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Drainage culverts as habitat linkages and factors affecting passage by mammals

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Summary

1. Drainage culverts are ubiquitous features in road corridors, yet little is known about the efficacy of culverts for increasing road permeability and habitat connectivity for terrestrial wildlife. Culvert use by small- and medium-sized mammals was investigated along roads in Banff National Park, Alberta, Canada. An array of culvert types was sampled varying in dimensions, habitat and road features during the winters of 1999 and 2000. Expected passage frequencies were obtained by sampling relative species abundance along transects at the ends of each culvert.

2. Weasels *Mustela erminea* and *M. frenata* and deer mice *Peromyscus maniculatus* used the culverts for passage most frequently, whereas red squirrels *Tamiasciurus hudsonicus* and snowshoe hares *Lepus americanus* were the most common small mammals in the study area according to transects sampled near each culvert.

3. Species' performance indices (observed crossing vs. expected crossing) were calculated for five species by comparing their tracks inside and adjacent to 36 culverts. Culvert performance indices were significantly different between the five species: culvert attributes influenced species' use but different attributes appeared to affect use by different species.

4. At all scales of resolution (species, species group and community level), traffic volume, noise levels and road width ranked high as significant factors affecting species' use of the culverts. Passage by American martens *Martes americana*, snowshoe hares and red squirrels all increased with traffic volume, the most important variable. Coyote *Canis latrans* use of culverts was negatively correlated with traffic volume. Increasing noise and road width appeared to be negative influences on culvert passage by coyotes, snowshoe hares and red squirrels.

5. Structural variables partially explained passage by weasels and martens. Weasel passage was positively correlated with culvert height but negatively correlated with culvert openness. Martens preferred culverts with low clearance and high openness ratios. High through-culvert visibility was important for snowshoe hares but not for weasels. The passage by weasels and snowshoe hares was positively correlated with the amount of vegetative cover adjacent to culverts.

6. For many small- and medium-sized mammals drainage culverts can mitigate the potentially harmful effects of busy transport corridors by providing a vital habitat linkage. To maximize connectivity across roads for mammals, future road construction schemes should include frequently spaced culverts of mixed size classes and should have abundant vegetative cover present near culvert entrances. Further work is required to assess the effects of culverts on population demography and gene flow adjacent to large roads.

Key-words: Banff National Park, barrier effect, connectivity, habitat fragmentation, mitigation measures, passage efficacy, road ecology.

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Introduction

Ecological theory about road corridors highlights their functional role as conduits, barriers (or filters), habitats, sources and sinks (Bennett 1991; Forman 1995). These effects can be of major ecological significance (Forman & Alexander 1998; Spellerberg & Morrison 1998). Many roads are barriers or filters to horizontal processes such as animal movement. Further, as roads are upgraded to accommodate greater traffic densities the rate of successful wildlife crossings might decrease significantly (Barnett, How & Humphreys 1978; Lovallo & Anderson 1996; Philcox, Grogan & Macdonald 1999), becoming in some cases the leading cause of animal mortality (Maehr, Land & Roelke 1991; Van der Zee *et al*. 1992; Clarke, White & Harris 1998) and effectively fragmenting otherwise connected habitats (Trombulak & Frissell 2000).

A recent review of the ecological effect of roads reported that barrier effects might emerge as the greatest ecological impact of roads with vehicles (Forman & Alexander 1998). In an increasing number of landscapes, the regular movements of animals involve road crossings. Efforts to increase road permeability and mitigate potential barrier effects might offset the risk of isolating or reducing populations (Opdam *et al*. 1993; Canters 1997). Specifically, wildlife underpasses and overpasses have been designed to facilitate the movements of wildlife (Bekker, Hengel & van der Sluijs 1995). Although not designed for animal passage, drainage culverts are ubiquitous features in road and rail corridors. However, practically nothing is known about their effectiveness for increasing road permeability and habitat connectivity for smaller mammals. Proximity to cover and culvert dimensions has been reported as important factors affecting use by small- and medium-sized terrestrial vertebrates (Hunt, Dickens & Whelan 1987; Yanes, Velasco & Suárez 1995; Rodríguez, Crema & Delibes 1996).

The Trans-Canada highway (TCH) is a major transportation corridor through Banff National Park (BNP), Alberta, Canada. The highway and other roads bisect critical montane and subalpine habitats in Banff's Bow River Valley on which many mammals depend. Over 70% of montane habitat in BNP is within the transportation corridor. At present, the TCH consists of 47 km of four-lane highway; however, there are plans to upgrade the remaining 30 km to four lanes within the next 5–10 years (Clevenger & Waltho 2000). This doubling in width and associated increases in traffic volumes present greater difficulties for animal crossings. Culverts along the TCH may allow safe crossings and thus increase permeability of this busy road corridor.

We investigated the use of drainage culverts by small- and medium-sized mammals along roads in BNP. Although the TCH was of primary concern, we sampled an array of culvert types along roads varying in width, traffic volume and landscape. Our specific objectives were to: (i) determine what species used drainage culverts to cross roads; (i) evaluate whether culverts served all species equally or whether some culverts limited habitat connectivity across roads in species-specific ways; (iii) model species' responses to structural, landscape and road-related attributes and identify which were most important in explaining animal passage and culvert effectiveness; and (iv) provide recommendations for incorporating small- and medium-size mammal requirements into drainage culvert design and transportation corridor planning.

Study area

The work was carried out in the Bow River Valley along the Trans-Canada transportation corridor in BNP (51°15′ N, 115°30′ W). Situated approximately 120 km west of Calgary, Banff is the most heavily visited national park in Canada with over 5 million visitors per year. Most of these visitors arrive by private vehicle or motor coach along the TCH. The highway is also a major commercial motorway between Calgary and Vancouver. On average, daily traffic volume at the park east entrance is more than 14 000 vehicles per day, year-round, peaking at more than 35 000 vehicles per day during summer. Use is currently increasing at a rate of 3% per year (Parks Canada Highway Service Centre, Calgary, Alberta).

The transportation corridor also contains the Canadian Pacific Railway mainline, access roads to Banff town site and several important two-lane roads, highways 93, 40 and 1A. The study was carried out along the TCH (two-lane and four-lane sections with and without central reservations) and highway 1A (two-lane with no central reservations).

The Bow River Valley is situated within the front and main ranges of the Canadian Rocky Mountains. Topography is regarded as mountainous, with elevations from 1300 m to over 3400 m, and valley floor width from 2 to 5 km. The climate is continental and characterized by relatively long winters and short summers (Holland & Coen 1983). Mean annual snowfall at the town of Banff is 249 cm. The transportation corridor traverses the montane ecoregion. Vegetation in the park encompasses montane, subalpine and alpine ecoregions. Montane habitats are found in low elevation valley bottoms and characterized by Douglas fir *Pseudotsuga menziesii* (Mirbel) Franco, white spruce *Picea glauca* (Moench) Voss, lodgepole pine *Pinus contorta* Dougl. ex Loud., aspen *Populus tremuloides* Michx. and natural grasslands. Subalpine and alpine ecoregions primarily consist of Engelmann spruce *Picea engelmanii* Parry ex. Engelm. and subalpine fir *Abies lasiocarpa* (Hook.) Nutt. forests interspersed with riparian shrub communities, subalpine grasslands and avalanche terrain, giving way to open shrub–forb meadows in the alpine ecoregion (Achuff & Corns 1983).

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Table 1. Names and definitions of 19 variables used in a multivariate analysis of factors influencing mammal passage at 36 drainage culverts in Banff National Park, Alberta, Canada (1999–2000)

Attribute group Attribute	Code	Definition
STRUCTURAL		
Width*	W	Culvert width (m)
Height	HT	Culvert height (m)
Length*	L	Culvert length (m)
Openness	OP	Culvert openness (= width × length/height)†
Aperture	AP	Mean percentage through-culvert visibility taken from each opening and measured in 25% increments between 0% and 100%
Road-culvert angle	R_ANG	= (X_{dist} × angle created by X_{dist} and Y_{dist}), where X_{dist} = horizontal distance from road edge to culvert opening; Y_{dist} = vertical distance below road grade level to culvert opening.
LANDSCAPE		
Habitat type	HAB	1 = forest-open mix, 2 = closed forest
Percentage forest cover	FOR	Measured as percentage forest cover along two 100-m transects‡
Percentage shrub cover	SHRUB	Percentage shrub cover measured along two 100-m transects‡
Percentage open*	OPEN	Percentage open habitat measured along two 100-m transects‡
Distance to cover	D_COV	Distance to cover in metres (trees or shrubs > 1·5 m high)
Distance to nearest passage structure	D_STR	Distance to nearest mitigation passage in metres (wildlife crossing structure or full-length culvert)
Elevation	ELEV	Elevation (m)
Topography	TOPO	1 = flat uniform, 2 = uneven terrain
ROAD-RELATED		
Road width	RD_W	Width between outer edges of road pavement (m)
Verge width*	VER_W	Width from pavement edge to ecotone created by road (m)
Road clearance*	RD_CL	Distance of road width + verge width (m)
Noise level	NOISE	Mean of 16 A-weighted decibel (dbl) readings taken 5 m from culvert opening at 15-s intervals during 4 min. Readings were taken on a single day between 10:00 h and 14:00 h
Traffic volume	T_VOL	Mean annual average daily traffic volume

*Removed from multivariate analysis due to multicollinearity.
†Reed & Ward (1985).
‡Transect 1 on the culvert axis extended 100-m from the opening. Transect 2 in front of the opening and 50-m out on both sides.

Methods

DRAINAGE CULVERTS

We quantified small- and medium-sized mammal use of 36 drainage culverts along the TCH (distance = 55 km) and highway 1A (distance = 24 km). Drainage culvert selection was stratified by habitat type and culvert size. Only full-length culverts were sampled, i.e. those fully spanning the road width without openings in the central reservation. We characterized each culvert with continuous ($n = 17$) and categorical ($n = 2$) variables encompassing structural, landscape and road-related attributes (Table 1).

OBSERVED PASSAGE FREQUENCIES

We monitored the passage of animals at each culvert using sooted track-plates (75 × 30 cm; Zielinski & Kucera 1995). Multiple plates were used to cover the bottom of the culvert. No baits were used. We checked track-plates weekly and recorded each species' presence, estimated the number of species crossings and the direction of travel. We noted the presence of species' tracks in the snow within a 20-m radius of culvert openings. If tracks indicated the culvert was used but there was no recording on the track-plate(s) we counted this as passage. Mammal species for which tracks were recorded in this study included coyote *Canis latrans* Say, American marten *Martes americana* Turton, weasels *Mustela erminea* L. and *M. frenata* Lichtenstein, snowshoe hare *Lepus americanus* Erxleben, red squirrel *Tamiasciurus hudsonicus* Erxleben, bushy-tailed wood rat *Neotoma cinerea* Ord, deer mice *Peromyscus maniculatus* Wagner, voles (Arvicolinae) and shrews *Sorex* sp.

ANALYSES

If the 36 drainage culverts occurred in a homogeneous habitat landscape that included random distribution of species, then the following assumptions may apply: (i) the 36 drainage culverts served the same population of individuals and (ii) each individual was aware of all 36 culverts and could choose between culverts based on culvert attributes alone. These assumptions, however, were unrealistic as individual ranges within species such as red squirrel and deer mice were at least an order or two of magnitude less than the spatial scale of the 36 culverts. It was most likely that drainage culverts instead served their own unique subpopulations. It was therefore necessary to examine observed crossing frequencies for each drainage culvert in the context of local culvert-specific expected crossing frequencies (i.e. performance indices).

Expected passage frequencies were obtained from measures of relative abundance of each species in the vicinity of each culvert. At the ends of each culvert a 500-m transect perpendicular to the road was established. Each transect was divided into 10 50-m segments. Transects were surveyed for tracks of small- and medium-sized mammals between 24 and 48 h after snowfall. On each segment we tallied the number of animal tracks crossing it. To reduce any potential biases incurred from non-randomly distributed tracks, we registered only the presence (> 1 track) or absence of tracks in each 50-m segment of any given transect. Relative abundance for each species was quantified on the number of transect segments that were consistent with the range of their movements near the culverts. For small mammals (shrews, voles and deer mice) we counted detections on the first three segments (1–3) closest to the culverts, for medium-size mammals (snowshoe hares, red squirrels and wood rats) on segments 1–6, and for larger mammals (weasels, martens and coyotes) on segments 1–10. We then derived species' performance indices using the following formula:

$$PR_i = Log\left(\left(\left(\left(\frac{Obs_i + 0{\cdot}5}{Exp_i + 0{\cdot}5}\right)^2 + \left(\frac{Obs_i - 0{\cdot}5}{Exp_i - 0{\cdot}5}\right)^2 \times \left(\left|\frac{Exp_i + 0{\cdot}5}{Obs_i - 0{\cdot}5}\right|\right) \times 10^{(Obs_i - Exp_i)}\right)\right)^{0{\cdot}5}\right)$$

where Pr_i is the species' performance index for species i, Obs_i is the observed crossing frequencies for species i, and Exp_i is the expected crossing frequencies for species i. Performance indices were designed such that the higher the performance index the more effectively the culvert appeared to facilitate species' crossings. Specifically, the performance index gave a higher value to species' crossings where (i) the absolute difference between observed and expected crossing frequencies was greater but their relative difference was the same, and (ii) the absolute difference between observed and expected crossing frequencies was the same but the total number of observed crossings was greater.

We examined the premise that drainage culverts served species equally by testing the null hypothesis that performance indices did not differ between species. In the event that we rejected the null hypotheses, we proceeded with two steps to determine which of the culvert attributes were most closely associated with species' performance indices.

Prior to carrying out a multivariate analysis, we screened variable data for normality, linearity, multicollinearity and outliers using bivariate scatterplots, correlation matrices and residual analysis plots (Neter, Wasserman & Kutner 1985; Tabachnick & Fidell 1996). To reduce the effects of multicollinearity we selectively removed one independent variable from any pair of independent variables having a correlation coefficient higher than 0·75 (Morrison, Marcot & Mannan 1992). Outliers were removed from an analysis if standard residuals fell outside two standard deviations from the mean.

We performed forward stepwise multiple regressions on the performance indices of the culverts for small- and medium-sized mammals (Tabachnick & Fidell 1996). For each species we ranked the regression models thus obtained according to the absolute value of each model's coefficient of determination. This process allowed for the identification and ordering of culvert attributes (in order of importance) associated with each species' performance index; however, it failed to separate ecologically significant attributes from those that appeared significant but were statistical artefacts of the culvert themselves. Principal components analysis (PCA) was used to examine which sets of species formed coherent subsets that were relatively independent of one another (Ramsey & Schafer 1997). We then used principal components regression to evaluate the importance of the independent variables in facilitating passage by each species group at the culverts. For the two categorical variables (7, 14), performance indices were compared using the Mann–Whitney *U*-test (Zar 1999). We used the Statisica kernel release 5·5 statistical package for all analyses (StatSoft 2000).

Results

Data on small- and medium-sized mammal movement at 36 culverts were collected during winter (January–April) 1999 and 2000. During this period we checked each culvert at least 12 times. A total of 618 crossings by a minimum of nine species was recorded. Weasels and deer mice used the culverts most (28% and 29% of all detections, respectively), followed by bushy-tailed wood rats and American martens (Fig. 1). Shrews were detected at 22 of the culverts (61%), weasels at 21 culverts (58%), and martens and deer mice at 18 (50%). Coyotes, bushy-tailed wood rats and voles used the fewest number of culverts ($n = 2$ culverts). Species' use of individual culverts ranged from 0 to 6. The average number of species detected at the culverts was 2·8 (SD = 1·6).

Relative abundance transects were sampled six times. Tracks of eight of the nine species were recorded a total of 6990 times along 228 km of permanent transects. This included tracks for all species crossing transects including more than one track per segment. For calculating relative abundance we noted species presence (> 1 track) in the 50-m segments a total of 3155 times. Red squirrels and snowshoe hares together accounted for more than 50% of all species detections, whereas martens and weasels combined made up 39% (Fig. 1). The small mammal community (wood rats, deer mice, voles and shrews) accounted for only 1·6% of

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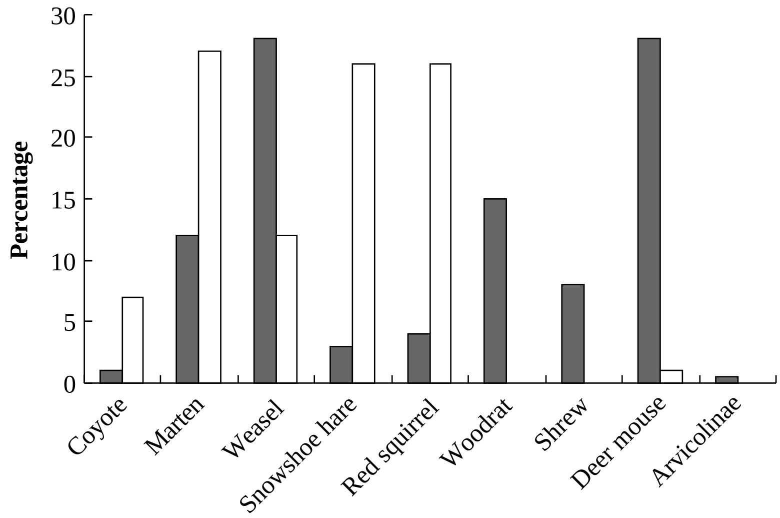

Fig. 1. Percentage occurrence of nine mammal species using drainage culverts (solid bars; $n = 618$ crossings) and found on adjacent snow transects (white bars; $n = 3155$ detections) in Banff National Park, Alberta, Canada (1999–2000). Expected detections were based on snow transect sampling (see the Methods).

crossings on transects. Because of the inability to detect small mammals on transects, we excluded these four species from the subsequent multivariate analysis. The following analyses focused on five medium-sized mammal species (coyote, marten, weasel, snowshoe hare and red squirrel).

The results showed that culvert performance indices were significantly different between the five species [Kruskal–Wallis ANOVA, H(4, 140) = 60·4, $P < 0{\cdot}001$]. Therefore, we rejected the null hypothesis that species' use of culverts was uniform and focused on determining which attribute of culverts was most likely to influence use by individual species, species groups and the mammal community.

Of the 17 continuous variables, five were excluded from the multiple regression analysis due to multicollinearity: road clearance, verge width, culvert length, amount of open habitat and culvert width (Table 1). In the stepwise regression analysis five models were developed for species' responses to the culvert attributes. For all five species the multiple regression models described a significant proportion of the variation in performance ratios ($P < 0{\cdot}003$). Coefficients of determination (R^2) for the models ranged from 0·47 in red squirrels to 0·81 in snowshoe hares. Of the five models, 25 of 95 (= 5 × 19 variables) variables were statistically significant. Ten (40%) of the 25 variables pertained to road-related features, nine (36%) landscape features and six (24%) structural attributes (Table 2). However, significant culvert attributes and their rank order in the models differed between species. For example, noise level (negative correlation) was the most significant culvert attribute for snowshoe hares, whereas traffic volume (negative correlation) was the most important attribute affecting coyote performance indices. Similarly, culvert height was the most significant attribute for weasels, but was of little importance for the other species except martens.

Traffic volume was a significant predictor of performance index for four of the five species and ranked as the most important of all attributes in determining passage for three of the taxa (Table 2). It was the most important attribute for coyotes, martens and red squirrels, and ranked fourth for snowshoe hares. For all species except coyotes, the relationship was positive: the higher the traffic volume, the greater the use of culverts by martens, snowshoe hares and red squirrels. Noise was a significant factor explaining culvert use by four of five taxa. It had high explanatory power for snowshoe hare and red squirrel passage at culverts; however, it ranked low for carnivores (weasels 6, martens 5). The relationship between noise levels and passage in all models was negative. For two taxa, road width was found to be a significant factor (coyotes 2, red squirrels 4) influencing culvert use. The correlation between culvert use and road width was negative for both species. Coyotes and red squirrels had a tendency not to use culverts on wide roads.

Structural attributes such as culvert height and openness were significant attributes influencing performance indices for two of five taxa. Weasel passage was positively correlated with culvert height but negatively correlated with culvert openness. Conversely, martens preferred culverts with low clearance and high openness ratios. The amount of culvert aperture significantly influenced passage for the two species. Weasels had a tendency to use culverts with low aperture, whereas high through-culvert visibility was important for snowshoe hares. Landscape attributes had low explanatory value in determining the effectiveness of culverts. However, the distance to the nearest passage structure was an important variable for martens. The greater the distance between passages the higher the likelihood of martens using a culvert for cross-highway travel.

Habitat type did not influence passage for any of the five species except coyotes ($U = 404{\cdot}5$, d.f. = 1, $P = 0{\cdot}003$), which had a tendency to use culverts located in

Table 2. Results of multivariate linear regressions on the performance indices of 36 drainage culverts for five mammal species in Banff National Park, Alberta, Canada. Significant coefficient of determinations and their slope are rank-ordered to show their relative importance in explaining factors facilitating passage. For attribute definitions see Table 1

Attribute	Beta	SE	*P*-value	Rank
Coyote				
T_VOL	−0·53	0·15	0·001	1
RD_W	−0·43	0·13	0·004	2
SHRUB	−0·22	0·1	0·038	3
Marten				
T_VOL	0·78	0·18	0·001	1
OP	0·58	0·21	0·01	2
HT	−0·51	0·23	0·038	3
NOISE	−0·50	0·15	0·003	4
D_STR	0·42	0·11	0·001	5
Weasel				
HT	0·88	0·30	0·007	1
AP	−0·64	0·24	0·015	2
OP	−0·61	0·28	0·037	3
D_COV	−0·57	0·19	0·006	4
FOR	−0·36	0·15	0·022	5
NOISE	−0·34	0·15	0·035	6
Snowshoe hare				
NOISE	−0·69	0·12	0·001	1
ELEV	−0·43	0·1	0·001	2
FOR	−0·41	0·12	0·002	3
T_VOL	0·36	0·16	0·037	4
AP	0·31	0·11	0·011	5
SHRUB	0·21	0·1	0·049	6
Red squirrel				
T_VOL	0·67	0·24	0·011	1
NOISE	−0·62	0·19	0·002	2
RD_W	−0·61	0·18	0·002	3

areas of closed forest. Similarly, topography only affected snowshoe hare passage; culverts in uneven terrain were used more than culverts located in level terrain (U = 422, d.f. = 1, P = 0·001).

We identified two distinct groups of species based on performance indices using PCA (Fig. 2). Two factors were extracted: factor 1 had high loadings (> 0·70) for martens, snowshoe hares and red squirrels; factor 2 had high loadings (> 0·70) for coyotes and weasels. We performed multiple regression analysis on the two species groups using two methods. First, we ran the multiple regression analysis using factor scores from the PCA (Table 3). The analysis produced a significant model for both species groups (P < 0·002). Coefficients of determination (R^2) were 0·56 for factor 1 and 0·55 for factor 2. Road width had the highest explanatory power (negatively correlated) for species grouped in factor 1, followed by noise levels (negatively correlated) and culvert distance to cover (positively correlated). For species grouped in factor 2, we found road width (negatively correlated) was the only factor that influenced species' passage at the culverts.

Secondly, we ran the multiple regression analysis using combined performance indices calculated for the species in each group (Table 3). The analysis produced a significant model for both species groups (P < 0·001). Coefficients of determination (R^2) were 0·56 for species group 1 (martens, snowshoe hares and red squirrels) and 0·58 for species group 2 (coyotes and weasels). Species group 1 responded to four culvert attributes. Traffic volume was the most important variable (positively correlated), followed by road width, noise levels and elevation (all negatively correlated). Five variables affected passage of species from group 2. Distance to cover, traffic volume and the amount of forest cover were negatively correlated with passage, whereas road-culvert angle was positively correlated. The amount of shrub cover (negatively correlated) partially explained passage of species.

Finally, we performed multiple regression analysis on performance indices for all five species together (Table 4). The analysis produced a significant model

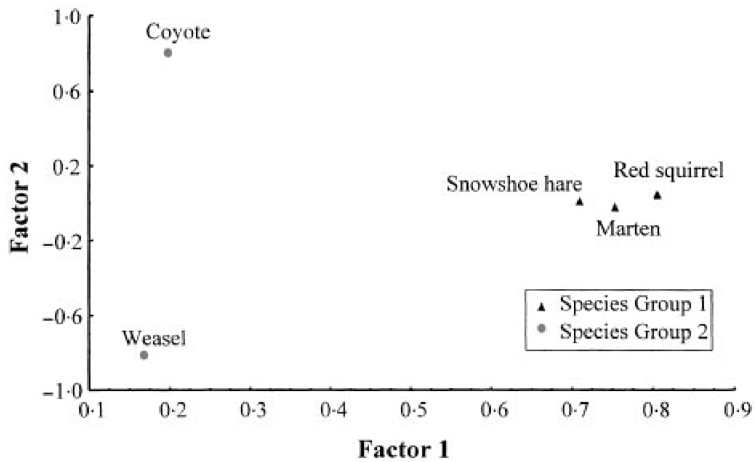

Fig. 2. Factor loadings for five mammal species from principal components analysis (Varimax normalized rotation of axes) of performance indices of 36 drainage culverts in Banff National Park, Alberta, Canada. Two distinct groups were identified for use in multiple linear regression: group 1, marten, red squirrel and snowshoe hare (black triangles); group 2, coyote and weasel (black dots). Road width, noise levels and distance to cover were significant correlates associated with factor 1. Road width was the only significant correlate for factor 2.

Table 3. Results from principal components analysis (PCA) to identify species groups based on their interactions with 36 culverts in Banff National Park, Alberta, Canada. Both species groups had significant regression models that explained culvert use ($P < 0{\cdot}002$). Coefficients of determination (R^2) were 0·56 for factor 1 and 0·55 for factor 2. Significant coefficient of determinations are rank-ordered from principal components regression using factor scores from PCA and regression analysis performed on combined performance index data for the species in each of the two groups

Attribute	Beta	SE	*P*-value	Rank
Factor 1* (marten, snowshoe hare, red squirrel)				
RD_W	–0·72	0·24	0·007	1
NOISE	–0·68	0·19	0·002	2
D_COV	0·37	0·17	0·039	3
Factor 2* (coyote, weasel)				
RD_W	–0·83	0·14	0·001	1
Group 1† (marten, snowshoe hare, red squirrel)				
T_VOL	0·75	0·21	0·001	1
RD_W	–0·66	0·17	0·001	2
NOISE	–0·66	0·16	0·001	3
ELEV	–0·37	0·16	0·025	4
Group 2† (coyote, weasel)				
D_COV	–0·79	0·14	0·001	1
T_VOL	–0·62	0·15	0·001	2
FOR	–0·54	0·15	0·002	3
R_ANG	0·48	0·15	0·004	4
SHRUB	–0·37	0·13	0·01	5

*Multiple regression analysis using factor scores from PCA.
†Multiple regression analysis performed on combined performance index data for the species in each of the two groups.

Table 4. Results of multivariate linear regressions on the combined performance indices of 36 drainage culverts for five mammal species as a group in Banff National Park, Alberta, Canada. Significant coefficient of determinations and their slope are rank-ordered to show their relative importance in explaining factors facilitating passage at the community level. For attribute definitions see Table 1

Attribute	Beta	SE	*P*-value	Rank
T_VOL	0·72	0·2	0·001	1
NOISE	–0·71	0·16	0·001	2
RD_W	–0·61	0·17	0·001	3
ELEV	–0·36	0·15	0·026	4

($P < 0{\cdot}001$). The coefficient of determination (R^2) was 0·58. We found the most significant culvert attribute influencing the mammal community's performance index was traffic volume (positive correlation). Noise levels, road width and elevation were all negatively correlated.

Discussion

Our results suggested that culvert attributes influence species' use but different attributes appeared to affect use by different species. One common theme at all scales of resolution – individual species, species group and community level – was that traffic volume, and to a lesser degree noise levels and road width, ranked high as a significant factor affecting species' use of the culverts.

One would expect that as road width increased medium-sized forest mammals would be increasingly vulnerable. The risk of predation while attempting to cross exposed road corridors may be greater as well (Korpimaki & Norrdahl 1989; Rodríguez, Crema & Delibes 1996). Coyotes, being the largest of the mammal species studied, tended to use culverts less in high traffic density situations, whereas three of the four smaller mammals (martens, snowshoe hares and red squirrels), and not surprisingly the three-species group, showed greater use of the passages. Forest-associated mammal species generally avoid open areas without overstorey or shrub cover (Buskirk & Powell 1994; Ruggiero *et al.* 1994) and we would expect the same response to an open road corridor (Oxley, Fenton & Carmody 1974; Mader 1984; Swihart & Slade 1984). Culvert use by these species might be a response to this fragmented and unsafe habitat and a result of learned behaviour passed on by surviving individuals selecting culverts for cross-highway travel.

Noise consistently ranked highly as a negative factor influencing culvert passage at all resolutions, ranking second most important at the community level. Marten, weasel, snowshoe hare and red squirrel passage at the culverts was negatively correlated with noise levels, suggesting that traffic-related disturbances may cause some species to reduce their activity near the highway, or avoid the area altogether. Research near busy highways in Massachusetts, USA, and the Netherlands has focused on areas of reduced bird abundance, which were believed to be a consequence of traffic noise (Reijnen *et al.* 1995; Reijnen, Foppen & Meeuwsen 1996; Forman & Deblinger 2000). Studies of terrestrial wildlife also concur that buffer areas around roads are generally avoided, the size of the buffer depending on traffic volume (McLellan & Shackleton 1988; Thurber *et al.* 1994; Mace *et al.* 1996; Gibeau 2000).

The dimension of the tunnels is considered to be one of the most important variables in the design of passageways for vertebrates (Reed, Woodward & Pojar 1975; Ballon 1985; Hunt, Dickens & Whelan 1987). Martens, weasels and, to a lesser extent, snowshoe hares responded most to the structural attributes of culverts. Martens had a tendency to use culverts with low clearance and high openness ratios, whereas weasels used culverts with high clearance, low openness ratios and low through-culvert visibility. These results may largely be explained by habitat preferences of the two mustelids. Martens prefer areas with dense canopy cover and complex understoreys (Buskirk & Powell 1994; Ruggiero *et al.* 1994), whereas weasels rely entirely on a hunting strategy that requires travelling through burrows and runway systems of rodents and through all kinds of cover into which these prey could escape (King 1989). High through-culvert visibility would be of little importance for weasels because a large part of the time they hunt underground. Conversely, low through-culvert visibility is believed to inhibit passage use by lagomorphs and carnivores (Beier & Loe 1992; Rodríguez, Crema & Delibes 1996; Rosell *et al.* 1997). In our study culvert passage by snowshoe hares was partially explained by aperture and those with high through-culvert visibility.

Landscape variables may also be important attributes influencing the use of culverts. The presence or amount of vegetative cover at passage entrances has been considered an essential component for designing effective tunnels (Hunt, Dickens & Whelan 1987; Rodríguez, Crema & Delibes 1996). It is believed that increased cover provides greater protection and security for animals approaching the passages. Our results indicated that distance to cover and the amount of it within the vicinity of culverts was a significant factor determining passage for weasels and snowshoe hares, and to a lesser extent coyotes. Elevation and topography adjacent to the culvert were significant attributes influencing the performance index of snowshoe hares. The importance of these attributes may be more an artefact of local habitat conditions than of direct significance on species' passage.

The predominance of weasels and martens at the culverts contrasted sharply with the scarcity of hare and red squirrels, despite the latter being some of the most prevalent species detected on the transects (Fig. 1). The inverse relationship between predator and prey species with respect to culvert use is noteworthy. There is some evidence from England that the presence of badgers *Meles meles* L. can disrupt the use of tunnels under roads by hedgehogs *Erinaceus europaeus* L. (Doncaster 1999). Whether this may be occurring in our study area remains to be investigated. Scent-marking (faeces) by martens and weasels was commonly observed at culvert entrances throughout the sampling period and may be the behavioural mechanism whereby prey species could detect and avoid the predator (Gorman 1984; Curio 1993; Jedrzejewski, Rychlik & Jedrzejewska 1993; Kats & Dill 1998).

From this study we found that road-related factors had the greatest influence on mammal passage at culverts. Structural and landscape attributes of culverts were lesser predictors of culvert use. These results concur with those of Yanes, Velasco & Suárez (1995) and Rodríguez, Crema & Delibes (1996), who found that factors related to the road and the landscape best explained animal use, whereas culvert design and dimensions had little effect. Of the five species only weasels appeared to be unaffected by road-related attributes of culverts. Weasels, and to a lesser extent martens, appeared to be affected by the structural attributes of culverts. When considering the relative density of species in our study area, mammalian carnivores accounted for the greatest amount of passage use. Others have found, to the contrary, that small mammals constituted the majority of crossings (Yanes, Velasco & Suárez 1995; Rodríguez, Crema & Delibes 1996).

Our results suggest that for many small- and medium-sized mammals drainage culverts can mitigate the potentially harmful effects of busy transportation corridors. For forest-associated wildlife, like most of the species we studied, culverts appear to provide a means of crossing open habitat created by road corridors (in some places up to 100 m wide), providing a vital habitat linkage. Open roadside habitat has been shown to be important for the movement and dispersal of small mammals (Huey 1941; Getz, Cole & Gates 1978; Underhill & Angold 2000). For weasels and their prey the open roadside verges, which cut up and fragment the heavily forested Bow Valley, may also be important habitat. Our findings suggest that, for mammalian carnivores, the culverts appear to be critical in linking habitats and maintaining habitat connectivity. During this work we were unable to determine whether the low use of culverts by prey species was because crossings were not attempted or because they preferred crossing above the road. Further work is required to assess the effects of culverts on population demography and gene flow adjacent to roads with high traffic volumes.

In our study area the mean distance between all mitigation passages (large wildlife crossing structure or full-length culvert) in the two road corridors we sampled was 465 m (SD = 411 m, range = 1·2 – 2658 m, $n = 275$). To ensure cross-highway connectivity and gene flow it will be important to have at least one culvert or passage within an individual's home range (Gerlach & Musolf 2000). Given the average home range size of the species in our study (Chapman & Feldhamer 1982) and the existing distribution of culverts along roads, this condition can be met for only the two largest mammal species (coyote and marten). Drainage culvert costs to highway infrastructure projects are trivial. To improve the permeability of roads for small- and medium-sized mammals we recommend that, first, culverts be placed at more frequent intervals (150–300 m) to provide sufficient opportunities for animals of all body sizes to avoid crossing busy roads. Secondly, if a road does not have large wildlife crossing structures in place, we recommend a mixed size class of culverts to accommodate the greatest variety of species possible. The size of the culverts will depend on the size of the fauna most likely to be interacting with the road. Large culverts (1·0–1·5 m diameter) will facilitate passage for medium-sized mammals (e.g. coyote), while small culverts (0·5–1·0 m diameter) will best serve small mammals (marten and smaller). Lastly, we advise that vegetative cover be present near culvert entrances to enhance passage by carnivores and small mammals.

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