Relationships among grizzly bears, highways, and habitat in the Banff-Bow Valley, Alberta, Canada

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Abstract: Banff National Park and surrounding lands constitute one of the most developed landscapes in the world where grizzly bears (*Ursus arctos*) still survive. We examine the relationships among roads, grizzly bears, and their habitat in a protected area with low road density but dominated by a major transportation corridor and highway system. We examined grizzly bears' spatial response to roads, road-crossing behaviour, crossing-location attributes, and habitat and temporal patterns of cross-road movements. Grizzly bears used areas close to roads more than expected, particularly roads with low traffic volume (low volume). Habituated bears were closer to roads than wary bears. Males were closer to low-volume roads than females but crossed roads less than females during the berry season. Bears were more likely to cross low-volume roads than high-volume roads and were more likely to cross at points with higher habitat rankings. In addition, bears were more likely to cross high-volume roads when moving from areas with low habitat values to areas with high habitat values. Efforts to prevent loss of habitat connectivity across highways should involve maintenance of high-quality grizzly bear habitat adjacent to roads and should address the effects of traffic volume on the road-crossing decisions of grizzly bears.

Résumé : Le parc national de Banff et les terres avoisinantes représentent un des paysages les plus développés au monde dans lesquels les grizzlis (*Ursus arctos*) survivent toujours. Notre étude examine les relations entre les routes, les grizzlis et leur habitat dans une région protégée avec une faible densité de routes, mais traversée par un important corridor de transport et un axe routier majeur. Nous avons étudié la réaction spatiale des grizzlis aux routes, leur comportement de traversée des routes, les caractéristiques de leurs points de traversée et les structures spatiales et temporelles reliées aux déplacements de traversée. Les grizzlis utilisent les espaces près des routes plus que prévu, particulièrement celles qui ont peu de circulation (volume faible). Les ours habitués se tiennent plus près des routes que les ours méfiants. Les mâles se tiennent plus près des routes à faible volume de circulation que les femelles, mais ils traversent les routes moins volontiers que les femelles durant la saison des petits fruits. Les ours sont plus susceptibles de traverser des routes à faible plutôt que forte circulation et de traverser aux endroits où l'habitat est de plus grande qualité. De plus, les ours sont plus susceptibles de traverser des routes à forte circulation lorsqu'ils se déplacent d'un habitat de faible qualité à un autre de qualité supérieure. Dans le but de prévenir la perte de connectivité entre les habitats à travers les routes, il faudrait maintenir près des routes des habitats de qualité pour les grizzlis et étudier les effets du volume de la circulation sur les décisions des ours de traverser la route.

[Traduit par la Rédaction]

Introduction

Many landscapes are undergoing extensive and rapid change as a consequence of human activities (Hansson and Angelstam 1991; Houghton 1994). One of the major changes associated with landscape modification is the fragmentation and loss of habitat (Bennett 1999). Less conspicuous than other forms of habitat disturbance, linear features such as roads can have immense and pervasive impacts on wildlife populations (Forman and Alexander 1998; Trombulak and Frissell 2000). In an increasing number of landscapes, the regular movements of animals involve road crossings.

In view of their great mobility and extensive spatial requirements for survival, large mammalian carnivores are vul-

nerable to road effects (Noss et al. 1996; Woodroffe and Ginsberg 2000). Currently, many wide-ranging predatory species are a source of conservation concern worldwide (Landa et al. 1997; Breitenmoser 1998; Sanderson et al. 2002), and the need to protect them from the harmful consequences of roads is paramount (Kerley et al. 2002).

Landscape fragmentation due to human activities and blockage of wildlife movement in the Bow Valley are major stressors affecting the Banff National Park (BNP) ecosystem (Banff – Bow Valley Study 1996). The Trans-Canada Highway (TCH) is a potential barrier to large-mammal movement in the mountain parks and the significantly larger Central Rocky Mountain ecosystem. Given the national importance of the cross-country transportation corridor (McGuire and
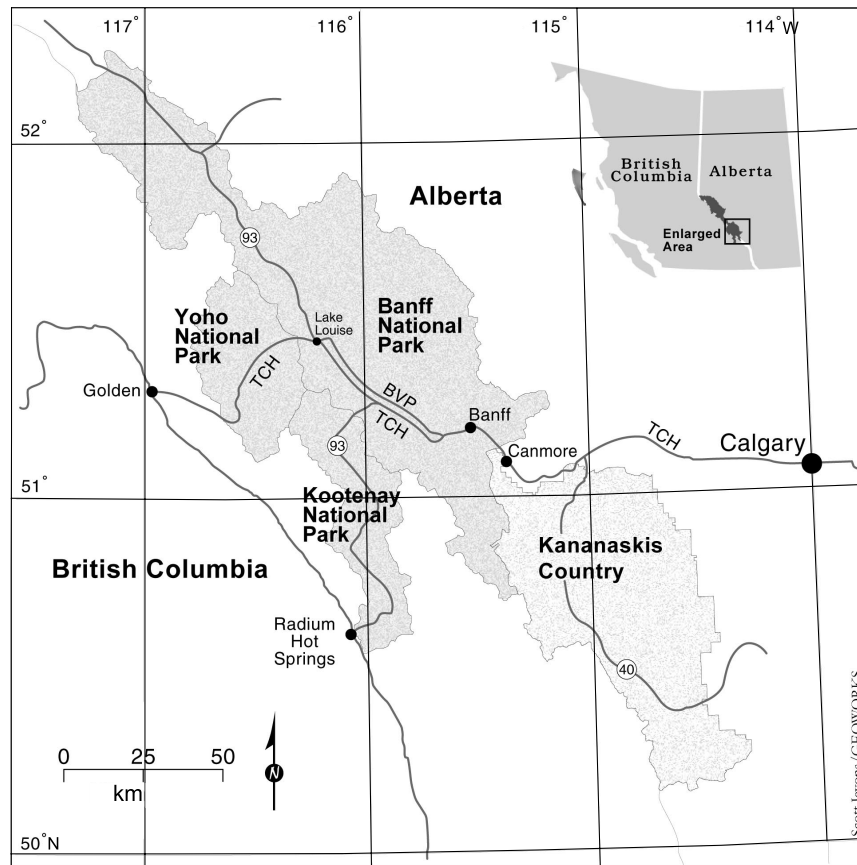
Fig. 1. Map of the study area and roads used to investigate grizzly bear (*Ursus arctos*) and road relationships in the Central Canadian Rocky Mountains. TCH, Trans-Canada Highway.

Morrall 2000) and popular attraction of BNP, highway traffic volumes are currently rising at a rate of 3% per year (Parks Canada Highway Service Centre, Calgary, Alta., unpublished data).

BNP and surrounding parklands constitute one of the most developed landscapes in the world where grizzly bears (*Ursus arctos*) still survive. However, their populations have been debilitated by the effects of human development and activity in their preferred lowland montane habitat (Banff – Bow Valley Study 1996; Gibeau et al. 2002). Reduced landscape connectivity and impeded movements due to roads may result in higher mortality, lower reproduction, and ultimately smaller populations and lower population viability. These deleterious effects have underscored the need to maintain and restore essential movements of grizzly bears and other large carnivore species across the TCH and other roads in the Rocky Mountain region (Parks Canada 1997; Carroll et al. 2001).

Over the last two decades, several authors have described the relationships between grizzly bears and roads (Archibald et al. 1987; Mattson et al. 1987; McLellan and Shackleton 1988; Kasworm and Manley 1990; Mace et al. 1996), but the Banff – Bow Valley is unlike the landscapes where these investigations took place. Previous studies examined grizzly bear response to roads in areas with a relatively dense road network, low traffic volumes, and (or) a long history of legal and illegal killing of grizzly bears and other wildlife. In this paper, we examine the relationships between roads, grizzly

bears, and their habitat in a protected area with overall low road density but dominated by a major transportation corridor and highway system. Specifically, we examine grizzly bears' spatial response to roads, road-crossing behaviour, crossing-location attributes, and habitat and temporal patterns of cross-road movements. We discuss the implications of our findings in the context of maintaining viable grizzly bear populations and sustainable transport systems in the Canadian Rocky Mountains.

Study area

Our research was located in the Central Canadian Rocky Mountains. The study area encompassed 11 400 km² of mountainous terrain located 50–180 km west of Calgary (population 800 000) in southwestern Alberta and southeastern British Columbia (Fig. 1). The area comprised mountain landscapes in BNP and Kootenay and Yoho national parks and adjacent Alberta provincial lands in Kananaskis County. We focused primarily on the TCH transportation corridor in the Bow Valley of BNP.

There are few places in the world where the intersection of transportation corridors with wildlife corridors is as significant as in the Canadian Rocky Mountain national parks. BNP and Yoho are the only national parks in North America to have a major transportation corridor bisecting them. BNP is the most heavily visited national park in North America, with over 5 million visitors per year. The highway is also a

major commercial motorway between Calgary and Vancouver. In 1998, annual daily traffic volume at the park east entrance was 14 600 vehicles per day and summer annual traffic volume was 21 500 vehicles per day (Parks Canada Highway Service Centre, unpublished data). Traffic volumes decrease as you travel west along the highway.

The TCH runs along the floor of the Bow Valley, sharing the valley bottom with the Bow River, several small towns (population <10 000) and several high-speed, two-lane primary roads that serve as arterial transportation routes. Traffic volumes on the primary roads (Highways 93 and 40 and Bow Valley Parkway) ranged between 2000 and 3000 vehicles per day in 1998. Several low traffic volume (low-volume), two-lane paved secondary roads complete the transportation system through most of the low-elevation valleys. There are few gravel roads in the study area. Hereinafter, we refer to the TCH as a high-volume road and to primary roads as low-volume roads. We restrict our analysis to interactions between grizzly bears and these two road types.

The geography of the central and eastern portions of the study area is dictated by the geology of the Front ranges of the Rocky Mountains. This geography influences the distribution and movement of wildlife in the park. The parallel north-northwest–south-southeast oriented limestone ridges and shale valleys create a landscape much more conducive to north–south than east–west movement. The few large valleys, the Bow Valley being the most prominent, that dissect the Front and Central ranges are recognized as critical, not only in maintaining regional-scale east–west movements of animals but also in providing a vital link between the valleys nested among the Front ranges of the park. For the same reasons, the Bow Valley is also one of the most important transportation corridors in the region.

Situated within the Front and Main ranges of the Canadian Rocky Mountains, the study area has a continental climate characterized by long winters and short summers (Holland and Coen 1983). The roads in our 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 (*Picea englemannii*), trembling aspen (*Populus tremuloides*), and natural grasslands.

Methods

Data collection

Grizzly bears in the study area were captured in foot snares or culvert traps as set out in the protocol of Jonkel (1993). Captured bears were immobilized with Telazol® following Taylor et al. (1989) and then ear-tagged and tattooed for permanent identification (Raine and Riddell 1991; Gibeau 2000). To determine the age of bears not known from birth, a premolar was extracted and sectioned (Stoneberg and Jonkel 1966). Bears were fitted with radio collars and allowed to recover before release. Our methods of capturing and handling grizzly bears met the standards set by the Canadian Council on Animal Care.

We obtained radiolocations from fixed-wing aircraft at about 1-week intervals (April–November) and by triangulating from the ground every 1–3 days using standard tech-

niques (Kenward 1987; Samuel and Fuller 1996). Rugged mountain topography in the study area limited our ground-based monitoring of bear movements to areas adjacent to roads and trails. Through testing with radio collars placed in known locations, our radiotelemetry error was estimated to be on average approximately 150 m. We plotted locations to ±100 m on a 1 : 50 000 ecological land classification map (Holland and Coen 1983) or 1 : 20 000 orthophotographs, referenced to a Universal Transverse Mercator coordinate and later converted to digital geographic information system (GIS) maps. Radiolocation data were also obtained from five grizzly bears equipped with global positioning system (GPS) collars between June and September 2001 (location error ≤15 m). The entire data set includes 14 998 locations collected between 1988 and 2001. Of these, 51% were obtained by ground telemetry, 20% by aerial telemetry, and 31% by GPS collars.

A total of 74 bears (42 females and 32 males) were radio-collared during the study, although various subsets of these individuals were used in the analyses based on sample size, their location relative to roads, and the constraints of the individual analyses. We defined seasons as preberry (den emergence to 15 July) and berry (16 July to den entry) based on major changes in the primary food plants consumed by grizzly bears (Hamer and Herrero 1983). We divided study-area roads into two classes based on amount of traffic: a high-volume road (TCH) and low-volume roads (Highways 93 and 40 and Bow Valley Parkway). In addition, we classified bears as either habituated or wary of human activity based on field experience and definitions given by Herrero (1985) to examine the potential effect of habituation on our results. There were no food-conditioned bears in our sample. All analyses were performed with and without locations from habituated bears included in the sample.

Because roads were used in triangulating to estimate study-animal locations, there were inherent biases when using ground-based telemetry data to examine animal distribution in relation to roads (White and Garrott 1990). The probability of receiving radio signals and obtaining fixes on animals decreases with increasing distance from roads. Therefore, data from animals found near roads tend to be collected more than those located further away. Aerial-based telemetry, if data are collected from all study animals within the study area systematically, is an effective technique that does not bias location data toward road networks. However, our collection of aerial-based telemetry data was only conducted once each week, resulting in low sample size. To minimize biases and maximize sample size in our analyses, we chose to use combined ground- and aerial-based radio-location data.

Spatial response to roads

Band analysis

We analyzed the distribution of grizzly bear locations within 3000 m of roads. Roads were buffered with successive 200 m wide parallel bands repeated to a distance of 3000 m on both sides of the road (i.e., 15 bands). To reduce autocorrelation in the data, we excluded locations that were obtained <10 h apart. We considered locations separated by 10 h or more to be independent because bears could travel between the most distant bands on either side of the road

during this time interval (McLellan and Shackleton 1988). For most analyses, locations were grouped by sex and stratified by season. However, in certain cases, data for male grizzly bears were not stratified by season due to low sample size. We assigned each location to a corresponding band buffering a road as well as calculating an exact distance from each location to the nearest road.

We used a χ^2 contingency table analysis to examine preference or avoidance of bands adjacent to the two road types for each sex–season category. Because we pooled data for this analysis, expected frequencies were determined based on the area of the bands surrounding the entire road type, not just within an individual's home range. We used Bailey's confidence intervals (Bailey 1980; Cherry 1996) to determine statistically significant relationships within each band.

By including bands to a distance of 3000 m from roads, our results may be biased towards higher use of bands closer to roads, owing to the inclusion of high-elevation areas in the outer bands (because roads tend to lie on valley bottoms). This bias may be more pronounced on low-volume roads that lie in valleys with narrower valley bottoms. To account for this bias, we repeated the analysis using only bands within 2000 m of roads and below an elevation of 2000 m. In both the 3000- and 2000-m analyses, we included the Cascade fire road as a control to determine whether the distribution of telemetry locations occurred as a valley bottom effect rather than a road-related effect because this road has no motorized traffic. Currently, the Cascade fire road functions as a hiking trail rather than a road.

Distance analysis

We generated random points within the same area used in the band analysis based on the number of radiolocations associated with each road type. Random points were generated based on a normal distribution with the same mean X and Y coordinates and standard deviations as the empirical data. We calculated distances from each empirical data point and from each random point to the nearest road. We compared distances between road types using t tests and between male and female grizzly bear locations and random points using a one-way ANOVA for each road type and season. We also tested for differences in distance to road between habituated and nonhabituated bears on low- and high-volume roads using two-way ANOVAs with sex and habituation state (i.e., habituated or wary) as class variables.

Index of road crossing

We examined the permeability of roads to grizzly bear movements using a crossing-index analysis (Brody and Pelton 1989; Lovallo and Anderson 1996; Apps 1999). We generated a movement path for each bear using the "point to polyline" option in the Animal Movement extension in ArcView® GIS (Hooge and Eichenlaub 1998; Environmental Systems Research Institute 1999). We determined crossing locations by intersecting the movement path of each bear with the digitized road layer and determined whether the crossing occurred on a low- or high-volume road. We described each animal's home range using minimum convex polygon home range estimates (Mohr 1947).

We calculated a crossing index for each bear based on the equation of Serrouya (1999) and the restrictions that we imposed below:

$$I_{ijk} = C_{ijk}/M_{ij}/L_{ijk}$$

where I is the crossing index for bear i during season j across a road of traffic volume k, C is the number of crossings made by bear i during season j across a road of traffic volume k, M is the total number of movements made by bear i during season j, and L is the length of road of traffic volume k in the home range of bear i during season j. A movement is defined as the straight-line distance between two consecutive points.

We also calculated road density within each individual home range as

$$D_{ik} = L_{ik}/A_i$$

where D is the density of a road of traffic volume k in the home range of individual i, L is the length of a road of traffic volume k in the home range of individual i, and A is the home range area of individual i. We calculated a second version of the crossing index not standardized by road length (C_{ijk}/M_{ij}) for comparison of road density effects between sex and season.

Criteria were developed to determine whether individual movements were suitable for inclusion in the crossing index calculation. We did this to maximize crossing location accuracy on the digitized road layer. We only included movements if the time between two consecutive locations spanning a road was <24 h and the movement was <10 km long. A minimum of 20 movements was needed to calculate a road-crossing index for a grizzly bear.

We examined the effect of sex and season on crossing indices separately for low- and high-volume roads. For low-volume roads, we used a two-way ANOVA with sex and season as the categorical variables. We log transformed crossing-index data to satisfy the assumptions of normality and heteroscedasity and to eliminate a correlation between mean and variance that occurred in our data. Only 11 bears (7 males and 4 females) crossed high-volume roads. As our sample size was small, we used nonparametric statistics (Mann–Whitney U test) to test for differences between sexes and seasons on high-volume roads. We tested for differences between low- and high-volume roads using a nonparametric Wilcoxon signed-rank test. To increase sample size, we pooled data for sex and season before performing this test. We ran simple linear regressions to determine the influence of road density on the crossing index not standardized by road length (C_{ijk}/M_{ij}, see above) for each sex–season category on low- and high-volume roads. We considered nonsignificant ($p > 0.05$) or negative regression coefficients to indicate that bears avoided roads (Lovallo and Anderson 1996). Finally, where sample size permitted, we repeated all analyses with habituated bears removed. We compared road-crossing indices between habituated and nonhabituated bears on low-volume roads during the berry season and preberry season using t tests.

Crossing-location attributes

To describe the attributes of grizzly bear crossing locations, we used the same two movement criteria as in the crossing-index calculation. We used logistic regression (maximum likelihood estimates) to predict the probability of bear road crossings as a function of landscape and road-related attributes. We used logistic regression because the explanatory variables that we used consisted of continuous and categorical data (Press and Wilson 1978). We chose variables to describe site-specific attributes of each estimated crossing location.

Seven explanatory variables (one categorical and six continuous) were used to describe crossing locations. Traffic volume was a categorical variable, as crossing locations were assigned to either low- or high-volume roads. Density of open vegetation (grass and shrubs) was a measure of the amount of open vegetation. We described the proximity to deciduous vegetation (stands of aspen trees) and we measured the distance to the nearest major drainage. Terrain ruggedness (TR) was calculated within a 750-m radius based on the following formula:

$$TR = (CDr)(AVr)/(CDr + AVr)$$

where CD is the density of contour lines within a given kernel, AV is the variability of eight cardinal aspects within a given kernel, and r is kernel size.

TR quantified the complexity of terrain (Nellemann and Thomsen 1994) and classified the landscape into gradient units (0–1) where the higher the value the greater the topographic diversity (Gibeau 2000). Habitat potential for grizzly bears within the national parks was derived from ecological land classification polygons (Holroyd and Van Tighem 1983). Habitat-quality values were calculated as described in Kansas and Riddell (1995) and ranged continuously from 0 to 10. Because habitat quality data were only available for the national parks, we performed two analyses: (1) using bear road-crossing locations within the national parks and including habitat quality as a predictor variable and (2) using bear road-crossing locations within the overall study area without habitat quality as a predictor variable. Elevation was derived from a 1 : 50 000 digital elevation model.

We compared the site-specific attributes of the empirical crossing locations with attributes of an equal number of random locations on the study area roads and with attributes of random locations on the national park roads. Random points were distributed along low- and high-volume roads in proportion to the length of the two road types in the given area. The dependent variable (crossing) was then coded as either cross (1) or no-cross (0, random point). We used empirical road-crossing locations and random locations for which we had a complete set of independent variables in the analyses. We analyzed the following subsets of data for the overall study area and within the national parks using logistic regression analysis: (*i*) all data, (*ii*) data for males, (*iii*) data for females, (*iv*) data for females during the preberry season, and (*v*) data for females during the berry season.

Data for males were not subdivided into seasons, owing to small sample size. Finally, all analyses were repeated with habituated bears removed from the sample of study area ($n = 368$) and national park ($n = 262$) road-crossing locations.

We used the log-likelihood ratio test (Hosmer and Lemeshow 1989) to determine significance of models to discriminate between crossing 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 predictor variable coefficients was based on χ^2 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 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 each model. Prior to performing the regression analysis, we tested potential explanatory variables for multicollinearity (Menard and Lewis-Beck 1995). When variables were correlated ($r > 0.7$), we removed one of the two variables from the analysis. Variable coefficients with a p value ≤ 0.10 were considered significant because predictors often ranked high in importance relative to other variables even when p values were between 0.05 and 0.10.

Habitat and cross-road movements

Risks to grizzly bears associated with crossing roads may be offset by benefits such as access to higher quality habitat or resources. We predicted that cross-road movements of bears would reflect a move towards higher quality habitat. We also predicted that this directional change would be more apparent on the busier, high-risk, high-volume roads than on low-volume roads. Cross-road movements were defined by two consecutive radiolocations on opposite sides of a road <10 km apart and obtained within 24 h. We compared the grizzly bear habitat potential values (Kansas and Riddell 1995) at the start location of each road-crossing movement with values at the end of the movements using paired *t* tests. We performed tests on data for low- and high-volume roads with data pooled for sex and season and by sex and season for each road type. We only used data within the national parks for this analysis.

Results

Spatial response to roads

Distance analysis

Grizzly bears were closer to low-volume than to high-volume roads regardless of sex or season (*t* tests, $p < 0.001$). There was no significant difference in distance to high-volume roads between random locations and the distribution of male or female grizzly bears during either season (both ANOVAs, $p > 0.05$).

Grizzly bear distribution in relation to low-volume roads during the preberry and berry seasons was significantly different from that expected by chance (ANOVA, $F_{[534]} = 141.3$, $p < 0.001$ and $F_{[544]} = 200.7$, $p < 0.001$, respectively). Post hoc tests indicated that there were statistically significant differences between random locations and both male and female grizzly bears and between male and female grizzly bear locations. For both seasons, male and female grizzly

bears were closer to low-volume roads than expected by chance; female bears were located further from low-volume roads than male bears (Tukey's HSD test, $p < 0.001$ for all comparisons) (Fig. 2). We found the same results when habituated bear radiolocations were removed from the sample. However, the locations of habituated bears tended to be closer to roads than those of wary bears (low-volume roads ANOVA, $F_{[3,3588]} = 42.77$, $p < 0.001$; high-volume roads ANOVA, $F_{[3,2182]} = 27.80$, $p < 0.001$). On low-volume roads, habituated females were closer to roads than wary females ($p < 0.001$) and habituated males showed the same trend relative to wary males, although it was not significant ($p = 0.098$). On high-volume roads, habituated males were closer to roads than wary males, wary females, or habituated females ($p < 0.001$ for all three pairwise comparisons).
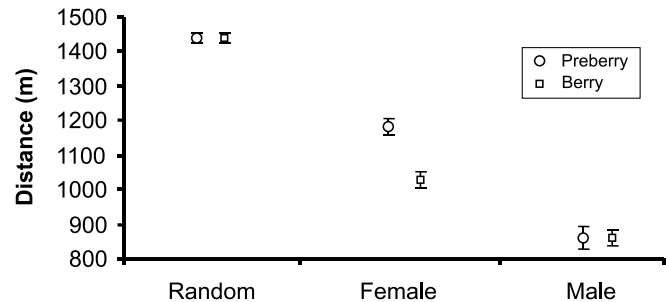
Band analysis

3000-m band analysis

Female grizzly bears used the Cascade fire road bands differentially during each season (all tests, χ^2, df = 14, $p < 0.050$). Analysis of confidence intervals revealed a general pattern of preference for bands within 800 m of roads, use of areas between 800 and 2400 m from roads in proportion to available, and avoidance of bands >2400 m (Fig. 3A). Males (with data combined for the two seasons) showed no preference for or avoidance of bands, perhaps due to the small sample size. During the preberry season, female grizzly bears were found in the area 400–800 m from roads disproportionately more than expected and less than expected in areas >2600 m from roads. In the berry season, female grizzly bears used areas <600 m from roads more than expected by chance and avoided bands >2400 m from roads.

Male and female grizzly bears used low-volume road bands differentially during each season (all tests, χ^2, df = 14, $p < 0.050$). Analysis of confidence intervals revealed a general pattern of preference for bands within 1000 m of roads, use of areas between 1000 and 2000 m from roads as available, and avoidance of bands >2000 m from roads (Fig. 3B). During the preberry season, female grizzly bears were found within 400 m of roads disproportionately more than expected and less than expected in areas >2200 m from roads. Male grizzly bears were found more than expected within 800 m of roads and less than expected >1800 m from roads. In the berry season, female grizzly bears used areas <600 m from roads more than expected by chance and avoided bands >1800 m from roads. Male grizzly bears were found within 1000 m of roads disproportionately more than expected and less than expected in areas >1600 m from roads.

There were significant differences in male and female grizzly bear use of high-volume road bands (all tests, χ^2, df = 14, $p < 0.050$). Male and female grizzly bears used areas within 1200 m of roads as available (Fig. 3C). There were slight differences in band use between seasons. During the preberry season, female grizzly bears tended to use areas 2000–2400 m from roads disproportionately more than expected and used areas >2600 m from roads less than expected. Male grizzly bears used areas within 2600 m from roads in proportion to their availability and areas >2800 m less than expected.

Fig. 2. Least squares mean (±SE) distance to low-volume roads for female and male grizzly bears during preberry (female, $n = 1202$; male, $n = 545$) and berry seasons (female, $n = 1279$; male, $n = 566$). Random locations ($n = 3605$) were generated within 3000 m of the road and based on a normal distribution with the same mean X and Y coordinates and standard deviations as the observed data.

2000-m band analysis

Female grizzly bears used the Cascade fire road bands differentially during each season (all tests, χ^2, df = 9, $p < 0.050$). Males (with data lumped for the two seasons) showed no preference for or avoidance of bands, perhaps because of the small sample size (Fig. 4A). During the preberry season, female grizzly bears were found between 400 and 600 m from roads disproportionately more than expected and less than expected in areas between 1400 and 1600 m from roads. In the berry season, female grizzly bears used areas <400 m from roads more than expected by chance and avoided bands between 1000 and 1800 m from roads.

Male and female grizzly bears used low-volume road bands differentially during each season (all tests, χ^2, df = 9, $p < 0.050$). Analysis of confidence intervals revealed a general pattern of preference for bands within 800 m of roads, use of areas between 800 and 1200 m from roads in proportion to available, and avoidance of bands >1200 m from roads (Fig. 4B). During the preberry season, female grizzly bears avoided areas between 800 and 1000 m from roads. Male grizzly bears were found more than expected between 200 and 800 m from roads and less than expected >1400 m from roads. In the berry season, female grizzly bears used areas <400 m from roads more than expected by chance and avoided bands between 1400 and 1600 m from roads. Male grizzly bears were found between 200 and 800 m from roads disproportionately more than expected and less than expected in areas >1200 m from roads.

Female grizzly bears used high-volume road bands differently than their availability in only two cases (χ^2, df = 9, $p < 0.050$). During the preberry season, female grizzly bears used the band between 600 and 800 m more than expected, and during the berry season, they used the band between 1200 and 1400 m less than expected (Fig. 4C). Males did not show preference for or avoidance of high-volume roads.

Index of road crossing

We calculated low-volume road-crossing indices for 18 grizzly bears (6 males and 12 females) during the preberry season and for 17 grizzly bears (5 males and 12 females) during the berry season. High-volume road-crossing indices

Fig. 3. Seasonal grizzly bear response to three road types: the Cascade fire road (A), low-volume roads (B), and high-volume roads (C). Avoidance (dark grey shading) or preference (light grey shading) of bands adjacent to low-volume roads was based on a χ^2 analysis of observed versus expected (based on area) distribution of grizzly bear locations within 200 m wide parallel bands 3000 m on both sides of the road. Areas used in proportion to availability are not shaded.
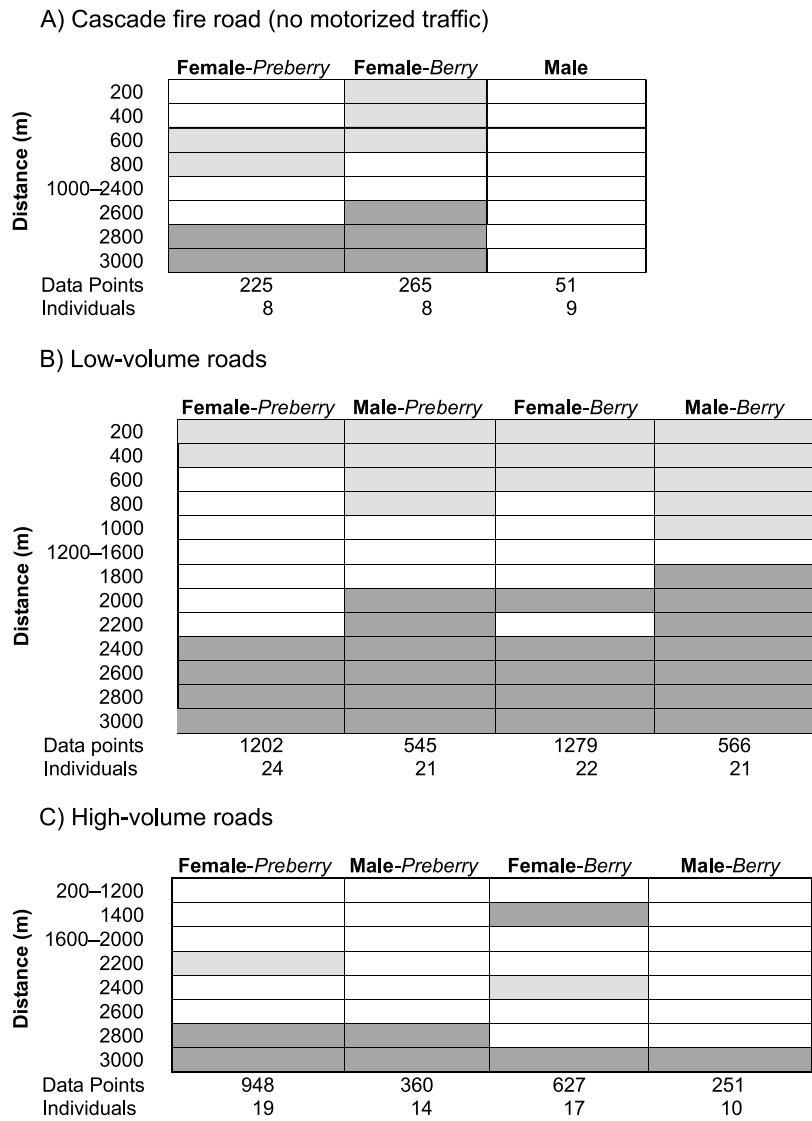

were calculated for 10 grizzly bears (4 males and 6 females) during the preberry season and 7 grizzly bears (2 males and 5 females) during the berry season (Table 1). A total of 789 grizzly bear road crossings were recorded between 1988 and 2001; 43% consisted of female grizzly bears crossing low-volume roads during the berry season. Conversely, only five crossings were made by male grizzly bears (0.6% of the total) on high-volume roads during the berry season.

Road-crossing behaviour on low-volume roads was influenced by sex and season (ANOVA, $r^2 = 0.87$, $F_{[3,31]} = 79.2$, $p < 0.001$). Sex ($F_{[1,31]} = 137.8$, $p < 0.001$), season ($F_{[1,31]} = 77.0$, $p < 0.001$), and the interaction between sex and season ($F_{[1,31]} = 84.4$, $p < 0.001$) all explained significant variation in the model. Male grizzly bears had significantly lower berry-season crossing indices than preberry-season crossing indices and lower indices than female grizzly bears during either season (Tukey's HSD test, df = 31, $p < 0.001$).

There was no effect of sex or season on road-crossing frequencies for bears on high-volume roads (all Mann–Whitney U tests, $p > 0.05$). Furthermore, we did not detect an effect of road type on crossing indices (Wilcoxon's matched pairs test, $n = 12$, $Z = 0.78$, $p > 0.05$). Seven of the 12 bears in this analysis had higher crossing indices on low-volume roads than on high-volume roads. Five bears had higher crossing indices on high-volume roads than on low-volume roads. However, with the exception of males during the berry season, all sex–season categories showed a trend toward greater mean crossing indices on low-volume roads.

For female bears, there was a significant (positive) relationship between berry-season crossing indices on low-volume roads and road density (Table 2). Marginally significant relationships were documented between female preberry-season and male berry-season crossing indices on low-volume roads and road density ($p < 0.10$). There were

Fig. 4. Seasonal grizzly bear response to three road types, the Cascade fire road (A), low-volume roads (B), and high-volume roads (C), for data below 2000 m in elevation. Avoidance (dark grey shading) or preference (light grey shading) of bands adjacent to low-volume roads was based on a χ^2 analysis of observed versus expected (based on area) distribution of grizzly bear locations within 200 m wide parallel bands 2000 m on both sides of the road. Areas used in proportion to availability are not shaded.

A) Cascade fire road (no motorized traffic)

B) Low-volume roads
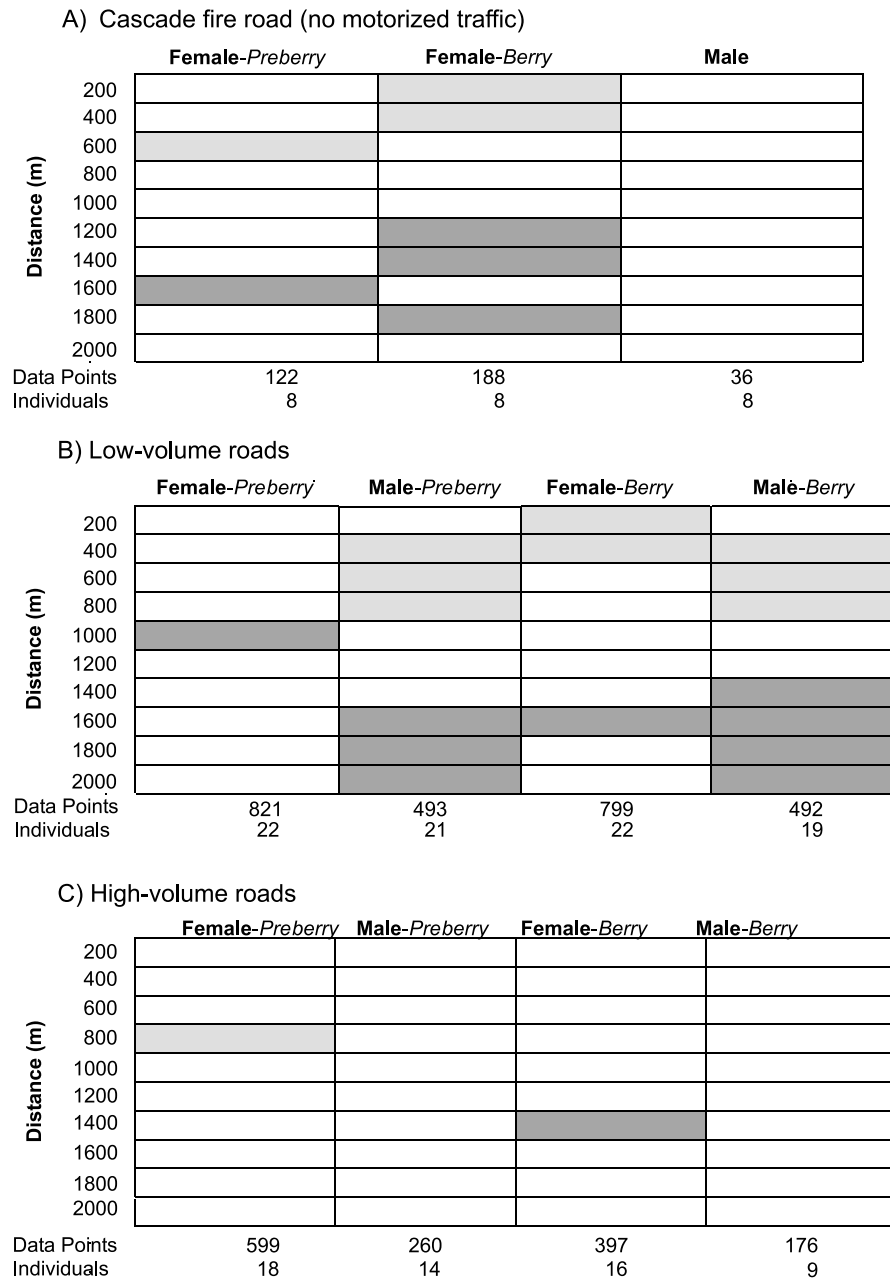
C) High-volume roads

no significant relationships between crossing indices on high-volume roads and road density, suggesting that bears avoided crossing high-volume roads. Removing habituated bears from the analyses did not affect the results. Furthermore, the crossing indices of habituated bears did not differ from those of nonhabituated bears during either the preberry ($t = 0.376$, df = 16, $p = 0.851$) or the berry season ($t = 0.105$, df = 15, $p = 0.366$).

Crossing-location attributes

We excluded elevation from the analysis of crossing-location attributes because of high correlation ($r > 0.7$) with

other predictor variables. All 10 logistic regression models describing crossing-location attributes were statistically significant ($p < 0.001$). Values of R^2 were low, from 0.049 to 0.162, and cross-validation classification rates were moderate to high, from 54.2% to 87.7% (median = 65.3%) (Table 3).

Overall, traffic volume was most important in explaining grizzly bear road crossings, ranking first or second in importance in 6 of the 10 models. Based on odds ratios, crossings were, on average, 80% less likely to occur on high-volume roads than on low-volume roads. The probability of bear crossings decreased going from low-volume to high-volume

Table 1. Summary of grizzly bear (*Ursos arctos*) road-crossing behaviour on two different road types in the Central Canadian Rocky Mountains from 1988 to 2001.

Season		High-volume roads		Low-volume roads	
		Females	Males	Females	Males
Preberry	No. of bears	6	4	12	6
	No. of road crossings	68	16	134	48
	Crossing index (m^{-1})	2.11×10^{-6}	1.02×10^{-6}	4.71×10^{-6}	1.62×10^{-6}
	±SE	5.71×10^{-7}	5.57×10^{-7}	1.21×10^{-6}	3.55×10^{-7}
Berry	No. of bears	5	2	12	5
	No. of road crossings	120	5	340	58
	Crossing index (m^{-1})	2.73×10^{-6}	7.87×10^{-7}	4.99×10^{-6}	1.98×10^{-9}
	±SE	1.56×10^{-6}	3.00×10^{-7}	1.35×10^{-6}	6.61×10^{-10}

Note: Crossing-index values are given as means for all individuals in each sex–season category and are calculated as $I_{ijk} = C_{ijk}/M_{ij}/L_{ijk}$ (see Methods).

Table 2. Relationship between crossing rate and road density for two road types within individual grizzly bear home ranges.

	Season	R^2	df	F	p
Low-volume roads					
Females	Preberry	0.24	1,10	4.488	0.060*
	Berry	0.29	1,10	5.470	0.041**
Males	Preberry	0.08	1,3	1.323	0.330
	Berry	0.45	1,4	5.046	0.088*
High-volume roads					
Females	Preberry	−0.20	1,5	0.003	0.957
	Berry	−0.25	1,3	0.189	0.693
Males	Preberry	0.31	1,2	2.321	0.267

Note: Male berry-season values on high-volume roads were not calculated because of the low sample size ($n = 2$); *, $p < 0.10$; **, $p < 0.05$.

Table 3. Results of logistic regression analyses of factors explaining grizzly bear road-crossing occurrence from five data sets.

	Study area[a]					National parks[b]				
	All data	Males	Females	Females, preberry season	Females, berry season	All data	Males	Females	Females, preberry season	Females, berry season
Traffic volume	−2	−3	−2		−2	−2	−1			−2
Proximity to deciduous vegetation	3	−4	3	3	3		−3		3	−4
Density of open vegetation	−1	−2	−1	−1	−1					
Proximity to major drainage	−4		−4	−2					−2	
Terrain ruggedness		1				−1		−1		−1
Habitat quality[c]						3	2	2	1	3
R^2	0.049	0.085	0.050	0.085	0.053	0.086	0.162	0.110	0.112	0.158
Cross-validation (%)	56.5	86.0	54.2	79.7	59.7	62.4	87.7	61.2	78.9	68.1

Note: Numbers indicate rank of importance of significant ($p < 0.10$) variables. Sign indicates influence on the odds ratio (negative decreases odds that the data point is a road-crossing location; positive increases odds that the data point is a road-crossing location). Model variance and validation results are provided.

[a]Study-area analysis includes data from the overall study area ($n = 789$ crossings).

[b]National parks analysis only includes crossings that occurred within the national parks ($n = 558$ crossings).

[c]Habitat not included in the study area analysis because of lack of habitat information outside the national parks (see Methods).

roads in all models. The amount of open vegetation was the most important variable determining the probability of bear crossings in the study-area analysis, ranking first or second in importance in all five models. In all significant models, the probability of crossings increased as the amount of open vegetation decreased, i.e., more crossings in more densely vegetated areas.

The amount of open vegetation was replaced by habitat quality as the most consistent predictor of crossings in the national park analysis. Habitat quality was a significant vari-

able in all five models and ranked first or second in importance in three of the models. The probability of crossing increased with increasing habitat potential in all five models. Grizzly bear crossings were explained by low terrain ruggedness in the national park analysis and primarily by female bears. The proximity to major drainages was significant in 4 of the 10 models. In each case, the probability of a crossing decreased as distance from drainage increased. This relationship appeared to be particularly important for females during the preberry season.

Habitat and cross-road movements

Males moved into areas of significantly higher habitat quality when crossing high-volume ($t = -2.26$, df = 63, $p = 0.027$) but not low-volume roads ($t = 0.24$, df = 141, $p = 0.810$). During the preberry season, females also moved into areas of significantly higher habitat quality when crossing high-volume roads ($t = -2.13$, df = 24, $p = 0.044$). All other sex and season categories were nonsignificant. Analyses performed without data from habituated bears showed the same results.

Discussion

Transportation infrastructure in western North America is a prominent and growing landscape feature and an obvious potential stressor on grizzly bear populations in terms of both habitat fragmentation and mortality (Forman et al. 2003). Grizzly bears are particularly vulnerable to road effects, owing to their need to travel widely to meet life requisites and their sensitivity to human disturbance (Weaver et al. 1996; Servheen et al. 1998). Consequently, road networks may be considered one important determinant of the status of grizzly bears as "threatened" in the United States (Servheen et al. 1999) and as a species of "special concern" in western Canada (COSEWIC 2002); nevertheless, the relationship between grizzly bears and highways has received little attention in the literature. The dearth of information is particularly evident in relation to high-speed, high traffic volume transportation corridors.

Our study is a first attempt to provide information on the interaction between grizzly bears and a major transportation corridor. We believe that this information is valuable on both a local scale and a broader geographic scale. In our study area, the long-term trend and prospects are for increasing traffic volumes. Thus, information describing grizzly bear interaction with local highways will aid land managers responsible for maintaining viable populations and transportation planners in charge of mitigating road effects on sensitive species. Because the literature lacks such information, our study will also provide useful information in other areas seeking to mitigate against the effects of such roads on local grizzly bear populations.

We found that grizzly bears tended to be closer to roads with low traffic volume than to those with high traffic volume. Other populations of bears have shown similar patterns of bear distribution. Black bears (*Ursus americanus*) in coastal North Carolina were found significantly farther from primary roads than from secondary roads immediately after crossing them (Brandenburg 1996). Similarly, grizzly bears in northwest Montana increased their distance to roads when

the roads opened after seasonal closures (Kasworm and Manley 1990). Busy roads may result in increased stress for individuals in close proximity to them. Northern spotted owls (*Strix occidentalis caurina*), for example, living close to forest roads experienced higher levels of a stress-induced hormone than owls living in areas without roads (Wasser et al. 1997). Thus, our results are largely intuitive given the mortality risks and the greater disturbance associated with busy roads. In general, wildlife tends to be less common near busy roads, effectively resulting in a road-avoidance zone that has been interpreted as largely due to traffic noise (Forman and Alexander 1998).

Our results indicated that the distribution of grizzly bears was influenced by gender. Several populations of grizzly bears show sex-related variation in habitat use adjacent to roads (Mattson et al. 1987; McLellan and Shackleton 1988; Gibeau 2000; Wielgus et al. 2002). In Yellowstone National Park (YNP), adult female and subadult grizzly bears suffered a greater reduction in habitat use due to the presence of roads than adult males, possibly because of competitive exclusion by dominant males (Mattson et al. 1987). We found that male grizzly bears were closer to low-volume roads than females, a pattern also reported for grizzly bears in the Selkirk Mountain ecosystem (Wielgus et al. 2002). In contrast, grizzly bears in the Flathead River Basin in southeastern British Columbia showed the opposite trend (McLellan and Shackleton 1988). McLellan and Shackleton (1988) predicted that in areas with steeper terrain than that found in their study area, males would be more likely to use productive low-elevation areas, which are closer to roads, while females would be restricted to high-elevation sites. Our results support this hypothesis, although we are unable to test whether the greater proximity of males to roads was a result of dominance hierarchy (males excluding females), mutual avoidance, or a means of females increasing their fitness. Adult females often select areas with a high degree of security for raising cubs (Gibeau 2000), which in some cases means avoiding males.

Previous work has shown significant differences in grizzly bear response to roads, trails, and human development (Tracey 1977; Mattson et al. 1987; Kasworm and Manley 1990; Mace et al. 1996). We found that grizzly bear spatial distribution differed relative to high- and low-volume roads. Both sexes were closer to low-volume roads than expected by chance but not to high-volume roads. Similarly, bears selected for areas close to and avoided areas distant from low-volume roads but not high-volume roads. Although our study contradicts previous findings (Harding and Nagy 1980; Archibald et al. 1987; Mattson et al. 1987; Kasworm and Manley 1990; Mace et al. 1996), it is noteworthy that these patterns only occurred on low-volume roads. BNP grizzly bears displayed similar behaviour toward a road with no motorized vehicle traffic (Cascade fire road) as toward low-volume roads. Thus, bear distribution relative to low-volume roads is probably a result of habitat associations rather than an attraction to low-volume roadsides. Our research suggests that grizzly bears in our study area utilize high-quality valley-bottom habitat adjacent to low-volume roads. Adjacent to high-volume roads, greater disturbance results in reduced affinity for roadside habitat, leading to a different pattern of grizzly bear distribution.

Several authors suggest that grizzly bears become accustomed to predictable occurrences (Herrero 1985; Jope 1985) including traffic (McLellan and Shackleton 1989), and habituation may permit some bears to exploit habitats close to roads, particularly if human use is spatially and temporally predictable (Tracey 1977; Jope 1985; McLellan and Shackleton 1989; Olson et al. 1990; Hellgren et al. 1991). We found that habituated grizzly bears were closer to roads than wary grizzly bears. Our results lead us to believe that bears use high-quality habitat near roads as they become habituated to highway traffic. On low-volume roads, where vehicle disturbance is less severe, bears adapt to the use of roadside habitat more readily, resulting in different patterns of distribution around the two road types. Unlike previous studies, bears in our study area were not hunted. Thus, the main disturbance from roads in our study area was traffic noise and other nonlethal encounters. Given the high traffic volumes in our study area, traffic noise is relatively constant and predictable and has no negative stimulus associated with it. Therefore, it is likely that bears learn to use habitat adjacent to roads.

The association or indifference of BNP grizzly bears to roads does not suggest that roads do not affect their movements. There is ample evidence that highways can limit bear movements in the Bow Valley and adjacent lands (Serruoya 1999; Gibeau 2000; this study). Although grizzly bears were found closer than expected to low-volume roads, they will not necessarily readily cross all road types or survive crossings. Our results indicate that grizzly bears were reluctant to cross high-volume roads like the TCH and crossings were generally associated with movements into better habitat. Low-volume roads were more permeable to grizzly bears than the TCH. Because grizzly bears are more likely to cross low-volume roads and because there are no mitigation measures on these roads, grizzly bear – vehicle collisions are more prevalent on low-volume roads (Benn 1998; Clevenger et al. 2002). Similar relationships between differential road permeability and incidence of large-mammal roadkills were found in Mikumi National Park, Tanzania (Newmark et al. 1996). Although permeability for grizzly bears is greater on low-volume roads, mortality is a concern and should be mitigated. Since 1981, nine grizzly bears have been killed on highways in our study, six on low-volume roads and three on high-volume roads.

Only one study has reported on grizzly bear response to roads in a protected area (Mattson et al. 1987). Grizzly bear habitat use in YNP did not differ significantly from expected during autumn; however, bears tended to avoid areas <500 m from roads in spring and summer. Two factors likely contribute to the differences between grizzly bear behaviour in YNP and BNP. The first is that although YNP is a heavily visited national park, it does not receive consistent high traffic volumes like BNP, and as a result, bears may not habituate to traffic noise as readily as the bears in our study area. The second explanation, which we believe to be more plausible, is related to the differing physiographical and human landscape characteristics of the two areas. The Central Canadian Rockies are rugged mountains ranging between 1400 and 3400 m in elevation with narrow, montane valley bottoms, whereas the YNP landscape is typified by more open, undulating terrain composed of extensive central plateaus

between 2000 and 2400 m (Knight and Eberhardt 1985). The lower elevation montane ecozone is prime grizzly bear habitat in BNP (Gibeau 2000) but is dominated by human development, including the TCH. Therefore, grizzly bear access to high-quality habitat in BNP is low relative to that in the YNP ecoregion. This suggests that bears are likely forced into close cohabitation with road systems and human development and thus find road avoidance more difficult.

Our study on grizzly bears and Serrouya's (1999) study on black bears are the first to examine the effects of a major transportation corridor on the movements of bears. The TCH has peak traffic volumes of over 25 000 vehicles per day during summer (Parks Canada, unpublished data). Brandenburg (1996) reported black bear behaviour relative to roads with traffic volumes up to 10 000 vehicles per day. To our knowledge, no other studies have examined the behaviour of large carnivores in relation to highways with traffic volumes in excess of 10 000 vehicles per day. For both road types in our study area, grizzly bears crossed roads in areas where habitat quality was high. However, when grizzly bears crossed high-volume roads, they moved into areas of higher quality habitat. This pattern did not occur on low-volume roads, suggesting that there is a trade-off between the risks of crossing roads and benefits in terms of access to higher quality habitat. Furthermore, road crossings were more likely to occur in areas where dense vegetation was adjacent to roads. Bear preference for cover when moving near or crossing roads has been observed elsewhere (McLellan and Shackleton 1989; Brandenburg 1996). Cover may be an important requirement for successfully crossing roads and providing security from road-related disturbance.

Several studies have examined the effects of traffic volume and road density on road-crossing indices of large carnivores (Brody and Pelton 1989; Beringer et al. 1990; Lovallo and Anderson 1996; Serrouya 1999). Most have shown a negative influence of traffic volume on road-crossing indices; however, Serrouya (1999) found no effect of road type on the crossing indices of black bears in BNP. Similarly, we found no significant effect of road type on the crossing indices of grizzly bears, although, with the exception of males during the berry season, all sex–season categories showed a trend toward greater crossing indices on low-volume roads. Furthermore, crossing indices were positively correlated with road density for low- but not high-volume roads. Although the latter result may occur due to low sample size, the pattern suggests that bears avoid crossing high- but not low-volume roads.

We find it difficult to explain why male grizzly bears cross low-volume roads less than females during the berry season, even though they are found closer to them, which was the main result of the crossing index analysis. One possibility is that when the breeding season is over, males move less and are therefore less likely to cross roads. Nonetheless, we believe that the results of the three major analyses presented in this paper (spatial distribution, crossing attributes, and crossing indices) taken together strongly indicate that grizzly bear interactions with roads are negatively influenced by traffic volume. Serrouya (1999) also found that an alternative analysis technique (a simulated-movement model) provided stronger results than a crossing-index analysis for explaining black bear movements relative to roads.

Two patterns emerged from our study: the avoidance of high-volume roads in a major transportation corridor and the importance of high-quality habitat in determining grizzly bear movement decisions relative to roads. Our study examined grizzly bears movements in relation to highway traffic volumes much higher than those considered in the past. Further, low-volume roads in our study area have traffic volumes that exceed those on the busiest roads in most previous studies. Nonetheless, we found a clear dichotomy in the behaviour of bears relative to high- and low-volume roads. The reduced cross-valley permeability caused by the presence of the TCH may result in harmful population effects in view of the great mobility and extensive spatial requirements of grizzly bears (Forman et al. 2003). Because the TCH only acts as a partial barrier (or filter), it is unlikely that isolation effects will occur in this population. However, the cumulative effects of human use and development and railways and highways within the Bow Valley can limit access to important habitats, thereby negatively affecting grizzly bears in the BNP ecosystem (Gibeau et al. 2002).

Given the negative effect of traffic volume described in this paper, and the fact that traffic volumes continue to increase on the TCH, we suggest that wildlife managers and transportation planners in the Bow Valley adopt a proactive approach to their management decisions. We suggest that efforts to prevent loss of habitat connectivity across the TCH should include maintenance of high-quality grizzly bear habitat adjacent to roads and should address the effects of traffic volume on the road-crossing decisions of grizzly bears. Furthermore, efforts made to increase the permeability of roads to grizzly bears must take into account and mitigate for collisions with motor vehicles as a potential source of mortality and the cumulative effects of human use on grizzly bear movement.

Highways affect wildlife by increasing mortality and reducing movements and ultimately landscape connectivity. These factors do not affect populations equally. The effects of road-related mortality on local populations may be seen as early as in one or two generations, while loss of connectivity may take several generations to manifest (Forman et al. 2003). Given the continuing increase in highway traffic and elevated risk of grizzly bear mortality on these roads, we believe that continuous highway fencing and wildlife passages will be the most effective mitigation (see Clevenger et al. 2002) for maintaining a viable grizzly bear population in BNP and the significantly larger Central Rocky Mountain ecosystem.

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