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Demographic Connectivity for Ursid Populations at Wildlife Crossing Structures in Banff National Park

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Abstract: *Wildlife crossing structures are one solution to mitigating the fragmentation of wildlife populations caused by roads, but their effectiveness in providing connectivity has only been superficially evaluated. Hundreds of grizzly (Ursus arctos) and black bear (Ursus americanus) passages through under and overpasses have been recorded in Banff National Park, Alberta, Canada. However, the ability of crossing structures to allow individual and population-level movements across road networks remains unknown. In April 2006, we initiated a 3-year investigation into whether crossing structures provide demographic connectivity for grizzly and black bears in Banff National Park. We collected hair with multiple noninvasive methods to obtain genetic samples from grizzly and black bears around the Bow Valley. Our objectives were to determine the number of male and female grizzly and black bears that use crossing structures; examine spatial and temporal patterns of crossings; and estimate the proportions of grizzly and black bear populations in the Bow Valley that use crossing structures. Fifteen grizzly (7 female, 8 male) and 17 black bears (8 female, 9 male) used wildlife crossing structures. The number of individuals detected at wildlife crossing structures was highly correlated with the number of passages in space and time. Grizzly bears used open crossing structures (e.g., overpasses) more often than constricted crossings (e.g., culverts). Peak use of crossing structures for both bear species occurred in July, when high rates of foraging activity coincide with mating season. We compared the number of bears that used crossings with estimates of population abundance from a related study and determined that substantial percentages of grizzly (15.0% in 2006, 19.8% in 2008) and black bear (17.6% in 2006, 11.0% in 2008) populations used crossing structures. On the basis of our results, we concluded wildlife crossing structures provide demographic connectivity for bear populations in Banff National Park.*

Keywords: connectivity, fragmentation, noninvasive genetic sampling, populations, roads, *Ursus americanus*, *Ursus arctos*, wildlife crossing structures

Conectividad Demográfica para Poblaciones de Úrsidos en Estructuras para Cruce de Vida Silvestre en el Parque Nacional Banff

Resumen: *Las estructuras para el cruce de vida silvestre son una solución para mitigar la fragmentación de poblaciones de vida silvestre provocada por los caminos, pero su efectividad para proporcionar conectividad ha sido evaluada solo superficialmente. Se han registrado cientos de pasadas de osos grizzli (Ursus arctos) y osos negros (U. americanus) en los cruces del Parque Nacional Banff, Alberta, Canadá. Sin embargo, se desconoce la capacidad de las estructuras de cruce para permitir movimientos individuales y a nivel población. En abril 2006, iniciamos una investigación de 3 años para conocer si las estructuras de cruce proporcionan conectividad demográfica para osos grizzli y negros en el Parque Nacional Banff. Recolectamos pelo mediante múltiples métodos no invasivos para obtener muestras genéticas de osos grizzli y negros alrededor del Valle Bow. Nuestros objetivos fueron determinar los patrones espaciales y temporales de los cruces; y estimar las proporciones de las poblaciones de osos grizzli y negros que utilizan estructuras de cruce. Quince osos grizzli (7 hembras, 8 machos) y 17 osos negros (8 hembras, 9 machos) utilizaron estructuras de cruce. El número de individuos detectados en las estructuras de cruce se correlacionó estrechamente con el número de pasadas en espacio y tiempo. Los osos grizzli utilizaron estructuras de cruce abiertas (e.g., puentes) más frecuentemente*

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que los cruces compactos (e.g., alcantarillas). El pico del uso de estructuras de cruce para ambas especies de osos ocurrió en julio, cuando las altas tasas de actividad forrajera coinciden con la temporada de apareamiento. Comparamos el número de osos que utilizaron cruces con estimaciones de la abundancia poblacional de un estudio relacionado y determinamos que porcentajes sustanciales de las poblaciones de osos grizzli (15.0% en 2006, 19.8% en 2008) y de osos negros (17.6% en 2006, 11.0% en 2008) utilizaron las estructuras de cruce. Con base en nuestros resultados, concluimos que las estructuras de cruce proporcionan conectividad demográfica a poblaciones de osos en el Parque Nacional Banff.

Palabras Clave: caminos, conectividad, estructuras para el cruce de vida silvestre, fragmentación, muestreo genético no invasivo, poblaciones, *Ursus americanus*, *Ursus arctos*

Introduction

Road networks are one of the most ubiquitous anthropogenic features on the planet, and they pose a major threat to Earth's biodiversity (Forman et al. 2003). The presence of roads is highly correlated with changes in species composition, population sizes, and ecological processes (Trombulak & Frissell 2000). Roadways, particularly ones with higher traffic volumes, can negatively affect wildlife populations through direct mortality and habitat fragmentation (Fahrig & Rytwinski 2009). Traffic on roads is a substantial source of mortality for many vertebrate populations, but road-caused mortality rates rarely limit population abundance. Barrier effects caused by road avoidance are thought to be a much bigger ecological problem (Forman & Alexander 1998). Roads constrain wildlife movements and thus decrease landscape connectivity and disrupt ecosystem functions such as individual survival and reproduction, population persistence and evolution, predator–prey dynamics, and resource competition. Provision of wildlife crossing structures combined with exclusion fencing is one solution to keeping animals off roadways while maintaining or restoring animal movements, but the ability of wildlife crossings to provide connectivity for populations fragmented by roads has yet to be properly evaluated (Corlatti et al. 2009; Kaplan 2009).

Patches of habitat that are connected will have greater species richness, diversity, and persistence than isolated patches (MacArthur & Wilson 1967). Corridors are designed to link patches of fragmented habitat and thus to stabilize population dynamics and community processes. Wildlife crossing structures are "in essence site-specific movement corridors" that are "designed to link critical habitats and provide safe movement of animals across busy roads" (Clevenger & Wierzchowski 2006). Potential demographic benefits of mitigating roads with crossing structures include increased survival from lower road mortality, increased survival and fecundity from greater access to patchily distributed resources (i.e., food and shelter), and increased recruitment from emigration. Ecological connectivity will become increasingly important as climate changes (Krosby et al. 2010). Wildlife crossings may help mitigate some effects of climate change by allowing animals to change movements (i.e., latitude, elevation) in response to rising temperatures and by allowing the flow of genes so that populations can adapt to and evolve with changing environmental conditions. Despite these potential benefits, conservation biologists have hotly debated the conservation value of corridors, including engineered wildlife crossing structures, for over 20 years (e.g., Noss 1987; Simberloff & Cox 1987; Beier & Noss 1998). The debate has understandably focused on whether wildlife crossings and other landscape corridors designed to increase population viability are worth the relatively high costs (e.g., Hobbs 1992; Simberloff et al. 1992; Dixon et al. 2006).

The ability of wildlife crossing structures to connect populations remains surprisingly unknown considering there is an aggressive global campaign currently underway to incorporate crossing structures into construction projects (Forman 2000; Ament et al. 2008; Mata et al. 2008). Exclusion fencing can reduce wildlife–vehicle collisions for some species (Clevenger et al. 2001; Jaeger & Fahrig 2004), and a variety of species use wildlife crossings to traverse busy highways (Clevenger & Waltho 2000; Clevenger & Waltho 2005). Nonetheless, there have been few studies on the effectiveness of crossing structures that go beyond documentation of the number of species that use them and their frequency of use (e.g., Cain et al. 2003; Ng et al. 2004; Gagnon et al. 2011).

One of the world's most developed and well-known systems of wildlife crossings is located in Banff National Park (BNP) in the Central Rocky Mountains of Alberta, Canada. With over 4 million visitors per year, BNP is one of the world's most visited national parks and this high level of human visitation acts as a major stressor on the ecosystem (Ford et al. 2010). Some of the seminal publications on road ecology have come from studying the 2 overpasses (>US $2 million/structure) and 23 underpasses built in the 1980s and 1990s to reduce wildlife–vehicle collisions and restore or maintain wildlife movement across the 4-lane section of the Trans-Canada Highway (TCH) (Clevenger & Waltho 2000; Clevenger et al. 2001; Clevenger & Waltho 2005). The TCH is Canada's busiest highway (17,970 vehicles/day on average in BNP) and the nation's primary east–west transportation route (Ford et al. 2010). Given the extent and duration of

road-mitigation efforts in BNP along with its protected status and biodiversity, BNP is viewed the world over as the quintessential place to study the effectiveness of road mitigation measures.

Recent evidence indicates that healthy populations of apex consumers (e.g., carnivores) are critical to maintaining top-down ecological processes, but many carnivore species are declining rapidly worldwide (Estes et al. 2011). Wide-ranging, large-bodied carnivores that inhabit BNP such as grizzly (*Ursus arctos*) and black bears (*Ursus americanus*) are susceptible to road-caused population fragmentation due to their low densities and reproductive rates and large home ranges (Brody & Pelton 1989; Proctor et al. 2005; Rytwinski & Fahrig 2011). Wildlife crossing structures in BNP and the bears that use them represent the ideal study system and model study species to address huge gaps in our understanding of how, when, and why road mitigation measures provide connectivity for individuals and populations.

Until recently, remote cameras and track pads have been the most frequently used methods to evaluate the effectiveness of wildlife crossing structures (Long et al. 2008; Ford et al. 2009), but these methods cannot reliably distinguish individuals or genders, so the research questions they can address are limited (Clevenger & Sawaya 2010). For instance, hundreds of passages of grizzly and black bears through wildlife crossing structures (hereafter passages) have been recorded with track pads at wildlife crossing structures in BNP. However, due to methodological limitations, the ability of crossing structures to serve as movement corridors for multiple individuals of different sexes remains completely unknown. Recent interest in road ecology has focused on the use of molecular genetics to investigate transportation effects on wildlife (Balkenhol & Waits 2009). Samples collected via noninvasive genetic sampling can identify male and female individuals and may provide information on abundance, vital rates, and genetic interchange, but managers have been reluctant to embrace genetic-monitoring methods because they are relatively new (Schwartz et al. 2006). Genetic data have been used frequently to assess genetic connectivity, but they may also be used to assess demographic connectivity, the degree to which population growth and vital rates are affected by individual movements between populations (Lowe & Allendorf 2010). A new noninvasive genetic sampling method allows assessment of the ability of wildlife crossings to connect ursid populations (Clevenger & Sawaya 2010).

In April 2006, we initiated a 3-year evaluation of the effectiveness of wildlife crossing structures to provide demographic connectivity for grizzly and black bear populations in the Bow Valley of BNP. We used the hair collection method developed by Clevenger and Sawaya (2010) to sample crossing structures. In a related study, Sawaya et al. (2012) used a combination of hair traps and rub tree surveys to collect genetic samples from grizzly and black bears in the Bow Valley. Here, our main objectives were to determine the minimum number of individual male and female grizzly and black bears that use wildlife crossing structures to traverse the TCH, examine the spatial and temporal patterns of individual bear movements at crossing structures, and estimate the proportions of the bear populations in the Bow Valley that use crossing structures to traverse the TCH.

Methods

Study Area

Our study area in the Bow Valley of BNP was 2246 km^2 and located approximately 120 km west of Calgary, Alberta, east of the Continental Divide in the central Rocky Mountains (Supporting Information). The lower Bow Valley is a human-dominated landscape with the TCH, the Banff Townsite (8000 residents), a golf course, 3 ski areas, a railway, and a secondary highway. Between 1982 and 1997, a 45-km stretch of TCH, extending west from the eastern park boundary, was widened from 2 to 4 lanes for safety reasons (McGuire & Morrall 2000). Twenty-five wildlife crossing structures, 2 overpasses and 23 underpasses (e.g., box culverts, creek, and open-span bridges), and 2.4-m high fencing were constructed to facilitate wildlife movement and reduce wildlife–vehicle collisions, respectively, along the 4-lane section of the TCH (Ford et al. 2010). Detailed ecological descriptions of the study area are in Holroyd and Van Tighem (1983) and Holland and Coen (1983).

Hair Sampling

We conducted hair sampling concurrently with track pad monitoring at 20 of 25 wildlife crossing structures in the Bow Valley from 15 May to 18 October 2006, 22 April to 29 October 2007, and 22 April to 18 October 2008 (Supporting Information). Five wildlife crossings were not included because they receive high levels of human use and low levels of bear use (Clevenger & Waltho 2005). To collect hair samples we stretched 2 lengths of barbed wire perpendicular to the line of movement of passing bears (Clevenger & Sawaya 2010). We collected hair samples in conjunction with track pad monitoring. Track pads consisted of strips of sandy loam 1.5- to 2-m wide perpendicular to the line of bear movement and spanning the length of the wildlife crossing (Clevenger & Waltho 2000; Clevenger & Waltho 2005). We checked track pads every 2 days and recorded species, direction of travel, and number in group (Ford et al. 2009). We based species identification on diagnostic characteristics of tracks (Halfpenny 2001). We calculated total number of passages by summing discrete crossing events over the 3-year sampling period.

For hair sampling at the crossing structures, we secured 2 metal stakes at each end of a track pad, and attached the 2 strands of wire at 30 cm and 70 cm,

respectively. Page wire and brush were piled at the ends of the wire to funnel animals through the hair-sampling system. Illustrations and detailed descriptions of the hair-sampling system and related pilot study are in Clevenger and Sawaya (2010). We checked the barbed wire for hair every 2 days in conjunction with track pad monitoring. We collected hair samples from each barb separately and collected discrete clumps of hair below the wire. We placed samples in paper envelopes labeled with a uniquely numbered barcode and sterilized every barb from which we collected hair with an open flame to prevent DNA contamination. We stored hair samples at room temperature in plastic bins containing silica desiccant. Detailed descriptions of genetic analyses are available in Supporting Information.

In a previous study, Sawaya et al. (2012) used 2 noninvasive genetic sampling methods, hair traps (Woods et al. 1999) and bear rubs (Kendall et al. 2009), to collect hair from black and grizzly bear populations near the TCH and to estimate grizzly and black bear population abundance in the Bow Valley in 2006 and 2008. Detailed descriptions of hair collection, genetic analyses, and abundance estimation methods and results used to estimate the proportions of the bear populations in the Bow Valley that use crossing structures to traverse the TCH are in Sawaya et al. (2012).

Demographic Connectivity

We considered a group of individuals of the same species was demographically connected if they co-occurred in space and time and had an opportunity to interact. We based these criteria on the ecological paradigm definition of population cohesiveness proposed by Waples and Gaggiotti (2006). We first examined individual patterns of bear passages across wildlife crossings along the TCH. We used multilocus genotypes to count the number of unique male and female bears that used crossing structures each year and over the 3 years of sampling. Many crossing events resulted in the collection of multiple hair samples from the same individual, but were only counted as single passages. Some individuals were detected at the same wildlife crossing structure on multiple occasions, but were counted only once per crossing structure. Some individuals were repeatedly detected at the same type of wildlife crossing structure, but were counted only once per crossing structure type. Some individuals were detected more than once in a given month or during more than 1 month in the same year or across years but were counted only once per month or year. We calculated mean and standard error for frequency of individual bear passages by year and across years. We used graphs to visualize spatial (i.e., crossing structure) and temporal (i.e., month) patterns of individual bear use. We calculated spatial and temporal correlation coefficients to determine the relation between the number of passages recorded at track pads and the number of individuals.

We assessed population-level connectivity by comparing minimum counts of grizzly and black bears detected at crossing structures with abundance estimates of grizzly and black bears in the Bow Valley of BNP from Sawaya et al. (2012). We estimated the minimum proportion of each population that used crossing structures by dividing the minimum number of male and female bears detected at crossing structures in a year by the respective annual superpopulation abundance estimates from Sawaya et al. (2012) for each species and sex.

Results

Hair Sampling

We recorded 91 grizzly bear passages at track pads in 2006, 115 in 2007, and 180 in 2008 (Supporting Information). We recorded 129 black bear passages at track pads in 2006, 98 in 2007, and 88 in 2008 (Supporting Information). We collected 348 hair samples from wildlife crossings in 2006, 416 in 2007, and 553 in 2008 (Supporting Information). Many samples came from the same individual bears or nontarget species such as cougars (*Puma concolor*) and wolves (*Canis lupus*). We collected hair from all wildlife crossings ($n = 20$) monitored in all years, but not all passages recorded at track pads yielded useable DNA or DNA from the target species. We identified individuals from 37% of grizzly ($n = 386$) and 33% of black bear passages ($n = 315$) recorded at track pads between 2006 and 2008.

Demographic Connectivity

We identified 15 grizzly bears (8 males, 7 females) and 17 black bears (9 males, 8 females) that used the wildlife crossing structures over the course of the study. We identified 11 grizzly and 11 black bears that used crossings in 2006, 12 grizzly and 8 black bears in 2007, and 10 grizzly and 9 black bears in 2008 (Table 1). A high percentage of individual grizzly bears detected at crossings were detected in >1 year (71% of females and 75% of males). A lower percentage of black bears were detected in >1 year (37% of females and 55% of males). Fifty-seven percent of female and 37% of male grizzly bears were detected in all 3 years of sampling compared with only 25% of female and 11% of male black bears. The average number of passages per individual was higher for grizzly bears than for black bears (Supporting Information). Variability in individual passage frequency was high for both species. Of the 247 total passages that produced useable DNA samples, grizzly bear males had the highest number of total passages ($n = 97$) and the highest mean number of passages per individual ($\bar{x}$ [SD] = 12.1 [12.8]). One grizzly bear male accounted for 34 of the 97 (35.1%) passages by male grizzly bears for which we had useable DNA, including the highest number we recorded for a single

Table 1. Number of individual bears detected in Bow Valley of Banff National Park, Alberta, Canada, with 3 noninvasive genetic sampling methods* (barbed wire hair sampling at wildlife crossings, hair traps, and bears rubs) between April 2006 and October 2008.

Detection method	*2006*	*2007*	*2008*	*Total*
Wildlife crossings				
grizzly bears	11	12	10	15
males	6	6	5	8
females	5	6	5	7
black bears	11	8	9	17
males	7	4	4	9
females	4	4	5	8
Hair traps				
grizzly bears	31	N/A	39	42
males	16	N/A	12	20
females	15	N/A	17	22
black bears	40	N/A	57	76
males	16	N/A	19	30
females	24	N/A	38	46
Bear rubs				
grizzly bears	40	46	43	73
males	25	30	24	44
females	15	16	19	29
black bears	2	11	6	16
males	1	9	2	12
females	1	2	4	4

**Some individuals detected with more than one method or in more than one year.*

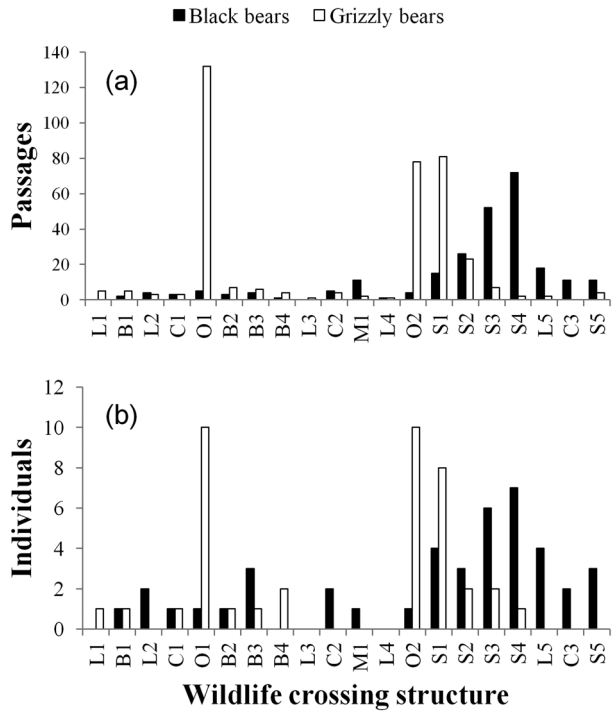

Figure 1. Total number of grizzly and black bear (a) passages through crossing structures and (b) individuals detected at each wildlife crossing structure between 2006 and 2008. Number of passages is the sum of unique crossing events recorded at track pads over 3 years. Number of individuals is the sum of unique individuals detected at a given crossing structure on the basis of DNA analysis of hair samples over 3 years. Crossing structures: M, medium culvert (n = 1); B, box culvert (n = 4); L, large culvert (n = 5); C, creek bridge (n = 3); S, open-span (n = 5); and O, overpass (n = 2). Crossing structures are ordered from west (left) to east (right).

year, 17. One grizzly bear female accounted for 18 of 47 (38.3%) female grizzly bear passages. Single individuals accounted for an even larger percentage of black bear passages (24 of the 55 [43.6%] passages by 1 male and 21 of 48 [43.8%] female black bear passages by a single female).

The number of grizzly and black bear passages was spatially correlated with the number of unique individuals detected at wildlife crossing structures (Pearson's $r = 0.89$ for black bears and $r = 0.95$ for grizzly bears) (Fig. 1). Grizzly bear passages and individuals were highly concentrated at 2 overpasses and 1 open-span underpass to the west of Banff townsite, whereas black bear passages were evenly distributed and more concentrated to the east (Fig. 1). High proportions of grizzly bear males and females were detected at the most open types of wildlife crossings, overpasses and open-span underpasses (Fig. 2a). Over 70% of female and 75% of male grizzly bears detected at wildlife crossings over the study period were detected at 1 of just 2 overpasses (Fig. 2a). The proportion of black bears detected at each crossing type was more evenly distributed (Fig. 2b).

The number of grizzly and black bears detected at wildlife crossings during each month was highly correlated with the number of passages detected with track pads ($r = 0.99$ for black bears and $r = 0.98$ for grizzly bears) (Fig. 3). The number of grizzly bear individuals identified that used wildlife crossings peaked in July, but increased slightly in September (Fig. 3a). The peak in number of black bear individuals and passages in July was higher than the peak for grizzly bears (Fig. 3b).

From Sawaya et al. (2012), we obtained precise abundance estimates for grizzly and black bears during 2006 and 2008 in the Bow Valley from which we determined that, in each year, >10% of the populations of both species used wildlife crossings to traverse the TCH. We estimated the minimum proportion of the grizzly bear population that used crossings was 15.0% in 2006 and 19.8% in 2008 (Table 2). We estimated the minimum proportion of the black bear population that used crossings was 17.6% in 2006 and 11.0% in 2008 (Table 3).

Discussion

To justify the continuation of expensive road mitigation projects, transportation agencies and wildlife managers

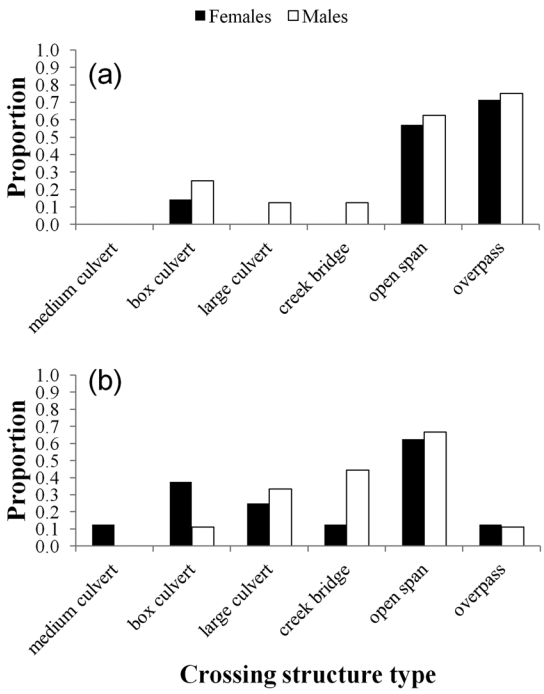

Figure 2. Proportion of total number of (a) grizzly and (b) black bears detected at each of 6 types of crossing structures monitored with noninvasive genetic sampling between 2006 and 2008. Proportions are based on the number of unique individuals detected at a crossing type over 3 years. Number of individuals is the sum of unique individuals detected at a given crossing structure type; individual identity was determined from DNA analysis of hair samples collected at wildlife crossings over 3 years. Crossing structures are ordered from more constricted (left) to more open (right): medium culvert (n = 1), box culvert (n = 4), large culvert (n = 5), creek bridge (n = 3), open-span (n = 5), and overpass (n = 2).

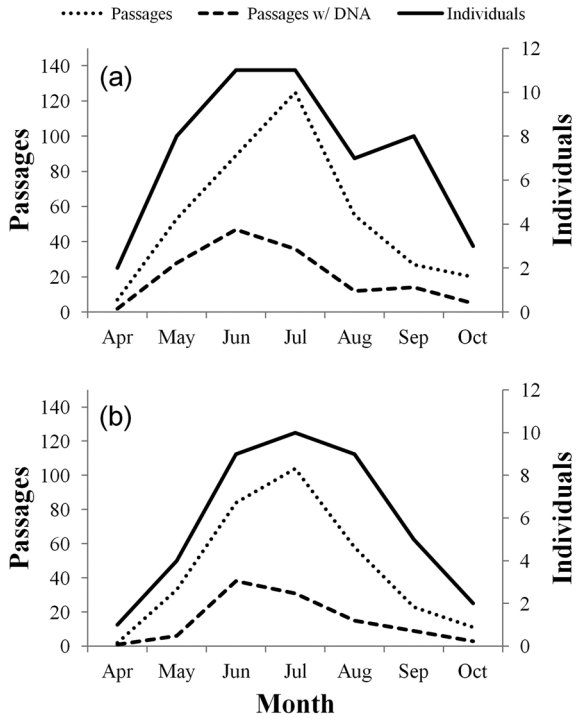

Figure 3. Total number of individual (a) grizzly and (b) black bears detected each month with noninvasive genetic sampling at wildlife crossings in Banff National Park, Alberta between 2006 and 2008. Number of passages is the sum of unique crossing events recorded at track pads over 3 years (species identification on the basis of tracks). Number of passages for which DNA samples were acquired (i.e., passages with DNA) is the sum of unique crossing events that produced a hair sample with amplifiable DNA. Number of individuals is the sum of unique individuals detected at a given crossing structure; individual identity was determined from DNA analysis of hair samples collected at wildlife crossings over 3 years.

Table 2. Total minimum number of grizzly bears and proportion of population detected using wildlife crossings to traverse the Trans-Canada Highway in the Bow Valley of Banff National Park, Alberta, Canada, in 2006 and 2008.

Year and sex	*Minimum number*	*Abundance estimate*[a]	*SE* ($\hat{N}$)	*No. detected at crossings*	*Population detected at crossings (%)*[b]
2006					
males	32	39.9	4.7	6	15.0
females	25	33.6	5.3	5	14.9
total	57	73.5	7.2	11	15.0
2008					
males	26	28.1	2.1	5	17.8
females	22	22.3	0.6	5	22.4
total	48	50.4	2.2	10	19.8

[a] *Model-averaged abundance estimates from Sawaya et al. (2012).*
[b] *Estimated by dividing the number detected at the wildlife crossings by the abundance estimate.*

Table 3. Total minimum number of black bears and proportion of population detected using wildlife crossings to traverse the Trans-Canada Highway in the Bow Valley of Banff National Park, Alberta, Canada, in 2006 and 2008.

Year and sex	*Minimum number*	*Abundance estimate*[a]	*SE* ($\hat{N}$)	*No. detected at crossings*	*Population detected at crossings (%)*[b]
2006					
males	19	30.2	7.3	7	23.2
females	24	32.3	4.9	4	12.4
total	43	62.6	9.0	11	17.6
2008					
males	22	28.3	4.1	4	14.1
females	41	53.5	5.7	5	9.3
total	63	81.8	7.2	9	11.0

[a]*Model-averaged abundance estimates from Sawaya et al. (2012).*
[b]*Estimated by dividing the number detected at the wildlife crossings by the abundance estimate.*

need to know whether wildlife crossings provide connectivity for individuals and populations. Rarely has empirical data on individual use of wildlife crossings been collected that provides population-level context to those movements (Corlatti et al. 2009; Kaplan 2009). Ours is the first in-depth examination of individual movements, spatial and temporal patterns of use, and population-level connectivity afforded by wildlife crossing structures. On the basis of our data, we conclude that crossing structures provide connectivity for ursid populations.

Although many of the hair samples we collected at crossings could not be used in genetic analyses, we were able to identify individuals from 37% of grizzly and 33% of black bear passages; thus, we had a conservative minimum count of bears that used wildlife crossings to traverse the TCH.

An examination of spatial patterns of individual bear use of wildlife crossing structures revealed that the type of crossing structure is important in determining where certain species are likely to cross. A much higher percentage of male and female grizzly bears used large, open crossings than black bears, whereas black bears used smaller, more constricted crossings more often than grizzly bears (Fig. 2). These findings are consistent with track-pad counts of Clevenger and Waltho (2005). Considering the high use of individual grizzly bears of more open, less constricted crossings, we recommend transportation planners and engineers consider overpasses and open-span underpasses when constructing crossings for grizzly bears. It appears that black bears are more adaptable and use a wider variety of crossing types than grizzly bears (Fig. 2), so mitigation targeted for black bears could involve a broader array of smaller crossing types.

Given the high degree of variability in the number of passages per individual (Supporting Information), it was surprising to find that the number of passages determined from track-pad counts was highly correlated with the number of individuals for both bear species (Fig. 1). This provides some independent validity to studies of crossing structure effectiveness that make assumptions about higher-order processes solely on the basis of track-count data. Our results demonstrate that wildlife crossings provide spatial connectivity by allowing frequent movements by a number of individuals in a variety of locations and through a number of different types of crossing structures.

We also found some interesting temporal patterns. The peak in grizzly and black bear passages in July (Fig. 3) was not surprising because bears would use crossings most in midsummer because it corresponds with mating season, dispersal, and the highest level of foraging activity in the montane valley bottom habitat. We also predicted an abrupt decline in bear use of the crossings as movements decreased due to increased foraging efficiency after buffaloberry (*Shepherdia canadensis*) patches ripen in late July (Hamer & Herrero 1987). The number of passages we recorded per month at crossings also was highly correlated with the number of individuals detected per month (Fig. 3).

The number of male and female black and grizzly bears that used crossings was surprisingly consistent across years (Table 1), especially when considering the upward trend in grizzly bear passages and the recent downward trend in black bear passages (Supporting Information). These opposing trends are complicated by the apparent relation between the number of track-pad detections and number of individuals (Figs. 1 & 3). The number of grizzly and black bears that used passages was fairly constant across years (Table 1). A very high percentage of grizzly bears used wildlife crossings from year to year, but we resampled far fewer black bears across years. The upward trend in grizzly bear passages coupled with the relatively stable number of individuals that used crossing structures suggests the increase in grizzly bear use may be explained by increasingly frequent use by a few individuals that disproportionately used crossing structures. Previous researchers have proposed that there may be a strong learning curve for some species to find and use wildlife crossings, and the strong upward trend we found (Supporting Information) shows the importance of long-term monitoring of crossing structures (Clevenger & Waltho 2005; Gagnon et al. 2011).

We provided a population-level context to our wildlife crossing data by obtaining precise estimates of abundance from a previous study, Sawaya et al. (2012), and directly comparing estimates with the minimum number of individuals we detected with hair sampling. Results of Hastings' (1993) examination of the complex interactions between dispersal and population dynamics with logistic equations suggest that discrete patches are demographically connected (i.e., coupled) if $\geq$10% of the population migrates between patches (Waples & Gaggiotti 2006; Lowe & Allendorf 2010). Relatively large percentages of the populations of grizzly (15–20%) and black bears (11–18%) in the Bow Valley used wildlife crossings to traverse between the north and south sides of the TCH. These minimum percentages are especially conservative when considering that our counts of bears that used crossings were absolute minimum numbers and these numbers were divided by maximum population sizes (i.e., superpopulation estimates). Also, many bears are unlikely to have home ranges overlapping or bordering the TCH; therefore, most bears would have no need to use the crossings to access food or mates. Regardless, nearly equal proportions of males and females of both species were detected at crossings in 2 separate years; a particularly encouraging finding because Proctor et al. (2005) found significant fragmentation effects and male-biased dispersal of grizzly bears across a major east–west highway in Alberta and British Columbia, Canada.

Although the minimum numbers of individuals that used crossings were relatively consistent from year to year, the population estimates for grizzly bears decreased and the estimates for black bears increased from 2006 to 2008. Changes in abundance explain much of the variability in minimum estimates of the proportions of individuals using crossings between years, but the opposing trend shown in passages from track pads (Supporting Information) reinforces the evidence that the number of passages is driven by a few individuals, irrespective of abundance. It is clear that it takes time for grizzly bears to learn how and where to incorporate wildlife crossings into home range movements. But as grizzly bears learn to use crossing structures it appears they will use crossings with more regularity. In situations where adult survival is low (e.g., hunted populations), grizzly bears may not survive long enough to learn to use wildlife crossings; therefore, crossings may not be as effective for unprotected populations as they are for protected populations.

Ideally, wildlife crossings should increase the permeability of roads and, therefore, survival of animals that live near them, but direct and indirect effects of road mitigation are complicated and difficult to evaluate without premitigation data (Roedenbeck et al. 2007). Wildlife crossings can positively affect bear survival by reducing roadkill, increasing access to food and shelter, and allowing escape from predation by other bears. Repeated visual observations of bears foraging in the small strip of riparian habitat between the highway and the Bow River suggest wildlife crossings in BNP play a role in allowing access to seasonal food resources that may be especially important to one of the most fragmented, food-stressed, and human-influenced populations of grizzly bears on Earth (Gibeau et al. 2002; Chruszcz et al. 2003). Even though just a few individuals accounted for the majority of female grizzly and black bear crossings in our study, their use of crossings could be crucial to maintaining bear population viability because even slight changes in adult female survival can strongly affect population growth rates for grizzly and black bears in BNP (Hebblewhite et al. 2003; Garshelis et al. 2005).

Indirect effects of road mitigation are rarely considered, but they could be as influential on population viability as direct effects. Stress can affect physiology, behavior, and demography of wildlife (Romero 2004). Animals that use crossings may experience reduced stress, which may lead to increased health (i.e., survival) and reproductive fitness. Survival may be negatively affected if wildlife crossings allow movements into areas with high habitat quality and high mortality (e.g., railways, urban developments). Wildlife crossings are no guaranteed solution for landscape and species conservation and the potential merits of building each crossing should be weighed against the costs and potential direct and indirect effects of road mitigation.

On the basis of our results, we suggest wildlife crossings provide connectivity for grizzly and black bear populations in BNP. Further study is warranted to understand the ability of wildlife crossings to prevent genetic isolation and enhance population viability. The one-to-ten-migrant-per-generation rule of thumb proposes a threshold of genetic interchange that should minimize short-term effects of inbreeding while allowing for local adaptive differentiation (Mills & Allendorf 1996; Wang 2004). Although movement does not necessarily translate to the flow of genes (Riley et al. 2006; Strasburg 2006), wildlife crossings may help maintain genetic connectivity. In short, our results demonstrate the ability of wildlife crossing structures to provide spatial and temporal connectivity for wildlife populations across a major transcontinental transportation corridor.

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Supporting Information

Map of Bow Valley study area and sampling locations in Banff National Park, Alberta (Appendix S1), summary of noninvasive genetic sampling effort and collection success (Appendix S2), description of methods of genetic analyses and results (Appendix S3), number of grizzly and black bear passages at wildlife crossing structures between 1997 and 2008 (Appendix S4), and descriptive statistics for frequency of passages at wildlife crossing structures by individual grizzly and black bears (Appendix S5). The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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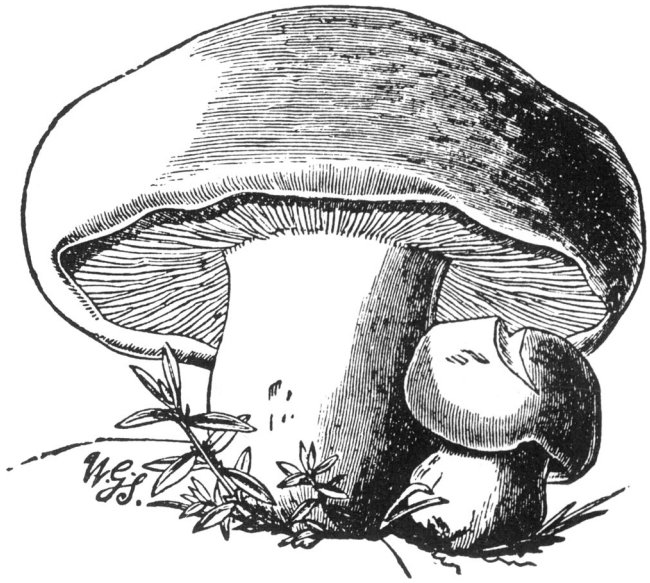
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