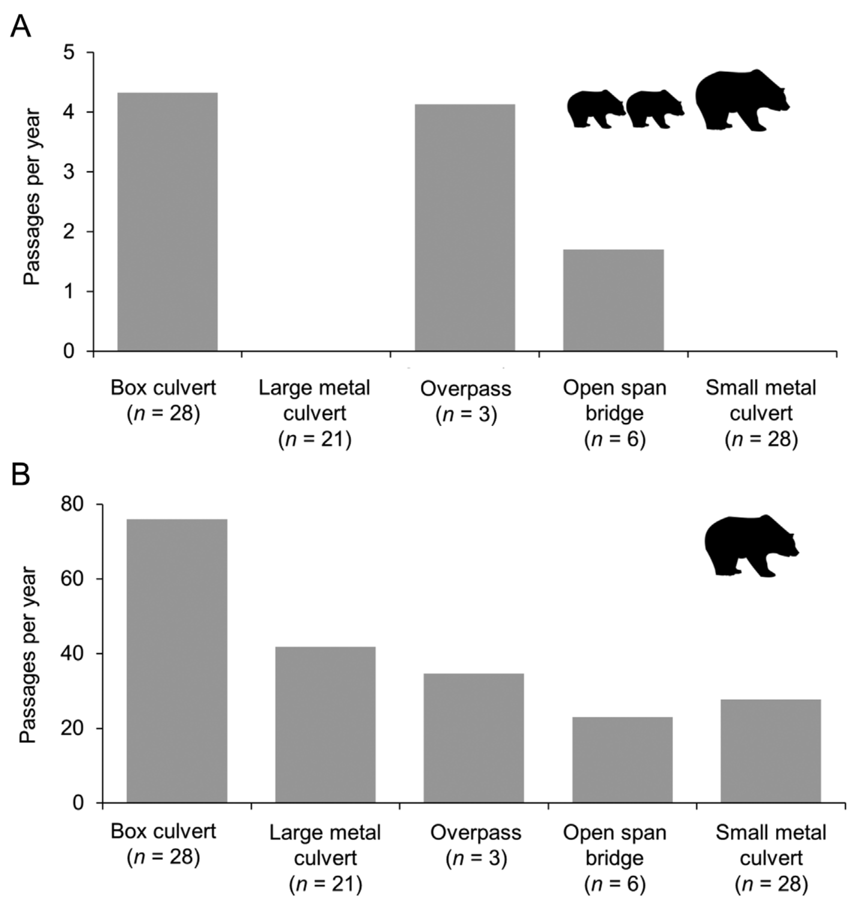

Figure 3. Economic model showing the expected grizzly bear passages per year for (A) family groups and (B) singletons for 5 designs of crossing structure in Banff National Park, Alberta, Canada. The number of crossing structures that could be built with a hypothetical budget of US\$5,000,000 is shown in parentheses under the bars and based on the construction cost incurred in Banff National Park. The y-axis shows the total number of passages per year if only one crossing structure design is used. Details on crossing structure design and cost are described in the online supporting information file.

2014, 58% were caused by collisions on roads or railways (Forshner et al. 2015). Adult female survival, along with juvenile survival (cub, yearling, subadult), are the most sensitive parameters affecting growth in this population of bears (Garshelis et al. 2005). Thus, in areas where facilitating the safe movement of dispersing, breeding individuals is a priority for population recovery, installing overpasses and adjoining fencing is the surest means to mitigate negative effects of highways.

Second, ensuring some proportion of crossing structures is "family friendly" might increase use of the entire crossing structure system; thus, making all designs more cost-effective. Social learning behavior or the transmission of behavior from adult female to young shapes the foraging preferences, movement patterns, and interactions with people for young grizzly bears (Gilbert 1999, Nielsen et al. 2013, Morehouse et al. 2016). In the case of crossing structure use, adult bears may be more willing to approach and then cross mitigated highways if they have used crossing structures as young. This learning behavior may explain the growth in use of crossing structures over time, because it outpaces estimates of population growth for this area (Garshelis et al. 2005). Future research—perhaps via simulation modelling—will need to determine the optimal proportion of family-friendly crossing structures.

Third, ensuring that both adult males and family groups have a number of options to cross the highway may reduce intraspecific predation. Adult male bears often kill young bears and will displace family groups from prime habitat (Wielgus and Bunnell 1994, Cristescu et al. 2013). A highway containing too few crossing structures may therefore inadvertently facilitate predation on young by adult males. Overpasses provide the most reliable means to ensure that all bears traverse this highway, but the availability of underpasses in our study area also allows less-selective singleton bears (including adult males) to cross the highway with lower risk of encountering family groups. In other words, from a Single Large or Several Small perspective, a balance of a few large structures (overpasses and open-span bridges) and several smaller structures (box and metal culverts) are effective for reducing intraspecific predation by adult males on young.

Although we found that family groups almost exclusively used overpasses and open-span bridges, their occasional use of box culverts and the relatively low cost of this design combined to make these designs as cost-effective as overpasses. However, use of box culverts by family groups only occurred in 2 of the 8 years (2011–2012) that we used cameras (as opposed to track-pads) to record animal movement. We cannot determine how many different family groups made these passages, but our results suggest that use of crossing structure designs other than overpasses or open-span bridges is too infrequent, and therefore not recommended for the restoration of connectivity for family groups. Moreover, the number of crossing structures used in Banff is quite rare among current highway mitigation complexes and most mitigation systems built in the future will likely consist of smaller highway segments and fewer crossing structures (Ford et al. 2011, Huijser et al. 2016). As such, when presented with few options to cross highways, it is even more important that highly-selected crossing structure designs (i.e., overpasses and open-span bridges) are used for grizzly bear management.

Our study is the first to assess the design and cost-effectiveness of mitigation measures for the cross-road movement of breeding individuals in a North American large-carnivore population. Previous studies have identified relatively equal use of crossing structures by male and female grizzly bears, despite a fairly consistent finding of male-biased road crossing at unmitigated road sections (see online supporting information, Table S3). Moreover, grizzly bear populations bisected by highways containing crossing structures have lower genetic isolation-by-distance than highways without crossing structures—an effect caused by a lack of female movement across unmitigated highways (Proctor et al. 2012, 2015; Sawaya et al. 2014). The findings from these previous studies, combined with our results, suggest that a highway with crossing structures that do not address the behavioral patterns of family groups is equivalent in function to a highway without crossing structures altogether.

MANAGEMENT IMPLICATIONS

We detected a trend of increasing use of all crossing structure designs with time when assessing this grizzly bear population in aggregate (pooling ages and sex), with the steepest rise in use at overpasses. In earlier publications using a portion of these data (1997–2008), we concluded that overpasses were critical for the maintenance of population connectivity because many underpasses were not being used by grizzly bears (Clevenger et al. 2009, Ford et al. 2009*b*). After collecting an additional 6 years of data, we stand by this conclusion, but for different reasons. As singleton grizzly bears learned to use different crossing structure designs over time, the relative importance of overpasses diminished for that segment of the population. Indeed, box culverts emerged as one of the most cost-effective means of facilitating movement for single bears (a group inclusive of dispersing subadults that are critical to gene flow) across the highway. However, to the extent that the survival of family groups is coupled with population growth, overpasses are critical to the viability of grizzly bears in the Rocky Mountains. Thus, our results support the installation of different crossing structure designs to optimize the behavioral ecology and demographic connectivity of grizzly bears. In addition to meeting the needs of different demographic classes within the grizzly bear population, increasing the diversity of crossing structures provides connectivity benefits to other species that vary in their preference for different crossing structure designs. Finally, our results illustrate that for long-lived and slowly reproducing species such as grizzly bears, monitoring effects of infrastructure on individual behavior over the long term (>5 yr) is needed to develop accurate and cost-effective approaches to wildlife management.

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SUPPORTING INFORMATION

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

Table S1. Characteristics of 5 crossing structure designs used along the Trans-Canada Highway in Banff National Park, Alberta, Canada.

Table S2. Performance of 5 crossing structure designs used along the Trans-Canada Highway in Banff National Park, Alberta, Canada.

Table S3. Studies describing road-mediated demographic filtering of grizzly bear movements in North America.

Figure S1. Examples of the 5 crossing structure designs used along the Trans-Canada Highway in Banff National Park, Alberta, Canada.