

## 6.5 MODELLING THE SPATIAL DISTRIBUTION OF HUMAN-CAUSED GRIZZLY BEAR MORTALITIES IN THE CENTRAL ROCKIES ECOSYSTEM OF CANADA

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### ABSTRACT

We examined the spatial patterns of 297 human-caused grizzly bear mortalities from 1971 to 2002 within the Central Rockies Ecosystem (CRE) of Canada to explore relationships between mortalities and variables reflecting human development, terrain, and vegetation. Using logistic regression, we modelled the distribution of grizzly bear mortalities based on local landscape attributes as well as examining variation among demographic status, seasons, and mortality type. Grizzly bear mortalities were concentrated in 3 main regions of the CRE: (1) Lake Louise; (2) Banff town site; and (3) Alberta Provincial lands near the Red Deer River. We found no evidence for environmental differences in mortality locations between sexes or season, while sub-adult male and legal harvest mortalities were more dispersed than other mortalities. Models describing the relative risk of mortality were positively associated with human access, water, and edge features, while negatively associated with terrain ruggedness and greenness indices. Model predictions fit well with independent data. Overall, relatively little of the landscape was secure from human-caused mortality for grizzly bears. This would be most directly remedied by controlling access.

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### INTRODUCTION

Large carnivores are particularly vulnerable to extinction because of their low density, high trophic level, and low reproductive rates (Russell et al., 1998; Purvis et al., 2000a; 2000b). Anglo-European settlement of previously ‘unoccupied’ lands together with increasing human density have been well correlated with historic carnivore extirpations (Woodroffe, 2000; Mattson and Merrill, 2002). Currently, however, effective land-management policies can be important determinants of population persistence (Channell and Lomolino, 2000; Linnell et al., 2001; Homewood et al., 2001). For North American grizzly bears, *Ursus arctos*, populations and distributions have been substantially reduced in the past century (Mattson and Merrill, 2002). Much of this loss has occurred in the contiguous United States and southern Canada (McLellan, 1998) and can be explained by historic conflicts between humans and bears reflecting pioneering attitudes and corresponding to two of Diamond’s (1989) evil quartets of extinction: overkill and habitat destruction/fragmentation.

Much research on grizzly bear conservation has focused on habitat selection and the spatial distribution of grizzly bear habitats using radiotelemetry data (e.g., Mace et al., 1996; 1999; Waller and Mace, 1997; Nielsen et al., 2002). Common factors used to describe bear occurrence include landcover or vegetation type (Mace et al., 1996; McLellan and Hovey, 2001), distance to streams and forest edge (Nielsen et al., 2002; Theberge 2002) vegetation indices from satellite data, such as greenness (Mace et al., 1999; Stevens, 2002), and terrain ruggedness (Theberge, 2002; Naves et al., 2003). Although substantial information on the spatial occurrence of bears exists, relatively little has been done to examine how spatial factors, especially human-related features, influence human-caused grizzly bear mortality in local populations (see however, Johnson et al., 2005; Mattson and Merrill, 2004). It is well accepted that survival, particularly of adult females, is the most important factor shaping population growth and long-term viability of grizzly bear populations (Wiegand et al., 1998; Pease and Mattson, 1999; Boyce et al., 2001; McLoughlin et al., 2003). Given the threatened status and/or nature of many remaining grizzly bear populations, including those in the Central Rockies Ecosystem (McLellan, 1998), the identification of mortality sinks (Knight et al., 1988) is crucial to the future conservation of grizzly bears. Mortality risk maps may be useful for describing habitat-based



population viability (Boyce, 2002) or the identification of bear habitats and core areas with high conservation value based on multidimensional habitat models of survival and reproduction (Naves et al., 2003). Although methods are well developed for survival modelling (Cox and Oakes, 1984), most areas of current grizzly bear range lack the required information on individual exposure and death. Alternative approaches that make use of ad hoc government mortality records are required. Development of regional spatial mortality risk models for grizzly bears would be an important contribution to conservation.

Grizzly bear populations within Canada, although not as reduced as within the contiguous United States, still face substantial pressures from habitat degradation and reduced population growth rates caused from excessive mortality (McLoughlin et al., 2003). Currently, only 37% of the 3.5-million-km<sup>2</sup> grizzly bear range is considered secure, with the remaining 63% considered vulnerable (Banci et al., 1994). Risks associated with these vulnerable populations are the expansion and development of resource extraction activities, including oil and gas exploration and development, timber harvesting, and mining. Previous research on human-caused grizzly bear mortality has shown a strong relationship between bear mortalities and roads (McLellan, 1989). As resource extraction activities enter an area, initially without much access, road construction provides entry for hunters, poachers, and settlers, the major cause of grizzly bear mortality (McLellan, 1989). Even in 'pristine' landscapes such as national parks where grizzly bears are protected from hunting, as much as 100% of known adult grizzly bear mortalities occurred within 500 m of roads or 200 m of high use trails (Benn and Herrero, 2002). Likewise, examinations of survival and mortality in the Greater Yellowstone Ecosystem revealed the highest risk of mortality for grizzly bears in areas of high road density and for those animals experiencing repeated management actions (Boyce et al., 2001; Johnson et al., 2005). Most often, researchers have focused on habitat selection and assumed that the identification of areas most frequently occupied by animals represent high quality habitats or contribute to fitness (Garshelis, 2000). In certain circumstances, however, areas frequented by animals and therefore identified as 'high' quality habitat within habitat models, can be considered attractive sinks where risk of mortality is high (Delibes et al., 2001; Naves et al., 2003). Identifying attractive sinks as high quality habitat would be misleading for management and conservation action. Research that identifies mortality sinks, or the opposite secure high-quality sites, as it relates to human features, terrain, and vegetation, is important if our goal is to maintain viable future populations of grizzly bears.

In this paper, we develop predictive models and maps that describe the distribution of human-caused grizzly bear mortalities for the Alberta and Yoho National Park portions of the Central Rockies Ecosystem of southern Canada. Our goal was to understand, through modelling, the relationships among bear mortality locations and landscape-level physiographic and human variables. More specifically, we were interested in: (1) examining the spatial density of grizzly bear mortalities; (2) evaluating possible differences in the physiographic attributes of mortality locations relative to demographic status, season, and mortality type; and (3) developing predictive models that estimate the relative probabilities of bear mortality (risk) given multi-variable combinations of physiographic variables. Our working hypothesis is that grizzly bear mortalities are related to factors describing human accessible habitats in those locations where bears are likely to frequent. Mattson et al. (1996a; 1996b) conceptualises this as the frequency of contact between bears and humans. At increasingly larger spatial and temporal scales, however, the lethality of contact can differ based on jurisdictional boundaries and temporal changes in management regime (Mattson et al., 1996a; 1996b; Mattson and Merrill 2002). We attempt to examine spatial expressions of these concepts in the Central Rockies Ecosystem of Canada using empirical modelling of grizzly bear mortality locations, animal use locations, and geographic information system (GIS) data typical of most grizzly bear habitat models.

## STUDY AREA

This study encompassed a 29,264-km<sup>2</sup> area of the Central Rockies Ecosystem (CRE) in southern Alberta and a small portion of adjacent British Columbia, Canada (Figure 1). This study area encompasses a portion of the known distribution of grizzly bears in western Canada. This area included Banff and Yoho National Parks and an Alberta Provincial area south of Banff referred to as Kananaskis Country. The area was bordered to the west by the Continental Divide and Yoho National Park, being no further than 117.0°W longitude. The northern boundary was primarily along Highway 11 and occurred south of 52.5°N latitude.



The southern border was at latitude 50.0°N, while the east border was irregular in shape, but no further east than 114.0°W longitude. Legal harvest of grizzly bears, through a limited entry spring hunt since 1988, occurred in the areas outside of Banff and Yoho National Parks and Kananaskis Country (Figure 1). Mountainous terrain dominated the study area with elevations varying from 839 m along the North Saskatchewan River at Rocky Mountain House to 3,588 m along the Continental Divide. Given a strong gradient in elevation, a diverse array of local ecosystems and plant communities existed, but most generally could be divided into the following 5 ecoregions: (1) alpine; (2) sub-alpine; (3) upper boreal-cordilleran; (4) aspen parkland; and (5) montane.

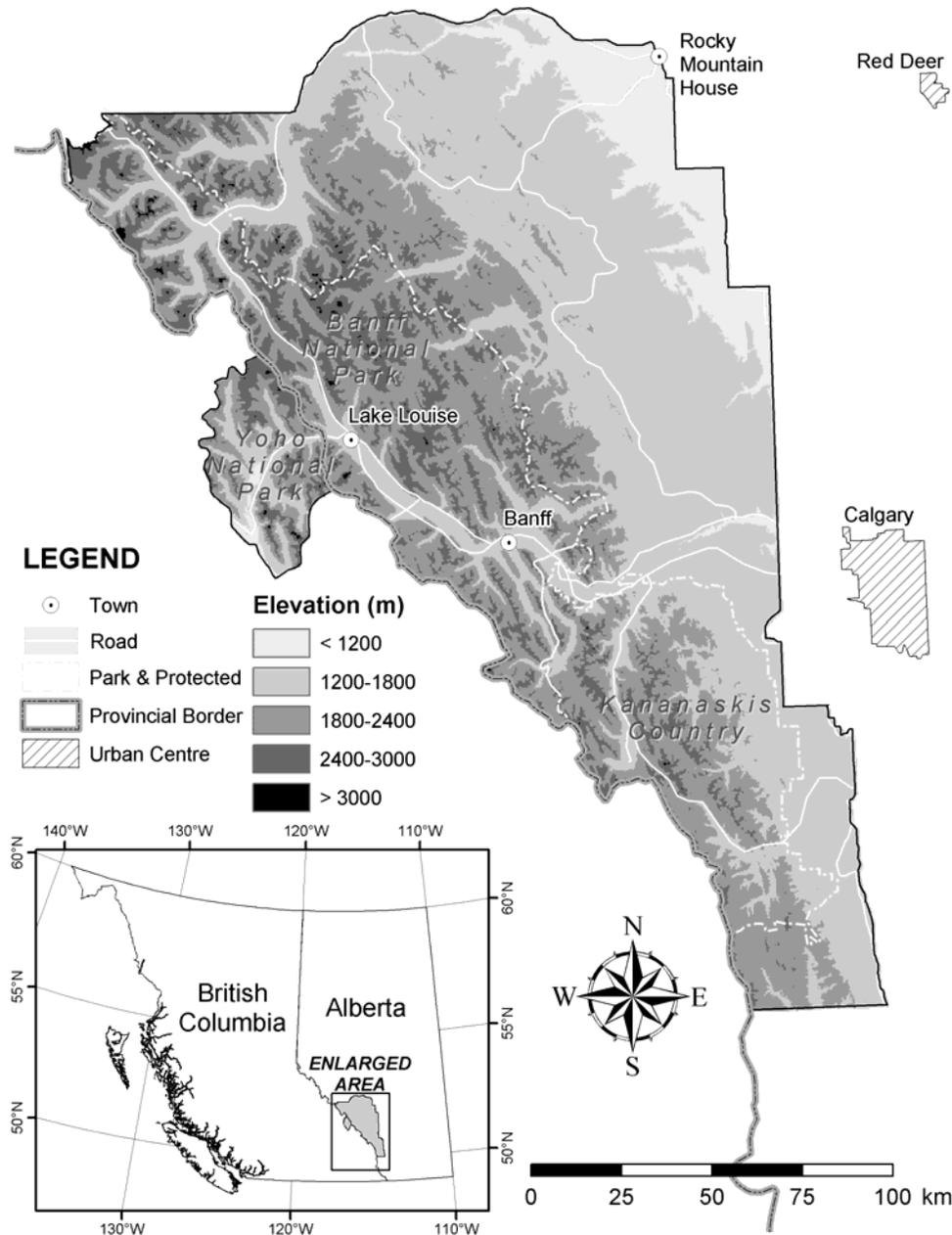


Figure 1. Study area map depicting elevation, study area boundary, Province border, places, and general location within Alberta and British Columbia, Canada (small inset map in lower left corner).



## METHODS

### Mortality location data

We collected grizzly bear mortality information across the CRE for a 32-year period from 1971 to 2002. Mortalities were defined as both dead bears and those bears translocated a sufficient distance to be considered eliminated from the population. For each mortality record, the location (UTM coordinates), accuracy of location, month, year, sex, age, and cause of mortality were obtained from National Park and Provincial management records (Benn, 1998; Benn and Herrero, 2002). However, because locations of mortalities in Alberta were provided at the scale of the township, and some mortalities in the National Parks were imprecise or missing, persons involved with the mortality event were interviewed to associate specific coordinates on a map and locations were then digitised into a GIS. For spatial mortality models, we used 279 accurate and reasonably accurate locations that were associated with human-caused events. Bear mortalities from human causes were classified into 2 classes: (1) legal harvest; and (2) non-harvest/other (self-defense, First Nation, accidents, railroads, highway, problem wildlife, research, and translocation).

### GIS (spatial) predictor variables

We generated 7 geographical information system (GIS) layers that were related to land cover, terrain, and humans. Land cover was estimated from Landsat TM satellite imagery dated from 1995 to 1998 and occurring at a 30-m pixel resolution. Land cover was initially classified into 9 classes: conifer forest, deciduous forest, shrub, avalanche, grass, cropland, ice/snow, rock/bare soil, and water (Wierzchowski, 2000). This map was further simplified by reclassifying the image into 5 more general land cover categories. These reclassified categories were conifer forest, deciduous forest, shrub (shrub and avalanche), grassland (grass and cropland), and non-vegetated areas (ice/snow, rock/bare soil, and water). From the classified land cover imagery, we further derived a grid (30-m pixel) representing the distance (km) to edge of any nearest land cover.

Using the same satellite imagery, we derived a greenness index based on a tasselled-cap transformation of the Landsat TM bands (Crist and Ciceron, 1984), which has been found to relate to leaf area index (LAI) and vegetation productivity (White et al., 1997; Waring and Running, 1998). Greenness has previously proven useful for identifying grizzly bear use in mountainous regions (Manley et al., 1992; Mace et al., 1996; 1999; Gibeau et al., 2002; Nielsen et al., 2002; Stevens, 2002), and as such has been recognized as a surrogate of grizzly bear habitat quality (Stevens, 2002). Using hydrographic GIS data, we also derived a 30-m grid that represented the distance (km) to any nearest water feature (water body, permanent stream, intermittent stream, indefinite stream). As a final distance metric, we calculated, again in a 30-m grid, the distance (km) to nearest linear human use feature (motorized or non-motorized), but did not include exploratory seismic lines that are common to areas outside of the Parks. To characterize terrain, we generated a terrain ruggedness index (TRI) within 300-m circular moving windows, as previous examinations have found this scale to be an important predictor of bear occurrence (Theberge, 2002).

## DATA ANALYSIS

### Spatial densities of grizzly bear mortalities

To qualitatively examine spatial patterns and concentrations of grizzly bear mortalities, we used 3 separately scaled moving windows to calculate the total density of mortality locations in a GIS. These moving window analyses corresponded to a scale of, (1) 520-km<sup>2</sup> (12,869-m radius) or the estimated average multi-annual 95% fixed kernel home range for female grizzly bears in the CRE (Stevens, 2002); (2) 900-km<sup>2</sup> (16,929-m radius) or the approximated lifetime home range of a female grizzly bear in Yellowstone (Blanchard & Knight, 1991); and (3) 1,405-km<sup>2</sup> (21,153-m radius) or the estimated average multi-annual 95% fixed kernel home range for male grizzly bears in the CRE (Stevens, 2002). All human-caused mortalities over the past 32 years were summed within moving windows and applied to 100-m pixels (1-ha grid) in a GIS map. All pixels with a mortality density of 0 were qualitatively considered secure sites, while those exceeding 31 mortalities ( $\geq 1$  mortality/yr) were qualitatively considered high mortality zones.



## Mortality differences among demographic status, season, and mortality type

We used logistic regression to assess relationships between landscape attributes of mortality locations (GIS predictor variables) and the categories of demographic status, season, and mortality type (response variables). Sex was contrasted for either female (1) or male (0) observations, while for sex-age class composition, we tested for sub-adult (3-5-yr-old) male mortalities (1) versus all the other (0) mortalities (e.g., young, adult, and sub-adult females). To examine whether seasonal differences were present, we compared mortalities that occurred during the berry season (1) with those mortalities that occurred outside of the berry season (0). We defined the berry season to be the period from 1 August to 31 October. During this time, grizzly bears in the region forage on Canada buffaloberry *Shepherdia canadensis* and numerous species of blueberry and huckleberry *Vaccinium* spp. (Hamer and Herrero, 1987; Hamer et al., 1991; Nielsen et al., 2003). Finally, we examined whether environmental differences existed in mortalities associated with legal harvest locations (1) compared to other human-caused mortalities (0) outside of protected areas.

## Random versus mortality locations- mortality distribution models

To characterize the landscape within the defined study area, we generated a sample of random (2-dimensional uniform distribution) locations with a sampling intensity of 1 point per 5-km<sup>2</sup> ( $n = 5,852$ ). These random landscape locations (0) were contrasted with human-caused, mortality locations (1) using an availability-presence design with the following log-linear form:

$$w(\mathbf{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k),$$

where  $w(\mathbf{x})$  represents the relative mortality distribution function (low to high mortality rank) and  $\beta_i$  the mortality coefficient estimated from environmental predictors  $x_i$  (Manly et al., 1993). Coefficients for the model were estimated using logistic regression. A global mortality distribution model representing all recorded mortalities was developed along with specific models for significant demographic status, season, and mortality type classes identified as significant in the previous section.

To validate our models, we partitioned mortality data prior to model building into a model-training (80%) and model-testing (20%) data set. Model-training data and random (pseudo-absences) locations were used to develop model coefficients, while model-testing data were used for within sample independent validation. Using the test data, we examined the predictive capacity of the model (validation) by comparing model predictions to the observed number of withheld mortalities (Boyce et al., 2002).

## Radiotelemetry versus mortality locations- the mortality risk model

Because the previous comparison between random and mortality locations does not consider the conditional nature of the mortality process (i.e., bears can only be killed where they are present, not necessarily all [random] locations), we also used logistic regression to contrast the location of grizzly bear mortalities with sites used by grizzly bears. We determined grizzly bear use by collecting 3,089 VHF radiotelemetry locations from 60 sub-adult and adult (35 female: 25 male) grizzly bears between 1994 and 2001. Similar methods were used for developing a mortality risk model as those in the previous section with the distinction being that radiotelemetry (0), not random locations, were contrasted with mortality (1) locations. For this analysis, all mortalities located outside the 100% minimum convex polygon (MCP) home range of individual radio-collared grizzly bears were excluded. We interpreted coefficients from the mortality risk model to represent those areas where grizzly bears are likely to die given that they selected particular habitats and resources (a form of conditional probability not satisfied with a comparison of random locations). Finally, we compared the ranked predictions of mortality distribution model with the mortality risk model using a weighted Kappa ( $\hat{K}_w$ ) statistic (Monserud and Leemans, 1992; Næsset, 1996). We consider Kappa values greater than 0.75 to indicate very good to excellent agreement (1.0 is perfect), while values between 0.4 and 0.75 indicate fair to good agreement, and finally values less than 0.4 to indicate poor agreement (Landis and Koch, 1977).



## RESULTS

### Spatial densities of grizzly bear mortalities

Regardless of the scale examined, grizzly bear mortalities were concentrated within 3 regions of the Alberta study area; (1) Lake Louise; (2) Banff town site; and (3) Alberta Provincial lands near the Red Deer River northwest of Calgary (Figure 2). For the 900- and 1405-km<sup>2</sup>-scales, mortality densities within moving windows exceeded 31 mortalities for the above 3 identified areas, equivalent to  $\geq 1$  mortality event/year and qualitatively considered a high mortality zone. At the 520-km<sup>2</sup>-scale, only Lake Louise stood out in having more than 31 mortality events, although a very small area west of Banff also showed high mortality. Total area occupied in a high mortality zones ranged from 1.4% at the 520-km<sup>2</sup>-scale to 13.2% for the 1,405-km<sup>2</sup>-scale (Table 1). In contrast, the total area considered secure from human-caused mortalities (no recorded mortality events) ranged from 7.2% for the 1,405-km<sup>2</sup>-scale to 23.9% for the 520-km<sup>2</sup>-scale (Table 1).

However, 22% to 32% of secure habitat was in areas of non-habitat (Figure 2, Table 1) suggesting an even more restricted extent for security over the past 32-years.

Table 1. Percent composition of qualitatively defined secure (0 recorded mortalities), secure but non-habitat (rock, snow, ice, water), and high mortality density sites (>31 mortality events) for the Central Rockies Ecosystem of Canada. Mortality density estimates were based on moving windows of three scales, the first relating to local female home range sizes (520-km<sup>2</sup>), the second Yellowstone lifetime home range sizes (900-km<sup>2</sup>), and third local male home range sizes (1,405-km<sup>2</sup>).

Variable	Percent of Landscape		
	520-km <sup>2</sup>	900-km <sup>2</sup>	1405-km <sup>2</sup>
Secure	23.9	13.9	7.2
Secure, non-habitat	21.8	23.2	32.0
High mortality density	1.4	3.8	13.2

### Mortality differences among demographic status, season, and mortality type

The landscape features at mortality locations for male and female grizzly bears were not differentiated by logistic regression ( $\chi^2 = 8.38$ ,  $p = 0.497$ , d.f. = 9) (Table 2). Conversely, we found strong differences between sub-adult males and other sex-ages. The sub-adult male model was significant overall ( $\chi^2 = 27.77$ ,  $p = 0.001$ , d.f. = 9) with distance to access feature and edge variables significant. Generally, sub-adult male mortalities were further from edges than other sex-age classes (Table 2). In addition, sub-adult male mortalities were more likely to be further from human access features than adult, young, and sub-adult female mortalities.



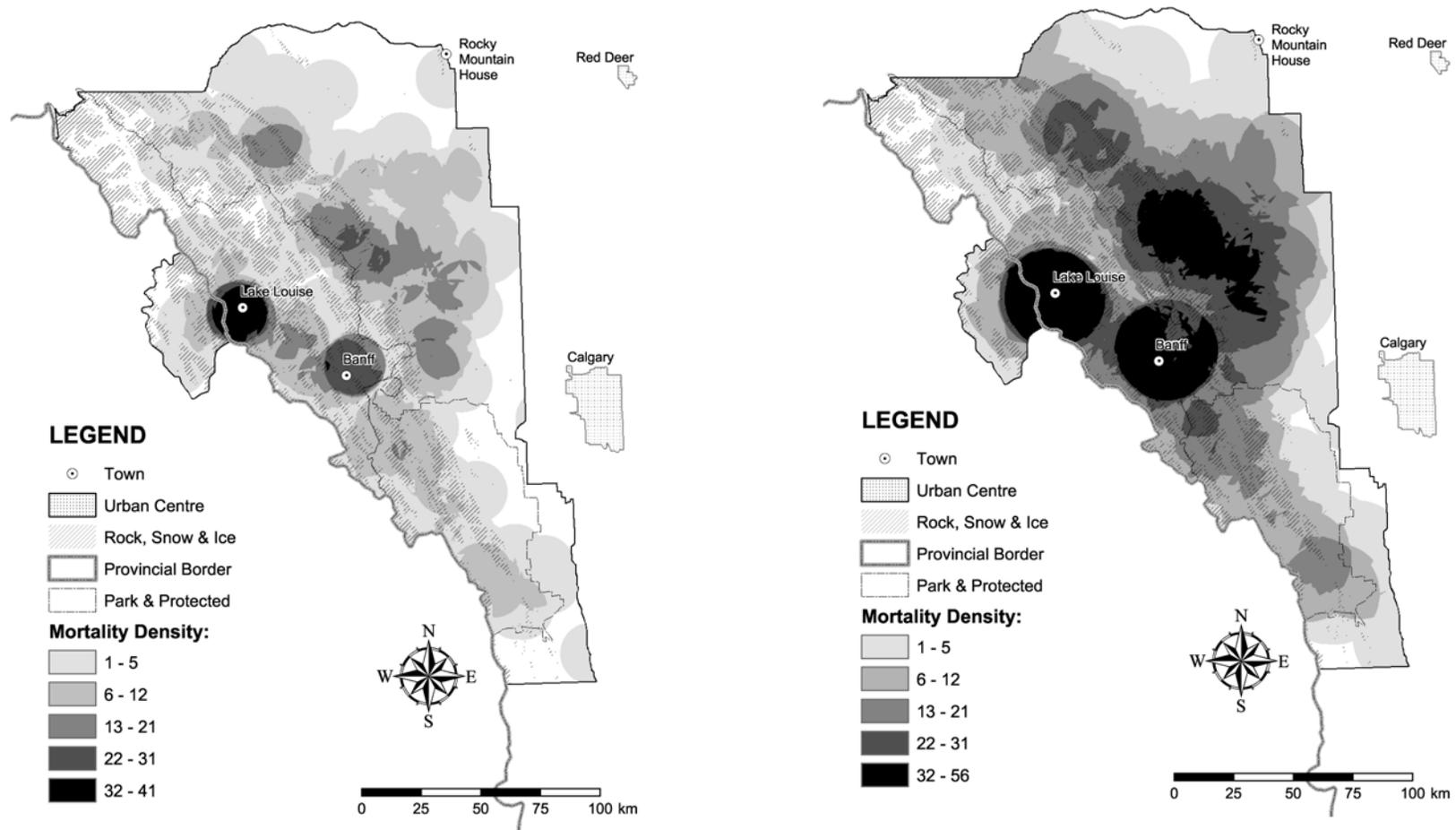


Figure 2. Distribution and concentration (density of recorded mortalities) of grizzly bear mortalities within the study area at 2 scales relating to the multi-annual 95% fixed kernel home ranges for female (a. 520-km<sup>2</sup>) and male (b. 1,405-km<sup>2</sup>) grizzly bears. Note the differences between scales and the high concentration of mortalities near Banff and Lake Louise town sites as well as the east slopes northwest of Calgary. A third scale relating to the lifetime home range of a Yellowstone grizzly bear (900-km<sup>2</sup>) is not shown but is intermediate between the scales depicted.



Table 2. Estimated coefficients (Coeff.) for GIS environmental predictor variables used to estimate if any spatial mortality differences existed among specific demographic status, sex-age, season, or mortality class when compared with other mortalities (e.g., berry season compared with non-berry season). Conifer forest was used as the reference category (indicator contrast) for comparisons with other landcover classes.

Variable	Female			Sub-adult male			Berry Season			Legal harvest		
	Coeff.	S.E.	<i>p</i>	Coeff.	S.E.	<i>p</i>	Coeff.	S.E.	<i>p</i>	Coeff.	S.E.	<i>p</i>
Landcover type												
Deciduous forest	0.109	0.463	0.814	-0.906	0.628	0.149	-0.046	0.455	0.919	0.075	0.590	0.899
Grassland	-0.021	0.461	0.964	-0.096	0.561	0.864	0.358	0.470	0.446	-0.341	0.577	0.555
Non-vegetated	0.636	0.745	0.393	§			0.726	0.749	0.332	-0.846	1.118	0.449
Shrub	0.010	0.356	0.978	-0.338	0.428	0.430	0.355	0.375	0.344	0.302	0.467	0.518
Greenness	0.010	0.073	0.891	0.005	0.090	0.959	0.048	0.074	0.511	-0.170	0.088	0.052
Distance to edge	-4.580	5.424	0.398	11.700	5.620	0.037	-9.293	5.749	0.106	11.977	6.119	0.050
Distance to water	-0.266	0.673	0.693	-1.732	1.040	0.096	0.741	0.671	0.270	-0.841	0.946	0.374
Distance to access	-0.736	0.370	0.047	0.942	0.353	0.008	-0.520	0.355	0.143	0.780	0.359	0.030
Terrain variability	3.251	3.464	0.348	-5.222	4.520	0.248	0.785	3.457	0.820	3.532	4.100	0.389
Constant	-0.317	0.750	0.672	-0.824	0.922	0.371	-0.952	0.773	0.218	0.641	0.947	0.498

§Estimated coefficient convergence failed due to perfect classification (no sub-adult male mortalities recorded in non-vegetated areas).

We did not find any temporal effects associated with berry season (August 1 to October 31), as the overall model was non-significant ( $\chi^2 = 12.04$ ,  $p = 0.211$ , d.f. = 9). Finally, comparisons of legal harvest with other human-caused mortalities showed strong spatial environmental differences for mortality locations with a significant overall model ( $\chi^2 = 23.30$ ,  $p = 0.006$ , d.f. = 9) and significant variables for distance to habitat edge and access features. Legal harvest locations occurred further from edges and access features compared with other mortalities, interpreted to mean that hunters must go further from a road to harvest bears and in other contexts, such as problem bears, human-caused mortality occurs nearer to roads.

### Random versus mortality locations- mortality distribution models

Irrespective of differences in demographic status, season, and mortality type, the global mortality distribution model significantly ( $\chi^2 = 144.91$ ,  $p < 0.001$ , d.f. = 9) described grizzly bear mortalities within the studied portion of the CRE. Mortalities were positively associated with access, water, and edge features (i.e., negative coefficients for distance to feature), while negatively associated with terrain ruggedness and greenness indices (Table 3). Only the shrub land cover class proved to be significantly different from that of conifer forests, having higher mortality ranks. Spatial model predictions for the global model showed strong patterns of high mortality along the eastern slopes of the Rockies and human accessible areas within the Parks (Figure 3). Using the independent withheld testing data (validation) we found our global mortality distribution model to be predictive overall with scaled bins of relative mortality ranks relating to the number of mortality locations falling within those bins ( $D = 1.0$ ,  $p < 0.001$ ; Figure 4).

Models describing sub-adult male mortalities were significant ( $\chi^2 = 93.19$ ,  $p < 0.001$ , d.f. = 9) showing an association with water, low greenness sites, less rugged terrain, and in shrub habitats (Table 3). In contrast, the distance variables for edge and access features, although negative (more likely to be near that feature), were not significant. For the other sex-age class, however, mortalities were strongly related to edges and access features, with a significant model overall ( $\chi^2 = 79.43$ ,  $p < 0.001$ , d.f. = 9). Similar to sub-adult males, mortalities for the other sex-age class were in low greenness sites and in less rugged terrain. Not only were other sex-age class mortalities more likely to occur in shrub habitats, but also in grassland areas



(Table 3). In comparison to other sex-age classes, sub-adult male mortalities tended to occur further from edges and access features, nearer to water, and in less rugged terrain.

Models describing legal harvest mortalities were significant overall ( $\chi^2 = 48.11, p < 0.001, \text{d.f.} = 9$ ), showing a strong association with water and less rugged terrain. Hunters were apparently successful in focusing their attention to streamside habitats, where animals are typically concentrated during the spring hunting season. There were non-significant, but consistent negative (nearer to features as for previous groups) relationships for access, edges, and greenness. For land cover types, only the shrub category was significantly different from that of closed conifer stands (Table 3). Non-harvest mortalities, on the other hand, were not only more likely to occur in shrub habitats, but also in grasslands with a significant model overall ( $\chi^2 = 57.07, p < 0.001, \text{d.f.} = 9$ ). Distance to edge and access also were important indicators of non-harvest mortalities. Both were strongly negative, suggesting that vegetation edges and human-accessible areas were more dangerous for non-harvested grizzly bears. Greenness, distance to water, and terrain variability were non significant, but were still negative, suggesting a weak association. In contrast to non-harvest mortalities, legal harvests mortalities tended to occur further from access and edge features, nearer to water, less likely in grasslands, and finally, in less rugged terrain.

### **Radiotelemetry versus mortality locations- the mortality risk model**

The mortality risk model, describing radiotelemetry versus mortality locations using GIS predictor variables, was significant overall ( $\chi^2 = 170.49, p < 0.001, \text{d.f.} = 9$ ). Mortality locations occurred in deciduous forest and shrub land cover classes more so than closed conifer stands (reference category). Also, grizzly bear mortalities were more likely to occur nearer to edge, access, and water variables (Table 4). Finally, grizzly bear mortalities were significantly related to areas of low greenness and minimal terrain ruggedness. Overall predictions of mortality classes and validations of withheld mortalities within these classes were similar for the mortality risk and mortality distribution models (Figure 4). Coefficient coverage between the random-versus-mortality and the radiotelemetry-versus-mortality models failed to reveal large differences, although stronger associations of mortality for less rugged terrain, near edges, and within the deciduous land cover class was evident for the mortality risk model (radiotelemetry versus mortality locations). Furthermore, a weighted Kappa statistic ( $\hat{K}_w = 0.78$ ) suggests very good to excellent agreement in the spatial predictions of mortality sites by the mortality distribution and mortality risk maps. Using the independent withheld testing data (validation) we found our global mortality risk model to be predictive overall with scaled bins of mortality risk relating to the number of mortality locations falling within those bins ( $D = 1.0, p < 0.001$ ; Figure 4). The similarities with our mortality distribution model (random versus mortality locations) suggest that the random versus mortality locations were not overly tied up in habitat selection, but instead related to those processes influencing human-caused grizzly bear mortality.



Table 3. Estimated coefficients (Coeff.) for models describing the relative probability of grizzly bear mortality within the Central Rockies Ecosystem of Canada by contrasting mortalities with random locations. Standard errors (S.E.) and inferences were based on a 499-sample bootstrap estimate. Conifer forest was used as the reference category (indicator contrast) for comparisons with other land cover classes.

Variable	Global model (all)			Sub-adult male			Other sex-age			Legal harvest			Non-harvest/Other		
	Coeff.	S.E.	<i>p</i>	Coeff.	S.E.	<i>p</i>	Coeff.	S.E.	<i>p</i>	Coeff.	S.E.	<i>p</i>	Coeff.	S.E.	<i>p</i>
<i>Landcover type</i>															
Deciduous forest	0.405	0.264	0.125	-0.098	0.539	0.856	0.415	0.359	0.248	0.398	0.487	0.413	0.536	0.493	0.277
Grassland	0.212	0.233	0.363	0.108	0.416	0.795	0.503	0.339	0.137	-0.138	0.53	0.795	0.931	0.361	0.01
Non-vegetated	-0.158	0.414	0.702	-0.629	3.108	0.84	0.592	0.487	0.224	-1.242	4.633	0.789	-0.14	4.622	0.976
Shrub	0.813	0.205	<0.001	0.784	0.318	0.014	1.023	0.276	<0.001	0.753	0.368	0.04	1.034	0.345	0.003
Greenness	-0.133	0.041	0.001	-0.144	0.076	0.057	-0.152	0.054	0.005	-0.146	0.076	0.057	-0.074	0.066	0.267
Distance to edge	-7.792	2.27	0.001	-6.005	3.032	0.048	-11.738	3.608	0.001	-3.251	2.545	0.201	-11.076	4.033	0.006
Distance to water	-2.274	0.549	<0.001	-3.524	1.291	0.006	-1.49	0.634	0.019	-3.499	1.252	0.005	-2.141	1.032	0.038
Distance to access	-1.63	0.474	0.001	-0.632	0.588	0.282	-2.901	0.91	0.001	-0.322	0.409	0.431	-2.652	0.889	0.003
Terrain variability	-8.09	1.599	<0.001	-10.598	2.533	<0.001	-6.74	2.048	0.001	-6.596	2.504	0.008	-4.086	2.471	0.098



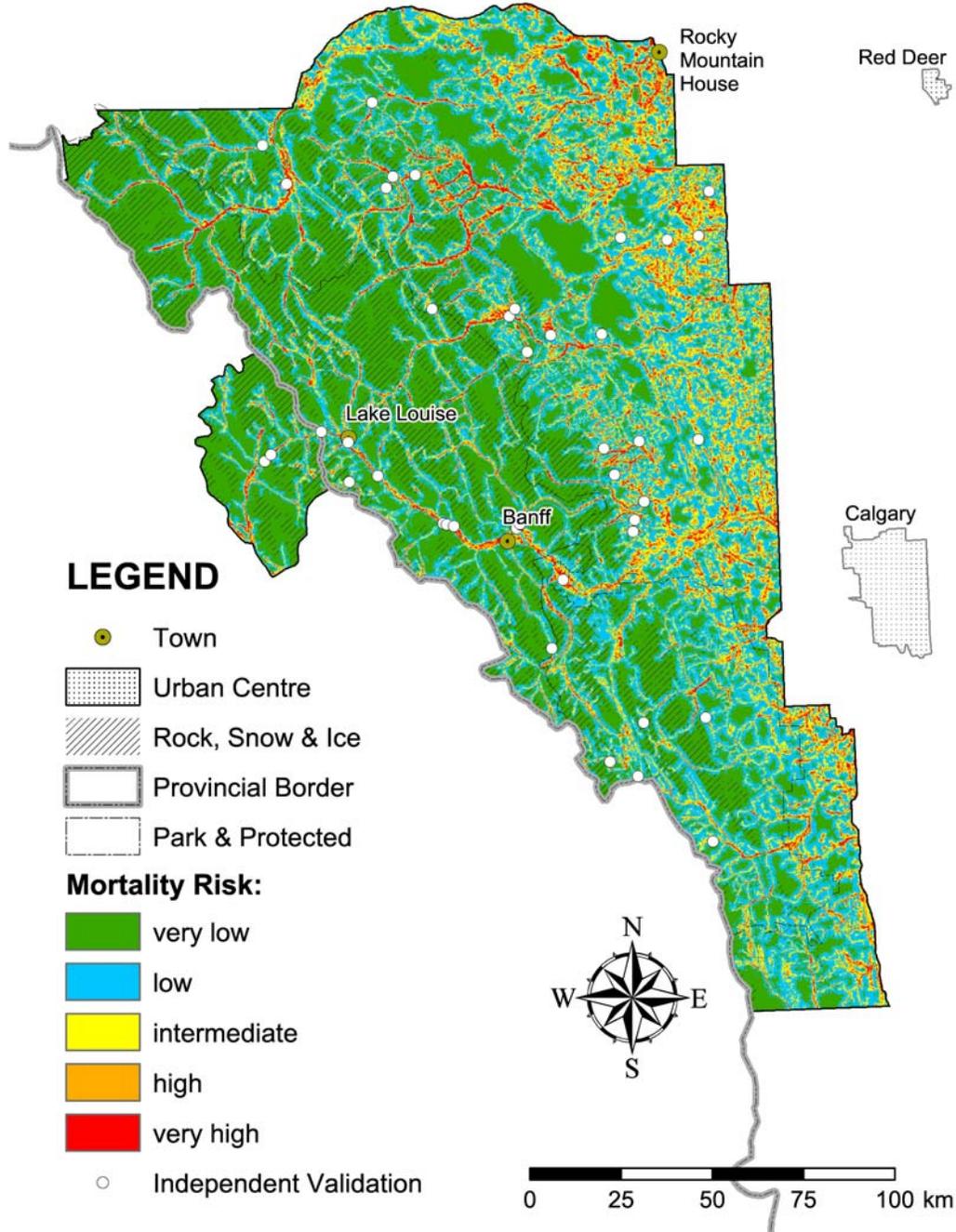


Figure 3. The distribution of mortality risk ranks from very low to very high based on the global mortality distribution (random versus mortality locations) model in the Central Rockies Ecosystem of Canada.



Table 4 . Comparison of the mortality distribution (random versus mortality locations) and mortality risk (radiotelemetry versus mortality locations) with bootstrapped standard errors and significance.

Variable	Mortality distribution model			Mortality risk model		
	Coeff.	S.E.	<i>p</i>	Coeff.	S.E.	<i>p</i>
<i>Landcover type</i>						
Deciduous forest	0.405	0.264	0.125	1.199	0.322	<0.001
Grassland	0.212	0.233	0.363	-0.034	0.378	0.928
Non-vegetated	-0.158	0.413	0.702	0.331	0.618	0.593
Shrub	0.813	0.205	<0.001	0.832	0.235	<0.001
Greenness	-0.133	0.041	0.001	-0.182	0.056	0.001
Distance to edge	-7.792	2.27	0.001	-12.969	4.895	0.008
Distance to water	-2.274	0.549	<0.001	-1.146	0.605	0.058
Distance to access	-1.630	0.474	0.001	-2.003	0.990	0.043
Terrain variability	-8.090	1.599	<0.001	-14.729	2.146	<0.001

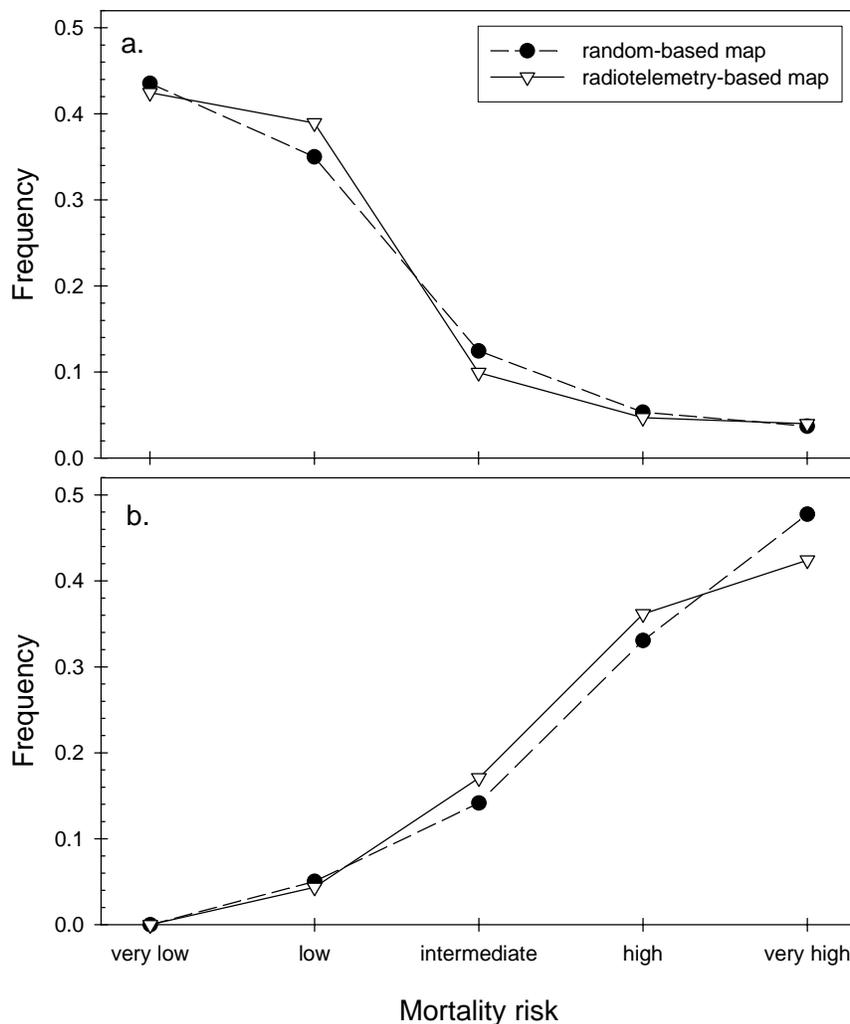


Figure 4. Percent composition of very low to very high mortality risk pixels in the Central Rockies Ecosystem of Canada based on the mortality distribution (random-based map) and the mortality risk (radiotelemetry-based map) models (a.). Area-adjusted frequency of withheld (testing data) mortality validations ( $n = 45$ ) falling within very low- to very high- mortality risk bins (b.). Although only a small fraction of mortality pixels are in high- and very high bins (a.), the majority of mortalities (per area) are occurring in these sites (b.).



## DISCUSSION

Grizzly bear mortalities were concentrated in three regions of the study area: (1) Lake Louise; (2) Banff town site; and (3) Alberta Provincial lands near the Red Deer River (Benn, 1998). Unlike Lake Louise and Banff, a large proportion of human-caused mortalities in the Red Deer River basin were caused by legal spring harvests. For 2 scales (900-km<sup>2</sup> and 1,405-km<sup>2</sup>), the number of mortalities within home-range-sized moving windows exceeded or equalled the number of years examined ( $\geq 1$  mortality/year) for these 3 regions suggesting very high mortality rates. Temporal variation in mortalities over the past 3 decades have, however, been evident for different regions, with some areas like the Banff town site exhibiting reduced rates of mortality in the past number of years (Benn, 1998; Benn and Herrero, 2002). Secure areas varied from 7.2% to 23.9%, although large proportions of these areas were considered to be non-habitat.

Comparisons of demographic status, season, and mortality type revealed spatial discriminations in mortalities for sub-adult male/non-sub-adult male and legal hunting/non-legal hunting locations, while sex and season differences were similar. We found no spatial differences in mortality for season (berry versus non-berry season), despite reported differences in total number of mortalities (Benn and Herrero, 2002). Benn and Herrero (2002) found that a high proportion of mortalities occurred in the berry season when bears were most likely to forage at low elevation sites for Canada buffaloberry, *Shepherdia canadensis*, fruits. Although grizzly bears were more likely to be 'killed' during the hyperphagic berry period when they were accessing habitats near humans (e.g., low elevation sites), these sites were spatially similar to those of other mortalities occurring in the non-berry seasons. This suggests that the spatial locations of mortality sinks (*sensu* Knight et al., 1988) were consistent and only the number (rate) of mortalities varied by season. For the sub-adult male and non-sub-adult male comparison, we found that sub-adult males tended to be 'killed' further from access and edge features when compared with non-sub-adult males, although variation in distance to access for sub-adults was high suggesting that animals were 'killed' both near and away from access features. Although we expected sub-adults to be further from edges through aggressive displacement by adult males (McLellan and Shackleton, 1988), we were surprised to find sub-adult male mortalities further from access features where you would expect most mortality events to occur regardless of sex-age class. Perhaps, sub-adult males were simply more broadly distributed across the landscape and this was reflected in mortality locations. Finally, the legal harvest versus non-legal harvest comparison revealed that legal harvests were further from edges and access features. This suggests that during the hunting season grizzly bears are further from edges and access or hunters were accessing more remote areas during the hunt.

For the global data set, the random-based mortality distribution model and the radiotelemetry-based mortality risk model revealed similar mortality patterns that were largely consistent with the literature and expected distribution of bears. Grizzly bear mortalities were positively associated with access, water, and edge features (e.g., nearer to those features or a negative coefficient). Previous research in the region has shown that bears select edge habitats and streamside areas (Nielsen et al., 2002; Theberge, 2002), but we also suspect that humans are more likely to be in these sites as well, thereby increasing the frequency of contact between bears and humans (Mattson and Merrill, 1996a; 1996b). Distance to access features, on the other hand, is more likely to describe the distribution of humans in space. Where bear habitat co-occurs with human access, however, interactions between bears and humans will escalate thereby increasing risk of human-caused mortality to bears. Although previous research in the area has shown positive associations between grizzly bear occurrence and both terrain ruggedness and the vegetation index greenness (Mace et al., 1999; Nielsen et al., 2002; Stevens, 2002; Theberge, 2002), we found negative associations for models describing mortality sites. Our models did not consider, however, the overall spatial pattern or patchiness of greenness like that of Stevens (2002), and thus may reflect the strong association of mortalities with edges, stream side areas, and roads, where pixel values for greenness are likely to be low. Likewise, for terrain ruggedness, we suspect that terrain patterns in mortalities is likely to be related more with human distribution than grizzly bear distribution as humans are less likely to venture into more rugged terrain, at least when compared to grizzly bears. Finally, for land-cover type classes, shrub (including avalanche) habitats were consistently more likely to have mortalities than the reference category closed conifer stands. We feel this reflects the strong concentration of bears within shrub and avalanche areas (Theberge, 2002).

Overall, global models describing the distribution of mortality risk were predictive and significant based on the occurrence of independent grizzly bear mortalities withheld for model validation. This suggests that mortalities were well described and predictable using readily available terrain, human, and vegetation GIS



data. This is further supported by the methods and results observed by Johnson et al. (2005) in the spatial description of grizzly bear survival in the Greater Yellowstone Ecosystem. Although our models were not based on the more powerful Cox regression methods (Cox and Oakes, 1984) for survival (1-mortality), as we did not track exposure and ultimately death for individual animals, our mortality risk model would likely closely match ranks from a survival model. Baseline survival functions from other studies might be used to scale our predictions. The fact that Johnson's (et al., 2005) survival model for Yellowstone and our mortality risk model for the CRE qualitatively provide similar responses to similar types of GIS data suggest that information from other areas can readily be used to describe areas of grizzly bear mortality risk, as human behaviour ultimately causing grizzly bear deaths appears to be consistent.

## MANAGEMENT IMPLICATIONS

Conservation models describing grizzly bear mortality locations in the CRE of Canada are needed for management and conservation planning. As would be expected, landscape attributes relating to human use, such as roads, trails, and terrain, correlated well with the locations of human-caused grizzly bear mortalities. Spatial mortality models, as those presented in this paper, can be used for management of humans in grizzly bear territories and the identification of potential restoration (road access control or deactivation) sites. Moreover, incorporation of risk models with existing animal occurrence models (e.g., Nielsen et al., 2002; 2003) may prove useful for assessments of population viability (Boyce and McDonald, 1999) and attractive sink dynamics (Delibes et al., 2001; Naves et al., 2003). We suggest that risk models be integrated with habitat models for identifying key habitat sinks and secure areas for active management and protection respectively.

Management and mitigation of potential habitat sinks may be necessary, at minimum during essential activities such as the hyperphagic berry period (August to October) or the spring limited entry bear hunt when the majority of animals are at high risk and killed by humans (Benn and Herrero, 2002). Concurrently, education programmes for the public and hunters may be necessary to reduce bear-human conflicts (Schirokauer and Boyd, 1998). Finally, management policies regarding problem wildlife may need further modification and/or examination of population impacts. Numerous animals were lost to the CRE by relocation and/or problem wildlife mortalities (Benn, 1998). The number of management actions a grizzly bear received increased substantially the risk of mortality (Boyce et al., 2001; Johnson et al., 2005). This suggests that behavioural patterns exhibited by some bears may place them at greater risk and those management policies and actions for these animals were not successful in ultimately reducing mortality. Managers should consider alternatives to animal relocation, such as aversive conditioning, while striving to minimize habituated and problem animals from first developing. Even with well-intended management plans, maintenance of viable grizzly bear populations in southern Canada is increasingly difficult given the rapid growth in human population, land use pressure, and recreation within grizzly bear range (McLellan, 1998). Addressing access management for grizzly bear populations, now being considered for threatened status by the Alberta government, may be necessary to stem localized mortality sinks. Implementation of human recreation and waste management policies in the National Parks has reduced local human-bear conflicts (Benn, 1998). We found that relatively little of the landscape was secure from human-caused mortality for grizzly bears. This would be most directly remedied by decreasing human access.

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