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Performance indices to identify attributes of highway crossing structures facilitating movement of large mammals

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Abstract

Studies assessing the efficacy of wildlife crossing structures often lead to spurious results because of their failure to address masking effects of confounding variables. Confounding variables include variation in human activity, density of crossing structures along the highway corridor, and equality of species' perceived access to each crossing structure. We investigated these issues for wide-ranging large carnivores and their prey species in Banff National Park, Alberta, using data obtained from systematic, year-round monitoring of 13 newly constructed crossing structures for wildlife (underpasses and overpasses) for 34 months post-construction. We standardized the first confounding variable by selecting crossing structures remote from areas of human activity. The second confounding variable we standardized by developing probability models of crossing structure usage assuming habitat homogeneity. We standardized the third confounding variable by developing species-specific, performance indices of crossing structures (= observed through passage usage–expected through passage usage). We regressed the species performance indices against 13 crossing structure variables encompassing structural, landscape, and human activity. Our results suggest that in absence of high human activity structural attributes best explained the performance indices for both large predator and prey species, while landscape and human-related factors were of secondary importance. Crossing structures that were high, wide and short in length strongly influenced passage by grizzly bears *Ursus arctos*, wolves *Canis lupus*, elk *Cervus elaphus*, and deer *Odocoileus* sp. More constricted crossing structures were favoured by black bears *Ursus americanus* and cougars *Puma concolor*. Distance to cover was the most important crossing structure landscape attribute for cougars (negative correlation) and was a significant factor determining passage for grizzly bears, elk and deer (all positive correlations). Our findings underscore the importance of: (a) integrating temporal and spatial variability a priori when addressing the efficacy of crossing structures, and; (b) demonstrate that species respond differently to crossing structure features. In light of these results, we suggest that to maximize connectivity across roads for multiple large mammal species, road construction schemes should include a diversity of crossing structures of mixed size classes. Mitigation planning in a multiple-species ecosystem is likely to be a challenging endeavour and long-term research will aid in the decision-making process.

Keywords: Banff National Park; Habitat fragmentation; Mammals; Road ecology; Wildlife crossing structure

1. Introduction

Over the last decade, federal land management and transportation agencies have become increasingly aware of the effects that roads have on wildlife (Bennett, 1991; Canters, 1997; Transportation Research Board, 1997). Significant advances in understanding these impacts have been made; however, the means to adequately mitigate these impacts are slower in coming (Evink, 2002; Transportation Research Board, 2002a).

In order to mitigate the effects of roads, crossing structures for wildlife are being designed and incorporated into road construction and improvement projects (Keller and Pfister, 1997; Spellerberg, 2002; Forman et al., 2003; Cain et al., 2003). Although federal land management and state transportation agencies are building costly structures for wildlife connectivity, long-term monitoring to determine the most effective approaches has not taken place (Evink, 2002). Currently

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there is limited knowledge of effective and affordable crossing structure designs for most wildlife species (Romin and Bissonette, 1996; Underhill and Angold, 2000; Transportation Research Board, 2002b).

One reason for the lack of available information is because few mitigation programs have implemented monitoring programs incorporating sufficient experimental design into pre- and post- construction evaluation. Thus, results obtained from most studies remain observational at best. Furthermore, those studies that collected data in more robust manners generally failed to address the need for wildlife habituation to such large-scale landscape change (Opdam, 1997). Habituation periods may take several years depending on the species as species experience, learn, and adjust their own behaviours to the wildlife structures (Clevenger et al., 2002a). The short monitoring periods frequently implemented are simply insufficient to draw reliable conclusions from (Forman et al., 2003).

Further, many earlier studies focused primarily on crossing structure relationships of single species, paying limited attention to multispecies or community level responses (see Forman et al., 2003 for review). Because poor crossing structure designs have the potential to decouple ecosystem level processes, for example, in the formation of prey-refuge zones in predator-prey relations (Woods et al., 1996; Clevenger and Waltho, 2000), most crossing structure designs are "selectively permeable". The apparent success of monitoring programs aimed at single species may fail to recognize the barrier effects imposed on other non-target species. Thus, systems can be severely compromised if land managers and transportation planners rely on simple extrapolation from data on individual species. To date we are unaware of any monitoring program that addresses this issue specifically.

Information deficiencies may also be due to the masking effects of confounding variables not considered in study designs (Underwood, 1997). Confounding variables are sources of variation that may bias or even mask the efficacy of one crossing structure design over another. Such variables include the variation in human use of the crossings (Clevenger and Waltho, 2000), density of crossing structures along the highway corridor, and the equality of species' perceived access to each crossing structure. If, for example, a species perceives crossing structure A as good, but not accessible, then it may choose crossing structure B (whose design is not favoured) for accessibility reasons alone. To control for these factors a robust experimental design requires a sufficiently large number of crossing structures - much larger than is realistically feasible for a public works project to finance.

In this paper, we investigate these issues using data obtained from systematic, year-round monitoring of 13 newly constructed crossing structures (underpasses and overpasses) for 34 months post-construction. These new crossing structures are sufficiently remote from centres of human activity (e.g., the town of Banff) that human use is significantly reduced and therefore not expected to be a dominant factor (Clevenger and Waltho, 2000). We standardized against the remaining confounding variables by developing species-specific, performance indices, and then tested for significant correlations against each of the crossing structure attributes. We then rank-ordered the significant coefficient of determinations and assumed that the higher the coefficient the greater importance that attribute had in influencing species passage (positive or negative). A multivariate analysis of this type allowed us to explore the extent and influence of numerous attributes associated with the crossing structures independent of confounding variables.

Our design allowed us to address relevant and current questions concerning the efficacy of crossing structures; specifically: (i) How to ascertain the strengths and weaknesses of design characteristics for a multiple large mammal species? and, (ii) What are the requirements for effective crossing structures designed for wide-ranging large carnivores and their prey species? Information on the effectiveness of mitigation measures in reducing barrier effects will provide critical information needed for future mitigation planning in the Bow Valley transportation corridor in Banff National Park.

2. Study area and methods

2.1. Study area

Our study was situated in the Bow River Valley along the Trans-Canada Highway (TCH) corridor in Banff National Park (BNP), Alberta, located approximately 120 km west of Calgary (Fig. 1). The TCH is the major transportation corridor through the park (park length = 76 km) carrying an estimated annual average daily traffic volume of 14,940 vehicles per day in 1999 and increasing at a rate of 3% per year (Highway Service Centre, Parks Canada, Banff, Alberta).

Upgrading the TCH from two to four lanes progressed in phases. The first 45 km of the TCH from the eastern park boundary is four lanes and bordered on both sides by a 2.4 m high wildlife exclusion fence (phases 1, 2 and 3A). Phase 1 and 2 (= 27 km), beginning at the eastern boundary, was completed in 1988 and has 11 wildlife underpasses. The phase 1 and 2 underpasses were the focus of our previous study of factors influencing underpass use (Clevenger and Waltho, 2000). Phase 3A (= 18 km) is a continuation of the two previous phases, was completed in late 1997, and has 11 wildlife underpasses and two wildlife overpasses. The remaining 30 km to the western park boundary (Alberta – British Columbia border, phase 3B) is two lanes and unfenced. Plans are to upgrade phase 3B to four lanes with mitigation within the next five years.

2.2. Wildlife crossing structures and monitoring

Our current study involved the 13 crossing structures recently constructed within phase 3A (Fig. 1). These crossing structures constituted four different structural designs: (1) two creek bridge underpasses (3 m high and 11 m wide expanded bridges that span creeks and rivers); (2) five elliptical, metal culvert underpasses (4 m high, 7 m wide); (3) four prefabricated concrete box underpasses (2.5 m × 3.0 m), and; (4) two 50-m wide wildlife overpasses.

Each crossing structure was characterized according to 13 independent variables encompassing structural, landscape and human activity attributes (Table 1). Structural variables included crossing structure width, height, length (including central median), openness = width × height/length (Reed and Ward, 1985); and noise level = mean of A-weighted decibel readings taken at the centre-point within the crossing structure and 5 m from each end. Landscape variables included distances to: nearest forest cover, closest major drainage, Canadian Pacific Railway (CPR), townsite, and the next nearest crossing structure. Human activity was quantified at the passages (as for wildlife described below) by counts of people on foot, bike, horseback. Crossing structure configuration was characterized as divided (separated structures with central median) or undivided (one structure with no central median).

We quantified large mammal use of crossing structures using methods described by Bider (1968). Specifically, to record evidence of crossing structure use (= observed data) tracking sections (2 × 4 m) were set at both ends of each structure. Tracking material consisted of a dry, loamy mix of sand, silt and clay, 3–4 cm deep. At 3–4 day intervals each crossing structure was visited and the tracking medium classified as adequate or inadequate depending on our ability to read tracks clearly. Species presence (wolves *Canis lupus*, cougars *Puma concolor*, black bears *Ursus americanus*, grizzly bears *Ursus arctos*, deer *Odocoileus* sp., and elk *Cervus elaphus*), species abundance, and human activity counts were recorded at each tracking section during each crossing structure visit. Observed through-passages were recorded for individuals if tracks in the same direction were present on both tracking sections. Tracking sections were then raked smooth in preparation for the next visit. At the wildlife overpasses, infra-red operated 35 mm cameras (Trailmaster^{TM}, Goodson and Associates, Inc., Lenexa, Kansas, USA) were used to supplement, rather than to replace, the track pad monitoring (Kucera and Barrett, 1993). The construction of all crossing structures was completed in October 1997; data were collected from November 1997 to August 2000 (34 months). Of 4494 crossing structure monitoring visits, 157 (3.5%) were classified as incomplete for data analyses.

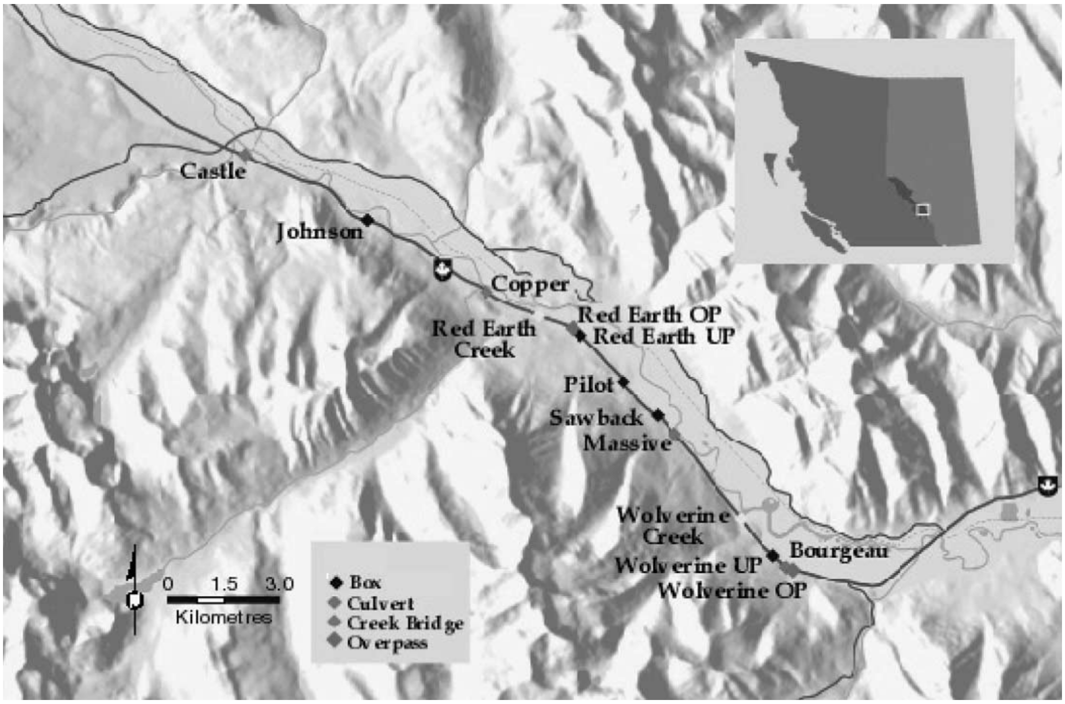

Fig. 1. Map of the study area in Banff National Park, Alberta, Canada, showing the location and type of wildlife crossing structures on phase 3A of the Trans–Canada Highway.

Table 1
Attributes of 13 wildlife crossing structures used in analysis of factors influencing wildlife passage in Banff National Park, Alberta

Attributes	Wildlife crossing structure												
	Wolverine OP	Wolverine UP	Bourgeau	Wolverine creek	Massive	Sawback	Pilot	Red Earth UP	Red Earth OP	Red Earth Creek	Copper	Johnson	Castle
Structural													
Width (m)	50.0	7.3	2.0	11.5	7.2	3.0	3.0	3.0	50.0	11.4	7.2	3.0	7.3
Height (m)	7.8	3.4	1.8	2.5	3.6	2.4	2.4	2.4	7.8	2.2	3.9	2.4	3.5
Length (m)	72.0	62.5	170.0	83.0	51.0	58.0	66.0	78.0	72.0	56.5	57.4	58.0	56.5
Openness	5.41	0.39	0.02	0.34	0.51	0.12	0.11	0.09	5.41	0.44	0.49	0.12	0.45
Noise level	52.7	55.4	74.7	66.1	54.3	58.3	56.6	56.8	54.8	71.2	54.1	55.3	64.1
Landscape (distance to)													
Crossing structure (km)	0.2	0.2	0.8	1.0	0.5	0.5	1.6	0.4	0.4	1.0	1.6	3.5	4.6
Forest cover (m)	27.0	9.0	4.0	22.0	32.0	6.0	9.0	12.0	42.0	24.0	7.5	10.5	35.4
Drainage (km)	1.64	1.41	0.63	0.0	0.0	0.37	1.77	1.25	0.86	0.0	1.0	1.77	0.3
CPR (km)	1.25	1.3	1.18	1.13	0.88	0.91	0.98	0.66	0.53	0.29	0.53	0.87	0.63
Townsite (km)	10.0	10.2	11.1	12.1	14.8	15.3	16.9	18.5	18.9	19.9	21.4	25.0	29.6
Human activity	15	9	5	4	8	14	19	22	8	97	5	7	70
Configuration	1	1	2	2	1	1	1	2	1	2	1	1	1

Notes: Height for overpasses equal to double maximum underpass height (= 3.9 m). CPR, Canadian Pacific Railway; Configuration (1 = undivided, 2 = divided); OP, overpass; UP, underpass.

With appropriate multivariate analyses (e.g., canonical and partial canonical correlation analysis), meaningful ecological relations may be teased out from the track and camera data (Sarakinos and Rasmussen, 1998). Such analyses, however, require: (a) adequate experimental design to control our confounding variables, and; (b) sufficient sampling replicates to obtain statistically meaningful results – some authors argue 30 replicates per variable (Morrison et al., 1992; Norman and Streiner, 1999). In our study both requirements were absent, i.e. manipulation or control of test variables in such a large-scale ecosystem-level study was unfeasible, and there were only 13 statistical replicates (crossing structures). We addressed both issues by developing species-specific performance indices and testing the indices against each of the crossing structure attributes.

2.3. Performance indices

We define species performance indices as the ratio of observed through-passage use to expected through-passage use. Performance indices function in such a way that the higher the index, the more effective the crossing structure appears to facilitate that species crossing. Our expected through-passage use, however, is more complex as it is defined within the context of two confounding variables: (i) variation in the density of crossing structures along the highway corridor (spatial variation), and; (ii) equality of species' perceived access to each crossing structure (spatial and seasonal variation). We address each confounding variable accordingly.

If the crossing structures were equally spaced along the length of the TCH, and the habitat template was continuously homogeneous, then we suggest the probability of large mammal species choosing any particular crossing structure in the absence of design differences to be 7.7% (i.e. $N_{\text{crossing structures}} = 13$; $P = 100/N_{\text{crossing structures}} = 0.077$). However, the distance between consecutive crossing structures is highly variable ranging from 0.24 to 3.7 km (mean distance = 1.5 km). In areas of TCH where the density of crossing structures is high, we suggest the absolute probability of any one structure being chosen is compromised by its close proximity to other nearby structures. By comparison, where crossing structures are relatively isolated from each other, we suggest the absolute probability of any one structure being chosen increases because each crossing structure approaches the only choice for the area. We therefore developed "absolute probabilities" as a function of distances between consecutive structures using the following equation:

$$P_{\text{CS}_n} = 100 \times ((\text{CS}_{n-1} + \text{CS}_{n+1})/2)/\text{CS}_{\text{total}},$$

where P_{CS_n} was the absolute probability for crossing structure (CS) n; $(\text{CS}_{n-1} + \text{C}_{\text{S}n+1})$ was the distance from crossing structure $n-1$ to $n+1$; and CS_{total} was the highway distance from the first crossing structure to the last (= 20.12 km). The absolute probabilities for any chosen crossing structure ranged from 2.7% to 18.1% (Table 2).

With respect to the second confounding variable, if the habitat template were continuously homogeneous (i.e. both spatially and temporally) then each species may have equal access to each of the crossing structures. However, the habitat template is not continuously homogeneous, but instead is fragmented and highly heterogeneous on multiple spatiotemporal scales. Mountain barriers and the seasonal flow of rivers versus ice cover divide the landscape into some permanent and some temporally isolated habitat fragments. Forest fires, meadows, aspen (*Populus tremuloides*) groves, and lodgepole pine (*Pinus contorta*) and spruce (*Picea* sp.) stands further contribute to habitat heterogeneity generating spatially and temporally dependent mosaics of shelter and food availability. Seasonal changes from winter and accumulated snow depth to summer may exacerbate habitat heterogeneity even further by limiting foraging abilities in deep snow (Telfer and Kelsall, 1984; Huggard, 1993).

Such spatial and temporal heterogeneity may be more significant when choosing an appropriate crossing structure to cross the TCH than any design features of the crossing structures themselves. If for example a crossing structure deemed favourable by design is isolated from a species' preferred habitat, then the perceived risks to use the crossing structure may dominate the decision making process of whether to use the crossing structure or not. Conversely, if the habitat quality surrounding a second inferiorly designed crossing structure is good then, by comparison to the first structure, the probability of the second structure being chosen may be significantly higher.

We approached this latter issue of spatial and temporal habitat heterogeneity with the aid of a geographic information system analysis (Environmental Systems Research Institute, 1998). From the center of each crossing structure we created buffers from 0 to 500 m, 500–1000 m, 1000–1500 m, 1500–2000 m, 2000–2500 m and 2500–3000 m. For each buffer we overlaid an ecological land classification map with five possible habitat suitability ratings (0, nil; 1, low; 2, moderate; 3, high; 4, very high) for each species per ecosite polygon (Holroyd and Van Tighem, 1983; Kansas and Raines, 1990). For a given buffer each habitat rating was multiplied by the absolute area it occupied to derive a "relative species occurrence" value. This was repeated for each buffer, at each crossing structure, for each of the six large mammal species in our study. We used seasonal habitat suitability data (winter and/or summer) to address temporal variation in the habitat template. Thus, for a given species, structures with a high proportion of high quality habitat surrounding them generate greater relative species

Table 2
Absolute and realized probabilities

Wildlife crossing structure	Absolute probabilities	Realized probabilities (as a function of buffer size)						
		0 m	500 m	1000 m	1500 m	2000 m	2500 m	3000 m
Wolverine OP	0.041	1.00	0.60	0.60	0.36	0.36	0.20	0.20
Wolverine UP	0.027	1.00	0.40	0.24	0.24	0.13	0.13	0.13
Bourgeau	0.045	1.00	1.00	0.27	0.22	0.22	0.22	0.22
Wolverine Creek	0.094	1.00	1.00	0.67	0.67	0.57	0.45	0.33
Massive	0.081	1.00	0.61	0.61	0.61	0.61	0.38	0.26
Sawback	0.052	1.00	0.39	0.39	0.39	0.24	0.24	0.24
Pilot	0.080	1.00	1.00	1.00	1.00	0.44	0.27	0.22
Red Earth UP	0.051	1.00	0.60	0.60	0.35	0.22	0.22	0.14
Red Earth OP	0.034	1.00	0.40	0.23	0.23	0.23	0.10	0.10
Red Earth Creek	0.062	1.00	1.00	0.65	0.42	0.22	0.22	0.17
Copper	0.129	1.00	1.00	1.00	1.00	0.68	0.57	0.47
Johnson	0.181	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Castle	0.126	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Absolute probabilities are the chance that any one wildlife crossing structure is selected as a function of all crossing structures present in the study. Realized probabilities are the chance opportunity that a given crossing structure is selected as a function of those crossing structures found only within the buffer.

occurrences compared to crossing structures without high quality habitat (Clevenger and Waltho, 2000).

The two confounding variables thus described occur independently of each other; however, by modelling the effects of the first variable into the second we can generate the "expected through passage usages".

If within a 500 m buffer zone a second crossing structure was found, we suggest the relative species occurrence for the target crossing structure is compromised by the probabilities of the second crossing structure being chosen instead (i.e. our first confounding variable). Thus for the Wolverine Overpass at 500 m, we expect 60% relative species occurrences because of the influence of the nearby Wolverine Underpass (Table 2; realized probabilities). At 3000 m, we expect only 20% relative species occurrence because of the further chance effect of the Bourgeau and Wolverine Creek Underpasses being used. By comparison, at Castle Underpass we expect 100% relative species occurrence even at 3000 m because no other crossing structures occur nearby. Thus, for each buffer we adjust the expected through-passage usages by the probability that, everything else being equal, the target crossing structure will be the one chosen. This step generated 78 data points ($= 6$ buffer zones $\times$ 13 crossing structures) for each species for each season (i.e. the "expected through-passage uses").

The ratio of observed through-passage use to expected through-passage use completes the performance indices. The indices function in a way that the higher the index the more effective the wildlife crossing structure appears to facilitate that species crossing.

2.4. Analyses

Using regression analyses (Jandel Scientific, 1994) we compared species performance indices against each of the crossing structure attributes, adjusting for multiple tests using Bonferroni adjustments (Waltho and Kolasa, 1996; Clevenger and Waltho, 2000). This generated 13 coefficients of determination for each species for each season. We rank ordered the coefficients of determination keeping only those that were statistically significant. We assumed that for each significant analysis ($P < 0.05$) the higher the coefficient of determination the higher the relative importance that crossing structure attribute had in influencing the passage by a particular species (positive influence or negative).

3. Results

We observed 4209 large mammal and human use through-passes (human use = 8%) from the 13 crossing structures monitored continuously from November 1997 to August 2000 (Table 3). The range in observed through-passage usage was high – the minimum observed was at Bourgeau Underpass ($n = 31$ through-passage usages) to a maximum at Red Earth Overpass ($n = 1099$). Through-passage use was effective to 91% of all approaches.

For each species, we tested species performance indices against each crossing structure attribute (seasonally dependent when applicable). The resultant statistically significant coefficients of determination are provided in Table 4.

3.1. Carnivores

At the guild level, carnivore models included summer analyses for black bear and grizzly bear, and summer and winter analyses for wolves and cougar. From these six models, 15 of 36 (42%) possible structural attributes

Table 3
Seasonal observed use of wildlife crossing structures by large mammal species in Banff National Park, Alberta, 1997–2000

Season/species	Wildlife crossing structure												
	Wolverine OP	Wolverine UP	Bourgeau	Wolverine Creek	Massive	Sawback	Pilot	Red Earth UP	Red Earth OP	Red Earth Creek	Copper	Johnson	Castle
Summer													
Black bear	7	5	14	4	6	3	19	16	3	2	5	11	18
Grizzly bear	7	0	0	0	1	0	1	1	2	2	0	0	1
Wolf	4	2	0	0	0	0	0	6	1	6	3	8	2
Cougar	4	8	11	18	5	1	5	8	0	9	8	10	0
Elk	92	79	1	127	128	51	64	81	435	69	140	8	407
Deer	397	56	3	5	101	16	22	27	506	22	65	6	169
Winter													
Wolf	3	0	0	0	0	0	0	4	0	0	0	0	12
Cougar	8	4	2	2	0	1	0	0	0	3	6	5	0
Elk	51	5	0	17	5	0	12	2	62	2	18	3	83
Deer	93	1	0	21	10	2	2	3	90	1	8	1	2

were found significant as were between 18 of 40 (45%) possible landscape variables (Table 4). Human influence had high explanatory power in only one of the models (i.e. wolves in summer).

At the species level, four crossing structure attributes were significantly correlated with black bear passage (Table 4). Distance to nearest drainage was the most important attribute facilitating passage and was positively correlated with crossing structure use ($r^2 = 0.120$, $P = 0.002$). Crossing structure openness was negatively correlated with black bear passage ($r^2 = 0.083$, $P = 0.011$), whereas structure length ($r^2 = 0.067$, $P = 0.022$) and distance to CPR tracks ($r^2 = 0.064$, $P = 0.025$) were both positively correlated with use.

For grizzly bears, six attributes were significantly correlated with crossing structure use. Five of the variables had high explanatory power. Crossing structure width ($r^2 = 0.534$, $P = 0.001$), height ($r^2 = 0.476$, $P = 0.001$), and openness ($r^2 = 0.544$, $P = 0.001$) were all positively correlated with passage, whereas noise levels were negatively correlated ($r^2 = 0.282$, $P = 0.001$). Grizzly bear passage was positively correlated with the distance to forest cover ($r^2 = 0.474$, $P = 0.001$).

Seasonality of wolves suggested correlation with eight attributes during the summer months, and two attributes during the winter months (Table 4). Specifically, crossing structure width ($r^2 = 0.138$, $P = 0.001$), height ($r^2 = 0.139$), openness ($r^2 = 0.142$, $P = 0.001$), distance to nearest townsite ($r^2 = 0.193$, $P = 0.001$) and amount of human use ($r^2 = 0.277$, $P = 0.001$) were significant factors and all positively correlated with wolf passage during summer. Wolves also tended to use structures that were near the CPR tracks ($r^2 = 0.121$, $P = 0.002$), far from drainages ($r^2 = 0.112$, $P = 0.003$) and relatively short in length ($r^2 = 0.097$, $P = 0.006$). During winter, distance to nearest townsite ($r^2 = 0.132$, $P = 0.001$) and nearest crossing structure ($r^2 = 0.238$, $P = 0.001$) had the highest explanatory power and were both positively correlated with passage.

Seasonality of cougars suggested correlation with nine attributes during the summer months and three during the winter (Table 4). Cougar passage in summer was negatively correlated with crossing structure height ($r^2 = 0.205$, $P = 0.001$), openness ($r^2 = 0.161$, $P = 0.001$), distance to forest cover ($r^2 = 0.494$, $P = 0.001$) and townsite ($r^2 = 0.262$, $P = 0.001$) and positively correlated with distance to CPR tracks ($r^2 = 0.202$, $P = 0.001$). Cougars demonstrated a negative relationship between passage and crossing structure width ($r^2 = 0.117$, $P = 0.002$) and distance to next structure ($r^2 = 0.093$, $P = 0.007$) but a positive relationship with crossing structure length ($r^2 = 0.074$, $P = 0.016$). Cougars had a tendency to use divided structures more than undivided structures ($t = 5.44$, $P = 0.002$). Winter passage by cougars was explained by fewer variables. Cougars tended to use crossing structures near forest

Table 4
Mean coefficient of determinations, their slope and level of significance for species models explaining wildlife crossing structure interactions in Banff National Park, Alberta (CS, crossing structure; CPR, Canadian Pacific Railway; HA, human activity)

Attributes	Black bear	Grizzly bear	Wolf		Cougar		Elk		Deer	
	Summer	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer
Structural										
Width	ns	+0.534**	ns	+0.138**	ns	−0.117**	+0.574**	+0.487**	+0.434**	+0.433*
Height	ns	+0.476**	ns	+0.139**	ns	−0.205**	+0.584**	+0.469**	+0.576**	+0.604**
Length	+0.067*	ns	ns	−0.097**	ns	+0.074*	ns	−0.247**	ns	−0.078*
Openness	−0.083*	+0.544**	ns	+0.142**	ns	−0.161**	+0.569**	+0.483**	+0.617**	+0.514**
Noise	ns	−0.282**	ns	ns	ns	ns	−0.177**	−0.164**	−0.271**	−0.226**
Landscape (distance to)										
CS	ns	ns	+0.238**	ns	ns	−0.093**	ns	ns	ns	ns
Forest	ns	+0.474**	ns	ns	−0.227**	−0.494**	+0.510**	+0.364**	+0.344**	+0.350**
Drainage	+0.120**	ns	ns	+0.112**		ns	ns	ns	ns	ns
CPR	+0.064*	−0.094**	ns	−0.121**	+0.266**	+0.202**	ns	ns	ns	ns
Townsite	ns	ns	+0.132**	+0.193**	−0.277**	−0.262**	ns	ns	ns	ns
HA winter	–	–	ns	ns	ns	–	ns	–	ns	–
HA summer	ns	ns	+0.096**	+0.277**	–	ns	–	+0.101**	–	+0.093**
Configuration	ns	ns	ns	ns	ns	$1 < 2^{**}$	ns	ns	ns	$1 > 2^{**}$

Note: ns, not significant.
[*] $0.01 > P < 0.05$.
[**] $0.001 > P < 0.01$.

cover ($r^2 = 0.227$, $P = 0.001$), townsites ($r^2 = 0.277$, $P = 0.001$) and far from CPR tracks ($r^2 = 0.266$, $P = 0.001$).

3.2. Ungulates

At the guild level, ungulate models included both summer and winter analyses for elk and deer. Structural attributes were found significant on 19 occasions (52 maximum possible = 4 models × 13 variables); landscape variables were found significant in four models (Table 4).

At the species level, seven attributes were correlated with summer crossing structure use by elk (Table 4). Elk passage was positively correlated and explained by structure width ($r^2 = 0.487$, $P = 0.001$), height ($r^2 = 0.469$, $P = 0.001$) and openness ($r^2 = 0.483$, $P = 0.001$). Crossing structure length ($r^2 = 0.247$, $P = 0.001$) and noise levels ($r^2 = 0.164$, $P = 0.001$) also were negatively correlated with elk passage. Elk passage showed a positive relationship with distance to forest cover ($r^2 = 0.364$, $P = 0.001$) and human use ($r^2 = 0.101$, $P = 0.005$). During winter, elk passage was positively correlated with crossing structure width ($r^2 = 0.574$, $P = 0.001$), height ($r^2 = 0.584$, $P = 0.001$), openness ($r^2 = 0.569$, $P = 0.001$) and negatively correlated with noise levels ($r^2 = 0.177$, $P = 0.001$). Elk tended to use crossing structures far from forest cover ($r^2 = 0.510$, $P = 0.001$) in winter.

Seasonality of deer use correlated with crossing structure attributes similarly (Table 4). During summer, deer passage was positively correlated with crossing structure width ($r^2 = 0.433$, $P = 0.001$), height ($r^2 = 0.604$, $P = 0.001$), openness ($r^2 = 0.514$, $P = 0.001$) and negatively correlated with noise levels ($r^2 = 0.226$, $P = 0.001$). The amount of human use was positively correlated with deer passage ($r^2 = 0.093$, $P = 0.006$). Undivided structures were selected by deer over divided ones ($t = 5.17$, $P = 0.001$). Structural variables were strongest variables influencing winter deer passage and positively correlated with crossing structure openness ($r^2 = 0.617$, $P = 0.001$), height ($r^2 = 0.576$, $P = 0.001$), width ($r^2 = 0.434$, $P = 0.001$) and negatively correlated with noise levels ($r^2 = 0.271$, $P = 0.001$). Deer had a tendency to use crossing structures far from forest cover ($r^2 = 0.344$, $P = 0.001$) in winter.

4. Discussion

A review of the literature suggests that there have been mixed results concerning the relative importance of factors affecting crossing structure efficacy. Some studies have argued that the location of a crossing structure, particularly in relation to habitat quality, is the most important feature (Foster and Humphrey, 1995; Yanes et al., 1995; Land and Lotz, 1996; Clevenger and Waltho, 2000; Ng et al., 2004). Other research has shown that structure design can be the most influential (Reed et al., 1975; Ballon, 1985; Norman et al., 1998; Cain et al., 2003). These discrepancies in how animals respond to crossing structures may largely be explained by taxon- and/or habitat-specific factors.

Contrary to our earlier analysis (Clevenger and Waltho, 2000), in this study, structural attributes largely explained performance indices for both predator and prey species, whereas landscape and human-related factors were of secondary importance. In Clevenger and Waltho (2000), we suggested that the overall weakness of structural attributes to explain species performance indices was due to confounding variables such as high levels of human use at the 12-year old phase 1 and 2 underpasses. As large mammal species learn to avoid underpasses with high human use, i.e., those close to the town of Banff, our results suggested structural attributes were then of secondary importance in determining crossing structure usage.

In the current study, we find structural attributes dominate species performance indices. We attribute the loss of human use influence to the fraction of human use activity found in phase 3A (97 human passes during 34 months monitoring) compared to phase 1 and 2 (894 passes during 35 months monitoring). The difference in human use activity results from the proximity of crossing structures in phase 1, 2 and 3A relative to Banff and hiking and bike trails. The average distance (±SD) in phase 1 and 2 is 3.0 ± 2.5 km; the average distance in phase 3A is 17.2 ± 5.9 km. It becomes apparent that in high human density settings, such as phase 1 and 2, human activity can clearly be a deterrent to wildlife passage at the crossing structures. However, in low human density settings (i.e., the present study), such confounding variables can be minimized.

A second explanation that may contribute to the different results was standardizing against spatial heterogeneity. As in Clevenger and Waltho (2000), we assumed each crossing structure was surrounded by its own unique habitat differentially preferred by the different species summer and winter. Such variance may bias the results towards crossing structure attributes associated with structures located in preferred habitats – independent of the structure attributes themselves. In this study, we assumed a second source of spatial heterogeneity – that is, variance in distances between consecutive crossing structures. We suspect such distances (mean distance $\pm$ SD $=$ 1.5 km $\pm$ 1.1 km) bias the results towards structure attributes most closely associated with isolated structures because they have an expected higher frequency of use by chance alone. For example, consider three crossing structures that serve two independent populations of equal size: the first crossing structure serves one population, and the second two crossing structures serve the second population. Everything else being equal, we expect the first single crossing structure to serve the first population by 100%, whereas the second two crossing structures to serve the second population by 50% each. Such degrees of isolation and proximity we believe can mask whatever ecological significance structural and landscape attributes may hold themselves.

We found it necessary therefore to perform our analyses not in the context of observed through-passage usage alone, but in the context of observed through-passage usage as a function of expected through-passage usage, i.e., the performance indices. Our performance indices thus were modelled to minimize the confounding biases of both sources of spatial heterogeneity.

With minimal human use activity confounding our analyses, and having standardized against the two sources of spatial heterogeneity, we assumed we were better able to assess how different species respond to structural and landscape attributes. Our results showed that at the guild level, structural and landscape factors were equally important in explaining carnivore passage, whereas structural attributes were the most dominant features affecting ungulate passage. For structural attributes, two clear patterns emerged from the analysis. First, crossing structures with high openness ratios (i.e. short in length, high and wide) strongly influenced passage by grizzly bears, wolves, elk and deer. Second, more constricted crossing structures (i.e. long in length, low, narrow and low openness ratios) best explained passage by black bears and cougars.

These patterns conform with evolved behaviours and life history traits for large mammals. Studies by others suggest grizzly bears and wolves, for example, are highly vulnerable to human-related disturbance and structures, and particularly roads (Noss et al., 1996; Mattson et al., 1996; Mladenoff et al., 1999; Gibeau et al., 2002). However, at the individual level, such vulnerability may be individually specific – a function of at least in part, sex and duration of habituation (Clevenger et al., 2002a). Reed et al. (1975) and Ward (1982) also observed that deer, elk and other ungulate prey species were reluctant to use confining structures. There is some evidence that crossing structures can be used by predators to capture prey (Hunt et al., 1987; Foster and Humphrey, 1995; see review by Little et al., 2002). Structures could potentially increase prey vulnerability by reducing the effectiveness of mechanisms available to prey species to avoid detection or escape. Such structures are generally exposed, restricted, and often narrow environments (Reed et al., 1975; Yanes et al., 1995; Clevenger et al., 2002b).

The more constricted crossing structures favoured by black bears and cougars might be explained by these species' requirements for hiding cover and avoidance of exposed, sparsely wooded habitats (Weaver et al., 1996). We suspect that affinity for cover may be heightened as these species enter inhospitable environments such as the TCH corridor and are faced with the task of traversing it. When given the option of crossing the highway at the exposed wildlife overpasses or adjacent underpasses (<200 m away), there is a greater tendency for both species to select the latter (Clevenger et al., 2002a).

Although we argue that structural attributes are most closely correlated with large mammal use, we do find two landscape variables repeatedly identified as being significant. Distance to cover was the most important landscape attribute for cougars (negative correlation) and was a significant factor determining passage for grizzly bears, elk and deer (all positive correlations). The presence or amount of vegetative cover at passage entrances has been considered an essential component for designing effective tunnels (Hunt et al., 1987; Rodríguez et al., 1996; Pfister et al., 1997). Increased cover provides greater protection and security for animals approaching the passages. Evolved life-history traits and behaviour of cougars confirms that increased cover near passages would be important for them. Conversely, open areas near passages would facilitate effective mechanisms for predator avoidance or escape by prey species such as elk and deer, and characterizes the preferred habitat of grizzly bears.

Noise appears to be an important attribute influencing species performance indices. Noise from vehicle traffic can stress animals and potentially restrict habitat use and their movements (Bowles, 1995; Wasser et al., 1997). In all of our models where noise was a significant factor, it negatively affected passage. Although repeated exposure to high noise levels can result in habituation (Valkenburg and Davis, 1985; Krausman et al., 1986), we do not suspect high noise levels enhance the function and performance of crossing structures.

The results from our two analyses provided a different suite of variables that were important in explaining passage by large mammals at the crossing structures in BNP. We might expect that at the level of individual structures, the importance of variables may differ. However, the variables differed at a larger scale, such as between the Lower and Middle Bow Valley. Although these two environments are relatively close geographically, there are considerable differences, particularly in the level of human disturbance. Further, if crossing structures are built along phase 3B in the future and a similar crossing-structure analysis is carried out, we might expect the key factors influencing passage to be different from the phase 1, 2 and phase 3A crossing structures.

An important outcome of our research is the demonstration that different large mammal species respond differently to structural and landscape-level attributes of crossing structures and that spatial and temporal scales are important in determining the efficacy of the measures. We caution that the results from our work are not universal in their application, as the influence of factors related to the efficacy of crossing structures might be expected to vary between landscapes and faunal communities. Additional long-term research of crossing structure performance from a range of landscapes with complex wildlife–human interactions will help develop a general model for land managers and transportation planners.

We suggest that because species respond differently to the features of crossing structures, mitigation planning in a multiple-species ecosystem will be a challenging endeavour. Moreover, crossing structures will only be as effective as the land and resource management strategies around them. Crossing structures are in essence small and narrow, site-specific habitat linkages or corridors. Consequently, for these measures to fulfil their function as habitat connectors, mitigation strategies must be contemplated at two scales. Site-level impacts from development and high levels of human activity near crossing structures will decrease habitat quality and likely disrupt animal movements, particularly of large predators (Smith, 1999; Clevenger and Waltho, 2000). Similarly, alteration of landscape elements at a broader regional-scale could impede or obstruct movements towards the structures, preventing animals from using them entirely, thus rendering them ineffective.

To maximize connectivity across roads for multiple large mammal species, road construction schemes in the future should include a diversity of crossing structures of mixed size classes. This strategy will likely provide greater permeability of roads by accommodating a variety of species and behavioural profiles. We believe that mitigating highways for wildlife is a long-term process that will last for many decades and affect individuals and populations alike (Opdam, 1997). Thus, highway mitigation strategies developed around land-use planning should not terminate with the construction process, but need to be proactive at both scales to ensure that crossing structures remain functional over time. This requires continuous long term monitoring, as exemplified in this study.

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