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Large carnivores are vulnerable to road effects because of their great mobility and extensive spatial requirements for survival. Wildlife crossing structures have mitigated harmful effects of roads for ungulate species, but there is limited information on how effective these structures are for large predators. We investigated the response of cougars *Puma concolor* to wildlife crossing structures along 45 kilometers of the Trans-Canada highway in Banff National Park, Alberta, Canada. Twenty-two crossing structures were monitored year-round for wildlife passage during 1996-2000. Cougar consistently used the wildlife crossing structures more than expected during winter months and less than expected during the summer. There was a significant positive correlation between passages made by cougar through wildlife crossing structures and those made by mule deer *Odocoileus hemionus* and white-tailed deer *O. virginianus*. There was no correlation between cougar and human use of the wildlife crossing structures. Cougar use of the five structure types differed from that expected. Open-span bridge underpasses were used more than expected, whereas creek bridge underpasses were used in proportion to their availability. All other crossing structure types were used significantly less than expected. The wildlife crossing structures that received the highest numbers of cougar passages were those situated close to high quality cougar habitat. The pattern of structure use was partly explained by the quality and distribution of cougar habitat near the structures as opposed to their physical features. Our results indicated that cougars tended to use underpasses more than wildlife overpass structures, and our study documents that cougars used crossing structures in a way that ensures habitat connectivity.

Key words: Alberta, Banff National Park, cougar, highway mitigation, performance evaluation, Puma concolor, wildlife crossing structure

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The impacts of roads on the environment are well documented and gaining increasing attention worldwide (Bennett 1991, Evink, Zeigler, Garrett & Berry 1996, Canters 1997, Forman & Alexander 1998, Hourdequin 2000). Aside from roads benefiting wildlife as habitat for plants or as corridors through the landscape, they can also disrupt animal movements, eliminate and alienate their habitat, and represent a source of mortality (see Spellerberg & Morrison 1998, Forman & Alexander 1998). Furthermore, as roads are upgraded to accommodate greater traffic volume, the rate of successful wildlife crossing decreases significantly (Barnett, How & Humphreys 1978, Swihart & Slade 1984, Brandenburg 1996, Ruediger 1996), becoming in some cases the leading cause of wildlife mortality (Maehr, Land & Roelke 1991, Calvo & Silvy 1996, Clarke, White & Harris 1998, Haxton 2000).

In view of their great mobility and extensive spatial requirements for survival, large carnivores are vulnerable to road effects (Noss, Quigley, Hornocker, Merrill & Paquet 1996, Servheen, Waller & Kasworm 1998). Currently many large predators are a source of conservation concern (Weaver, Paquet & Ruggiero 1996, Clevenger, Purroy & Campos 1997, Breitenmoser 1998, Corsi, Dupre & Boitani 1999) and the need to protect them from the harmful consequences of roads is paramount. The impacts which roads can have on populations of large predators is perhaps best illustrated by mortality statistics. The Ljubljana-Postojna highway in Slovenia opened in 1972, and by 1990 at least nine brown bears *Ursus arctos* had been killed by motor vehicles (Kaczensky, Knauer, Huber, Jonosovic & Adamic 1996). Similar mortality rates were reported for brown bears along major highways in Croatia (Huber, Kusak & Frkovic 1998). In both Slovenia and Croatia, high-speed motorways were believed to be barriers to large carnivore movements. Highways were responsible for nearly half of all documented mortality among Florida panthers *Puma concolor coryi* (Maehr et al. 1991). In southern California, the single most important cause of cougar *P. concolor* mortality was from motor vehicles (Beier & Barrett 1991).

Attempts to increase barrier permeability across road structures can be found in some road construction and upgrade projects. Despite the obvious need for information on the effectiveness of highway mitigation measures such as wildlife crossing structures (underpasses and overpasses) and fencing for large carnivores, most studies addressing this matter up until now have focused on ungulates (Reed, Woodward & Pojar 1975, Ballon 1985, Singer & Doherty 1985, Woods 1989, Groot Bruinderink & Hazebroek 1996, Putman 1997). Presently there is limited information on the efficacy of wildlife crossing structures for large carnivores (Foster & Humphrey 1995, Land & Lotz 1996, Clevenger & Waltho 2000). Initiatives such as the TEA-21 bill in the USA and program COST-341 in the European Union have heightened the concern for sustainable transport systems and incorporating mitigation passages in transportation planning schemes (U.S. Department of Transportation 1999, Button, Nijkamp & Priemus 1998). Decision-making by land managers and transportation planners regarding design requirements for effective structures is hampered by the dearth of information currently available.

The purpose of our study was to assess cougar use and response to wildlife crossing structures in order to establish how successful they were at mitigating the negative impacts of a major transportation corridor. We addressed the following questions: 1) whether there was a seasonal pattern to cougar use of the wildlife crossing structures; 2) whether a correlation existed between the wildlife crossing structures cougars use and those used by their main prey, white-tailed deer *Odocoileus virginianus* and mule deer *O. hemionus*; 3) how cougar reacted to certain wildlife crossing structures that were heavily used by humans; and 4) whether cougars selected for a particular type of wildlife crossing structure when accessing habitats separated by the transportation corridor.

Methods

Study area

We conducted the research in the Trans-Canada highway transportation corridor, situated in the Bow River Valley of Banff National Park (BNP) approximately 100 km west of Calgary, Alberta (Fig. 1). The highway is a major commercial motorway between Calgary and Vancouver. Annual average daily traffic volume at the park east entrance was 14,600 vehicles/day in 1998 and increasing at a rate of 3% per year (Highway Services, Parks Canada, Banff, Alberta). The first 45 kilometers of the highway (see Fig. 1) from the eastern park boundary (phase 1&2 and 3A) has four lanes and is bordered on both sides by a 2.4 m high wildlife-exclusion fence (phase 1&2 completed in 1988, phase 3A in late 1997). The fenced portion constitutes a potential barrier to large mammal movement. To mitigate this barrier effect, highway engineers constructed 20 wildlife underpasses and two wildlife overpasses. The effectiveness of such structures to facilitate large carnivore movements, however, is unknown.

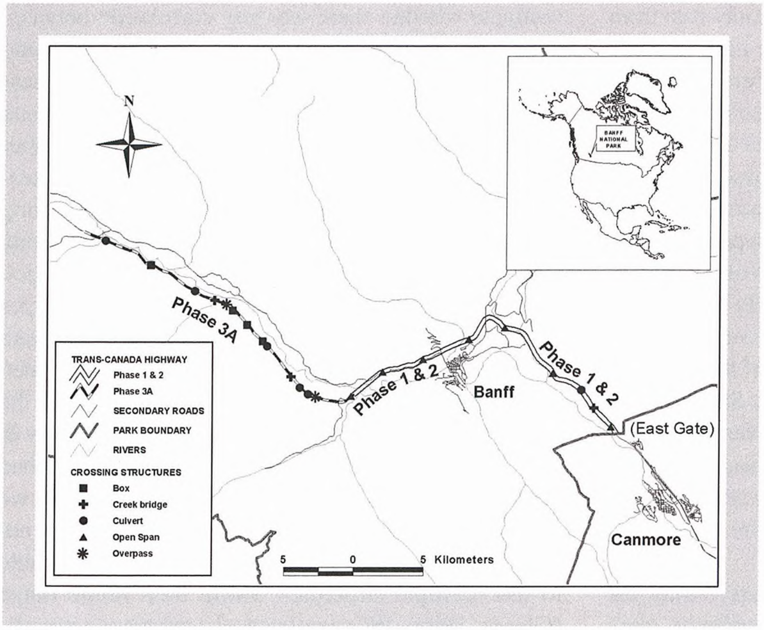

Figure 1. Location of the study area and the 22 wildlife crossing structures along the Trans-Canada highway, Banff National Park, Alberta, Canada.

The highway bisects critical montane (valley bottom) and subalpine habitats in the Bow River Valley on which many forest-associated mammals depend as over 70% of montane habitat in BNP is found in the corridor. BNP is situated within the Continental Ranges of the Southern Rocky Mountains. Elevations range from 1,300 m to over 3,000 m a.s.l. Valley floor width varies within 2-5 km. The climate is continental and characterised by relatively long winters and short summers (Holland & Coen 1983). Mean maximum snowfall at the town of Banff is 112 cm.

The Bow Valley is an important wintering area for populations of mule deer and white-tailed deer that migrate to subalpine elevations and return to the valley floor in winter. Vegetation consists of forests dominated by Douglas fir *Pseudotsuga menziesii*, white spruce *Picea glauca*, lodgepole pine *Pinus contorta*, aspen *Populus tremuloides* and natural grasslands.

Cougars inhabit the Bow Valley, and their movements correspond with the seasonal movements of both deer species (Jalkotzy & Ross 1991). Cougars prey on elk *Cervus elaphus*, mule deer and white-tailed deer; however, mule deer are the main prey of the cougar in the Rockies. Jalkotzy & Ross (1991) observed that 20 out of 32 cougar kills recorded in the Rocky Mountains were mule deer.

Data collection and analysis

We monitored cougar use of crossing structures between November 1996 and July 2000 (Table 1). As a consequence of phase 3A crossing structures not being completed until November 1997, and to avoid unequal

Table 1. Cougar frequency of passage and habitat quality indices at wildlife crossing structures in Banff National Park, Alberta, Canada, during 1997-2000. Wildlife overpasses are listed in italics along with neighbouring underpasses located within 2 km. The habitat quality index gives the summed habitat quality ratings (see Holland & Coen 1983) within a 1,000 m buffer of the wildlife crossing structure.

Crossing structure	Phase	Design type	No of passes	Habitat quality index
East gate	1&2	Open-span	43	92
Carrot	1&2	Creek bridge	20	183
Morrison	1&2	Metal culvert	32	198
Duthil	1&2	Open-span	46	180
Powerhouse	1&2	Open-span	27	117
Buffalo	1&2	Open-span	8	165
Vermilion	1&2	Open-span	25	154
Edith	1&2	Open-span	36	217
Healy	1&2	Open-span	34	105
Wolverine OP	*3A*	*Overpass*	*11*	*95*
Wolverine UP	*3A*	*Metal culvert*	*8*	*95*
Bourgeau	*3A*	*Metal culvert*	*12*	*115*
Wolverine Creek	3A	Creek bridge	15	131
Massive	3A	Metal culvert	5	86
Sawback	3A	Box culvert	2	79
Pilot	*3A*	*Box culvert*	*5*	*59*
Redearth UP	*3A*	*Box culvert*	*8*	64
Redearth OP	*3A*	*Overpass*	*0*	*72*
Redearth Creek	*3A*	*Creek bridge*	*12*	*79*
Copper	*3A*	*Metal culvert*	*14*	*96*
Johnston	3A	Box culvert	14	76
Castle	–*	Metal culvert	0	107

* This crossing was constructed in 1991, after completion of phase 1&2 but prior to phase 3A.

sampling intensities between structures, only data from November 1997 and onwards could be used in some of our analyses. There were four different designs among 22 crossing structures: seven open-span bridge underpasses (3 m high, 11 m wide), three creek bridge underpasses (open-span bridge underpasses with running water), six metal culvert underpasses (4 m high, 7 m wide); and four concrete box culvert type underpasses (2.5 m high, 3 m wide). Two 50-m wide overpasses were constructed on phase 3A, largely in response to concerns that phase 1&2 underpasses were not effective for mitigating barrier effects of the highway for large carnivores (Banff-Bow Valley Study 1996). All underpasses had dirt substrates. The overpasses were vegetated with a 10 species native grass seed mix, shrubs of *Elaeagnus commutata, Rosa acicularis, Shepherdia canadensis* and *Salix* sp., and white spruce trees 2-3 m high.

We measured passage at the structures using the methods described by Bider (1968). Specifically, track sections 2 m long and as wide as the structure were set at both ends to detect movement through the structures. Species presence (cougars and deer), their abundance and human activity counts were recorded at each tracking section during each underpass visit. Tracking material consisted of a dry, loamy mix of sand, silt and clay, 3-4 cm deep. At 3-4 day intervals each structure was visited and the tracking medium classified as adequate or inadequate depending on our ability to read tracks clearly. Through-passages were recorded for individuals if tracks in the same direction were present on both track sections. We then raked the track sections smooth in preparation for the next visit. At the overpasses, infra-red operated 35 mm cameras (Trailmaster™, Goodson and Associates, Inc., Lenexa, Kansas, USA) were used as a supplement to, rather than replacement of, the track section monitoring (Kucera & Barrett 1993).

To investigate whether there was a seasonal pattern in cougar use of the wildlife crossing structures, we grouped the data into the following seasons: autumn (September-November), winter (December-February), spring (March-May), and summer (June-August), and χ^2-statistics were calculated to test for significant seasonality in cougar use of crossing structures.

To ascertain whether there was any correlation between the type of wildlife crossing structure used by cougars and those used by both species of deer (the main prey of cougars), the number of visits made by each species to the 22 wildlife crossing structures was calculated and a Pearson's correlation was used to test for any association. Pearson's correlation test was also used to investigate whether there was any correlation between cougar and human (combined passages of hikers and bicyclists) use of wildlife crossing structures. To assess whether seasonality was a factor influencing cougar and human use of wildlife crossing structures, the number of passages made at Edith underpass during the four seasons by both cougars and humans was compared using a Pearson's correlation test. Finally, expected crossing structure use by cougars assumed random selection based on the proportional availability of the four types in the study area. The four crossing structure types were intermixed throughout the 45 kilometers of mitigated highway. Given the estimated number of cougars in the Bow Valley and average home range size (Jalkotzy & Ross 1991, Gloyne 1999), we assumed that cougars had access to different crossing structure types. Further, we recognize that sampling use of the structures was not independent as at least four resident cougars were able to use multiple structures within their home range (Gloyne 1999). We calculated χ^2-statistics to investigate whether there was a significant difference between the overall expected utilization of wildlife crossing structure types by cougars and their observed frequency of use. In case of significance ($P < 0.05$), observed and expected comparisons of structure types were made using the Bonferroni Z-statistic (Zar 1999).

Results

Cougar consistently used the wildlife crossing structures more than expected during winter and less than expected during summer ($\chi^2 = 95.40$, df = 9, $P < 0.0001$; Table 2); use during spring and autumn was not significantly different from that expected without seasonality. There was a significant positive correlation between passages made by cougar through wildlife crossing struc-

Table 2. Observed frequency of seasonal cougar passage at wildlife crossing structures in Banff National Park, Alberta, Canada, during 1997-2000. The expected passage frequency with no seasonality was 32.5 ($\chi^2 = 95.40$, df = 9, $P < 0.0001$).

Season	Year	Observed passage frequency
Summer	1997	5
Autumn	1997	8
Winter	1997/1998	43
Spring	1998	15
Summer	1998	6
Autumn	1998	21
Winter	1998/1999	44
Spring	1999	39
Summer	1999	77
Autumn	1999	67
Total		325

Table 3. Observed and expected frequency of cougar passage through wildlife crossing structure design types in Banff National Park, Alberta, Canada, during 1997-2000.

Design types	N	Observed passage frequency	Expected passage frequency[1]	Proportion used	Proportion available	P^2
Open span bridge	7	219	120	0.580	0.318	+ ****
Creek bridge	3	47	52	0.124	0.136	0
Metal culvert	6	71	103	0.188	0.272	- ***
Overpass	2	11	34	0.029	0.181	- ****
Box culvert	4	29	68	0.077	0.181	- ****
Total	22	377	377			

[1] Expected passage frequency assumes even distribution between design types (χ^2 = 48.34, P < 0.0001, df = 4).
[2] - = used less than expected (* = P < 0.05, ** = P < 0.01, *** = P < 0.001, **** = P < 0.0001);
0 = used in proportion to availability;
+ = used more than expected (* = P < 0.05, ** = P < 0.01, *** = P < 0.001, **** = P < 0.0001).

tures and those made by white-tailed and mule deer (r = 0.624, P < 0.002).

Cougar and human use of the wildlife crossing structures were not correlated (r = 0.274, P = 0.216). However, it is interesting to note that the third most important crossing structure for cougars in terms of frequency of use (Edith underpass) had the highest amount of human activity. At the Edith underpass there was no significant correlation between cougar and human use (r = -0.156, P = 0.148).

A total of 377 cougar passages at the crossing structures were used to determine their response to the different types available in the study area. Cougar use of the five structure types differed from that expected (χ^2 = 48.34, df = 4, P < 0.0001; Table 3). Open-span bridge underpasses were used more than expected, whereas creek bridge underpasses were used in proportion to their availability. All other crossing structure types (metal culverts, overpasses, box culverts) were used significantly less than expected.

To test whether crossing structure use could be explained by the quality and distribution of cougar habitat near the structures as opposed to their physical features, we tested habitat quality against structure design type. The difference between the two variables bordered significance (ANOVA: F = 2.91, df = 4, P = 0.053). When comparing the means among the structure types, only habitat quality between the open-span and box culverts approached significance (Bonferroni method: P = 0.06).

Discussion

There was a clear seasonal pattern in cougar use of the wildlife crossing structures, passage frequency being higher than expected during the winter and less than would have been expected (assuming no seasonality) during the summer. In a study on cougars carried out in the Big Horn Mountains in Wyoming, USA, Logan & Irwin (1985) found that there was a marked difference in the mean seasonal elevations of cougar distribution. In summer the average elevation of cougar occurrence was 2,039 m a.s.l., dropping to 1,933 m a.s.l. in the autumn. In the winter cougars were typically found at 1,881 m a.s.l., but it was during the spring that they were recorded at the lowest mean elevation of 1,837 m a.s.l.

The pattern of seasonal elevation change described above and by Jalkotzy & Ross (1991) most likely occurred in the Bow Valley during our study as reflected by the seasonal variation in the number of passages cougars make through the wildlife crossing structures. Without these mitigation measures in place, cougars would undoubtedly be more reluctant to cross the busy highway and would be put at great risk of being hit by motor vehicles while in the valley during winter and moving to and from higher elevations the remainder of the year (Maehr et al. 1991, Beier 1995, Sweanor, Logan & Hornocker 2000).

Mule deer and white-tailed deer are key components of cougar diet (Beier & Barrett 1991, Ross, Jalkotzy & Festa-Bianchet 1997); consequently, when cougar select a home range, an area where deer are present in reasonable numbers is an important consideration. In the BNP biophysical land classification, Holland & Coen (1983) used the numbers of deer present in a particular site as a guide to classify the site as either high, medium or low quality habitat for cougar.

Within the Bow Valley the wildlife crossing structures that received the highest numbers of cougar passages were those situated close to high quality cougar habitat, i.e., the parts of their home range which we would expect cougars to use most. Passage frequency and habitat quality values were highly correlated (Spearman's rank correlation: r = 0.605, P = 0.002). By definition based on Holland & Coen's (1983) classification, sizeable herds of deer are likely to be present within those same areas where cougars hunt and consequently will use the same wildlife crossing structures as cougar. Our results showed a positive correlation between these two variables with cougar and deer tending to use the same wildlife crossing structures.

Human use of the wildlife crossing structures in our study area is largely determined by the distance of the structures from the Banff townsite and the proximity of hiking and bike trails. The coincidence of cougar and human use at Edith underpass is contrary to many studies that suggest that large carnivores tend to avoid areas of human activity if possible (van Dyke, Brocke, Shaw, Ackerman, Hemker & Lindzey 1986, Mattson, Knight & Blanchard 1987, Jalkotzy & Ross 1993). Recent work in the same study area showed that large carnivores, including cougars, were less likely to use underpasses that had high levels of human activity (Clevenger & Waltho 2000). However, cougars exhibit a high degree of behavioural plasticity (Weaver et al. 1996) and elsewhere have been found to use habitat corridors in landscapes highly fragmented by urbanization (Beier 1995).

It is feasible that Edith underpass was the only crossing point within an individual cougar's home range and that it had little choice but to use the underpass despite frequent human activity, which was clearly not an absolute deterrent. This, however, may be possible by mutual avoidance as cougars are crepuscular and therefore mainly active at dawn and dusk (Seidensticker, Hornocker, Wiles & Messick 1973, van Dyke et al. 1986, Beier 1995), whereas human use of the underpasses is almost exclusively diurnal (A. Clevenger, pers. obs.).

Cougars had a tendency to use open-span underpasses more than other crossing structure types in the study area. Conversely, they used all other types, except creek bridges, less than expected. The structure type selection we observed could possibly be due to a greater abundance of cougars lower in the Bow Valley along phase 1&2. However, a study analysing the cougar tracks collected from the wildlife crossing structures suggested that there were four separate cougars using the 22 structures and they tended to use them exclusively. For the most part cougar home ranges did not overlap where the wildlife crossing structures were located, with the exception of two individuals using the same structures immediately west of the Banff townsite (Gloyne 1999). Although we used passage frequency data from the same period for both phases, higher passage at the open-span underpasses on phase 1&2 structures could be attributed to greater familiarity and longer adaptation time (ca 12 years) compared to the other newer structures located nearly exclusively on phase 3A (<3 years).

There are virtually no published studies comparing the efficacy of passage types, particularly underpass vs overpass designs. An important and resounding variable in mitigation planning is structure cost and where to best invest mitigation funds. Our results indicated that cougars tended to use underpasses (primarily open-span and to a lesser extent creek bridges) over the more costly wildlife overpass structures. Furthermore, a comparison of cougar use of overpasses with neighbouring underpasses located within 2 km (and therefore potentially available to the same individuals) confirmed that underpasses received greater use (see Table 1). Some features of the overpasses may discourage cougar use. The arched design of the BNP overpasses obstructs cross-highway field of view for cougars in addition to making them climb up into the 'unknown' while crossing. Others have stressed the importance for cougars to be able to view the habitat on the opposite side of a road prior to using passages (Foster & Humphrey 1995, Beier 1995). Cougars may also be inhibited by the lack of dense vegetation and overhead cover on the relatively new overpasses and therefore found the covered underpasses more secure routes of travel.

The function of a wildlife crossing structure essentially is to reduce road-related mortality and increase barrier permeability. We believe there are two main criteria for successful crossing structures and both are related to the intended purpose of the structures: reducing mortality and retaining natural connectivity.

Highway mortality has not been a major cause of death for cougars in BNP. Records kept since 1981 reported that five cougars were killed on the Trans-Canada highway, all relatively recently (BNP Warden Service, Banff, Alberta). Two cougars were killed on an unmitigated stretch of the highway, while three were killed on a fenced, mitigated section relatively close to crossing structures. The latter three mortalities indicate that the structures are not infallible and that the fence is not an insurmountable obstacle for cougars. Vehicle-related mortality has not been a major cause of death for cougars in BNP, but given the number of times they have used the crossing structures since our monitoring began in November 1996 (N = 520 passes), the presence of crossing structures has undoubtedly reduced the potential for cougars to be killed on the highway and allowed cougars to cross the highway to access parts of their home range.

Large carnivores are sensitive to the barrier effect caused by highways (Sweanor et al. 2000). Being able to effectively minimise these effects is essential, especially in areas where large carnivores are at risk from being extirpated. The crossing structures in BNP were effective for cougars in the sense that they used them regularly and in a way that provided connectivity between habitats on both sides of the highway. Although highway mortality has not been a major cause of mortality for cougars in our study area, the fact that three animals were killed on a mitigated stretch of highway highlights the importance of fence maintenance and the need for a more effective fence design to discourage climbing (or jumping) carnivores like cougars. Increasing the height of any new fences or installing an outrigger on the existing fence, i.e., a 1-m extension on top and at a right-angle away from the fence, would likely deter cougars from climbing over the fence and help prevent further cougar mortality.

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