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Source: *Conservation Biology*, Vol. 14, No. 1 (Feb., 2000), pp. 47-56
Published by: Blackwell Publishing for Society for Conservation Biology
Stable URL: http://www.jstor.org/stable/2641903
Accessed: 27/01/2010 13:35

Factors Influencing the Effectiveness of Wildlife Underpasses in Banff National Park, Alberta, Canada

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Abstract: *Wildlife crossing structures are intended to increase permeability and habitat connectivity across roads. Few studies, however, have assessed the effectiveness of these mitigation measures in a multispecies or community level context. We used a null model to test whether wildlife crossing structures serve large mammal species equally or whether such structures limit habitat connectivity across roads in species-specific ways. We also modeled species responses to 14 variables related to underpass structure, landscape features, and human activity. Species performance ratios (observed crossing frequency to expected crossing frequency) were evaluated for four large carnivore and three ungulate species in 11 underpass structures in Banff National Park, Alberta, Canada. Observed crossing frequencies were collected in 35 months of underpass monitoring. Expected frequencies were developed from three independent models: radio telemetry, pellet counts, and habitat-suitability indices. The null model showed that species responded to underpasses differently. In the presence of human activity carnivores were less likely to use underpasses than were ungulates. Apart from human activity, carnivore performance ratios were better correlated to landscape variables, and ungulate performance ratios were better correlated to structural variables. We suggest that future underpasses designed around topography, habitat quality, and location will be minimally successful if human activity is not managed.*

Factores que Influencían la Efectivadad de Pasadizos para vida Silvestre en el Parque Nacional Banff, Alberta, Canada

Resumen: *Las estructuras diseñadas para el cruce de vida silvestre tienen la intención de incrementar la permeabilidad y conectividad del hábitat a lo largo de las carreteras. Sin embargo, pocos estudios han evaluado la eficacia de estas medidas de mitigación en un contexto multi-especie o de comunidad. Utilizamos un modelo nulo para evaluar si las estructuras para el cruce de vida silvestre sirven de igual manera a las especies de mamíferos grandes, o si estas estructuras limitan la conectividad del hábitat a lo largo de carreteras de manera especie-específica. También modelamos las respuestas de las especies a 14 variables relacionadas con la estructura de los pasadizos, las características del paisaje y la actividad humana. Se evaluaron tasas de éxito por especie (frecuencia de cruces observados/frecuencia de cruces esperados) para cuatro carnívoros grandes y tres especies de ungulados en 11 estructuras de pasadizos en el parque nacional Banff, Alberta, Canada. Las observaciones de frecuencias de cruce esperadas se obtuvieron a partir de tres modelos independientes: radio telemetría, conteo de heces e índices de hábitat adeduado. El modelo nulo mostró que las especies responden de manera diferente a los pasadizos. En presencia de actividades humanas fue menos probable que los carnívoros utilizaran los pasadizos en comparación con los ungulados. Aparte de la actividad humana, las tasas de éxito para los carnívoros estuvieron mejor correlacionadas con variables estructurales. Sugerimos que los pasadizos diseñados en el futuro en base a la topografía, la calidad del hábitat y la ubicación, tendrán un mínimo éxito si la actividad humana no es manejada.*

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Paper submitted February 8, 1999; revised manuscript accepted July 10, 1999.

Introduction

The effect of heavily used roads on mammal populations has been the focus of many studies during recent years (Oxley et al. 1974; Mierau & Favara 1975; Mader 1984; Bennett 1991; Evink et al. 1996). These studies show that roads affect mammal populations in numerous ways, from habitat loss and habitat alienation (i.e., sensory disturbance) to physical barriers and road mortality (Adams & Geis 1983; Mansergh & Scotts 1989; Van der Zee et al. 1992; Brandenburg 1996). Among these effects, habitat fragmentation and physical barriers pose what many conservation ecologists consider the greatest obstruction to maintaining species diversity and ecological integrity (Wilcox & Murphy 1985; Saunders & Hobbs 1991; Dale et al. 1994; Forman & Alexander 1998).

Attempts to increase habitat connectivity and barrier permeability across road structures can be found in some road construction and upgrade projects. Wildlife overpasses and underpasses, for example, first constructed in the 1970s, are used as mitigation tools in many parts of the world today (Reed et al. 1975; Hunt et al. 1987; Romin & Bissonette 1996; Keller & Pfister 1997). Nonetheless, few studies have examined the efficacy of these mitigation structures (Romin & Bissonette 1996). Furthermore, the few that have been conducted are limited in their extent to single-species analyses (Reed et al. 1975; Ballon 1985; Schall et al. 1985; Singer & Doherty 1985; Woods 1990; Carsignol 1993; but see Foster & Humphrey 1995). No study has considered the usefulness of wildlife overpasses and underpasses at multispecies scales that encompass the large mammals.

Today, highway planners and land managers can ill afford the naïve luxury of single-species mitigation structures. Species do not function in isolation but are components of ecological systems that inherently fall into the category of organized complexity (Allen & Starr 1982; O'Neill et al. 1986). In an organized, complex system, species are dynamically linked to other species on multiple spatial and temporal scales (Kolasa & Pickett 1989; Pickett et al. 1989, 1997; Waltho & Kolasa 1996; Fiedler & Kareiva 1998). Therefore, any single-species mitigation structure is likely to have cascading effects, some positive and some negative, on nontarget species also. If a mitigation structure is to succeed, a multispecies approach is needed to evaluate the efficacy of such mitigation on nontarget species as well.

We evaluated whether underpass structures in Banff National Park, Alberta, Canada, serve all species (i.e., large mammals) equally, or whether such structures limit habitat connectivity across roads in species-specific ways. Furthermore, we aimed to determine which of 14 underpass variables species responded to most, with the anticipation that once these variables were identified the design of future mitigation measures could be improved.

Methods

We collected data along the Trans-Canada highway (TCH) in Banff National Park (BNP), Alberta, Canada (Fig. 1). The Trans-Canada highway in BNP runs along the floor of the Bow Valley (2–5 km wide), sharing the valley bottom with the Bow River, the township of Banff (population 9000), several high-volume two-lane highways, numerous secondary roads, and the Canadian Pacific Railway. The TCH is the major transportation corridor through the park (park length, 75 km), carrying an estimated 5 million visitors to the park per year, with an additional 5 million users en route between Calgary and Vancouver (Parks Canada Highway Services, unpublished data). The first 45 km of the TCH from the eastern park boundary (phase 1, 2, and 3A) is four lanes and bordered on both sides by a wildlife exclusion fence 2.4 m high (phase 1 completed in 1986, phase 2 in 1988, and phase 3A late 1997). The remaining 30 km to the western park boundary (Alberta–British Columbia border, phase 3B) is two lanes and unfenced. Plans exist to upgrade phase 3B to four lanes with fencing within the next 5–10 years.

The fenced portion constitutes an effective barrier to the movement of large mammals. To mitigate this barrier effect, highway engineers constructed 22 wildlife underpasses and two wildlife overpasses. The effectiveness of such structures to facilitate large mammal movements, however, is unknown. Because no two underpasses are similar in all structural and ecological aspects, we propose that species (i.e., large mammals) select underpasses that best correlate with their ecological needs and behavior. Attributes that best characterize high-use underpasses can then be integrated into new designs for an eventual phase 3B widening process. We tested this premise at three scales of ecological resolution: species, species groups, and large mammals. These scales were used because (1) we anticipate that the explanatory power of each attribute is dependent, at least in part, on the ecological resolution used (Rahel et al. 1984; Rahel 1990; Collins & Glenn 1991) and (2) the information needs of land managers and transportation planners with respect to mitigation structures can best be met by a variable scale approach. We chose only phase 1 and phase 2 underpasses for this study, however, because the recent completion of phase 3A mitigation structures does not permit sufficient time for wildlife habituation to occur at such landscape scales (A.P.C., unpublished data).

Wildlife Underpasses

We monitored 11 wildlife underpasses (Fig. 1): 9 cement open-span underpasses and 2 metal culverts. We characterized each underpass with 14 variables encompassing attributes of structural, landscape, and human activity

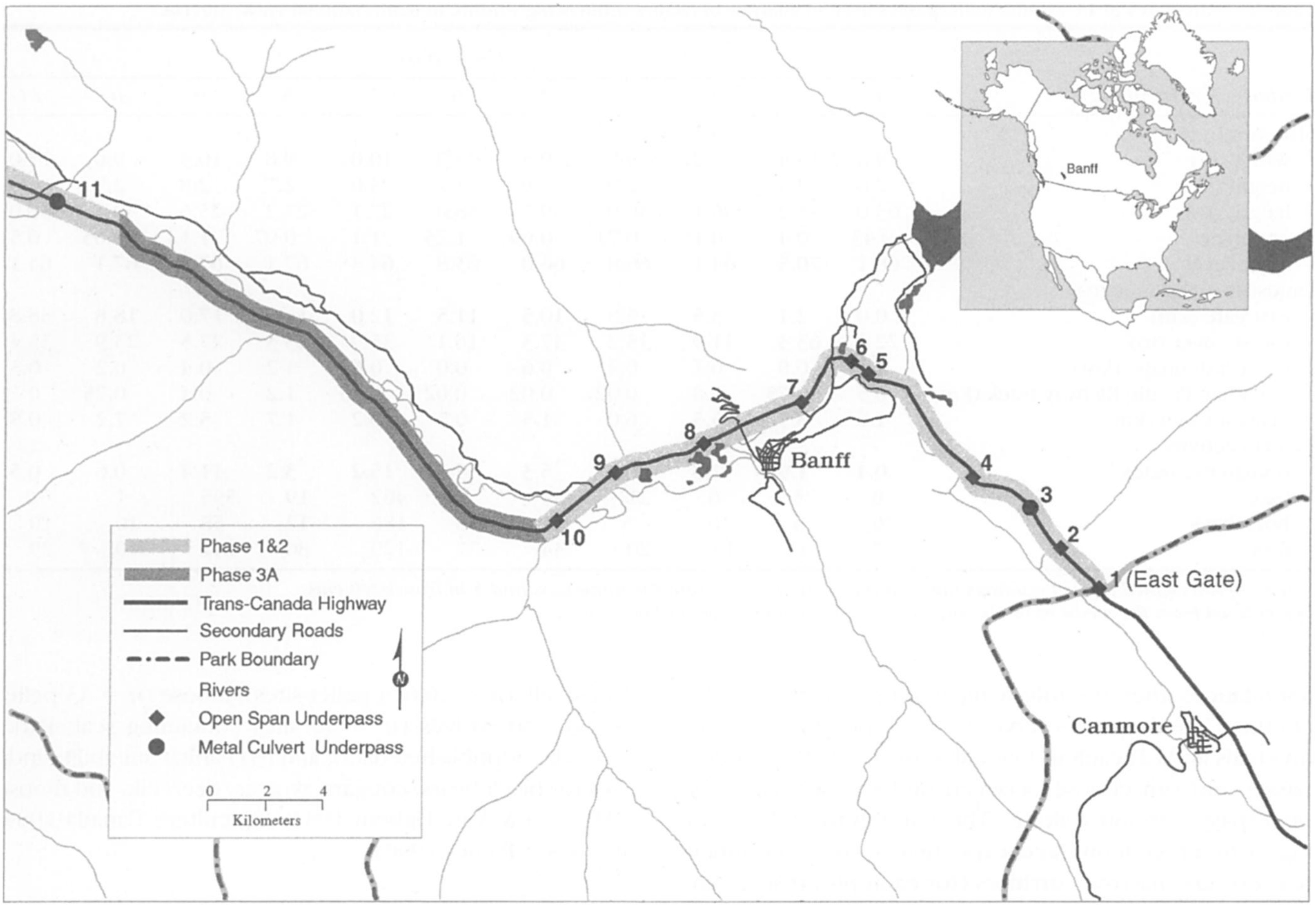

Figure 1. Location of study area and 11 wildlife underpasses along the Trans-Canada Highway (TCH) in Banff National Park, Alberta. Shaded sections of the TCH refer to phases: lightly shaded, phases 1 and 2; darkly shaded, phase 3A.

(Table 1). Structural variables included underpass width, height, length (including median), openness (width × height/length) (Reed & Ward 1985); and noise level (mean of *A*-weighted decibel readings taken at the center point within the underpass and 5 m from each end).

Landscape variables included distance to nearest forest cover, Canadian Pacific Railway, townsite, closest major drainage, and eastern-most park entrance (hereafter referred to as east gate). Human activity variables included types of human use in the underpasses characterized by counts of people on foot, bike, and horseback, and a human-use index calculated from the mean monthly counts of the three former variables combined.

Observed Crossing Frequencies

We measured wildlife use for the 11 underpasses using methods described by Bider (1968). Specifically, tracking sections (2 × 4 m) were set at both ends of each underpass to record evidence of underpass use. Tracking material consisted of a dry, loamy mix of sand, silt and clay 3–4 cm deep. At intervals of 3–4 days, we visited each underpass and classified the tracking medium as adequate or inadequate, depending on our ability to read tracks clearly. We recorded species presence (wolves [*Canis lupus*], cougars [*Puma concolor*], black bears [*Ursus americanus*], grizzly bears [*U. arctos*], deer [*Odocoileus* sp.], elk [*Cervus elaphus*], and moose [*Alces alces*]), species abundance, and human activity at each tracking section during each underpass visit. 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. Data were collected in this manner for two continuous monitoring periods: 1 January 1995–31 March 1996 (15 months) and 1 November 1996–30 June 1998 (20 months). Of 3311 underpass monitoring visits, 59 (1.8%) were classified as inadequate for data collection.

Expected Crossing Frequencies

If the 11 underpasses occur in a homogeneous-habitat landscape that includes random distribution of species

Table 1. Attributes of 11 wildlife underpasses used in analysis of factors influencing wildlife in Banff National Park, Alberta.

	Underpass										
Underpass attribute	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*
Structural											
width (m)	9.8	13.4	4.2	9.8	9.5	14.9	10.0	9.8	10.3	9.0	7.0
height (m)	2.8	2.5	3.5	2.9	2.9	3.2	3.0	2.7	2.8	2.9	4.0
length (m)	63.0	83.2	96.1	40.0	39.7	38.0	27.1	27.2	25.6	40.1	56.0
openness	0.43	0.4	0.15	0.71	0.69	1.25	1.1	0.97	1.12	0.65	0.5
noise level[a]	68.1	70.5	64.1	66.8	66.0	63.8	64.3	67.4	67.4	67.1	64.1
Landscape (distance to)											
east gate (km)	0.0	2.1	3.5	5.8	10.5	11.5	12.0	14.4	17.0	18.8	38.8
forest cover (m)	22.3	63.3	11.9	15.2	47.3	16.1	35.9	23.3	27.5	23.9	35.4
nearest drainage (km)	1.0	0.0	0.1	0.4	0.6	0.0	0.6	1.2	0.4	0.2	0.3
Canadian Pacific Railway track (km)	0.5	0.75	0.8	0.02	0.02	0.02	0.25	1.2	0.4	0.75	0.75
nearest town (km)	1.6	3.5	5.5	6.0	1.5	0.5	0.2	1.7	5.2	7.2	0.8
Human activity											
human-use index[b]	0.4	1.9	1.8	0.6	5.3	5.3	15.2	3.2	11.4	0.6	0.5
bike	0	5	6	21	189	8	462	19	595	1	0
horseback	6	3	6	5	42	138	186	12	58	10	10
foot	7	45	14	20	34	77	129	80	241	10	29

[a]*Mean of A-weighted decibel readings taken at the center point within the underpass and 5 m from each end.*
[b]*Calculated from the mean monthly counts of people on foot, bike, and horseback.*

abundances, then the following assumptions may apply: (1) the 11 underpasses serve the same population of individuals and (2) each individual is aware of all 11 underpasses and can choose between underpasses based on underpass attributes alone. The Banff Bow Valley is a highly heterogeneous landscape, that is, lakes, mountain barriers, and narrow corridors (for example) restrict underpass accessibility on multiple spatiotemporal scales. If habitat fragmentation is perceived as extreme, then we may assume that each underpass serves its own unique subpopulation. If this were true, then differences in observed crossings frequencies between underpasses would reflect differences in subpopulation sizes alone and not attributes of the underpasses themselves. Although these two sets of assumptions represent endpoints along a continuum of possible interactions, the relative extent that species interact with the habitat landscape and distribution of underpasses is unknown. It is therefore necessary to examine observed crossing frequencies in the context of expected crossing frequencies (i.e., performance ratios).

Expected crossing frequencies were obtained from three independent data sets that included radiotelemetry location data, relative-abundance pellet transects, and habitat-suitability indices. Because it remains unclear what proportion of individuals from these data sets uses the underpasses directly, we defined our expected crossing frequencies as equal to the abundance data found at radii 1, 2, and 3 km from the center of each underpass. Specifically, we used (1) radiotelemetry location data for black bears (n = 255 locations), grizzly bears (n = 221 locations), wolves (n = 2314 locations), and elk (n = 1434 locations; Parks Canada, unpublished data); (2) relative-abundance pellet transects for deer (n = 1579 pellet sites), elk (n = 26,614 pellet sites), moose (n = 43 pellet sites), and wolves (n = 30 sites containing scat; Parks Canada, unpublished data); and (3) habitat suitability indices for black bears, cougars, wolves, deer, elk, and moose (Holroyd & Van Tighem 1983; Agriculture Canada 1989; Kansas & Raines 1990).

Analyses

We derived species-performance ratios for each of the three independent data sets by dividing observed crossing frequencies by expected crossing frequencies. Performance ratios were designed such that the higher the ratio, the more effectively the underpass appeared to facilitate species crossings.

We examined the premise that wildlife crossing structures serve species equally by testing the null hypothesis that performance ratios do not differ between species (paired t test with Bonferroni adjusted probability values; SYSTAT 1998). We tested the null hypothesis for each of the three performance models—radiotelemetry, habitat suitability indices, and log-transformed pellet counts—partly because no one model includes the complete species composition.

In the event that we rejected the null hypothesis, we proceeded with three steps to determine which of the 14 underpass attributes were most closely associated with species performance ratios. First, we standardized all performance ratios to a mean of zero and a standard deviation of one to remove absolute differences between the three models.

Second, we used a family of simple curvilinear and polynomial regression curves to optimize the fit between species-performance ratios and each underpass attribute (Jandel Scientific 1994). We used the following criteria to choose the optimal equation for each regression analysis. (1) the regression model had to be statistically significant (at $p < 0.05$). (2) The beta coefficient for the highest ordered term had to be statistically significant. (3) Once an equation met the above criteria, we compared its F statistic with the F statistic for the next equation that also met these criteria but had one less ordered term. We chose the model with the higher F statistic and (4) iterated the above process for equations with consecutively fewer terms. (5) If no curvilinear or polynomial equation was accepted, we chose the simple linear regression model (equation 41; Appendix 1) to describe the relationship, assuming that it had not already been chosen through the iterative process. (6) If these criteria failed to produce a significant regression model for species per se and underpass attribute per se, we deleted the underpass attribute as being a significant factor influencing the species-performance ratio.

Third, for each species we ranked the regression models thus obtained according to the absolute value of each model's coefficient of determination. This three-step process allowed for the identification and ordering of underpass attributes (in order of importance) associated with each species performance ratio, but it failed to separate ecologically significant attributes from those that appeared significant but were statistical artifacts of the underpasses themselves.

The three-step process was repeated for each of the three scales of ecological resolution. For species groups, however, it was first necessary to identify group types according to similarities in species performance ratios as compared to some arbitrary definition. We used principal component analysis (PCA) to identify these species groups. Because none of the performance models contains a full species list, it was necessary to include all species performance ratios from each of the models into the single PCA.

Results

From 1 January 1995 to 30 June 1998 (excluding 1 April to 31 October 1996) 14,592 large-mammal underpass visits were recorded. Ungulates were 78% of this total, carnivores 5%, and human-related activities 17% (Table 2). Individual underpasses ranged from 373 visits to 2548 visits. Specific to wildlife, elk were the most frequently observed species ($n = 8959$, 74% of all wildlife), followed by deer ($n = 2411$, 20%), and then wolves ($n = 311$, 2.5%). The through-passage rate for wildlife species was high (mean 98%, SD = 1.9).

For each underpass, species-performance ratios significantly differed between species (paired t test with Bonferroni adjusted probability; $p < 0.001$). We therefore rejected the null hypothesis and focused instead on identifying the underpass attributes that most likely influenced a species's underpass use.

For individual species, the rank order of significant attributes was not significantly different between performance models (paired t test, all within-species comparisons not significant at $p < 0.05$). We therefore provide mean rank scores only (Table 3). The rank order of significant attributes, however, does differ between species (paired t test, Bonferroni adjusted probability values; $p < 0.05$). For example, we found that underpass distance from the east gate (positive correlation) was the most significant underpass attribute affecting black bear performance ratios, whereas underpass length (negative correlation) was the most significant attribute affecting elk performance ratios (Table 3).

At the second scale of ecological resolution, species groups, we used PCA to identify two group types (Factor 1, Fig. 2). The two groups were readily identifiable as large predators/omnivores (hereafter referred to as carnivores) and ungulates. For carnivores the most significant underpass attribute influencing the group's performance was distance to townsite (positively correlated), followed by human activities such as hiking (negatively correlated), human use index (negatively correlated), and horseback riding (negatively correlated). Landscape and structural variables were the least significant attributes influencing the group's performance ratio (i.e., distance to nearest drainage, negatively correlated; underpass openness, negatively correlated; Table 4).

In contrast, we found that the most significant underpass attributes influencing ungulates were structural and landscape factors. Specifically, the rank order was 1, underpass openness (negatively correlated); 2, noise level (positively correlated); 3, underpass width (negatively correlated), and 5, distance to nearest drainage. Human activity attributes, although significant, were ranked lower: 4, horseback riding (negatively correlated), and 6, hiking (negatively correlated; Table 4).

At the third scale of ecological resolution, large mammals (i.e., all species together), we found that the most significant underpass attribute influencing the community's performance ratio was structural openness (negatively correlated; Table 4). Distance to townsites was the second most significant attribute (positive correlation), followed by human activity (human-use index, horseback riding, hiking, and biking, all negatively correlated).

Discussion

There were no significant differences in the rank order of the 14 underpass attributes between the three performance ratio models (radiotelemetry, pellet count, and habitat suitability indices). This suggests that although the subpopulation that each underpass serves is unknown our confidence in using performance ratios as a means to standardize differ-

Table 2. Observed use of wildlife underpasses by carnivores and ungulates in Banff National Park, Alberta, 1995–1998.

	Underpasses										
Species	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*
Black bear	10	20	43	37	13	8	0	4	8	34	16
Grizzly bear	0	0	0	2	0	0	0	0	0	5	0
Cougar	5	29	3	30	7	0	4	4	20	15	0
Wolf	1	7	3	28	3	5	1	5	77	146	35
Deer	554	42	294	253	215	21	61	338	288	291	54
Elk	825	201	331	1199	1062	467	1576	1522	821	683	272
Moose	1	0	1	0	0	0	0	0	0	0	0

ences in species abundance between underpasses is high. More importantly, however, these results permit us to test the null hypothesis independently of the actual grain in which species interact with the habitat template.

Our results suggest that underpass attributes differentially influence species performance ratios. Depending on the ecological resolution (i.e., species, species groups, large mammals), however, different underpass attributes were interpreted as dominant. One common thread at all resolutions was that human influence—whether it was distance to townsite or human activity within an underpass—consistently ranked high as a significant factor affecting species-performance ratios. At the species level, for example, results from six of the seven species ranked at least one human attribute as the first or second most important attribute influencing the species-performance ratio. At the group level, carnivores showed a positive correlation between underpass performance ratios and distance from town and a negative correlation to human activity. The inverse relation between the two human-related attributes occurred because the townsites served as sources of human populations from which human activity originates. The closer an underpass was to the town of Banff or Canmore, the greater the human use activity observed (Mattson et al. 1987; Kasworm & Manley 1990; McCutchen 1990; Jalkotzy & Ross 1993; Gibeau et al. 1996; Paquet et al. 1996; but see Rodriguez et al. 1997).

Ungulates, however, failed to respond to human activity in the same manner. Although significant negative correlations in performance ratios were observed, the relative importance of human activity ranked below that of structural attributes. Elk habituation to human presence close to town may, at least in part, have masked the performance ratios of unhabituated elk farther from town (Woods et al. 1996). At the community level, the most important attribute influencing species performance ratios was structural openness. The second most important attribute, however, was distance to the townsites (positive correlation).

These results lend support to the Banff National Park management plan, which emphasizes stricter limits on human development and more effective methods of managing and limiting human use within the park (Parks Canada 1997). The BNP management plan also recommends improving the effectiveness of phase 1 and 2 underpasses by "retrofitting." In this context we suggest that in such a multispecies system the most efficient

Table 3. Species level rank ordering of mean coefficient of determinations and their slope for models explaining underpass interactions in Banff National Park, Alberta.

Underpass attributes	*Black bear*	*Grizzly bear*	*Cougar*	*Wolf*	*Deer*	*Elk*	*Moose*
Width	8 −				4 −	3 −	5 −
Height			3 −	3 +		10 +	
Length	7 +					1 −	4 +
Openness	4−				5 −	4 +	1 −
Noise level	12 +		1 +		3 +	8 +	
Distance to							
east gate	1 −			2 +			3 −
forest cover	11 −	3 −	4 +		6 −	11 −	6 −
nearest drainage	9 −			7 −	2 +	2 +	
Canadian Pacific Railway track		4 −		5 +	8 +		
nearest town	3 +	1 +	2 +	1 +		12 +	
human activity							
human-use index	6 −	2 −		6 −		5 −	8 −
bike	10 −			4 −		6 −	7 −
horseback	5 −				1 −	7 −	2 −
foot	2 −		5 −	8 −	7 −	9 −	9 −

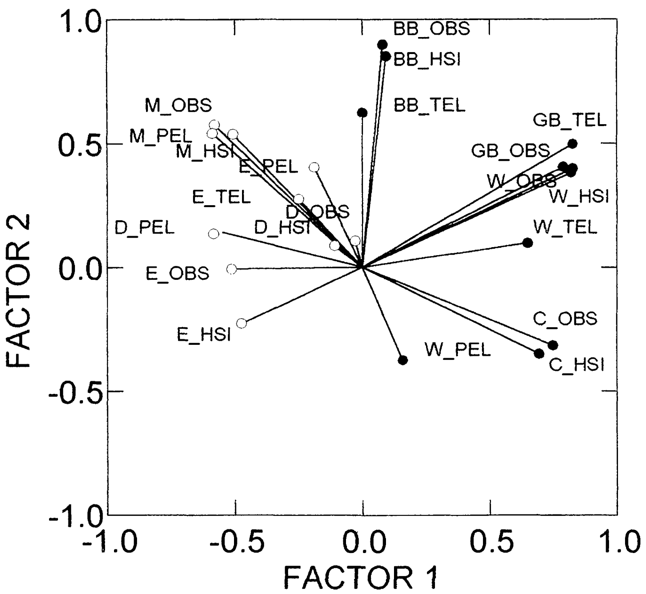

Figure 2. Principal component analysis of models of observed and expected underpass use for wildlife in Banff National Park, Alberta. Models were developed from observation data (OBS), radiotelemetry location data (TEL), relative-abundance pellet-transect data (PEL), and habitat suitability index data (HSI) for black bears (BB), grizzly bears (GB), cougars (C), wolves (W), deer (D), elk (E), and moose (M). Two discrete groups were identified along factor 1: large predators/omnivores (●) and herbivores (○).

(and probably economic) approach to retrofitting is to manage human activity near each underpass. Specifically, we recommend that foot trails be relocated and human use of underpasses be restricted. Continual monitoring of wildlife passage frequencies at these structures will permit Parks Canada to evaluate how this management strategy may translate into greater permeability of the Trans-Canada Highway and habitat connectivity for all wildlife populations in the Bow Valley.

Landscape variables other than distance to town may also be important attributes influencing species-performance ratios. Carnivores had a greater tendency to use underpasses close to drainages systems, for example, whereas ungulates tended to avoid them. Drainage systems are known travel routes for wildlife, particularly in narrow glacial valleys such as Banff's Bow Valley. The inverse relationship between carnivores and ungulates with respect to drainages may reflect processes such as predator-prey interactions rather than any direct effect of landscape attributes on underpass use. Recent studies have shown that predators can have important effects on the community structure of prey species (Lima & Dill 1990; Dickman 1992; Jedrzejewski et al. 1993). For example, deer are known to keep to the periphery of wolf territories (Hoskinson & Mech 1976; Mech 1977) and re-

Table 4. Rank ordering of mean coefficients of determination and their slope for models explaining underpass interactions at the level of species groups and large mammals in Banff National Park, Alberta.

Underpass attributes	*Carnivores*	*Ungulates*	*Large mammals*
Width		3 −	6 −
Height			10 −
Length		8 +	11 +
Openness	5−	1 −	1 −
Noise level	7+	2 +	8 +
Distance to			
east gate		10 −	13 +
forest cover		7 −	12 −
nearest drainage	6 −	5 +	
Canadian Pacific			
Railway track		12 +	9 +
nearest town	1+	13 +	2 +
Human activity			
human-use index	3 −	9 −	3 −
bike	8 −	11 −	7 −
horseback	4 −	4 −	4 −
foot	2 −	6 −	5−

duce their feeding effort when exposed to odors of wolves and other predator species (Muller-Schwarze 1972; Sullivan et al. 1985). Furthermore, there is some evidence that the presence of badgers (*Meles meles*) can disrupt their prey species (hedgehogs [*Erinacceus europaeus*]) use of tunnels under roads in England (C. Doncaster, unpublished data).

The results from our analyses also suggest that structural attributes were significant in species-performance ratios, especially for ungulates. Ungulates preferred underpass structures with a low openness ratio, narrow width, and long tunnel dimensions. We doubt, however, that such species prefer constricted underpasses over larger and more open underpasses. Previous studies have shown that ungulates were reluctant to use underpasses <7 m wide or <2.4 m high (Reed et al. 1975; Yanes et al. 1995; Rosell et al. 1997). Therefore, in a series of post-hoc regression analyses, we found that openness was significantly correlated to length, noise, and distance to town (linear regression, $p < 0.05$). These post-hoc tests suggested that the importance of these structural attributes may be statistical artifacts.

Although there is limited information on the suitability of underpass design for large carnivores (but see Rodriguez et al. 1997), it is understood underpasses that are long and low in clearance inhibit use by carnivores (Hunt et al. 1987; Beier & Loe 1992; Foster & Humphrey 1995). Results from our analyses agree in part with this expectation because wolf performance ratios were positively correlated with underpass height; for other carnivore species, however, attributes of underpass structure contributed little.

It is possible that the overall weakness of structural attributes in explaining species performance ratios may be due to each species's individual familiarization with the 12-year-old underpasses. Individuals require time to adapt to underpass structures (Reed et al. 1975; Waters 1988; Bunyan 1990; Land & Lotz 1996; A.P.C., unpublished data); once adaptation has occurred, the dynamics of human activity and attributes of landscape heterogeneity may play a larger role in determining species-performance ratios than the structural attributes themselves (Gibeau & Herrero 1998).

The underpass attributes varied in importance between both species and ecological resolutions. The multiscale approach we used demonstrates that the informational needs of a state transportation planner responsible for site-specific mitigation for deer (Reed et al. 1975; Romin & Bissonette 1996) will likely be different from those of a land manager in BNP mandated to maintain ecosystem integrity of a 650,000-ha national park. Independent of the ecological resolution used, however, species-performance ratios were consistently negatively correlated with some measure of human activity. Therefore, the best designed and landscaped underpasses may be ineffective if human activity is not controlled.

Acknowledgments

J. Mamalis, B. Bertch, A. Whitehead, Z. Callaway, K. Wells, P. Smillie, C. St-Pierre, and M. Brumfit assisted in the data collection. We thank Parks Canada Highway Services Centre (PCHSC) and Banff National Park, World Wildlife Fund-Canada, and the Agricultural Research Foundation at Oregon State University for providing funding for the research. T. McGuire (PCHSC) was instrumental in providing necessary funds for the project. T. Hurd and C. White (Banff National Park) helped secure administrative and logistical support. D. Zell provided support for the geographic information system. The following researchers generously allowed us to use their data for this analysis: M. Hebblewhite, C. Callaghan, P. Paquet, M. Gibeau, S. Herrero, and T. Hurd. We thank M. Hourdequin, E. Main, G. Meffe, and two anonymous reviewers for critically reading earlier versions of this manuscript.

Literature Cited

Adams, L. W., and A. D. Geis. 1983. Effects of roads on small mammals. Journal of Applied Ecology **20**:403–415.

Agriculture Canada. 1989. Ecosites of the Lower Bow Valley Banff National Park East Gate-Castle Junction. Map Reproduction Centre, Department of Energy, Mines and Resources, Ottawa, Ontario, Canada.

Allen T. F. H., and T. B. Starr, editors. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago.

Ballon, P. 1985. Premieres observations sur l'efficacie des passages a gibier sur l'autoroue A36. Pages 311–316 in Routes et faune sauvage. Service d'Etudes Techniques de Routes et Autoroutes, Bagneaux, France.

Beier, P., and S. Loe. 1992. A checklist for evaluating impacts to wildlife movement corridors. Wildlife Society Bulletin **20**:434–440.

Bennett, A. F. 1991. Roads, roadsides and wildlife conservation: a review. Pages 99–118 in D.A. Saunders and R.J. Hobbs, editors. Nature conservation 2: the role of corridors. Surrey Beatty & Sons, Chipping Norton, New South Wales.

Bider, J. R. 1968. Animal activity in uncontrolled terrestrial communities as determined by a sand transect technique. Ecological Monographs **38**:274–291.

Brandenburg, D. M. 1996. Effects of roads on behavior and survival of black bears in coastal North Carolina. M.S. thesis. University of Tennessee, Knoxville.

Bunyan, R. 1990. Monitoring program of wildlife mitigation measures. Trans-Canada Highway twinning: phase II. Final report. Parks Canada, Banff National Park, Alberta, Canada.

Carsignol, J. 1993. Passages pour la grande faune. Atelier Central de l'Environnement, Paris.

Collins S. L., and S. M. Glenn. 1991. Importance of spatial and temporal dynamics in species regional abundance and distribution. Ecology **72**:654–664.

CTGREF. 1978. Autoroute et grand gibier. Note technique 42. Groupement technique forestier. Ministere de l'Agriculture, Paris.

Dale, V. H., S. M. Pearson, H. L. Offerman, and R. V. O'Neill. 1994. Relating patterns of land-use change to faunal biodiversity in the Central Amazon. Conservation Biology **8**:1027–1036.

Dickman, C.R. 1992. Predation and habitat shift in the house mouse, *Mus domesticus.* Ecology **73**:313–322.

Evink, G., D. Ziegler, P. Garrett, and J. Berry. 1996. Highways and movement of wildlife: improving habitat connections and wildlife passageways across highway corridors. Proceedings of the Florida Department of Transportation/Federal Highway Administration transportation-related wildlife mortality seminar. Florida Department of Transportation, Tallahassee.

Fiedler P., and P. M. Kareiva, editors. 1998. Conservation biology for the coming decade. Chapman & Hall, New York.

Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics **29**:207–231.

Foster, M. L., and S. R. Humphrey. 1995. Use of highway underpasses by Florida panthers and other wildlife. Wildlife Society Bulletin **23**: 95–100.

Gibeau, M. G., and S. Herrero. 1998. Roads, rails and grizzly bears in the Bow River Valley, Alberta. Pages 104–108 in G. Evink, D. Ziegler, P. Garrett, and J. Berry, editors. Proceedings of the international conference on wildlife ecology and transportation. Publication FL-ER-69-98. Florida Department of Transportation, Tallahassee.

Gibeau, M. G., S. Herrero, J. L. Kansas, and B. Benn. 1996. Grizzly bear population and habitat status in Banff National Park. Report. Banff-Bow Valley Task Force, Banff, Alberta.

Holroyd, G. L., and K. J. Van Tighem. 1983. Ecological (biophysical) land classification of Banff and Jasper national parks. Volume 3. The wildlife inventory. Canadian Wildlife Service, Edmonton, Alberta, Canada.

Hoskinson, R. L., and L. D. Mech. 1976. White tailed deer migration and its role in wolf predation. Journal of Wildlife Management **40**:429–441.

Hunt, A., H. J. Dickens, and R. J. Whelan. 1987. Movement of mammals through tunnels under railway lines. Australian Zoologist **24**:89–93.

Jalkotzy, M., and I. Ross. 1993. Cougar responses to human activity at Sheep River, Alberta. Arc Wildlife Services, Calgary, Alberta, Canada.

Jandel Scientific. 1994. Tablecurve 2D. Version 3 for Win32. Jandel Scientific, San Rafael, California.

Jedrzejewski, W., L. Rychlik, and B. Jedrzejewska. 1993. Responses of bank voles to odours of seven species of predators: experimental data and their relevance to natural predator-vole relationships. Oikos **68**:251–257.

Kansas, J. L., and R. M. Raines. 1990. Methodologies used to assess the relative importance of ecological land classification units to black bears in Banff National Park, Alberta. International Conference on Bear Research and Management **8**:155-160.

Kasworm, W., and T. Manley. 1990. Road and trail influences on grizzly and black bears in northwest Montana. International Conference on Bear Research and Management **8**:79-84.

Keller, V., and H. P. Pfister. 1997. Wildlife passages as a means of mitigating effects of habitat fragmentation by roads and railway lines. Pages 70-80 in K. Canters, editor. Habitat fragmentation & infrastructure. Ministry of Transportation, Public Works & Water Management, Delft, The Netherlands.

Kolasa J., and S. T. A. Pickett. 1989. Ecological systems and the concept of biological organization. Proceeding of the U.S. National Academy of Sciences **86**:8837-8841.

Land, D., and M. Lotz. 1996. Wildlife crossing designs and use by Florida panthers and other wildlife in southwest Florida. Pages 323-328 in G. Evink, D. Ziegler, P. Garrett, and J. Berry, editors. Highways and movement of wildlife: improving habitat connections and wildlife passageways across highway corridors. Florida Department of Transportation, Tallahassee.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology **68**:619-640.

Mansergh, I. M., and D. J. Scotts. 1989. Habitat continuity and social organization of the mountain pygmy-possum restored by tunnel. Journal of Wildlife Management **53**:701-707.

Mattson, D. J., R. R. Knight, and B. M. Blanchard. 1987. The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. International Conference on Bear Research and Management **7**:259-273.

Mader, H. J. 1984. Animal habitat isolation by roads and agricultural fields. Biological Conservation **29**:81-96.

McCutchen, H. E. 1990. Cryptic behavior of black bears in Rocky Mountain National Park, Colorado. International Conference on Bear Research and Management **8**:65-72.

Mech, L. D. 1977. Wolf-pack buffer zones as prey reservoirs. Science **198**:320-321.

Mierau, G. W., and B. E. Favara. 1975. Lead poisoning in roadside populations of deer mice. Environmental Pollution **8**:55-64.

Muller-Schwarze, D. 1972. Responses of young black-tailed deer to predator odours. Journal of Mammalogy **53**:393-394.

O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen, editors. 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton, New Jersey.

Oxley, D. J., M. B. Fenton, and G. R. Carmody. 1974. The effects of roads on small mammals. Journal of Applied Ecology **11**:51-59.

Paquet, P. C., J. Wierczhowski, and C. Callaghan. 1996. Summary report on the effects of human activity on gray wolves in the Bow River Valley, Banff National Park, Alberta. Report. Banff-Bow Valley Task Force, Banff, Alberta, Canada.

Parks Canada. 1997. Banff National Park management plan. Ministry of Canadian Heritage, Ottawa, Ontario, Canada.

Pickett, S. T. A., J. Kolasa, S. Collins, and J. J. Armesto. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. Oikos **54**:129-136.

Pickett, S. T. A., R. S. Ostfeld, M. Shackak, and G. E. Likens, editors. 1997. The ecological basis of conservation: heterogeneity, ecosystems, and biodiversity. Chapman & Hall, New York.

Rahel, F. J 1990. The hierarchical nature of community persistence: a problem of scale. American Naturalist **136**:328-344.

Rahel, F. J., J. D. Lyons, and P. A. Cochran. 1984. Stochastic or deterministic regulation of assemblage structure? It may depend on how the assemblage is defined. American Naturalist **124**:583-589.

Reed, D. F., and A. L. Ward. 1985. Efficacity of methods advocated to reduce deer-vehicle accidents: research and rationale in the USA. Pages 285-293 in Routes et faune sauvage. Service d'Etudes Techniques de Routes et Autoroutes, Bagneaux, France.

Reed, D. F., T. N. Woodward, and T. M. Pojar. 1975. Behavioral response of mule deer to a highway underpass. Journal of Wildlife Management **39**:361-367.

Rodriguez, A., G. Crema, and M. Delibes. 1997. Factors affecting crossing of red foxes and wildcats through non-wildlife passages across a high-speed railway. Ecography **20**:287-294.

Romin, L. A., and J. A. Bissonette. 1996. Deer-vehicle collisions: status of state monitoring activities and mitigation efforts. Wildlife Society Bulletin **24**:276-283.

Rosell, C., J. Parpal, R. Campeny, S. Jove, A. Pasquina, and J. M. Velasco. 1997. Mitigation of barrier effect on linear infrastructures on wildlife. Pages 367-372 in K. Canters, editor. Habitat fragmentation and infrastructure. Ministry of Transportation, Public Works and Water Management, Delft, The Netherlands.

Saunders, D. A., and R. J. Hobbs. 1991. Nature conservation 2: the role of corridors. Surrey Beatty & Sons, Chipping Norton, New South Wales.

Schall, A., L. D. Humblot, and D. Guilminot. 1985. Premieres donnees sur la frequentation de passages a faune par la cerf, Autoroute A26, Haute Marne, Nord-Est de la France. Pages 269-274 in Routes et faune sauvage. Service d'Etudes Techniques de Routes et Autoroutes, Bagneaux, France.

Singer, F. J., and J. L. Doherty. 1985. Managing mountain goats at a highway crossing. Wildlife Society Bulletin **13**:469-477.

Sullivan, T. P., L. O. Nordstrom, and D. S. Sullivan. 1985. Use of predator odors as repellents to reduce feeding damage by herbivores II. Black-tailed deer (*Odocoileus hemionus columbianus*). Journal of Chemical Ecology **11**:921-935.

SYSTAT. 1998. Version 8.0 for Windows. Evanston, Illinois.

Van der Zee, F. F., J. Wiertz, C. J. F. Ter Braak, R. C. van Apeldorn, and J. Vink. 1992. Landscape change as a possible cause of the badger *Meles meles* L. decline in The Netherlands. Biological Conservation **61**:17-22.

Waltho, N., and J. Kolasa. 1996. Stochastic determinants of assemblage patterns in coral reef fishes: a quantification by means of two models. Environmental Biology of Fishes **47**:255-267.

Waters, D. 1988. Monitoring program mitigative measures, Trans-Canada Highway twinning: phase I. Final report. Parks Canada, Banff National Park, Alberta, Canada.

Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. American Naturalist **125**:879-887.

Woods, J. G. 1990. Effectiveness of fences and underpasses on the Trans-Canada Highway and their impact on ungulate populations project. Report. Parks Canada, Banff National Park Warden Service, Banff, Alberta, Canada.

Woods J. G., L. Cornwell, T. Hurd, R. Kunelius, P. Paquet, and J. Wierzchowski. 1996. Elk and other ungulates. Pages 149-156 in J. Green, C. Pacas, L. Cornwell, and S. Bayley, editors. Ecological outlooks project: a cumulative effects assessment and futures outlook of the Banff Bow Valley. Department of Canadian Heritage, Ottawa, Ontario, Canada.

Yanes, M., J. M. Velasco, and F. Suarez. 1995. Permeability of roads and railways to vertebrates: the importance of culverts. Biological Conservation **71**:217-222.

Appendix 1

Curvilinear regression equations used to optimize the fit between species-performance ratios and each underpass attribute.

Number	*Equation*
1	$\ln y = a+bx+cx^2+dx^3$
2	$y^2 = a+bx+cx^2+dx^3$
3	$y^{0.5} = a+bx+cx^2+dx^3$
4	$y^{-1} = a+bx+cx^2+dx^3$
5	$y = a+b(\ln x)^{-1}+c(\ln x)^{-2}+d(\ln x)^{-3}$
6	$y = a+b(x)^{-1}+c(x)^{-2}+d(x)^{-3}$
7	$y = a+b\ln x+c(\ln x)^2+d(\ln x)^3$
8	$y = a+b(\ln x)^2+c\ln x+d(\ln x)^{-1}$
9	$y = a+bx+cx^2+d(x)^{-1}$
10	$y = a+bx+cx^2+dx^3$
11	$\ln y = a+bx+cx^2$
12	$y^2 = a+bx+cx^2$
13	$y^{0.5} = a+bx+cx^2$
14	$y = a+b(\ln x)^{-1}+c(\ln x)^{-2}$
15	$y = a+b(x)^{-1}+c(x)^{-2}$
16	$y = a+b\ln x+c(\ln x)^{-1}$
17	$y = a+b(\ln x)^2+c\ln x$
18	$y = a+bx+c(x)^{-1}$
19	$y = a+bx+cx^2$
20	$\ln y = a+bx$
21	$y = a+be^{-x}$
22	$y = a+b(x)^{-2}$
23	$y = a+b\ln x(x)^{-2}$
24	$y = a+b(x)^{-1.5}$
25	$y = a+b(x)^{-1}$
26	$y = a+b\ln x(x)^{-1}$
27	$y = a+b(x)^{-0.5}$
28	$y = a+b(\ln x)^{-1}$
29	$y = a+b\ln x$
30	$y = a+bx^{0.5}$
31	$y = a+bx(\ln x)^{-1}$
32	$y = a+b(\ln x)^2$
33	$y = a+bx^{0.5}\ln x$
34	$y = a+be^{x}$
35	$y = a+bx^3$
36	$y = a+bx^{2.5}$
37	$y = a+bx^2\ln x$
38	$y = a+bx^2$
39	$y = a+bx^{1.5}$
40	$y = a+bx\ln x$
41	$y = a+bx$