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Spatial patterns and factors influencing small vertebrate fauna road-kill aggregations

Anthony P. Clevenger[a,b,*], Bryan Chruszcz[c], Kari E. Gunson[c]

[a]*Faculty of Environmental Design, University of Calgary, Calgary, AB, Canada T1N 2N4*
[b]*Department of Forestry, Wildlife and Fisheries, University of Tennessee, Knoxville, TN 37901-1071, USA*
[c]*Parks Canada, Box 900, Banff, AB, Canada T0L 0C0*

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Abstract

We examined the spatial patterns and factors influencing small terrestrial vertebrate road-kill aggregations in the Bow River Valley, Alberta, Canada. We surveyed roads varying in traffic volume, configuration and adjacent landscape attributes for road-kills between 1997 and 2000. The spatial pattern of road-kills was described using neighbour *K* statistics. We investigated the importance of road-kills at three taxonomic levels using logistic regression. Mammal and bird road-kill indices were consistently higher on a low volume parkway than on the high-speed, high volume Trans-Canada highway (TCH). Birds were more vulnerable to collisions than mammals on the TCH. Road-kill aggregations were nonrandomly distributed. Parkway road-kills were aggregated on small scales and characterized by low clustering intensities compared to the TCH. Road-kills were less likely to occur on raised sections of road. Road-kills tended to occur close to vegetative cover and far from wildlife passages or culverts. Our findings reveal how two distinct road types can have different effects in terms of vertebrate mortality and their spatial pattern. We recommend a series of mitigation measures for existing roads or future road planning projects. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Banff National Park; Mortality; Road ecology; Road-kills; Spatial pattern

1. Introduction

Studies of vehicle-caused wildlife mortality have covered a broad taxonomical spectrum, yet collisions with deer and other large mammals such as moose *Alces alces* and elk *Cervus elaphus* have stimulated much of the research (Reed et al., 1979; Woods, 1990; Lavsund and Sandegren, 1991). Research results have largely been descriptive and anecdotal reporting on surveys or counts of animals killed by vehicles, age and sex characteristics of road-kills, and seasonal patterns. Although counts of dead animals can be useful for evaluating the magnitude of road-kills, they are inadequate for understanding the relationship between roads and wildlife.

The importance of habitat and road variables influencing bird collisions with vehicles has long been recognized (Barnes, 1936; Finnis, 1960). Previous analyses of factors explaining road-kills have focused primarily on large mammals (Bellis and Graves, 1971; Bashore et al., 1985; Groot Bruinderink and Hazebroek, 1996), whereas few formal studies have investigated the role of road and landscape variables influencing small fauna road-kills (Oxley et al., 1974; Fahrig et al., 1995; Massemin and Zorn, 1998; Philcox et al., 1999).

Research on large mammal road-kill aggregations has demonstrated that they do not occur randomly but are spatially clustered (Puglisi et al., 1974; Child, 1998; Hubbard et al., 2000; Clevenger et al., 2001a; Joyce and Mahoney, 2001). Wildlife tends to be linked to specific habitats and adjacent land use types. Thus, landscape spatial patterns would be expected to play an important role in determining road-kill locations and rates (Forman and Alexander, 1998). Explanatory factors of wildlife road-kills vary widely between species and taxa. To understand the importance of such factors and processes, it is first necessary to be able to measure and describe the spatial pattern of road-kill aggregations.

Where vehicle speed and/or road density are high, road traffic has been shown to have a severe local effect

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* Corresponding author. Present address: 3–625 Fourth Street, Canmore, Alberta, Canada T1W 2G7. Tel.: +1-403-760-1371; fax: +1-403-762-3240.

E-mail address: tony_clevenger@pch.gc.ca (A.P. Clevenger).

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on animal road-kills (Rosen and Lowe, 1994; Drews, 1995; Jones, 2000). Increased traffic flows in Banff National Park (BNP) have raised concerns about increased road-kills of wildlife (Banff-Bow Valley Study, 1996). One strategic goal of the BNP management plan was to reduce wildlife road-kills on the Trans-Canada highway (TCH) and other roads in and adjacent to the park (Parks Canada, 1997). The lethal impacts of park roads on large mammals has been investigated (Woods, 1990; Clevenger et al., 2001a), yet virtually nothing is known about road-kills of smaller vertebrate fauna. To support efforts to mitigate road impacts at all levels of species organization, management needs to be able to identify where particular individuals, species, taxa, and vertebrate communities are susceptible to high road-kill rates along roads.

We quantified road-kill occurrence among small terrestrial vertebrates in the Bow River Valley. We identified seasonal and geographic patterns of road-kills. We tested whether road-kills occurred randomly and, in the event they were spatially clustered, whether road-kill aggregation characteristics were taxa-specific. Finally, we evaluated the relative importance of factors associated with road-kills of small terrestrial vertebrates on a variety of roads varying in vehicle traffic, road configuration and adjacent landscape attributes.

2. Methods

2.1. Study area

This study took place in the Central Canadian Rocky Mountains in western Alberta approximately 100 km west of Calgary (Fig. 1). The area encompasses the Bow River watershed comprising mountain landscapes in BNP and adjacent Alberta Provincial lands in Kananaskis Country. Topography is mountainous, elevations range from 1300 to over 3400 m, and valley floor width varies from 2 to 5 km.

We selected two roads within our study area, both had varying traffic volumes, vehicle speeds, road configurations, and adjacent habitat. The first road was a 117 km section of the TCH between the town of Seebe and Kicking Horse Pass. This part of the highway traverses provincial land (=44%) as well as BNP (=56%), terminating at the western boundary of the park and border between British Columbia and Alberta. The TCH runs along the floor of the Bow Valley sharing the valley bottom with the Bow River, the Canadian Pacific Railway and several small towns with $\leqslant$10,000 people. Average traffic volume at the park east entrance was more than 14,000 vehicles per day year-round in 1997, and reached peaks of more than 35,000 vehicles per day during summer months (Parks Canada Highway Service Centre, unpublished data). The stretch of highway we studied consisted of two and four lane segments including four lane segments with a dividing centre median. The average vehicle speed ranged from 90 to 120 km per hour.

The second road in the study was the Bow Valley Parkway (hereafter referred to as the Parkway) within BNP. The Parkway also runs along the floor of the Bow Valley and is parallel to the TCH. Average daily traffic volume in 1997 ranged from 1068 to 3231 vehicles per day during summer (Parks Canada Highway Service, unpublished data). The Parkway is two lanes wide and the average vehicle speed was 60–70 km per hour.

The Bow River Valley is situated within the front and main ranges of the Canadian Rocky Mountains. The roads in this study traversed montane and subalpine ecoregions. Vegetation consisted of open forests dominated by Douglas fir *Pseudotsuga menziesii*, white spruce *Picea glauca*, lodgepole pine *Pinus contorta*, Englemann spruce *P. englemannii,* aspen *Populus tremuloides* and natural grasslands.

2.2. Road-kill survey data collection

From September 1997 to August 2000, we surveyed the TCH and the Parkway by vehicle for road-killed wildlife in BNP and adjacent Kananaskis Country. We sampled roads on snow-free days between the months of April and November; surveys were not conducted during winter or days with snow because of decreased detection and snow removal on roads. We focused our attention specifically on small fauna, defined as terrestrial vertebrate species coyote *Canis latrans*-sized and smaller.

Surveys began within 1 h after sunrise. We noted the weather during the previous 24 h. One route surveyed the TCH from the Banff townsite to the junction of Highway 40 in Kananaskis Country (sample distance = 105.6 km). The other route sampled the TCH from Banff townsite to Kicking Horse Pass (sample distance = 80.1 km) and the Parkway (sample distance = 62.4 km). Two lanes of road was the standard road sampling width. The two survey routes were alternated each day. Two observers performed the survey, one driving 10–20 km per hour below the posted speed limit, the other searching for road-killed animals on the road surface. When a road-killed animal was discovered, we attempted to identify the species, determine the sex and age. We marked the road-kill location on the road pavement edge with florescent spray paint and obtained the geographic coordinate location of all road-kills using a differentially-correctable, global positioning system (GPS) unit (Trimble Navigation Ltd., Sunnyvale, California, USA). We divided the sampling period into two seasons: spring-early summer (1 April–15 July), late summer-autumn (16 July–31 October). A road-kill index was calculated as the frequency of road-kills per

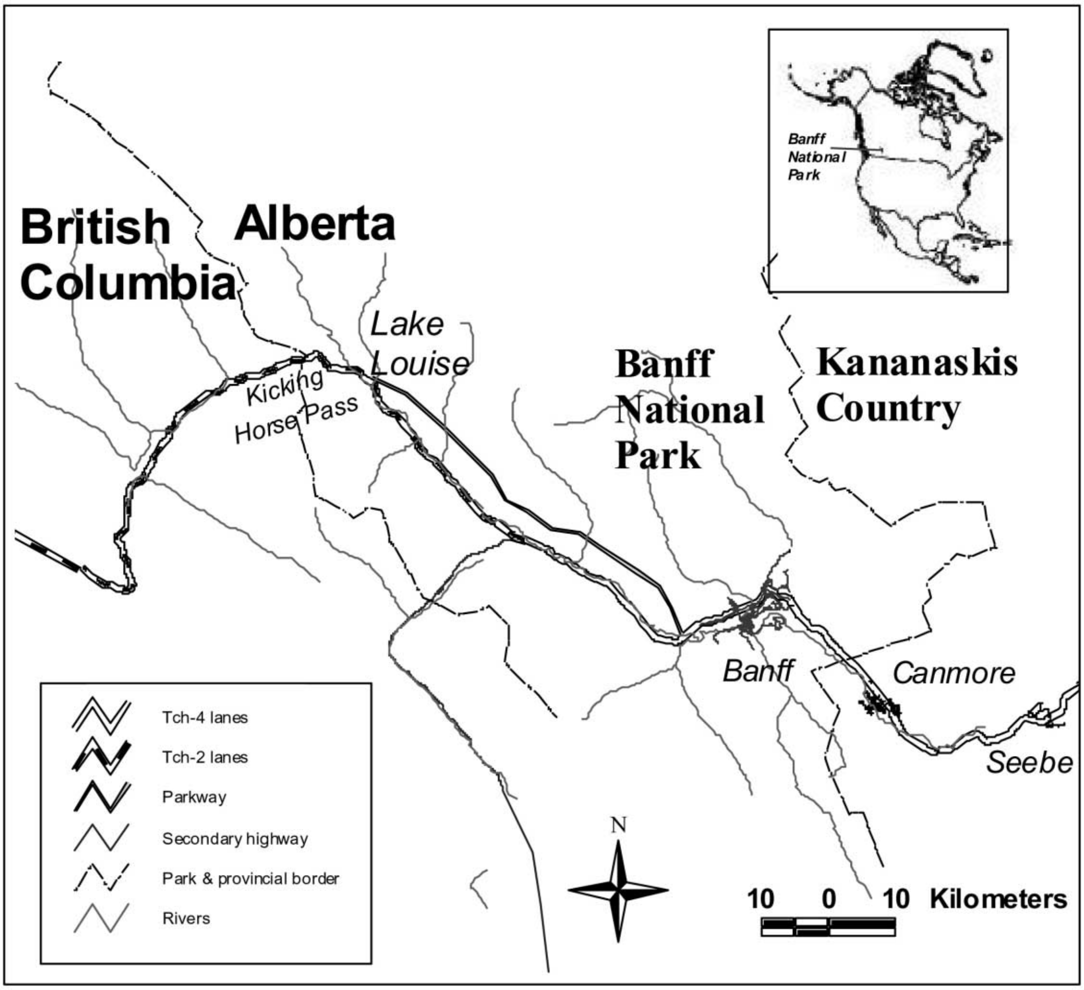

Fig. 1. Location of study area and roads sampled for small vertebrate fauna road-kills in the Central Canadian Rocky Mountains, 1997–2000.

1000 km of road surveyed. For each road type we calculated the proportion of road-kills by taxa.

2.3. Description of spatial pattern of road-kills

The distributions of animals killed on roads we sampled were 1-dimensional because the width of the area sampled (2-lanes = ca. 9 m) was small compared with the survey length (60–120 km). Ripley's *K*-statistic describes the dispersion of data over a range of spatial scales (Ripley, 1981; Cressie, 1991). We calculated Ripley's *K*-statistic for avian and mammalian road-kills on the TCH and the Parkway. We used the *K*-statistic as defined by Levine (2000), but modified for points distributed in one dimension (i.e. distributions along a line). The resulting algorithm was coded in Avenue™ and run in ArcView© GIS (Environmental Systems Research Institute, 1998). The algorithm counted the number of neighbouring road-kills within a specified scale distance (t) of each road-kill and these counts were summed over all road-kills. We standardized the totals by sample size (N) and road length (RL) to allow for comparison between the four categories (mammal kills on TCH, mammal kills on Parkway, bird kills on TCH, and bird kills on Parkway). The process was repeated for incrementally larger scale distances up to RL for the two road types. Thus the *K*-statistic (adapted from Levine, 2000, and O'Driscoll, 1998) was defined as:

$$K(t)_{\text{obs}} = \frac{\text{RL}}{N^2} \sum_{\substack{i=1 \\ i \neq j}}^{N} \sum_{j=1}^{N} I(d_{ij})$$

where d_{ij} was the distance from road-kill i to road-kill j and $\text{I}(\text{d}_{\text{ij}})$ was an indicator function that returns 1 if $d_{ij} \leqslant$ distance and zero otherwise (O'Driscoll, 1998). We used a scale distance increment of 624 m for all four categories to allow for a minimum of 100 bins on the shorter of the two roads (i.e. Parkway).

To assess the significance of *K*-values we ran 100 simulations of the above equation based on random distributions of points for each of the four categories. We displayed results as plots of $L(t)$ versus linear scale distance t, where $L(t)$ was the average number of extra neighbours within the scale distance t of any given road-kill in the distribution. The extra neighbours were those which were not expected if all the road-kills were arranged randomly along the survey route. Thus, $L(t)$ is a measure of the intensity of clustering and was calculated as the difference between the observed K-value and the mean of the K-values for the 100 simulations. For a random distribution $L(t)=0$. Positive values of $L(t)$ indicated clustering and negative values indicate dispersion (O'Driscoll, 1998). We also presented the 95% confidence limits calculated as the upper or lower 95th percentile of the random simulations minus the mean of the random simulations. We defined significant clustering as any value of $L(t)$ above the upper confidence limit and significant dispersion as any value of $L(t)$ below the lower confidence limit.

2.4. *Analysis of factors explaining road-kill occurrence*

We used logistic regression (maximum likelihood estimates) to predict the probability of occurrence of road-kills as a function of landscape and road variables. Logistic regression was selected because the explanatory variables we used consisted of continuous and categorical data (Press and Wilson, 1978). We chose variables to describe site-specific attributes of each road-kill site. Ten explanatory variables were used to describe each road-kill site (Table 1). Indicator or dummy variables were created for each categorical variable with one reference comparison variable (HABITAT = open, MEDIAN = absent, TOPOG = level, TR_VOL = low). The variable D_PASS was not included in analysis of factors explaining bird or bird species road-kills.

We investigated the importance of road-kills at three taxonomic levels, individual species, species groups (mammals and birds), and the small vertebrate community. We compared the site-specific attributes of road-kill locations to attributes of 300 random locations along the sampled roads. Random points were distributed along the TCH and Parkway in proportion to the length of the two road types in the study area. We used a hand-held, GPS unit to locate random points on the road and collect the same site-specific attributes from each location as the road-kills. The dependent variable (Road-kill) was then coded either kill (1) or no-kill (0, random point). At the species level we performed logistic regression on species that had more than 50 road-kills and all associated site measurements (= common raven *Corvus corax*, red squirrel *Tamiasciurus hudsonicus* and snowshoe hare *Lepus americanus*). All of the observed road-kill locations for which we had a complete set of independent variables were used at the species group (mammals: $n=272$ locations; birds: $n=296$ locations) and community level ($n=604$ locations).

We used the log-likelihood ratio test (Hosmer and Lemeshow, 1989) to determine significance of models to discriminate between road-kill locations and random locations based on location attributes. We assessed the improvement of fitted models over null models according to the difference in (-2) log-likelihood ratios. Significance of explanatory variable coefficients was based on chi-square tests of Wald statistics (Hosmer and Lemeshow, 1989). Standardized effect coefficients were not calculated, however we multiplied logistic regression coefficients (β) by the standard deviation of the respective variables to assess the relative importance of the

Table 1
Definition and description of variables used in the analysis of factors explaining road-kill occurrence

Variable name	Definition
Continuous variables	
D_COVER [a]	Mean distance (m) to vegetative cover (trees and shrubs $\geqslant 1$ m high) taken from both sides of road
D_PASS[b]	Distance (m) to nearest wildlife crossing structure or drainage culvert
D_TOWN [c]	Distance (m) to nearest town
D_WATER [c]	Distance (m) to nearest water (wetland, lake, stream)
ELEV [c]	Elevation (m)
N_JERSEY [a]	Number of Jersey barriers in roadway (road centre or edges)
Categorical variables	
HABITAT [a]	Forest, forest-open mix, water (wetland, lake, stream), open (meadows, barren ground)
MEDIAN [a]	Median absent (0) or present (1) between lanes
TR_VOL[c]	High = $\geqslant$21 000 vehicles/day, summer average daily traffic volume (SADT); moderate = 11,000–14,000 vehicles/day (SADT); low = $\leqslant$3000 vehicles/day (SADT)
TOPOG [a]	Roadside topography (bold line represents pavement):  Buried (1) Raised (2) Buried-Raised (3) Level (4) Part buried (5) Part raised (6)

[a] Variable measure obtained from field measurement.
[b] Variable not included in analysis of factors explaining bird or bird species kills.
[c] Variable measure obtained from a geographic information system or other source.

explanatory variables within the model. We call this parameter the standardized estimate coefficient. Interpretation of logistic regression coefficients was made in terms of statements about odds ratios. We also included cross-validation classification accuracies for random points, observed points, and combined overall points for each model. Prior to performing the regression analysis we tested potential explanatory variables for multicollinearity (Menard, 1995). When variables were correlated ($r > 0.7$) we removed one of the two variables from the analysis. Final models and variable coefficients with a P-value $\leqslant 0.10$ were considered significant unless otherwise stated. We used the SPSS statistical package version 7.5 for all analyses (SPSS, 1996).

3. Results

3.1. Species composition and temporal pattern of road-kills

Our surveys sampled a total of 65,253 km of roads. Of this distance, 14,659 km were surveyed on the Parkway and 50,594 km on the TCH. Sampling took place on 554 days; 226 (40%) of those days no road-kills were found. The average number of sampling days without recorded road-kills was highest in May and October and lowest in July and August.

A total of 677 animals (56 identified species) were collected at 669 sites. These included 313 mammals (18 species), 316 birds (36 species) and 48 amphibians (two species) (Table 2). Mammals made up 46% of the road-kills followed by birds (47%) and amphibians (7%). All of the recorded road-kills were wild species endemic to the study area. Of the endemic species residing in habitats traversed by the surveyed roads, 46% of 37 mammal species, 34% of 106 bird species, and two of five amphibian species were represented in our road-kill sample. Only one reptile species, wandering garter snake *Thamnophis elegans*, occurred within the study area but was not recorded as a road-kill. Of the five most frequently killed mammals, three were widespread and abundant, and two were locally abundant. Four of the most frequently killed birds were roadside foragers and one was the most common species in the area.

Road-kills were the highest during summer. The greatest number of road-kills occurred in July ($n = 226$), followed by August ($n = 155$) and June ($n = 81$). Road-kills were most prevalent among mammals in April, among birds from May to August, and among amphibians from June to August (Fig. 2). We compared road-kill indices for the three taxa between years. We did not include 1997 because only 3 months of data were collected. Road-kill indices were similar between years ranging from 7.9 to 10.7 road-kills per 1000 km sampled (Table 3).

Of 253 road-killed animals recorded on the Parkway, 54% ($n = 137$) were mammals, 29% ($n = 74$) birds, and 17% ($n = 42$) amphibians. Mammal road-kill indices were highest each year on the Parkway and overall three times greater (9.1 road-kills/1000 km vs. 2.9 road-kills/1000 km) than the TCH (Table 3). Similarly, bird road-kill indices were higher each year on the Parkway than the TCH each year, particularly in 2000, and overall indices were slightly greater than that of the TCH. Of 417 road-kills on the TCH, 58% ($n = 242$) were birds, 41% ($n = 170$) mammals and 1% ($n = 5$) amphibians. For each of the three years road-kill frequencies were higher for birds than mammals on the TCH, whereas mammal road-kill frequencies were consistently higher than birds on the Parkway. Amphibian road-kill frequencies were higher on the Parkway than the TCH. However, in 1999 we documented two periods of tiger salamander *Ambystoma tigrinum* mass migrations across the TCH both resulting in a minimum of 183 road-kills (Clevenger et al., 2001b).

3.2. Description of spatial pattern of road-kills

The distribution of road-kills was heterogeneous and significantly more clustered than would be expected in a random arrangement over a wide range of scales ($P < 0.05$; Fig. 3). For both mammals and birds there was significant clustering of road-kills at small spatial scales on the Parkway. Peaks in $L(t)$ occurred at a scale distance of 2 km in birds and 4 km in mammals, but the range of spatial scales over which clustering was significant was larger in mammals (0–13 km) than birds (0–4 km). Both taxonomic groups also displayed minima representing significant dispersion (i.e. at 10 and 20 km in birds and 27 and 53 km in mammals).

Clustering was significant on the TCH over a larger range of spatial scales compared to the Parkway and there was no significant dispersion at any spatial scale (Fig. 3). This result was consistent for both mammals [scale of maximum $L(t) = 14$ km, range of scales for significant clustering = 0–62 km] and birds (scale of maximum $L(t) = 31$ km, range of scales for significant clustering = 0–69 km). Road-kill aggregations were three to four times more severe on the TCH than the Parkway [considering the maximum $L(t)$ values from the four plots; Fig. 3].

3.3. Analysis of factors explaining road-kill occurrence

The three species models were statistically significant (all $P < 0.001$). The variance explained by the models and overall cross-validation accuracies were highest for the red squirrel model ($R^2 = 0.82$; 96%) followed by raven ($R^2 = 0.41$; 90%) and snowshoe hare ($R^2 = 0.37$; 82%) models (Table 4). Road topography was most important in explaining raven road-kills. Ravens were

Table 2
Frequency of small vertebrate road-kill in the Central Canadian Rocky Mountains, 1997–2000 (Domestic animals were excluded)

Common name	Scientific name	*N*	% of taxa	% of total kills
Mammals				
Red squirrel	*Tamiasciurus hudsonicus*	90	28.7	13.3
Snowshoe hare	*Lepus americanus*	77	24.6	11.4
Deer mouse	*Peromyscus maniculatus*	39	12.4	5.8
Columbian ground squirrel	*Spermophilus columbianus*	26	8.3	3.9
American marten	*Martes americana*	15	4.8	2.2
Coyote	*Canis latrans*	14	4.5	2.1
Mink	*Mustela vison*	6	1.9	<1
Muskrat	*Ondatra zibethicus*	6	1.9	<1
Meadow vole	*Microtus pennsylvanicus*	6	1.9	<1
Red-backed vole	*Clethrionomys gapperi*	6	1.9	<1
Striped skunk	*Mephitis mephitis*	3	1.0	<1
Western jumping mouse	*Zapus princeps*	3	1.0	<1
Beaver	*Castor canadensis*	2	0.6	<1
Least chipmunk	*Eutamias minimus*	2	0.6	<1
Unidentified mammal		6	1.9	<1
Species with one road-kill		4	1.2	<1
Total mammals		313		
Total species		18		
Birds				
Common raven	*Corvus corax*	60	18.9	8.9
American robin	*Turdus migratorius*	50	15.8	7.4
American crow	*Corvus brachyrhynchos*	33	10.4	4.9
Black-billed magpie	*Pica pica*	32	10.1	4.7
Gray jay	*Perisoreus canadensis*	19	6.0	2.8
Chipping sparrow	*Spizella passerina*	16	5.1	2.4
Ruffed grouse	*Bonasa umbellus*	9	2.8	1.3
White-crowned sparrow	*Zonotrichia leucophrys*	7	2.2	1.0
Yellow-rumped warbler	*Dendroica coronata*	7	2.2	1.0
Pine siskin	*Carduelis pinus*	6	1.9	<1
Hermit thrush	*Catharus guttatus*	5	1.6	<1
Dark-eyed junco	*Junco hyemalis*	5	1.6	<1
Great horned owl	*Bubo virginianus*	4	1.3	<1
Lincoln sparrow	*Melospiza lincolnii*	3	1.0	<1
Mallard	*Anas platyryhncos*	3	1.0	<1
Northern saw-whet owl	*Aegolius acadicus*	3	1.0	<1
Spruce grouse	*Dendragapus canadensis*	3	1.0	<1
Clark's nutcracker	*Nucifraga columbiana*	2	0.6	<1
Belted kingfisher	*Ceryle alcyon*	2	0.6	<1
Merlin	*Falco columbarius*	2	0.6	<1
Swainson's thrush	*Catharus ustulatus*	2	0.6	<1
Species with one road-kill		15	4.7	2.2
Unidentified passerine		10	3.2	1.5
Unidentified sparrow		4	1.3	<1
Unidentified bird		5	1.6	<1
Unidentified raptor		2	0.6	<1
Unidentified swallow		2	0.6	<1
Unidentified duck		2	0.6	<1
Unidentified gull		2	0.6	<1
Unidentified owl		1	0.3	<1
Total birds		316		
Total species		36		
Amphibians				
Western toad	*Bufo boreas*	45	93.8	7.2
Tiger salamander	*Ambystoma tigrinum*	2	4.2	<1
Unidentified amphibian		1	2.1	<1
Total amphibians		48		
Total species		2		

91% (odds ratio = 0.086) less likely to be killed on raised sections of road relative to level roads. Habitat type also ranked high influencing road-kills as ravens were less likely to be killed on roads in forested and forest-open mix habitats. Elevation and proximity to towns were significant factors and both negatively correlated with road-kills. Red squirrel road-kills were only explained by the proximity of towns (negative correlation). Topography was the most important variable explaining snowshoe hare road-kills. Hares were less likely to be killed on road sections that were raised and to a lesser extent combined buried-raised sections compared to level. Road-killed hares were found close to cover and far from safe passages (culverts or crossing structures).

Models for mammals, birds and the small vertebrate community were significant (all $P<0.001$). Model variance and cross-validation accuracies were high (Table 4). Six variables explained the occurrence of mammal road-kills. Topography had the highest explanatory power as mammals were less likely to be killed on raised roads relative to level roads. Mammals also had a tendency to be killed on roads close to cover, at low elevations and far from safe passages. Birds were 92% (odds ratio = 0.088) less likely to be killed on raised roads compared to roads in level terrain. Habitat type also ranked high influencing road-kills as birds were less likely to be killed on roads in forested and forest-open mix habitats relative to open habitats. There was a greater tendency for birds to be killed on roads with centre medians (85% more likely; odds ratio = 1.852) and low in elevation. At the community level, topography was most important in explaining road-kills. Vertebrate taxa were 93% (odds ratio = 0.067) less susceptible to road-kills on raised roads relative to level sections and 45% (odds ratio = 0.546) less vulnerable on combined buried-raised sections of road. Animals were more likely to be killed on roads at low elevations and close to towns.

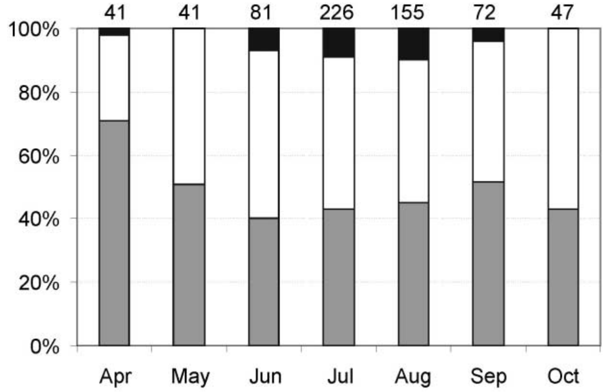

Fig. 2. Monthly composition of small vertebrate road-kills in the Central Canadian Rocky Mountains, 1997–2000. Categories are: mammals, grey bars; birds, white bars; amphibians, black bars. Sample sizes at top of columns.

4. Discussion

4.1. *Species composition and temporal pattern of road-kills*

Compared to the sampling effort undertaken to quantify road-kill occurrence in our study area kill rates were remarkably low. We surveyed 65,000 km of road during 550 days and documented 674 road-killed animals. Previous studies have reported greater numbers of road-kills while sampling shorter road sections during shorter periods (Fahrig et al., 1995; Ashley and Robinson, 1996; Kline and Swann, 1998). The low kill rates we report may be explained by climatic conditions in

Table 3
Road-kill indices and frequency of small vertebrate road-kill by road type and year in the Central Canadian Rocky Mountains, 1998–2000

Taxa	Road	1998		1999		2000		Total	
		Kills per 1000 km	N (%)[a]	Kills per 1000 km	N (%)[a]	Kills per 1000 km	N (%)[a]	Kills per 1000 km	N (%)[a]
Mammals	TCH	3.0	38 (34)	3.4	62 (44)	2.7	43 (43)	2.9	143 (40)
	BVP	12.6	54 (56)	8.0	45 (52)	6.5	33 (53)	9.1	132 (54)
	Total	4.9		4.5		3.5		4.3	
Birds	TCH	4.8	73 (65)	4.0	77 (54)	3.6	57 (57)	4.2	207 (58)
	BVP	4.8	22 (23)	4.9	26 (30)	5.6	23 (37)	5.1	71 (29)
	Total	4.8		4.2		4.0		4.4	
Amphibians	TCH	0.1	2 (1)	0.1	3 (2)	0.0	0 (0)	0.1	5 (2)
	BVP	4.3	20 (21)	3.3	16 (18)	1.7	6 (10)	3.2	42 (17)
	Total	1.1		0.8		0.4		0.8	
Total		10.7		9.5		7.9		9.4	

[a] Frequency and percent composition of road-killed taxa by road type.

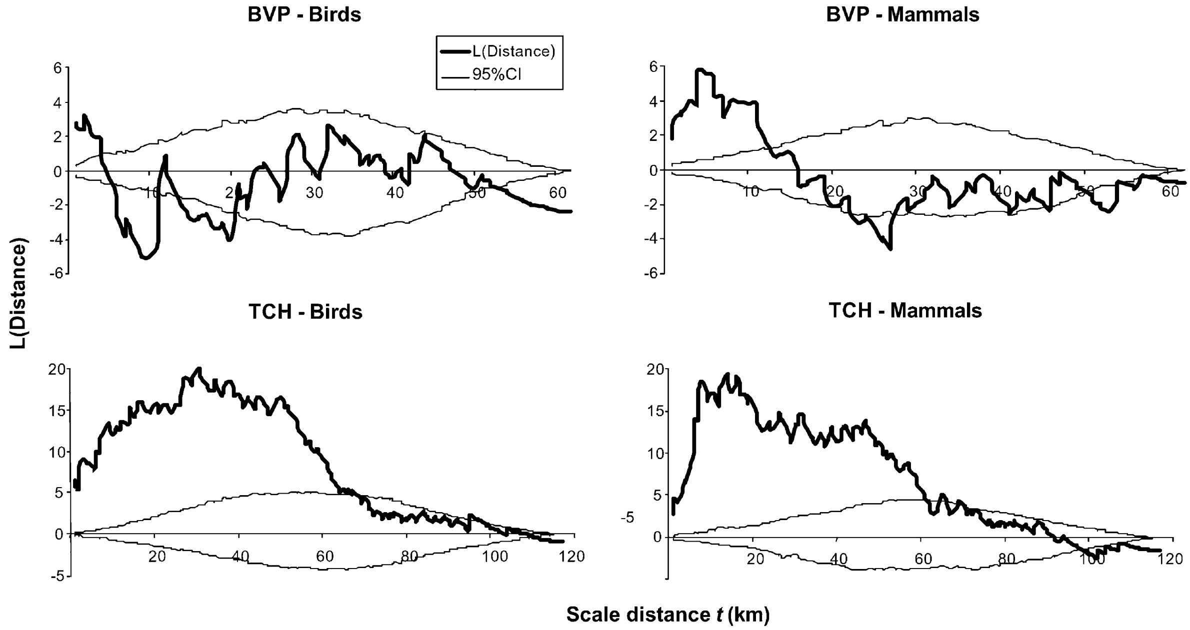

Fig. 3. Plots of the L-statistic [$L(t)$] as a function of scale for distribution of small vertebrate road-kills on the Trans-Canada Highway (TCH) and Bow Valley Parkway (BVP). The thick solid line represents the observed number of neighbours per road-kill along the survey route minus the mean expected number of neighbours if the road-kills were distributed randomly. If the road-kills were distributed randomly $L(t)=0$. The distribution is significantly clustered or dispersed ($P<0.05$) at scale distance t when $L(t)$ is above or below the 95% confidence interval (thin solid line), respectively.

Table 4

Species, group and community level ordering of significant ($P<0.10$) standardized estimate coefficients and their sign in analysis of factors explaining road-kill occurrence. Numbers indicate rank of importance of variable. Sign indicates influence on odds ratio (negative decreases odds that data point is a road-kill; positive increases odds that data point is a road-kill). Model variance and validation results are provided

Variable	Raven	Red squirrel	Snowshoe hare	Mammals	Birds	Community
D_COVER			3−	3−		
D_PASS[a]			5+	5+		
D_TOWN	5−	1−	6−	6−	6−	4−
D_WATER						
ELEV	4−		4−	4−	5−	3−
N_JERSEY						
HABITAT—forest	3−				2−	
HABITAT—forest-open	2−				3−	
MEDIAN					4+	
TR_VOL[b]						
TOPOG—raised	1−		2−	1−	1−	1−
TOPOG—raised/buried			1−	2−		2−
Model R^2	0.41	0.82	0.37	0.58	0.54	0.53
Cross-validation accuracy (%)[c]	90	96	82	80	79	79

[a] Variable not included in analysis of factors explaining bird or bird species road-kills.

[b] TR_VOL was significant for mammals ($P=0.019$) and the small vertebrate community ($P=0.0002$); however, neither of its constituent dummy variables proved significant and therefore rankings are not displayed in the table.

[c] Overall cross-validation accuracy using random and observed data.

our study area, characterized by short summers and brief activity periods for many small vertebrates. Further, four of the five amphibian species in the Bow Valley are considered uncommon; only the western toad *Bufo boreas* is widespread and relatively abundant (Holroyd and Van Tighem, 1983) compared to other temperate zones of North America where large numbers have been recorded as road-kills (Wilkins and Schmidly, 1980; Palis, 1994; Fahrig et al., 1995; Ashley and Robinson, 1996).

Small vertebrate road-kills showed seasonal patterns for the three taxa that were consistent with life history phenology, particularly breeding and dispersal. These findings are in agreement with results from previous road-kill studies of small and large fauna (Allen and McCullough, 1976; Ashley and Robinson, 1996; Philcox et al., 1999; Joyce and Mahoney, 2001). Overall road-kill indices were highest during summer months of July and August. However, road-kill indices were highest for mammals in spring, which suggests that road-kills may be largely explained by breeding activity. Bird road-kills were high from May through August indicating that breeding and dispersal activities may make them more susceptible to road-related mortality. Although amphibian road-kills were highest between June and August, they were episodic and generally associated with rainfall events (Clevenger, personal observation).

Our results showed that mammals were more vulnerable to being killed on the narrower and less traveled Parkway. For birds, however, two of our road-kill measures (road-kill index and proportion of kills per road type) indicated their road-kills tended to be higher on the wider and busier TCH. The work by Oxley et al. (1974) is the only study we are aware of that has examined kill rates between taxa on roads that vary in traffic intensity and width. They found birds were more susceptible to road-kills on high traffic volume roads (5000–10,000 vehicles/day, summer average daily traffic volume, SADT) in Ontario. However, they had mixed results regarding road-kill rates among mammals. Small, forest-adapted species such as *Tamia striatus, Sciurus carolinensis* and *Tamiasciurus hudsonicus* had higher road-kill rates on roads with moderate traffic volume (1500–4000 SADT) and lower rates on wide, high traffic volume roads. Conversely, medium-sized mammals including *Lepus americanus* showed increasing road-kill rates with increasing traffic volume and road width. We found relatively low kill rates for small- and medium-sized mammals on the TCH. One reason may be that traffic speed and volumes on the TCH were substantially higher than the Ontario study (100 vs. 70 km/h and 24,000 vs. 5000–10,000 SADT, respectively). Although many of the forest-associated mammals killed on the Parkway reside in the TCH corridor (Clevenger et al., 2001c), we suspect that disturbance generated from a highway of this magnitude may effectively deter animal movements onto or across the roadway (Barnett et al., 1978; Swihart and Slade, 1984; Woodward, 1990). The higher incidence of bird road-kills along the TCH compared to mammals may be explained by greater abundance or vulnerability to road-kills (Mumme et al., 2000).

The level of threat from traffic to an amphibian population depends on a number of factors. The juxtaposition of ponds or preferred habitats may or may not necessitate road crossing to access seasonal habitat. The tiger salamander migration across the TCH was episodic, resulting in hundreds of road-kills in one location (Clevenger et al., 2001b), however, when calculating road-kill indices we treated this singular event as one road-kill. Nevertheless, we found amphibians more vulnerable to road-kills on the Parkway than the TCH and believe this can largely be explained by more wetland habitat adjacent to the Parkway.

4.2. Description of spatial pattern of road-kills

Neighbour *K* statistics are well suited for the description of one-dimensional spatial distributions (Ripley, 1981; Getis and Franklin, 1987). The range of scales over which clustering appears significant is dependent on the intensity of the distribution. Our results showed that small vertebrate road-kills were nonrandomly distributed and clustered along both roads. Distributions of mammal and bird road-kills on the TCH and Parkway were significantly clustered at scales ranging from two to more than thirty kilometres.

We are not aware of previous studies describing the structure and scale of road-kill aggregations. Clustering of wildlife-vehicle collisions, however, has been reported elsewhere (Puglisi et al., 1974; Huijser, 2000). Clustering of large mammal road-kills previously has been explained by animal distribution, abundance, dispersal, and road-related factors including local topography, vegetation, vehicle speed, and fence location or type (Puglisi et al., 1974; Allen and McCullough, 1976; Case, 1978; Clevenger et al., 2001a).

Parkway bird road-kills were clustered on small scales and the intensity of clustering (i.e. the number of extra neighbouring road-kills) was low compared to mammals. The opposite was found for aggregations of bird road-kills on the TCH as the scale of clustering was long and clustering intensity was high with respect to mammal road-kills. Variation in aggregation characteristics (i.e. clustering or dispersion) between taxa and road types may reflect different responses of animals to their habitat, spatial and temporal variability in habitat quality, or local terrain conditions that might facilitate or block movement across roads. An example in this study was the correlation between road-kills with factors such as roadside topography and adjacent habitat structure that we discuss later.

Species-specific traits of birds likely make them vulnerable to road-kill. This increased vulnerability of birds, for example, could be due to their high variability in foraging and flight behaviours. Massemin and Zorn (1998) suggested that local population density and flight behaviour of barn owls *Tyto alba* were related to high road-kills. We found distinct differences between the road-kill aggregation characteristics on the TCH and Parkway. The scale and intensity of road-kill clusters was markedly higher on the TCH compared to the Parkway. One possible explanation for the disparate patterns may stem from differences in road configuration and traffic flow on the two roads. Roads like the Parkway with many curves and low traffic speed might result in a more discontinuous pattern of road-kills (i.e. aggregations of kills on smaller spatial scales) compared to a high speed, linear motorway with little variation in speed where kill aggregations may encompass broader segments of road.

4.3. Analysis of factors explaining road-kill occurrence

The literature suggests that vehicle speed and traffic volume are probably the most important factors explaining wildlife collisions (Trombulak and Frissell, 2000). More recent road-kill studies of large and small vertebrates confirm these findings (Rolley and Lehman, 1992; Fahrig et al., 1995; Inbar and Mayer, 1999; Joyce and Mahoney, 2001). The results from our study show that roadside topography strongly influences small vertebrate road-kills and how two distinct road types can have different effects in terms of vertebrate mortality and their spatial pattern.

Raised or partially raised roads had the highest explanatory power for all species and taxa but red squirrels. The models predicted that raised roads resulted in fewer road-kills relative to level roads. Bird road-kills were less likely to occur on raised roads adjacent to forested habitat. Massemin and Zorn (1998) found the opposite as barn owls were more likely to be hit while crossing elevated sections of road near open fields in France. This might be expected given the flight behaviour of barn owls, typically low to the ground while hunting. Further, compared to open habitat, wooded sections of road may naturally force birds to fly higher above roads when crossing between forest edges (Bekker et al., 1995).

Traffic volume was not an important factor explaining road-kills. Disturbance, particularly road noise, generated from high-speed motorways like the TCH has been shown to affect birds, extending up to 2 km from an adjacent road (Van der Zande et al., 1980; Reijnen and Foppen, 1994; Reijnen et al., 1995), and also degrades the surrounding habitat (Ortega and Capen, 1999). Clarke et al. (1998) suggested that high volume roads may discourage badgers *Meles meles* from attempting to cross major roads in England. We believe the lack of association between road-kills and traffic volume in our study is likely explained by the alienating effect of the highway which primarily deters animal movements across the roadway.

There was a tendency for snowshoe hare and mammal road-kills to occur close to vegetative cover. These results accord with others reporting that concentrations of road-killed animals generally occur where wooded areas or cover adjoins both sides of a road (Hodson, 1962; Bellis and Graves, 1971; Bennett, 1991). It is believed that increased cover provides greater protection and security for animals approaching roads. However, the lack of cover and low connectivity may inhibit animal movement across roads particularly forest interior species (Bennett et al., 1994; Andreassen et al., 1996; Desrochers and Hannon, 1997; St. Clair et al., 1998), ultimately leading to reduced road permeability.

The proximity to safe passage (drainage culvert or wildlife crossing structure) below roads in our study area was positively correlated with snowshoe hare and mammal road-kills. In a previous study we showed that for many small- and medium-sized mammals drainage culverts can mitigate harmful effects of busy transportation corridors (Clevenger et al., 2001c). For forest-associated wildlife like most of the species we studied, these passages may provide a safe means of crossing open habitat created by road corridors (some places up to 100 m wide) and a vital habitat linkage. In a post-hoc analysis we found that snowshoe hare road-kills occurred where passages were located farther away than expected by chance (Mann–Whitney *U* test, $Z=1724$, $P=0.070$). This suggests that when passages are relatively far apart there may be a greater tendency for animals to cross above the road, whereas when in close proximity they are more likely to use them for safe passage.

Few studies have examined how fauna utilize centre medians with respect to roadside verges and adjacent habitat (Ferris, 1979; Adams, 1984). The role of centre medians in animal dispersal across transportation corridors has received even less attention (Forman and Alexander, 1998). The general belief is that medians function as safe areas or habitats for animals attempting to cross busy highways and facilitate successful crossings; however, road-kill rates may be affected by the pattern of wooded and grassy areas in the median strip (Bellis and Graves, 1971). Empirical studies have convincingly demonstrated that many forest-dwelling birds are reluctant to cross gaps in forest cover as narrow as 50 m (Desrochers and Hannon, 1997; St. Clair et al., 1998), a distance much narrower than most four lane highways. Thus, the width of gaps created by roads should influence their motivation or willingness to cross. We found that birds were more likely to be killed on roads with a centre median. Using playback experiments in the same study area, St. Clair (unpublished data) suggested that highway sections with forested medians were less significant barriers to forest birds than open grassy medians. The increased road-kill rate on divided sections of road, therefore, may be explained by a greater propensity for birds to cross the narrower gaps but at the same time increase their vulnerability to collisions with vehicles.

4.4. Conclusions

The trade off between management of roadways for landscape permeability and management for reduction of road-kills becomes apparent from our results. The two management objectives may be potentially conflicting. Effective road-kill reduction measures will limit travel of animals over roads, but in essence will reduce connectivity by restricting movements within a population. Providing ample opportunities for below road passage (e.g. culverts) may be a means of managing for both objectives. Earth berms, vegetation and drift fences are proven means of leading animals to below road passage entrances and preventing them from traveling over the road (Bekker et al., 1995; Huijser and Bergers, 2000).

The low road-kill rates indicated by our study do not imply that the roads have a negligible effect on small vertebrate populations in the Bow Valley as local populations may have already been depressed from decades of cumulative road-kills and crossing behaviours may have been selected out of the population. However, without adequate experimental design to obtain demographic data from control and treatment areas in relation to roads we will never be able to estimate how severe the impacts may be at the population level.

Based on the results of our study there are a series of mitigation measures that can be contemplated in future road planning projects. We recommend that simple below road passages (e.g. metal culverts) be installed at frequent intervals (150–300 m; see Clevenger et al., 2001c) to provide opportunities for animals of all body sizes to avoid crossing roads. Drainage culvert costs to highway infrastructure projects are small and the ecological benefits considerable. Cover should be provided close to passage entrances to enhance animal use. At curves in roads where visibility is reduced the verges should be widened to discourage crossings. However, along straight sections cover should extend as close to the road as permitted by road construction standards.

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