# Permeability of the Trans-Canada Highway to Wildlife in Banff National Park: Importance of Crossing Structures and Factors Influencing Their Effectiveness

*Anthony P. Clevenger*
*Department of Forestry*
*The University of Tennessee*
*Knoxville, TN*

**Abstract**

Highway mitigation measures have been designed to increase permeability and habitat connectivity for wildlife living in transportation corridors. Unfortunately, post-construction performance evaluations are rarely carried out to determine mitigation measure effectiveness, modify them if necessary, and learn from past experiences. In Banff National Park, Alberta, 11 wildlife underpasses (WUP) were constructed during the last decade to allow wildlife movement across a 4-lane section of the Trans-Canada highway (TCH). This paper evaluates wildlife use of the WUP and examines the importance of structural and environmental features that may enhance wildlife use of them. WUP were intensively monitored during 12 months. WUP were characterized by eight continuous variables and three categorical variables. Simple correlations were used to examine relationships between monthly crossing rate and WUP variables. Stepwise multiple regression analyses developed models with one or more variables explaining relative use of WUP. Elk and deer used the WUP more frequently than carnivores. Among large carnivores, black bears were most frequent users. Monthly crossing rates varied during the year and reflected seasonal activity patterns. Underpass use by large carnivores was negatively correlated with human use levels and was greatest at divided underpasses. WUP quality was best predicted by human use levels, and WUP openness and length, yet human use was the most important factor. Ungulate use was positively correlated with human use and negatively correlated with underpass length. Regression analysis showed that human activity and openness were the most important model components. The results suggested that possible barrier effects of the TCH may be reduced by WUP, but long term studies are needed to assess TCH effects on species' fitness. Park management of human activity around WUP will be crucial for success. The requirements of sensitive species should take precedence in design of quality WUP.

**Introduction**

The effect of roads on animal populations has been the focus of numerous studies during the last few decades (Oxley et al. 1974, Muskett and Jones 1980, Bennett 1991, Evink at al. 1996). Some well documented impacts of roads on animal populations include: habitat loss, habitat alienation due to sensory disturbances, barrier effects, and mortality (Adams and Geis 1983, Mansergh and Scotts 1989, Paquet 1993, van der Zee et al. 1992). Of all these, barrier effects or habitat fragmentation, poses what many conservation biologists consider the greatest threat to biological diversity (Harris 1984, Saunders and Hobbs 1991, Noss and Cooperrider 1994).

Measures have been designed to increase permeability and habitat connectivity and mitigate barrier effects of roads. The first wildlife crossing structures were constructed in the 1970's (Reed et al. 1975, SETRA 1978, Hunt et al. 1987) and many more have been constructed since then. Nevertheless, few rigorous evaluations regarding crossing structure effectiveness have been carried out (Romin and Bissonette 1996).

Research aimed at quantifying wildlife use of crossing structures (hereafter referred to as wildlife underpasses) has focused mostly on ungulates (Reed et al. 1975, Ballon 1985, Schall et al. 1985, Singer and Doherty 1985, Woods 1990, Carsignol 1993) and rarely on carnivores (Foster and Humphrey 1995). Only recently studies have begun addressing what structural and environmental factors might influence underpass use by wildlife (Foster and Humphrey 1995, Yanes et al. 1995, Rodriguez et al. 1996, Rosell et al. 1997). Virtually nothing is known regarding differences in effectiveness between overpasses and underpasses, or between underpass types and configurations.

Performance evaluations of wildlife crossing structures are essential for determining effectiveness, making recommendations for improving them if necessary, and designing more effective measures in the future. Compared to other mitigation measures, crossing structures, particularly those for large mammals, are costly (Camut 1985, Gounot 1985, Leeson, this volume). Proper evaluations will aid resource managers and highway planners when making decisions regarding the number, placement and type of wildlife crossing structures along a section of highway.

This paper evaluates the patterns of wildlife use of underpasses along a 4-lane section of the Trans-Canada highway (TCH) in the central Canadian Rocky Mountains of Alberta. Secondly, I examine the relative importance of structural and environmental attributes, as factors determining the quality of underpass as perceived by wildlife.

**Study area**

The work was carried out in the Bow River Valley along the TCH corridor in Banff National Park (BNP, Figure 1). Situated approximately 100 km west of Calgary, BNP is the most heavily visited national park in Canada with over 4 million visitors per year. Most of these visitors arrive by private vehicle or motor coach along the TCH. The highway also is a major commercial motorway between Calgary and Vancouver. Annual average daily traffic volume at the park east entrance was 13,800 vehicles/day in 1994 and increasing at a rate of 3% per year (R. MacMahon, Parks Canada, pers. comm.).

The transportation corridor also contains the Canadian Pacific Railway (CPR) mainline, access roads to Banff town site and several important two-lane highways (highways 93 and 40) and secondary roads (highway 1A). The study was conducted primarily along the easternmost 27 kilometers of twinned (4-lane) TCH in BNP (Phase 1 and 2). Ten conventional highway wildlife underpasses were constructed between 1986-88 along Phases 1 and 2 to permit wildlife movement across the twinned TCH. One additional underpass west of Phase 1 and 2 was constructed at Castle Junction interchange in 1991.

A 2.4 m high page-wire fence borders twinned sections of TCH. All underpasses are located along twinned sections of highway.

The location of the wildlife underpasses relative to the TCH are shown in Figure 1. Seven of the 11 underpasses are cement open-span underpasses, two are bridges over creeks, and two are metal culverts. Divided sections of the highway are made up of two separate structures.

The Bow River Valley in BNP is situated within the Continental Ranges of the Southern Rocky Mountains. Elevations range from 1,300 m to over 1,600 m at the Continental Divide. Valley floor width varies from 2-5 km. The climate is continental and characterized by relatively long winters and short summers (Holland and Coen 1983). Mean annual snowfall at the town of Banff is 249 cm. The transportation corridor traverses the Montane Ecoregion. Vegetation consists of open forests dominated by Douglas fir (*Pseudotsuga menziesii*), white spruce (*Picea glauca*), lodgepole pine (*Pinus contorta*), aspen (*Populus tremuloides*) and natural grasslands.

## Methods

### *Data collection*

Data from monitoring animal movements through wildlife underpasses on the TCH were used to assess relative use of underpasses by wildlife. Wildlife visits and through-passages at underpasses were quantified by identifying tracks of animals on track sections at each underpass (Bider 1968). Track sections were on level ground at underpass ends and measured roughly 2m long and 4m wide. Tracking material consisted of a dry, loamy mix of sand, silt and clay, 3-4cm deep. During each monitoring check, on each track section the tracks of animals present were identified, their direction of travel recorded, and the surface raked smooth. At each check, the tracking medium was classified as operative or inoperative depending on the ability to read tracks clearly.

Underpasses were checked at 3-4 day intervals. Tracks of unidentified canids and small and medium-sized mammals were recorded but not included in this article. Wildlife in this study consisted of wolves (*Canis lupus*), coyotes (*C. latrans*), cougars (*Felis concolor*), black bears (*Ursus americanus*), grizzly bears (*U. arctos*), deer (*Odocoileus sp.*) and elk (*Cervus elaphus*). Other species were recorded using the underpasses (bighorn sheep *Ovis canadensis*, mountain goats *Oreamnos americanus*, moose *Alces alces*), however, due to small samples sizes they were excluded from the analysis. Twelve months of data were collected on wildlife movement through the underpasses between 1 November 1996 to 31 October 1997.

### *Data analysis*

To determine what attributes most influence the use of underpass, wildlife were divided in two guilds: large carnivores (wolves, cougars, black and grizzly bears) and ungulates (deer and elk). Nine of the 11 underpasses were considered in the analysis. Cascade underpass was excluded because of inconsistent and overall sub-optimal tracking conditions. East gate underpass was left out due to its staggered as opposed to in-line configuration thereby negating comparisons of structural variables. The analysis was based on through-passages by species from the two groups at the underpasses. Presence-absence data, independent of number of individuals, were used in estimating crossing rates. For each underpass, the monthly crossing index was calculated as the number of through-passes divided by the total number of through-passes at all nine underpasses during the same month. Bear crossing data were collected only during active months (May through October). The amount of human activity (hikers, bikers, skiers, horses) at each underpass was quantified in the same manner as the monthly crossing rate for wildlife.

In order to characterize the underpasses, eight continuous variables and three categorical variables were measured (see Table 1). Continuous variables included:

Length (L): underpass length (excluding median width);
Width (W): underpass width;
Height (HT): underpass height;
Openness (OPEN): calculated from the three former variables according to the formula (width x height)/length (Reed and Ward 1985);
Sound level (SL): mean of A-weighted decibel readings;
Forest cover (DFOR): distance to nearest forest cover;
CP Railway (DCPR): distance to CP Railway tracks;
Human activity (HUM): mean monthly index of human use;
Measurements of underpass dimensions were means if structures were not uniform in size. Sound level readings were taken 5m in front of underpass entrances and in the center. Distance to forest cover and CP Railway tracks represents the mean of measurements taken from both underpass ends.

Three categorical variables were:
Habitat (HAB): forest (0); forest/open mix (1).
Underpass configuration (CONF): divided (0); undivided (1).
Underpass type (TYPE): open-span (0); culvert (1).

Distances between consecutive underpass along the TCH were randomly distributed (Runs test, 2-tail P=0.52; mean distance between underpasses = 2.7 km) indicating that crossing rates from consecutive underpasses were independent of each other.

The relationship between the monthly crossing rate and each of the underpass variables was examined by simple correlation (continuous variables) and non-parametric Mann-Whitney U tests (categorical variables). Variables were log-transformed where this provided a better fit for correlations. Forward stepwise multiple regression analyses were then performed (Statistix 1996) to develop models with combinations of one or more variables that explain the relative use of underpasses. Statistical significance was set at $P<0.10$ in all analyses. The underlying assumption in these analyses is that the monthly crossing rate is a measure of the quality of that underpass as sensed by large carnivores or ungulates.

## RESULTS

### *Wildlife underpass use*

For the 12-month period, the average number of monthly monitoring checks at the 11 structures was 8.5 and the average number of days between checks was 3.7 (range = 3.2 - 7.4 days). There were a total of 2,458 visits by wildlife to the underpasses (Table 2). Total number of species' track detections at the underpasses ranged from 148 (Carrot Creek) to 482 (Buffalo). Carrot Creek had the lowest total number of animal through-passes. The through-passage rate was highest at Buffalo, Cascade, Edith, Powerhouse and Vermilion underpasses. Through-passage rate was lowest at East gate (88%). There were a total of 170 failed passages (5%), i.e., where species did not travel through the underpasses. Monitoring checks recording no tracks occurred most often at Morrison Coulee and Carrot Creek.

Elk were most frequently detected at the wildlife underpasses (n=1,338, 54%), followed by deer (n=538, 22%) and coyotes (n=373, 15%; Table 3). Among large carnivores, black bear tracks were found 97 times (4%) at the underpasses, wolves 77 times (3%) and cougars 29 times (1%). One wolf pack (Bow Valley pack) was responsible for practically all the underpass use (75 out of 77 through-passes), whereas one member of the Cascade pack used the underpasses twice during winter. Overall through-passage rate was high (mean = 98%, n=7), ranging from cougars and grizzly bears (100%) to elk and deer (96%). Elk, deer and coyotes used all of the underpasses, while black bears were found traveling through nine, wolves six and cougars five. Two radio-collared adult male grizzly bears used three different underpasses.

Monthly crossing rates for all wildlife in the study area were low from December through April, increased sharply from May to July, and then decreased to September (Fig. 2). There was an abrupt increase in activity during November prior to the onset of winter. There were slight differences between large carnivore and ungulate crossing rates over the course of the year (Fig. 3 & 4). Crossing rates for both groups were lowest in winter. However, they differed in that large carnivores were more active than ungulates in early spring, whereas ungulates sustained higher crossing rates during the autumn compared to carnivores.

*Factors influencing use*

Correlations between underpass variables and the monthly crossing index for wildlife suggested that several variables were important correlates of underpass quality (Table 4). For large carnivores, the amount of human activity was significant and showed a strong negative correlation with underpass usage. Underpass length was positively correlated with large carnivore crossing indices but was not significant. Higher rates of passage were associated with divided underpass types and were significantly different from undivided types (P=0.07, two-tail test). All other variables showed weak correlations.

Results from stepwise linear regression analyses of the crossing indices for large carnivores is summarized in Table 5. Underpass quality was best predicted by three attributes, levels of human activity, openness and underpass length, which together explained 60% of the variance. Human activity was the most important factor alone, accounting for more than half of the variance (30%).

Correlations for the relationship between underpass use by ungulates and underpass variables suggested that two variables were important in determining underpass quality (Table 4). Level of human activity and underpass length were highly correlated with ungulate use, the former being positive whereas the latter negative. Ungulates were indifferent to underpass configuration, underpass type, and type of habitat in the vicinity of an underpass failing to show any correlations.

Underpass quality for ungulates was best predicted by three variables, levels of human activity, openness and height, which combined accounted for 50% of the variance (Table 5). Level of human activity and underpass openness were the most important model components explaining 42% of the variation found. Underpass length did not explain significant additional variation.

**Discussion**

Is the Trans-Canada highway permeable to wildlife? The results indicated that during the 12-month period the underpasses were readily used by most species of large carnivores and ungulates in BNP. For some species such as elk, deer, coyotes, black bears and at least one wolf pack, crossing structures were used regularly suggesting that possible barrier effects may be reduced. The proportion of through-passages was high and may be a result of animals becoming accustomed to the structures after 10 years. During a 5-year monitoring period post-twinning Phase 1, average through-passage rates for elk and deer were 50% and 83%, respectively (Waters 1988). Significantly greater through-passage rates (>96%) occurred along newly constructed underpasses in Phase 2 (Bunyan 1990)and was best explained by prior habituation to underpasses on Phase 1.

Monthly crossing rates from this study varied greatly over the course of the year and were concordant with prior knowledge of seasonal animal activity and movement patterns in the Bow Valley. Possible reasons for the low crossing rates of large carnivores during September and October may be related to greater or more uniformly distributed food resources. Reduced underpass use during these months also might have resulted from decreased bear activity prior to denning as bears accounted for half of the large carnivores sampled.

Factors influencing use. Large carnivore use of wildlife underpasses was correlated with several variables; however, human use levels was shown to be the most important and best predicted high quality underpasses. Due to their location, several underpasses are key passages for recreationists to cross the TCH and access popular hiking, biking or horseback riding trails in the park. In essence, these underpasses are conduits with elevated levels of human use and similar to well-used trails.

The influence of humans on underpass use by large carnivores is not surprising. In BNP and elsewhere, large carnivores generally avoid areas of human activity including trails. Research on wolf movements in relation to linear structures (roads, trails, railways, etc.) in the Bow Valley showed that they tended to avoid areas within 200m of trails (Paquet et al 1996). Grizzly bear survival is strongly linked to areas far from human use areas. In BNP, 100% of all grizzly bear mortality occurs less than 500m and 200m from roads and trails, respectively (Gibeau et al. 1996). Similar negative responses of black bears and cougars to trails and human use have been reported in other areas including national parks (Mattson et al. 1987, Kasworm and Manley 1990, McCutchen 1990, Jalkotzy and Ross 1993).

Underpass use by ungulates also was best predicted by the level of human use. However, contrary to large carnivores, a strong positive correlation was found. Most of the underpasses with high human use levels are situated close to the town of Banff as these provide convenient and quick access to popular hiking and horse trails. The a synchronized use of underpasses by large carnivores and ungulates can best be explained by two separate phenomena. First, large carnivores are underutilizing or avoiding the underpasses closest to areas of significant human activity for reasons explained above. The second is a result of a dramatic change in elk distribution in the Bow Valley following wolf recolonization in the early 1980's. The simultaneous recovery of wolves and increased numbers of elk in and around the town of Banff suggests that elk seek out wolf-free zones as refugia from predation (Paquet et al. 1996). Deer were also considered in the analyses, however, elk accounted for 75% of the ungulate data.

Underpass dimensions rather than landscape attributes associated with them have taken precedence in determining optimal structures for ungulates (Foster and Humphrey 1995). Previous studies indicated that ungulates were wary of using underpasses that were narrower than 7m wide or lower than 2.4 m high (Reed et al. 1975, CTGREF 1978, Velasco et al. 1992, Rosell et al. 1997). All but one of the underpasses in this study were greater than 7m wide (mean=9.8m, SD=2.8) and all were greater than 2.4m high (mean=3.0, SD=0.4).

Underpasses with high openness ratios were also high quality underpasses as perceived by ungulates. Reed et al. (1975) recommended an openness ratio for underpasses for mule deer greater than 0.6 when calculated in meters. Seven of the nine BNP underpasses surpassed this parameter (median=0.85, range=0.21-1.16).

Divided highway underpasses were recommended over undivided or bridged structures because they are less expensive, but more importantly the latter resemble a tunnel and may inhibit use (Foster and Humphrey 1995). The results shown here partially support that proposal as large carnivores tended to use divided underpasses more than undivided ones; ungulates did not select for one type over the other.

*Are the underpasses effective in reducing barrier effect?* The total number of underpass visits and through-passages was high for some species (elk, deer, coyote), moderate for others (black bear, one wolf pack, cougar) and extremely low for one other species (grizzly bear, one other wolf pack). For species that used the underpasses regularly, the data indicate that possible fragmentation effects due to the TCH might be reduced considerably. However, to determine whether the TCH (and railway) are fragmenting wildlife populations in BNP and the Bow Valley we need to know something about crossings and movements prior to highway construction, which unfortunately is impossible. Without question cross-valley and cross-TCH movements today are filtered due to human activity, availability of quality crossing points and underpasses along the TCH, and behavioral variability in animals. As a result, travel patterns for most animals, particularly large carnivores, have been modified and the number of crossings are much lower than in the past. Is this significantly affecting the fitness of animal populations in the Bow Valley? To answer this question we will need to carry out studies of highway effects, closely monitoring species' movements and life history requirements in the transportation corridor. Because many of the species of special concern are long-lived and have low reproductive rates (e.g., grizzly bear), any deleterious indirect effects of the highway are most likely incremental and cumulative and many years of research will be required to assess highway effects.

The results indicate that managing human activity around wildlife crossing structures will be of utmost importance if the structures are to be effective in allowing wildlife to permeate linear features such as the

TCH (see Gibeau and Herrero, this volume). This has serious implications in BNP given the current rates of growth in visitor numbers and development. The findings described here lend greater support to the BNP management plan, emphasizing that stricter limits to growth be imposed and calling for more effective methods of managing and limiting human use (Banff-Bow Valley Study 1996). The permeabilityof the TCH has to be improved and guaranteed by a general strategy that includes wildlife crossing structures as one measure among others.

In addition to restricting human use, underpasses with a large aperture should be designed in the future. Carrot Creek, Duthil and Edith underpasses were shown to be high quality underpasses for large carnivores and ungulates alike, primarily because of their high openness ratio. Five-mile bridge, an unconventional wildlife underpass along the TCH, is one of the few places large carnivores (including grizzly bears) choose to cross the TCH (Gibeau and Heuer 1996). The bridge spans over the Bow River, the highway 1A, and the CPR mainline and is best characterized by its great breadth and openness.

Though few habitat or landscape attributes were measured in this analysis, none were shown to be significant in determining quality wildlife underpasses. Nevertheless, topography and vegetation are probably important in determining underpass quality, and location is likely the most critical factor in guaranteeing success. For example, large carnivores cross high-speed motorways not through the best designed underpass, but rather through the underpass that is best aligned with a major drainage (Beier and Loe 1992, Clevenger, unpubl. data).

In this analysis we have attempted to address each of these factors as best possible and carry out a rigorous evaluation of the factors most important in determining high quality underpass for the two guilds. The results suggest that in BNP underpasses with low human use are most important and most effective in allowing large carnivores to permeate highways and prevent habitat fragmentation. To design quality underpasses the requirements of sensitive species such as large carnivores should take precedence. As such, species with generalized habitat needs and greater adaptability to human disturbance also will be accommodated.

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**Table 1**
**Characteristics of nine wildlife underpasses (WUP) used in analysis of factors influencing wildlife use.**

| WUP | L (m) | W (m) | HT (m) | OPEN | SL (db) | DFOR (m) | DCPR (m) | HUM | HAB | CONF | TYPE |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Carrot Creek | 28.8 | 13.4 | 2.5 | 1.16 | 66.9 | 63.3 | 750 | 1.9 | 1 | 0 | 0 |
| Morrison Coulee | 67.5 | 4.2 | 3.5 | 0.21 | 60.7 | 11.9 | 800 | 1.8 | 0 | 0 | 1 |
| Duthil | 28.0 | 9.8 | 2.9 | 1.01 | 64.8 | 15.2 | 20 | 0.6 | 0 | 0 | 0 |
| PowerHouse | 27.5 | 9.5 | 2.9 | 1.00 | 64.1 | 47.3 | 20 | 5.3 | 1 | 0 | 0 |
| Buffalo | 27.1 | 10.0 | 3.0 | 1.10 | 69.0 | 35.9 | 250 | 15.2 | 1 | 1 | 0 |
| Vermilion | 27.2 | 9.8 | 2.7 | 0.97 | 70.3 | 23.3 | 1200 | 3.2 | 0 | 1 | 0 |
| Edith | 25.6 | 10.3 | 2.8 | 1.12 | 71.2 | 27.5 | 400 | 11.4 | 1 | 1 | 0 |
| Healy | 28.0 | 9.0 | 2.9 | 0.65 | 66.5 | 23.9 | 750 | 0.6 | 1 | 0 | 0 |
| Castle | 56.0 | 7.0 | 4.0 | 0.50 | 61.7 | 35.4 | 750 | 0.5 | 1 | 1 | 1 |

L: length; W: width; H: height; OPEN: openness ratio; SL: sound level; DFOR: distance to forest cover; DCPR: distance to CP Railway; HUM: human activity index; HAB: habitat; CONF: configuration; TYPE: WUP type. See methods for definition of variables.

**Table 2**

**Summary data from 11 wildlife underpasses (WUP) along twinned sections of the TCH in Banff National Park, November 1996 – September 1997. Figures in bold type indicate highest and lowest categorical values (excluding Castle).**

| WUP (# of checks) | Total Visits[a] | Number of TP's[b] (%) | Number of failed TP's[b] | No Tracks[c] |
|---|---|---|---|---|
| East gate (97) | 286 | 253 (88) | 33 | 14 |
| Carrot Creek (97) | 148 | 142 (96) | 6 | 33 |
| Morrison Coulee (100) | 202 | 179 (89) | 23 | 36 |
| Duthil (102) | 320 | 311 (97) | 9 | 8 |
| PowerHouse (100) | 331 | 329 (99) | 2 | 8 |
| Cascade (98) | 328 | 326 (99) | 2 | 5 |
| Buffalo (97) | 482 | 479 (99) | 3 | 9 |
| Vermilion (99) | 395 | 390 (99) | 5 | 2 |
| Edith (100) | 432 | 427 (99) | 5 | 8 |
| 5-Mile bridge (98) | 181 | 176 (97) | 5 | 27 |
| Healy (97) | 304 | 298 (98) | 6 | 7 |
| Castle (44) | 97 | 96 (99) | 1 | 13 |

[a] *Total visits: Total number of species tracks detected.*
[b] *TP: Through-passage.*
[c] *Number of checks recording no tracks present.*

**Table 3**

**Species detections and through-passages at 11 wildlife underpasses (WUP) along twinned sections of the Trans-Canada highway in Banff National Park, Alberta. Figures in bold type indicate highest and lowest categorical values.**

| Guild Species | Total visits[a] | # of TP's[b] (%) | # of failed TP's[b] | WUP[c] visited |
|---|---|---|---|---|
| *Ungulates* | | | | |
| Elk | 1,338 | 1,290 (96) | 48 | All (12) |
| Deer | 538 | 518 (96) | 20 | All (12) |
| *Carnivores* | | | | |
| Coyote | 373 | 365 (98) | 8 | All (12) |
| Wolf | 77 | 76 (99)[d] | 1 | CC, CA, CJ, DH, H, ED |
| Black bear | 97 | 94 (99) | 1 | CC, CA, CJ, DH, EG, ED, H, MC, PH |
| Grizzly bear | 6 | 6 (100) | 0 | DH, H, PH |
| Cougar | 29 | 29 (100) | 0 | CC, DH, EG, ED, MC |

[a]=*Total visits: Total number of times species' tracks detected at underpasses.*
[b]=*TP: Through-passage.*
[c]=*WUP: B=Buffalo; CC=Carrot Cr; CA=Cascade; CJ=Castle; DH=Duthil; EG=East gate; ED=Edith; H=Healy; MC=Morrison Coulee; PH=PowerHouse; V=Vermilion; 5M=5-Mile bridge.*
[d]=*Consists of 74 through-passes by Bow Valley pack and two through-passes by one member of the Cascade pack.*

**Table 4**

(a) Correlation coefficients for the relationship between use of nine underpasses by wildlife and underpass variables. (b) Mean values for underpass use (tested using Mann-Whitney). $\underline{n}$=9 for both large carnivores and ungulates.

| Variables | Large carnivores | Ungulates |
|---|---|---|
| (a) Length | 0.47 | -0.76*** |
| Width | -0.10 | 0.26 |
| Height | -0.09 | -0.42 |
| Openness | -0.02 | 0.16 |
| Sound level | 0.25 | 0.36 |
| Human activity | -0.60** | 0.75*** |
| Distance to forest | -0.26 | 0.05 |
| Distance to CPR | -0.04 | 0.13 |
| (b) Habitat | | |
| 0 Forest | 10.6 | 4.7 |
| | NS | NS |
| 1 Forest/open mix | 11.9 | 3.5 |
| Configuration | | |
| 0 Divided | 16.5 | 4.0 |
| | ** | NS |
| 1 Undivided | 3.0 | 3.9 |
| Type | | |
| 0 Open-span | 11.6 | 4.3 |
| | NS | NS |
| 1 Culvert | 10.1 | 2.7 |

*$\underline{P}$<0.10, **$\underline{P}$<0.05, ***$\underline{P}$<0.01.
NS, not significant.

**Table 5**

Stepwise multiple regression analyses of monthly use indices of underpasses in relation to underpass variables*.

| Dependent Variable | Independent variables & variance explained ($r^2$) Step1 | Step2 | Step3 | Step4 | Total variance from significant steps |
|---|---|---|---|---|---|
| Large carnivore monthly use Index | HUM 29.6% | L 11% | OPEN 12% | SL 7% | 59.6% |
| Ungulate monthly use index | HUM 22.4% | OPEN 19.8% | HT 8.0% | L 0% | 50.2% |

*: HUM=human use; L=length; OPEN=openness ratio; SL=sound level; HT=height (see Methods for description).

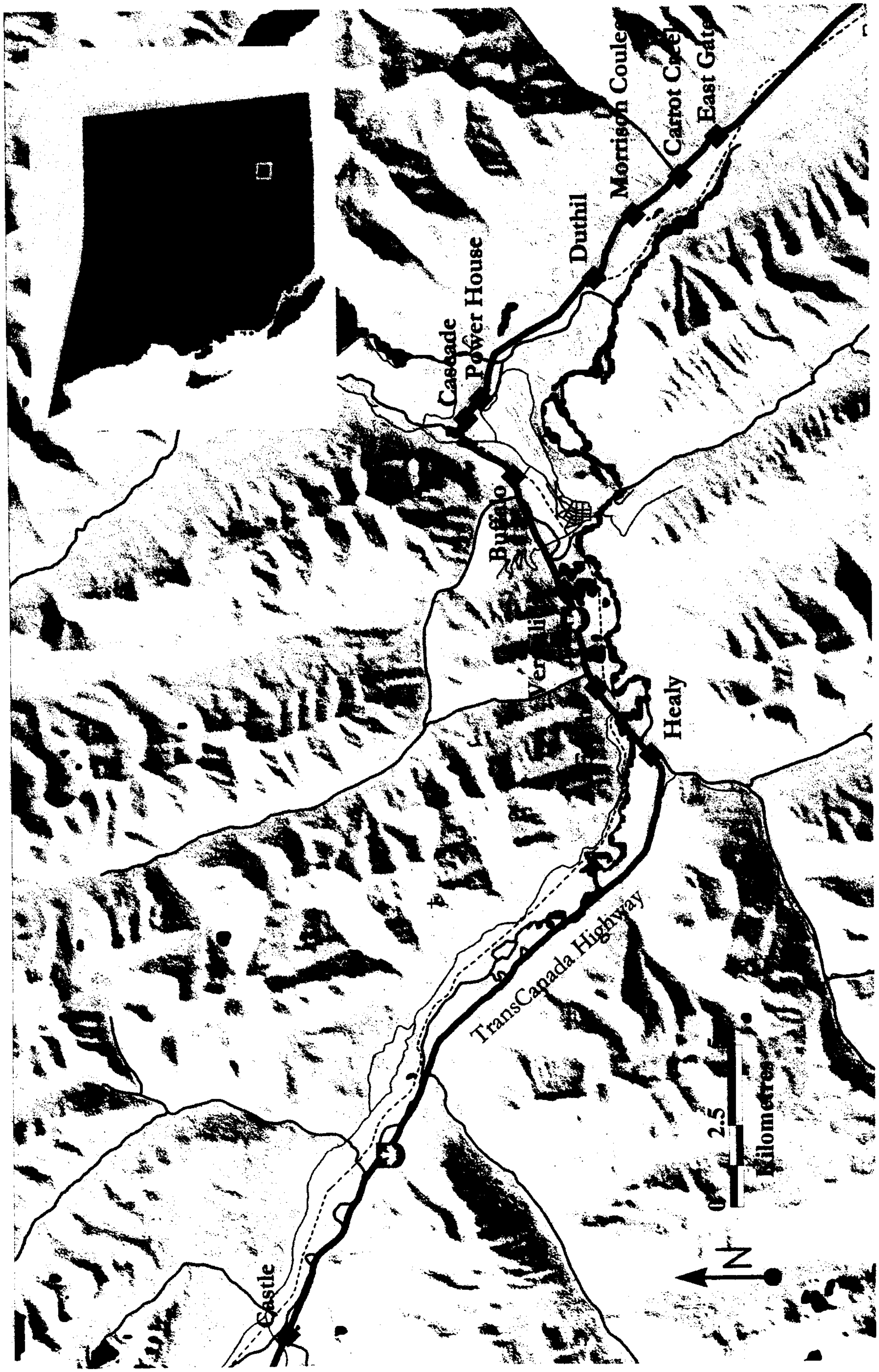


**Figure 1.**
**Location of study and wildlife underpasses along twinned sections of the Trans-Canada Highway in Banff National Park, Alberta.**

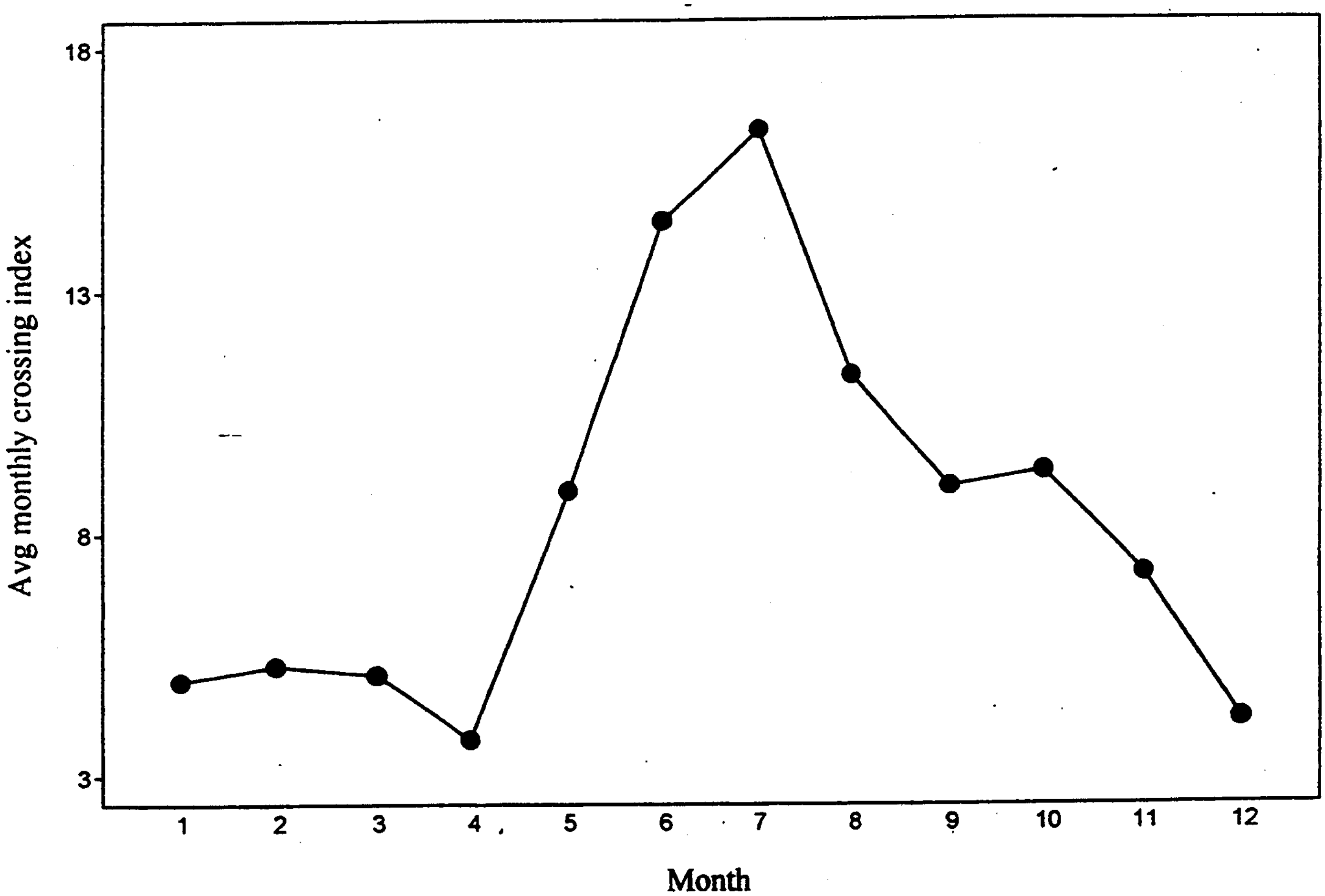


**Figure 2.**
**Mean monthly crossing rates of wildlife at underpasses in Banff National Park, Alberta.**

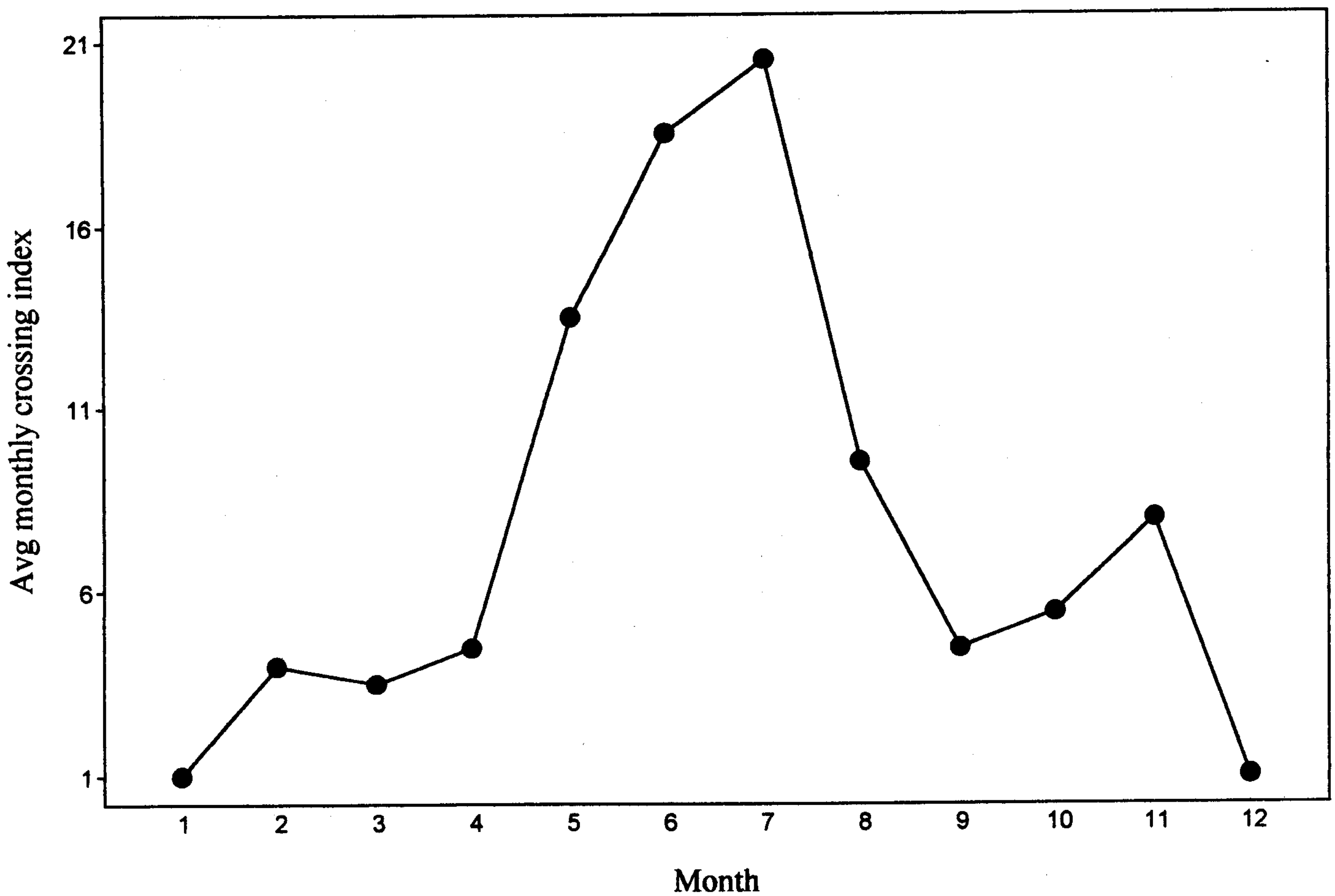


**Figure 3.**
**Mean monthly crossing rates of large carnivores at underpasses in Banff National Park, Alberta.**

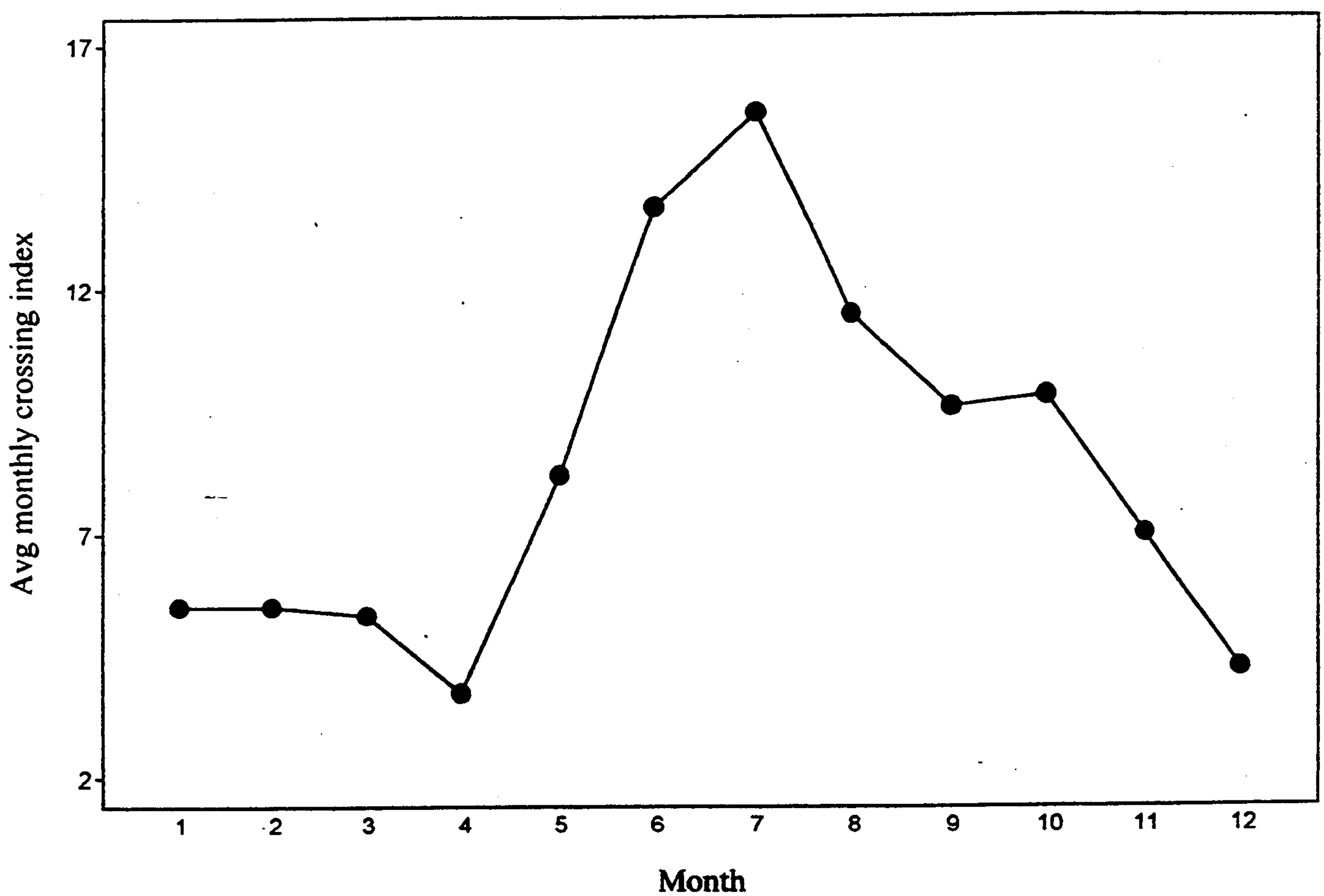


**Figure 4.**
**Mean monthly crossing rates of ungulates at underpasses in Banff National Park, Alberta.**