DRY DRAINAGE CULVERT USE AND DESIGN CONSIDERATIONS FOR SMALL- AND MEDIUM-SIZED MAMMAL MOVEMENT ACROSS A MAJOR TRANSPORTATION CORRIDOR

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Abstract

Drainage culverts are ubiquitous features in road and rail corridors. Yet practically nothing is known about the effectiveness of culverts for increasing road permeability and habitat connectivity for small- and medium-sized mammals. We quantified mammal use of dry drainage culverts to cross a major transportation corridor. We used a null model to evaluate whether culverts serve all species equally or whether some culverts limit habitat connectivity across roads in species-specific ways. We also modeled species response to structural, landscape, and road-related attributes and identified which are most important in explaining animal passage rates and culvert effectiveness. Species performance ratios (i.e., observed passage frequency / expected passage frequency) were evaluated for eight small- and medium-sized mammal taxa to 24 culverts along the Trans-Canada highway in Banff National Park, Alberta. Observed passage frequencies were collected from three winter months of culvert monitoring. Carnivores (weasels Mustela sp., martens Martes americana) used more culverts and used them more frequently than small mammals (hares Lepus americanus, red squirrels Tamiasciurus hudsonicus, mice, shrews Sorex sp.). Small mammals were most prevalent on transects outside the culverts. The null model showed that species responded to culverts differently. We found that passage use was positively correlated with traffic density, road width, road clearance and culvert length. All species except coyotes (Canis latrans) and shrews preferred small culverts with low openness ratios. Weasels and shrews preferred culverts with cover nearby. Our results indicate that drainage culverts can mitigate harmful effects of a high-speed motorway. To maximize road permeability for small fauna, we recommend frequently spaced culverts (150-300 m) of varying sizes situated in close proximity to shrub or tree cover.

Introduction

Despite heightened recognition of the harmful effects of roads, road density continues to increase in North America and Europe as does motor vehicle travel. Currently there are more than 6.2 million kilometers of public roads in the United States traversed by 200 million vehicles (National Research Council 1997). By 2002, Europe intends to have 54,000 kilometers of roads designated as Atrans-European networks@ (TENs) and of these 13,000 kilometers will have been built since 1993 (Button et al. 1998). In the coming millennium great challenges lie ahead in the field of road ecology as the integration of transportation planning and environmental management begins to evolve.

The detrimental effects of such a road-construed landscape on wildlife ecology is only now being addressed (Saunders and Hobbs 1991, Canters 1997, Evink et al. 1996, 1998; Forman and Alexander 1998). These studies show, at least in part, that avoidance of otherwise suitable habitat occurs near roads for elk *Cervus elaphus* (Witmer and deCalesta 1985, Edge et al. 1987), bobcats *Felis rufus* (Lovallo and Anderson 1996) and bears *Ursus* sp. (Brody and Pelton 1989, Mace et al. 1996). Second, road effects restrict population movements thus fragment and potentially isolate otherwise continuous populations distributions. Furthermore, as roads are upgraded to accommodate greater traffic volume the rate of successful wildlife crossings decreases significantly (Barnett et al. 1978, Swihart and Slade 1984, Brandenburg 1995, Ruediger 1997) becoming in some cases the leading cause of wildlife mortality (Calvo and Silvy 1997, Gibeau and Heuer 1997, Clarke et al. 1998).

Attempts to increase habitat connectivity and barrier permeability across roads can be found in some road construction and upgrade projects (Foster and Humphrey 1995, Rosell et al. 1997, Clevenger and Waltho 2000). Mitigation passages or crossing structures have been designed to perforate road barriers and maintain horizontal natural processes across the land (Forman 1995). Surprisingly, the efficacy of such mitigation has received little attention, and the few studies carried out are limited to single species and do not contemplate multiple species responses. Although not designed for animal passage, drainage culverts are ubiquitous features in road and rail corridors. However, practically nothing is known about the effectiveness of culverts for increasing road permeability and habitat connectivity for smaller mammals. Proximity to cover and culvert dimensions was reported to be important factors contributing to passage of small- and medium-sized mammals (Hunt et al. 1987, Yanes et al. 1995, Rodriguez et al. 1996).

The Trans-Canada highway (TCh) is a major transportation corridor through Banff National Park (BNP). The highway bisects critical montane and subalpine habitats in the Bow River Valley of which many forest-associated mammals depend. Over 70% of montane habitat in BNP is found in the corridor. Presently the TCh consists of 47 kilometers of 4-lane highway; however, plans are to upgrade to four lanes the remaining 30 kilometers within the next 5-10 years. Doubling the highway width and associated increases in traffic volumes will result in greater difficulties for animal crossings. TCh culverts may function as conduits for efficient and safe travel and increase permeability of this busy road corridor.

In this paper we investigated small- and medium-sized mammal use of drainage culverts along the Trans-Canada corridor in Banff National Park, Alberta. Areas selected for sampling varied in road width, traffic volume, and landscape. Our specific objectives have been to: 1) determine what species use drainage culverts to cross the TCh; 2) evaluate whether culverts serve all species equally or whether some culverts limit habitat connectivity across roads in species-specific ways; 3) model species response to structural, landscape, and road-related attributes and identify which are most important in explaining animal passage rates and culvert effectiveness; and 4) provide recommendations for incorporating micro- and mesofauna requirements into drainage culvert design and transportation corridor planning.

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 5 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 14,600 vehicles/day in 1998 and increasing at a rate of 3% per year (Parks Canada, unpubl. data).

The transportation corridor also contains the Canadian Pacific Railway (CPR) mainline, access roads to Banff townsite and several important two-lane highways (highways 93 and 40) and secondary roads (highway 1A). The study was carried out along a 55 km section of the TCh. The first 45 km of the TCh from the eastern park boundary (phase 1 & 2, and phase 3A) is four lanes and bordered on both sides by a 2.4 m high wildlife fence. Phase 1 was completed in 1986, phase 2 in 1988, and phase 3A late 1997.

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 forests dominated by Douglas fir (Pseudotsuga menziesii), white spruce (Picea glauca), lodgepole pine (Pinus contorta), aspen (Populus tremuloides) and natural grasslands.

Methods

Drainage culverts

We quantified small- and medium-sized mammal use of 24 drainage culverts along a 55 km section of the TCh between 14 January and 29 March 1999. Drainage culvert selection was stratified by operational duration, habitat type, and culvert size. Only full-length culverts were sampled, i.e., fully spanning the road width without openings in the median.

We characterized each culvert with 18 variables encompassing structural, landscape and road attributes (Table 1 and 2). Structural variables included culvert (1) width, (2) height, (3) length, (4) openness (width x height/length ; Reed and Ward 1985), (5) age, and (6) aperture.

Landscape variables included (7) percent forest cover, (8) percent shrub cover, (9) percent open, (10) distance to cover, (11) distance to nearest mitigation passage, (12) snow depth, and (13) elevation. Road-related variables included (14) road width, (15) verge width, (16) road clearance, (17) noise level, and (18) traffic volume.

Observed passage frequencies

We monitored passage of animals at each culvert using sooted track-plates (75 cm x 30 cm; Zielinski and Kucera 1995). Multiple plates were used to cover the bottom of the culvert. No baits were used. We checked track-plates weekly and species= presence, estimated number of individuals and direction of travel were recorded. We noted the presence of species tracks in 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 in this study were coyote (Canis latrans), American marten (Martes americana), weasel (Mustela sp.), snowshoe hare (Lepus americanus), red squirrel (Tamiasciurus hudsonicus), deer mice (Peromyscus maniculatus), voles (Arvicolinae), and shrews (Sorex sp.).

Analyses

If the 24 drainage culverts occur in a homogeneous habitat-landscape that include random distribution of species abundances, then the following assumptions may apply: (1) the 24 drainage culverts serve the same population of individuals and (2) each individual is aware of all 24 culverts and can choose between culverts based on culvert attributes alone. These assumptions, however, are unrealistic as individual ranges within species such as red squirrel or deer mice are at least an order or two magnitude less than the spatial scale of the 24 culverts (range = 55 km). It is most likely that drainage culverts instead serve their own unique subpopulations. It is therefore necessary to examine observed crossing frequencies for each drainage culvert in the context of local culvert-specific expected crossing frequencies (i.e., performance ratios).

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 24-48 hours after snowfall. On each segment we tallied the number of animal tracks detected crossing the transect. To reduce any potential biases incurred from non-randomly distributed tracks, relative abundance indices were determined by registering the presence (>1 track) or absence of tracks in each 50 m segment. Relative abundance was quantified on the first three segments (1-3) for small mammals (shrews, voles, deer mice), segments 1-6 for hares, red squirrels, and woodrats, and segments 1-10 for the remaining mammals (weasels, martens, coyotes).

We then derived species performance ratios using the following formula:

where Pr_i is the species performance ratio 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 ratios were designed such that the higher the performance ratio the more effective the underpass appears to facilitate species crossings. Specifically, the performance ratio gives higher value to species crossings where (a) the absolute difference between observed and expected crossing frequencies is greater but their relative difference is the same, and (b) the absolute difference between observed and expected crossing frequencies is the same but the total number of observed crossings is greater (Table 3).

We examined the premise that drainage culverts 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). In the event that we rejected the null hypotheses, we proceeded with two steps to determine which of 18 culvert attributes species performance ratios were most closely associated with. First, we used a family of simple curvilinear and polynomial regression curves to optimize the fit between species performance ratios and each culvert attribute (Tablecurve 2D; Jandel 1994). We used the following criteria to choose the most optimal equation for each regression analysis: (1) the regression model must be statistically significant (at $p < 0.05$); (2) the beta coefficient for the highest ordered term must be statistically significant; (3) once an equation meets the above criteria we compared its F statistic with the F statistic for the next equation that also meets these criteria but has one less ordered term. We chose the model with the higher F statistic; (4) iterate 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 ($y = a + bx$) to describe the relationship, assuming it has not already been chosen through the iterative process; and (6) if these criteria failed to produce a significant regression model for per se species and per se culvert attribute, we deleted the culvert attribute as being a significant factor influencing the species performance ratio (Clevenger and Waltho 2000).

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

Results

Data on mammal movement at 24 culverts was collected between 14 January and 29 March 1999. During this period we checked each culvert 11 times. A total of 546 crossings by a minimum of nine species were recorded (Table 4). Weasels used the culverts most (31% of all detections) followed by deer mice and American martens. Weasels were detected at 19 of the culverts (79%), shrews at 16 (67%), deer mice at 14 (58%), and martens at 13 (54%). Voles used the fewest number of culverts ($n = 3$), then red squirrels ($n = 4$) and coyotes ($n = 4$). Species use of individual culverts ranged from 0 to 7. Average number of species detected at the culverts was 3.5 (SD = 1.7).

Relative abundance transects were sampled six times between 9 February and 6 April 1999. Seven of the nine species were detected 4,483 times along 156 km of permanent transects. We noted species presence (≥ 1 track) in the 50 m segments a total of 1,946 times (Table 5). Red squirrels and hares accounted for more than 50% of all species= detections, whereas martens and weasels combined made up 38%.

Test of null hypothesis

The results showed that culvert performance ratios were significantly different between species (paired t test with Bonferroni adjusted probability; $P<0.001$). We therefore rejected the null hypothesis and identified the culvert attributes that explained culvert use by the species and taxa in this study.

Attributes influencing culvert use

The importance of the culvert attributes differed between species. As an example, we found that the amount of forest cover adjacent to the culvert (negative correlation) was the most significant culvert attribute for weasels, whereas traffic volume (positive correlation) was the most important attribute affecting red squirrel performance ratios (Table 6). Similarly, distance to cover was the most significant attribute for voles, but was of little importance for all other species except weasels.

Traffic volume was the most important of all attributes in determining passage for six of the eight taxa. It was the most important attribute for martens and red squirrels, and ranked second and third for hares and voles, respectively. For all species except coyotes, the relationship was positive. The higher the traffic volume, the greater the use of culverts by martens, weasels, hares, red squirrels, and voles.

For five taxa road width was found to be a significant factor (first for coyotes, fifth for weasels and red squirrels) influencing culvert use. The correlation between culvert use and road width was positive for all species except coyotes. The wider the road the more a culvert was used by weasels, hares, red squirrels, and voles.

Structural attributes such as age of culvert and openness were significant attributes influencing performance ratios for four of the eight taxa. Coyotes and martens had a tendency to use older culverts as opposed to weasels, hares, and red squirrels that used newer culverts. Passage by red squirrels and voles were negatively correlated with culvert openness, whereas it was positively correlated for coyotes. Landscape attributes had low explanatory value in determining the effectiveness of culverts. However, the amount of forest cover, mean snow depth, and distance to cover were important variables for some species.

Discussion

Our results suggest that culvert attributes influence species use in different ways. Depending on the species different attributes weigh more heavily than others in ultimately determining the effectiveness of a culvert for safe cross-highway travel. One common theme between all species was that traffic volume, and to a lesser degree road width, ranked high as a significant factor affecting species use of the culverts. Road width, road clearance, culvert length, and traffic volume were all strongly correlated (Figure 2) suggesting that higher traffic densities translate to wider roadways, longer culverts, and greater road clearance.

One would expect that as a road widens small- and medium-sized forest mammals would be increasingly more vulnerable to becoming road-kills. The risk of predation while attempting to cross exposed road corridors also may be greater as well (Korpimaki and Norrdahl 1989, Rodriguez et a. 1996). Coyotes being the largest of the mammal species studied tended to use culverts less in high traffic density situations, whereas five of the seven smaller mammals (martens, weasels, hares, red squirrels, voles) showed greater use of the passages. Forest-associated mammal species generally avoid open areas where no overstory or shrub cover exists (see Buskirk and Powell 1994) and we would expect the same response to an open road corridor (Oxley et al. 1974, Mader 1984, Swihart and Slade 1984). Culvert use by these species might be an adaptation to this fragmented and unsafe habitat and a result of learned behavior passed on by surviving individuals selecting culverts for cross-highway travel.

The dimension of the tunnels is considered as one of the most important variables in the design of passageways for vertebrates (Reed et al. 1975, Ballon 1986, Rosell et al. 1997, Hunt et al. 1987). Contrary to our results, small- and medium-sized mammal use of culverts was negatively correlated with road width and culvert length in Spain (Yanes et al. 1995). We found that small culverts with low openness ratios were preferred by all mammals except coyotes and shrews. Similar results for small mammals were reported by Rodriguez et al. (1996) and support the notion that predation risks may be greater in large tunnels and culverts (Hunt et al. 1987). Furthermore, low visibility (culvert aperture) is believed to inhibit passage use by lagomorphs and carnivores (Beier and Loe 1992, Rodriguez et al. 1996, Rosell et al. 1997). Passage by red squirrels and voles in our study was partially explained by culvert aperture.

The presence or amount of cover (shrubs or trees) at passage entrances has been considered an essential component for designing effective tunnels (Hunt et al. 1987, Rodriguez et al. 1996, 1997; Rosell et al. 1997). It is believed that increased cover provides greater protection and security for animals approaching the passages. Our results indicated that distance to cover was the most important culvert attribute for voles and was a significant factor determining passage for coyotes and weasels (all negative correlations). Snow depth was negatively correlated with culvert use for all species but coyotes and shrews. This attribute ranked either first or second in importance for martens, hares, and red squirrels.

Elevation and age of the culvert were significant attributes influencing performance ratios for five of eight species. Both had high positive loadings (Figure 2) indicating a strong interdependence between the two attributes. The importance of these attributes may be more an artifact 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 squirrel passage despite the latter being most prevalent of all species detected on the transects. The inverse relationship between predator and prey species with respect to culvert use is noteworthy. There is some evidence that the presence of badgers (Meles meles) can disrupt their prey species (hedgehogs [Erincaceus europaeus]) use of tunnels under roads in England (C. Doncaster, unpubl. data). Whether this may be occurring in our study area remains to be investigated. Scent-marking (feces) by martens and weasels was commonly observed at culvert entrances throughout the sampling period and may be the behavioral mechanism whereby prey species could detect and avoid a potential risk of predation (Gorman 1984, Jedrzejewski et al. 1993, Doncaster 1994, Ward et al. 1997)

We found that passage frequencies were highest for carnivore species. This result contrasts with those of Yanes et al. (1995) and Rodriguez et al. (1996), who found that small mammals constituted the majority of crossings. We were unable to identify small mammal tracks to species and therefore quantifying passage at the culverts can be problematic. Nonetheless, meadow voles (Microtus pennsylvanicus) and red-backed voles (Clethrionomys gapperi) are the dominant species in the road corridor and adjacent habitat (A. Clevenger, unpubl. data) and most likely constituted the majority of voles detected. We were unable to determine whether voles actually utilized the full-length of the culverts or Aloitered@ inside. Rodriguez et al. (1996) reported small mammals travelling through culverts up to 64 m in length. The average length of the culverts we sampled was 43 m (SD = 17), which suggests that cross highway movements of small mammals through culverts could have been realized.

Our results suggest that for many small- and medium-sized mammals drainage culverts can mitigate harmful effects of the bustling TCh transportation corridor. For forest-associated species like most of the species we studied culverts appear to provide a safe means of crossing open habitat created by the TCh corridor (some places up to 100 m wide) and a vital habitat linkage. Open roadside habitat has been shown to be important for movement and dispersal of small mammals (Microtus sp., Huey 1941, Getz et al. 1978). For weasels and their prey the open roadsides of the TCh corridor, which bisects the heavily forested Bow Valley, also may be important habitat and the culverts a critical linkage for maintaining connectivity.

To improve the permeability of roads for small- and medium-sized mammals we recommend that: (1) culverts be placed at frequent intervals (150-300 m) to provide sufficient opportunities for animals to avoid having to cross busy roads, (2) if a road does not have mitigation passages for large wildlife in place, a mixed size class of culverts is recommended. Size of the culverts will depend on the size of fauna likely interacting with the road, (3) 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 accommodate small mammals (marten and smaller), and (4) cover near culverts may enhance passage by carnivores and small mammals.

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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 5 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 14,600 vehicles/day in 1998 and increasing at a rate of 3% per year (Parks Canada, unpubl. data).

The transportation corridor also contains the Canadian Pacific Railway (CPR) mainline, access roads to Banff townsite and several important two-lane highways (highways 93 and 40) and secondary roads (highway 1A). The study was carried out along a 55 km section of the TCh. The first 45 km of the TCh from the eastern park boundary (phase 1 & 2, and phase 3A) is four lanes and bordered on both sides by a 2.4 m high wildlife fence. Phase 1 was completed in 1986, phase 2 in 1988, and phase 3A late 1997.

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 forests dominated by Douglas fir (Pseudotsuga menziesii), white spruce (Picea glauca), lodgepole pine (Pinus contorta), aspen (Populus tremuloides) and natural grasslands.

Methods

Drainage culverts

We quantified small- and medium-sized mammal use of 24 drainage culverts along a 55 km section of the TCh between 14 January and 29 March 1999. Drainage culvert selection was stratified by operational duration, habitat type, and culvert size. Only full-length culverts were sampled, i.e., fully spanning the road width without openings in the median.

We characterized each culvert with 18 variables encompassing structural, landscape and road attributes (Table 1 and 2). Structural variables included culvert (1) width, (2) height, (3) length, (4) openness (width x height/length; Reed and Ward 1985), (5) age, and (6) aperture.

Landscape variables included (7) percent forest cover, (8) percent shrub cover, (9) percent open, (10) distance to cover, (11) distance to nearest mitigation passage, (12) snow depth, and (13) elevation. Road-related variables included (14) road width, (15) verge width, (16) road clearance, (17) noise level, and (18) traffic volume.

Observed passage frequencies

We monitored passage of animals at each culvert using sooted track-plates (75 cm x 30 cm; Zielinski and Kucera 1995). Multiple plates were used to cover the bottom of the culvert. No baits were used. We checked track-plates weekly and species' presence, estimated number of individuals and direction of travel were recorded. We noted the presence of species tracks in 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 in this study were coyote (Canis latrans), American marten (Martes americana), weasel (Mustela sp.), snowshoe hare (Lepus americanus), red squirrel (Tamiasciurus hudsonicus), deer mice (Peromyscus maniculatus), voles (Arvicolinae), and shrews (Sorex sp.).

Analyses

If the 24 drainage culverts occur in a homogeneous habitat-landscape that include random distribution of species abundances, then the following assumptions may apply: (1) the 24 drainage culverts serve the same population of individuals and (2) each individual is aware of all 24 culverts and can choose between culverts based on culvert attributes alone. These assumptions, however, are unrealistic as individual ranges within species such as red squirrel or deer mice are at least an order or two magnitude less than the spatial scale of the 24 culverts (range = 55 km). It is most likely that drainage culverts instead serve their own unique subpopulations. It is therefore necessary to examine observed crossing frequencies for each drainage culvert in the context of local culvert-specific expected crossing frequencies (i.e., performance ratios).

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 24-48 hours after snowfall. On each segment we tallied the number of animal tracks detected crossing the transect. To reduce any potential biases incurred from non-randomly distributed tracks, relative abundance indices were determined by registering the presence (>1 track) or absence of tracks in each 50 m segment. Relative abundance was quantified on the first three segments (1-3) for small mammals (shrews, voles, deer mice), segments 1-6 for hares, red squirrels, and woodrats, and segments 1-10 for the remaining mammals (weasels, martens, coyotes).

We then derived species performance ratios using the following formula:

$$PR_i = Log\left(\left(\left(\left(\frac{Obs_i + 0.5}{Exp_i + 0.5}\right)^2 + \left(\frac{Obs_i - 0.5}{Exp_i - 0.5}\right)^2\right) * \left(\left|\frac{Exp_i + 0.5}{Obs_i - 0.5}\right| * 10^{(Obs_i - Exp_i)}\right)\right)^{0.5}\right)$$

where Pr_i is the species performance ratio 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 ratios were designed such that the higher the performance ratio the more effective the underpass appears to facilitate species crossings. Specifically, the performance ratio gives higher value to species crossings where (a) the absolute difference between observed and expected crossing frequencies is greater but their relative difference is the same, and (b) the absolute difference between observed and expected crossing frequencies is the same but the total number of observed crossings is greater (Table 3).

We examined the premise that drainage culverts 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). In the event that we rejected the null hypotheses, we proceeded with two steps to determine which of 18 culvert attributes species performance ratios were most closely associated with. First, we used a family of simple curvilinear and polynomial regression curves to optimize the fit between species

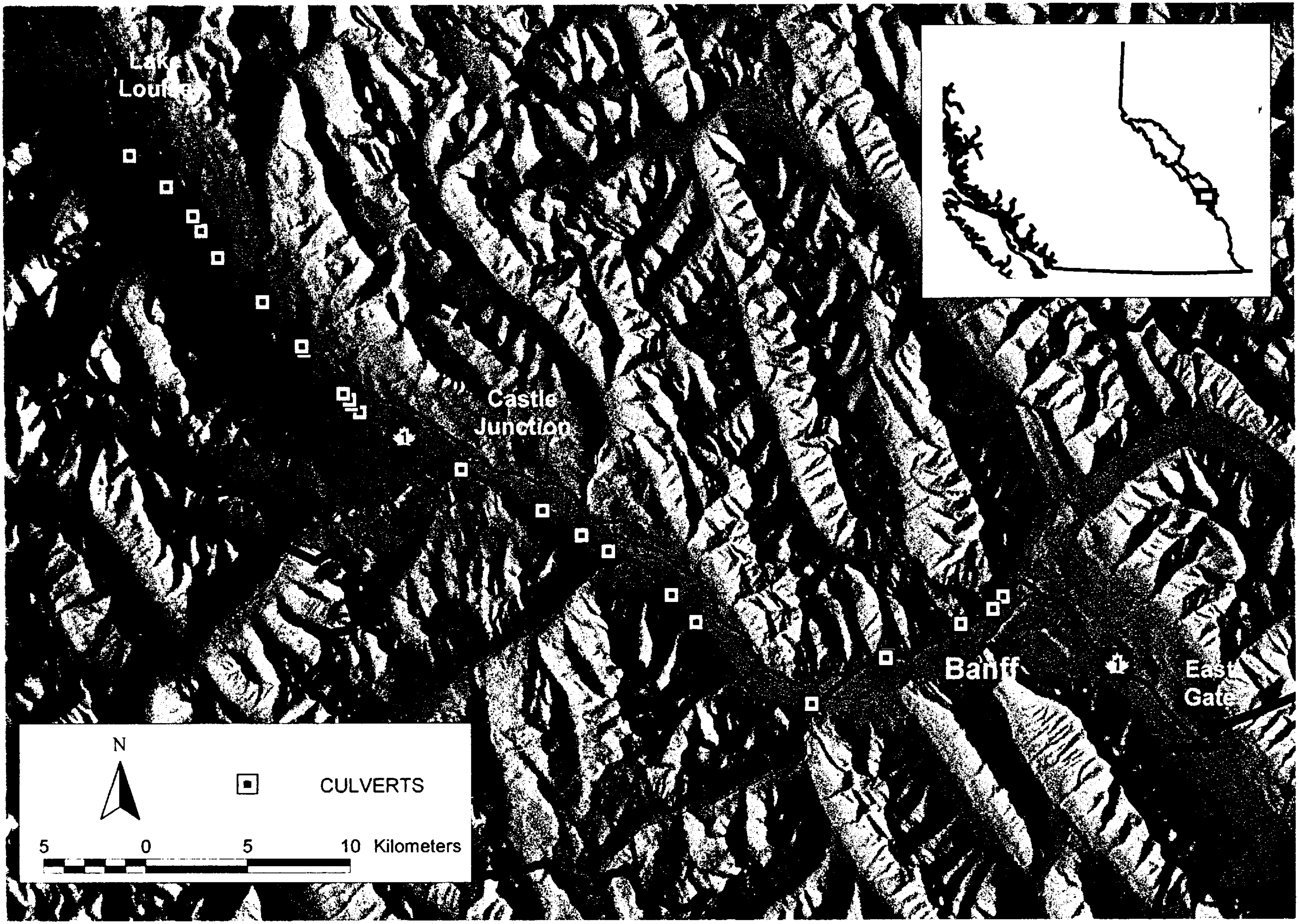

Figure 1. Location of culverts sampled along the Trans-Canada highway in Banff National Park

Table 1. Names and definitions of 18 attributes measured at 24 drainage culverts in Banff National Park, Alberta.

Attribute group Attribute name	Code	Definition
Structural		
Width	W	Culvert width (m)
Height	HT	Culvert height (m)
Length	L	Culvert length (m)
Openness	OPN	Culvert openness (= width x length/height)[a]
Age	AGE	Number of years since installed
Aperture	AP	Mean percent through-culvert visibility taken from each opening and measured in 25% increments between 0-100%
Landscape		
Percent forest cover	FOR	Measured as % forest cover along 2-100 m transects[b]
Percent shrub cover	SHR	% shrub cover measured along 2-100 m transects[b]
Percent open	O	% open habitat measured along 2-100 m transects[b]
Distance to cover	DC	Distance to cover in meters (trees or shrubs >1.5m high)
Distance to nearest structure	DST	Distance to nearest mitigation passage in meters (wildlife crossing structure or full-length culvert)
Snow depth (cm)	SNO	Mean of 3 depth measurements taken 5 m from culvert opening
Elevation	ELEV	Elevation (m)
Road-related		
Road width	RD_W	Width between outer edges of road pavement (m)
Verge width	VG_W	Width from pavement edge to ecotone created by road (m)
Road clearance	RD_CL	Distance between ecotones across road (m)
Noise level	N	Mean of 16 A-weighted decibel (dbl) readings taken at 15 sec intervals during 4 minutes at 5 m from culvert opening
Traffic volume	TVOL	Mean annual average daily traffic volume

[a]:Reed and Ward 1985.

[b]:Transect1: on the culvert axis extends 100 m from the opening. Transect2: in front of the opening and 50 m out on both sides.

Table 2a. Structural attributes of 24 drainage culverts used in analysis of factors influencing small- and medium-sized mammal use in Banff National Park, Alberta. See Table 1 for Variable codes and definitions.

Culvert	W	HT	L	OPN	AP	AGE
1	1.2	0.9	38.3	0.030	1.0	12
2	0.6	0.6	41.9	0.008	1.0	12
3	1.1	1.0	37.8	0.029	1.0	12
4	0.9	0.5	42.0	0.012	0.0	12
5	0.6	0.7	52.3	0.007	0.0	12
6	0.9	0.6	70.0	0.007	0.3	9
7	1.2	1.0	59.0	0.020	1.0	1
8	2.0	1.7	63.1	0.054	0.8	1
9	1.2	1.1	79.2	0.017	0.0	1
10	0.9	0.9	65.4	0.012	0.0	1
11	0.9	0.8	54.7	0.013	0.8	1
12	1.0	0.9	78.0	0.011	0.4	1
13	0.9	0.9	30.5	0.025	0.9	44
14	2.1	1.5	27.5	0.119	1.0	44
15	0.9	0.9	27.4	0.030	0.9	44
16	0.9	0.9	30.9	0.025	0.9	44
17	0.7	0.7	30.1	0.017	1.0	44
18	1.0	0.5	27.6	0.018	0.6	44
19	2.1	1.3	32.3	0.082	0.8	44
20	0.8	0.6	41.1	0.011	0.5	44
21	0.8	0.9	31.5	0.022	1.0	44
22	0.9	0.9	29.3	0.027	0.8	44
23	0.9	0.7	25.4	0.024	0.5	44
24	0.9	0.8	30.8	0.024	0.8	44

Table 2b. Landscape attributes of 24 drainage culverts used in analysis of factors influencing small- and medium-sized mammal use in Banff National Park, Alberta. See Table 1 for Variable codes and definitions.

Culvert	FOR	SHR	O	DC	DST	SNO	ELEV	TOPO
1	13.0	10.3	76.8	11.5	1120	17.0	1402	4
2	35.3	0.3	64.5	7.7	370	10.1	1402	4
3	23.5	5.0	71.5	4.7	1620	13.7	1405	5A
4	4.3	16.8	79.0	35.5	94	9.5	1418	3C
5	3.0	2.0	95.0	19.6	43	16.9	1414	3C
6	26.3	19.5	54.3	2.5	400	29.0	1402	4
7	25.5	4.8	69.8	10.0	1	43.5	1411	5B
8	28.5	9.0	62.5	7.1	40	55.3	1409	5B
9	28.8	8.0	63.3	3.8	630	65.4	1422	5B
10	34.0	0.0	66.0	19.0	370	68.2	1430	3C
11	29.8	0.0	70.3	39.9	610	64.6	1422	3A
12	22.0	2.5	75.5	30.4	10	63.6	1434	4
13	28.5	1.8	69.8	14.0	450	59.6	1463	4
14	34.8	2.0	63.3	8.1	135	65.3	1463	4
15	38.0	0.5	61.5	11.7	135	58.1	1463	4
16	28.3	0.0	71.8	13.3	500	58.3	1463	4
17	23.8	1.3	75.0	7.8	220	61.1	1493	4
18	72.5	4.0	88.8	12.5	220	66.2	1493	5B
19	36.5	0.0	63.5	9.9	350	56.1	1500	4
20	35.8	4.8	59.5	33.0	460	72.0	1496	5A
21	41.8	0.0	58.3	13.2	200	63.2	1507	4
22	44.5	1.5	54.0	10.5	310	65.3	1510	5B
23	13.0	11.8	75.3	9.2	0.5	81.2	1522	4
24	18.8	22.3	59.0	14.7	460	82.9	1525	4

Table 2c. Road-related attributes of 24 drainage culverts used in analysis of factors influencing small- and medium-sized mammal use in Banff National Park, Alberta. See Table 1 for variable codes and definitions.

Culvert	RD_W	VG_W	RD_CL	N	TVOL
1	26.0	15.1	56.2	62.3	14,600
2	26.0	13.3	52.6	60.1	14,600
3	26.0	12.1	50.1	60.9	14,600
4	26.0	6.1	38.2	57.6	14,600
5	26.0	5.6	37.2	58.0	14,600
6	43.0	16.0	75.0	58.8	14,600
7	42.2	20.2	82.6	54.0	8,680
8	42.2	17.2	76.5	61.8	8,680
9	40.8	12.6	65.9	56.2	8,680
10	42.2	8.4	59.0	56.1	8,680
11	37.5	23.4	84.2	60.9	8,680
12	43.0	29.0	101.0	52.3	8,680
13	13.4	17.0	47.3	58.8	7,420
14	15.2	13.0	41.2	61.7	7,420
15	15.0	10.5	35.0	62.2	7,420
16	15.0	14.8	44.6	63.3	7,420
17	13.7	13.2	40.0	62.3	7,420
18	13.7	12.6	38.9	64.3	7,420
19	15.0	12.1	39.2	62.8	7,420
20	15.0	15.2	45.3	60.6	7,420
21	14.0	11.2	36.3	63.2	7,420
22	14.5	10.2	34.9	63.6	7,420
23	13.8	7.9	29.6	65.7	7,420
24	15.9	7.8	31.4	64.2	7,420

Table 3. Rank order of the Performance Ratio

Observed Crossing Frequenices	Expected Crossing Frequenices	Performance Ratio	Rank
4	0	4.212	1
4	1	3.514	2
4	2	2.323	3
2	0	2.289	4
2	1	1.536	5
1	0	1.500	6

Table 4. Observed use of drainage culverts by small- and medium-sized mammals[a] during winter in Banff National Park, Alberta, 1999.

Culvert	CALA	MAAM	MUSP	LEAM	TAHU	ARSP	PEMA	SOSP	N[a] (Σspp.)
1	0	0	11	0	0	0	79	2	92 (3)
2	0	0	0	0	0	0	14	1	15 (2)
3	0	0	8	0	0	0	0	1	9 (2)
4	0	0	2	0	2	0	0	0	4 (2)
5	0	2	27	0	0	1	6	1	104 (5)
6	0	5	13	0	0	2	3	1	24 (5)
7	1	5	5	1	1	0	8	4	25 (7)
8	1	4	23	0	2	2	30	3	65 (7)
9	1	1	27	1	0	0	0	0	30 (4)
10	0	8	4	1	0	0	0	1	14 (4)
11	4	0	10	0	0	0	1	1	16 (4)
12	0	6	13	3	0	0	6	0	28 (4)
13	0	1	0	0	0	0	1	1	3 (3)
14	0	6	2	4	0	0	5	5	22 (5)
15	0	0	0	0	0	0	0	0	0
16	0	0	7	0	1	0	0	0	8 (2)
17	0	0	1	0	0	0	0	0	1 (1)
18	0	0	2	0	0	0	3	0	5 (2)
19	0	7	2	1	0	0	3	10	23 (5)
20	0	0	10	1	0	0	0	2	13 (3)
21	0	1	0	1	0	0	0	0	2 (2)
22	0	2	0	0	0	0	1	2	5 (3)
23	0	0	1	0	0	0	0	7	8 (2)
24	0	3	2	0	0	0	1	1	7 (4)
N[b]	7	51	170	13	6	5	161	43	456
N[c]	4	13	19	8	4	3	14	16	

[a]: CALA=coyote, MAAM=marten, MUSP=weasel, LEAM=snowshoe hare, TAHU=red squirrel, ARSP=voles, PEMA=deer mouse, SOSP=shrews.
N[a]: Total number of species detections at culvert.
N[b]: Total number of detections for species.
N[c]: Number of culverts that species was detected.

Table 5. Relative abundance of small- and medium-sized mammals[a] at drainage culverts during winter in Banff National Park, Alberta, 1999. Abundance was determined by presence (≥1 track; 1) or absence (0) on 50 m segments on each transect.

Culvert	CALA	MAAM	MUSP	LEAM	TAHU	ARSP	PEMA	SOSP	Total
1	11	1	7	0	4	0	4	0	**27**
2	7	2	8	0	1	0	5	0	**23**
3	2	15	16	2	9	0	2	0	**46**
4	11	5	10	1	14	0	0	0	**41**
5	11	5	10	1	14	0	0	0	**41**
6	20	16	11	36	23	1	6	0	**113**
7	11	32	14	11	38	0	2	0	**108**
8	14	46	18	13	44	1	1	0	**137**
9	9	19	19	18	16	0	0	0	**81**
10	6	42	12	31	14	0	2	0	**107**
11	17	16	15	18	6	1	0	0	**73**
12	9	31	13	18	23	0	0	0	**94**
13	0	16	10	40	18	0	3	0	**87**
14	0	16	10	40	18	0	3	0	**87**
15	4	19	6	23	32	0	1	0	**85**
16	4	19	6	23	32	0	1	0	**85**
17	2	22	9	21	26	0	1	0	**81**
18	2	22	9	21	26	0	1	0	**81**
19	0	18	9	13	28	0	0	0	**68**
20	3	6	31	13	21	0	0	0	**74**
21	6	30	8	43	30	1	0	0	**118**
22	6	30	8	43	30	1	0	0	**118**
23	1	20	6	27	38	0	0	0	**92**
24	1	12	8	27	31	0	0	0	**79**
Total	**157**	**460**	**273**	**483**	**536**	**5**	**32**	**0**	**1,946**
Percent	**8**	**24**	**14**	**25**	**27**	**<1**	**2**	**0**	

[a]: CALA=coyote, MAAM=marten, MUSP=weasel, LEAM=snowshoe hare, TAHU=red squirrel, ARSP=voles, PEMA=deer mouse, SOSP=shrews.

Table 6. Rank ordering of significant coefficient of determinations (bold type) and their slope explaining culvert interactions of small and medium-sized mammals in Banff National Park, Alberta.

ATTRIBUTES	Coyote			Marten			Weasel		
	r^2	Rank	Slope	r^2	Rank	Slope	r^2	Rank	Slope
Landscape									
Forest	0.096		Pos	0.192	**5**	**Neg**	0.261	**1**	**Neg**
Shrub	0.364	**7**	**Neg**	0.133		Pos	0.030		Pos
Open	0.033		Pos	0.053		Pos	0.173	**8**	**Pos**
Dist_Cov	0.191	**11**	**Neg**	0.034		Pos	0.213	**4**	**Neg**
SnwDpth	0.228	**9**	**Pos**	0.315	**2**	**Neg**	0.099		Neg
Nearest_Str	0.065		Pos	0.159		Pos	0.017		Neg
Elevation	0.498	**4**	**Pos**	0.019		Neg	0.200	**6**	**Neg**
Structural									
Age	0.567	**2**	**Pos**	0.226	**4**	**Pos**	0.214	**3**	**Neg**
Width	0.030		Pos	0.187	**6**	**Neg**	0.045		Neg
Height	0.121		Pos	0.271	**3**	**Neg**	0.124		Pos
Length	0.555	**3**	**Neg**	0.075		Neg	0.239	**2**	**Pos**
Openness	0.301	**8**	**Pos**	0.148		Neg	0.094		Neg
Aperture	0.145		Pos	0.039		Neg	0.165	**10**	**Neg**
Road									
Noise	0.203	**10**	**Pos**	0.069		Pos	0.027		Neg
Verge_Wdth	0.103		Neg	0.136		Neg	0.082		Neg
Rd_Wdth	0.592	**1**	**Neg**	0.161		Neg	0.202	**5**	**Pos**
Rd_Clear	0.399	**6**	**Neg**	0.097		Neg	0.171	**9**	**Pos**
TrfcVol	0.425	**5**	**Neg**	0.330	**1**	**Pos**	0.178	**7**	**Pos**

Table 6. Continued.

ATTRIBUTES	Hare			Red_Squirrel			Shrew			Deer mouse			Vole		
	r^2	Rank	Slope	r^2	Rank	Slope	r^2	Rank	Slope	r^2	Rank	Slope	r^2	Rank	Slope
Landscape															
Forest	0.236	**8**	**Neg**	0.058		Neg	0.030		Neg	0.053		Neg	0.110		Neg
Shrub	0.042		Pos	0.033		Neg	0.014		Pos	0.047		Pos	0.197	**4**	**Pos**
Open	0.309	**4**	**Pos**	0.127		Pos	0.018		Neg	0.036		Pos	0.045		Pos
Dist_Cov	0.059		Pos	0.122		Pos	0.031		Neg	0.019		Pos	0.331	**1**	**Neg**
SnwDpth	0.454	**1**	**Neg**	0.395	**2**	**Neg**	0.016		Pos	0.134		Neg	0.144		Neg
Nearest_Str	0.032		Pos	0.349	**3**	**Pos**	0.127		Neg	0.163		Neg	0.032		Neg
Elevation	0.308	**5**	**Neg**	0.291	**4**	**Neg**	0.054		Pos	0.125		Neg	0.193	**5**	**Neg**
Structural															
Age	0.322	**3**	**Neg**	0.221	**8**	**Neg**	0.033		Pos	0.097		Neg	0.137		Neg
Width	0.072		Neg	0.130		Neg	0.459	**1**	**Pos**	0.074		Pos	0.113		Neg
Height	0.047		Neg	0.096		Neg	0.266	**3**	**Pos**	0.071		Pos	0.151		Neg
Length	0.278	**6**	**Pos**	0.106		Pos	0.050		Neg	0.099		Pos	0.183	**7**	**Pos**
Openness	0.055		Neg	0.223	**7**	**Neg**	0.385	**2**	**Pos**	0.054		Pos	0.229	**2**	**Neg**
Aperture	0.113		Neg	0.172	**9**	**Pos**	0.057		Pos	0.071		Pos	0.190	**6**	**Neg**
Road															
Noise	0.079		Neg	0.085		Neg	0.052		Pos	0.007		Neg	0.040		Neg
Verge_Wdth	0.142		Neg	0.037		Neg	0.030		Neg	0.034		Pos	0.107		Neg
Rd_Wdth	0.255	**7**	**Pos**	0.283	**5**	**Pos**	0.023		Neg	0.121		Pos	0.163	**8**	**Pos**
Rd_Clear	0.126		Pos	0.250	**6**	**Pos**	0.045		Neg	0.121		Pos	0.063		Pos
TrfcVol	0.397	**2**	**Pos**	0.397	**1**	**Pos**	0.026		Neg	0.127		Pos	0.206	**3**	**Pos**