University of Alberta

HABITAT ECOLOGY, CONSERVATION, AND PROJECTED POPULATION VIABILITY OF GRIZZLY BEARS (*Ursus arctos* L.) IN WEST-CENTRAL ALBERTA, CANADA

by

Scott Eric Nielsen ©

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Dedication

In dedication to the loving memory of my father Roger (1945–2003).

Abstract

Grizzly bear (*Ursus arctos* L.) populations in Alberta are threatened by habitat loss and high rates of human-caused mortality. Effective management and conservation require not only an understanding of grizzly bear habitat ecology, but also spatial depictions of these relationships. The goal of this thesis was to examine and model habitat factors, both natural and anthropogenic, related to habitat selection, mortality, and persistence of grizzly bears in west-central Alberta, Canada.

Contrary to most previous studies, I found grizzly bears selected clearcuts, although patterns of clearcut use were temporally (seasonal and diurnal) and spatially (microsite, silvicultural history, landscape metrics, etc.) dependent. Critical food resources found within clearcuts provided an attractive alternative to natural openings and young seral forests that were rare within the foothills. Spatial models of human-caused mortality risk suggest, however, that use of such habitats resulted in an ecological trap situation, where animals lacked the cues necessary to distinguish the high-risk condition. Examinations of seasonal habitat selection among 3 sex-age classes supported a resource competition hypothesis of habitat segregation over that of an infanticide hypothesis. Comparisons of genetic relatedness and habitat selection further suggested that maternal-parent-offspring rearing shaped individual habitat selection more so than genetic relatedness.

Using a 2-dimension model of habitat occupancy and mortality risk, I present a framework for grizzly bear habitat conservation in Alberta, developing habitat indices and relative habitat states that can be used to identify existing high-quality, secure habitats and restore high-quality, risky habitats. Using a spatially explicit forest simulation model, I further assessed the population viability of grizzly bears for a 100-

year period by tracking habitat indices, relative habitat states, and the status of potential territory units for two-pass (current management) and natural disturbance-based forestry. Road densities increased over 100 years from 0.35 km/km^2 to 1.16 and 1.39 km/km^2 for two-pass and natural disturbance-based forestry respectively. Despite a potential 10% increase in animal density and potential carrying capacity, effective (secure) territory units declined by 54 to 67%. All effective territories, even by year 30, were located within or adjacent to protected mountain parks, suggesting a substantial decline in foothill populations.

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First and foremost, I wish to thank my wife Charlene for her unwavering support and encouragement throughout this process.

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Finally, I wish to thank the bears and all those who care enough to help conserve for future generations what Aldo Leopold, the father of wildlife biology, calls the noblest of North American mammals, the grizzly bear.

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Chapter 1

General Introduction

Low reproductive rates and densities (large area requirements) predispose grizzly bears (*Ursus arctos* L.) to being vulnerable to population decline and making their subsequent recovery slow (Russell et al., 1998; Purvis et al., 2000). During the past century, populations and distribution of grizzly bears have declined substantially in North America (Figure 1-1). Losses in some regions, such as the contiguous United States and Mexico, exceed 99% with little hope of large-scale recovery (Servheen, 1990; see however, Pyare et al., 2004). Such declines have undoubtedly arisen from human-bear conflict and habitat loss, as increased human densities have been well correlated with extirpation (McLellan, 1998; Woodroffe, 2000; Mattson and Merrill, 2002). Ultimately, the loss of large carnivores, such as grizzly bears, can lead to a decoupling of ecological relationships, including nutrient cycling and plant growth (Pastor et al., 1993; McLaren and Peterson, 1994; Tardiff and Stanford, 1998), behavioural modification of prey (Berger 1999; Berger 2001), and loss of biodiversity (Berger et al., 2001). Regardless of the potential for decoupling, the persistence of large carnivores in ecosystems is nevertheless considered an important indicator of ecosystem health (see however, Andelman and Fagan, 2000) and philosophically essential (Leopold, 1933; 1949). As such, grizzly bears have been used as a focal (surrogate species) and/or flagship (majestic and charismatic) species for conservation (Noss et al., 1996; 2002; Carroll et al., 2001).

Currently, grizzly bears are considered threatened within the contiguous United States (Servheen, 1990) and a species of special concern in Canada (Ross, 2002). Although Canada has witnessed the extirpation of the prairie population in parts of Alberta, Saskatchewan and Manitoba (Figure 1-1), Canada still contains approximately 27,000 individuals over an area of 2.574 million km^2 in western and northwestern Canada (Ross, 2002). Canadian populations, however, are not without risk of future population decline, thus their status as a species of special concern. Industrial, residential, and recreational developments all threaten existing populations. This is especially relevant for populations along the southern fringe of their distribution in British Columbia and Alberta (McLellan, 1998; Proctor et al., 2004). In Alberta, populations have recently been estimated at 500 animals on Provincial lands and perhaps a few hundred within National Parks (Stenhouse et al., 2003). Although these estimates are admittedly crude, most would agree that continual loss of critical habitat and perhaps more importantly, high rates of human-caused mortality (Benn, 1998; McLellan et al., 1999; Benn and Herrero, 2002), threaten the long-term persistence of grizzly bears in Alberta.

Critical to the needs of management and conservation of grizzly bears in Alberta are assessments of the impact of industrial resource extraction (i.e., forestry, oil and gas exploration/development and open pit coal mining) on grizzly bear habitats and populations. More specifically, spatially explicit models (i.e., maps) that predict and describe habitat quality, population density, mortality risk, and/or projected population viability are needed. Although numerous studies of grizzly bear habitats in the Central Rockies region have been completed and have added to our knowledge of local bear ecology (e.g., Hamer and Herrero, 1987; Hamer et al., 1991; Waller and Mace, 1997; Mace et al., 1996; 1999; Gibeau, 1998; McLellan and Hovey, 2001; Nielsen et al., 2002; 2003; Stevens, 2002; Theberge, 2002; Apps et al., 2004; Mueller et al., 2004), no single practice or framework for guiding management and conservation of grizzly bears has emerged. This has partially been a consequence of the nature of the species as a habitat generalist, exhibiting a wide range of behaviours dependent on available habitats, foods, and human activities, making it difficult to generalize local models to other populations. Equally, however, few have attempted to integrate habitat relationships for grizzly bears with population or demographic factors in the Central Rockies, as the species is long-lived and difficult to study. There is no doubt that long-term collection of life history information is needed to be gathered for understanding and monitoring of population trends, much like what has occurred in Yellowstone (Craighead et al., 1995), but exploiting existing data sources to make conservation recommendations also is necessary to prevent near-future declines. Commonly, what is available to the conservation biologist is information on animal presence or use from aerial surveys or radiotelemetry studies and sometimes a distribution of mortality locations from government management databases (e.g., hunting, problem wildlife, vehicle-wildlife collisions, etc.). Formulating a process that uses these data to identify and track critical habitat conditions and mortality, perhaps as a relative index or state, would undoubtedly provide improvements in conservation planning and wildlife management for populations suffering decline. This thesis attempts to address such management needs, as well as provide a general assessment of grizzly bear habitat requirements.

Objectives

I intend to provide an analysis of the habitats of grizzly bears in west-central Alberta. More specifically, I attempt to provide a framework for developing spatially explicit habitat and population level tools for management and conservation of grizzly bears in Alberta, while also examining the factors (natural and anthropogenic) leading to habitat occupancy, mortality, and persistence for a 9,752-km^2 study area (Figure 1-2) in west-central Alberta, Canada. To accomplish this goal, I rely heavily on the resource selection function (RSF) methods for characterizing and predicting animal-habitat (use) relationships (Manly et al., 1993, 2002; Boyce and McDonald, 1999). As well as providing practical applications for management and conservation of grizzly bears in Alberta, I test some theoretical questions relating to grizzly bear habitat selection.

Chapters in this thesis, which total 9 including the general introduction and conclusion, are organized into independent papers (i.e., paper format thesis), some of which (chapters 2, 3, and 4) have been published. Excluding specific University of Alberta guidelines, the format of each chapter follows that of the journal *Biological Conservation.* Below I provide a brief description of each chapter following the general introduction (chapter 1).

In chapters 2 and 3, I address the influence of clearcut harvesting on habitat use and food resources. Specifically, I assess how silviculture, age, landscape metrics, and local environmental site conditions (soils, elevation, etc.) influence patterns of clearcut use by bears and the distribution of critical food resources including fruit. In chapter 4, I examine the influence of environmental and human factors on the spatial distribution of human-caused grizzly bear mortalities. For this, I collaborated with the East Slopes Grizzly Bear Project (ESGBP) to model risk of human-caused mortality, ultimately for use in the Foothills Model Forest project. In chapter 5, I test the hypothesis that sexual segregation is responsible for habitat selection, as well as provide a more general assessment of habitat use for 3 sex-age classes (adult female, adult male, and sub-adult animals) in 3 food-related seasons. In chapter 6, I examine the influence of genetic relatedness on habitat selection, testing whether relatedness alone or maternal parent-offspring rearing (learning experiences) helps shape the selection of habitats by grizzly bears. In chapter 7, I develop a two-dimensional habitat model for adult females by integrating mortality results from chapter 4 with habitat selection results in chapter 5, and present a set of habitat indices and habitat states for conservation and wildlife management. In chapter 8, my final data chapter, I examine the projected changes in these habitat indices and habitat states over a 100-year period of time for two forestry scenarios (two-pass forestry vs. natural disturbance-based forestry). I also assess population viability by estimating habitat-based animal densities, generating animal territories for adult females, and assessing the risk of mortality per territory unit (effective versus non-effective territory). Taken together, I believe these chapters help address the habitat ecology, conservation, and population viability of grizzly bears in west-central Alberta, Canada. I hope these models not only help enlighten grizzly bear management for west-central Alberta, but also provide, more generally, a framework for grizzly bear conservation elsewhere.

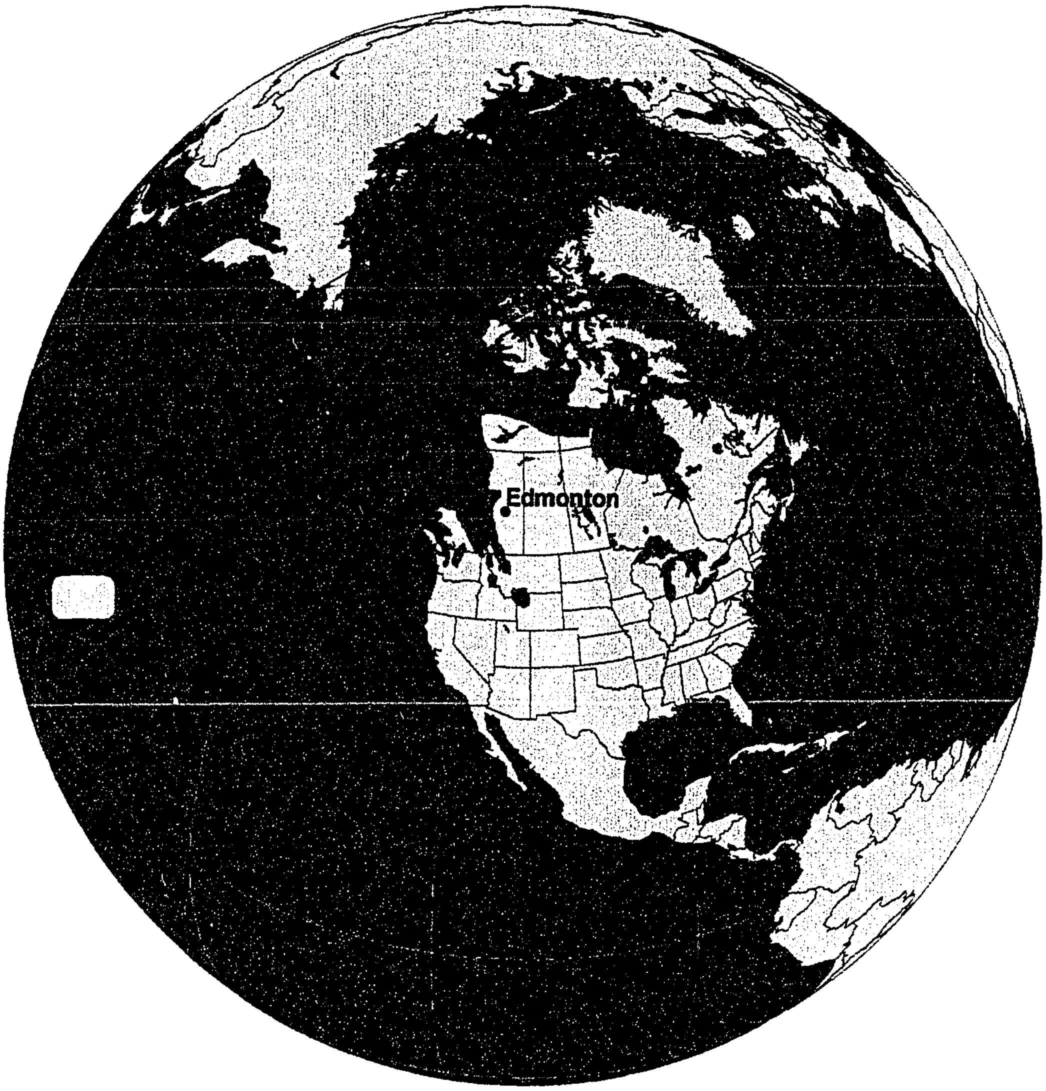

Figure 1-1. Historic (19th century, *circa* 1900) and current (21st century, *circa* 2000) distribution of grizzly (brown) bears (*Ursus arctos* L.) in North America.

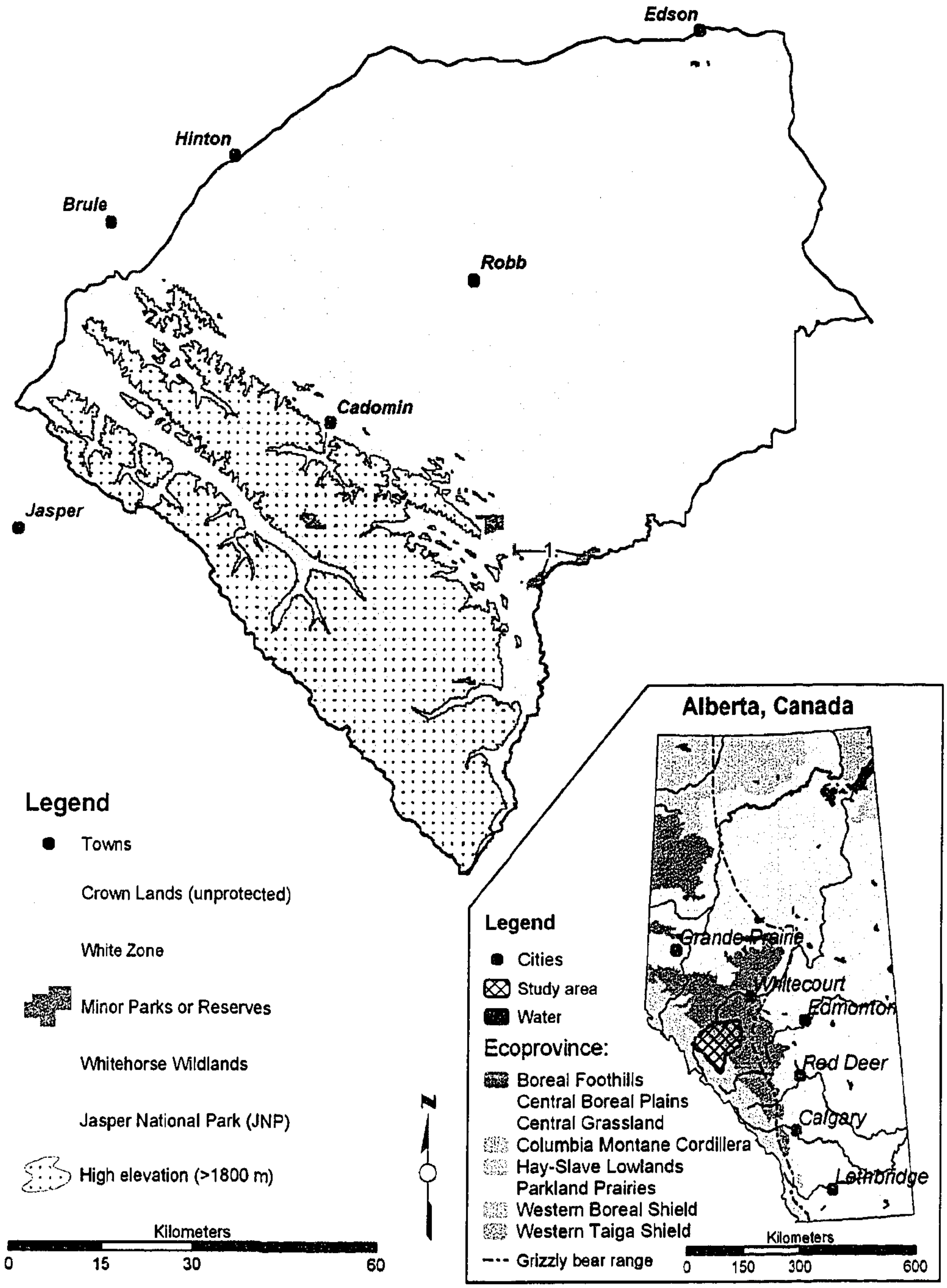

Figure 1-2. Study area map depicting management zones, towns, and high elevation (>1800 m) sites. Minor parks or reserves numbered include, 1) Brazeau Canyon; 2) Cardinal Divide; and 3) Grave Flats. Inset map of Alberta in lower right illustrates Ecoprovince, current grizzly bear range, and study area within Alberta.

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Chapter 2

Grizzly bears and forestry I: Selection of clearcuts by grizzly bears in west-central Alberta, Canada[1]

1. Introduction

Industrial resource extraction activities, including forestry, threaten the persistence of grizzly bears (*Ursus arctos* L.) in North America (Banci et al., 1994; Clark et al., 1996; McLellan, 1998) by fragmenting secure (free of human disturbance) habitats and increasing human access to previously remote landscapes. This is especially evident in the Central Rockies Ecosystem of Canada where unprecedented growth of human population and resource extraction has co-occurred (Schneider et al., 2003). For grizzly bears, increased human access has amplified human-caused mortality, the primary source of death for grizzly bears (McLellan and Shackleton, 1988; Benn and Herrero, 2002; Nielsen et al., 2004a). General habitat selection and assessments of road impacts have been widely studied for grizzly bears (McLellan and Shackleton, 1988; Mace et al., 1996; 1999; McLellan and Hovey, 2001; Gibeau et al., 2002; Wielgus et al., 2002). Although forest planning will largely determine overall habitat quality, configuration, and composition of future grizzly bear habitats in forested landscapes, few of these studies have assessed selection patterns by grizzly bears for different forest activities. With continual industrial resource extraction activities expected, viability of grizzly bear populations within managed forest landscapes is uncertain and in need of study.

High-quality grizzly bear habitats generally are considered roadless areas with a mosaic of early seral-staged forests and natural openings in proximity to secure forest stands providing day beds and hiding cover (Herrero, 1972; Blanchard, 1980; Hamer and Herrero, 1987). Fire suppression, however, threatens open-structured habitats, including those required by grizzly bears. Suppression of fire in western North America over the past half century has led to increased woody encroachment of natural openings and extensive succession of early seral or open structured stands (Payne, 1997). Widespread succession without further disturbance can lead to local population declines in grizzly

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[1] This chapter was published on 27 September 2004 (volume 199, issue 1, pp. 51–65) in *Forest Ecology and Management* by Nielsen, S.E., Boyce, M.S., Stenhouse, G.B. Reprinted with permission from Elsevier.

bears (McLellan and Hovey, 2001). Forest management, through development of early seral stage communities, therefore offers an opportunity for management of grizzly bear habitat and ultimately populations. Previous examinations of habitat use, however, have shown consistent avoidance of regenerating clearcuts suggesting potential loss of habitat (Zager et al., 1983; Waller, 1992; McLellan and Hovey, 2001). Most recently, Wielgus and Vernier (2003) found grizzly bears used clearcuts as available (neither selected nor avoided). Previous grizzly bear work, however, has focused on mountainous landscapes where open habitats were not limiting and often greater in extent than clearcuts. Few if any studies have examined how selection for regenerating clearcuts occurs in foothill boreal-like environments typical of west-central Alberta, where forests predominate and natural openings are rare. Moreover, little has been done to examine specific conditions of clearcut use by grizzly bears with respect to food seasons, time of day, and local site and management history conditions. Instead, most have assumed that clearcuts are homogenous and selection consistent among seasons and times of day. Identifying any site and terrain conditions, silvicultural treatments, and clearcut designs that enhance or reduce grizzly bear habitat is important for determining future forest management and conservation planning, as many of North America's grizzly bear populations reside in areas undergoing forest management.

Here we explore selection of habitats by grizzly bears in the upper foothills of west-central Alberta, a forested landscape that has been intensively managed for nearly 50 years. We test the widely held hypothesis that clearcuts were avoided by grizzly bears by examining 4 years of global position system (GPS) radiotelemetry data. In the foothills of west-central Alberta we suspected clearcut selection was occurring, as natural openings were not extensively available. Our specific objectives for this paper were three-fold: (1) determine differences in grizzly bear selection of clearcuts (patch or third-order selection) by season; (2) describe selection by season for individual clearcuts (within-patch or fourth-order selection) based on scarification, age, distance-to-edge, perimeter-to-edge ratio, and micro-site terrain characteristics; and finally, (3) examine whether there were any differences in selection of clearcuts during diurnal or crepuscular/nocturnal periods. In a companion paper (Nielsen et al., 2004b), we characterize how critical food resources vary within clearcuts to help interpret habitat use patterns observed herein.

2. Study area

A study area was delineated for a 2,677-km^2 landscape located in the eastern foothills of the Canadian Rocky Mountains of west-central Alberta (53°15′N, 117°30′W; Figure 2-1). We chose this area because of its long history of forestry and available detailed records of management actions. Within this area, a total of 525-km^2 (19.6% of the area) of forest has been harvested for timber (clearcutting) since 1956 (Figure 2-2). Surrounding regenerating clearcuts were closed conifer forests (41.4%), numerous minor forest (e.g., open conifer, deciduous, etc.), and to a lesser extent non-forest (e.g., herbaceous, shrub, etc.) classes (Franklin et al., 2001; Table 2-1). Closed conifer, the dominant land cover category, was composed of lodgepole pine (*Pinus contorta*), and to a lesser extent three species of spruce (*Picea glauca*, *P. mariana*, and *P. engelmannii*). Minor areas of trembling aspen (*Populus tremuloides*) or balsam poplar (*P. balsamifera*), often mixed with other shrubs including willow (*Salix* spp.), were scattered throughout the area, but most notable in lower elevations or riparian zones. We refer to all land cover and land use activities occurring outside of clearcut boundaries as matrix.

Natural sub-region classification based on climate, vegetation, soils, and topography was best described as upper foothills (Achuff, 1994), with elevations varying from 953 and 1975 m in rolling low mountainous terrain. Summer and winter temperatures averaged 11.5 and –6.0° C respectively, with a normal annual precipitation of 538 mm (Beckingham et al., 1996). Prior to 1950, periodic stand-replacing fires were the primary disturbance, averaging 20% of the landscape burned per 20-year period yielding a 100-year fire cycle (Andison, 1998). Since the 1950s, however, there has been a reduction in fires to the region being associated with the initiation of industrial forestry and fire suppression (Tande, 1979; Andison, 1998; Rhemtulla, 1999). Although some stands in remote regions are in advanced stages of succession due to fire suppression, large areas have or continue to be harvested providing the only major mechanism of disturbance. As most grizzly bear foraging in the front slopes of the Canadian Rockies occurs in open forests or meadows (Hamer and Herrero, 1987), clearcuts within heavily forested regions, such as the foothills of west-central Alberta, provide an opportunity or alternative source of food normally only associated with young fire-regenerating stands (Nielsen et al., 2004b).

3. Methods

3.1. Grizzly bear location data

From 1999 to 2002, we captured and collared 8 (5 female, 3 male) sub-adult (2–4 yrs of age) and 13 (7 female, 6 male) adult (≥5 yrs of age) grizzly bears from areas within or surrounding the forestry study area using standard aerial darting and leg snaring techniques (Cattet et al., 2003). Bears were fitted with either a Televilt GPS (global-positioning-system)-Simplex or an ATS (Advanced Telemetry Systems) GPS radiocollar. Radiocollars were programmed to acquire locations at intervals of every 4-hr, excluding a few collars that were programmed to take a fix every 1-hr. Following retrieval of GPS collars and/or remote uploading of collars, grizzly bear locations were imported into a geographic information system (GIS) and used to delineate 100% minimum-convex-polygon (MCP) home ranges (Samuel and Fuller, 1994). These home ranges were used to identify "available" locations for each individual using a random-point generator in ArcView 3.2. Sampling intensities for available locations within MCP home ranges were standardized to 5 points/km^2. For selection analyses on the broader landscape (clearcut versus matrix habitats), all locations falling within the defined study area were used, while selection within clearcuts was examined using only those locations falling within clearcut boundaries.

To account for variation in habitat use through time (Schooley, 1994; Nielsen et al., 2003), we stratified grizzly bear location data into three seasons based on food habits and selection patterns for the region (Hamer and Herrero, 1987; Hamer et al., 1991; Nielsen et al., 2003). The first season, hypophagia, was defined as den emergence (typically in April) to 14 June. During this season, bears fed on roots of *Hedysarum* spp. and in some instances on carrion. The second season, early hyperphagia, was defined as 15 June to 7 August. During this season, bears fed on ants (myrmecophagy), in some instances ungulate calves, and frequently on green herbaceous material including *Heracleum lanatum*, graminoids, sedges, and *Equisetum arvense*. The third season, late hyperphagia, was defined as 8 August to denning. During this season, bears sought out berries from *Shepherdia canadensis* and *Vaccinium* spp. followed by late season digging for *Hedysarum* spp. Resource selection functions (RSFs) were developed for both clearcut selection and within-clearcut selection using these three seasons. We did not explore year-to-year variation in habitat selection as sample sizes precluded seasonal and yearly stratification of data.

Given that grizzly bears have shown avoidance of non-secure (areas of human activity) areas during diurnal periods (Gibeau et al., 2002), we further assessed whether selection of clearcuts occurred more than expected during crepuscular and nocturnal periods. Diurnal hours were defined as the period occurring between 0700 and 1900 hr, while crepuscular and nocturnal hours were defined as occurring between 1900 and 0700 hr. Our definitions of diurnal and crepuscular/nocturnal periods were general only and did not account for changes in sunrise or sunset. To ensure that acquisition rates for these periods were not biased for the global dataset, we assessed the proportion of locations acquired during each period using 2×2 contingency χ^2 test and an expected 50:50 ratio.

3.2. Patch-level selection of clearcuts (third-order scale)

We compared seasonal GPS radiotelemetry locations with random or available locations to assess habitat selection for clearcut (1) and matrix habitats (0). Analyses were evaluated at the third-order (patch) scale (Johnson, 1980) following a 'design III' approach, where the individual identity of the animal was maintained for use and available samples (Thomas and Taylor, 1990). For each season, we calculated a resource selection function (RSF) at the level of the population using the following model structure from Manly et al. (2002):

$$w(x) = \exp(\beta x) \qquad (2\text{-}1),$$

where $w(x)$ is the resource selection function (relative probability of occurrence) and β the selection coefficient for the dummy variable x used to indicate whether locations (use or available) were within (1) or outside (0) of clearcut polygons. Logistic regression was used to estimate β in the program Stata (2001). We specified the robust cluster option to calculate our variance around the estimated coefficient using the Huber-White sandwich estimator (White, 1980; Nielsen et al., 2002). Sandwich estimators assumed that observations were independent across clusters, but not necessarily independent within clusters (Long and Freese, 2003). Bear was specified as the cluster, thereby matching the design III approach of the analysis (unit of replication) and avoiding autocorrelation and/or psuedoreplication of locations within individual bears. We further corrected for habitat and terrain-induced GPS-collar bias (Obbard et al., 1998; Dussault et al., 1999; Johnson et al., 2002) by using probability sample weights for grizzly bear locations (Frair et al., 2004). Probability sample weights were based on local models predicting GPS fix acquisition as a function of terrain and land cover characteristics (Frair et al., 2004). For the clearcut selection model we report results as an odds ratio based on the exponentiated form of β. Reported odds ratios were interpreted as the likelihood that grizzly bears were using clearcuts compared with matrix habitats for a particular season. Use of clearcuts by grizzly bears in concordance with availability would therefore be represented as 1.0, while selection would be >1.0 and avoidance <1.0. Finally, we tested whether GPS radiotelemetry data associated with clearcut use occurred more in diurnal or crepuscular/nocturnal periods by using a 2×2 contingency χ^2 test and an expected 50:50 ratio.

3.3. Within-patch selection of clearcuts (fourth-order scale)

For analyses of selection within clearcuts, we selected all locations occurring within clearcut polygons and divided our observations into 2 groups following a random sample test set validation. The first group, the model-training group, represented a random 85% sub-sample used for model development, while the remaining sub-sample (15%), the model-testing group, was used for assessing model performance by independent validation. Given that observations were within-clearcut patches, our analytical design followed a fourth-order scale of habitat selection (Johnson, 1980). Individual identity of animals (design III; Thomas and Taylor, 1990) was also maintained. Using model-training data and explanatory map variables (Table 2-2) for each season we developed RSF models by assuming the following structure from Manly et al. (2002):

$$w(\boldsymbol{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k) \qquad (2\text{-}2),$$

where $w(\boldsymbol{x})$ is the resource selection function for a vector of predictor variables, x_i, and β_i's are the corresponding selection coefficients. Logistic regression was used to estimate selection coefficients in Stata (2001). Linear predictor variables (Table 2-2) were assessed for collinearity through Pearson correlations (r) and variance inflator function

(VIF) diagnostics. All variables with correlations (r) >|0.6|, individual VIF scores >10, or the mean of all VIF scores considerably larger than 1 (Chatterjee et al., 2000) were assumed to be collinear. Area of clearcut and area-to-perimeter ratio were the only correlated ($r = 0.68$) variables, and thus were not considered together for inclusion in the same model. No further evidence of collinearity was evident using VIF tests. Using independent explanatory map variables, we generated 5 *a priori* candidate models (Table 2-3). Each candidate model corresponded to a set of similar variables or combination of variables that we hypothesized as being important for grizzly bears. We evaluated model selection for the 5 candidate models using Akaike's information criteria (AIC; Burnham and Anderson, 1998; Anderson et al., 2000). Akaike weights (w_i) were used to determine the approximate 'best' model given the data and candidate models tested. Methods for controlling autocorrelation and GPS radiotelemetry bias, explained in the previous section, were similarly used here.

Using testing data, we assessed the predictive performance of models by comparing map predictions with frequency of within-sample independent testing data (grizzly bear use locations) in specified bins (Boyce et al., 2002). A total of 10 quantile bins were generated based on the distribution of predicted habitats in the study area from the AIC-selected seasonal model. These bins ranked from habitats with low relative probability of occurrence (1) to habitats with high relative probably of occurrence (10). Models that performed well were characterized by having successively more model-testing GPS radiotelemetry locations in higher value habitat bins, while poor habitat bins contained few animal locations. We used a Spearman rank correlation (r_s) to assess the relationship among number of observed grizzly bear model-testing locations per bin and bin rank (Boyce et al., 2002). We considered a model to be predictive if r_s was positive and significant.

3.4. Site-specific predictor variables

Age of clearcut, in years, for each radiotelemetry and available location was determined from a GIS forestry polygon database provided by Weldwood of Canada Ltd. (Hinton, Alberta). Size of clearcut, in km^2, also was used as a predictor to assess whether small clearcuts were more attractive to grizzly bears from a security or ecotone basis. To determine clearcut size, we maintained all original clearcut boundaries. Finally, silviculture and/or site preparation data were joined with GIS harvest polygons and stratified into nine separate treatments and a control (no treatment) to test for local clearcut site history effects (Table 2-4).

We assessed the influence of two landscape metrics on grizzly bear habitat selection. These metrics were distance-to-clearcut edge (km) and area (km^2)-to-perimeter (km) ratio. A 10-m grid was used to determine distance-to-edge (matrix habitat) using the straight-line distance function in the Spatial Analyst extension of ArcGIS 8.1. The area-to-perimeter ratio was calculated for each polygon based on the estimated clearcut size and perimeter from a GIS.

To assess how terrain and local site conditions influenced the pattern of habitat selection for grizzly bears, we used a 26.7 m digital elevation model (DEM). From the DEM, we estimated elevation (km) for each use or available location. We further derived two terrain related variables from the same DEM. First, we estimated an index of soil wetness commonly referred to as the compound topographic index (CTI), previously found to correlate with several soil attributes including horizon depth, silt percentage, organic matter, and phosphorous (Moore et al., 1993; Gessler et al., 1995). A CTI grid was calculated using the spatial analyst extension in ArcView 3.2 and a CTI script from Rho (2002). Second, we used the DEM to derive total potential direct incoming solar radiation (WH/m^2) for summer solstice (day 172) using the Solar Analyst 1.0 extension in ArcView 3.2.

4. Results

4.1. Patch-level selection of clearcuts (third-order scale)

A total of 10,127 locations from 21 grizzly bears were recovered from the identified study area. Of these, 2,381 or 23.5% of locations were located within clearcut polygons. The selection of clearcuts compared with all other landcover categories (matrix) varied by season (Table 2-5). During hypophagia, grizzly bears selected clearcut habitats close to that which was expected based on availability. The estimated odds ratio for clearcut selection was 1.14 (95% CI = 0.88 to 1.46) times that of the landscape matrix. In contrast, for early hyperphagia, we found higher rates of clearcut selection. During this season, clearcuts were significantly selected over that of matrix habitats with an odds ratio of 1.56 (CI = 1.31, 1.85). Bears were therefore on average more than one and a half times more likely to select clearcuts over matrix habitats. Finally, during late hyperphagia, grizzly bears once again selected clearcut habitats close to that which would be expected based on habitat availability, although slightly less than matrix habitats with an estimated odds ratio of 0.85 (CI = 0.59, 1.23). Fine-scale temporal patterns of clearcut use differed for diurnal and crepuscular/nocturnal periods. Clearcuts were used more than expected during crepuscular/nocturnal periods ($\chi^2 = 5.69$, 1 d.f., $p = 0.017$). No evidence of bias in diurnal versus crepuscular/nocturnal acquisitions in animal locations was evident for the global dataset ($\chi^2 = 1.25$, 1 d.f., $p = 0.264$), suggesting that the selection of clearcuts for the crepuscular/nocturnal period was a biological effect.

4.2. Within-patch selection of clearcuts (fourth-order scale)

4.2.1. Hypophagia

A total of 734 GPS radiotelemetry locations from 14 grizzly bears were acquired from clearcuts during hypophagia. Of the 5 *a priori* models assessed for the season, the comprehensive model showed the greatest AIC support (Table 2-6). During this period, grizzly bears selected intermediate-aged (~30 yrs) clearcuts (Figure 2-4) that were more complex in shape (negative area-to-perimeter ratio), while animal locations were consistently closer to clearcut edges than random locations (Table 2-7). There did not appear to be any relationship among grizzly bear location and the compound topographic index (CTI) of soil wetness, although the terrain variable of potential direct incoming solar radiation did appear to be important. Grizzly bears selected for areas of low solar radiation during this season. Lastly, silvicultural treatments were selected within the final model. Responses of site preparation treatments compared to control sites without any treatment varied from positive to negative. In general, bears selected for clearcuts that were scarified with bracke, dragging, shark-fin barrel dragging, disc-trenching, excavator, and plow treatments, although only shark-fin barrel dragging had a strong consistent effect (Figure 2-3; Table 2-7). In contrast, bears tended to avoid (compared with controls) blade and Donaren mound clearcuts, although neither treatment was overly different from that of controls (Table 2-7). For between treatment effects, only plow (selection) and Donaren mound (avoidance) treatments were near to being different from one another when comparing 95% confidence intervals. Predictive accuracy of the AIC-selected hypophagia model using withheld model-testing data was good with a significant positive Spearman rank correlation ($r_s = 0.915$, $p<0.001$), suggesting potential utility in using hypophagia clearcut habitat maps for conservation.

4.2.2. Early hyperphagia

A total of 1,005 GPS radiotelemetry locations from 15 grizzly bears were acquired from clearcuts during the early hyperphagia period. Of the 5 *a priori* models assessed, the terrain model showed the greatest AIC support (Table 2-6). During this period, areas with high levels of direct incoming solar radiation were best associated with animal locations, while elevation and soil wetness (CTI) were only weakly related to bear locations (Table 2-7). Predictive accuracy of the AIC-selected early hyperphagia model using model-testing data was good with a significant positive Spearman rank correlation ($r_s = 0.964$, $p<0.001$), again suggesting potential utility in mapping seasonal clearcut habitat.

4.2.3. Late hyperphagia

A total of 642 GPS radiotelemetry locations from 9 grizzly bears were acquired from clearcuts during the late hyperphagia period. Of the 5 *a priori* models assessed, the comprehensive model showed the greatest AIC support (Table 2-6). During this period, coefficients for direct potential incoming solar radiation and soil wetness (CTI) largely overlapped (95% C.I.) 0 suggesting a weak relationship, while age of clearcut and perimeter-to-edge ratio, although partially overlapping 0, were influential (Table 2-7). Grizzly bears tended to use clearcuts that were irregular in shape and either young or more preferably old (up to 46 yrs; Figure 2-4). Like that of hypophagia, distance-to-edge of clearcut was strongly negative (i.e., increasing distance from edge corresponded to decreasing levels of use) suggesting hiding cover or ecotone relationships. Finally, silvicultural treatments again appeared in the AIC-selected model. Bears tended to select for areas that were scarified with bracke and shark-fin barrel dragging, although confidence intervals were large and overlapping zero (Figure 2-3; Table 2-7). Avoidance of Donaren mound, dragging, disc-trencher, excavator, and plow treatments were suggested, but again noisy. No differences were evident between silvicultural treatments. Predictive accuracy of the AIC-selected late hyperphagia model using model-testing data was good with a significant positive Spearman rank correlation ($r_s = 0.770$, $p=0.009$), suggesting potential utility in mapping seasonal clearcut habitat. The predictive relationship, however, was less significant than the previous two seasons warranting greater caution in use.

5. Discussion

We reject the hypothesis that grizzly bears avoid clearcuts. We found that grizzly bears selected clearcuts during early hyperphagia, while we could not show a statistical avoidance or selection of clearcuts during hypophagia (non-significant trend of clearcut selection) and late hyperphagia (non-significant trend of clearcut avoidance). Except for a recent study by Wielgus and Vernier (2003), this seasonal selection of clearcuts (according to availability) contradicts previous examinations of habitat selection by grizzly bears (Zager et al., 1983; Waller, 1992; McLellan and Hovey, 2001). However, most previous work has occurred in mountainous terrain where natural openings (e.g., alpine meadows) and/or large naturally regenerating forests (burns) were available to bears. We suggest that the general lack of large natural openings in our foothill landscape made clearcuts an attractive alternative habitat. Ultimately, the availability of early seral-staged forests or natural openings may explain whether grizzly bears will use clearcuts, as grizzly bears are known to prefer mosaic areas of forest and non-forest habitat (Herrero, 1972). Where fire suppression and succession has led to little if any forest openings, grizzly bears have adapted by utilizing closely related anthropogenic sites, such as clearcuts. Long-term grizzly bear research in Yellowstone has shown a general flexibility or adaptive nature to grizzly bear foraging, maximizing their nutrition through learned behaviour (Craighead et al., 1995). Nielsen et al. (2004b) found the occurrence of critical grizzly bear foods, including roots and tubers, herbaceous materials, and ants, to be more common in clearcuts than surrounding forests. Grizzly bears in the foothills of west-central Alberta may have adapted, like that of Yellowstone bears, to changes in landscape composition and associated food resources. Although clearcuts provided a possible resource surrogate for natural openings and young fire-regenerated forests, the associated risk of human-caused mortality due to increased human access may offset this benefit (Nielsen et al., 2004a).

Grizzly bears not only used clearcuts differentially according to season, but also according to time of day. Overall, there was a trend for grizzly bear use of clearcuts during crepuscular/nocturnal periods, rather than diurnal hours. Although our definitions of diurnal and crepuscular/nocturnal periods did not follow actual sunrise and sunset patterns, our results do point to differences in fine temporal scales, suggesting that activity (bedding versus foraging) and perhaps local security may be important. Previous work on habitat selection for grizzly bears in neighboring Banff National Park support changes in habitat selection between diurnal and nocturnal periods. Gibeau et al. (2002) found that selection of high-quality habitats near areas of human activity were greatest during the nocturnal period when security was highest. Alternatively, use of clearcuts at night may simply reflect thermal demands, especially in mid-to-late summer when high daytime temperatures may force animals to bed in forest stands, with foraging in clearcuts and other open areas restricted to the cooler crepuscular and nocturnal periods. Regardless of the mechanism, short-term (daily) temporal variation in habitat use of clearcuts was observed suggesting that further research into the subject is needed. This is especially relevant as most historic grizzly bear habitat assessments have used VHF radiotelemetry data that was largely collected during diurnal periods, perhaps helping further explain the disparity between our results (seasonal selection of clearcuts) and other studies (avoidance of clearcuts).

Site-specific (within-patch) habitat selection models proved predictive for each season, suggesting that terrain, silviculture, and landscape metrics were important determinants of local clearcut use. Clearcuts cannot therefore be considered uniform in habitat quality, as is usually the case for most grizzly bear habitat work. Small-scale differences in terrain, silviculture, and landscape metrics within or between clearcuts can result in major differences in predicted animal occurrence. Changes, however, were not consistent between seasons as bears were presumably responding to spatio-temporal fluctuations in the availability of critical food resources that individually responded to local environmental gradients and site history characteristics (Nielsen et al., 2004b). Researchers examining grizzly bear habitats should consider introducing environmental covariates that describe age, landscape metrics, silviculture, and terrain.

Landscape metric variables, distance-to-edge and edge-to-perimeter ratio were consistent predictors of grizzly bear use for both the hypophagia and late hyperphagia periods. Grizzly bears occurred nearer to clearcut edges, while also selecting for clearcuts that were more irregular in shape. These landscape factors, taken together with the observed crepuscular/nocturnal use of clearcuts, help support the hypothesis that hiding cover and/or local security-related issues are important considerations in habitat selection by grizzly bears (Gibeau et al., 2002).

Silvicultural effects on habitat selection for the hypophagia and late hyperphagia seasons varied from negative to positive. Bracke and shark-fin barrel dragging were selected over that of control treatments (no silviculture) for both seasons, but only shark-fin barrel dragging for the hypophagia season had a strong positive effect. In comparison, clearcuts with Donaren mound or blade site preparation were avoided for each season, although confidence intervals were too variable to be certain of this effect. For between-treatment comparisons, Donaren mound (avoidance) and plow (selection) treatments in the hypophagia season were noteworthy of a difference. Grizzly bear use of clearcuts based on silvicultural treatment likely reflected differences in available food resources, as Nielsen et al. (2004b) observed both negative (*Hedysarum* spp. and *Shepherdia canadensis*) and positive (*Equisetum* spp.) changes in food occurrence with mechanical scarification.

Age of clearcut was also an important predictor of grizzly bear use. Intermediate aged (~30-yrs) clearcuts were most frequently selected during hypophagia, while recent and old (up to 46-yrs) clearcuts were selected more than intermediate aged clearcuts during late hyperphagia. The use of intermediate-aged sites during hypophagia most likely reflected distribution of *Hedysarum* spp., as bears readily seek out roots from *Hedysarum* during this season (Hamer and Herrero, 1987; Hamer et al., 1991). Further, Nielsen et al. (2004b) found *Hedysarum* occurrence to be greatest in clearcuts with approximately 25% canopy cover. As canopy cover was correlated with clearcut age (r = 0.66), sites with more *Hedysarum* also were likely to be intermediate in age. In comparison, selection of recent and old clearcuts during late hyperphagia likely reflected late season foraging for fruit-bearing species such as *Shepherdia canadensis* in old clearcuts and *Rubus idaeus* and herbaceous foods in young clearcuts.

Finally, micro-site terrain features were more important predictors of bear use than landscape metrics or silviculture during early hyperphagia. Grizzly bears selected for areas with high incoming direct solar radiation, which supports myrmecophagy activities (Elgmork and Unander, 1999; Swenson et al., 1999). Ants, typically foraged by bears during early hyperphagia (Hamer and Herrero, 1987; Hamer et al., 1991), tend to be associated with dry, warm slopes (Crist and Williams, 1999; Nielsen et al., 2004b) and occur with greater abundance in clearcuts than unharvested forests (Knight, 1999; Nielsen et al., 2004b). We did not find a strong relationship between grizzly bear use of clearcuts and the soil wetness index, despite the importance of the variable for describing the occurrence of a number of critical grizzly bear foods (Nielsen et al., 2004b).

Habitat selection models for the three examined seasons were predictive based on assessments of independently withheld data suggesting utility in habitat mapping for management and conservation purposes. Such maps could describe both fine-scale differences in habitat quality within clearcuts and coarse-scale differences between clearcuts. Managers could use resulting habitat maps to identify on-the-ground conservation actions, such as determining which roads are in need of deactivation or seasonal closure. Without restricting human access to identified high-quality habitats, risk of mortality will increase, as humans and bears will be placed in close proximity to one another (Mattson et al., 1996; Nielsen et al., 2004a).

6. Conclusion

Grizzly bears selected clearcuts in the foothills of west-central Alberta. Selection, however, occurred differentially depending on micro-site terrain, landscape metrics, silvicultural history, and season. Management or even enhancement of grizzly bear habitat through forest management appears feasible, especially for areas that lack extensive natural openings or recent fires. We suggest that future forest planning strive to maximize grizzly bear habitat by: (1) increasing perimeter-to-edge ratio for clearcut shapes; (2) using low impact and/or positively associated site preparation treatments like Bracke and shark-fin barrel dragging; and (3) limiting human access to areas predicted as high-quality habitat. Use of prescribed fire, as a silvicultural treatment, also should be considered along with establishment of food plots for negatively impacted grizzly bear foods (Nielsen et al, 2004b). Limiting human access to high-quality sites helps address population-level factors. In particular, risk of human-caused mortality increases significantly for areas with open public roads (Benn and Herrero, 2002; Nielsen et al., 2004a; Johnson et al., 2005). Without addressing habitat occupancy and mortality concurrently, attractive sink conditions may develop where animals are drawn to locations where survival is low (Knight et al., 1988; Delibes et al., 2001). Public education programs targeted at reducing illegal mortalities have been successful elsewhere (Schirokauer and Boyce, 1998) and should also be considered. Finally, long-term forest management will likely modify habitat use by grizzly bears, as the proportion of harvested to non-harvested habitats change. Future research should consider how grizzly bear habitat use changes as the landscape-level context of forest harvesting changes.

Table 2-1. Area (km^2) and percent composition of land cover classes within the 2,677-km^2-study area near Hinton, Alberta. Land cover classes were determined from a remote sensing classification (Franklin et al., 2001) and forestry GIS data on clearcuts.

Land cover class	Area (km^2)	Percent
closed conifer	1109.2	41.4
clearcut	525.2	19.6
mixed forest	401.2	15.0
wetland-open bog	184.0	6.9
closed deciduous	117.9	4.4
wetland-treed-bog	94.9	3.5
road/rail/pipeline/well site	76.9	2.9
non-vegetated	34.4	1.3
open conifer	31.5	1.2
shrub	31.2	1.2
other anthropogenic	26.6	1.0
herbaceous	17.6	0.7
water	15.4	0.6
burn	7.8	0.3
open deciduous	3.0	0.1
alpine/subalpine	0.2	0.01
Total	2,677	100

Table 2-2. Explanatory map variables used for assessing grizzly bear habitat selection of clearcuts in the upper foothills of west-central Alberta, Canada.

Variable code	Description	Type	Range
age	Age of clearcut (years)	linear	0 to 46
area	Area (km^2) of clearcut	linear	0.003 to 2.683
area:perim	Area-(km^2) to-perimeter (km) ratio	linear	0.009 to 2.885
cti	Compound topographic (wetness) index	linear	7.34 to 24.45
distedge	Distance-to-edge of clearcut (km)	linear	0 to 0.8465
elev	Elevation of location (km)	linear	974 to 1712
scarYN	Scarified clear-cut	categorical	Yes or No
scartype	Scarification method	categorical	10 Categories
solar	Direct solar radiation (WH/m^2) on Day 172	linear	2391 to 4380

Table 2-3. *A priori* seasonal candidate models used to describe habitat selection within clearcuts by grizzly bear in the upper foothills of west-central Alberta, Canada. Model number, name, and structure are provided.

Model number	Model name	Model structure
1	Scarification model	age+age^2+scarYN+area
2	Silviculture model	age+age^2+scartype+area
3	Terrain model	cti+cti^2+elev+elev^2+solar
4	Landscape model	distedge+area:perim
5	Comprehensive model	age+age^2+cti+cti^2+solar+scartype+distedge+area:perim

Table 2-4. Mechanical silviculture and site preparation treatments assessed for grizzly bear habitat selection.

Scarification type	Description
BLAD	Blade (modified)
BRAC	Bracke
DONM	Donaren mound
DRAG	Drag (light or heavy)
DRSF	Drag- shark fin barrels
DSTR	Disc trencher
EXCA	Excavator mound
OTHR	Other method (hand and unknown)
PLOW	Plough (Crossley, C&H, C&S ripper)
NONE	Control (no silvicultural site preparation recorded)

Table 2-5. Seasonal estimates of habitat selection for clearcuts (1) by grizzly bears compared to matrix habitats (0; reference category) in the upper foothills of west-central Alberta, Canada.

		Robust	95% C.I.		Odds	95% C.I.	
Season	Coeff.	S.E.	lower	upper	Ratio	lower	upper
hypophagia	0.128	0.128	-0.124	0.379	1.137	0.883	1.461
early hyperphagia	0.443	0.088	0.270	0.616	1.557	1.310	1.852
late hyperphagia	-0.162	0.189	-0.531	0.208	0.850	0.588	1.231

Table 2-6. AIC-selected models for hypophagia, early hyperphagia, and late hyperphagia periods. Number of parameters (K_i), model −2 loglikelihood (−2LL), AIC, change in AIC (Δ_i) from lowest model, and Akaike weights (w_i) of model support are reported.

Season and candidate model	K_i	−2LL	AIC	Δ_i	w_i
1. *Hypophagia*					
Scarification model	5	5947.4	5957.4	103.1	<0.001
Silviculture model	13	5914.9	5940.9	86.6	<0.001
Site model	5	6013.8	6023.8	169.5	<0.001
Landscape model	3	6023.1	6029.1	174.8	<0.001
Comprehensive model	17	5820.3	5854.3	0.0	1.0
2. *Early hyperphagia*					
Scarification model	5	7634.7	7644.7	180.2	<0.001
Silviculture model	13	7575.7	7601.7	137.2	<0.001
Site model	5	7454.5	7464.5	0.0	1.0
Landscape model	3	7641.2	7647.2	182.7	<0.001
Comprehensive model	17	7522.0	7556.0	91.5	<0.001
3. *Late hyperphagia*					
Scarification model	5	4914.1	4924.1	163.5	<0.001
Silviculture model	13	4830.2	4856.2	95.6	<0.001
Site model	5	4938.0	4948.0	187.4	<0.001
Landscape model	3	4906.3	4912.3	151.7	<0.001
Comprehensive model	17	4726.6	4760.6	0.0	1.0

Table 2-7. Estimated seasonal AIC-selected model coefficients. Due to perfect avoidance relating to low sample sizes for the scarification treatment (scartype) ‘OTHR’, this category was not estimated.

Variable	Hypophagia		Early Hyperphagia		Late Hyperphagia	
code	Coef.	S.E.	Coef.	S.E.	Coef.	S.E.
age	0.098	0.027			-0.081	0.061
§age^2	-0.145	0.059			0.207	0.114
cti	-0.172	0.225	-0.108	0.105	0.157	0.169
§cti^2	0.694	0.930	0.762	0.430	0.029	0.629
elev			0.025	0.016		
§elev^2			-0.079	0.058		
§solar	-1.164	0.321	0.889	0.298	-0.170	0.791
scartype:						
BLAD	-0.268	0.292			-0.300	0.866
BRAC	0.593	0.417			0.407	0.857
DONM	-1.745	1.239			-0.711	1.050
DRAG	0.387	0.501			-0.358	1.084
DRSF	0.783	0.365			0.205	0.934
DSTR	0.166	0.476			-0.273	0.649
EXCA	0.089	0.701			-0.658	1.200
PLOW	0.470	0.245			-0.343	0.842
distedge	-2.253	1.038			-3.518	0.643
area:perim	-4.850	1.805			-5.816	3.808

§Coefficients for elev2 and solar are reported at 1,000 times their value, while age2 and cti2 are 100 times their actual value.

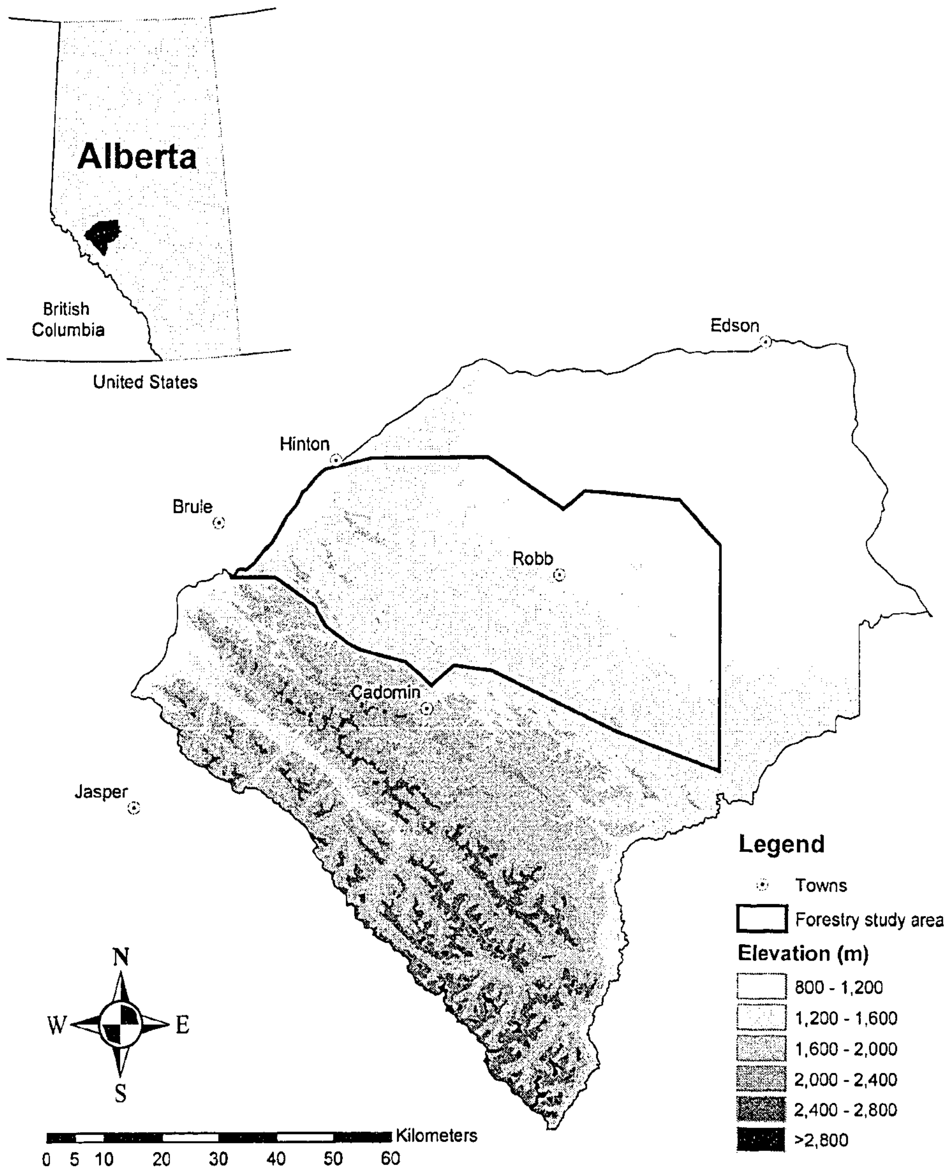

Figure 2-1. Study area map depicting elevation, local towns, overall Foothills Model Forest (FMF) study region (map extent), and secondary forestry study area for examining habitat selection related to clearcut harvesting in west-central Alberta, Canada. Location of FMF study area within Alberta is depicted in the upper left portion of the figure.

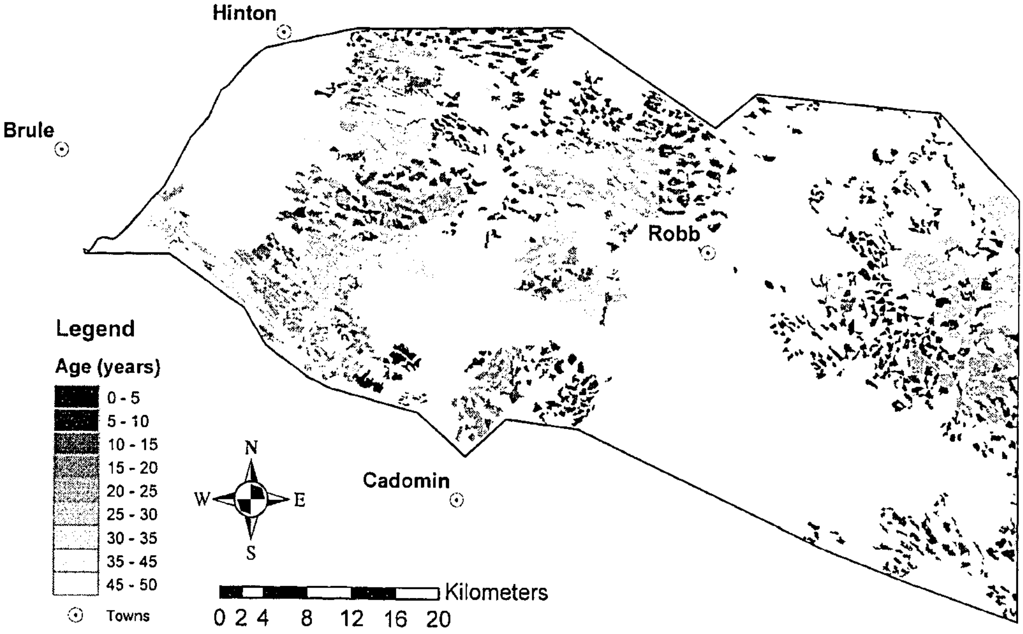

Figure 2-2. Mapped clearcuts by 5-year age class in the upper foothills of west-central Alberta, Canada.

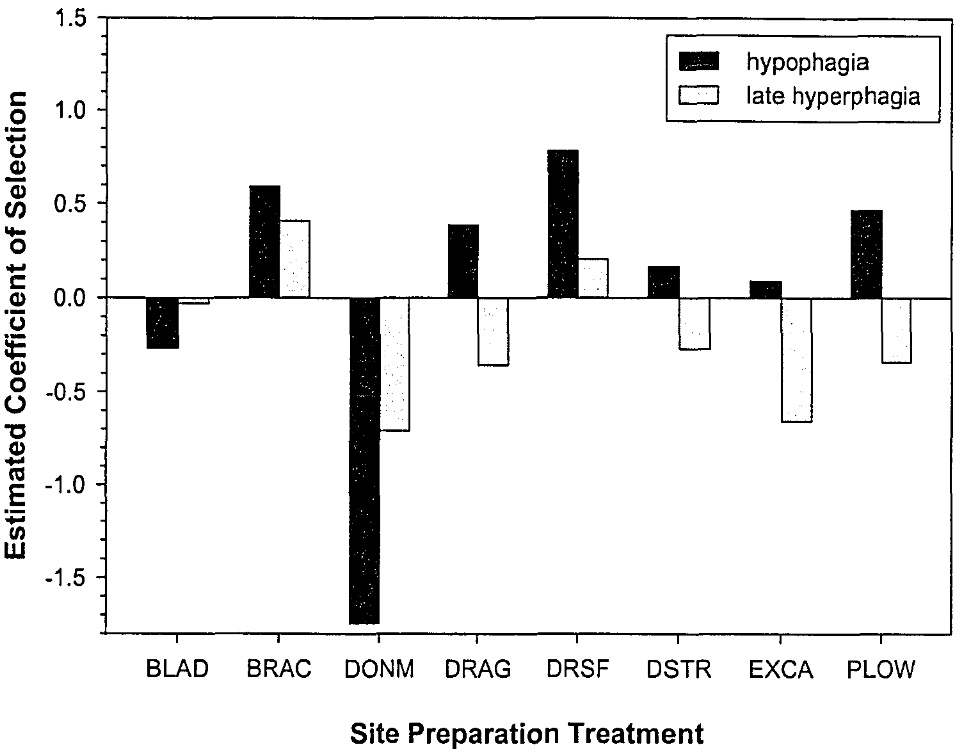

Figure 2-3. Estimated silvicultural coefficients for hypophagia and late hyperphagia seasons based on AIC-selected models and contrasts with no treatment (reference category). Category 'other' was withheld due to limitations in estimation caused by perfect collinearity from too few locations. Refer to Table 3-1 for description of treatment codes.

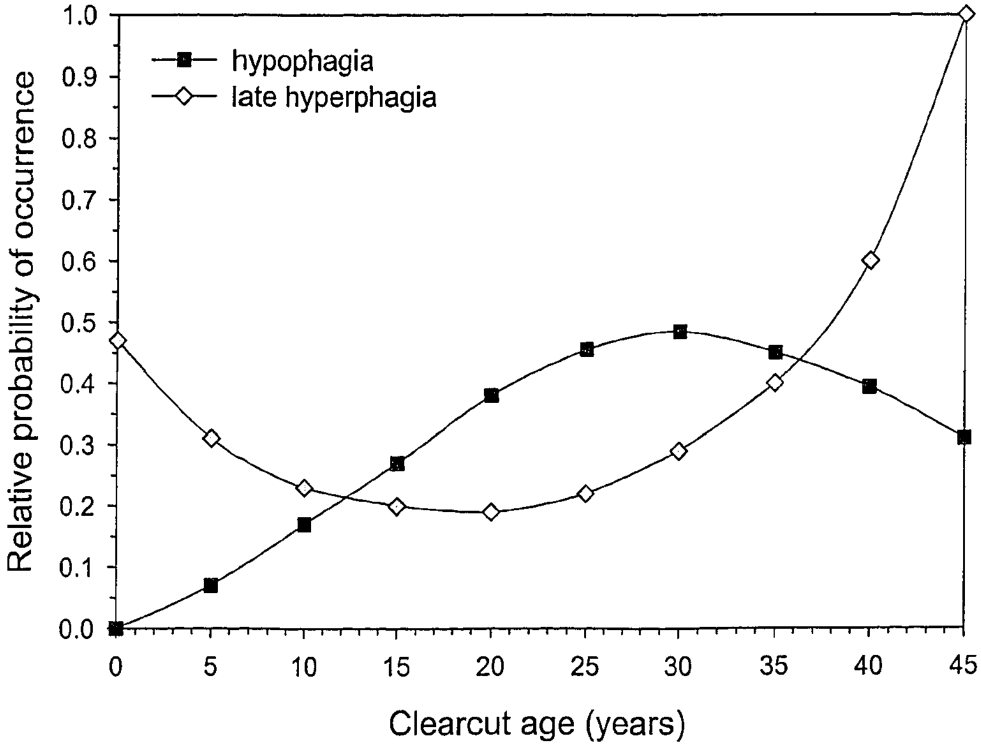

Figure 2-4. Relative probability of grizzly bear occurrence within west-central Alberta clearcuts as a function of clearcut age and season. All remaining covariates were held at their mean level. Only seasons that included clearcut age within AIC-selected models were depicted.

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Chapter 3

Grizzly bears and forestry II: distribution of grizzly bear foods in clearcuts of west-central Alberta, Canada[2]

1. Introduction

Understanding the potential impacts of forest management on rare or threatened species is a primary topic of forest ecology and conservation biology. In the Rocky Mountain ecosystems of the northern United States and southern Canada industrial resource extraction activities, including forestry, threaten the persistence of grizzly bear (*Ursus arctos* L.) populations (Banci et al., 1994; Clark et al., 1996; McLellan, 1998). Much of this threat relates to risk of human-caused mortality from increases in human access (McLellan and Shackleton, 1988; Benn and Herrero, 2002; Nielsen et al. 2004a). Forestry activities can further impact grizzly bears through changes in landscape composition, configuration, and structure (Reed et al., 1996; Tinker et al., 1998; Popplewell et al., 2003).

Optimal grizzly bear habitat has generally been considered a blend of forested and non-forested habitats (Herrero, 1972). One might therefore expect certain forest disturbances to be beneficial to bears, especially in fire-adapted forest ecosystems with a history of fire suppression (Tande, 1979; Andison, 1998; Rhumtella, 1999). As young fire-regenerated stands mature and effective fire suppression continues, timber harvesting provides a consistent mechanism of disturbance and forest renewal required for early seral specialists.

Despite a potential for habitat improvement, many studies have shown a pervasive avoidance of clearcuts by grizzly bears (Zager et al., 1983; Waller, 1992; McLellan and Hovey, 2001). Wielgus and Vernier (2003) and Nielsen et al. (2004b), however, observed use of clearcuts by grizzly bears in forest-managed landscapes. Nielsen et al. (2004b) suggested that differences between avoidance and selection of clearcuts were likely due to landscape and temporal contexts. The foothills of west-central Alberta

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lacked extensive natural openings, early seral fire-regenerated forests, and alpine meadows, which contrasted with other studies located in mountainous terrain where such habitats were common. As secure (free of human disturbance) high-quality habitats were readily available, there was little reason for selection of the non-secure alternative (i.e., clearcuts). Previous studies also have been based on VHF radiotelemetry data, where daylight locations are typical and seasonal data pooled. Nielsen et al. (2004b) found seasonal differences in selection of clearcuts, as well as greater use during the crepuscular and nighttime periods. Clearcuts appeared to provide an alternate habitat resource for certain landscape and temporal contexts, albeit a potentially risky one at that (Benn and Herrero, 2002; Nielsen et al., 2004a).

Loss of early seral forests and natural openings has the potential to cause population declines in bears (Beecham, 1980; 1983; Irwin and Hammond, 1985; Lindzey et al., 1986; Noyce and Coy, 1989; McLellan and Hovey, 2001). Young regenerating forests contain greater abundances of most critical bear foods including fruits, ants, ungulates, green herbaceous vegetation, roots and other subterranean foods (Martin, 1983; Zager et al., 1983; Irwin and Hammond, 1985; Knight, 1999). Availability of consistent high-quality foods shapes individual nutritional level and ultimately population size (Craighead et al., 1995). However, a general sense of how specific environmental factors and past management actions influence distribution patterns of food resources, especially within successional clearcuts, is lacking. Previous food modelling efforts have focused on protected mountainous ecosystems like Yellowstone (Mattson, 2000) or Jasper (Nielsen et al., 2003) National Parks, where forest harvesting does not occur and populations are generally considered secure. Given the potential for habitat and population change outside of protected areas, an examination of food resource availability and abundance for forest management areas is a conservation priority. Identification of food patches within forest management stands provides opportunities for protection, maintenance, and enhancement of grizzly bear habitats. Moreover, specific assessments of food resource availability allow for fine-level interpretations of selection and inferences of mechanism (Morrison, 2001). Ultimately the understanding of critical food resources will allow for better grizzly bear management and conservation.

Here we explore the distribution of grizzly bear foods in an attempt to better understand the observed behaviour of grizzly bears in west-central Alberta, Canada (Nielsen et al., 2004b). Specifically, we investigated how scarification, canopy cover, clearcut age, and terrain characteristics influenced the occurrence of 13 grizzly bear foods, while further examining how fruit occurrence and production varied for 6 fruit-bearing species. Our objectives were three-fold: (1) determine whether differences in grizzly bear foods occurred between upland forests, our reference condition, and clearcuts; (2) develop local models describing grizzly bear food occurrence within clearcuts; and (3) describe patterns reflecting fruit and non-fruit producing clearcuts, together with an overall comparison of fruit production between clearcuts and upland forest sites. We hypothesized that forest disturbance through clearcut harvesting enhances the occurrence and diversity of grizzly bear foods. Food resources were expected, however, to be patchy and responding to local environmental gradients and management history, thereby requiring additional environmental covariates. Relationships between food resources and clearcut harvesting should help explain patterns in grizzly bear habitat use as well as provide on-the-ground management solutions to conservation problems.

2. Methods

2.1. Field sampling

The environmental characteristics of the study area are described fully in Nielsen et al. (2004b). During the growing seasons (June–August) of 2001–02, we established 355 sample plots within clearcuts and 183 sample plots within reference forest stands. All reference forest stands used were in upland sites dominated by coniferous tree species having a minimum composition of 20% lodgepole pine and not disturbed by anthropogenic activities. Upland conifer stands are one of the primary targets for local clearcut harvesting. Based on geographical information system (GIS) fire history maps, reference forest plots averaged 105 (±37 SD) years of age. Sampling procedures were the same for both clearcuts and forest stands. We used a GIS to identify random coordinates stratified within clearcut and upland forest sites based on a land cover classification provided by Franklin et al. (2001). To ensure an approximately equal proportion of plots within different aged clearcuts, we used a stratified random design to assign random clearcut locations to 5-yr age classes. Age was not considered as a stratum for upland forest sites. A small number of randomly selected grizzly bear locations identified from global position system (GPS) radiotelemetry data were added as additional plots to increase sample size. We navigated to all field coordinates using a hand-held Garmin GPS III plus unit, attempting to locate the plot centre to within no more than 10 m of the coordinates.

At each field plot, we established a 20-m transect running south-to-north with the 10 m location being the plot centre. Five 0.5-m^2 (70.7 mm × 70.7 mm) herbaceous quadrats were established along each transect at 5 m intervals. Within these quadrats, we recorded the presence of 10 grizzly bear food items. The presence of *Shepherdia canadensis* was measured in the shrub-layer (plants >0.5 m in height) along a belt transect 1 × 20 m (20-m^2) in size. At each plot, we estimated fruit production for *Arctostaphylos uva-ursi*, *Shepherdia canadensis*, and all *Vaccinium* species. Berries were counted within herbaceous quadrats (*Arctostaphylos uva-ursi* and *Vaccinium* spp.) or belt transects (*Shepherdia canadensis*) using hand-held tally counters and standardized to a per hectare basis. A sub-sample of ripe fruit were weighed and used to estimate average fresh weight productivity (kg/ha) for each species. Given that berries were not present for the entire sampling period, we considered only those plots visited on or after July 15 and before September 1 to be available for characterizing fruit presence and productivity. Finally, we recorded the presence of ants (in mounds and/or woody debris) and ungulate pellets using meander searches within 10 m of either side of the established transect (20 × 20 m; 400-m^2). We consider ungulate pellets as an index of animal use and not a directly scalable measure of biomass or ungulate density. Caution should be given to interpretation of forest and non-forest occurrence of pellets, as biases are known to occur (Collins and Urness, 1979). All analyses reported here were at the level of the plot and thus all 5 herbaceous quadrats were combined. Taxonomy of vascular plants follows that of Voss (1994).

2.2. Predictor variables

We dummy coded each plot to identify whether it was in a clearcut (1) or forest stand (0). For models specifically examining food occurrence within clearcuts, we queried age and silvicultural history of sites using a GIS forestry database provided by Weldwood of Canada Ltd. (Hinton, Alberta). However, given the small sample of clearcuts visited relative to the availability of different silvicultural (site preparation) treatments, we were forced to dissolve silvicultural history into either scarified (1) or non-scarified (0) treatments, again using dummy coding.

To assess terrain-influenced conditions, we used a 26.7 m digital elevation model (DEM) that described the elevation and local micro-site conditions. From this DEM, we estimated elevation (km) for each plot. We further derived two terrain-related variables from the DEM. First, we calculated an index of soil wetness commonly referred to as the compound topographic index (CTI). CTI has previously been found to correlate with several soil attributes including horizon depth, silt percentage, organic matter, and phosphorous (Moore et al., 1993, Gessler et al., 1995). We used CTI as a surrogate for soil conditions, since a soil survey was not available for the entire area. CTI was calculated from the DEM using the spatial analyst extension in ArcView 3.2 and a CTI script from Rho (2002). Our second DEM-derived variable was a slope-aspect index (SAI) from Nielsen and Haney (1998), modified from the Beer's aspect transformation (Beers et al., 1966) and having the following form:

$$SAI = \sin(aspect + 225) \times (slope/45) \qquad (3\text{-}1),$$

where aspect and slope were derived from the DEM and measured in degrees. Slopes for all sites were $\leq 45°$, thus the sine wave was scaled from a flat line at a 0° slope to that of -1 (mesic northeast aspect) or $+1$ (xeric southwest aspect) at a 45° slope. Our final predictor variable was average canopy cover, estimated for each plot using a spherical densiometer (Lemon, 1956). Spherical densiometer readings were taken above each herbaceous quadrat facing the 4 cardinal directions (north, east, south, and west) and averaged over the entire plot (all five quadrats). Quadratic terms were fit for age, canopy, CTI and elevation given that non-linear relationships were likely (Vaughan and Ormerod, 2003).

2.3. Model building strategies and statistical methods

2.3.1. Grizzly bear food occurrence for clearcuts versus reference forests

We used logistic regression to contrast the occurrence of 13 grizzly bear foods (Table 3-1) for clearcuts (1) and upland forests (0). Important food resources were based on food habits reported elsewhere (Hamer and Herrero, 1987; Nagy et al., 1989; Hamer et al., 1991; McLellan and Hovey, 1995). We report all logistic regression results as odds ratios (Hosmer and Lemeshow, 1989) with the reference category being forest plots. These odds ratios were interpreted as the odds that grizzly bear foods were occurring in clearcuts compared with that of reference upland forest stands. We used a likelihood ratio χ^2 test to determine the significance of individual food models.

2.3.2. Distribution of grizzly bear foods in clearcuts

We examined grizzly bear food distribution for clearcuts by modelling their occurrence as a function of canopy, age, scarification, elevation, CTI, and SAI. Clearcut plots were divided into 2 groups following a random sample test set validation. The first group, the model-training group, represented a random 85% sub-sample of plots used for model development, while the remaining sub-sample (15%), the model-testing group, were used for assessing model performance by independent validation. Using model-training data and explanatory variables (Table 3-2), we developed logistic regression models describing the occurrence of each grizzly bear food item. Linear explanatory variables were assessed for collinearity prior to modelling through Pearson correlation (r) tests and variance inflator function (VIF) diagnostics. All variables with correlations (r) $>|0.6|$, individual VIF scores >10, or the mean of all VIF scores considerably larger than 1 (Chatterjee et al., 2000) were assumed to be collinear and not included within the same model structure. Using these guidelines, we found that age and canopy were strongly correlated ($r = 0.66$) and therefore were not considered for inclusion in the same candidate model. No further evidence of collinearity was evident.

Using these predictor variables, we generated 6 *a priori* candidate models (Table 3-3). We evaluated model selection using Akaike's information criteria (Burnham and Anderson, 1998; Anderson et al., 2000) with a small sample size correction (AIC_c). Akaike weights (w_i) were used to determine the approximate 'best' model given the data and candidate models tested for each bear food. We assessed fit and predictive accuracy of training data using Hosmer and Lemeshow (1980; 1989) goodness-of-fit χ^2 tests ($\hat{C}$) and receiver operator characteristic (ROC) area under the curve estimates. Significant $\hat{C}$ values indicated poor fit between the model and data, while ROC scores were assessed based on their value falling into one of three categories. Those ranging from 0.5 to 0.7

were taken to represent 'low' model accuracy, while values between 0.7 and 0.9 were considered 'good', and finally those above 0.9 were considered to have 'high' model accuracy (Swets, 1988; Manel et al., 2001).

We used our withheld model-testing data to further assess the fit ($\hat{C}$) and predictive performance (ROC) as model verification. Finally, as an additional validation, we assessed the predictive capacity of individual AIC$_c$-selected grizzly bear food models for 136 independent field plots collected for separate purposes within the same study area in 2002. Although these independent plots were collected at a different scale (5 quadrats 1-m^2 in size), we felt that a general secondary validation was worthwhile. To determine the predictive capacity of our models for these data, we chose a probability cut-off point for AIC$_c$-selected grizzly bear food models that maximized both specificity and sensitivity curves simultaneously (Swets, 1988). Using AIC$_c$-selected model coefficients, we estimated the probability of occurrence for each grizzly bear food item and predicted either a presence (≥cut-off point) or absence (<cut-off point) for each of the 136 independent plots. We estimated the percent correctly classified (PCC) for each species by determining the proportion of total plots correctly predicted. We considered models with a PCC of ≥70% to be reasonably predictive. Finally, using the AIC$_c$-selected model structure we estimated probabilities of occurrence for each variable and food item by exploring the range of predictions for that factor (within the observed range; Table 3-2), while holding all other variables in the model at their mean level. We plotted these predictions to provide visual interpretation of responses and estimated optima.

2.3.3. Distribution of fruit in clearcuts

To examine factors influencing the occurrence of fruit production within clearcuts, we again used logistic regression and the 6 *a priori* candidate models described in the previous section. A total of 6 species were examined for fruit production: 4 species of *Vaccinium*; *Arctostaphylos uva-ursi*; and *Shepherdia canadensis*. We used a conditional modelling strategy including only those locations where the species was present to examine fruit occurrence. At these species presence sites, we compared plots that lacked fruit production (0) with those where fruit production was present (1) during the fruiting period (July 15–August 31). Failure to discriminate the two events was interpreted to mean that berry production was random with respect to the examined variables and candidate models and thus simply mimicking the distribution of the species. Due to relatively low sample sizes resulting from the absence of species and/or berry-producing sites, along with our limited berry season, we combined both 2001 and 2002 field seasons. Similarly, *Vaccinium caespitosum* and *V. membranaceum* were too uncommon to model individually. Instead, we combined the two species into a *Vaccinium caespitosum-membranaceum* complex. We report the general frequency of fruit, given the presence of the species, while further estimating the position at which fruit occurrence was maximized for individual AIC_c-selected variables.

2.3.4. Fruit productivity for clearcuts and reference forests

Average productivity of *Arctostaphylos uva-ursi*, *Shepherdia canadensis*, and 4 species of *Vaccinium* were estimated for clearcut and upland forest stands on a per hectare basis. We examined fruit production for 2 separate conditions during the fruiting period: (1) presence-only sites, where average fruit production was estimated for only those plots where that species was initially present; and (2) all sites where, regardless of a conditional presence of the species, fruit production was estimated. Finally, we compared the difference in estimated average fruit production for all sites within clearcuts and forests for each species or species complex, along with the total fruit production, by using Mann–Whitney *U* tests.

3. Results

3.1. Grizzly bear food occurrence in clearcuts versus reference forests

Ants, *Equisetum* spp., *Hedysarum* spp., *Taraxacum officinale*, *Trifolium* spp., and *Vaccinium myrtilloides* had significantly higher occurrence in clearcuts than upland forest sites (Table 3-4). *Taraxacum officinale* had the largest odds ratio at 13.9, with an observed difference in plot frequency of 38.9% for clearcuts and only 4.4% for upland forests. Although not as substantial, *Trifolium* spp., ants, and *Hedysarum* spp. also had high odds ratios of 6.7, 5.4, and 4.3 respectively, while *Equisetum* spp. and *Vaccinium myrtilloides* had smaller, but still significant odds ratios of 2.4 and 1.8.

In contrast to those grizzly bear foods positively associated with clearcuts, 3 species, *Vaccinium caespitosum*, *V. membranaceum*, and *V. vitis-idaea*, were more likely to occur in upland forests (Table 3-4). Although *Vaccinium membranaceum* and *V. vitis-idaea* had similar odds ratios at 0.2, their observed frequency was substantially different. *Vaccinium membranaceum* occurred at a 6.2% and 22.4% frequency for clearcuts and upland forest stands respectively, while *V. vitis-idaea* was much more common with a frequency of 51.0% for clearcuts and 81.4% for upland forests. *Vaccinium caespitosum* occurrence was more similar between clearcuts and forests with an odds ratio of 0.6, but still significantly more likely to occur in upland forests. Finally, 4 grizzly bear foods lacked any significant difference in occurrence between clearcuts and forests. These included *Arctostaphylos uva-ursi*, *Heracleum lanatum*, *Shepherdia canadensis*, and ungulate pellets (Table 3-4).

3.2. Distribution of grizzly bear foods in clearcuts

Based on AIC_c weights (w_i) there was large variation in support for the 6 *a priori* candidate models tested (Table 4-5). Only the scarification-canopy model had little to no support for any one grizzly bear food. Excluding 3 species of *Vaccinium* that all had support for the terrain model, no obvious patterns were evident between candidate models and food groups. Using likelihood ratio (LR) χ^2 tests, we found all AIC_c-selected models to be significant (Table 3-5), although the proportion of deviance explained varied from a low of 2.8% for *Trifolium* spp. to a high of 31.3% for *Hedysarum* spp. There were no significant differences in fit between training data and selected models for any individual grizzly bear food using Hosmer and Lemeshow goodness-of-fit tests. Testing data, however, revealed poor fit for 4 species: *Equisetum* spp., *Hedysarum* spp., *Vaccinium membranaceum*, and *V. vitis-idaea* (Table 3-5). Classification accuracy (ROC) for model training data proved poor (0.5–0.7) for 5 of 13 grizzly bear foods and good (0.7–0.9) for the remaining 8 food items. Decreasing model accuracy was evident for testing data on all 4 species that revealed poor fit. Using independent sample data, we found 6 of the 11 food items tested to have reasonably good (>70% PCC) prediction (Table 3-5). Overall, we found that ants, *Arctostaphylos uva-ursi*, *Shepherdia canadensis*, and *Vaccinium myrtilloides* had consistently good fit, classification accuracy, and predictive capacity for both training and testing data. Other food items proved to be either inconsistent between training and testing data or low in classification accuracy suggesting that further examination and modelling was required.

The scarification variable emerged in 7 of 13 AIC_c-selected models, having strong negative effects on the occurrence of *Arctostaphylos uva-ursi*, *Hedysarum* spp., and *Shepherdia canadensis*, while weaker negative effects on ants and ungulate pellets (Table 3-6; Figure 3-1). In contrast, *Equisetum* spp. appeared to respond positively to scarification. Age or overstorey canopy was represented in 10 of 13 AIC_c-selected models (Table 3-6). Non-linear responses, with maximum occurrence at intermediate levels of overstorey canopy or age, was evident for 7 foods: ants, *Arctostaphylos uva-ursi*, *Equisetum* spp., *Hedysarum* spp., *Shepherdia canadensis*, ungulate pellets, and *Vaccinium vitis-idaea* (Figure 3-2a, 3-2b). *Taraxacum officinale* and *Trifolium* spp. decreased in occurrence as canopy increased, while occurrence of *Heracleum lanatum* increased with increasing canopy (Figure 3-2b).

Terrain-derived variables of compound topographic index (CTI), elevation, and slope-aspect index (SAI) were selected in 9 of 13 grizzly bear food models (Table 3-6). Non-linear responses for CTI and elevation were useful in describing ant, *Arctostaphylos uva-ursi*, and *Equisetum* spp. occurrence. Most other foods responded in a more linear manner, occurring with greater frequency in areas with low or high soil moisture (CTI), low or high elevation, or xeric or mesic slopes (Figure 3-2c, 3-2d, 3-2e).

3.3. Distribution of fruit in clearcuts

For all 6 species, the canopy model was selected as the most parsimonious model describing fruit occurrence. Little to no support was evident for other factors influencing fruit occurrence, once the presence of the species was fixed. *Arctostaphylos uva-ursi*, *Vaccinium caespitosum-membranaceum* complex, and *V. vitis-idaea* were predicted to occur with maximum fruit occurrence at intermediate canopy levels, 34, 34, and 64% respectively (Table 3-7; Figure 3-3). In contrast, *Shepherdia canadensis* and *Vaccinium myrtilloides* responded in a linear manner with maximum fruit occurrence predicted at 0 and 100% overstorey canopy respectively. Overall, *Arctostaphylos uva-ursi* fruit occurred in 45% of clearcut sites, *Vaccinium caespitosum-membranaceum* in 20% of sites, *Vaccinium vitis-idaea* in 36% of sites, *Shepherdia canadensis* in 68% of sites, and finally *Vaccinium myrtilloides* in 46% of sites (Table 3-7). In some cases, maximum occurrence of fruit differed from that of species occurrence. Fruit occurrence of *Shepherdia canadensis* was optimal at low to negligible overstorey canopy levels, while the maximum predicted occurrence for the species in clearcuts was at more intermediate canopy levels.

3.4. Fruit productivity for clearcuts versus reference forests

For clearcut locations where fruiting species were present, average fruit production ranged from 22,700 berries/ha for *Acrtostaphylos uva-ursi* to 200,400 berries/ha for *Shepherdia canadensis* (Table 3-8). In comparison, when disregarding the conditional presence of the species (all sites), these estimates dropped to 6,000 berries/ha for *Acrtostaphylos uva-ursi* to 36,900 berries/ha for *Shepherdia canadensis*. Total fruit production for clearcuts (all sites) was estimated at 127,300 berries/ha or an estimated fresh weight production of 22.9 kg/ha. In upland forest stands, fruit production for sites where the species was present was estimated to range from 26,000 berries/ha for *Vaccinium myrtilloides* to 150,200 berries/ha for *Vaccinium vitis-idaea* (Table 3-8). Disregarding the conditional presence of the species (all sites), fruit production dropped from an estimated abundance of 2,500 berries/ha for *Vaccinium myrtilloides* to 116,200 berries/ha for *V. vitis-idaea*. Total fruit production for upland forests was estimated at 177,100 berries/ha, the majority of which were from *Vaccinium vitis-idaea*, or an estimated fresh weight production of 32.3 kg/ha. Mann–Whitney *U* tests revealed that only *Vaccinium myrtilloides* and *V. vitis-idaea* fruit production differed for clearcut and upland forest sites (Table 3-8). *Vaccinium myrtilloides* had significantly greater production in clearcuts ($U = 2.22, p = 0.026$), while *Vaccinium vitis-idaea* had significantly greater production in upland forests ($U = -4.72, p < 0.001$). Although species-specific differences existed, total fruit production (berries/ha) was not found to significantly differ between clearcut and upland forest sites.

4. Discussion

Ants, *Equisetum* spp., *Hedysarum* spp., *Taraxacum officinale*, *Trifolium* spp., and *Vaccinium myrtilloides* had higher frequencies of occurrence in clearcuts compared to upland forest stands. Clearcut harvesting appeared to benefit these species through the disturbance of overstorey canopy structure, supporting our initial hypothesis. As would be expected and previously reported, the exotic species, *Taraxacum officinale* and *Trifolium* spp., responded favorably to clearcutting and mechanical disturbance

(Haeussler et al., 1999; Roberts and Zhu, 2002). Unlike these exotics, however, *Vaccinium cespitosum*, *V. membranaceum*, and *V. vitis-idaea* were all more likely to occur in upland forests, suggesting that clearcut harvesting was negatively impacting their occurrence. We found no evidence that *Arctostaphylos uva-ursi*, *Heracleum lanatum*, *Shepherdia canadensis*, and ungulate pellets occurred at different frequencies of occurrence for clearcuts and upland forest sites, although ungulate pellets have the potential for bias in distribution (Collins and Urness, 1979). Frequencies of *Arctostaphylos uva-ursi* and *Shepherdia canadensis* also should be interpreted with caution, as previous work suggests greater occurrence for early seral or open forests (Hamer, 1996; del Barrio et al., 1999). The lack of a difference suggests that clearcut harvesting may be impacting occurrence. Comparisons with similar open or naturally disturbed early seral forests would be required to more fully assess these differences.

Of the 6 *a priori* candidate models evaluated, only the scarification-canopy model had little to no support for any one grizzly bear food item. The remaining 5 candidate models that included the variables canopy cover, scarification, clearcut age, CTI, SAI, and elevation proved useful in describing local patterns of grizzly bear food occurrence for clearcuts. Goodness-of-fit ($\hat{C}$) and model accuracy (ROC) generally revealed model fit and predictive accuracy, while model validation revealed reasonable accuracy of predictions for the majority of grizzly bear foods. This suggests that maps describing food occurrence could be derived from the models presented here. Modelling efforts of nearby areas have already revealed the utility of using food-based models for predicting grizzly bear habitat (Nielsen et al., 2003). The same methods could be used to derive habitat quality maps for clearcuts.

Canopy cover and age of clearcut were strong predictors of food occurrence with most species peaking at intermediate canopy and age levels. The scarification variable, emerging in most AIC_c-selected models, had negative impacts on the occurrence of *Arctostaphylos uva-ursi*, *Hedysarum* spp., and *Shepherdia canadensis*, while weaker effects on ant and ungulate pellet occurrence. In contrast, *Equisetum* spp. and *Vaccinium vitis-idaea* appeared to respond positively to scarification. Previous work has shown negative affects from mechanical scarification of Ericaceae shrubs, suggesting that the destruction of rhizomes were to blame (Zager et al., 1983; Haeussler et al., 1999; Roberts and Zhu, 2002). Scarification also has been suggested for declines in *Shepherdia canadensis* abundance (Knight, 1999). Root and rhizome structure were likely to have been disturbed, preventing vegetative re-sprouting (Noste and Bushey, 1987). Methods to reduce the severity of mechanical scarification or implementation of post-scarification remediation activities may be necessary. Terrain variables, including elevation, compound topographic index (CTI), and slope-aspect index (SAI), were all found to be important predictors of food occurrence. Location of species optima varied from low elevation sites to xeric or mesic soils. Small-scale changes in terrain therefore had the potential to influence food occurrence within individual clearcuts. Remediation should recognize favourable resource niches when planning actions to enhance grizzly bear habitat. Enhancing habitats near human access, however, may result in increasing the risk of human-caused mortality for grizzly bears (Nielsen et al., 2004a). Therefore, human access will need to be managed for sites where active remediation is occurring.

Responses in fruit occurrence sometimes differed from that of plant occurrence. For the 6 fruit species examined, canopy cover was the only variable that was found to be useful for predicting fruit occurrence, once the species was present. *Shepherdia canadensis*, for instance, was most likely to occur at intermediate canopy levels, while fruit production peaked in open sites. Hamer (1996) found similar patterns between canopy and fruit production for *Shepherdia canadensis*. Fruit production was generally stable until canopy cover reached more than 50%, causing precipitous declines. Fruit occurrence for the other 5 species maximized at either intermediate or high canopy levels. Maintenance of canopy levels below or near 50% through silvicultural thinning of selected micro-sites favorable for fruit-bearing species could provide attractive seasonal grizzly bear habitat through enhancement of fruit production if human access is managed.

For all fruit-bearing species, the average estimated fresh weight production of clearcuts was 22.9 kg/ha, while upland forests averaged 32.3 kg/ha. However, no significant difference in total fruit production was evident, although *Vaccinium myrtilloides* and *V. vitis-idaea* were found to differ at the individual species level. *Vaccinium myrtilloides* had greater fruit production in clearcuts, while *V. vitis-idaea* had high fruit production in upland forests. Total fruit production for *Vaccinium* species was estimated at 15.1 kg/ha and 27.6 kg/ha for clearcut and upland forest stands respectively.

These productivity levels were more similar to those reported by Noyce and Coy (1989) for conifer stands in Minnesota (9 kg/ha), rather than for Russia at 188 kg/ha (Cherkasov, 1974) and 296 kg/ha (Kolupaeva, 1980) or Alaska at 270 kg/ha (Hatler, 1967). Higher productivity levels from Russia and Alaska may reflect historical artifacts from previous forest fires or other nutrient inputs necessary for large crops (Penney et al., 1997). Comparisons of fruit production for regenerating burns and clearcuts support this conclusion (Martin, 1983; Zager et al., 1983). Although silvicultural management of clearcuts rarely involves treatment with fire, such actions may be necessary to fulfill the natural functions missing in mechanical treatments. Although total fruit production was slightly greater for upland forest stands, availability of herbaceous foods, roots and tubers, and ants were greater in clearcuts. Food habit studies have shown the importance of these items in grizzly bear diets (Hamer and Herrero, 1987; Edge et al., 1990; Hamer et al., 1991; McLellan and Hovey, 1995; Elgmork and Unander, 1999; Knight, 1999; Swenson et al., 1999).

5. Conclusion

Despite management implications, little information is currently available regarding specific patterns of grizzly bear foods in clearcuts. We found that clearcuts in the foothills of west-central Alberta provided a diverse array of grizzly bear foods. Use of clearcuts by grizzly bears in the study area was greatest during the mid-summer period (early hyperphagia) when green herbaceous and ant feeding was at its greatest and lowest for the late-summer period (late hyperphagia) when foraging for fruit was at its highest (Nielsen et al., 2004b). This supports our food modelling results, as herbaceous material and ants were more diverse and abundant in clearcuts than forests, while fruit production was lower in clearcuts than forests. We suggest that for forested areas lacking extensive natural openings or recent fires (e.g., extensive fire suppression), clearcut harvesting provides a potential habitat surrogate if control of human access is addressed. Terrain, clearcut age, canopy cover, and scarification characteristics influenced local patterns of food occurrence, while canopy cover alone influenced fruit occurrence. Consistent with our hypothesis, a number of grizzly bear foods increased in occurrence following clearcut harvesting. Not all foods responded favorably, however, and thus methods of promoting grizzly bear food availability through forest management, including scarification and site preparation techniques, may be required. Active management, such as the planting of fruit-producing shrubs like *Shepherdia canadensis*, may further mitigate negative effects observed from mechanical scarification. Terrain-related micro-sites, however, should be identified for potential food plantings prior to application. Despite the maintenance and/or enhancement of grizzly bear foods in clearcuts, further control and/or management of human access will be required. If human access is not controlled, we suggest that food remediation activities occur in locations that are relatively secure from human access to avoid attractive sinks or ecological traps (Delibes et al., 2001; Nielsen et al., 2004a).

Table 3-1. List of grizzly bear foods examined in clearcuts and upland forest stands of west-central Alberta, Canada.

Grizzly bear food	Food item number	Type of food or feeding activity	Season of use
ants	1	myremocaphagy	summer
Arctostaphylos uva-ursi	2	fruits	spring and late summer
Equisetum spp.	3	herbaceous	summer
Hedysarum spp.	4	roots/tuber digging	spring and fall
Heracleum lanatum	5	herbaceous	summer
Shepherdia canadensis	6	fruits	late summer and fall
Taraxacum officinale	7	herbaceous	spring and summer
Trifolium spp.	8	herbaceous	spring and summer
ungulates (pellets)	9	carnivorous	spring to early summer/fall
Vaccinium caespitosum	10	fruits	late summer and fall
Vaccinium membranaceum	11	fruits	late summer and fall
Vaccinium myrtilloides	12	fruits	late summer and fall
Vaccinium vitis-idaea	13	fruits	late summer and fall

Table 3-2. Environmental variables used to predict the occurrence of grizzly bear foods within west-central Alberta clearcuts. Variable code used for candidate models, variable description, units (with range for non quadratic parameters), and data sources are presented.

Variable code	Variable description	Units and range	Data source
age	age	years (0 to 46)	GIS forest polygons
canopy	canopy	% canopy (0 to 100)	Field measurements
cti	compound topographic index (CTI)	index (8 to 21)	GIS model from DEM
elev	elevation	metres (957 to 1596)	DEM
scar	scarification	yes (1) or no (0)	GIS forest polygons
sai	slope-aspect index	index (-1 to 1)	GIS model from DEM

Table 3-3. *A priori* candidate models used for assessing distribution of grizzly bear foods within clearcuts of west-central Alberta. Model number, parameter structure (variables), name, and total number of parameters (including constant) used for calculating Akaike weights (w_i) for model selection.

Model number	Model structure	Model name	*K*
1	scar+age+age^2	scarification-age	4
2	scar+canopy+canopy^2	scarification-canopy	4
3	cti+cti^2+elev+elev^2+sai	terrain	7
4	canopy+canopy^2	canopy	3
5	scar+age+age^2+cti+cti^2+elev+elev^2+sai	mixed-age	9
6	scar+canopy+canopy^2+cti+cti^2+elev+elev^2+sai	mixed-canopy	9

Table 3-4. Frequency of occurrence for 13 grizzly bear foods within clearcut (*n* = 355) and reference forest (*n* = 183) plots. Odds ratio (± S.E.) of finding grizzly bear foods within clearcuts of west-central Alberta when compared to reference upland forest stands are reported from logistic regression models. Model likelihood ratio (LR) χ^2 test and associated significance (*p*) levels are reported.

Grizzly bear food item	Clearcut frequency	Forest frequency	Odds ratio	S.E.	Model LR χ^2	*p*
ants	65.9	26.2	5.44	1.098	78.42	<0.001
Arctostaphylos uva-ursi	21.7	19.1	1.17	0.267	0.49	0.485
Equisetum spp.	43.9	24.6	2.40	0.486	20.01	<0.001
Hedysarum spp.	10.7	2.7	4.27	2.069	12.29	0.001
Heracleum lanatum	4.2	5.5	0.76	0.320	0.41	0.523
Shepherdia canadensis	17.8	14.2	1.30	0.330	1.12	0.290
Taraxacum officinale	38.9	4.4	13.92	5.253	88.92	<0.001
Trifolium spp.	23.4	4.4	6.67	2.554	37.23	<0.001
ungulates (pellets)	36.1	39.9	0.85	0.159	0.76	0.385
Vaccinium caespitosum	37.8	49.7	0.61	0.113	7.09	0.008
Vaccinium membranaceum	6.2	22.4	0.23	0.229	28.87	<0.001
Vaccinium myrtilloides	14.7	8.7	1.79	0.540	4.02	0.045
Vaccinium vitis-idaea	51.0	81.4	0.24	0.517	50.22	<0.001

Table 3-5. AIC_c-selected models and Akaike weights (w_i) with corresponding metrics of overall model significance, fit, and classification accuracy using training and testing data. All model likelihood ratio (LR) χ^2 tests were significant at $p<0.05$. Percent deviance (Dev.) explained represented the reduction in the log likelihood from the null model. Probabilities for Hosmer and Lemeshow (1980) goodness-of-fit χ^2 statistic ($p\ \hat{C}$) were reported for model and data fit, while receiver operating characteristic (ROC) curves were used to assess model classification accuracy. Independent (Ind.) data from a concurrent study was used to assess the percent correctly classified (PCC) based on specified optimal probability cut-off levels.

	AIC_c selected	AIC_c	Model	% Dev.	Training data		Testing data		Optimal	Ind.
Grizzly bear food item	model	w_i	LR χ^2	explained	$p\ \hat{C}$	ROC	$p\ \hat{C}$	ROC	cut-off	PCC
ants	mixed-age	0.977	62.33	16.0	0.338	0.755	0.631	0.742	0.5452	-
Arctostaphylos uva-ursi	mixed-canopy	0.892	78.81	24.1	0.063	0.825	0.342	0.705	0.3120	72.79
Equisetum spp.	mixed-canopy	0.935	44.58	10.8	0.919	0.719	0.031	0.547	0.4838	87.50
Hedysarum spp.	mixed-canopy	0.997	62.59	31.3	0.442	0.860	<0.001	0.640	0.0934	91.18
Heracleum lanatum	canopy	0.690	6.11	5.7	0.545	0.667	0.151	0.378	0.0275	47.06
Shepherdia canadensis	mixed-age	0.692	80.96	28.9	0.960	0.862	0.470	0.814	0.2115	83.82
Taraxacum officinale	canopy	0.515	26.18	6.6	0.174	0.660	0.236	0.643	0.3522	64.71
Trifolium spp.	canopy	0.623	9.21	2.8	0.662	0.615	0.793	0.670	0.2569	58.09
ungulates (pellets)	scarification-age	0.548	18.25	4.6	0.958	0.644	0.564	0.604	0.4212	-
Vaccinium caespitosum	terrain	0.512	12.42	3.1	0.325	0.617	0.596	0.616	0.3840	47.06
Vaccinium membranaceum	terrain	0.608	14.58	10.7	0.151	0.716	0.027	0.612	0.0527	84.56
Vaccinium myrtilloides	terrain	0.681	51.31	19.4	0.306	0.806	0.722	0.750	0.1547	67.65
Vaccinium vitis-idaea	mixed-age	0.388	17.74	4.3	0.424	0.632	0.012	0.487	0.5231	86.03

Table 3-6. Estimated coefficients (β_i) and standard errors (in parentheses) for AIC$_c$-selected models describing the probability of occurrence for grizzly bear foods within clearcuts of west-central Alberta, Canada.

Grizzly bear food item	scarify	age	§age^2	canopy	§canopy^2	cti	cti^2	elev	§elev^2	sai	constant
ants	-0.579	0.303	-0.561			0.816	-0.027	-0.021	0.074	3.149	6.890
	(0.582)	(0.048)	(0.100)			(0.666)	(0.028)	(0.017)	(0.065)	(1.197)	(11.259)
Arctostaphylos uva-ursi	-0.836			0.033	-0.582	1.691	-0.064	0.030	-0.156	6.677	-23.496
	(0.596)			(0.020)	(0.255)	(0.859)	(0.036)	(0.027)	(0.111)	(1.895)	(17.123)
Equisetum spp.	0.768			0.005	-0.249	-0.296	0.025	0.044	-0.173	-1.862	-28.222
	(0.566)			(0.015)	(0.184)	(0.794)	(0.035)	(0.016)	(0.065)	(1.082)	(11.501)
Hedysarum spp.	-2.113			0.138	-2.648	-0.393	0.022	0.082	-0.367	-1.928	-44.268
	(0.858)			(0.040)	(0.731)	(1.000)	(0.040)	(0.045)	(0.187)	(2.733)	(27.005)
Heracleum lanatum				-0.008	0.304						-3.618
				(0.033)	(0.344)						(0.611)
Shepherdia canadensis	-1.246	0.228	-0.348			-0.469	0.011	0.055	-0.264	2.848	-26.675
	(0.627)	(0.094)	(0.167)			(0.766)	(0.031)	(0.045)	(0.185)	(1.991)	(27.218)
Taraxacum officinale				-0.031	0.119						0.189
				(0.015)	(0.179)						(0.203)
Trifolium spp.				-0.012	-0.035						-0.816
				(0.017)	(2.077)						(0.222)
ungulates (pellets)	-0.295	0.143	-0.234								-1.950
	(0.476)	(0.045)	(0.091)								(0.640)
Vaccinium caespitosum						-0.008	0.0002	0.039	-0.154	2.490	-25.035
						(0.595)	(0.025)	(0.017)	(0.066)	(1.049)	(11.228)
Vaccinium membranaceum						1.819	-0.092	-0.068	0.264	-3.831	30.785
						(2.700)	(0.128)	(0.023)	(0.089)	(2.212)	(20.154)
Vaccinium myrtilloides						1.070	-0.050	-0.020	0.045	1.357	10.587
						(1.234)	(0.055)	(0.027)	(0.110)	(1.863)	(17.696)
Vaccinium vitis-idaea	0.647	0.094	-0.243			-0.049	-0.0002	-0.041	0.154	0.235	26.136
	(0.501)	(0.041)	(0.087)			(0.586)	(0.025)	(0.015)	(0.060)	(0.995)	(10.423)

§Coefficients for age2 are 100, for canopy2 1,000, and for elev2 10,000 times their actual size.

Table 3-7. Percent frequency (freq.) of fruit, given the presence of the species, for clear-cuts in west-central Alberta. Estimated coefficients (β_i) for AIC$_c$-selected models describe the probability of fruit occurrence (given food item presence). Predicted optima (highest probability of occurrence) for fruit occurrence are reported. Coefficients for canopy^2 are 100 times their actual value.

	% freq.	Canopy		§Canopy^2		Constant		Predicted
Fruit species/group	of fruit	β	S.E.	β	S.E.	β	S.E.	optima
Arctostaphylos uva-ursi	45.0	0.122	0.063	-0.194	0.101	-1.016	0.700	34
Shepherdia canadensis	67.9	-0.003	0.052	-0.019	0.060	1.317	1.009	0
Vaccinium caespitosum-membranaceum	20.0	0.068	0.037	-0.101	0.050	-1.778	0.525	34
Vaccinium myrtilloides	45.5	0.008	0.047	0.020	0.061	-0.491	0.677	100
Vaccinium vitis-idaea	35.5	0.093	0.030	-0.073	0.032	-2.579	0.609	64

§Coefficients for canopy^2 are 100 times their reported value.

Table 3-8. Average (± S.E.) fruit production (reported by 1000's of berries) per hectare (ha) for 5 grizzly bear food groups in clearcuts and reference upland forest stands of west-central Alberta. Reported are estimates of berry production for sites where the species was present (presence-only) and for all sites regardless of its presence ($n = 180$) for only those plots occurring after July 14 when fruits are available. Estimated fresh weight production (kg/ha) for each food item is reported for all sites (an average clearcut or reference forest stand) based on an average berry field weight.

	Average berry	Clearcuts			Reference upland forest stands		
Grizzly bear food item	weight (g)	Presence-only	All sites[§]	kg/ha	Presence-only	All sites[§]	kg/ha
Arctostaphylos uva-ursi	0.186	22.7 ±6.2	6.0 ±6.2	1.11	30.0 ±11.1	5.7 ±2.3	1.05
Shepherdia canadensis	0.180	200.4 ±117.4	36.9 ±22.2	6.65	98.0 ±34.4	19.4 ±7.7	3.49
Vaccinium caespitosum-membranaceum	0.242	38.8 ±15.9	23.7 ±9.5	5.73	48.6 ±18.3	33.4 ±12.6	8.08
Vaccinium myrtilloides	0.142	124.6 ±45.4	27.1 ±10.6*	3.84	26.0 ±17.6	2.5 ±1.8*	0.35
Vaccinium vitis-idaea	0.165	47.9 ±14.1	33.7 ±10.1***	5.56	150.2 ±26.9	116.2 ±21.7***	19.18
Total			127.4	22.9		177.2	32.3

[§] Test of difference in fruit production for each species between clearcuts and reference forest stands (Mann-Whitney *U*-test). *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$

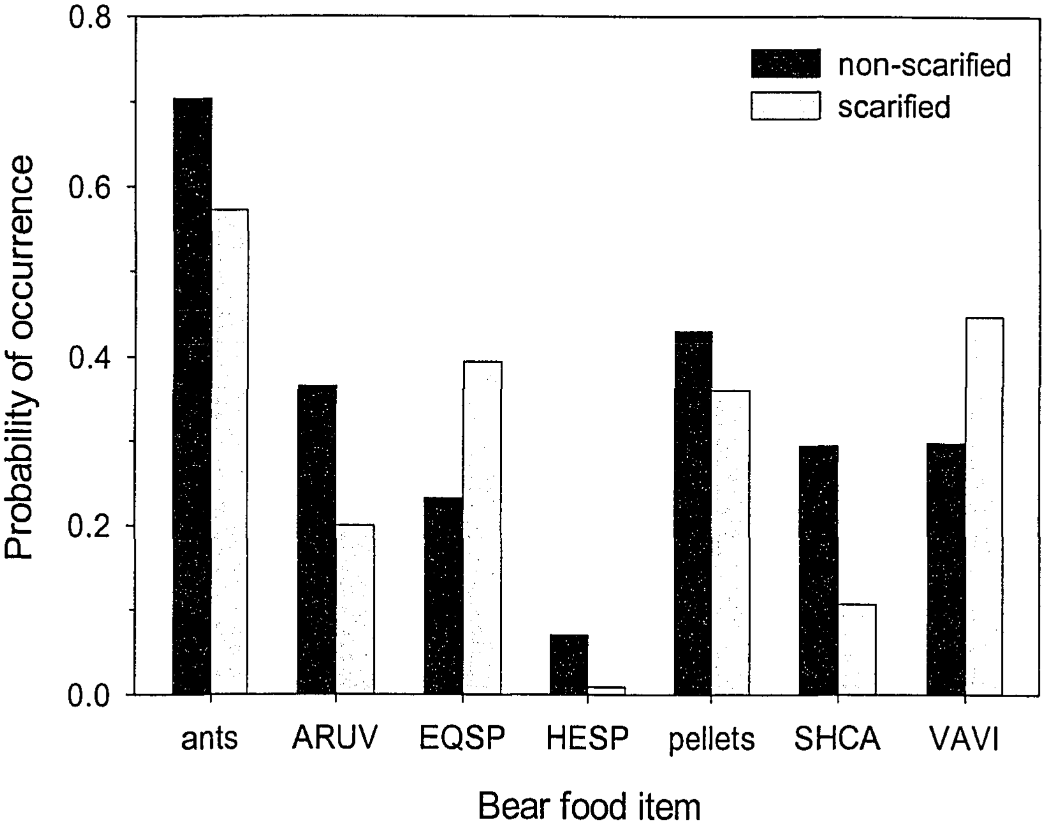

Figure 3-1. Predicted probability of occurrence for AIC_c-selected grizzly bear food items in scarified and non-scarified clearcuts. All other environmental factors included in the selected AIC_c model were held at their mean level.

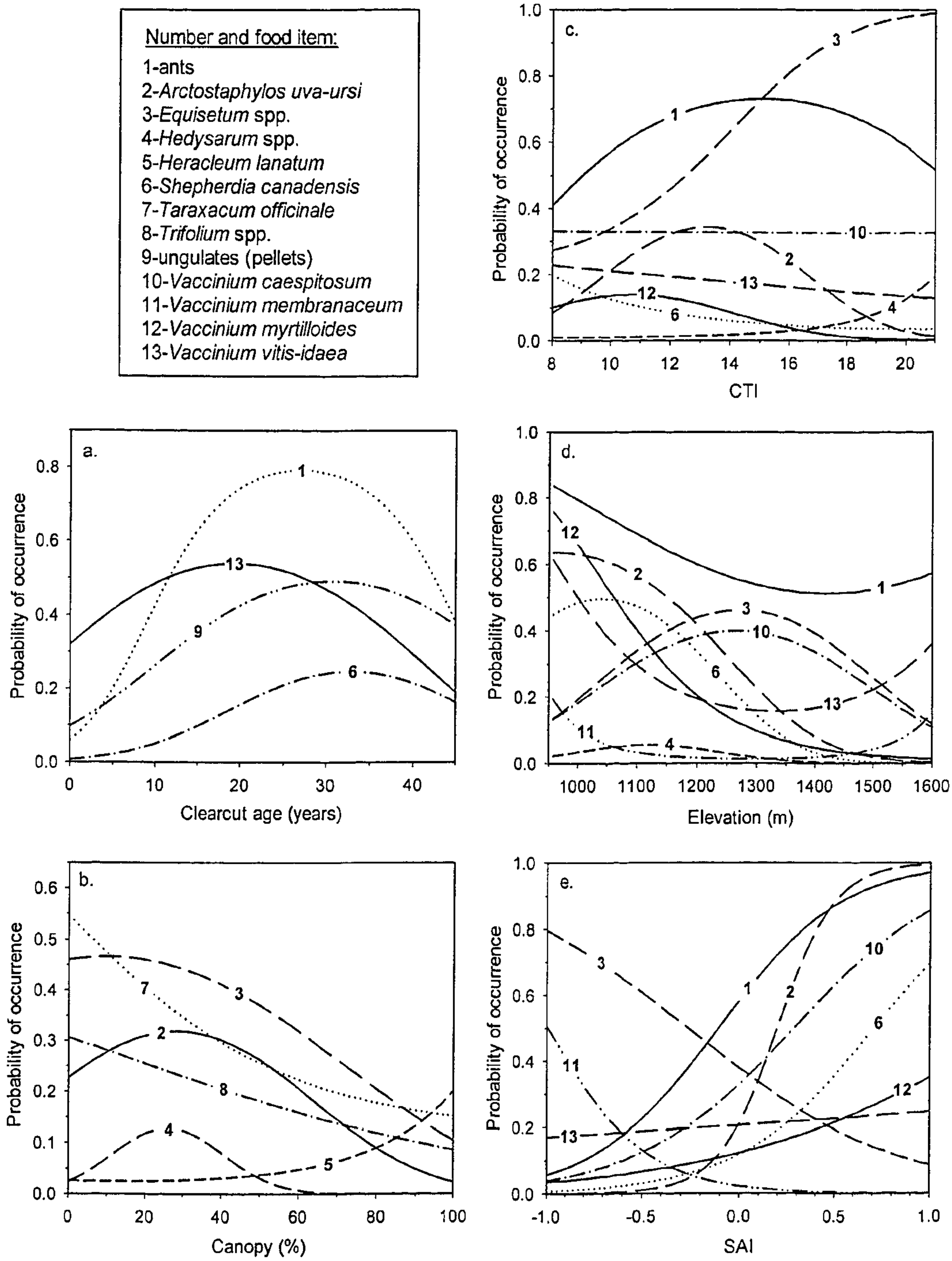

Figure 3-2. Predicted probability of occurrence for AIC$_c$-selected grizzly bear food items in each of the 5 environmental gradients used for describing food occurrence. For each gradient (graph's a. through e.), remaining factors in the selected AIC$_c$ models were held at their mean level. Numbers adjacent to each line correspond to the identification of grizzly bear food items defined in the upper left of the graph and in Table 4-1.

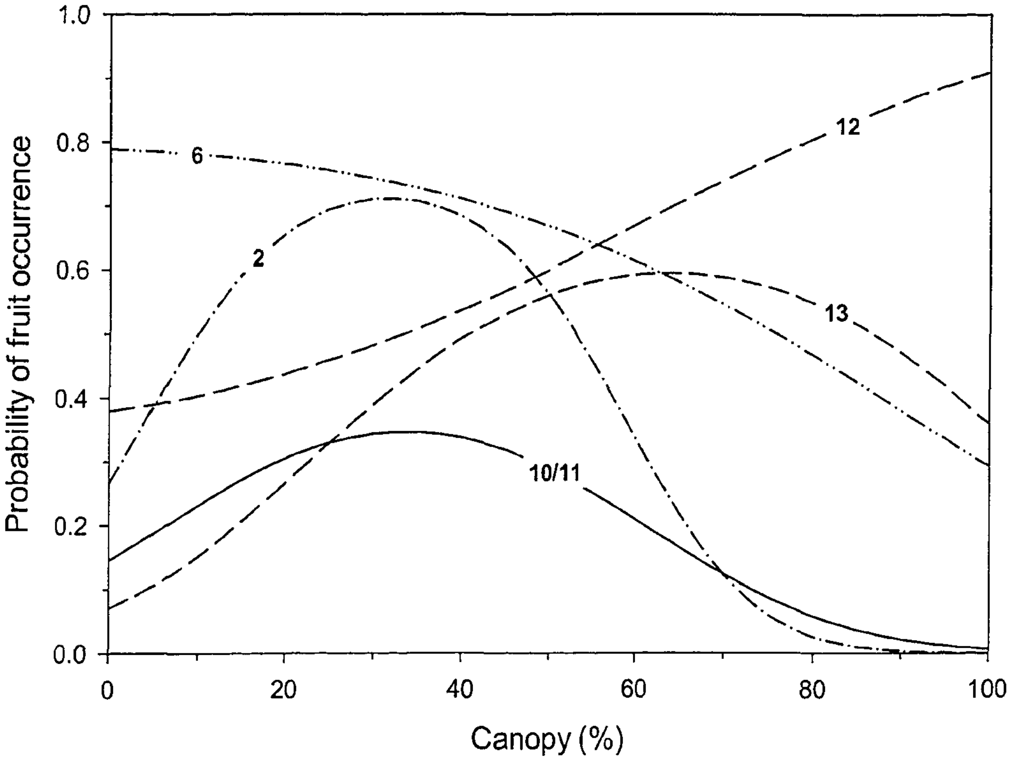

Figure 3-3. Predicted probability of fruit occurrence within clearcuts of west-central Alberta for sites where the fruit-bearing species was conditionally present. Numbers along each predicted line correspond to a bear food (2-*Arctostaphylos uva-ursi*, 6-*Shepherdia canadensis*, 10/11-*Vaccinium caespitosum* and *V. membranaceum*, 12-*Vaccinium myrtilloides*, and 13-*Vaccinium vitis-idaea*).

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Chapter 4

Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies Ecosystem of Canada[3]

1. 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,

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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^2 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.

2. Study Area

This study encompassed a 29,264-km^2 area of the Central Rockies Ecosystem (CRE) in southern Alberta and a small portion of adjacent British Columbia, Canada (Figure 4-1). 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 4-1). 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.

3. Methods

3.1. 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. Accuracy for each observation was categorized from accurate

(<100 m) and reasonable (within a stated distance to a known road, trail, or drainage development), to an estimate or unknown accuracy. For spatial mortality models, we used 279 accurate and reasonably accurate locations that were associated with human-caused events (e.g., we removed the relatively few natural mortality events and those with inaccurate assignments). 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).

3.2. 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). Based on ground truth locations, the overall accuracy of this map was 76% with a kappa index of agreement at 0.712 (J. Theberge and S. Jevons, unpublished data, 2002). This map was further simplified by reclassifying the image into 5 more general land cover categories, since a number of classes were rare and/or ecologically similar for our purposes. 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). Under this classification, there was an overall accuracy of 81%. 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). The equation for TRI, modified from that of Nellemann and Cameron (1996) and calculated in a GIS with a 30-m DEM, was as follows:

$$TRI = \frac{(\text{aspect variation} \times \text{average slope})/(\text{aspect variation} + \text{average slope})}{100} \qquad (4\text{-}1),$$

where aspect variation was measured in a 300-m circular window surrounding each pixel and calculated following the relative richness index of Turner (1989) as the proportion of total number of aspect classes in the moving window over the maximum number of aspect classes in the study area. Slope average was calculated for each pixel based on the average of slopes for all pixels within 300-m circular windows. Excluding TRI and distance to water, the remaining GIS predictor variables were temporally relevant to only the most recent mortality events. We thus make the assumption that the majority of features were established near to or before 30 years ago. We examined potential collinearity between the above linear predictors by using Pearson correlations and variance inflation factors (VIF). Collinearity was assumed if correlations were $>|0.6|$ or the VIF scores were much greater then one (Chatterjee et al., 2000). Given these examinations, we excluded elevation derived from a DEM for all models because it was correlated with both TRI ($r = 0.73$) and greenness ($r = -0.62$), and the VIF was much greater than 1 (VIF = 2.99).

3.3. Data analysis

3.3.1. 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^2 (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^2 (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^2 (21,153-m radius) or the estimated average multi-annual 95% fixed kernel home range for male grizzly bears in the CRE (Stevens, 2002). The 900-km^2-scale was used by Mattson and Merrill (2002) for examinations of grizzly bear extirpations in the contiguous United States, and could be considered a conservative estimate for the CRE since our home range estimates were not lifetime estimates. 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. Because mortality locations existed beyond the extent of the study area boundary, where GIS information was unavailable, we felt comfortable that potential edge biases in moving window density estimates were minimized. 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. We summed all secure and high mortality pixels to assess the total proportion of the study area that could be considered in either state over the past 32 years, while further assessing the proportion of secure areas in non-vegetated areas; considered non-habitat *a priori*. We do not address temporal changes in mortality because Benn (1998) and Benn and Herrero (2002) previously examined this issue.

3.3.2. 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). Of the documented grizzly bear mortalities, information regarding the sex and age of the animals was known for 244 and 254 locations respectively, while age and sex data were known for 232 observations. To examine potential differences in mortalities relating to demographic status, we evaluated either sex or sex-age class composition. 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). We selected sub-adult males for our comparison, because previous research has shown that differences in mortality rates exist for this group, but not for others (McLellan et al., 1999). 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). However, because all legal harvests (legal hunting mortalities) occurred outside of protected National parks (e.g., Banff and Yoho) and Kananaskis Country, we excluded these protected areas from this analysis. All mortality locations with attribute data identifying sex, sex-age class, legal harvest, and season were used for model fitting.

For each comparison, logistic regression was used to contrast each category or class (response variable) against the 6 uncorrelated environmental habitat, terrain, and human-related GIS variables hypothesized to influence bear mortality. Because the land cover variable was categorical, we used an indicator contrast with conifer forest as our reference cover type. Model significance was assessed using a likelihood ratio χ^2 test, while coefficient significance was based on a Wald χ^2 test. If model or coefficient significance was lacking, we interpreted such results to mean that tested demographic, season, or mortality categories were not useful for understanding the spatial distribution of grizzly bear mortalities, at least for those GIS environmental data tested. For significant demographic status, season, or mortality type classes, specific mortality distribution models were developed as described below.

3.3.3. 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^2 (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:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k), \qquad (4\text{-}2),$$

where w(x) represents the relative mortality distribution function (low to high mortality rank) and β_i the mortality coefficient estimated from environmental predictors x_i (Manly et al., 1993). Coefficients for the model were estimated using logistic regression. We used this structure, following the resource selection function literature (Manly et al., 1993; Boyce et al., 2002), as we were sampling our GIS for zeros (psuedo-absences) and hence not directly measuring absences. 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. Model significance was determined using those methods described previously, while standard error estimates and associated coefficient significance were calculated using a 499 bootstrap sample. Bootstrap estimates did not require any assumptions beyond the sample being representative of the underlying process and therefore were considered more robust (Manly, 1991).

To validate our models, we partitioned mortality data prior to model building into a model-training and model-testing data set. Model-training data and random (psuedo-absences) locations were used to develop model coefficients, while model-testing data were used for within sample independent validation. We approximated the ratio of training and testing data using Huberty's rule of thumb (Huberty, 1994) where 80% of the randomly chosen data were used for training and 20% were used for testing. 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). Mortalities were summed within 5 ranked bins representing low to high mortality predictions. Division of the 5 bins was based on a standard deviation classification of model predictions using the reclassification function in Spatial Analyst (ArcGIS 8.2). We used a Somer's *D* statistic, with jackknifed standard errors, to compare the number of withheld testing data mortalities within standardized bins (based on the area of that bin) and the ranking of that bin. A Somer's *D* test can be interpreted in a similar manner to that of a Spearman rank correlation, where concordance ranges from –1 to 1. A significant positive relationship would be interpreted as a model that was predictive and characterized by successively greater number of mortalities within increasing bin ranks (i.e., more mortalities were occurring in higher risk of mortality sites standardized for area).

3.3.4. 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 at 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 (equation 2) with the distinction being that radiotelemetry (0), not random locations, were contrasted with mortality (1) locations. In the context of survival modelling (Cox and Oakes, 1984), our radiotelemetry locations would closely match that of exposure, as these locations were sites where the animal was known to have occurred and survived. Radiotelemetry locations were considered to be accurate within 150 m of the estimated location (Gibeau, 2000). For this analysis, all mortalities located outside the 100% minimum convex polygon (MCP) home range of individual radio-collared grizzly bears were excluded. The merged MCP home ranges therefore represented our spatial extent for this analysis. Coefficients from this analysis were compared with the mortality distribution model (random versus mortality locations) to identify potential differences. 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). The weighted Kappa statistic was used instead of traditional Kappa given that categories of risk were ordered. 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).

4. Results

4.1. 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 4-2). For the 900- and 1405-km^2-scales, mortality densities within moving windows exceeded 31 mortalities for the above 3 identified areas, equivalent to ≥1 mortality event/year and qualitatively considered a high mortality zone. At the 520-km^2-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 high mortality zones ranged from 1.4% at the 520-km^2-scale to 13.2% for the 1,405-km^2-scale (Table 4-1). In contrast, the total area considered secure from human-caused mortalities (no recorded mortality events) ranged from 7.2% for the 1,405-km^2-scale to 23.9% for the 520-km^2-scale (Table 4-1). However, 22% to 32% of secure habitat was in areas of non-habitat (Figure 4-2, Table 4-1) suggesting an even more restricted extent for security over the past 32-years.

4.2. 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 4-2). 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 4-2). In addition, sub-adult male mortalities were more likely to be further from human access features than adult, young, and sub-adult female mortalities.

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.

4.3. 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 4-3). 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 4-3). 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 4-4).

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 4-3). 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 4-3). 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 ($\chi^2 = 48.11, p < 0.001$, 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 4-3). 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 ($\chi^2 = 57.07, p < 0.001$, 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.

4.4. Radiotelemetry versus mortality locations- the mortality risk model

The mortality risk model, describing radiotelemetry versus mortality locations using GIS predictor variables, was significant overall ($\chi^2 = 170.49, p < 0.001$, 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 4-4). 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 4-4). 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 4-4). 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.

5. 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^2 and 1,405-km^2), the number of mortalities within home-range-sized moving windows exceeded or equalled the number of years examined (≥ 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 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.

6. 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.

Table 4-1. 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^2), the second Yellowstone lifetime home range sizes (900-km^2), and third local male home range sizes (1,405-km^2).

	Percent of Landscape		
Variable	520-km^2	900-km^2	1405-km^2
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

Table 4-2. 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 land cover classes.

	Female			Sub-adult male			Berry Season			Legal harvest		
Variable	Coeff.	S.E.	*p*	Coeff.	S.E.	*p*	Coeff.	S.E.	*p*	Coeff.	S.E.	*p*
Land cover 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).

Table 4-3. 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.

	Global model (all)			Sub-adult male			Other sex-age			Legal harvest			Non-harvest/Other		
Variable	Coeff.	S.E.	*p*	Coeff.	S.E.	*p*	Coeff.	S.E.	*p*	Coeff.	S.E.	*p*	Coeff.	S.E.	*p*
Land cover type															
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

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

	Mortality distribution model			Mortality risk model		
Variable	Coeff.	S.E.	*p*	Coeff.	S.E.	*p*
Land cover type						
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

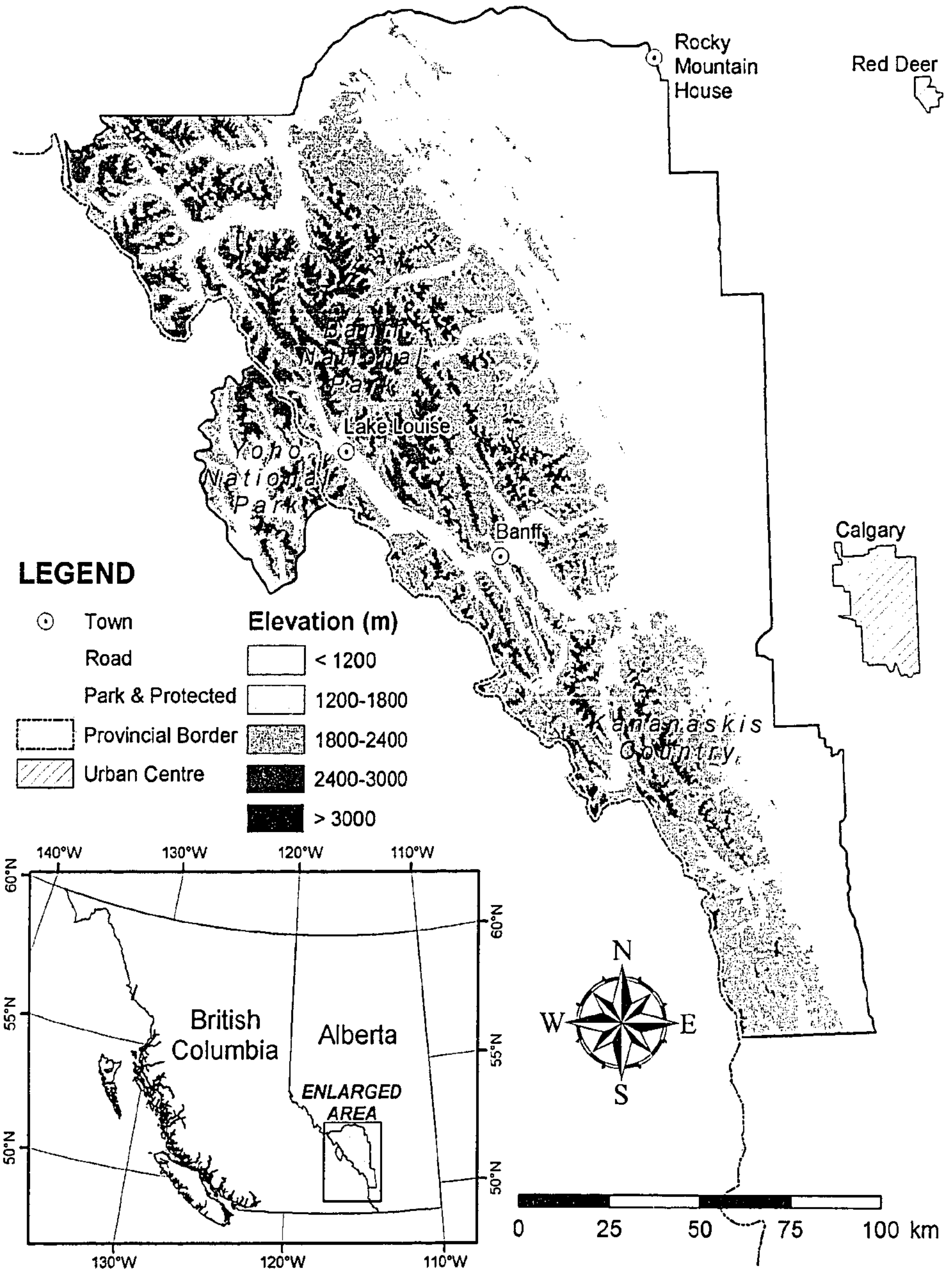

Figure 4-1. Study area map depicting elevation, study area boundary, Province border, places, and general location within Alberta and British Columbia, Canada (small inset map in upper left corner).

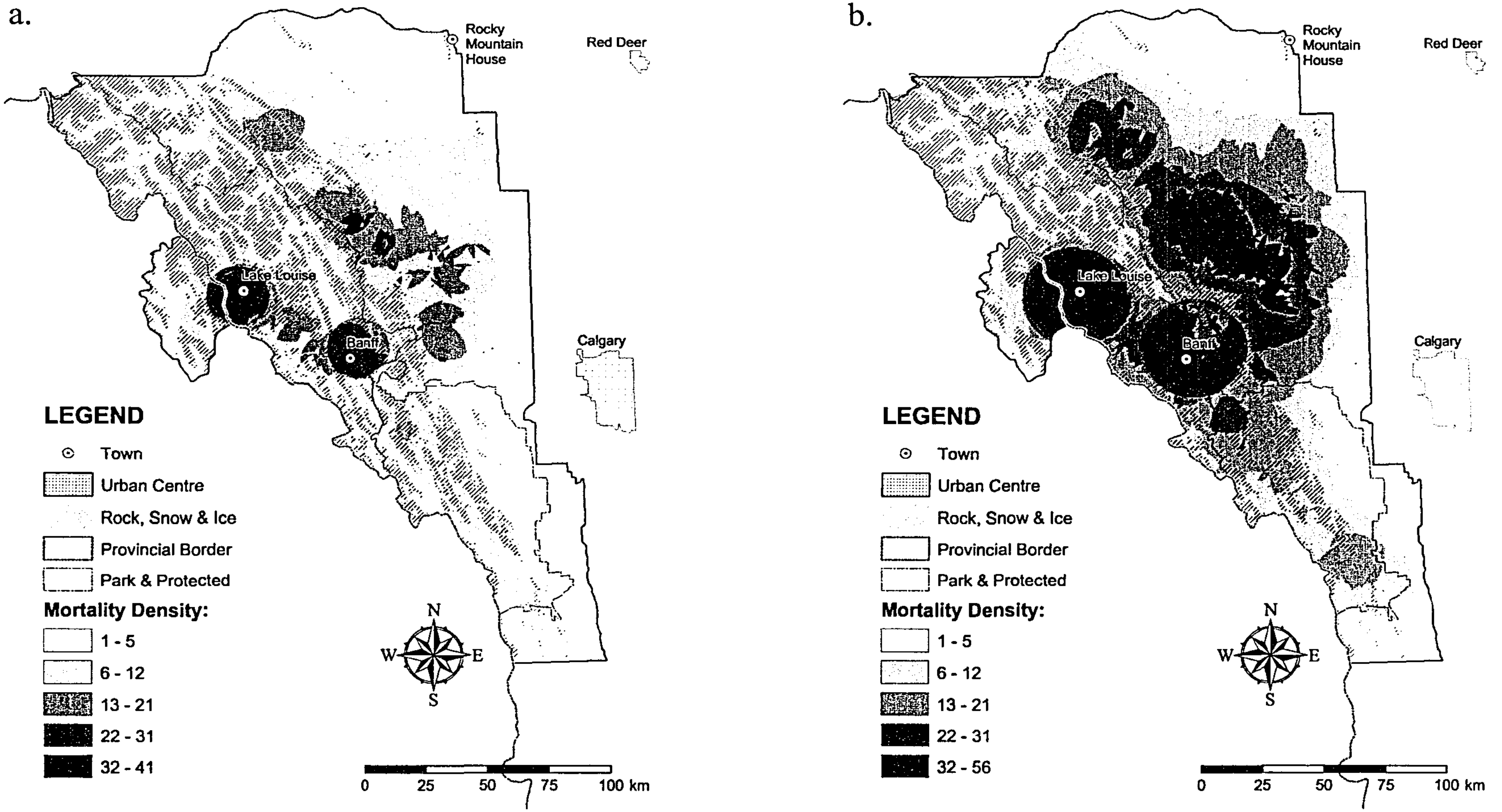

Figure 4-2. Distribution and concentration (density of recorded mortalities) of grizzly bear mortalities within the study area at 2 scales relating to the multi-annual 95% fixed kernel home ranges for female (a. 520-km^2) and male (b. 1,405-km^2) grizzly bears. Note the differences between scales and 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^2) is not shown but is intermediate between the scales depicted.

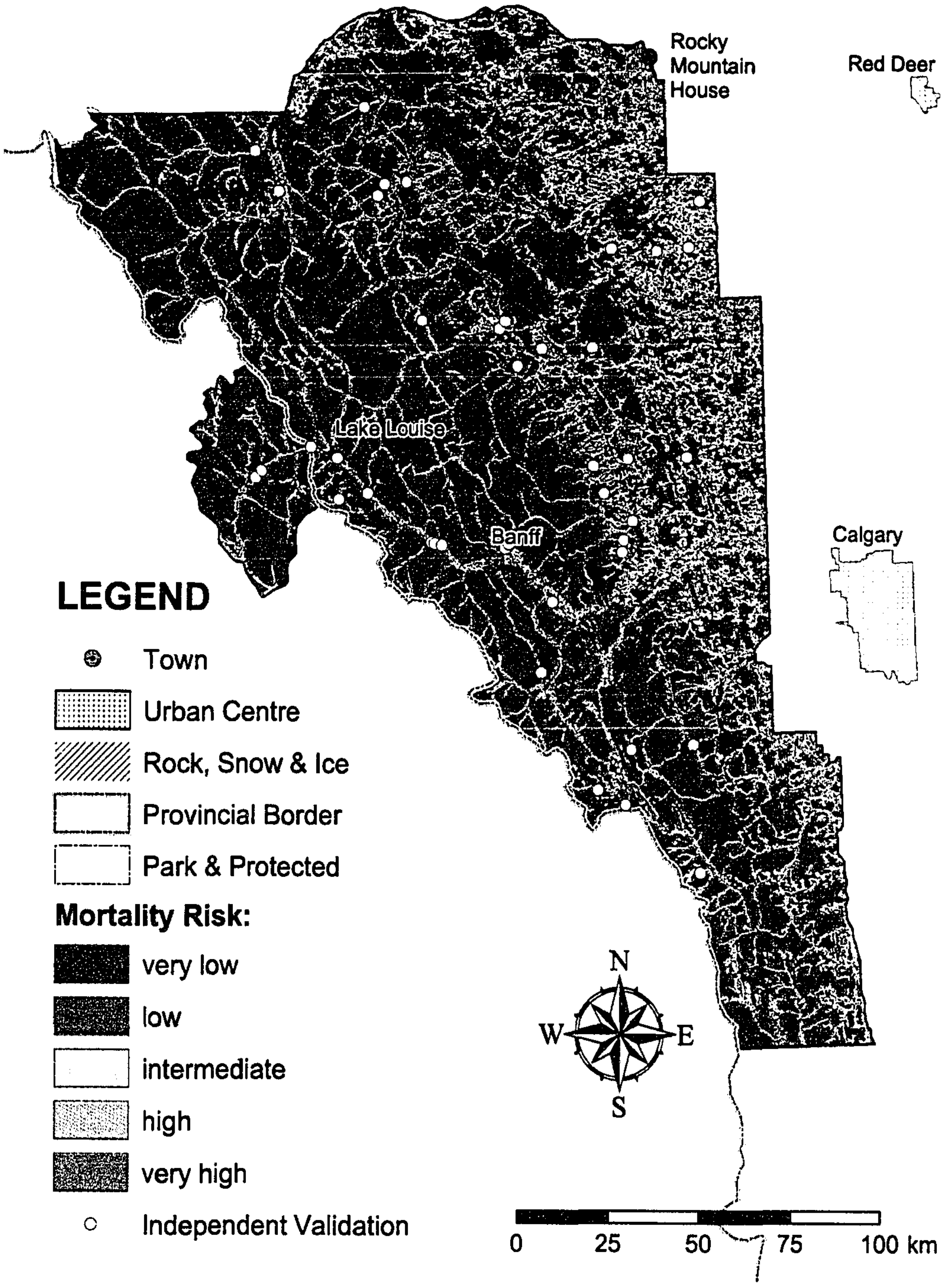

Figure 4-3. The distribution of mortality risk ranks from very low to very high based on the global mortality distribution (random versus mortality locations) model in the Central Rockies Ecosystem of Canada.

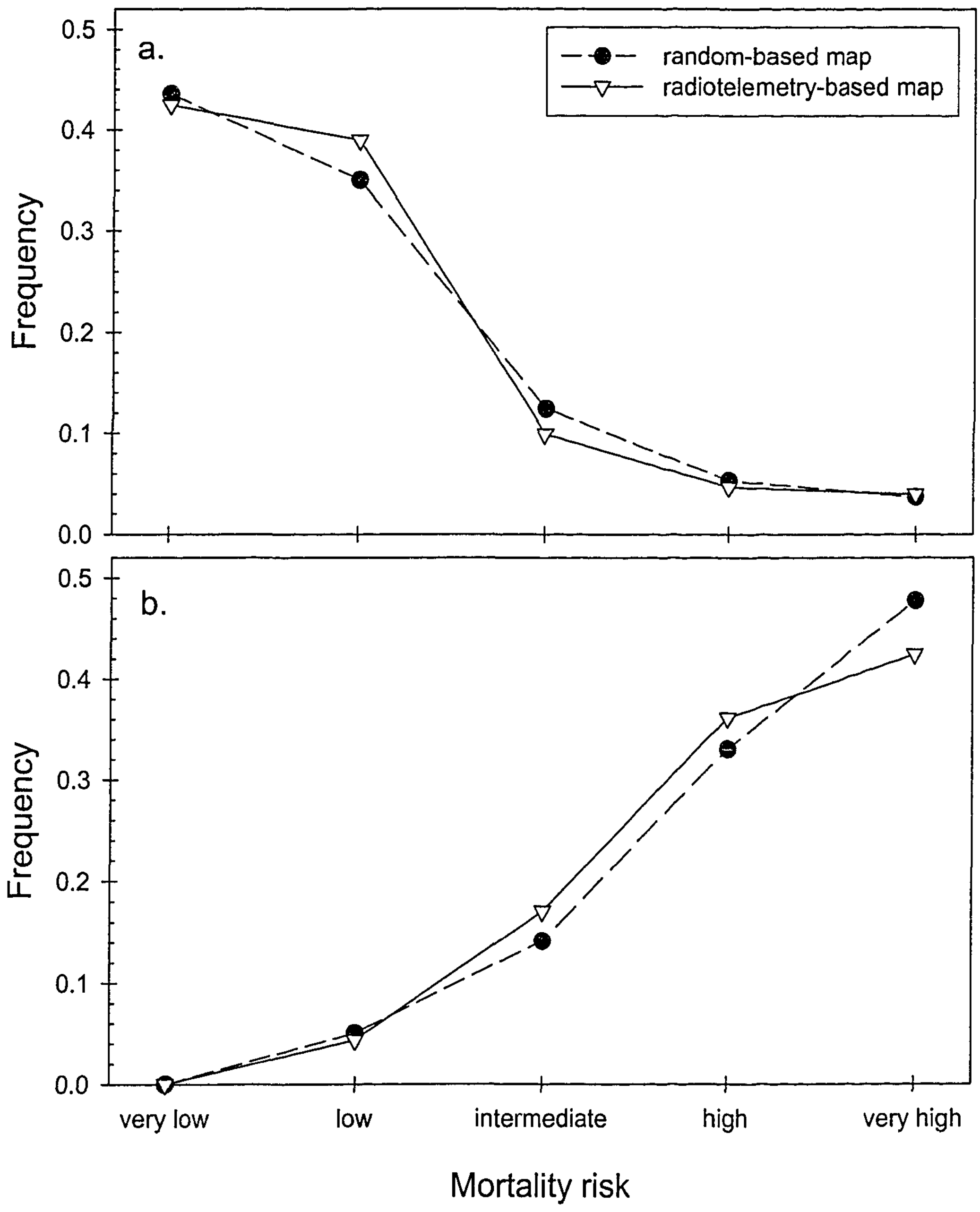

Figure 4-4. Percent composition of very low to very high mortality risk pixels in the Central Rockies Ecosystem of Canada based on the mortality distribution (random-based map) and the mortality risk (radiotelemetry-based map) models (a.). Area-adjusted frequency of withheld (testing data) mortality 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.).

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Chapter 5

Grizzly bear habitat segregation from resource competition

1. Introduction

Wildlife-habitat modelling is an important management and conservation tool, providing insights and predictions of species-habitat relationships (Boyce and McDonald, 1999). Most wildlife-habitat modelling, however, assumes individual-level variation in habitat selection to be unimportant. For instance, animal locations are often lumped together to reveal a population-level estimate of habitat selection or use. In fact, Bos and Carthew (2003) found only 10% of habitat selection papers compared selection differences among groups of animals or individuals. As Aebischer et al. (1993) points out, however, animals often form distinct groups that vary in their habitat use. Groups may vary by sex (Zharikov and Skilleter, 2002), age (Whitehead et al., 2002), body size (Ulfstrand et al., 1981), or a combination of factors. In fact, this natural grouping or segregation of animals into different habitats provides one mechanism for reducing intra-specific competition (Young, 2004), while further reinforcing social activities or learning behavior (Punzo and Ludwig, 2002; Schaik et al., 2003). As well as social and competitive reasons, segregation of habitats also may be caused by dietary or metabolic requirements associated with sexual size dimorphism (McNab, 1963). Grizzly bears for instance are highly sexually dimorphic (Nowak and Paradiso, 1983). Feeding trials for captive grizzly bears have shown smaller sized bears, such as females, are able to meet their energy requirements on vegetative diets alone, while larger sized bears, such as males, require meat to sustain their large body mass (Rode et al., 2001). Stable isotope assessments of wild grizzly bears support this conclusion with larger carnivorous diets for males and vegetative diets for the smaller bodied females (Jacoby et al., 1999). In combination with dietary differences, food-based hypotheses for habitat segregation also predict intra-specific competition with adult males excluding sub-dominant animals from high-quality food patches (Egbert and Stokes, 1976; Stringham, 1983).

Habitat segregation among sexes, however, may be a response to sexually selected infanticide pressures, where the killing of dependent young by nonsire males shortens the interval of the females' next conception, thereby conferring a reproductive advantage to the infanticidal male (Hrdy, 1979; Swenson et al., 1997). Infanticide has been observed for bears (Olson, 1993; Derocher and Wiig, 1999), although in one bear population infanticide of young by adult females was greater than that of adult males (Hessing and Aumiller, 1994). Regardless of direct observations of infanticide, studies examining sex-specific habitat selection have generally revealed differences in home ranges and/or habitats for adult female and male bears, suggesting that segregation from infanticide was a primary mechanism for these differences (Wielgus and Bunnell, 1994; 1995; Dahle and Swenson, 2003; Ben-David et al., 2004). However, not all grizzly bear populations consistently showed sexual segregation of habitats or population-level consequences (e.g., Berns et al., 1980; Nagy et al., 1983; Wielgus and Bunnell, 1995; Swenson et al., 1997; McLellan and Hovey, 2001). For example, Wielgus and Bunnell (1995) found a hunted grizzly bear population exhibited sexual segregation of habitats for adult females and males, while an un-hunted population did not. Reproductive rates and cub survivorship also varied among hunted and un-hunted populations, with reproductive rates and cub survival being lower in hunted populations (Swenson et al., 1997; Wielgus and Bunnell, 2000). These results suggest that sexually selected infanticide pressures and consequences are not consistent among populations and that disruption in social structure through removal of large dominant males may be an important mechanism responsible for instigating infanticide responses.

Regardless of the mechanism for habitat segregation, conservation requires accurate spatial maps of grizzly bear habitats, as grizzly bears are often used as an umbrella (large area requirements), flagship (majestic and charismatic), and/or focal species (surrogate species for regional planning) for regional conservation planning (Noss et al., 1996; Carroll et al., 2001). Population-level habitat maps that do not consider variations in sex-age groups or appropriate seasons will not likely prove predictive nor overly effective in inferring habitat responses, since seasonal or sex-age group variation will likely obscure important details of habitat requirements when combined. Appropriate temporal scales or method of representing seasonal variation, together with possible sex-age differences, are therefore important considerations in grizzly bear habitat mapping.

In this paper, we explore the interplay between season and sex-age class on habitat selection for grizzly bears in west-central Alberta, Canada, an area of Canada where grizzly bear populations are now being considered for threatened status. Our goals were to develop and describe seasonal and sex-age specific habitat selection models and compare sex-age and seasonal maps to better understand the importance of environmental and social hierarchy relationships. We hypothesize that two potential mechanisms shape seasonal selection of habitats by grizzly bear sex-age groups: (1) intra-specific competition for food resources (resource competition or food hypothesis) with agonistic aggression by adult males; and (2) sexually selected infanticide pressure (infanticide hypothesis). If intra-specific competition for food resources were a dominant factor, differences in habitat selection among sex-age groups would be predicted to be greatest during late hyperphagia (late-summer to early fall) when bears most directly compete for limited and spatially aggregated high-quality foods. In our case, fruit from *Vaccinium* species and especially that of *Shepherdia canadensis*. In contrast, differences in habitat selection among sex-age groups would be predicted to be lowest during early hyperphagia (mid-summer) when the abundance and availability of food resources, primarily herbaceous forbs, was greatest (i.e., habitat selection differences would rank: late hyperphagia > hypophagia > early hyperphagia). As well, we would predict differences in habitat selection to be most prominent for adult males, the larger and more dominant or aggressive sex, reflecting contest competition for food resources, while adult female and sub-adult animals should select habitats similarly, since body size and dominance hierarchy would be less well pronounced. In contrast, if sexually selected infanticide were the dominant factor determining habitat selection patterns among sex-age groups, we would predict differences in habitats to be most pronounced during hypophagia, followed by early hyperphagia and late hyperphagia (i.e., habitat selection differences should rank: hypophagia > early hyperphagia > late hyperphagia). During hypophagia bears begin mating and cubs are most sedentary and thus most vulnerable to infanticide, while in subsequent seasons the mating period ends and cubs become more mobile. Additionally, we predict adult female and adult male habitats to be most dissimilar, with sub-adult habitat selection more similar to adult males than adult females as sub-adults lack risk of infanticide. We compare support for these competing hypotheses by examining the agreement between seasonal habitat predictions for 3 sex-age groups: (1) adult females; (2) adult males; and (3) sub-adult animals.

2. Study area

We studied grizzly bears across a 9,752-km^2 landscape in west-central Alberta, Canada (53° 15′ 118° 30′; Figure 6-1). Two land use and land cover zones dominated the region. The first was the protected mountainous region of the west, and the second, the resource-utilized foothills of the east. Management of the mountainous region was divided between provincial (Whitehorse Wildlands Provincial Park; 173-km^2) and federal (Jasper National Park; 2,303-km^2) authority and characterized by extensive recreational use. Land cover in the mountains consisted of montane, conifer, and sub-alpine forests, along with alpine meadows (Achuff, 1994). In some high elevation areas, however, rock, snow, and ice (glaciers) predominate. In contrast, the eastern foothills contained a number of resource extraction activities, including forestry, oil and gas activities, and open pit coal mining. Large numbers of roads and seismic lines typify this landscape creating an extensive network of access points for human recreation. Timber harvesting has been active since the mid 1950s with additional exploration and development of natural gas resources since. A long history of coal mining also has been present in the area, partly influencing Anglo-European settlement along the mountains near the town of Cadomin. Land cover for the foothill region includes conifer, mixed, and deciduous forests, areas of open and treed-bogs (wetlands), small herbaceous meadows (including small agricultural fields near the town of Edson), and areas of regenerating (clearcut harvesting) forests (Achuff, 1994; Franklin et al., 2001). With large-scale forestry now dominating the eastern landscape, fire suppression has become increasingly evident (Andison, 1998; Rhemtulla, 1999). Historic stand-replacing fires averaged 20% of the landscape burned per 20-yr period and a 100-yr fire cycle (Andison, 1998). Climate is intermediate, with an average summer and winter temperature of 11.5° C and –6.0° C respectively, and a normal annual precipitation of 538 mm (Beckingham et al., 1996). Temperature and precipitation were strongly influenced by an elevation gradient ranging from 984 to 3,012 m. With a short growing season, lack of salmon and other high protein foods (Jacoby et al., 1999), grizzly bear populations in the area occur at relatively low densities (e.g., $\leq$14 animals/1000-km^2) compared with other interior grizzly bear populations of North America (Poole et al., 2001).

3. Methods

3.1. Grizzly bear location data

From 1999 to 2002, we captured and collared 32 grizzly bears using aerial darting, leg snaring, and immobilization techniques (Cattet et al., 2003). Bears were fitted with either a Televilt GPS (global-positioning-system)-Simplex or an ATS (Advanced Telemetry Systems) GPS radiocollar. Radiocollars were programmed to acquire a positional fix at intervals occurring between every 1-hr to 4-hr. We removed all animal locations occurring outside of the study boundary and used a minimum radiotelemetry sample size rule of 50 observations per individual per season as recommended by Leban et al. (2001). Applying this minimum radiotelemetry rule, we had 28,227 model-training locations from 22 female and 10 male animals (Table 5-1). We felt we were assured of a reasonable representation of grizzly bear habitat relationships given the large sample of radiotelemetry observations and individual animals used. Previous researchers have suggested a minimum number of animals at 10 (Aebischer et al., 1993) to 20 (Leban et al., 2001) and preferably up to 30 (Aebischer et al., 1993). In addition to these radiotelemetry observations, we collected also a second set of animal locations from 2003 for independent out-of-sample (out-of-time) model validation. These testing data totaled 6,521 locations from 19 individuals, including 10 animals not previously used for model building that were captured and collared during the 2003 season (Table 6-2). Using animal location data from 1999 through 2002, we delineated multi-annual 100% minimum-convex-polygon (MCP) home ranges (Samuel and Fuller, 1994) using Hawth's tools version 2 (Beyer, 2004), an extension for ArcGIS 8.3 (ESRI, 2002). We used these home ranges to identify *available* resources for each bear using a random-point generator in ArcView 3.2 (ESRI, 2002). Sampling intensities of random locations within MCP's were standardized to 5 points/km^2.

To account for variation in habitat use through time (Nielsen et al., 2003), we stratified animal locations into 3 separate seasons occurring between 1 May and 15 October. Seasons were defined from food habits and selection patterns for the region (Pearson and Nolan, 1976; Hamer and Herrero, 1987; 1991; Hamer et al., 1991; Nielsen et al., 2003). The first season, hypophagia, was defined as the period occurring from 1 May to 15 June.

During this spring season, bears readily fed on roots of *Hedysarum* spp., carrion or ungulate calves, and early green herbaceous material, such as clover *Trifolium* spp. and horsetails *Equisetum arvense*. The second season, early hyperphagia, was defined as the period occurring between 16 June and 15 August. During this season, bears normally fed on herbaceous forbs including cow-parsnip *Heracleum lanatum*, graminoids, sedges, and horsetails, and in some cases ants and ungulate calves. And finally the third season, late hyperphagia, was defined as the period from 16 August to 15 October. During this season, bears normally sought out berries from Canada buffaloberry *Shepherdia canadensis*, blueberries and huckleberries *Vaccinium* spp., followed by late season digging for *Hedysarum* spp. We did not stratify animal locations within season by year due to limitations in sample size. Although annual differences in habitat selection are bound to occur (Schooley, 1994), pooling of years provided an average seasonal estimate of habitat selection. Something that was more consistent with conservation and land use planning needs, as annual variations in habitat selection are not like to be addressed nor predictable for the future.

Beyond temporal differences in habitat selection, variation among individual grizzly bears or sex and/or age groups also was considered to be important. Previous habitat modelling for the area showed substantial differences among individuals (Nielsen et al. 2002). To account for some of this individual-level variation, we stratified animals into one of the 3 following groups: (1) adult female; (2) adult male; and (3) sub-adult animals. Adult animals were defined as those averaging 5–years of age or older while radiotracking, while sub-adult animals were defined as those animals averaging between 2 and 4 years of age. Given the above-defined season and sex-age groups, a total of 9 possible sex-age and season combinations were present. We maintained each stratum for habitat selection modelling.

3.2. Remote sensing and GIS predictor variables

An Integrated Decision Tree Approach (IDTA) land cover classification on a 30 m grid was generated for the study area using Landsat TM satellite imagery (1999–2002), a digital elevation model (DEM), GIS vegetation inventory data, and ground-truth field training sites (Franklin et al., 2001). Twenty-three land cover categories were identified with an overall classification accuracy of 83% (Franklin et al., 2001). We combined similar land cover classes into 10 major land cover groups that included 6 forest classes (closed conifer, open conifer, mixed, deciduous, treed-bog, and regenerating forest), 3 open classes (alpine/herbaceous, non-vegetated [including water], and open-bog/shrub), and finally a single anthropogenic class (Figure 5-1). We reclassified the resulting land cover map into a forest and non-forest grid to estimate our second variable, edge distance. This forest/non-forest grid was converted to a polyline and used to calculate straight-line distance to a polyline edge using the Spatial Analyst extension in ArcGIS 8.3 (ESRI, 2002). The resulting edge distance metric (converted to 100 m intervals) represented the distance from either an interior location within a forest to a nearby open edge or the distance from a location within an opening to a nearby forest edge. Previous grizzly bear research in the area has shown strong selection for edge habitats (Theberge, 2002; Nielsen et al., 2004a).

Forest age was estimated for closed conifer, deciduous, mixed, open conifer, and treed-bog pixels using Alberta Vegetation Inventory (AVI) data and fire history GIS maps from Foothills Model Forest (FMF; Hinton, Alberta). Likewise, we used GIS forest harvest polygon data from forestry stakeholders to associate ages of regenerating forests (clearcuts). All ages were simplified into an age class index that ranged from 1 to 15 (a value of 0 was given to all non-forested land cover pixels). Each age class in the index represented a 10-year period of succession following disturbance (e.g., age class 1 would be a 0 to 10-yr old forest or clearcut stand). All forest stands ≥ 140 years of age were assigned an age class of 15 and thus representing a single old growth value.

We modeled 3 terrain-derived variables using a 30 m DEM. These 3 variables included a soil wetness index called compound topographic index (CTI), a terrain ruggedness index (TRI), and global solar radiation for the mid-month day of June, July, and August. We used an AML (Arc Macro Language) from Evans (2002) to calculate CTI in an ArcInfo Workstation (ESRI, 2002). CTI, often referred to as wetness index, has been shown to correlate with several soil attributes including soil moisture, horizon depth, silt percentage, organic matter, and phosphorous (Moore et al., 1993; Gessler et al., 1995). Specific to wildlife modelling, CTI has previously been used to characterize grizzly bear habitat selection of clearcuts, as well as the occurrence of important grizzly bear food items (Nielsen et al., 2004a; 2004b). To estimate our second terrain-derived variable TRI, we modified an existing equation of TRI from Nellemann and Cameron (1996), as described fully in Nielsen et al. (2004c). TRI has previously been shown to be useful in describing habitat selection and risk of human-caused mortality for grizzly bears in the east slopes of the Canadian Rocky Mountains (Theberge, 2002; Nielsen et al., 2004c). Finally, we calculated, using AML's from Zimmermann (2000) in an ArcInfo Workstation (ESRI 2002), short wave and diffuse solar radiation for 3 summer days: June 15, July 15, and August 15. Estimates of short wave solar radiation were based on Zimmermann (2000), correcting for overshadowing of adjacent terrain found in Kumar, Skidmore and Knowles (1997). We used estimates from Kumar et al. (1997) for diffuse solar radiation, although the AML used was again from Zimmermann (2000). For both solar radiation estimates, we used 60-minute time intervals for incrementing daily solar path and a set latitude 53° 00′ N. We summed both short wave and diffuse solar radiation across all 3 days to estimate an index of summer global solar radiation. Solar radiation and more generally, slope-aspect relationships correlating with solar radiation, have proven important predictors of grizzly bear habitat (Nielsen et al., 2002; 2003; 2004a; Theberge, 2002). Global solar radiation values were only used for 3 common land cover classes that varied substantially within the study and were thought to be important. These included closed conifer, regenerating forest, and alpine/herbaceous classes. Each was treated as an interaction term between the categorical land cover class and global solar radiation estimates for each pixel in that class (Table 5-3). We additionally hypothesized that interactions between CTI (soil wetness) and age class, as well as CTI and edge distance, would be important descriptors of grizzly bear habitat (Table 5-3). We suspected that areas further from edges would be more likely to be used if those areas were wet (e.g., high CTI values). As well, we suspected that use of old growth stands would be greater if those areas were also wet. Finally, we fit quadratic (Gaussian) terms for CTI, TRI, and age class variables allowing for non-linear responses that we hypothesized *a priori* (Table 6-3).

3.3. Habitat selection modelling

We evaluated third-order (Johnson, 1980) habitat selection for grizzly bears across a 5-year period of time (1999–2003) using a *design III* approach, where the individual identities of animals were maintained (Thomas and Taylor, 1990). We divided our data into 2 groups. The first group, the model-training group, represented data from 1999 through 2002 and was used for model development, while the remaining 2003 sample year, the model-testing group, was used for assessing model performance through independent validation. Using the model-training data and explanatory remote sensing and GIS map variables, we developed RSF models for each sex-age and season combination using coefficients estimated by logistic regression and having the following model structure from Manly et al. (2002):

$$w(\mathbf{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k) \qquad (5\text{-}1),$$

where $w(\mathbf{x})$ was the resource selection function for a vector of predictor variables, x_i, and β_i's were the corresponding selection coefficients. Significance of individual parameters were assessed by Wald χ^2 tests (Hosmer and Lemeshow, 1989; Manly et al., 2002). We used Stata 7.0 (2001) for all statistical analyses. Linear predictor variables (Table 5-4) were assessed for collinearity prior to model building through assessments of Pearson correlations (r) and variance inflator function (VIF) diagnostics. All variables with correlations $>|0.6|$, individual VIF scores >10, or the mean of all VIF scores considerably larger than 1 (Chatterjee et al., 2000) were assumed to be collinear and not included in the model structure. No evidence of collinearity was evident for map predictor variables examined. Given that we hypothesized that all environmental covariates were important habitat factors, we chose to fit full models instead of using model selection methods.

We specified the robust cluster option in Stata (2001) to calculate our variance around estimated coefficients using the modified sandwich estimator (White 1980). Sandwich estimators assumed that observations were independent across clusters, but not necessarily independent within clusters (Hardin and Hilbe, 2001; Long and Freese, 2003). As the bear was specified as the cluster, we maintained the design III approach to the analysis where the unit of replication was considered the animal, not the individual observation, thereby accounting for psuedoreplication and/or autocorrelation. We further corrected for habitat and terrain-induced GPS-collar bias (Obbard et al., 1998; Dussault et al., 1999; Johnson et al., 2002) by using probability sample weights (Frair et al., 2004). Available (random) locations were all assigned a weight of 1 (i.e., samples were un-weighted), while weights for radiotelemetry observations were based on local models predicting GPS fix acquisition as a function of terrain and land cover characteristics in Frair et al. (2004).

3.4. Model mapping, assessment, validation, and comparison

We estimated RSF maps for each sex-age and season combination using eqn. 5-1 and the map calculator function in the spatial analyst extension of ArcGIS 8.3 (ESRI, 2002). RSF values were transformed, $T\,w(x)$, in a GIS using the following equation in map calculator,

$$Tw(x) = \frac{w(x)}{1 + w(x)} \qquad (5\text{-}2),$$

where $w(x)$ is the RSF prediction from equation 5-1. Transformations arranged RSF values into distributions that were easier to classify and interpret. Transformed RSF maps were binned into 10 ordinal classes, using a quantile classification in the spatial analyst extension of ArcGIS 8.3 (ESRI, 2002). Resulting maps provided a relative assessment of animal occurrence, ranging from a low value of 1 (low relative probability of occurrence) to a high value of 10 (high relative probability of occurrence). As 9 individual sex-age and season maps were derived, we further estimated an annual habitat rank for each pixel by averaging the 3 seasonal scores within sex-age groups. To better understand the importance of specific land cover categories, we estimated characteristic habitat values (mean, standard deviation, and mode) for each of the 10 land cover classes by sex-age and season combination. With the resulting land cover specific information, we report an average seasonal importance value (IV) for each sex-age and landcover class. Standard deviation of habitat rank values within land cover classes provided an index of variation in habitat selection within individual land cover classes, as a number of microsite factors (e.g., stand age, solar radiation, topographic ruggedness, etc.) and interaction terms were included in the habitat model thereby allowing flexibility in the predicted relative probability of occurrence within any one land cover patch.

We evaluated the predictive performance of each map by comparing the area-adjusted frequency of animal observations within each bin by the corresponding rank of that bin using a Spearman rank correlation (r_s) and Somer's *D* statistic (Boyce et al., 2002). The Somer's *D* statistic provided an assessment of variance (jackknifed standard errors) around *D* and therefore was considered a more meaningful alternative to the Spearman rank (r_s) analysis suggested by Boyce et al. (2002). Area-adjusted frequency, f, values for each bin were calculated as,

$$f = \frac{0.1}{a_i} \times u_i \qquad (5\text{-}3),$$

where a_i is the proportion of available study pixels and u_i the proportion of use observations within bin i. As we used 10 habitat bins for each map, an expected map proportion of 0.1 for each bin was used for standardizing available (a_i) pixels in each bin to get an area-adjusted frequency. Without adjusting for area, we might for instance, have found fewer use observations within certain bins that were rare on the landscape, despite having more observations per unit area. Both the rank correlation and correspondence (Somer's D) metrics ranged from a possible value of -1 (poor performance) to $+1$ (perfect performance). We considered a predictive model to be one that showed a significant and positive rank correlation and D statistic. Other statistical tests of model fit and performance, such as ROC (receiver operating characteristic) and Hosmer and Lemeshow (1980) goodness-of-fit were not assessed, since use-availability data invalidated traditional tests of model performance (Boyce et al., 2002). Instead, we have concentrated on the predictive performance of resulting maps. Two sets of validation data for each sex-age and season combination were evaluated. First, we assessed the relationship between map predictions and animal locations used for model training (radio-telemetry data from 1999 through 2002). This represented a within-sample test or more precisely an assessment of model fit and was therefore considered a liberal estimate of model performance. Second, we assessed the relationship between map predictions and an independent sample (out-of-sample) of animal locations collected from 2003 and not used for model building. We consider this out-of-sample model validation to be a more representative assessment of model predictive performance.

To determine whether differences existed between sex-age and season maps, we evaluated agreement between seasonal pixel values of maps within sex-age groups (9 possible combinations) and sex-age pixel values of maps within seasons (9 possible combinations, plus 3 additional seasonally averaged comparisons). We used the *combine* function in the spatial analyst extension of ArcGIS 8.3 (ESRI, 2002) to determine total number of pixels for each examined combination of maps within a 10 by 10 matrix representing the ordinal habitat bins for each map. For each resulting matrix comparison, we assessed degree of agreement using a weighted Kappa ($\hat{K}_w$) statistic (Næsset, 1996). A weighted Kappa was used, in contrast to the traditional Kappa ($\hat{K}$) statistic (Cohen, 1960), since values in the matrix were ordinal in nature (Næsset, 1996). Kappa values range from a perfect agreement at a value of 1 to a value of 0 where observed agreement was that which would be expected by chance alone. All weighted Kappa statistics were estimated using version 1.71 of the Analyse-it (2003) add-in for Microsoft Excel (Microsoft Corp., 2000). For ease of interpretation, we classified $\hat{K}_w$ values into 1 of 8 degree of agreement categories ranging from perfect to no agreement (Table 5-5). The 8 agreement classes were based on thresholds of $\hat{K}_w$ suggested by Monserud and Leemans (1992).

4. Results

4.1. Seasonal adult female habitat selection

4.1.1 Adult female hypophagia habitat selection

During hypophagia, adult female grizzly bear occurrence significantly correlated with intermediate terrain ruggedness (TRI), areas near to edges, and either young, but especially old forests (Table 5-5). As well, adult females were more likely to occur near edges or in older forests when those edges or forests were hydric in nature (e.g., high CTI values), as evidenced by the interaction of age, edge, and soil wetness (CTI) variables (Table 5-5). Global solar radiation within closed conifer forests, regenerating forests, and alpine areas, along with soil wetness were not significant predictors of adult female hypophagia occurrence. Individual land cover categories varied in importance and were most easily interpreted by the assessment of final habitat scores given the number of interaction terms in the model. Open conifer forests, alpine/herbaceous, and regenerating forests were selected most during hypophagia, while non-vegetated areas, closed conifer forests, and open-bog/shrub classes were least favored (Table 5-6). Model validation revealed that the adult female hypophagia map (Figure 5-2) fit in-sample data perfectly (Table 5-7), while predicting out-of-sample data significantly (Table 5-8), but much less strongly than in-sample data. Adult female grizzly bear occurrence (habitat rank) during hypophagia was predicted to occur most often in mid-to-high elevation sites within the mountains, throughout the Gregg and upper McLeod River basins, and the foothills near the town of Robb (Figure 5-2).

4.1.2. Adult female early hyperphagia habitat selection

During early hyperphagia, adult female grizzly bears were more likely to occur in areas with mesic soils, intermediate terrain ruggedness, areas near to edges, intermediate aged regenerating forests, alpine/herbaceous and closed conifer forests with low global solar radiation, regenerating forests with high global solar radiation, and edges that were hydric in nature (Table 5-5). Forest age alone did not appear to be an important predictor of animal occurrence, while adult females were marginally more likely to occur in old hydric forests as evidenced by the interaction of CTI and stand age. Examining land cover characteristics, adult females favored alpine/herbaceous, open conifer forest, and anthropogenic sites, while non-vegetated, mixed, and closed conifer forests were avoided (Table 5-6). Both in-sample (Table 5-7) and out-of-sample (Table 5-8) model validation proved significant for the early hyperphagia map (Figure 5-3). Adult female grizzly bear occurrence (habitat rank) during early hyperphagia was once again predicted to occur in mid-to-high elevation sites in the mountains, throughout the Gregg and upper McLeod River basins, and the foothills near the town of Robb (Figure 5-3).

4.1.3. Adult female late hyperphagia habitat selection

During late hyperphagia, adult female grizzly bear occurrence significantly correlated with areas near to edges, mesic to hydric soils, intermediate terrain ruggedness conditions, young and old forests, regenerating forest sites with high global solar radiation, closed conifer sites with low global solar radiation, old and hydric forests, and hydric edges (Table 5-5). Age of regenerating forests, along with global solar radiation in alpine/herbaceous sites, did not appear to influence adult female animal occurrence. Alpine/herbaceous, open conifer, and deciduous forests were most consistently selected, while anthropogenic, regenerating forests, and non-vegetated areas were least favored (Table 5-6). Although in-sample (Table 5-7) and out-of-sample (Table 5-8) model validation proved significant for the late hyperphagia map (Figure 5-4), rank correlations for the in-sample data were not as high as the previous 2 seasons, while out-of-sample correlations were higher than the previous 2 seasons. Similar to the previous 2 seasonal maps, adult female grizzly bear occurrence (habitat rank) during late hyperphagia occurred more often along mid-to-high elevation sites in the mountains, throughout the Gregg and upper McLeod River basins, and in the foothills near the town of Robb (Figure 5-4).

4.2. Seasonal adult male habitat selection

4.2.1. Adult male hypophagia habitat selection

During hypophagia, adult male grizzly bear occurrence significantly correlated with hydric soils, intermediate terrain ruggedness, intermediate aged regenerating forests, regenerating forest sites with low global solar radiation, and alpine/herbaceous sites with high global solar radiation (Table 5-9). Edge distance, forest age, global solar radiation in closed conifer forests, and the interaction of soil wetness with either stand age or edge distance failed to significantly explain the occurrence of adult male animals. Open-bog/shrub, open conifer forests, and treed-bog habitats were selected for most, while non-vegetated areas, mixed forests, and closed conifer forests were least favored (Table 5-6). Model validation revealed excellent fit for in-sample data (Table 5-7), while prediction of out-of-sample data was marginally non-significant (Table 5-8). Regardless of model predictive capacity, adult male grizzly bear occurrence (habitat rank) during hypophagia was predicted to occur most often throughout much of the lower foothill bogs between Robb and Edson, as well as regenerating forests and riparian areas in the Gregg and upper McLeod River basins, much of the Whitehorse Wildlands Provincial Park (WWPP), and drainages south of the Cardinal River (e.g., Thistle and Ruby creek) along the slopes of the front range (Fig. 5-5).

4.2.2. Adult male early hyperphagia habitat selection

During early hyperphagia, adult male grizzly bear occurrence significantly related to mesic soils, intermediate terrain ruggedness, areas near to edges, and alpine/herbaceous sites with low solar radiation (Table 5-9). Forest and regenerating forest age, global solar radiation within closed conifer and regenerating forests, and the interaction of soil wetness (CTI) with either stand age or edge distance failed to significantly contribute to seasonal adult male animal occurrence. Deciduous forests, anthropogenic areas, and open conifer forests were selected for most, while non-vegetated areas, closed conifer forests, and open-bog/shrub classes were least favored (Table 5-6). Model validation revealed excellent fit and prediction for in-sample (Table 5-7) and out-of-sample (Table 5-8) data respectively. Adult male grizzly bear occurrence (habitat rank) during early hyperphagia was predicted to occur most often in the WWPP, Gregg and upper McLeod River basins, high alpine meadows in the south part of Jasper National Park, the foothills near the town of Robb, and along riparian areas throughout the study area (Figure 5-6).

4.2.3. Adult male late hyperphagia habitat selection

During late hyperphagia, adult male grizzly bear occurrence significantly correlated with mesic/hydric soils, intermediate terrain ruggedness, areas near to edges, young and old forests, closed conifer forests with low global solar radiation, and regenerating forests with high global solar radiation (Table 5-9). As well, adult males were more likely to occur near edges or in older forests when those edges or forests were hydric in nature, as evidenced by the interaction term of soil wetness with age and edge distance. Treed-bog, open conifer forests, and deciduous forests were selected for most, while non-vegetated areas, closed conifer forests, and regenerating forest classes were least favored (Table 5-6). Model validation revealed excellent fit and prediction for in-sample (Table 5-7) and out-of-sample (Table 5-8) data respectively. Adult male grizzly bear occurrence (habitat rank) during late hyperphagia was predicted to occur most often in lower elevations, including riparian zones and lower foothill bogs (Figure 5-7).

4.3. Seasonal sub-adult habitat selection

4.3.1. Sub-adult hypophagia habitat selection

During hypophagia, sub-adult grizzly bear occurrence significantly correlated with soil wetness, young and old forests, areas near to edges, and edges that were moist in nature (Table 5-10). To a lesser degree, sub-adult animal occurrence also was related to areas with intermediate terrain ruggedness. In contrast, regenerating forest age, global solar radiation for all 3 land cover classes, and the interaction of soil wetness with stand age failed to significantly explain the occurrence of sub-adult animals. Alpine/herbaceous, open conifer forests, and deciduous forests were selected for most overall, while closed conifer forests, non-vegetated areas, and open-bog/shrub habitats were least favored (Table 5-6). Model validation revealed good fit of in-sample data (Table 5-7) and reasonable prediction of out-of-sample data (Table 5-8). Overall, sub-adult animal occurrence (habitat rank) during hypophagia was predicted to occur most often in mid-to-high elevation slopes in the mountains, with some areas of the Gregg and upper McLeod River basins and the foothills near Robb used (Figure 5-8).

4.3.2. Sub-adult early hyperphagia habitat selection

During early hyperphagia, sub-adult grizzly bear occurrence significantly related to forest age (younger stands), intermediate terrain ruggedness, and areas to near edges (Table 5-10). Marginally significant factors included low and high global solar radiation for closed conifer forests and regenerating forests respectively and the interaction of soil wetness and stand age. Soil wetness alone, along with regenerating forest age, global solar radiation in alpine/herbaceous areas, and the interaction of soil wetness and edge distance did not significantly relate to sub-adult animal occurrence. Deciduous forests, alpine/herbaceous sites, and open conifer forests were favored habitats, while non-vegetated, closed conifer forests, and mixed forests were avoided (Table 5-6). Model validation revealed excellent fit and prediction for in-sample (Table 5-7) and out-of-sample (Table 5-8) data respectively. In contrast to the hypophagia season, sub-adult grizzly bear occurrence (habitat rank) during early hyperphagia was predicted to occur more often in the foothills, with high quality patches in the interior mountains (Figure 6-9). There also appeared to be a clear relationship between animal occurrence and valley bottom/riparian areas. Areas of higher sub-adult occurrence (habitat rank) included the WWPP, the Gregg and upper McLeod Rivers, and the foothills near the town of Robb (Figure 5-9).

4.3.3. Sub-adult late hyperphagia habitat selection

During late hyperphagia, sub-adult grizzly bears were significantly correlated with intermediate terrain ruggedness, areas near to edges, alpine/herbaceous sites with low solar radiation, and the interaction of soil wetness with stand age or edge distance (Table 5-10). Sub-adult animals also were more likely to occur in edge habitats if they were wet or old forests if they were dry. Soil wetness, forest and regenerating age, and global solar radiation in closed conifer and regenerating forests were non-significant predictors of sub-adult animal occurrence. Overall, alpine/herbaceous, open conifer forests, and deciduous forests were most favored, while non-vegetated areas, closed conifer forests, and treed-bog habitats were least favored (Table 5-6). Similar to the early hyperphagia season, sub-adult grizzly bear occurrence (habitat rank) during late hyperphagia was predicted throughout the foothills, especially within riparian areas (Figure 5-10). Mountain patches of high quality habitat also were evident and again similar to that of the early hyperphagia map. Areas of higher sub-adult occurrence (habitat rank) included the WWPP, the Gregg and upper McLeod Rivers, and the foothills near the town of Robb (Figure 5-10).

4.4. Inter-seasonal map comparisons within sex-age groups

4.4.1. Inter-seasonal adult female map comparisons

For adult female animals, seasonal maps of predicted habitat rank appeared to be rather similar overall. Indeed, comparison of hypophagia and early hyperphagia periods revealed *very good* ($\hat{K}_w$ = 0.70) map agreement (Table 5-11). Change in mean habitat rank, however, was evident for mixed and deciduous forests (Table 5-6). On average, mixed forests appeared to be favored during hypophagia, while deciduous forests were preferred during early hyperphagia. Assessments of habitat selection (coefficient) confidence intervals (95%) revealed significant inter-seasonal selection differences for soil wetness, regenerating forest age, and global solar radiation within regenerating forests. During early hyperphagia, adult female bears were more selective of intermediate soil wetness (mesic sites) and regenerating forest age, as well as regenerating forests with greater global solar radiation (Table 5-5). For hypophagia and late hypophagia periods, comparisons revealed *good* ($\hat{K}_w$ = 0.63) map agreement (Table 5-11). The lower degree of agreement for hypophagia and late hyperphagia seasons appeared to be caused mostly from changes in selection of anthropogenic, deciduous forests, and regenerating forests classes. Anthropogenic and regenerating forests were on average lower in habitat rank during late hyperphagia, with deciduous forest being higher in habitat rank (Table 5-6). No evidence of inter-seasonal selection differences based on confidence intervals was evident for remaining variables (Table 5-5). Finally, comparison of early hyperphagia and late hyperphagia periods proved to be the most similar of seasons with *very good* ($\hat{K}_w$ = 0.72) map agreement (Table 5-11). Although maps were largely regarded to be similar, noticeably lower mean habitat ranks were evident for regenerating forests and anthropogenic classes during late hyperphagia (Table 5-6). As well, selection of low global solar radiation sites in alpine/herbaceous areas during early hyperphagia was significantly different from that of late hyperphagia when adult females selected alpine/herbaceous sites with high global solar radiation (Table 5-5).

4.4.2. Inter-seasonal adult male map comparisons

For adult male animals, seasonal maps of predicted habitat rank appeared to be more dissimilar than inter-seasonal comparisons of adult female maps. Comparison of hypophagia and early hyperphagia periods, however, revealed *good* ($\hat{K}_w = 0.57$) map agreement (Table 5-11). Noticeable change in mean habitat ranks for land cover classes were observed, with favored use of open-bog/shrub, open conifer forests, and treed-bog habitats during hypophagia and anthropogenic, deciduous forest, mixed forest, and regenerating forest during early hyperphagia (Table 5-6). Significant inter-seasonal differences were apparent for global solar radiation in regenerating forests and alpine/herbaceous sites (Table 5-9). Adult males were more likely to select alpine/herbaceous sites with low global solar radiation during early hyperphagia and high global solar radiation during hypophagia. For regenerating forests, however, the opposite trend was evident with high global solar radiation sites used more during early hyperphagia and low global solar radiation sites used more during hypophagia (Table 5-9). Comparison of hypophagia and late hypophagia habitats revealed *fair* ($\hat{K}_w = 0.46$) map agreement (Table 5-11). Mean habitat ranks of alpine/herbaceous, open-bog/shrub, open conifer, and regenerating forests decreased from hypophagia to late hyperphagia, while deciduous and mixed forests increased during the same period (Table 5-6). Two significant inter-seasonal variables were apparent, regenerating forest age and global solar radiation in alpine/herbaceous sites. Adult males tended to select intermediate-aged regenerating forests during hypophagia and young or old regenerating forests during late hyperphagia. Similar to the previous seasonal comparison, adult males selected sites with high global solar radiation during hypophagia and switched to low global solar radiation sites during late hyperphagia. Finally, comparison of early hyperphagia and late hyperphagia periods proved similar to that of the hypophagia and late hyperphagia comparison with *fair* ($\hat{K}_w = 0.46$) map agreement (Table 5-11). Changes in mean habitat ranks included declines in use of alpine/herbaceous, anthropogenic, and regenerating forests during late hyperphagia and increases in use of treed-bog habitats during early hyperphagia (Table 5-6). Despite only having fair agreement between maps, no further evidence of significant inter-seasonal changes in liner predictors were evident (Table 5-9).

4.4.3. Inter-seasonal sub-adult map comparisons

For sub-adult animals, seasonal maps of predicted habitat ranks appeared similar for some seasons and substantially different for others. Comparison of hypophagia and early hyperphagia periods revealed *fair* ($\hat{K}_w = 0.41$) map agreement (Table 5-11). There were noticeable changes in mean habitat ranks for land cover classes during hypophagia and early hyperphagia periods (Table 5-6). This included, the favored use of anthropogenic, deciduous forest, open-bog/shrub, and regenerating forests during early hyperphagia and greater selection for mixed forest, non-vegetated areas, open conifer forests, and treed-bog habitats during hypophagia. As well, there was a terrain-related shift in the occurrence of sub-adult bears (Table 5-10); moving from higher more rugged habitats in hypophagia (Figure 5-8) to lower elevation and less rugged areas during early hyperphagia (Figure 5-9). Comparison of hypophagia and late hypophagia maps revealed a similar, *fair* ($\hat{K}_w = 0.46$), map agreement as with the previous inter-seasonal comparison (Table 5-11). Mean habitat ranks of anthropogenic and deciduous forests increased from hypophagia to late hyperphagia, while non-vegetated areas declined during the same period (Table 5-6). Similar to the previous comparison, terrain-related differences were apparent for linear predictor variables, with sub-adults using higher elevation sites during hypophagia. Finally, comparison of early hyperphagia and late hyperphagia revealed *good* ($\hat{K}_w = 0.65$) map agreement (Table 5-11). Changes in mean habitat ranks for the period included reduced selection of open-bog/shrub and regenerating forest and increased selection of mixed forest during late hyperphagia when compared to early hyperphagia (Table 5-6). Assessment of significant differences in linear predictors revealed inter-seasonal changes for the interaction of forest age and soil wetness. Sub-adult animals tended to use younger and drier forest stands during late hyperphagia and older and wetter stands during early hyperphagia (Table 5-10).

4.5. Intra-seasonal sex-age comparisons

4.5.1. Hypophagia sex-age class comparison

During hypophagia, it was apparent that habitat selection varied based on sex-age class, especially for adult males. Comparison of adult female and male maps revealed *poor* ($\hat{K}_w = 0.37$) overall agreement (Table 5-12). Adult females tended to occur more frequently in alpine/herbaceous, mixed forests, non-vegetated areas, and regenerating forests, while adult males tended to be more common in open-bog/shrub and treed-bog habitats (Table 5-6). Assessment of linear predictor variables further revealed significant differences in the use of specific regenerating forest sites (Tables 5-5; 5-9). Adult males selected regenerating forests that were intermediate in age and low in global solar radiation, while adult females selected young or old regenerating forests with high global solar radiation. In contrast to poor agreement between adult female and male sex-age groups, adult female and sub-adult animals proved to be in *good* ($\hat{K}_w = 0.69$) agreement. Despite map agreement, noticeable differences were evident in the mean habitat ranks for anthropogenic and regenerating forests (Table 5-6). Adult females were more likely to select anthropogenic and regenerating forests than sub-adult animals. In support of these differences, sub-adult animals also tended to be less restricted to terrain ruggedness, often more likely to occur in higher elevation sites (Tables 5-5; 5-10). Finally, adult male and sub-adult habitat maps proved to be in *poor* ($\hat{K}_w = 0.30$) agreement (Table 5-12). Sub-adult animals were more likely to select alpine/herbaceous areas, deciduous forests, mixed forests, and non-vegetated areas, while adult males were more common in open-bog/shrub and treed-bog habitats (Table 5-6). Based on differences in linear predictors, sub-adult animals were again more likely to be found throughout high elevation sites (Tables 5-9; 5-10).

4.5.2. Early hyperphagia sex-age class comparison

During early hyperphagia, habitat selection was more similar among sex-age groups. Comparison of adult female and male maps revealed *good* ($\hat{K}_w = 0.55$) overall agreement (Table 5-12). Despite this good agreement, adult females tended to occur more frequently in alpine/herbaceous, mixed forests, non-vegetated areas, and open conifer stands, while adult males tended to be more common in deciduous forests and treed-bog habitats (Table 5-6). No significant differences were evident for remaining linear predictor variables when comparing sex-age groups (Tables 5-5; 5-9). Comparison of adult female and sub-adult maps revealed slightly higher agreement ($\hat{K}_w$ = 0.65), but still considered to be within the same map agreement class of *good* (Table 5-12). Based on mean land cover ranks, sub-adult animals tended to be more common in deciduous forests and open-bog/shrub, while adult females were more common in non-vegetated areas (Table 5-6). In comparing linear predictors, adult female distribution was more constrained to sites with intermediate soil wetness than sub-adult animals (Tables 5-5; 5-10). Finally, adult male and sub-adult habitat maps proved to be in *good* ($\hat{K}_w$ = 0.65) agreement (Table 5-12). It was evident from mean land cover ranks that adult males favored mixed forests and treed-bog habitats, while sub-adult animals were more common to alpine/herbaceous areas and open-bog/shrub habitats (Table 5-6). Significant differences in selection of soil wetness conditions were apparent (Tables 5-9; 5-10). Similar to adult females, adult males selected for intermediate soil wetness conditions, while soil wetness did not appear to be a factor for sub-adults.

4.5.3. Late hyperphagia sex-age class comparison

During late hyperphagia, habitat selection among sex-age groups was exceedingly variable. Comparison of adult female and male maps revealed *very poor* ($\hat{K}_w$ = 0.15) agreement (Table 5-12). Seasonal maps depicted high adult male occurrence throughout the lower foothills and mountain valleys (Figure 5-7), while adult female occurrence was concentrated to the mountainous region and within higher elevation sites (Figure 5-4). Mean land cover ranks supported this spatial differentiation in sex-age groups, as adult females were more likely to occur in alpine/herbaceous, non-vegetated, and open conifer habitats typical of the mountains, while adult males favored anthropogenic, mixed forests, and treed-bog habitats typical of the foothills (Table 5-6). Average and standard deviation of elevation for predicted high value habitat ranks (e.g., rank of 10) further illustrated the separation of adult female and male animals. Adult female habitats averaged 1805 m (±316) in elevation, while adult male habitats average only 1301 m (±364) in elevation. This was more than a 500 m average difference in elevation. Although selection of regenerating forests declined during late hyperphagia, comparisons of linear predictors revealed that when adult females selected regenerating forests, they tended to be sites with high global solar radiation (Table 5-5). In comparison, adult males tended to select regenerating forest sites low in global solar radiation (Table 5-10). Comparison of adult female and sub-adult maps revealed *fair* ($\hat{K}_w$ = 0.48) agreement (Table 5-12). Based on a comparison of mean land cover ranks, sub-adult animals were more likely to be present in anthropogenic areas, deciduous forests, and regenerating forests, while adult females were more likely to favor non-vegetated habitats (Table 5-6). Significant differences in adult female and sub-adult animals were evident for the interaction of soil wetness and stand age (Tables 5-5; 5-10). Adult females selected old and hydric forests, while sub-adults selected for young and xeric forests. Finally, adult male and sub-adult habitat maps proved to be in *poor* ($\hat{K}_w$ = 0.36) agreement (Table 5-12). Based on mean landcover ranks, adult males were more likely to occur in treed-bog habitats, while sub-adults were more common to alpine/herbaceous, anthropogenic, non-vegetated, and open conifer forest habitats (Table 5-6). Despite poor agreement, no significant difference in linear predictors were evident (Tables 5-9; 5-10)

5. Discussion

5.1. Habitat selection and inter-seasonal sex-age group variation

Seasonally specific grizzly bear habitat maps based on land cover, forest history, terrain, and landscape covariates proved accurate and predictive. Map comparisons revealed variations among season and sex-age groups, with degree of agreement between maps varying from *very poor* to *very good.* This suggests that seasonal variations and/or sex-age composition need to be considered when mapping grizzly bear habitats. Inter-seasonal comparisons within sex-age groups revealed adult female habitats to be most consistent, with *very good* to *good* Kappa agreement. Regardless of season, adult females selected alpine/herbaceous and open conifer forests, sites with mesic soils, intermediate terrain ruggedness, as well as habitats nearer to edges, edges that were hydric in nature, and old hydric forests. Selection for alpine/herbaceous, open conifer forests, intermediate terrain ruggedness, and edges were consistent with previous regional grizzly bear habitat evaluations (Waller and Mace, 1997; Theberge, 2002; Nielsen et al., 2003, 2004a; 2004b). Additional soil wetness and interactions terms for soil wetness and forest age or edge distance suggest that microsite conditions within land cover types were important predictors. We also found adult females selected regenerating forests (e.g., clearcuts) that were xeric in nature for all 3 seasons, while also preferring intermediate aged regenerating forests during early hyperphagia. Selection for xeric clearcuts during early hyperphagia likely reflects myrmecophagy (Hamer and Herrero, 1987; Elgmork and Unander, 1999; Knight, 1999; Swenson et al., 1999), as ants were most common in these sites (Nielsen et al., 2004b). Use of regenerating forests, however, declined substantially during late hyperphagia, consistent with observations by Nielsen et al. (2004a). Most previous studies have shown a general avoidance of harvested stands (Zager et al., 1983; Waller, 1992; Waller and Mace, 1997; McLellan and Hovey, 2001). We suggest that disparity in results was caused by landscape context and radiotelemetry methods, as the foothills region characteristic of our study lacked extensive open meadows making clearcuts a natural alternative, while GPS radio-telemetry data, unlike that of most VHF radio-telemetry studies, were collected throughout the day, including the crepuscular/nighttime period when bears were more likely to use clearcuts (Nielsen et al., 2004a). Despite some secondary seasonal variations in habitat selection, the overall pattern of adult female occurrence was rather consistent, suggesting a single habitat selection strategy was employed. That strategy appeared to be the selection of high elevation alpine and open conifer stands that were near to edges. Such sites are known to be rich in green herbaceous material and root digging opportunities (Hamer and Herrero, 1987; Hamer et al., 1991; Mattson, 1997), but less much less productive for fruiting of *Shepherdia canadensis*, a critical hyperphagic food abundant in low elevation sites (Hamer, 1996). Edges likely reflected a higher diversity in bear foods, but also may have reflected hiding cover needs.

For adult males, selection patterns were less consistent among seasons with map agreement between seasons varying from *fair* to *good*. Intermediate terrain ruggedness, mesic to hydric soils, and open conifer forests were the most consistently selected environmental factors. Inter-seasonal variation was evident for remaining land cover and environmental covariates. For example, intermediated aged regenerating forests were selected during hypophagia, no age relationship was evident for early hyperphagia, and finally young and old regenerating forests were selected during late hyperphagia.

Pooling of seasonal observations would therefore have resulted in little if any relationship for regenerating-forest age. Differences in microsite terrain features among seasons also were apparent. Alpine/herbaceous areas with high global solar radiation were selected during hypophagia, while alpine sites with low global solar radiation were selected during early and late hyperphagia. The selection for alpine areas with high global solar radiation in hypophagia likely reflected foraging of *Hedysarum* roots, since Hamer et al. (1991) found digging of *Hedysarum* roots to be greatest on steep xeric slopes early in the spring. In contrast, alpine sites with low global solar radiation were selected during early and late hyperphagia, perhaps reflecting cool, mesic sites where important herbaceous foods, such as *Herecleum lanatum*, occur (Nielsen et al., 2003). Finally, edge distance varied in importance from no effect during hypophagia to a moderate to strong affinity for edges during early and late hyperphagia respectively. As fruit production for species such as *Shepherdia canadensis* declines with increasing canopy (Hamer, 1996; Nielsen et al., 2004b), the strong selection for edges during late hyperphagia may reflect selection for fruit-bearing forest edges or ecotones. Overall, it appears that seasonal habitat selection strategies used by adult males were variable and likely reflected the availability of food resources.

Agreement between inter-seasonal sub-adult habitat maps ranged from *fair* to *good* suggesting similar seasonal variation in habitat selection to that witnessed for adult males. Regardless of the seasonal variation in final maps, sub-adult animals consistently selected alpine/herbaceous and open conifer stands, as well as sites nearer to edges. Environmental covariates that varied depending on season included, selection for wet edges during hypophagia and late hyperphagia, but not early hyperphagia. In addition, forest age was important with young and old forests selected during hypophagia. Finally, sub-adult animals were selecting xeric and young forests, as well as alpine sites with low global solar radiation during late hyperphagia. Although habitat selection varied through time, the overall patterns appeared to be intermediate between the highly variable adult males and the more consistent adult females.

5.2. Habitat selection by sex-age group: resource competition or infanticide?

Differences in habitat selection among sex-age groups, revealed rather consistent and *good* agreement between habitat maps during early hyperphagia, *good* to *poor* agreement during hypophagia, and finally *fair* to *very poor* agreement during late hyperphagia. The increasing segregation of sex-age classes as the season's progress agrees with previous regional sex-specific habitat selection assessments (Wielgus and Bunnell, 1994; Waller and Mace, 1997). Wielgus and Bunnell (1994) found differences in habitat use for adult female and adult male grizzly bears to be highest during late summer. Waller and Mace (1997) found that this period also was characterized by segregation of adult female and male animals along an elevational gradient, with adult females averaging 147 m higher in elevation. This elevational separation of sexes has been observed elsewhere as well (Russell et al., 1979; Nagy et al., 1983). Consistent with these studies, we too observed an elevation segregation of adult male and female animals. During late hyperphagia, for instance, adult female habitats (top habitat rank) averaged more than 500 m higher in elevation than adult male habitats. As low elevation sites during this period were much more likely to contain abundant populations of the critical fruit-bearing *Shepherdia canadensis* (Hamer and Herrero, 1987; Nielsen et al., 2003), the selection of low elevation sites by adult males and high elevation sites by adult females suggests that either infanticide or resource competition was operating. Our results were more consistent with predictions of the resource competition and food hypothesis, however, as adult female and sub-adult animals were more similar regardless of season, while adult male habitats were often dissimilar to either of the 2 remaining sex-age groups. This is different than Wielgus and Bunnell (1994; 1995), where although adult females avoided food-rich, male-dominated habitats in Kananaskis Country in southwestern Alberta, sub-adult animals did not avoid adult males suggesting that the infanticide hypothesis for sexual segregation was the mechanism. Even in a stable population where Wielgus and Bunnell (1995) found no infanticide effects, sex-age classes tended to be similar unlike our population. Although we did not separate adult females by reproductive status (i.e., presence of cubs, yearlings, or no dependent young), neither did Wielgus and Bunnell (1994; 1995). The fact that we found sub-adult avoidance of male habitats still suggests that resource competition and not sexually selected infanticide was the dominant factor shaping habitat segregation among sex-age groups.

Mapping of grizzly bear habitats using habitat selection methods should consider the affects of sex-age composition and model habitats separately for individual sex-age groups. When a single sex-age group needs to be selected for assessing conservation strategies, we suggest that adult female habitats be chosen, since they undoubtedly represent the most important and sensitive demographic sex-age class in grizzly bear populations (Wiegand et al., 1998; Boyce et al., 2001). This has normally been the case for many grizzly bear studies. However, if the goal of the study is to describe and map high-quality food-based habitats, it might be prudent to examine adult male habitat selection, as resource competition may drive adult females and sub-adult animals from spatially aggregated high-quality food resource sites.

6. Conclusions

In west-central Alberta, adult female grizzly bear habitats were similar among seasons, but selection was dissimilar to adult male habitats during hypophagia and especially during late hyperphagia when food resources were most concentrated and limiting. All 3 sex-age groups selected habitats similarly during the resource abundant early hyperphagia period, while hypophagia was intermediate between early and late hyperphagia differences. The similarity among sex-age groups during a period of resource abundance and the dissimilarity among sex-age groups during the critical hyperphagic fruiting period, questions whether sexually selected infanticide was resulting in habitat segregation of adult females and males. As well, sub-adult habitats tended to be consistently more similar to adult female habitats rather than adult male habitats, contrary to what would be expected with infanticide pressures (Wielgus and Bunnell, 1994; 1995). Our results support instead predictions from a resource competition-based hypothesis (Egbert and Stokes, 1976; Stringham, 1983). As our analyses focused on habitat segregation only, future examinations of cub survival (Swenson et al., 1997; Wielgus and Bunnell, 2000) should be considered to elucidate whether population-level effects are present. Sex-age group and seasonal variation in habitat selection should carefully be considered in wildlife-habitat modelling and conservation mapping of grizzly bears. Use of habitat conservation maps from population-level habitat models that pool seasons and sex-age groups are not likely to be representative of the complexity of grizzly bear habitat requirements.

Table 5-1. Identification, sex (M-male; F-female), age class (adult: ≥5 yrs; sub-adult: 2-4 yrs), age during radio-tracking, multi-annual 100% minimum convex polygon (MCP) home range size (km^2), and number of radio-telemetry locations by season (from 1999 through 2002), abbreviated as S-1 (hypophagia), S-2 (early hyperphagia), and S-3 (late hyperphagia).

Bear				Radiotelemetry locations (season #)			
identity	Sex/age class	[§]Age	MCP (km^2)	S-1	S-2	S-3	Total
GB01	M-adult	8.5	1,629	433	250	84	767
GB02	F-adult	6.5	694	328	379	97	804
GB03	F-adult	6.7	849	374	671	586	1,631
GB04	F-adult	6	471	458	641	532	1,631
GB05	M-adult	12.5	3,745	636	786	500	1,922
GB06	M-adult	16.5	1,491	303	210	-	513
GB07	F-adult	5	416	66	-	-	66
GB08	M-adult	15.5	1,827	311	437	280	1,028
GB10	F-adult	14.5	659	385	825	549	1,759
GB11	F-adult	8	484	171	151	-	322
GB12	F-adult	6.5	1,860	558	488	277	1,323
GB13	F-subadult	4	2,045	-	63	-	63
GB14	M-adult	10.5	2,638	139	136	58	333
GB16	F-adult	6	591	124	606	664	1,394
GB17	M-adult	8.5	1,694	672	378	-	1,050
GB20	F-adult	5.5	987	633	708	316	1,657
GB23	F-adult	12	666	261	912	419	1,592
GB24	M-adult	6.5	4,314	227	384	422	1,033
GB26	F-subadult	3	1,447	53	95	95	243
GB27	F-adult	12	2,928	217	388	355	960
GB28	F-adult	7	1,300	370	600	780	1,750
GB33	M-subadult	4	4,710	409	818	872	2,099
GB34	F-adult	21	799	-	90	109	199
GB35	F-subadult	4	294	122	219	188	529
GB36	F-subadult	3.5	1,064	198	154	155	507
GB37	F-subadult	4	742	82	150	167	399
GB38	F-adult	15	311	86	126	191	403
GB40	F-subadult	3.5	1,000	272	268	238	778
GB42	F-adult	18.5	1,271	-	275	297	572
GB50	M-subadult	4	903	81	87	-	168
GB54	M-subadult	4	1,467	-	63	-	63
GB100	F-subadult	3.5	606	128	289	251	668
			TOTAL	8,098	11,647	8,482	28,227

[§] Age calculated as average age of animal during radiotelemetry

Table 5-2. Identification, sex (M-male; F-female), age class (adult ≥5 yrs; sub-adult 3-5 yrs), age in 2003, and number of radiotelemetry locations from 2003 used for validation (by season). Abbreviations for seasons are defined in Table 1. Italicized bear identification number indicates an independent out-of-sample animal captured in 2003 and not used for model building.

Bear		Age	Radiotelemetry locations (season #)			
identity	Sex/age class	(2003)	S-1	S-2	S-3	Total
GB03	F-adult	10	64	174	221	459
GB07	F-adult	8	30	-	-	30
GB10	F-adult	18	102	134	142	378
GB12	F-adult	10	199	170	-	369
GB23	F-adult	15	105	138	115	358
GB28	F-adult	10	234	242	273	749
GB33	M-adult	7	162	147	-	309
GB40	F-adult	6	163	181	216	560
GB43	M-subadult	3	113	191	264	568
GB44	M-subadult	3	160	167	194	521
GB45	M-adult	6	43	19	-	62
GB48	F-adult	5	23	58	54	135
GB55	M-subadult	4	101	205	137	443
GB58	M-subadult	3	28	167	79	274
GB60	F-adult	21	103	-	-	103
GB61	F-subadult	2	124	253	295	672
GB62	M-adult	5	-	14	88	102
GB100	F-adult	6	97	132	180	409
GB106	F-subadult	2	-	20	-	144
		TOTAL	1,851	2,412	2,258	6,521

Table 5-3. Remote sensing and GIS map predictor variables used for modelling the relative probability of occurrence of grizzly bears in the Yellowhead study area, Alberta, Canada.

Model variable	Variable code	Linear or non-linear	Units/Scale	Data range
Land cover:				
alpine/herbaceous	alpine	category	n.a.	0 or 1
anthropogenic	anthro	category	n.a.	0 or 1
closed conifer	clscon	category	n.a.	0 or 1
deciduous forest	decid	category	n.a.	0 or 1
mixed forest	mixed	category	n.a.	0 or 1
non-vegetated	nonveg	category	n.a.	0 or 1
open-bog/shrub	opnbog	category	n.a.	0 or 1
open conifer	opncon	category	n.a.	0 or 1
regenerating forest	regen	category	n.a.	0 or 1
treed-bog	treedbg	category	n.a.	0 or 1
edge distance	edge	linear	100 m	0 - 35
compound topographic index	cti	non-linear	unitless	1.89 - 31.7
terrain ruggedness index	tri	non-linear	unitless	0 - 0.29
forest age	for-age	non-linear	10-yr age class	1 - 15
regenerating clearcut age	cut-age	non-linear	10-yr age class	1 - 5
solar radiation × alpine	solar×alp	linear	kJ/m^2	17,133 - 91,836
solar radiation × clscon	solar×clscon	linear	kJ/m^2	21,698 - 91,835
solar radiation × regen	solar×regen	linear	kJ/m^2	57,110 - 91,831
cti × age	cti×age	linear	unitless	0 - 402
cti × edge distance	cti×edge	linear	unitless	0 - 522

Table 5-4. Threshold values used for separating different degrees of agreement classes for the weighted Kappa ($\hat{K}_w$) statistic based on those suggested by Monserud and Leeman (1992).

Degree of agreement	Lower bound	Upper bound
None	0.00	0.05
Very poor	0.05	0.20
Poor	0.20	0.40
Fair	0.40	0.55
Good	0.55	0.70
Very good	0.70	0.85
Excellent	0.85	0.99
Perfect	0.99	1.00

Table 5-5. Estimated seasonal habitat selection coefficients for adult (≥5 years of age) female grizzly bears in the Yellowhead region of west-central Alberta, Canada. Models were based on GPS radiotelemetry data (bias-corrected) collected from 15 adult female animals during the 1999 through 2002 seasons. Robust standard errors (Std. Err.) and significance levels (*p*) were based on modified sandwich estimates of variance among animals.

Variable	*hypophagia*			*early hyperphagia*			*late hyperphagia*		
code	Coef.	Std. Err.	*p*	Coef.	Std. Err.	*p*	Coef.	Std. Err.	*p*
alpine	-0.253	0.851	0.767	2.935	0.319	<0.001	0.218	0.941	0.817
anthro	0.038	0.567	0.947	0.385	0.293	0.189	-0.114	0.344	0.740
closcon	0.585	0.716	0.414	3.502	1.305	0.007	2.530	0.703	<0.001
decid	0.574	0.255	0.024	0.630	0.262	0.016	1.366	0.309	<0.001
mixed	0.727	0.212	0.001	0.079	0.299	0.791	0.778	0.553	0.159
nonveg	0.036	0.286	0.901	0.488	0.175	0.005	0.510	0.445	0.252
opnbog	-0.152	0.329	0.643	0.018	0.293	0.950	0.322	0.502	0.522
opncon	1.236	0.243	<0.001	1.268	0.255	<0.001	1.909	0.348	<0.001
regen	-3.653	1.583	0.021	-10.089	1.716	<0.001	-8.865	2.856	0.002
treedbg	0.863	0.243	<0.001	0.783	0.327	0.017	1.346	0.377	<0.001
edge	-0.281	0.063	<0.001	-0.274	0.045	<0.001	-0.302	0.061	<0.001
cti	-0.070	0.053	0.183	0.176	0.040	<0.001	0.107	0.049	0.029
[†]cti^2	0.349	0.182	0.055	-0.677	0.169	<0.001	-0.294	0.195	0.130
tri	21.516	6.541	0.001	34.959	6.496	<0.001	34.009	7.564	<0.001
tri^2	-93.66	28.67	0.001	-170.01	26.79	<0.001	-147.07	31.84	<0.001
for-age	-0.269	0.080	0.001	-0.150	0.101	0.138	-0.219	0.058	<0.001
[†]for-age^2	1.095	0.469	0.019	0.279	0.544	0.609	0.766	0.364	0.036
cut-age	-0.640	0.565	0.258	1.202	0.151	<0.001	-0.262	0.390	0.545
cut-age^2	0.123	0.087	0.159	-0.189	0.027	<0.001	0.097	0.075	0.197
[§]solar×clscon	-0.019	0.092	0.840	-0.382	0.164	0.020	-0.207	0.093	0.026
[§]solar×regen	0.496	0.290	0.087	0.998	0.225	<0.001	0.934	0.355	0.009
[§]solar×alp	0.133	0.119	0.264	-0.171	0.037	<0.001	0.166	0.123	0.180
[†]cti×age	0.583	0.187	0.002	0.562	0.316	0.075	0.633	0.126	<0.001
cti×edge	0.015	0.006	0.012	0.014	0.004	0.001	0.017	0.005	<0.001

[†] estimated coefficients and standard errors reported at 100 times their actual value

[§] estimated coefficients and standard errors reported at 10,000 times their actual value

Table 5-6. Mean, variation (SD-standard deviation) and mode grizzly bear occurrence (relative) values (bins) for individual land cover classes by sex-age and season.

Land cover	*hypophagia*			*early hyperphagia*			*late hyperphagia*			*seasonal average*			
class	mean	SD	mode	mean	SD	mode	mean	SD	mode	mean	SD	mode	rank
1. *Adult female*													
alpine	9.6	1.6	10	9.6	1.6	10	9.6	1.6	10	9.5	1.6	10	1
anthro	7.2	2.3	7	7.5	2.3	7	4.4	2.4	3	6.0	2.2	5	4
closcon	4.0	2.3	2	4.7	2.5	2	5.1	2.5	2	4.3	2.3	2	10
decid	6.4	2.2	8	7.4	1.8	8	8.3	1.4	9	7.0	1.8	8	3
mixed	6.1	2.1	8	4.2	2.1	2	5.3	2.1	3	4.9	2.0	3	8
nonveg	4.9	3.3	1	4.5	3.4	1	4.9	3.2	1	4.5	3.2	1	9
opnbog	5.3	1.4	5	5.2	1.4	4	5.2	1.4	5	5.0	1.3	4	7
opncon	9.6	0.8	10	9.5	1.1	10	9.8	0.6	10	9.4	0.9	10	2
regen	7.5	1.8	9	7.1	2.1	9	3.2	2.6	1	5.6	1.9	4	6
treedbg	5.7	1.9	4	5.8	1.8	5	6.4	1.6	5	5.6	1.7	4	5
2. *Adult male*													
alpine	8.0	2.5	10	7.9	2.8	10	6.5	3.0	10	7.2	2.6	10	4
anthro	6.4	2.0	7	8.0	2.4	10	6.3	1.8	7	6.6	1.9	7	5
closcon	4.8	2.0	4	5.0	2.2	3	5.6	2.5	3	4.8	1.9	5	9
decid	6.6	1.6	7	9.0	1.4	10	8.7	1.9	10	7.8	1.4	8	3
mixed	4.6	1.8	4	6.2	1.9	5	6.4	1.9	7	5.4	1.7	5	7
nonveg	2.9	2.5	1	2.4	2.2	1	2.5	2.6	1	2.4	2.2	1	10
opnbog	9.4	0.6	9	5.1	1.6	4	5.7	1.2	5	6.5	1.0	6	6
opncon	9.2	1.2	10	7.9	2.4	10	7.6	2.6	10	8.0	2.0	9	2
regen	5.2	3.0	3	6.6	2.3	9	4.2	1.2	4	5.0	1.7	6	8
treedbg	8.7	0.9	8	7.7	1.3	7	9.2	1.1	10	8.2	1.0	9	1
3. *Sub-adult*													
alpine	9.6	1.6	10	9.1	2.1	10	9.2	2.0	10	9.2	1.8	10	1
anthro	5.4	2.0	4	8.3	2.4	10	7.7	2.2	9	6.8	2.0	8	4
closcon	4.3	2.7	2	4.6	2.2	3	4.7	2.3	3	4.2	2.1	3	9
decid	7.8	1.4	8	9.4	1.0	10	9.7	0.9	10	8.5	0.9	9	3
mixed	6.0	1.8	6	4.9	1.9	3	6.3	2.1	8	5.4	1.7	4	7
nonveg	5.1	3.3	1	3.2	3.0	1	3.7	3.2	1	3.7	2.6	1	10
opnbog	5.3	1.3	5	7.6	1.1	7	6.2	1.1	6	6.0	1.1	6	5
opncon	9.5	0.9	10	8.5	2	10	9.2	1.5	10	8.8	1.2	9	2
regen	5.4	2.6	3	7.0	1.8	9	5.2	2.3	5	5.5	1.6	4	6
treedbg	6.1	1.4	5	5.0	1.6	4	5.4	1.9	5	5.2	1.4	5	8

Table 5-7. In-sample map validation representing the predictive accuracy of seasonal, sex-age class habitat selection models (binned map) based on location data used to train the model.

	Number	Number of	Spearman rank		Somer's *D*		
Model/Map	of bears	locations	r_s	*P*	*D*	S.E.	*P*
adult female, season 1	14	4,058	1.0	<0.001	1.0	<0.001	<0.001
adult female, season 2	15	6,876	0.988	<0.001	0.956	0.067	<0.001
adult female, season 3	13	5,172	0.867	0.001	0.778	0.183	<0.001
adult male, season 1	7	2,721	0.988	<0.001	0.956	0.067	<0.001
adult male, season 2	7	2,581	1.0	<0.001	1.0	<0.001	<0.001
adult male, season 3	7	1,384	0.939	<0.001	0.822	0.145	<0.001
sub-adult, season 1	10	1,418	0.952	<0.001	0.867	0.111	<0.001
sub-adult, season 2	10	2,206	0.976	<0.001	0.911	0.082	<0.001
sub-adult, season 3	9	2,005	1.0	<0.001	1.0	<0.001	<0.001

Table 5-8. Out-of-sample map validation representing the predictive accuracy of seasonal and sex-age class habitat selection models (binned map) based on location data gathered in 2003.

	Number	Number of	Spearman rank		Somer's *D*		
Model/Map	of bears	locations	r_s	*P*	*D*	S.E.	*P*
adult female, season 1	9	1,097	0.733	0.016	0.689	0.281	0.014
adult female, season 2	7	1,171	0.649	0.043	0.644	0.318	0.043
adult female, season 3	6	1,147	0.867	0.001	0.778	0.183	<0.001
adult male, season 1	2	205	0.588	0.074	0.467	0.249	0.061
adult male, season 2	3	180	0.927	<0.001	0.822	0.125	<0.001
adult male, season 3	1	88	0.879	0.001	0.733	0.245	0.003
sub-adult, season 1	6	549	0.934	<0.001	0.822	0.100	<0.001
sub-adult, season 2	7	1,061	0.964	<0.001	0.911	0.111	<0.001
sub-adult, season 3	6	1,023	0.952	<0.001	0.867	0.111	<0.001

Table 5-9. Estimated seasonal habitat selection coefficients for adult (≥5 years of age) male grizzly bears in the Yellowhead region of west-central Alberta, Canada. Models were based on GPS radiotelemetry data (bias corrected) collected from 7 adult male animals during the 1999 through 2002 seasons. Robust standard errors (Std. Err.) and significance levels (*p*) were based on modified sandwich estimates of variance among animals.

Variable	*hypophagia*			*early hyperphagia*			*late hyperphagia*		
code	Coef.	Std. Err.	*p*	Coef.	Std. Err.	*p*	Coef.	Std. Err.	*p*
alpine	-1.856	1.037	0.073	2.653	0.810	0.001	2.307	1.078	0.032
anthro	-0.365	0.395	0.356	0.397	0.350	0.256	-0.516	0.706	0.465
closcon	-0.208	1.053	0.843	0.310	1.431	0.828	-3.420	3.246	0.292
decid	-0.278	0.698	0.690	0.492	0.478	0.304	-0.202	0.432	0.640
mixed	-0.581	0.718	0.418	-0.099	0.458	0.829	-0.758	0.185	<0.001
nonveg	-0.325	0.210	0.122	-0.199	0.425	0.640	-0.107	0.170	0.528
opnbog	0.399	0.481	0.406	-0.128	0.413	0.756	-0.795	0.171	<0.001
opncon	0.522	0.429	0.224	0.219	0.354	0.537	0.026	0.562	0.963
regen	2.333	1.449	0.107	-4.081	2.761	0.139	3.731	1.372	0.007
treedbg	0.360	0.677	0.595	0.436	0.443	0.324	-0.267	0.603	0.658
edge	0.021	0.213	0.922	-0.180	0.083	0.030	-0.516	0.142	<0.001
cti	0.132	0.068	0.050	0.275	0.078	<0.001	0.107	0.068	0.116
†cti^2	-0.057	0.284	0.842	-0.882	0.453	0.051	-0.089	0.394	0.821
tri	17.263	5.469	0.002	31.996	6.487	<0.001	11.544	8.812	0.190
tri^2	-93.16	23.34	<0.001	-181.94	33.68	<0.001	-113.69	36.42	0.002
for-age	-0.106	0.090	0.239	-0.037	0.048	0.448	0.064	0.149	0.665
†for-age^2	0.737	0.651	0.257	0.307	0.194	0.113	-0.147	1.418	0.917
regen-age	3.027	0.801	<0.001	1.024	0.935	0.274	-0.346	0.153	0.024
regen-age^2	-0.431	0.121	<0.001	-0.143	0.141	0.309	0.032	0.018	0.077
§solar×clscn	-0.023	0.192	0.905	-0.061	0.199	0.760	0.334	0.433	0.441
§solar×regen	-0.884	0.205	<0.001	0.297	0.296	0.315	-0.477	0.136	<0.001
§solar×alp	0.281	0.121	<0.001	-0.234	0.097	0.016	-0.198	0.077	0.010
†cti×age	0.200	0.375	0.594	0.022	0.374	0.954	-0.100	0.313	0.749
cti×edge	-0.023	0.024	0.344	0.003	0.006	0.602	0.019	0.013	0.145

†estimated coefficients and standard errors reported at 100 times their actual value

§estimated coefficients and standard errors reported at 10,000 times their actual value

Table 5-10. Estimated seasonal habitat selection coefficients for sub-adult (2–5 years of age) grizzly bears in the Yellowhead region of west-central Alberta, Canada. Models are based on GPS radiotelemetry data (bias corrected) collected from 10 sub-adult animals during the 1999 through 2002 seasons. Robust standard errors (Std. Err.) and significance levels (*p*) were based on modified sandwich estimates of variance among animals.

Variable	*hypophagia*			*early hyperphagia*			*late hyperphagia*		
code	Coef.	Std. Err.	*p*	Coef.	Std. Err.	*p*	Coef.	Std. Err.	*p*
alpine	-0.684	1.118	0.541	2.033	1.185	0.086	1.861	0.881	0.035
anthro	-0.735	0.702	0.295	0.094	0.268	0.728	-0.587	0.378	0.121
closcon	1.518	1.849	0.412	1.173	0.798	0.142	1.060	0.894	0.236
decid	0.058	0.640	0.927	0.586	0.397	0.140	0.370	0.441	0.402
mixed	-0.104	0.741	0.889	-0.337	0.320	0.292	-0.697	0.455	0.126
nonveg	-1.050	0.654	0.108	-0.069	0.210	0.744	-0.322	0.435	0.459
opnbog	-0.692	0.702	0.324	0.002	0.244	0.992	-0.853	0.344	0.013
opncon	0.312	0.794	0.694	0.289	0.272	0.288	0.050	0.528	0.925
regen	1.365	2.998	0.649	-3.701	1.920	0.054	-0.249	2.990	0.934
treedbg	0.012	0.783	0.988	-0.071	0.297	0.811	-0.632	0.342	0.064
edge	-0.366	0.097	<0.001	-0.298	0.099	0.002	-0.528	0.151	<0.001
cti	-0.085	0.086	0.325	-0.074	0.049	0.129	0.007	0.058	0.897
†cti^2	0.583	0.268	0.029	0.345	0.210	0.101	0.010	0.262	0.968
tri	10.556	5.567	0.058	26.266	10.756	0.015	22.280	6.919	0.001
tri^2	-12.611	7.576	0.096	-151.47	45.44	0.001	-122.36	31.19	<0.001
for-age	-0.138	0.060	0.022	-0.127	0.058	0.029	0.138	0.097	0.157
†for-age^2	0.631	0.244	0.010	0.409	0.518	0.430	-0.855	0.824	0.300
regen-age	0.302	0.885	0.733	0.362	0.578	0.532	-1.281	0.905	0.157
regen-age^2	-0.007	0.116	0.950	-0.064	0.096	0.505	0.164	0.141	0.244
§solar×clscn	-0.226	0.299	0.451	-0.165	0.086	0.055	-0.234	0.148	0.114
§solar×regen	-0.341	0.419	0.416	0.329	0.194	0.090	0.143	0.364	0.693
§solar×alp	0.098	0.168	0.559	-0.159	0.105	0.132	-0.178	0.080	0.026
†cti×age	0.095	0.437	0.827	0.485	0.258	0.060	-0.997	0.398	0.012
cti×edge	0.031	0.007	<0.001	0.013	0.011	0.240	0.030	0.009	<0.001

†estimated coefficients and standard errors reported at 100 times their actual value

§estimated coefficients and standard errors reported at 10,000 times their actual value

Table 5-11. Degree of agreement between seasonal habitat maps within sex-age groups, as estimated from weighted Kappa ($\hat{K}_w$) statistics and thresholds for degree of agreement from Monserud and Leemans (1992).

Map comparison	Weighted Kappa ($\hat{K}_w$)	Degree of agreement
1. *Adult female*		
hypophagia vs. early hyperphagia	0.70	very good
hypophagia vs. late hyperphagia	0.63	good
early hyperphagia vs. late hyperphagia	0.72	very good
2. *Adult male*		
hypophagia vs. early hyperphagia	0.57	good
hypophagia vs. late hyperphagia	0.46	fair
early hyperphagia vs. late hyperphagia	0.46	fair
3. *Sub-adult*		
hypophagia vs. early hyperphagia	0.41	fair
hypophagia vs. late hyperphagia	0.42	fair
early hyperphagia vs. late hyperphagia	0.65	good

Table 5-12. Degree of agreement between sex-age habitat maps within season, as estimated from weighted Kappa ($\hat{K}_w$) statistics and thresholds for degree of agreement from Monserud and Leemans (1992).

Map comparison	Weighted Kappa ($\hat{K}_w$)	Degree of agreement
1. *Hypophagia*		
adult female vs. adult male	0.37	poor
adult female vs. sub-adult	0.69	good
adult male vs. sub-adult	0.30	poor
2. *Early hyperphagia*		
adult female vs. adult male	0.55	good
adult female vs. sub-adult	0.65	good
adult male vs. sub-adult	0.65	good
3. *Late hyperphagia*		
adult female vs. adult male	0.15	very poor
adult female vs. sub-adult	0.48	fair
adult male vs. sub-adult	0.36	poor
4. *Multi-seasonal (average of 3 seasons) models*		
adult female vs. adult male	0.37	poor
adult female vs. sub-adult	0.72	very good
adult male vs. sub-adult	0.46	fair

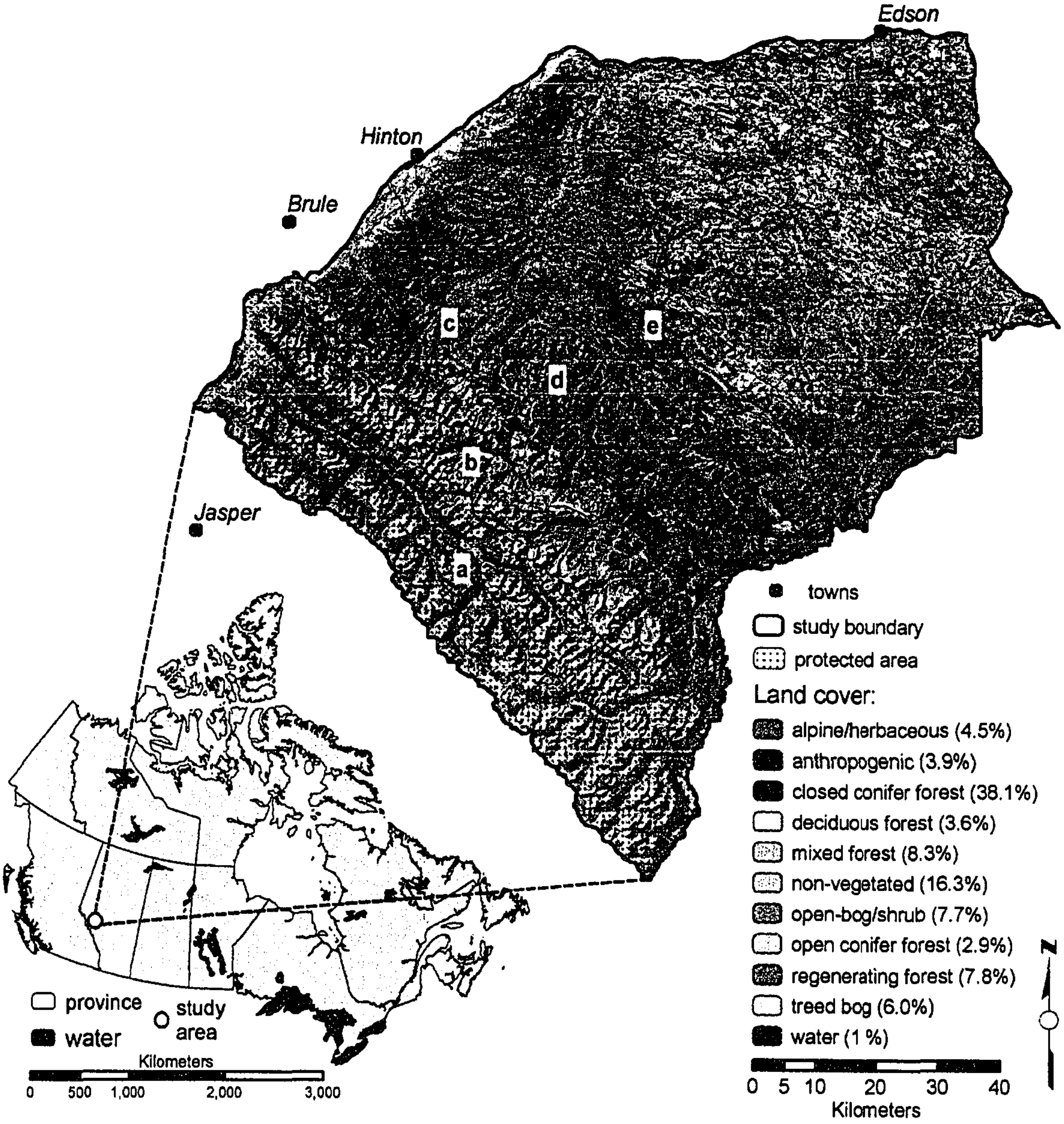

Figure 5-1. Grizzly bear study area in west-central Alberta (53° 15′ N, 118° 30′ W) and location within Canada (lower left figure) shown. Land cover, towns, and protected areas are depicted. Letters represent protected areas or specific regions mentioned in the text, including (a) Jasper National Park (JNP), (b) Whitehorse Wildlands Provincial Park (WWPP), (c) Gregg River, (d) upper McLeod River, and (e) the lower foothills near the town of Robb.

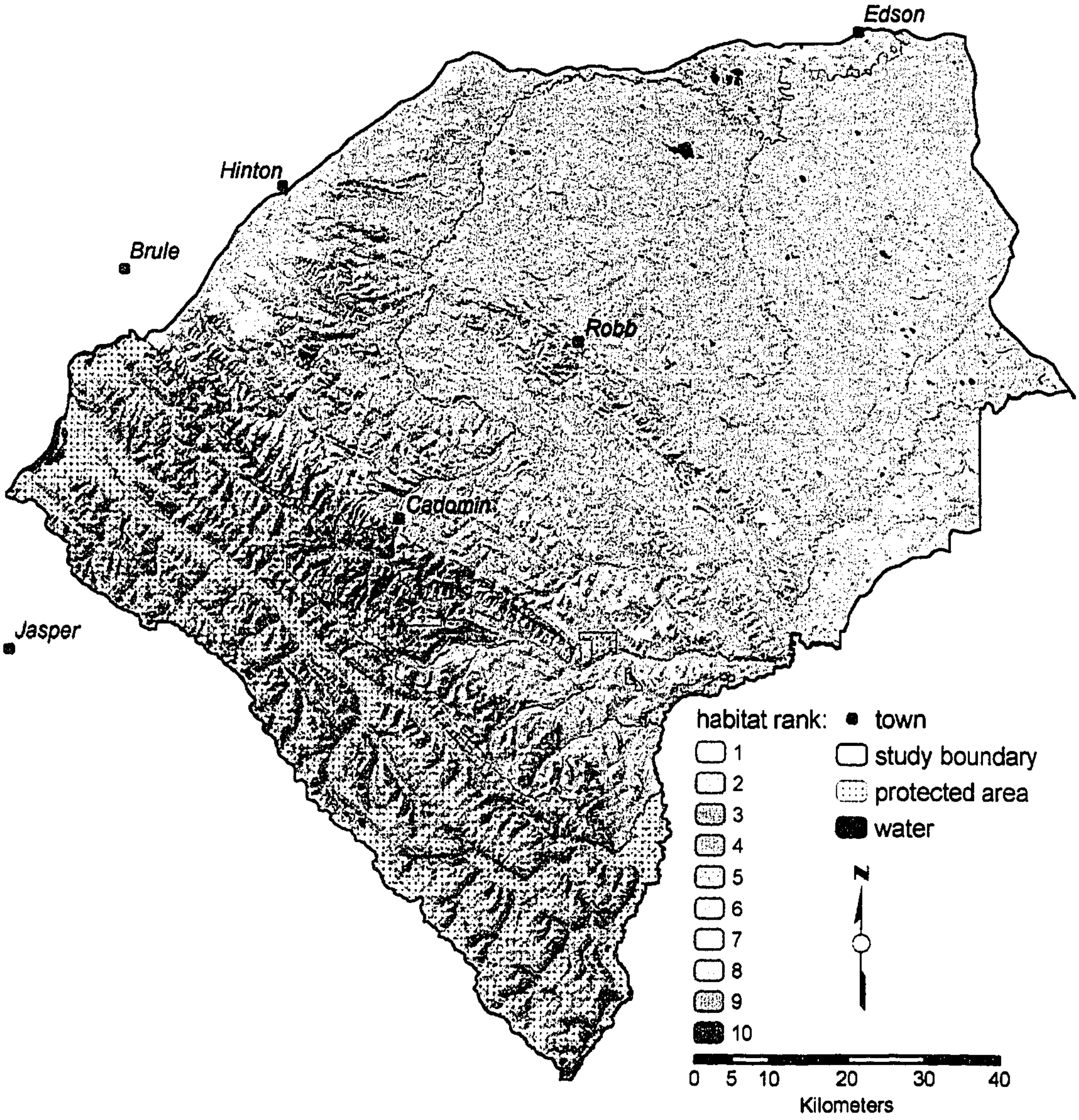

Figure 5-2. Predicted adult female grizzly bear habitat rank (relative probability of occurrence bin) for hypophagia (1 May to 15 June).

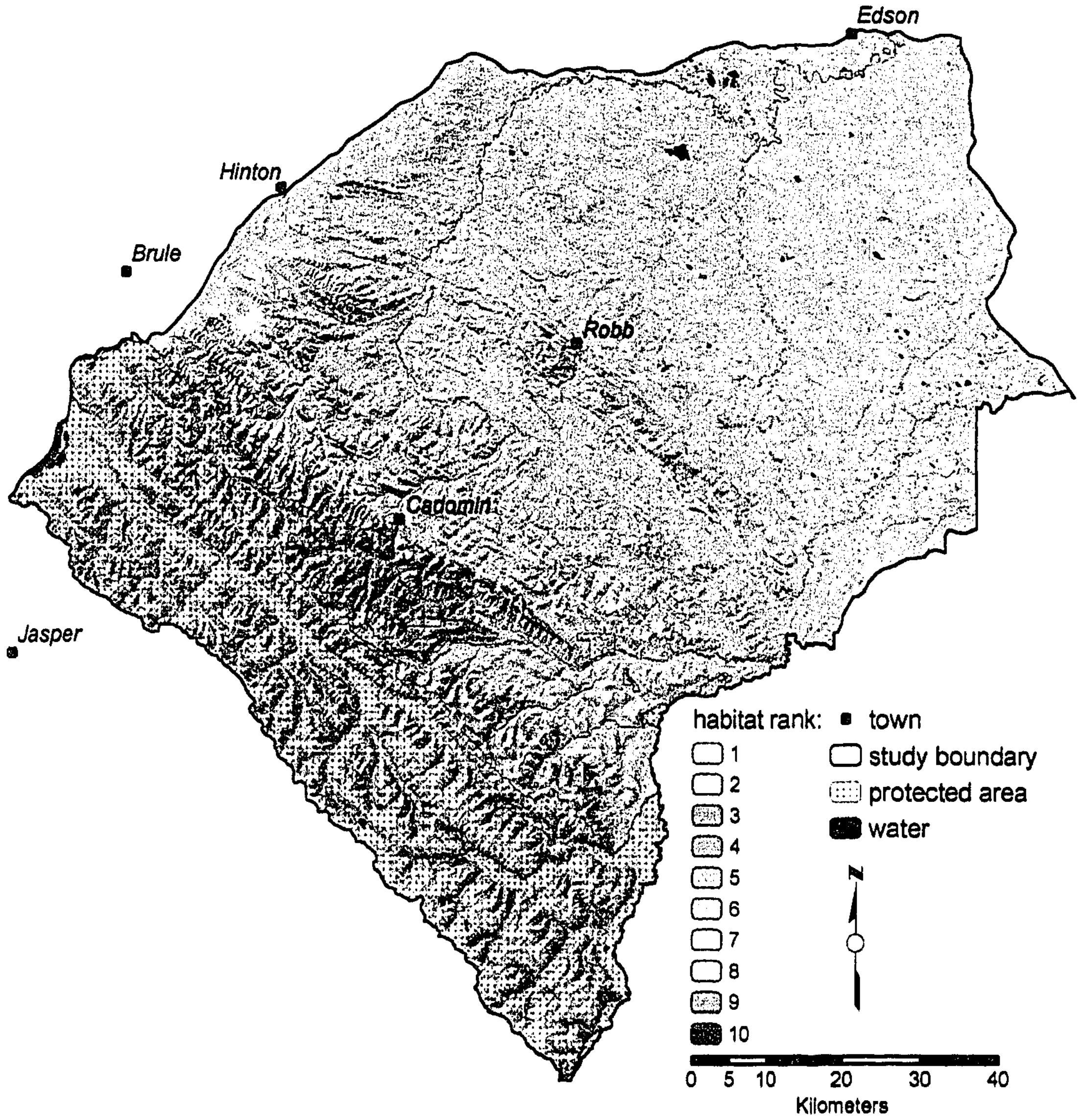

Figure 5-3. Predicted adult female grizzly bear habitat rank (relative probability of occurrence bin) for early hyperphagia (16 June to 15 August).

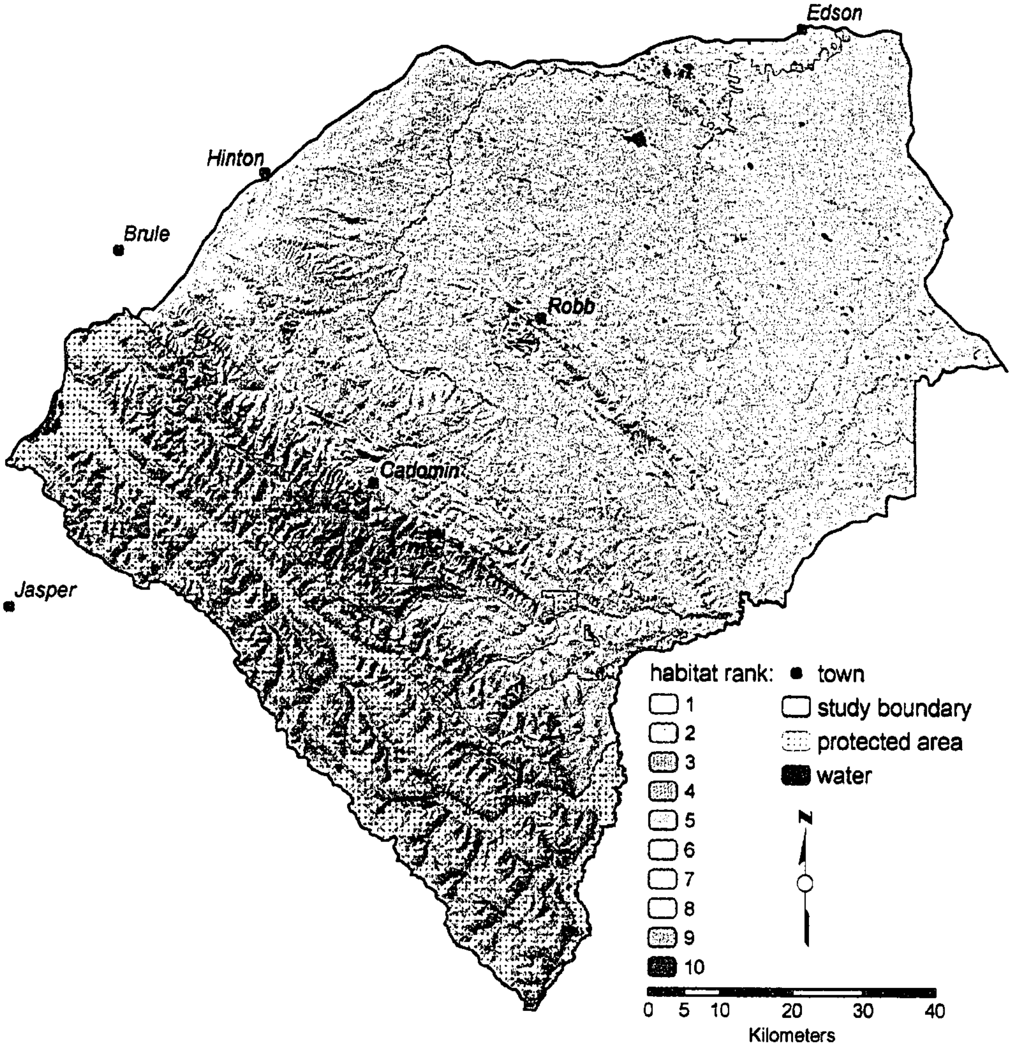

Figure 5-4. Predicted adult female grizzly bear habitat rank (relative probability of occurrence bin) for late hyperphagia (16 August to 15 October).

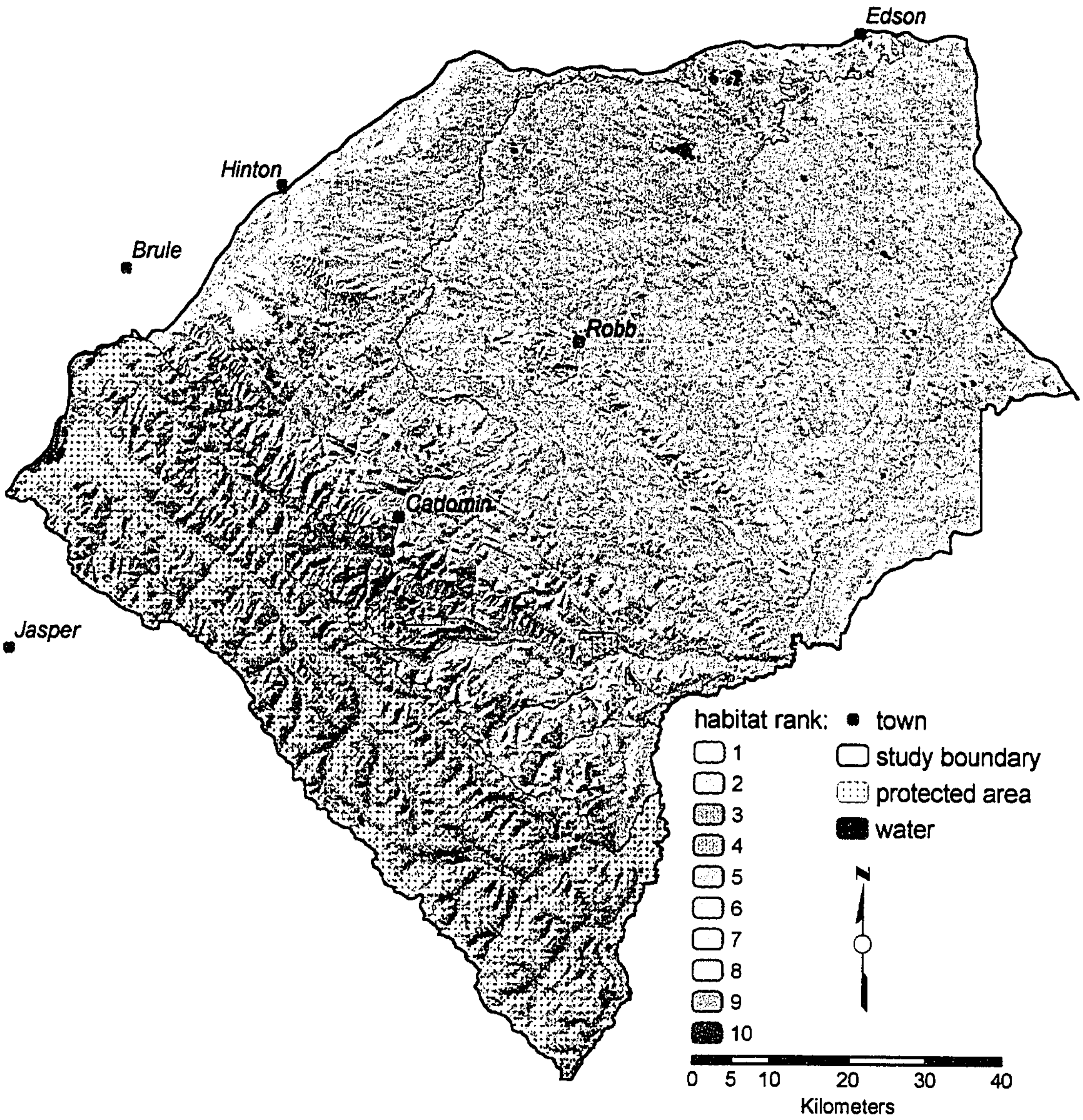

Figure 5-5. Predicted adult male grizzly bear habitat rank (relative probability of occurrence bin) for hypophagia (1 May to 15 June).

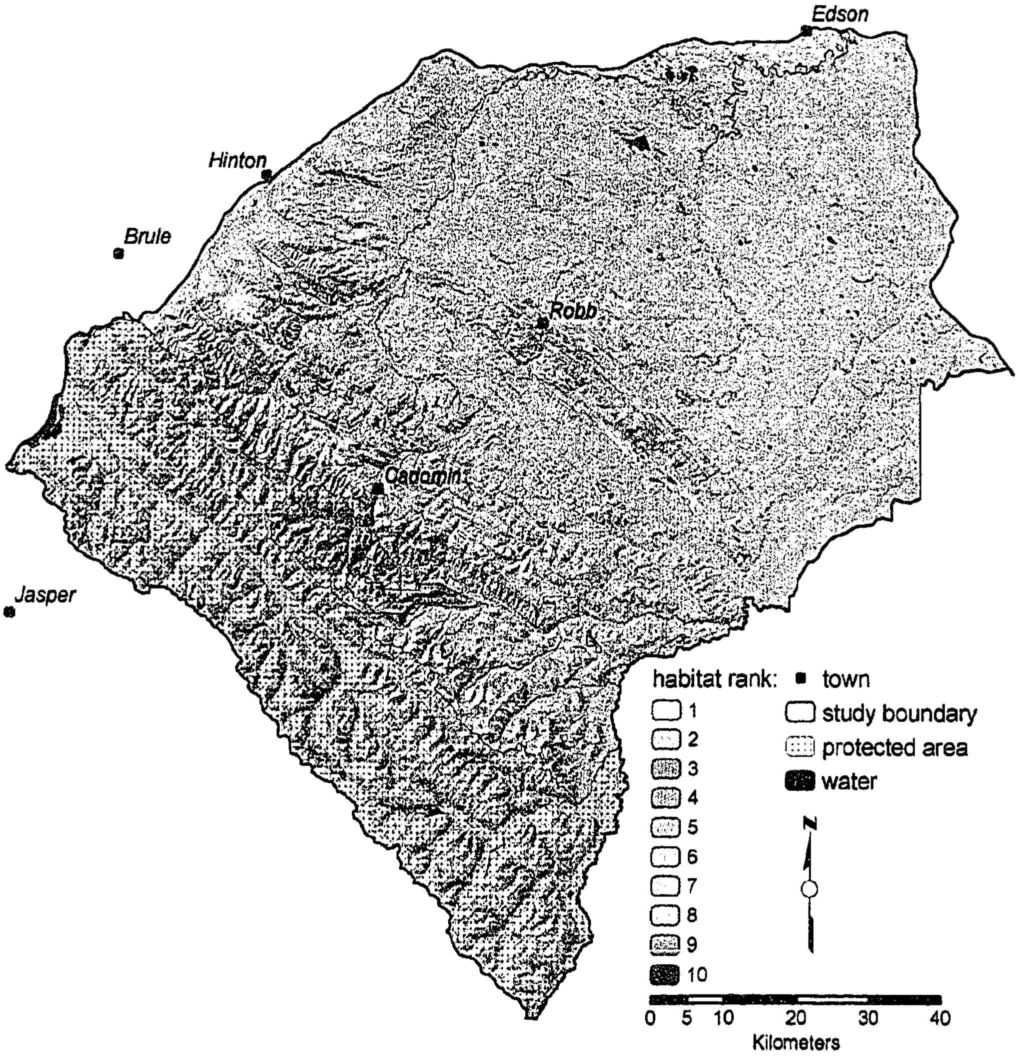

Figure 5-6. Predicted adult male grizzly bear habitat rank (relative probability of occurrence bin) for early hyperphagia (16 June to 15 August).

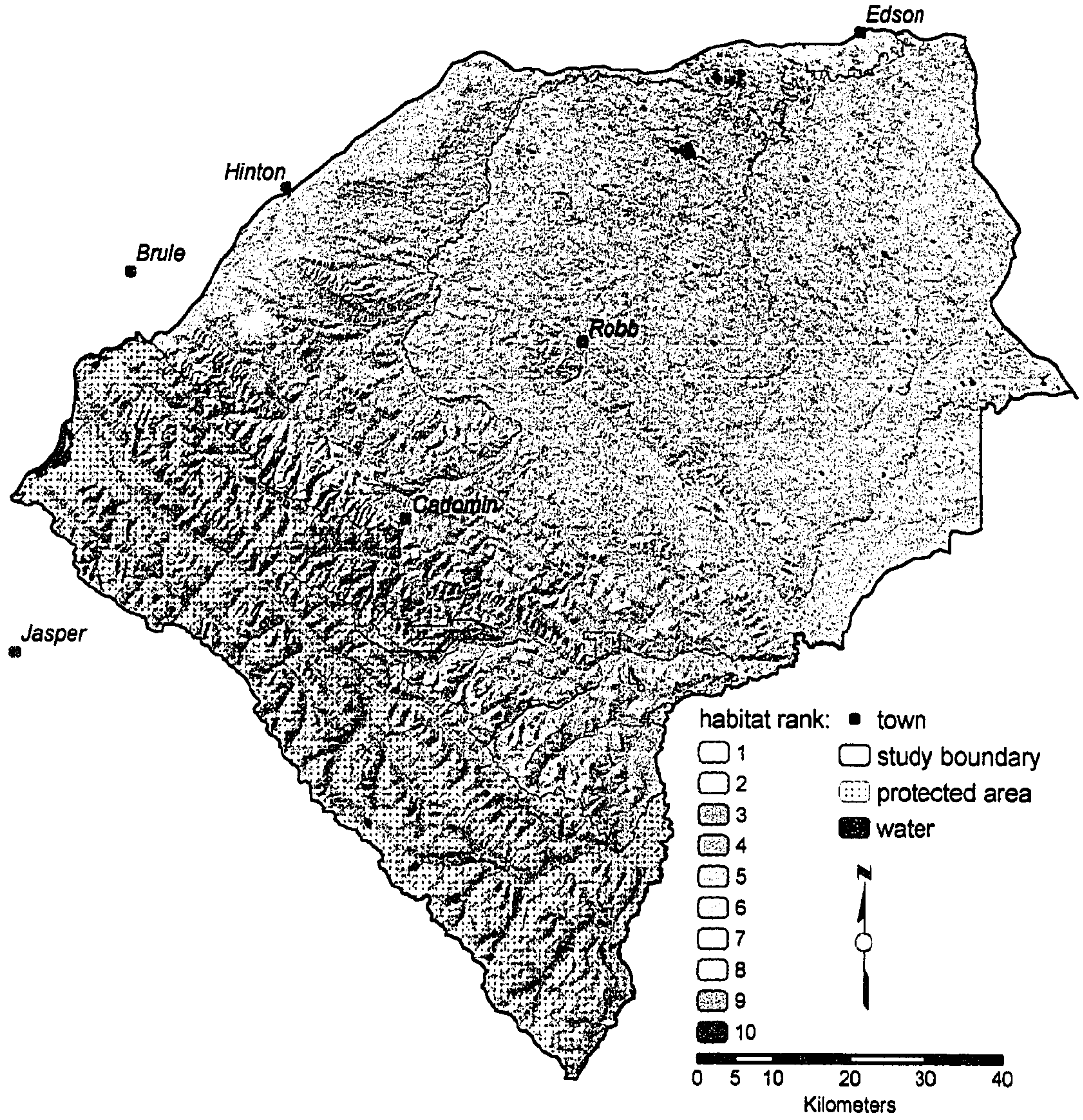

Figure 5-7. Predicted adult male grizzly bear habitat rank (relative probability of occurrence bin) for late hyperphagia (16 August to 15 October).

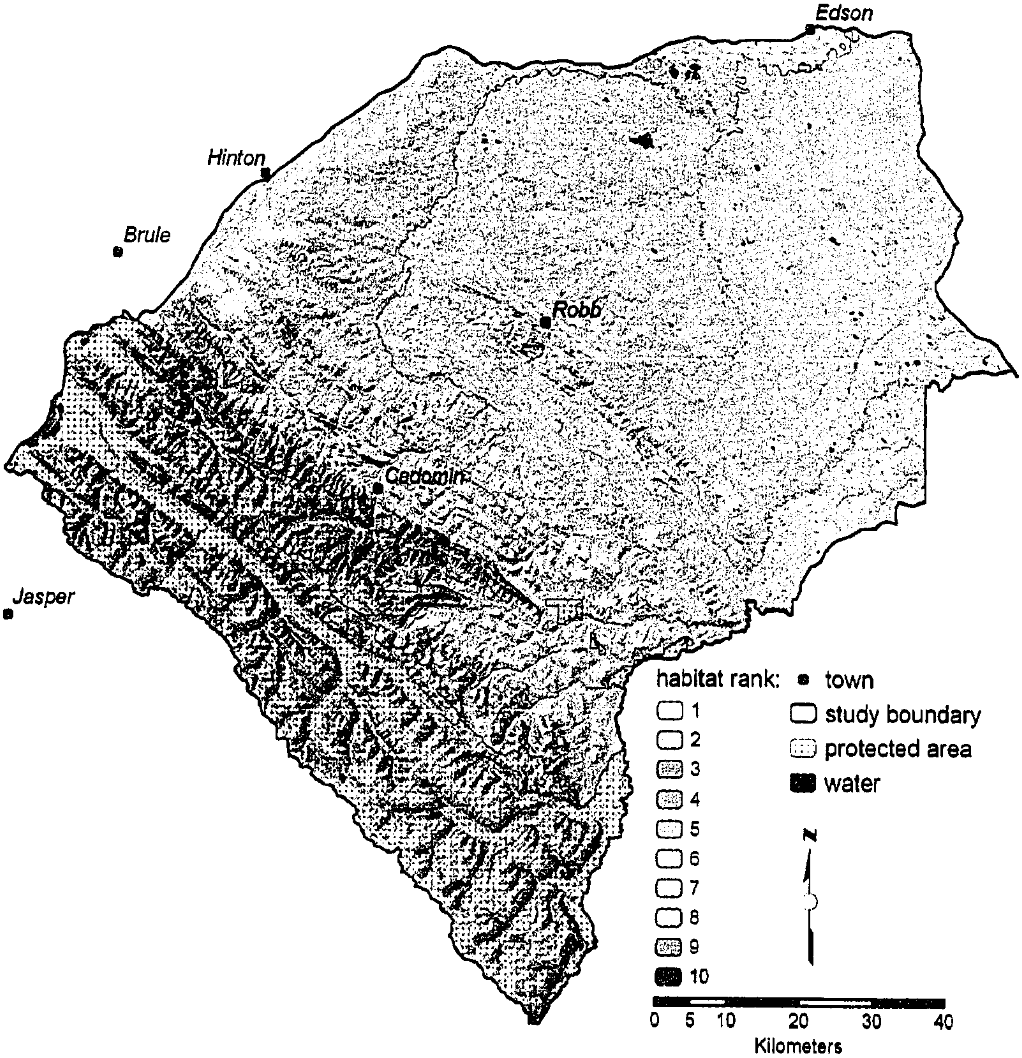

Figure 5-8. Predicted sub-adult grizzly bear habitat rank (relative probability of occurrence bin) for hypophagia (1 May to 15 June).

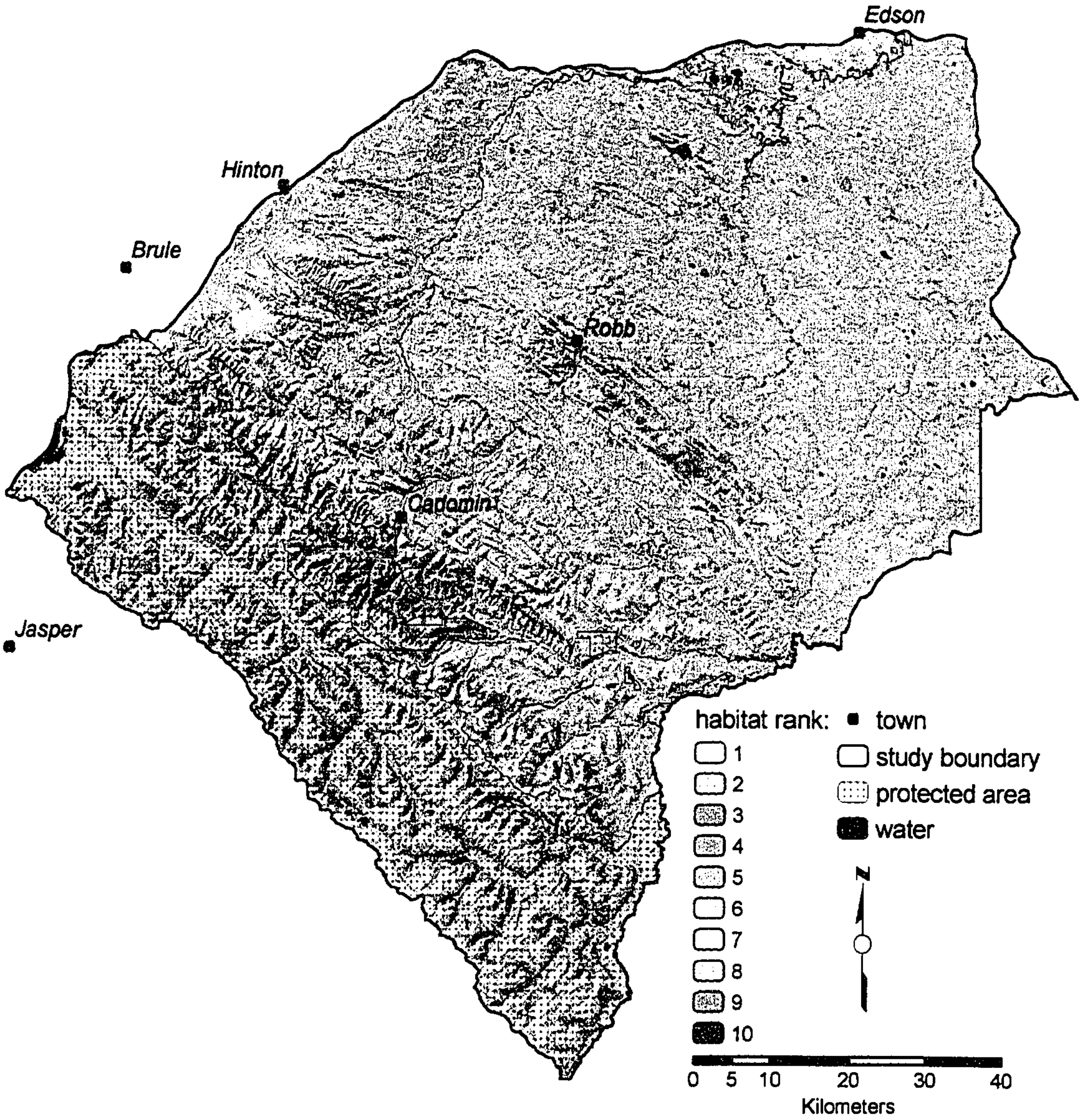

Figure 5-9. Predicted sub-adult grizzly bear habitat rank (relative probability of occurrence bin) for early hyperphagia (16 June to 15 August).

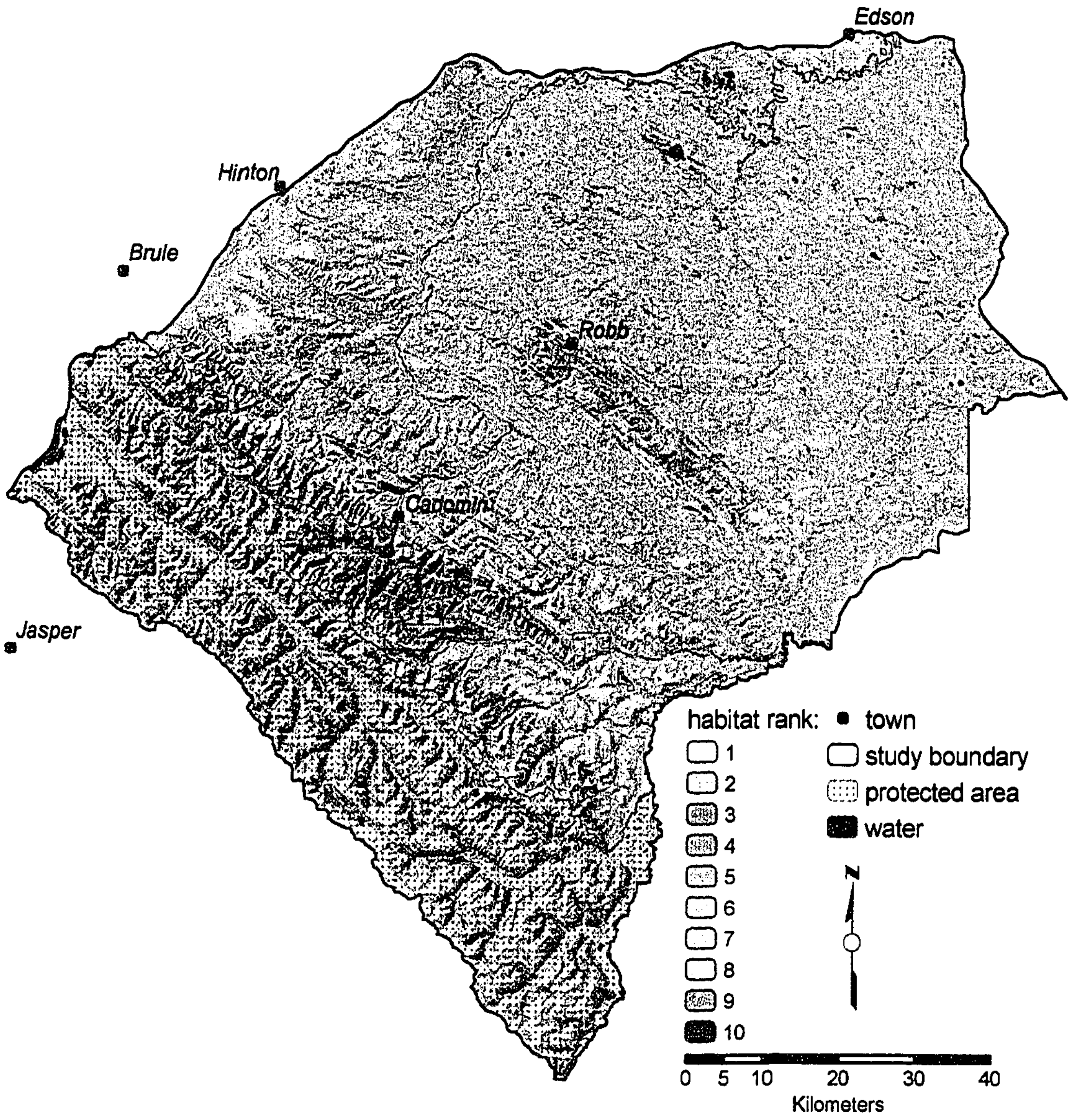

Figure 5-10. Predicted sub-adult grizzly bear habitat rank (relative probability of occurrence bin) for late hyperphagia (16 August to 15 October).

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Chapter 6

Does learning or genetic relatedness shape habitat selection in grizzly bears?

1. *Introduction*

Theoretical and practical applications of habitat selection have received much attention (Fretwell and Lucas, 1970; Rosenzweig, 1981; Mysterud and Ims, 1998; Manly et al., 2002). As well as providing a framework from which to map critical habitats for conservation of threatened species (Boyce and McDonald, 1999), assessments of habitat selection have provided an important foundation from which to understand evolutionary processes, including ecological plasticity, competition among sympatric species, and species formation (Darwin, 1859; Grinnell, 1928; Mayr, 1942). In the process of selecting habitats, those individuals most adept at selecting the necessary resources (e.g., food, shelter, attracting mates, etc.) likely will have the highest survival and reproduction (fitness), passing along these presumably favorable genes. Whether such favourable genes influence habitat selection in subsequent generations is still unknown, but this may be ultimately important for understanding evolutionary process and the conservation of rare or threatened species.

A genetic basis for habitat selection, for instance, has been suggested for *Drosophila* (Kekic et al., 1980; Klaczko et al., 1986; Hoffmann and McKechnie, 1991) and molluscs (Giesel, 1970; Byers, 1983), but the evidence has not been consistent (Jaenike and Holt, 1991). For example, despite previous perceived *Drosophila* habitat selection-genetic relationships, Taylor and Powell (1978) found that *Drosophila* progeny did not return to the habitats from which their parents were collected when released. Regardless, most examples to date have focused on precocial species, such as insects and molluscs where parental care and social interaction were limited or absent.

In contrast, habitat selection for altricial and social animals would be expected to be influenced by parent-offspring rearing and/or social learning experiences while young (Punzo and Ludwig, 2002; Schaik et al., 2003; Haughland and Larsen, 2004). For instance, Haugland and Larsen (2004) found that juvenile red squirrels settled within their habitat of origin during dispersal, suggesting that experience within the natal territory was important. Davis and Stamps (2004) refer to this phenomenon as natal habitat preference induction (NHPI), demonstrating the presence of NHPI in a broad range of taxa. Species-environment relationships can be important as well. We expect that innate (genetic) behavioural responses would be favoured for species inhabiting stable environments where the same behavioural response should always be optimal (Dukas, 1998; see however, Mery and Kawecki, 2004), while learning is thought to be especially advantageous in unstable or variable environments (Stephens, 1991), where the species must adapt to be successful (i.e., survive and reproduce). Although the best test for determining the contribution of inheritance in habitat selection is to experimentally monitoring habitat preferences for offspring when released (Taylor and Powell, 1978; Jaenike and Holt, 1991). Such a test is not realistic or feasible for many species, like grizzly bears (*Ursus arctos*). Recent developments in genetic profiling of free-ranging wildlife (Woods et al., 1999; Mowat and Strobeck, 2000), however, now make it possible to estimate genetic relatedness for individuals within a population (Queller and Goodnight, 1989). In combination with large global position system (GPS) radiotelemetry datasets that allow individual-level definitions of habitat selection (Nielsen et al., 2002), the assessment of genetic or learning contributions to habitat selection is now possible.

Here, we test the degree to which genetic relatedness or parent-offspring rearing shapes the pattern of habitat selection for a population of grizzly bears in west-central Alberta, Canada. We expect that because grizzly bears are flexible omnivores inhabiting variable environments, learning should play a strong role in shaping habitat selection patterns. Specifically, we hypothesize that related female bears will select habitats similarly, as maternal parent-offspring rearing that typically lasts at least 2 years should to lead to habitat 'learning' (experience) and natal habitat preference induction. We further hypothesize, however, that habitat selection among related male bears will not be correlated to the degree of that of females, since paternal contribution of offspring rearing is lacking. However, as male-male sibling pairs would occur in approximately (assuming a 50:50 sex ratio) 1/4 of all liters of 2, some correlations may result between habitat selection and relatedness for male animals. If a relationship between relatedness and habitat selection were found for females, but none for males, we would support a habitat-based learning hypothesis for habitat selection. In contrast, our competing genetic-relatedness hypothesis would predict a genetic contribution to habitat selection behaviours and thus similar correlations between relatedness and habitat selection values regardless of sex. If however, a weak correlation between relatedness and habitat selection existed for male animals and a stronger relationship was evident for female animals, we would not be able to distinguish whether habitat-learning alone (due to male-male sibling relationships) or both habitat-learning and relatedness contributed to habitat selection.

2. Methods

2.1. Grizzly bear habitat use data

From 1999 to 2002, we captured and collared 32 adult (>4 yrs of age) and sub-adult (3-4 yrs of age) grizzly bears in west-central Alberta, Canada (53° 15′ N, 118° 30′ W) using standard aerial darting, leg snaring, and immobilization techniques (Cattet et al., 2003). Bears were fitted with either a Televilt GPS (global-positioning-system)-Simplex or an ATS (Advanced Telemetry Systems) GPS radiocollar and programmed to acquire locations at intervals of either 1-hr or 4-hrs. During the 4-year period, 31,849 locations from the 32 animals were acquired from within a defined 9,752-km^2-study area in west-central Alberta, Canada. Animal locations were stratified into 3 seasons between 1 May and 15 October to account for variation in habitat use through time (Nielsen et al., 2002; 2003). Characteristics and timing of the 3 seasons are defined in more detail in Table 6-1. Using the 3 defined seasons and a minimum sampling rule of 50 observations per season-bear combination (Leban et al., 2001), we identified 28,227 animal observations (Table 6-2) and used these data to assess individual-level habitat use by grizzly bears based on 11 habitat (landcover/landuse) classes (Table 6-3).

For each animal and season, we assessed the proportion use, u_i, of habitat i by simply comparing the number of observations, n_i, observed in each habitat i with the total number of observations for each animal and season combination across all 11 habitats or,

$$u_i = n_i / \Sigma n \qquad (6\text{-}1).$$

To account for GPS radiotelemetry bias (Johnson et al., 2002; Frair et al., 2004), we used probability sample weights from a model describing the probability of acquiring a GPS acquisition, $p_{(fix)}$, based on local habitat and terrain covariates (Frair et al., 2004).

After applying $p_{(fix)}$ models for the landscape in a GIS (geographical information system) for both Televilt and ATS GPS radiocollars, we used zonal statistics to estimate average $p_{(fix)}$ values by habitat (Table 6-4). Our bias-adjustment of n_i was therefore defined as,

$$\text{adj-}n_i = 1/p_{(fix)} \times n_i \qquad (6\text{-}2).$$

Bias-adjusted values of n_i were fit back into equation 6-1 to estimate a bias-adjusted proportion use, u_i, for each habitat by animal and season. As 3 seasons were examined for habitat use, we used only those habitats that proved rather invariant results temporally, as determined through previous habitat-selection modelling (S. Nielsen, unpublished data). In total, 7 of the 11 habitats examined appeared to be used similarly among seasons. These were alpine/herbaceous, deciduous forest, mixed forest, non-vegetated, open conifer, riparian, and treed-bog habitats. To assess habitat selection, we required an assessment of habitat availability (Manly et al., 2002). We estimated habitat availability by generating multi-annual 100% minimum convex polygon (MCP) home ranges for each animal. Within individual home ranges, we calculated the proportion availability, a_i, of each habitat class i by summing the map pixels within each class and comparing these to the sum of all home range map pixels. Based on our assessments of use and availability, we defined a habitat selection ratio, $w_{(x)}$, for each animal following that of Manly et al. (2002):

$$w_{(x)} = u_i \,/\, a_i \qquad (6\text{-}3),$$

where u_i was the seasonal bias-adjusted proportion use for habitat i defined by equation 6-1 and 6-2 and a_i was the proportion availability of habitat i based on 100% MCP assessments. Pairwise Pearson correlations (r) for individual animals were estimated based on a comparison of $w_{(x)}$ values for each of the 7 habitats. The resulting matrix was labeled S for habitat selection. As well, we generated a pairwise correlation matrix of our habitat availability for the same 7 habitats, labeling this matrix as A for habitat availability.

2.2. Genetic relatedness

Root hairs were collected from 91 marked and unmarked grizzly bears in west-central Alberta, Canada. Grizzly bear hairs from unmarked individuals were sampled using hair-snagging techniques for mark-recapture population estimates (Woods et al., 1999; Mowat and Strobeck, 2000), while hairs from radiocollared animals were collected during capture. DNA was extracted using 15 microsatellite loci with 10 alleles at the most polyallelic locus. Based on the DNA profiling of each hair sample, we calculated pairwise genetic relatedness for individual animals using version 5.0 of the program RELATEDNESS (Queller and Goodnight, 1989). All animals were equally weighted. From the pairwise relatedness matrix, we separated the 32 radiocollared animals of interest into a single matrix that we called G for genetic relatedness.

2.3. Comparing genetic relatedness and animal habitat selection

We used a Mantel test (Mantel, 1967) with randomization (Manly, 1997) to assess the correlation among matrices of habitat selection (S) and genetic relatedness (G). We controlled for habitat availability (A), however, using a partial Mantel test, as habitat selection can vary as a function of habitat availability (Mysterud and Ims, 1998; Mysterud et al., 1999). We separated pairwise matrices by sex to compare male-male and female-female animal groups, thus allowing us to compare our competing hypotheses, as well as removing sex-based behavioural differences that have been previously criticized for genetic-habitat selection assessments (Jaenike and Holt, 1991). As Mantel tests most typically use distance matrices instead of correlations, we defined new distance matrices by subtracting all correlations from 1. We use the same symbols of S, G, and A to define distance matrices for habitat selection, genetic relatedness and habitat availability respectively. Partial Mantel tests were performed in EXCEL® using the XLSTAT® add-in with 50,000 randomizations for significance of matrix correlations under a one-tailed test of significance.

3. Results

Habitat selection ratios varied substantially among individuals (Table 6-5). Differences between sexes, however, were less well pronounced, but still significantly different for alpine/herbaceous and deciduous forest classes (Figure 6-1). Male grizzly bears selected deciduous forests more than female bears, while females selected alpine/herbaceous areas more than males. Partial Mantel tests revealed that correlations between relatedness and habitat selection matrices varied by sex. After accounting for habitat availability, related female grizzly bears were more likely to select habitats in a similar manner than unrelated female animals ($r_{(S,G|A)} = 0.192$, $p = 0.021$; Figure 6-2a).

In contrast, use of habitats by individual male grizzly bears was not correlated ($r_{(S,G|A)} = -0.044$, $p = 0.431$; Figure 6-2b) with genetic relatedness.

4. Discussion

Habitat selection varied among individuals and between sexes. That variation was partially explained by genetic relatedness, however, because female grizzly bears were more likely to select similar habitats. In contrast, related males did not select similar habitats. Given the lack of a relationship for males and evidence for a relationship for females, we support our habitat-learning hypothesis. Assuming genes for habitat selection are not sex-linked, we do not find support for the genetic relatedness hypothesis and the hypothesis that genetic relatedness and habitat learning were operating simultaneously. Maternal parent-offspring rearing in grizzly bears therefore appears to play a role in the shaping of habitat selection strategies in bears. The importance of maternal parent contact for habitat learning also has been shown for young *Hogna carolinensis* spiderlings (Punzo and Ludwig, 2002). Punzo and Ludwig (2002) demonstrated that maternal contact (as compared with isolation) increased subsequent hunting efficiency and spatial learning of spiderlings following dispersal. Likewise, Schaik et al. (2003) found that female orang-utans that spent time in female social groups beyond that of the maternal parent had much greater tool-use specialization than male orang-utans, the dispersing sex. Although both of these examples point to the importance of learning through parental or social contact, we have demonstrated for grizzly bears that learning experiences alone appear to predict grizzly bear habitat selection without evidence for a genetic (innate) contribution. To our knowledge, we are the first to directly test genetic versus learning influence of habitat selection *in situ*. Our results also are consistent with previous suggestions that for highly variable environments, typical of grizzly bear habitats, learning should be promoted over inherited behaviours, as the same response will not always be optimal (Dukas, 1998).

Despite finding a correlation among relatedness and habitat selection for female grizzly bears, a large proportion of variance was left un-explained; perhaps the result of intra-specific competition among related animals having overlapping home ranges or ecologically important temporal effects. Food resource variation, including different fruiting intervals for mass fruiting species, may be one ecologically important temporal effect (Hamer and Herrero, 1987; Mattson et al., 1992; Felicetti et al., 2003). Some parent-offspring pairings may have occurred between mass fruiting intervals, preventing 'learning' experiences from occurring and thus influencing resource use in subsequent years. As well as ecological factors, sampling factors also may have influenced results because some animals were radiocollared in different years. As bears are habitat generalists that respond to variations in available food resources, they can show substantial variation in annual habitat selection (Hamer and Herrero, 1987; Schooley, 1994).

5. Conclusion

The multi-year bond between maternal parent and dependent offspring contributes to subsequent habitat-selection behaviours in grizzly bears. Davis and Stamps (2004) refer to this as natal habitat preference induction, being supported across a wide range of taxa. Because learning might occur between siblings (thus not limited to maternal parent pairing), additional tests or observations of the nature of sibling learning in grizzly bears is needed.

Table 6-1. Defined seasons used for assessing habitat use by grizzly bears in west-central Alberta, Canada. Seasonal breaks based on foraging activities reported for the region (e.g., Hamer and Herrero, 1987; Hamer et al., 1991; Nielsen et al., 2003).

Season	Start date	End date	Characteristic foraging items
Hypophagia (S-1)	1-May	15-Jun	roots from *Hedysarum* spp., carrion and young ungulate calves
Early hyperphagia (S-2)	16-Jun	15-Aug	ants (myrmecophagy), *Heracleum lanatum*, graminoids, sedges, and *Equisetum arvense*
Late hyperphagia (S-3)	16-Aug	15-Oct	fruit (frugivory) of *Vaccinium* spp. and *Shepherdia canadensis,* roots from *Hedysarum* spp.

Table 6-2. Identification, sex (M-male; F-female), multi-annual 100% minimum convex polygon (MCP) home range size, and number of radiotelemetry locations by season for habitat use assessments.

Bear		100% MCP	Radiotelemetry locations			
Identity	Sex	Range (km^2)	S-1	S-2	S-3	Total
GB01	M	1,629	433	250	84	767
GB02	F	694	329	379	97	805
GB03	F	849	374	671	586	1,631
GB04	F	471	458	641	532	1,631
GB05	M	3,745	636	786	500	1,922
GB06	M	1,491	303	210	-	513
GB07	F	416	66	-	-	66
GB08	M	1,827	311	437	280	1,028
GB10	F	659	385	825	549	1,759
GB11	F	484	171	151	-	322
GB12	F	1,860	558	488	277	1,323
GB13	F	2,045	-	63	-	63
GB14	M	2,638	139	136	58	333
GB16	F	591	124	606	664	1,394
GB17	M	1,694	672	378	-	1,050
GB20	F	987	633	708	316	1,657
GB23	F	666	261	912	419	1,592
GB24	M	4,314	227	384	422	1,033
GB26	F	1,447	53	95	95	243
GB27	F	2,928	217	388	355	960
GB28	F	1,300	370	600	780	1,750
GB33	M	4,710	409	818	872	2,099
GB34	F	799	-	90	109	199
GB35	F	294	122	219	188	529
GB36	F	1,064	198	154	155	507
GB37	F	742	82	150	167	399
GB38	F	311	86	126	191	403
GB40	F	1,000	272	268	238	778
GB42	F	1,271	-	275	297	572
GB50	M	903	81	87	-	168
GB54	M	1,467	-	63	-	63
GB100	F	606	128	289	251	668
		TOTAL	8,098	11,647	8,482	28,227

Table 6-3. Land cover classes used to represent grizzly bear habitats for assessing habitat use. Composition (%) of habitats within the study area are provided, as well as the original remote sensing class used to define grizzly bear habitats from Franklin et al. (2001).

Land cover class	Percent composition	Original remote sensing classes extracted from Franklin et al. (2001)
closed conifer forest	37.2	closed coniferous forest
open conifer forest	2.7	open coniferous forest
deciduous forest	3.4	closed & open deciduous forests
mixed forest	7.9	mixed forest
alpine/herbaceous	4.4	alpine/sub-alpine >1800m & herbaceous <1800 m
open-bog/shrub	6.3	open-bog & shrub <1800 m
treed-bog	5.4	treed-bog
non-vegetated	17	rock, snow/ice, shadow, & water
anthropogenic	3.9	road/rail line, pipleline, well site, & urban
regenerating forest	7.5	clearcuts and recent burns
riparian	4.3	n.a. (obtained through GIS model)

Table 6-4. Average probability of acquiring a fix for 2 GPS collar brands by land cover type based on a model applying $p_{(fix)}$ to the study area from Frair et al. (2004). Zonal statistics in a GIS were used to determine the average $p_{(fix)}$ value within individual land cover classes.

	GPS collar bias- $p_{(fix)}$	
Land cover type	Televilt	ATS
alpine/herbaceous	0.834	0.904
anthropogenic	0.877	0.930
closed conifer forest	0.752	0.852
deciduous forest	0.783	0.872
mixed forest	0.891	0.939
non-vegetated	0.780	0.867
open-bog/shrub	0.865	0.924
open conifer forest	0.712	0.817
regenerating forest	0.854	0.916
riparian	0.826	0.898
treed-bog	0.724	0.833

Table 6-5. Selection ratios, $w_{(x)}$, average seasonal bias-adjusted proportion use, u_i, and proportion availability, a_i, within individual multi-annual 100% MCP home ranges for 7 temporally invariant habitat classes used to describe individual-level habitat selection of grizzly bears in west-central Alberta, Canada.

Bear ID	alpine/herbaceous			deciduous forest			mixed forest			non-vegetated			open conifer forest			riparian			treed-bog		
and sex	u_i	a_i	$w_{(x)}$	u_i	a_i	$w_{(x)}$	u_i	a_i	$w_{(x)}$	u_i	a_i	$w_{(x)}$	u_i	a_i	$w_{(x)}$	u_i	a_i	$w_{(x)}$	u_i	a_i	$w_{(x)}$
GB01-M	0.244	0.098	2.495	0.031	0.005	6.777	0.001	0.005	0.191	0.235	0.616	0.382	0.126	0.045	2.780	0.097	0.015	6.642	0.059	0.013	4.615
GB02-F	0.288	0.096	2.989	0.008	0.004	1.857	0.002	0.003	0.552	0.387	0.714	0.542	0.104	0.040	2.590	0.037	0.017	2.121	0.034	0.014	2.390
GB03-F	0.356	0.122	2.919	0.011	0.006	1.850	0.005	0.003	1.714	0.225	0.509	0.442	0.134	0.090	1.484	0.014	0.015	0.966	0.009	0.011	0.832
GB04-F	0.462	0.192	2.414	0.030	0.023	1.306	0.006	0.011	0.509	0.213	0.402	0.530	0.127	0.090	1.408	0.010	0.009	1.022	0.029	0.021	1.373
GB05-M	0.046	0.088	0.520	0.054	0.020	2.663	0.102	0.048	2.124	0.059	0.245	0.240	0.070	0.050	1.396	0.065	0.022	2.960	0.031	0.009	3.576
GB06-M	0.373	0.146	2.554	0.024	0.007	3.350	0.004	0.004	0.919	0.171	0.584	0.292	0.124	0.050	2.455	0.026	0.007	3.708	0.024	0.005	4.710
GB07-F	0.001	0.005	0.208	0.036	0.034	1.065	0.133	0.098	1.348	0.048	0.013	3.856	0.012	0.016	0.761	0.157	0.068	2.317	0.036	0.018	2.069
GB08-M	0.253	0.101	2.490	0.045	0.020	2.284	0.019	0.031	0.631	0.086	0.266	0.324	0.149	0.072	2.055	0.026	0.019	1.343	0.052	0.015	3.480
GB10-F	0.442	0.138	3.209	0.007	0.004	1.868	0.001	0.001	0.786	0.222	0.624	0.357	0.100	0.046	2.202	0.041	0.012	3.266	0.016	0.004	3.780
GB11-F	0.010	0.007	1.429	0.010	0.019	0.523	0.079	0.070	1.141	0.014	0.030	0.447	0.010	0.007	1.429	0.191	0.065	2.932	0.026	0.022	1.143
GB12-F	0.007	0.003	2.281	0.047	0.048	0.990	0.219	0.141	1.552	0.035	0.018	1.934	0.007	0.008	0.852	0.098	0.070	1.395	0.061	0.066	0.917
GB13-F	0.020	0.004	5.154	0.061	0.028	2.195	0.172	0.102	1.694	0.041	0.021	1.929	0.001	0.005	0.217	0.061	0.054	1.122	0.207	0.099	2.085
GB14-M	0.029	0.021	1.359	0.246	0.039	6.359	0.114	0.101	1.124	0.033	0.042	0.782	0.036	0.024	1.523	0.046	0.051	0.897	0.024	0.022	1.092
GB16-F	0.502	0.173	2.899	0.038	0.011	3.600	0.009	0.006	1.393	0.172	0.490	0.351	0.096	0.089	1.073	0.006	0.008	0.711	0.042	0.012	3.609
GB17-M	0.028	0.022	1.286	0.015	0.027	0.564	0.074	0.105	0.702	0.033	0.045	0.717	0.024	0.023	1.024	0.076	0.051	1.479	0.016	0.013	1.284
GB20-F	0.041	0.027	1.502	0.023	0.019	1.229	0.086	0.110	0.778	0.019	0.036	0.515	0.021	0.019	1.093	0.081	0.044	1.827	0.011	0.009	1.213
GB23-F	0.044	0.032	1.368	0.080	0.035	2.268	0.056	0.078	0.716	0.038	0.072	0.531	0.151	0.038	3.971	0.017	0.051	0.333	0.040	0.017	2.283
GB24-M	0.003	0.013	0.274	0.029	0.030	0.973	0.111	0.139	0.800	0.030	0.021	1.412	0.012	0.016	0.749	0.094	0.060	1.578	0.020	0.019	1.047
GB26-F	0.035	0.004	8.775	0.068	0.028	2.384	0.048	0.095	0.504	0.118	0.019	6.114	0.006	0.004	1.341	0.180	0.062	2.913	0.038	0.101	0.370
GB27-F	0.030	0.006	4.825	0.080	0.034	2.386	0.085	0.099	0.856	0.053	0.021	2.491	0.050	0.013	3.937	0.051	0.055	0.912	0.068	0.069	0.988
GB28-F	0.362	0.095	3.827	0.012	0.007	1.864	0.003	0.007	0.444	0.283	0.416	0.681	0.131	0.069	1.917	0.033	0.022	1.507	0.020	0.024	0.831
GB33-M	0.020	0.019	1.073	0.121	0.039	3.145	0.098	0.088	1.105	0.049	0.092	0.537	0.018	0.020	0.908	0.103	0.052	1.990	0.056	0.069	0.807
GB34-F	0.340	0.111	3.072	0.011	0.005	2.140	0.001	0.005	0.204	0.253	0.595	0.425	0.043	0.050	0.855	0.108	0.017	6.195	0.015	0.016	0.956
GB35-F	0.629	0.196	3.213	0.007	0.012	0.542	0.001	0.008	0.128	0.222	0.519	0.427	0.064	0.058	1.107	0.004	0.007	0.486	0.008	0.014	0.580
GB36-F	0.057	0.023	2.465	0.041	0.024	1.710	0.106	0.129	0.827	0.039	0.039	1.010	0.021	0.020	1.051	0.072	0.044	1.638	0.013	0.009	1.438
GB37-F	0.107	0.063	1.695	0.022	0.028	0.762	0.039	0.062	0.627	0.072	0.151	0.478	0.060	0.045	1.322	0.041	0.026	1.593	0.016	0.010	1.698
GB38-F	0.155	0.086	1.795	0.043	0.023	1.903	0.041	0.030	1.372	0.062	0.117	0.526	0.079	0.052	1.516	0.004	0.017	0.254	0.006	0.006	1.164
GB40-F	0.084	0.047	1.778	0.052	0.024	2.128	0.047	0.072	0.654	0.111	0.118	0.946	0.138	0.035	3.921	0.037	0.041	0.908	0.031	0.011	2.702
GB42-F	0.200	0.103	1.944	0.026	0.018	1.431	0.016	0.025	0.627	0.166	0.411	0.404	0.115	0.040	2.859	0.012	0.002	6.833	0.001	0.001	1.000
GB50-M	0.006	0.012	0.470	0.044	0.022	1.965	0.135	0.149	0.908	0.006	0.017	0.332	0.011	0.010	1.055	0.093	0.048	1.922	0.011	0.009	1.137
GB54-M	0.009	0.022	0.394	0.026	0.024	1.079	0.071	0.089	0.792	0.009	0.031	0.285	0.009	0.024	0.366	0.088	0.045	1.969	0.001	0.011	0.089
GB100-F	0.030	0.063	0.478	0.055	0.035	1.576	0.067	0.059	1.139	0.055	0.150	0.368	0.070	0.049	1.421	0.016	0.031	0.521	0.037	0.014	2.624

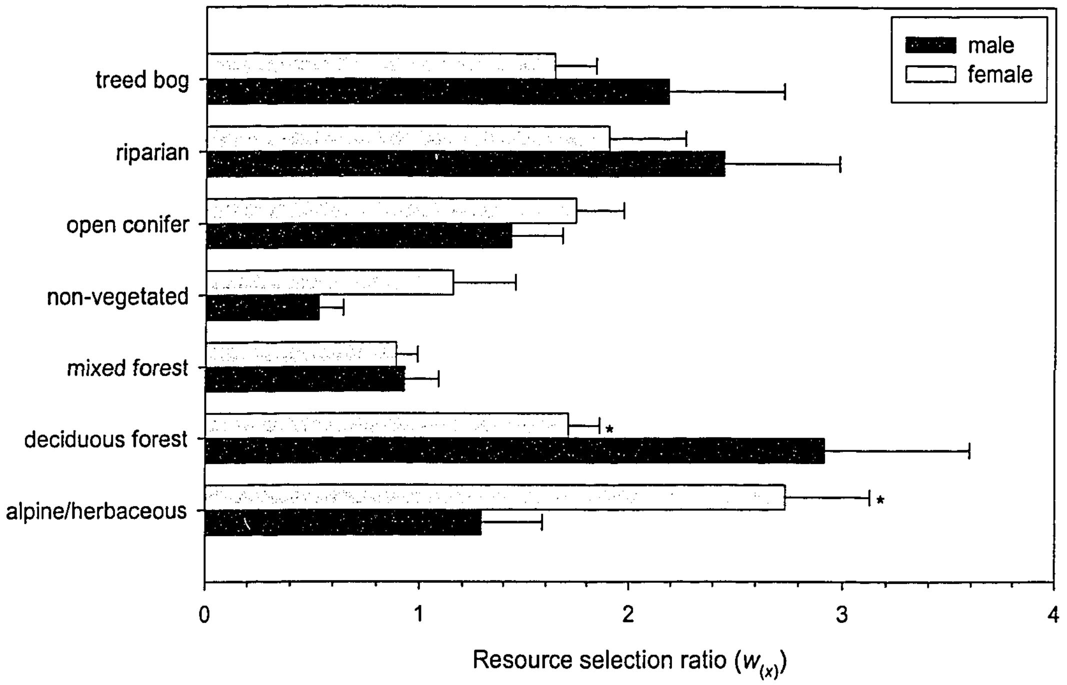

Figure 6-1. Mean and standard error (bars) of resource selection ratios, by sex, for 7 examined land cover classes. The symbol, *, following a female land cover estimate indicates significant (p <0.05) differences in selection ratios between sexes based on Hotelling T^2 tests.

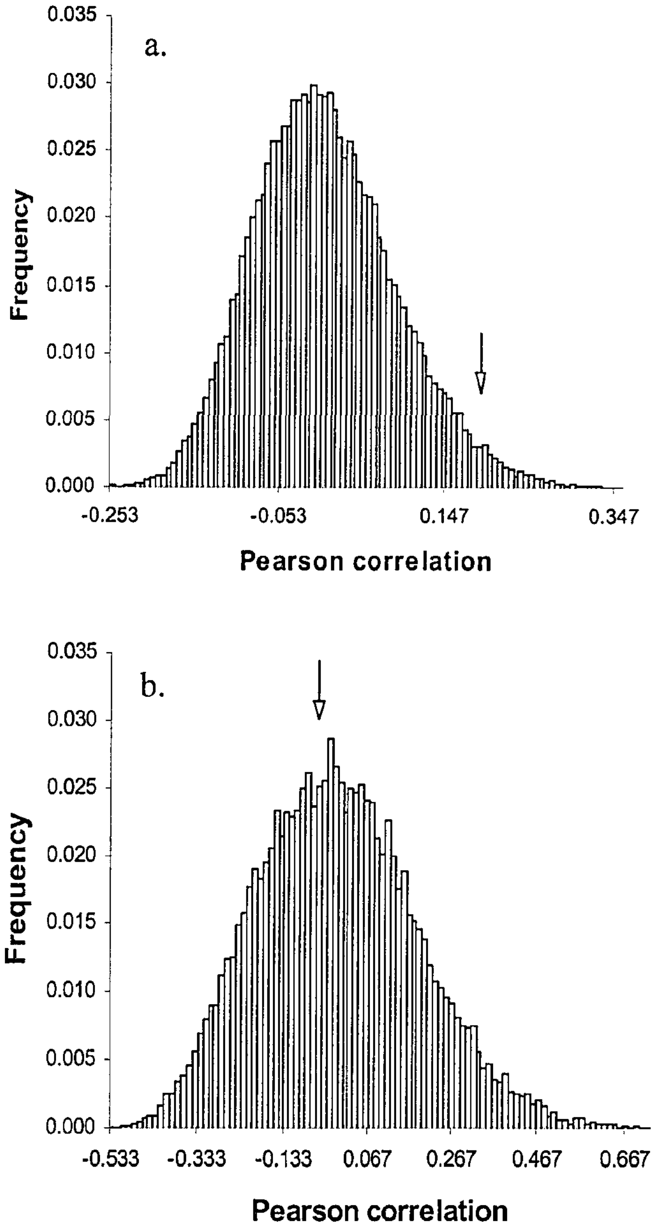

Figure 6-2. Pearson (*r*) correlations for habitat selection and genetic relatedness matrices (dissimilarity) after controlling for habitat availability using a partial Mantel test with randomization (50,000 permutations). The distributions of resulting correlations are depicted as frequencies, with the actual observed correlation indicated with an arrow. Female grizzly bear (*n* = 22) correlations are shown in a., while male grizzly bear (*n* = 10) correlations are shown in b.

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Chapter 7

A habitat-based framework for grizzly bear conservation in Alberta

1. Introduction

Understanding the distribution and abundance of species in space and time is the primary definition of ecology (Krebs, 1985). With the recent advent of geographic information systems (GIS), together with widespread availability of digital geo-spatial data, predicting species occurrence and/or abundance has become commonplace (Boyce and McDonald 1999; Scott et al., 2001). Such predictions can be made over a wide variety of scales, including global (Rodrigues et al., 2004), regional (Raxworthy et al., 2003), landscape (Mladenoff et al., 1995), patch (Dunham et al., 2001), and multi-scale (Johnson et al., 2002; 2004) levels. Applications of such models include climate-change assessments (Tellez-Valdes and Davila-Aranda, 2003), restoration or range expansion (Mladenoff et al., 1995; Boyce and Waller, 2003), ecological risk assessment (McDonald and McDonald, 2002), and conservation gaps or reserve design (Flather et al., 1998; Yip et al., 2004). Ultimately, understanding large-scale patterns and temporal changes to rare, threatened or endangered species helps focus conservation needs (Dobson et al., 1996; Channell and Lomolino, 2000; Mattson and Merrill, 2002).

Describing species occurrence, or even that of abundance, however, does not necessarily parallel habitat relationships for populations, as occurrence and abundance can be poor surrogates for demographic performance (Van Horne, 1983; Hobbs and Hanley, 1990; Tyre et al., 2001). Relating life history traits to habitats is therefore critical for understanding habitat processes and ultimately the management of species of conservation concern (Franklin et al., 2000; Breininger and Carter, 2003). Without understanding such functions, one risks assuming that animal occurrence or abundance relates directly to habitat quality, something that clearly is not always the case. For instance, some sites considered high in habitat quality from an occupancy standpoint may be low in survival and/or final recruitment. These 'attractive' habitat patches can produce local population sinks, and therefore have been called attractive sinks (Delibes et al., 2001; Naves et al., 2003) or ecological traps (Dwernychuk and Boag, 1972; Ratti and Reese, 1988; Donovan and Thompson, 2001). Recognizing this phenomenon within conservation habitat models and resulting planning maps is therefore crucial for fully representing habitat quality. For many species, however, we lack the necessary data to formulate habitat-specific demographic parameters and waiting for such data to be collected for long-lived species with low reproductive rates might simply result in documenting the decline or extirpation rather than providing an initial recommendation for the conservation problem. No doubt, collection of long-term life history information needs to be gathered for understanding, but exploiting existing data sources also is necessary for short-term conservation management. Commonly, what is available to the conservation biologist is information on animal occupancy from aerial surveys or radiotelemetry studies and sometimes a distribution of mortality locations from government management databases (e.g., hunting, problem wildlife, vehicle-wildlife collisions, etc.). Formulating a process that identifies attractive sink habitats, as well as some form of source or secure habitats, would be useful in conservation planning and wildlife management for species suffering population declines.

One species ideally suited for exploring conservation habitat modelling from an occupancy and survival framework is grizzly bears *Ursus arctos* L. Grizzly bears are an important keystone species (Tardiff and Stanford, 1998) that have declined substantially throughout North America in the past century (McLellan, 1998; Mattson and Merrill, 2002), largely due to vulnerability from late maturation, low density, extremely low reproductive rates, and a high trophic level (Bunnell and Tait, 1981; Russell et al., 1998; Purvis et al. 2000a; 2000b; Woodroffe, 2000). Given their sensitivity to population decline and historic population losses together with a large area requirement, grizzly bears have been used as umbrella, flagship, and/or focal species for regional conservation planning (Noss et al., 1996; Carroll et al., 2001), although the utility of such conservation surrogates has been questioned (Andelman and Fagan, 2000; Caro et al., 2004). Regardless of whether grizzly bears are surrogates for anything beyond the species itself, any conservation process will require spatially explicit models that predict habitats and limiting factors. Many approaches have been used, but perhaps one of the most popular has been habitat selection modelling using digital geospatial data and a sample of radiotelemetry observations (Waller and Mace, 1997; Mace et al., 1996; 1999; McLellan and Hovey, 2001; Nielsen et al., 2002; 2003). Resulting habitat or resource selection models, however, only provide an assessment of animal occurrence or use, which as previously mentioned may not represent critical life history traits and processes. Even spatial models that predict grizzly bear abundance (Apps et al., 2004), although adding additional information, still lack an explicit mechanism to identify conservation actions or monitor trends. What is needed is an approach that merges habitat-related occurrence or animal abundance models with critical life history parameters.

For grizzly bears, it is widely accepted that survival, especially that of females, is the most sensitive parameter for population growth (Knight and Eberhardt, 1985; Wiegand et al., 1998; Boyce et al., 2001). Most grizzly bear mortalities are human-caused (McLellan et al., 1999; Benn and Herrero, 2002) and often related to human access (Nielsen et al., 2004a). Incorporating some form of survival within habitat maps would therefore be helpful. Although population-level estimates of survival have been estimated for grizzly bears (e.g., McLellan et al., 1999), few have attempted to define or index these in a spatial manner necessary for targeting on-the-ground management or mitigation (see however, Nielsen et al., 2004a; Johnson et al., 2005). Recently, Naves et al. (2003) used a spatial framework for defining brown bear habitats in northern Spain that incorporated both survival and reproduction simultaneously. Such modelling and mapping approaches are attractive management tools for identifying on-the-ground conservation targets because they record attractive sinks where animals are likely to be present, but suffer high mortality rates, and source or secure habitats where animals are present and enjoy high survival. Both habitat states provide managers with 2 separate conservation strategies: (1) preservation and protection of existing source and secure areas to impede habitat degradation; and (2) mitigation of sites where habitat conditions are excellent, but risk of mortality is high and manageable.

Here we develop a framework for identifying attractive sink and source-like habitats for grizzly bears in west-central Alberta. Such an approach is especially needed for Alberta where grizzly bears have been recommended for *threatened* status. Alberta currently lacks, however, an effective approach for identifying habitats for protection or management based on existing information on occupancy of habitats and mortality risk. Despite the recognition of population declines and the importance of secure habitats, management of Alberta grizzly bear populations is still largely based on a 1988 assessment of land cover and human disturbance (Stenhouse et al., 2003). Here we define grizzly bear habitats using empirical models of animal occurrence and risk of human-caused mortality specific to the east slopes of the Alberta Rocky Mountains. Using this 2-dimensional habitat framework, we define indices of attractive sink and safe-harbor (source-like or secure) habitats as well as a classification of 5 habitat states including, non-critical habitat, secondary sink, primary sink (similar to high index values of attractive sink habitats), secondary habitat, and primary habitat (similar to high index values safe harbor habitats). We emphasize, however, that these indices and states are relative, as we did not model habitat-specific population growth. Such habitat definitions therefore have their greatest value in tracking temporal changes in habitats or highlighting areas in need of conservation action. To this end, we describe the potential utility of this 2-dimensional habitat model and resulting indices for west-central Alberta, while suggesting the application of these methods throughout the Province.

2. Study Area

Our 9,752-km^2-study landscape was located in west-central Alberta, Canada (53° 15′ N 118° 30′ W; Figure 7-1). Two land use zones dominated the region: (i) the protected mountains in the west, and (ii) the resource-utilized foothills in the east. Management of the protected mountains were divided between provincial (i.e., Whitehorse Wildlands; 173-km^2) and federal (i.e., Jasper National Park; 2,303-km^2) authority and characterized by recreational use. Mountainous land cover classes consisted of montane forests, conifer forests, sub-alpine forests, and alpine meadows (Achuff, 1994; Franklin et al., 2001). As well, some high elevation areas of rock, snow, and ice (glaciers) predominate. In contrast to the protected mountains, the eastern foothills were characterized by a number of resource extraction activities, including forestry, oil and gas, and open-pit coal mining. Large numbers of roads and seismic lines typify the foothills. Coal mining has had a long history to the region, influencing initial Anglo-European settlement of the foothills and eastern front ranges near the town of Cadomin. Timber harvesting has been active since the mid 1950s with additional exploration and development of natural gas resources since. Land cover for the foothill region includes conifer, mixed, and deciduous forests, areas of open and treed-bogs, small herbaceous meadows (including small agricultural fields near the town of Edson), and areas of regenerating (fire and clearcut harvesting) forests (Achuff, 1994; Franklin et al., 2001). Climate within the area was intermediate, with an average summer and winter temperature of 11.5° C and –6.0° C respectively, and a normal annual precipitation of 538 mm (Beckingham et al., 1996). Temperature and precipitation, however, were strongly influenced by elevation that ranges from 984 to 3,012 m. With a short growing season, lack of salmon and other high protein foods (Jacoby et al., 1999), these interior grizzly bears occur at relatively low densities (e.g., ≤ 4 animals/1000-km^2).

3. Methods (a framework for assessing grizzly bear habitat)

3.1. Modelling the relative probability of adult female occupancy

We used a resource selection model specific to adult females during late hyperphagia from Nielsen (2005) to define the relative probability of adult female occurrence. We chose a single sex-age group, as Nielsen (2005) found differences in habitat selection between sub-adult, adult male and adult female grizzly bears. As adult female grizzly bears represented the most sensitive sex-age class for population change (Knight and Eberhardt, 1985; Wiegand et al., 1998; Boyce et al., 2001), we chose to concentrate on this sex-age group. As well as sex-age group differences, Nielsen (2005) also found seasonal variation in habitat use to be common, supporting previous habitat-relationship examinations for the region (Hamer and Herrero, 1987; Hamer et al., 1991; Nielsen et al., 2002; 2003). We chose to examine only late hyperphagia, defined to be 16 August to 15 October, as this season was considered the most critical foraging period for grizzly bears, corresponding to the ripening of fruit from *Vaccinium* spp. and *Shepherdia canadensis* (Hamer and Herrero, 1987; Hamer et al., 1991; Nielsen et al., 2004c).

A total of 5,172 late hyperphagia radiotelemetry observations were collected from 13 adult females between 1999 and 2002. Nielsen (2005) used these data to develop (training) a habitat model that predicted the relative probability of adult female occurrence. The model was assumed to take an exponential form (Manly et al., 2002):

$$H_f = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_{24} x_{24}) \qquad (7\text{-}1),$$

where H_f represented the relative probability of occurrence for adult females within any study area pixel (30 m × 30 m), β_1 the selection coefficient for x_1 representing the land cover category alpine/herbaceous, β_2 the selection coefficient for x_2 representing the land cover category for anthropogenic, and so on for all 24 categorical and continuous environmental predictor variables used to describe grizzly bear habitat occurrence (Tables 7-1; 7-2). These 24 variables included 10 land cover categories, distance to nearest edge, a terrain-derived index of soil wetness, an index of terrain ruggedness, forest or regenerating forest age, global solar radiation within 3 land cover types (interactions), and the interactions of soil wetness with either edge distance or forest age. Nielsen (2005) binned map predictions into 10 ordinal habitat classes, ranging from a low relative probability of occurrence at 1 to a high relative probability of occurrence at 10 (Figure 7-2). Based on average bin values within land cover classes, adult females favored alpine/herbaceous, open conifer, and deciduous forests, while tending to avoid anthropogenic, regenerating forests, and non-vegetated areas. General distribution corresponded to mid-to-high elevation sites in the mountains, throughout the Gregg and upper McLeod River basins, and in the foothills near the town of Robb (Figure 7-2). Evaluations of the map performance using 1,201 independent radiotelemetry observations collected from 7 adult females during 2003 revealed a significant predictive fit (Nielsen, 2005).

3.2. Modelling risk of human-caused grizzly bear mortality

We used a model from Nielsen et al. (2004a) to define risk of human-caused mortality for adult grizzly bears in west-central Alberta. The risk model, developed just south of our study area, described the distribution of grizzly bear mortalities based on a comparison of the locations of human-caused grizzly bear mortalities with random landscape locations using common landscape covariates that represented human encroachment and bear habitat. We used a model specific to adult animals, as the distribution of sub-adult mortalities were found to differ from that of other sex-age classes, while no variation in the spatial distribution of adult male and female mortalities were evident (Nielsen et al., 2004a). Risk of human-caused mortality for adult female grizzly bears, R_f, was fit for the present study area using coefficients reported from Nielsen et al., (2004a) and defined as,

$$R_f = \exp(0.415d + 0.503g + 0.592n + 1.023s + -0.152r + -11.738z + -1.490w + -2.901a + -6.740t) \qquad (7\text{-}2).$$

Environmental covariates included, deciduous forest (d), grassland and crop (g), non-vegetated areas (n), and shrub (s) land cover categories (0 or 1); greenness (r), an index of vegetative productivity (White et al., 1997; Waring and Running, 1998) based on a tasseled-cap transformation of Landsat TM bands (Crist and Cicone, 1984); and distance to nearest edge (z), water (w) or human access (a) feature measured in kilometers. Resulting predictions of human-caused mortality risk (R_f) were highest when near edges, water, and access, as well as in areas with lower greenness values and in shrub habitats (Nielsen et al., 2004a). Using eqn. 7-2, we calculated R_f for the given study area using the map calculator function of the spatial analyst extension in ArcGIS 8.3 (ESRI, 2002). Predicted values of R_f were scaled in a similar manner to that of H_f (10 ordinal bins using a quantile method), where the relative risk of mortality ranged from a low of 1 to a high of 10 (Figure 7-3). We again refer to the resulting quantile map as R_f, or index of human-caused mortality risk for grizzly bears. Assessment of mortality locations occurring within the defined study suggested good fit to the R_f model with 10 of 13 (6 of 6 for female bears) documented human-caused grizzly bear mortalities with accurate coordinates occurring in $R_f > 5$.

3.3. Defining attractive sink and safe harbor indices

Using the adult female habitat occupancy (H_f) and a mortality risk (R_f) maps, we defined a 2-dimensional grizzly bear habitat model that related the relative probability of occurrence for bears with their relative risk of mortality. For conservation purposes, we were interested in identifying 2 habitat conditions, attractive sink habitats (Delibes et al., 2001; Naves et al., 2003), also known as ecological traps (Dwernych and Boag, 1972; Ratti and Reese, 1988; Donovan and Thompson, 2001); and the corollary safe-harbor sites (source-like areas). Attractive sink and safe-harbor indices were assumed to correlate with mortality risk and reproduction respectively. We define attractive sink and safe harbor indices as,

$$AS_f = H_f \times R_f \qquad (7\text{-}3)$$

and

$$SH_f = H_f \times (11 - R_f) \qquad (7\text{-}4),$$

where AS_f and SH_f were indices of attractive sink and safe harbor habitats for adult females respectively, H_f an index of habitat occupancy for adult females from equation 7-

1, and R_f an index of human-caused mortality risk for adult animals from equation 7-2. As H_f was assumed to be proportional to the relative probability of use, when multiplied by the relative probability of mortality risk, R_f, using equation 7-3, a relative index of the of use and mortality risk resulted. Given that both H_f and R_f scaled from 1 to 10, AS_f and SH_f indices ranged from a possible low value of 1 to a high value of 100 (Figure 7-4). High AS_f values were taken to represent habitats in which bears were both likely to occur and at risk of human-caused mortality (e.g., low survival), whereas high SH_f values were assumed to indicate habitats in which bears were likely to occur, but also were low in mortality risk (e.g., high survival). From a conservation perspective, AS_f sites were those areas in need of mitigation, while SH_f sites were areas needing continual protection or preservation from future human development. To understand the distribution of SH_f and AS_f sites within the study, we assessed the proportion of the landscape within AS_f or SH_f conditions based on very low (1–20), low (21–40) mid (41–60), high (61–80), and very high (81–100) AS_f or SH_f values (Fig. 4). We summarized AS_f and SH_f pixels by management authority, as well as characterizing (mean and standard deviation) each index within individual land cover categories to better understand spatial patterns of the two indices and where protection and mitigation are needed.

3.4. Defining habitat states

As well as defining safe-harbor and attractive-sink indices, we also suggest a model of 5 relative habitat states based on the 2 dimensions of H_f (habitat occupancy) and R_f (mortality risk). Although losing information through categorization, such simplification may be necessary for certain conservation and management actions, such as trading markets (Sandor et al., 2002; Woodward et al., 2002). We defined the 5 habitat states to be non-critical habitat, primary sink, secondary sink, primary habitat, and secondary habitat, based on the division of H_f into 3 categories and R_f into 2 classes (Figure 7-5). Although producing 6 possible states, 2 states were merged into a single habitat state called non-critical habitat and defined as $H_f < 5$, regardless of R_f. Non-critical habitats were not considered to be matrix habitats where bear occupancy never occurred, but rather where they were rare in occurrence. Secondary habitats were defined as H_f with values between 5 and 7 and $R_f < 6$ (e.g., low risk, but also lower in habitat occupancy). Primary habitats, on the other hand, were defined as those sites with $H_f > 7$ and $R_f < 6$

(e.g., low risk, but higher in habitat occupancy). Secondary sinks were defined as those sites with H_f between 5 and 7 and $R_f > 5$ (e.g., high risk, but lower in habitat occupancy). Lastly, primary sinks were defined to be those sites with $H_f > 7$ and $R_f < 6$ (e.g., low risk, but higher in habitat occupancy). Primary sinks would correspond to higher values of the attractive-sink index, while primary habitats would be most similar to higher values of the safe-harbor index. Again, we summarize habitat states for the study area by management authority, as well as describe proportions of each state within individual land cover categories to better understand the distribution of defined habitat states.

4. Results

4.1. Index of attractive-sink habitat

The majority (67.8%) of the study area was dominated by very low attractive sink (AS_f) values with decreasing amounts of low (17.6%), mid (9.1%), high (4.2%), and very high (1.3%) categories (Figure 7-6). Although high and very high AS_f categories totaled just over 5% of the landscape, they were concentrated within the study area to the foothills near Robb, many of the upper foothill river valleys, and mountain passes and drainage networks in Whitehorse Wildlands and adjacent Jasper National Park (Figure 7-6). Average attractive sink values for the 5 examined protected areas, the white zone and crown lands revealed low to very low overall ratings (Table 7-3). Attractive sink values for Jasper National Park (JNP), however, were nearly half those of Brazeau Canyon, Cardinal Divide, Grave Flats, Whitehorse Wildlands, the white zone, and crown lands.

Values of the AS_f index also varied among land cover classes (Table 7-3). Non-vegetated and deciduous forests had the lowest and highest AS_f values respectively, ranging from very low to middle values of the index. Although regenerating forests and closed conifer forests were not as low as non-vegetated areas, they too averaged very low AS_f values. Only the deciduous forest class was classified with a mid AS_f level. Anthropogenic and open-bog/shrub classes, however, were near to being similar to deciduous forests with AS_f scores averaging more than 30. Alpine/herbaceous, mixed forests, open conifer forest, and treed-bog habitats all were similar in average AS_f values, with low scores ranging from 25 to 27.8 (Table 7-3).

4.2. Index of safe-harbor habitat

For the safe-harbor (SH_f) index, very low scores (category) dominated (34.9%) the study area (Figure 7-7). However, unlike that of the AS_f index, more similar amounts of low (23.8%), mid (16.8%), high (13.7%), and very high (10.9%) SH_f categories were evident, although decreasing slightly in composition for each. High and very high values were most common to intermediate elevations within mountain valleys and along the Front Range (Figure 7-7). Some of the lower foothills near Robb, however, also were apparent in containing high safe harbor levels, but much more limited and isolated. Examinations of SH_f values within protected and non-protected areas revealed greater differentiation of SH_f values than AS_f values, varying from high to very low values (Table 7-3). Cardinal Divide and the white zone had very low SH_f values, while Whitehorse Wildlands had high SH_f values. Brazeau Canyon, Grave Flats and JNP all averaged mid SH_f values, although JNP was noticeably higher than the relatively similar Brazeau Canyon and Grave Flats sites. Finally, crown lands averaged low SH_f values, although near to being similar to Brazeau Canyon and Grave Flats.

Safe-harbor values also varied substantially among land cover classes from very low to very high levels (Table 7-3). Alpine/herbaceous, followed closely by open conifer forest had very high and high SH_f values respectively, while the anthropogenic class was very low in SH_f values. Regenerating forest, open-bog/shrub and mixed forest also had low SH_f values (Table 7-3). Intermediate (mid-SH_f values) between alpine/herbaceous and anthropogenic classes was closed conifer and deciduous forests, non-vegetated areas and treed-bog habitats.

4.3. 2-Dimensional habitat states

For the given study area and defined hypothetical habitat states, we predicted 39.6% of the study area to be non-critical, 9.8% to be secondary sink, 6.7% to be primary sink, 22.0% to be secondary habitat, and 21.9% to be primary habitats (Figure 7-8). These percentages varied by individual land cover categories with the highest proportion of primary habitats occurring in open conifer (81.1%) and alpine/herbaceous (80.7%) classes and the lowest amounts of primary habitat in open-bog/shrub (2.6%) and anthropogenic (1.3%) classes (Table 7-4). Secondary habitat conditions were common for treed-bog (48.3%) and non-vegetated (48.3%) classes, while secondary habitats were rare for the high valued alpine/herbaceous (0.6%) or open conifer (0.7%) classes. Primary sink habitats were most prominent for deciduous forests (32.3%) and to a lesser degree open conifer (18.0%) and alpine/herbaceous (15.4%) classes. Closed conifer and regenerating forests had low amounts of primary sink habitats (Table 7-4). Both classes, however, were low in habitat quality as supported by the classification of non-critical habitats, with the majority of regenerating forests (72.6%), anthropogenic (57.9%) and closed conifer (44.7%) sites considered non-critical. Finally, secondary sinks were most common for open-bog/shrub (35.7%) and anthropogenic (24.3%) classes, while least frequent for alpine/herbaceous (0.1%) and open conifer forest (0.2%) sites (Table 7-4).

Within the examined protected and non-protected management zones, Whitehorse Wildlands had the highest proportion of primary habitats and the lowest proportion of non-critical habitats and secondary sinks (Table 7-4). Although having a larger proportion of primary habitats, Whitehorse Wildlands did have a low, but noticeable composition of primary sinks. In contrast to Whitehorse Wildlands, JNP had moderate proportions of primary and non-critical habitats, reflecting the distinction between high elevation rocky peaks and glaciers that were poor in habitat quality and high-quality alpine meadows (Table 7-4). Although JNP was moderate in total habitat value, both primary and secondary sinks were rather rare overall, indicating a high level of security from human-caused mortality. Moreover, many sites predicted as primary or secondary sinks inside JNP, especially those in the southern portion of the study, were likely to have been primary or secondary habitats, as risk of human-caused mortality was potentially over-estimated in this region, since these backcountry wilderness areas receive relatively little human activity. The Cardinal Divide, being adjacent to JNP and Whitehorse Wildlands, had the greatest proportion of non-critical habitats and the lowest proportions of primary and secondary habitats for protected areas (Table 7-4). As well, primary sinks were the most dominant for the Cardinal Divide of all the management zones. This indicated that what little habitat was available for bears at the Cardinal Divide sites, they were non-secure in nature. Grave Flats and Brazeau Canyon both contained moderate proportions of secondary habitats with lesser amounts of primary habitats. However, unlike that of Grave Flats, Brazeau Canyon had higher proportions of non-critical habitats and lower proportions of primary sinks (Table 7-4). Finally, the white zone and crown lands showed high proportions of non-critical habitat, although crown lands did contain moderate amounts of secondary and primary habitats unlike that of the white zone that contained very little of either.

5. Discussion

5.1. A conservation strategy using habitat indices

The index of attractive-sink habitat was on average rather low for examined management zones and land cover classes in west-central Alberta. Selected areas, however, had concentrated high and very high categories of attractive sink, indicating a co-occurrence of high mortality risk and animal occupancy. This was most evident for deciduous forest stands, foothill valleys near the town of Robb, front slopes and valleys near Cadomin. Significant numbers of grizzly bear mortalities can result in these rare, yet concentrated sites. For instance, Nielsen et al. (2004a) found that the majority (~80%) of independently validated human-caused grizzly bear mortalities for the Central Rockies Ecosystem (CRE) occurred in areas of high and very high mortality risk, which constituted less than 10% of the landscape. For the Banff and Yoho National Parks (within the CRE), where portions of high and very high risk were even lower, Benn and Herrero (2002) documented an average annual human-caused mortality of 4.3 bears/year for the period 1971 to 1998. For a protected (national park) population that lacked hunting and industrial resource pressures, these mortalities combined with natural causes of death can be a significant conservation concern. Including Provincial lands where hunting and resource extraction occurred, average annual mortality was even higher at 7.6 bears/year, representing an estimated mortality rate of 6.1 to 8.3% of the population, depending on the population estimate, but exceeding the Provincial allowable threshold of 6% none the less (Benn, 1998). Apparently, even isolated but concentrated levels of attractive sink can lead to mortality sinks (*sensu* Knight et al., 1988). Limiting human access and/or modifying habitat quality to make areas where bears are likely to encounter humans less attractive or accessible to bears or humans should be considered, especially those attractive sinks that occur near contiguous areas of safe harbor habitats. Although not as evident during late hyperphagia, grizzly bears also readily used clearcuts in the foothills during pre-berry seasons (Nielsen et al., 2004b). As we considered only late hyperphagia, identification of attractive sinks at clearcut sites during earlier seasons also should be considered.

Unlike the attractive-sink index, the index of safe-harbor habitats identified existing high-quality and secure grizzly bear habitats. To achieve effective grizzly bear conservation, these areas should receive highest priority for conservation. Maps of safe-harbor habitats differed from traditional radiotelemetry-based maps of grizzly bear occurrence in Alberta (e.g., Nielsen et al., 2002; 2003; Theberge, 2002), because they also consider security (low mortality risk), similar to concepts of habitat effectiveness and security (i.e., Gibeau, 1998; Gibeau et al., 2001). For west-central Alberta, safe-harbor values averaged from very low to very high depending on land cover class and management zone. Generally, high-valued safe-harbor habitats were most common to the front slopes of the Rocky Mountains, along with isolated foothills ranges in the east (especially near the town of Robb), and interior valleys or side slopes in Jasper National Park. Overall, Whitehorse Wildlands averaged the highest safe-harbor values for management zones, indicating the significance of this park for grizzly bear conservation. Alpine/herbaceous and open conifer stands also proved high to very high in average safe-harbor values, consistent with previous regional habitat assessments promoting secure open herbaceous areas and open forested conditions (Hamer and Herrero, 1987; Hamer et al., 1991; McLellan and Hovey, 2001; Nielsen et al., 2002; 2003; Theberge, 2002).

Selective harvesting of mature forest stands during winter with immediate removal (decommission) of temporary winter forest roads provides one approach for improving habitat quality and limiting human-caused mortality risk. Care should be given towards the silvicultural practice employed for site preparation and shape of harvest blocks. Grizzly bears have been shown to select clearcuts based on method of scarification and shape of clearcut (Nielsen et al., 2004b). Irregular-shaped clearcuts proved more attractive to bears, while silvicultural practices can influence food resource availability (Nielsen et al., 2004c). As forests and regenerating clearcuts age, attractive sink and safe harbor values change, even without changes to the human footprint. Given the dynamic nature of grizzly bear habitats, future scenarios should be employed to consider long-term impacts of resource management practices during forest and resource planning. We consider the identification of attractive sink and safe harbor sites as an essential element of grizzly bear management. Indices of attractive sink provide a mechanism for identifying areas in most need of management attention to minimize the likelihood of contact between humans and bears, while safe-harbor sites identify habitats in most need of continual protection or inclusion in a system of reserves, both a conservation priority for grizzly bears in Alberta.

5.2. A conservation strategy using habitat states

Instead of using attractive sink and safe-harbor indices, which were continuous metrics of non-secure and secure habitat, we proposed an alternate approach that identified categorical states based again on the 2-dimensional model of habitat occupancy and mortality risk (similar to Naves et al., 2003). Using thresholds of mortality risk (2 categories) and habitat occupancy (3 categories), we defined non-critical habitats, secondary and primary sinks, and secondary and primary habitats. Primary habitats closely corresponded to high safe-harbor scores, while primary sinks were correlated with high attractive sink values. Proportions of each habitat state varied among management zone and land cover class with overall composition dominated by non-critical habitat, followed by secondary habitat, primary habitat, secondary sink, and primary sink. Although primary sinks were low in overall composition, they were once again concentrated to river bottoms and valleys throughout the study area. For some regions of Whitehorse Wildlands, and especially that southern Jasper National Park, primary and secondary sinks were potentially over-predicted as levels of recreational use for many areas were much lower than the baseline model from Nielsen et al. (2004a) in Banff National Park. In fact, total grizzly bear mortalities since the mid-1970s in Jasper National Park have been substantially lower than in Banff National Park, despite Jasper National Park being larger in size (Benn and Herrero, 2002). Replacing primary and secondary sinks with primary and secondary habitats for low recreational use trails in Jasper and Whitehorse Wildlands should be considered. Regardless, patterns of primary and secondary sinks and habitats within crown lands, where the majority of human activities and conservation concerns reside, appear reasonable.

We propose that stakeholders involved in grizzly bear management and conservation on Alberta crown lands consider tracing changes within the 5 hypothetical habitat states during resource planning. Specifically, we suggest a process of habitat balancing with the goal of minimizing loss of secondary and especially primary habitats. If resource management actions modify secondary or primary habitats to secondary or primary sinks through increase in human access, equivalent amounts of secondary or primary sinks should be restored through management of human access (see Figure 7-9). Trading markets could also be used to balance existing habitat states (Sandor et al., 2002; Woodward et al., 2002) based on a cap in current habitat conditions. Of course, forest disturbance and succession modifies habitat conditions along a successional gradient. As such, habitat changes can occur regardless of human activity, leading to possible beneficial or detrimental changes for grizzly bears. Habitat conditions should therefore be considered dynamic, rather than static. This is especially true for seasonal habitats, as grizzly bear habitat occupancy changes with seasonal trends in food resources (Nielsen et al., 2003).

Future scenario modelling of habitat states should be considered in all long-term management planning. Landscape configuration should be considered so that restoration activities taking place are best situated to habitats most accessible to bears (i.e., not placed in isolated patches). Finally, primary and secondary habitats can be used for reserve planning, as these sites represent remaining secure habitats. A network of grizzly bear conservation reserves should be considered for the East Slopes of Alberta where large contiguous regions of primary and secondary habitat reamian. Necessarily, such reserves would need to encompass multiple territory units. Road development within such reserves should be limited or requiring strict human access control, restoration of similar habitats elsewhere and finally deactivation and re-vegetation of roads following final extraction of resources.

6. Conclusion and management recommendations

Grizzly bear habitat modelling rarely considers spatial predictions of survival, the most important life history trait for bears, focusing on occupancy patterns instead. As survival can vary among different habitats and human-related landscape patterns (Naves et al., 2003, Nielsen et al., 2004a; Johnson et al., 2005), relying on animal occurrence alone for assessments of habitat quality is questionable. One risks promoting habitats that are effectively attractive sinks where occupancy and reproduction may be high, but survival is low (Delibes et al., 2001). In Alberta, grizzly bears are being considered for threatened status. Hence managers require better tools for inventorying grizzly bear habitats, identifying key sites for protection, and finally identifying those areas in greatest need of management attention. Using a 2-dimensional habitat model of occupancy and mortality risk, we developed habitat indices and habitat states for the purpose of better identifying these grizzly bear conservation needs. Indices of attractive sink, and the corollary safe-harbor habitats, were calculated from the 2 dimensions to describe patterns of non-secure and secure high-quality habitats. As well, we proposed habitat states that allow an accounting of grizzly bears habitats in context of management and future planning, perhaps under a habitat balancing or cap and market trading system (Sandor et al., 2002; Woodward et al., 2002). Primary habitats were identified for continual protection of secure habitats and reserve planning, while primary sinks depicted areas in most need of mitigation of mortality risk. We recommend land use planners consider this model for conservation of grizzly bears in Alberta. To minimize losses of grizzly bears on the landscape, when industrial resource extraction modifies an existing primary or secondary habitat, restoration of equivalent primary or secondary sinks in other sites should be considered. Non-critical habitats, on the other hand, could be managed without strict mitigation. However, landscape patterns should be considered when targeting restoration sites, as isolated restoration sites within a matrix of risky habitat should be avoided. Management of human behaviour (storage of food, garbage and horse feed) preventing habituation of bears and development of problem bears, a major source of human-caused mortality (Benn, 1998; Benn and Herrero, 2002), should be considered. An effective education program provides an important mechanism for successfully reducing bear-human conflict (Schirokauer and Boyd, 1998). Finally, future scenario modelling should be employed to understand long-term impacts of resource development and forest succession on grizzly bear habitat needs.

Table 7-1. Remote sensing and GIS environmental predictor variables used for modelling the relative probability of occurrence for adult female grizzly bears during late hyperphagia in west-central Alberta, Canada.

Model variable	Variable code	Linear or non-linear	Units/Scale	Data range
Land cover:				
alpine/herbaceous	alpine	category	n.a.	0 or 1
anthropogenic	anthro	category	n.a.	0 or 1
closed conifer	clscon	category	n.a.	0 or 1
deciduous forest	decid	category	n.a.	0 or 1
mixed forest	mixed	category	n.a.	0 or 1
non-vegetated	nonveg	category	n.a.	0 or 1
open-bog/shrub	opnbog	category	n.a.	0 or 1
open conifer	opncon	category	n.a.	0 or 1
regenerating forest	regen	category	n.a.	0 or 1
treed-bog	treedbg	category	n.a.	0 or 1
edge distance	edge	linear	100 m	0 - 35
compound topographic index	cti	non-linear	unitless	1.89 - 31.7
terrain ruggedness index	tri	non-linear	unitless	0 - 0.29
forest age	for-age	non-linear	10-yr age class	1 - 15
regenerating clearcut age	cut-age	non-linear	10-yr age class	1 - 5
solar radiation × alpine	solar×alp	linear	kJ/m^2	17,133 - 91,836
solar radiation × clscon	solar×clscon	linear	kJ/m^2	21,698 - 91,835
solar radiation × regen	solar×regen	linear	kJ/m^2	57,110 - 91,831
cti × age	cti×age	linear	unitless	0 - 402
cti × edge distance	cti×edge	linear	unitless	0 - 522

Table 7-2. Estimated habitat selection coefficients for adult female grizzly bears in west-central Alberta, Canada based estimates from Chapter 5 of Nielsen (2004). Robust standard errors and significance levels (*p*) were estimated from modified sandwich estimates of variance among animals with categorical contrasts from deviance coding.

Environmental variable	Coefficient	Standard Error	*p*
alpine/herbaceous	0.218	0.941	0.817
anthropogenic	-0.114	0.344	0.740
closed conifer forest	2.530	0.703	<0.001
deciduous forest	1.366	0.309	<0.001
mixed forest	0.778	0.553	0.159
non-vegetated	0.510	0.445	0.252
open-bog/shrub	0.322	0.502	0.522
open conifer forest	1.909	0.348	<0.001
regenerating forest	-8.865	2.856	0.002
treed-bog	1.346	0.377	<0.001
edge distance	-0.302	0.061	<0.001
cti	0.107	0.049	0.029
†cti^2	-0.294	0.195	0.130
tri	34.009	7.564	<0.001
tri^2	-147.07	31.84	<0.001
for-age	-0.219	0.058	<0.001
†for-age^2	0.766	0.364	0.036
cut-age	-0.262	0.390	0.545
cut-age^2	0.097	0.075	0.197
§solar×clscn	-0.207	0.093	0.026
§solar×regen	0.934	0.355	0.009
§solar×alp	0.166	0.123	0.180
†cti×age	0.633	0.126	<0.001
cti×edge	0.017	0.005	<0.001

†estimated coefficients and standard errors reported at 100 times their actual value
§estimated coefficients and standard errors reported at 10,000 times their actual value

Table 7-3. Characteristics (mean, standard deviation [SD], and category) of attractive sink (AS_f) and safe harbor (SH_f) indices for management zones and land cover classes.

Management zone or	Attractive sink (AS_f)			Safe harbor (SH_f)		
Land cover type	Mean	SD	Category	Mean	SD	Category
a. Management zone						
Brazeau Canyon (Wildland Park)	23.8	18.9	low	42.9	23.4	mid
Cardinal Divide (Natural Area)	22.9	30.9	low	19.4	17.7	very low
Grave Flats (Natural Area)	29.3	24.1	low	41.2	20.9	mid
Jasper (National Park)	12.5	17	very low	53.8	32	mid
Whitehorse (Wildland Park)	21.2	21.6	low	64.5	28.2	high
White-zone (Private)	24.6	21.4	low	15.5	16.8	very low
Crown lands	21.6	20.0	low	35.8	25.4	low
b. Land cover class						
alpine/herbaceous	25	25.3	low	80.2	29.1	very high
anthropogenic	38.4	22.5	low	10.5	11.4	very low
closed conifer forest	14.2	13.9	very low	42.2	24.7	mid
deciduous forest	40.5	28.9	mid	50.3	25.6	mid
mixed forest	26.7	19.8	low	32.1	20.3	low
non-vegetated	10.8	17	very low	42.7	30.9	mid
open-bog/shrub	32.5	20.1	low	24.5	17.2	low
open conifer forest	27.8	23.9	low	79.9	24.5	high
regenerating forest	14	14.9	very low	21.5	21.9	low
treed-bog	25.7	18.9	low	44.2	18.5	mid

Table 7-4. Percent composition of 5 hypothetical habitat categories for protected areas (a.) and land cover classes (b.) based on a 2-dimensional classification of habitat occupancy (H_f) and mortality risk (R_f) maps.

Management zone or Land cover type	Non-critical habitat	Secondary sink	Primary sink	Secondary habitat	Primary habitat
a. Management zone					
Brazeau Canyon (Wildland Park)	29.2	10.2	4.8	32	23.9
Cardinal Divide (Natural Area)	61.7	6.7	17.4	8.4	5.7
Grave Flats (Natural Area)	19.2	12.6	15.4	36.2	16.6
Jasper (National Park)	33.6	2.2	4.6	20	39.6
Whitehorse (Wildland Park)	16.0	0.9	10.9	14.5	57.6
White zone (Private)	63.2	14.8	9.7	8.0	4.2
Crown lands	41.9	12.4	7.2	22.9	15.6
b. Land cover class					
alpine/herbaceous	3.2	0.1	15.4	0.6	80.7
anthropogenic	57.9	24.3	14.6	1.9	1.3
closed conifer forest	44.7	5.2	2.9	27.5	19.7
deciduous forest	0.7	11.3	32.3	14.7	41
mixed forest	38.8	19.5	8.7	23.2	9.9
non-vegetated	9.2	16.9	10.3	48.3	15.4
open-bog/shrub	34.6	35.7	5.5	21.7	2.6
open conifer forest	0	0.2	18	0.7	81.1
regenerating forest	72.6	5.2	2.7	11.9	7.7
treed-bog	9.2	16.9	10.3	48.3	15.4

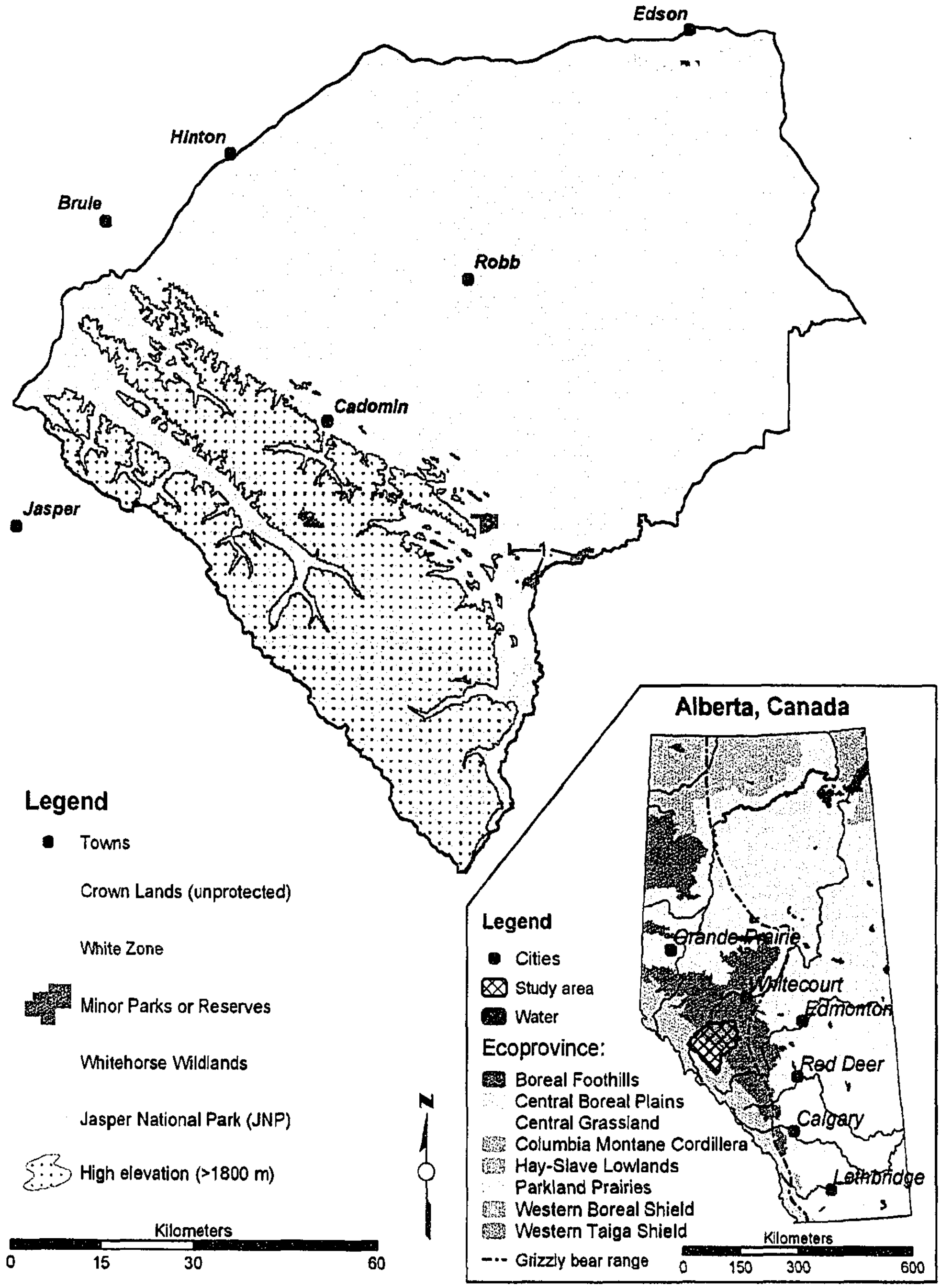

Figure 7-1. Study area map depicting management zones, towns, and high elevation (>1800 m) sites. Minor parks or reserves mentioned include, 1) Brazeau Canyon; 2) Cardinal Divide; and 3) Grave Flats. Inset map of Alberta in lower right illustrates Ecoprovince, grizzly bear range, and study area within Alberta.

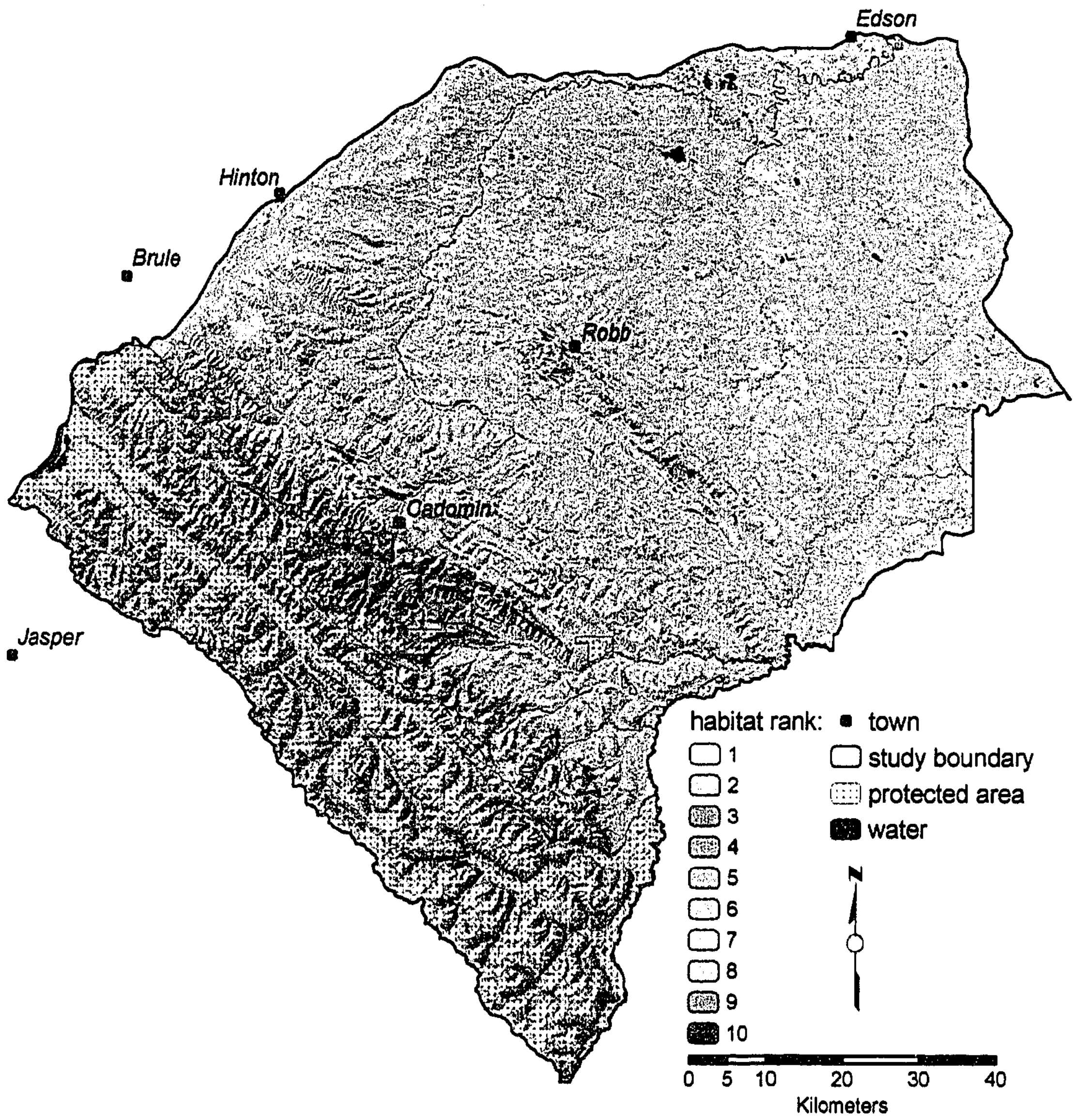

Figure 7-2. Predicted relative probability of occurrence in ordinal bins for adult female grizzly bears during late hyperphagia (16 August to 15 October). A habitat rank of 1 represents low relative probability of occurrence, while 10 represents high relative probability of occurrence.

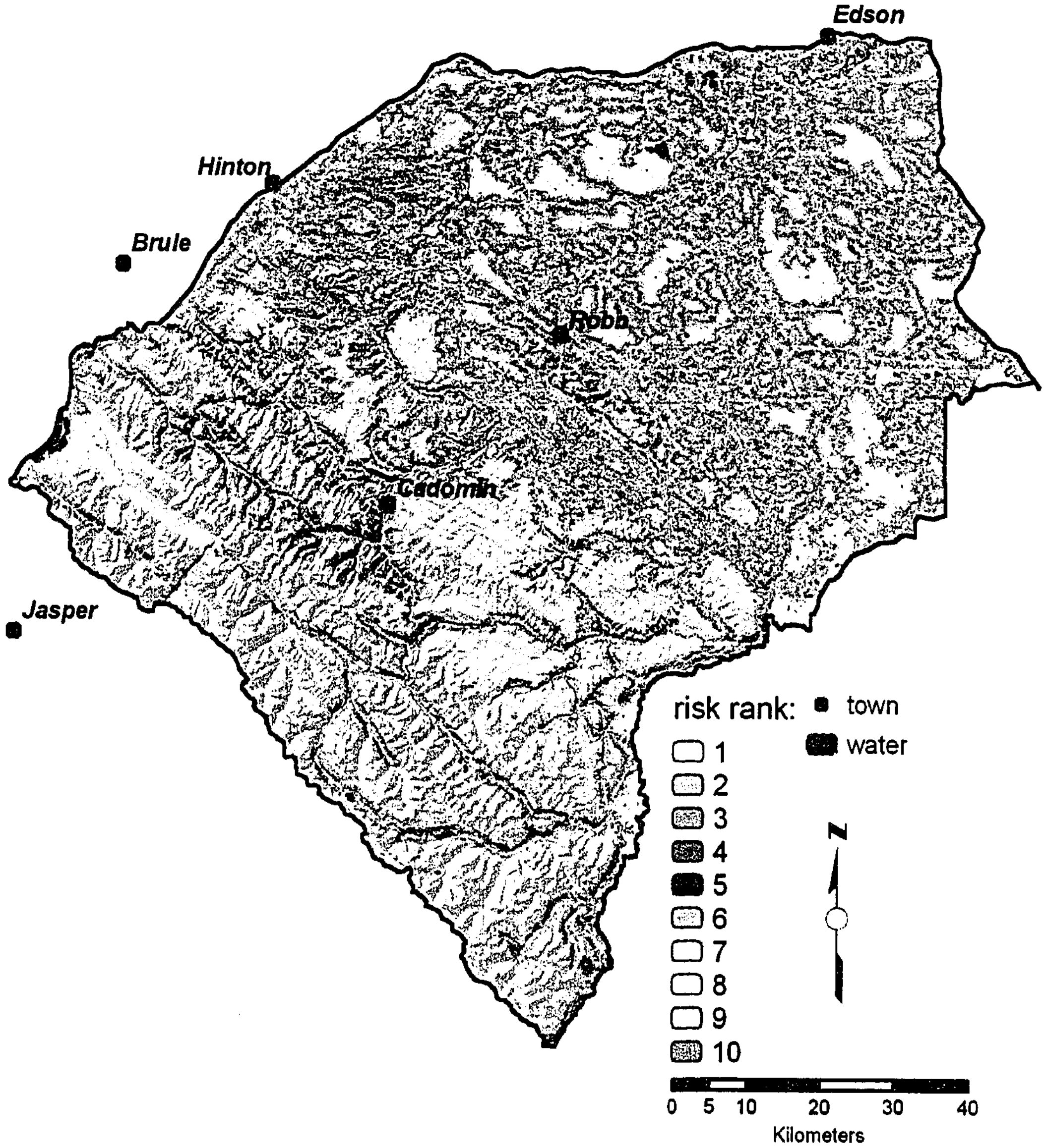

Figure 7-3. Risk (ordinal bins) of human-caused mortality for adult female grizzly bears in west-central Alberta, Canada. A risk rank of 1 represents low relative probability of mortality, while 10 represents high relative probability of mortality.

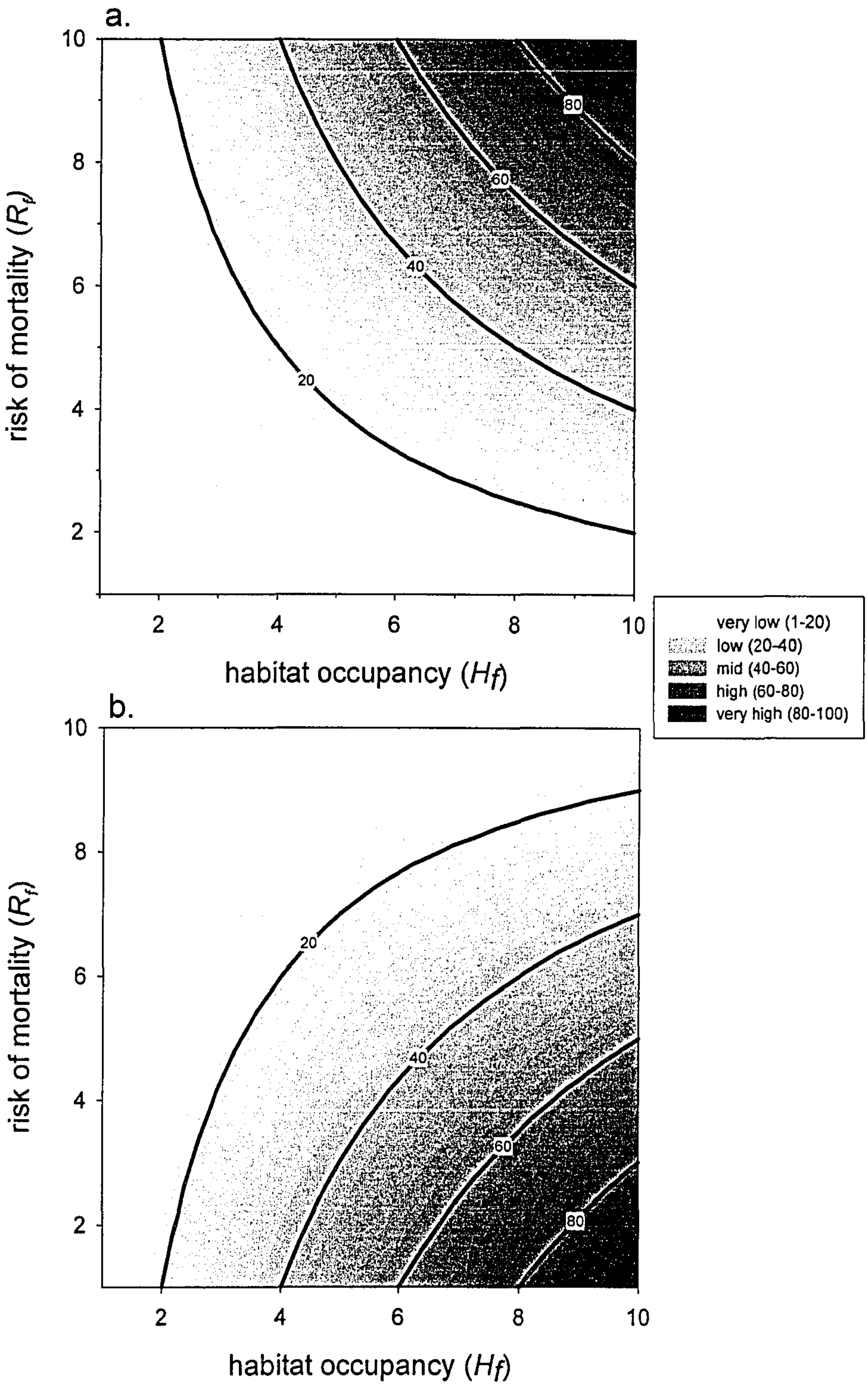

Figure 7-4. Graphic representation of attractive sink (a.) and safe harbor (b.) indices based on adult female habitat (H_f) and human-caused mortality risk (R_f) models.

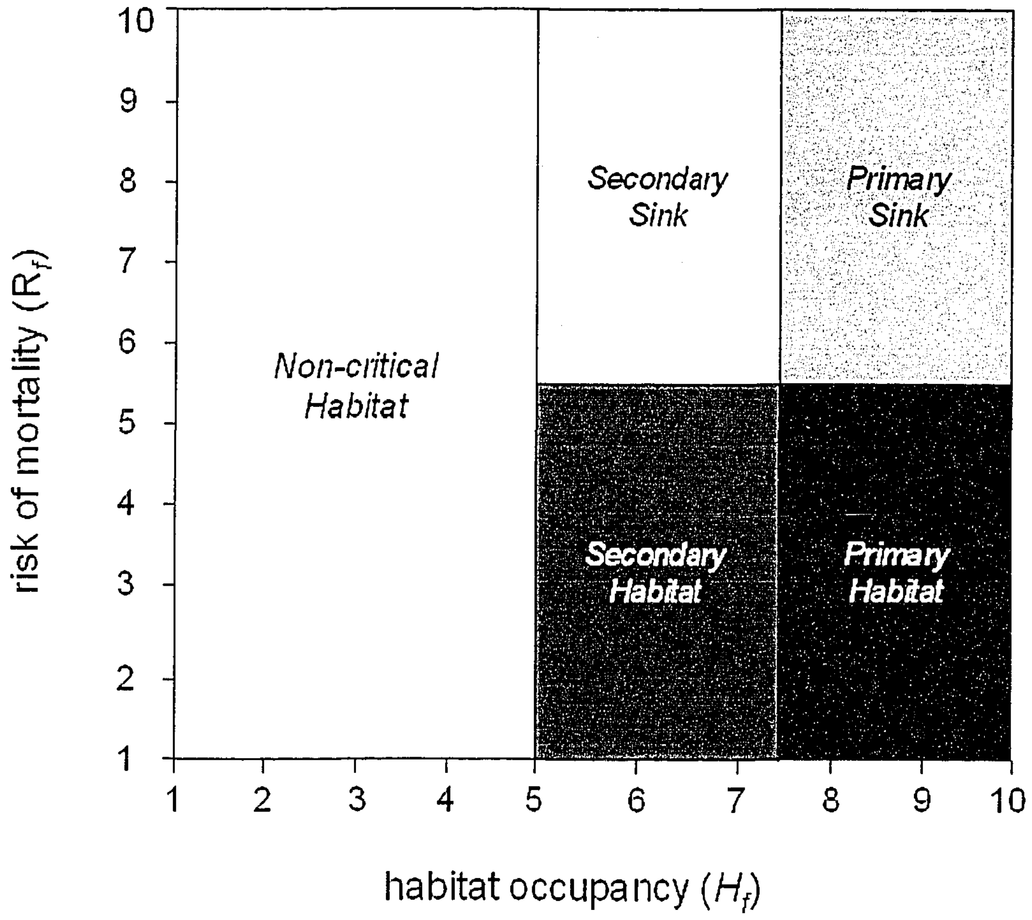

Figure 7-5. Graphic representation of the 5 defined hypothetical habitat states based on habitat (H_f) and risk (R_f). These states include safe harbor, refuge, matrix, attractive sink, and sink habitats.

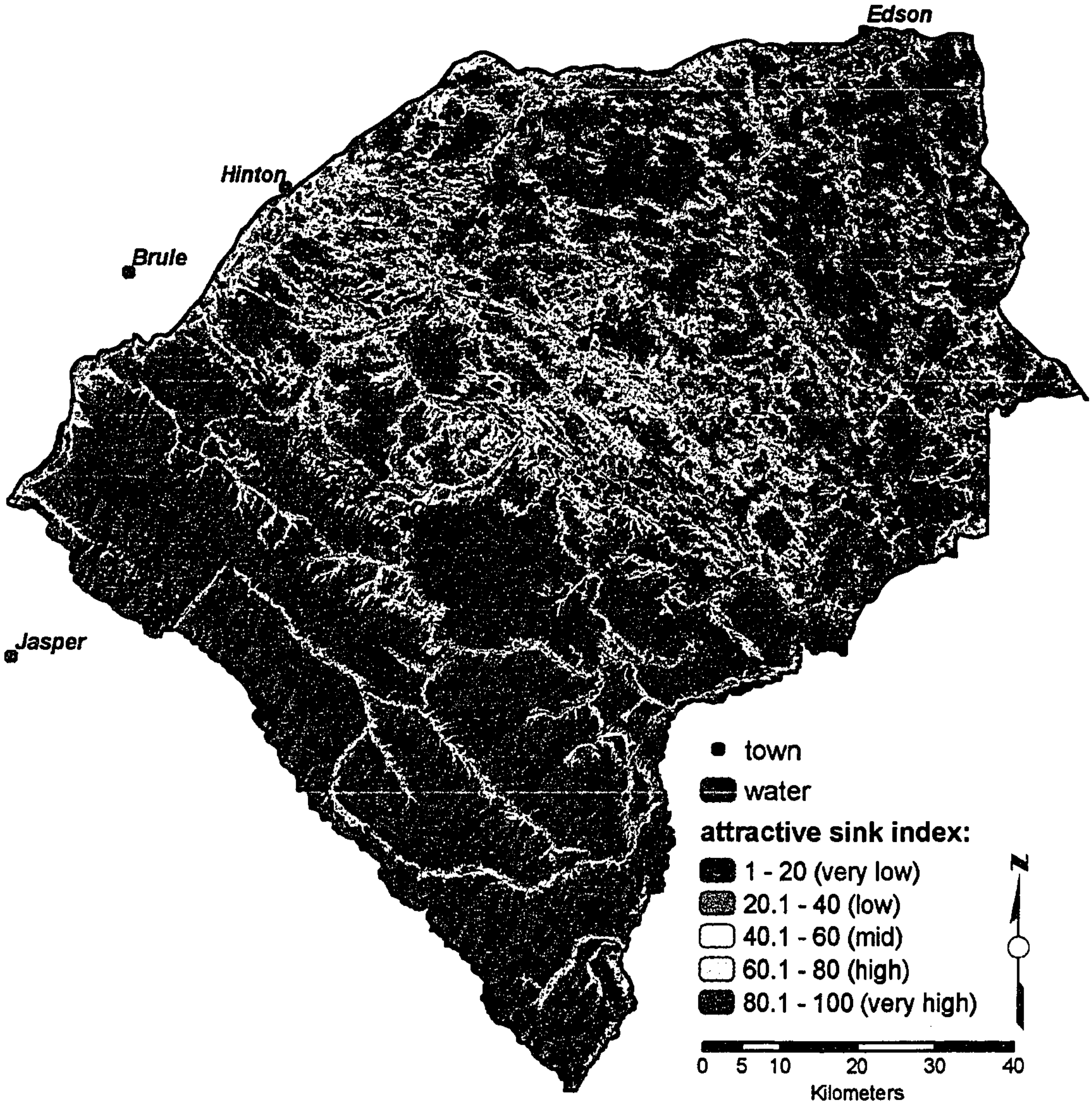

Figure 7-6. Index of attractive sink (AS_f) habitats for adult female grizzly bears during late hyperphagia in west-central Alberta, Canada. High and very high attractive sink values represent those habitats where animals are both likely to occur and at high risk of mortality, hence the need for mitigation.

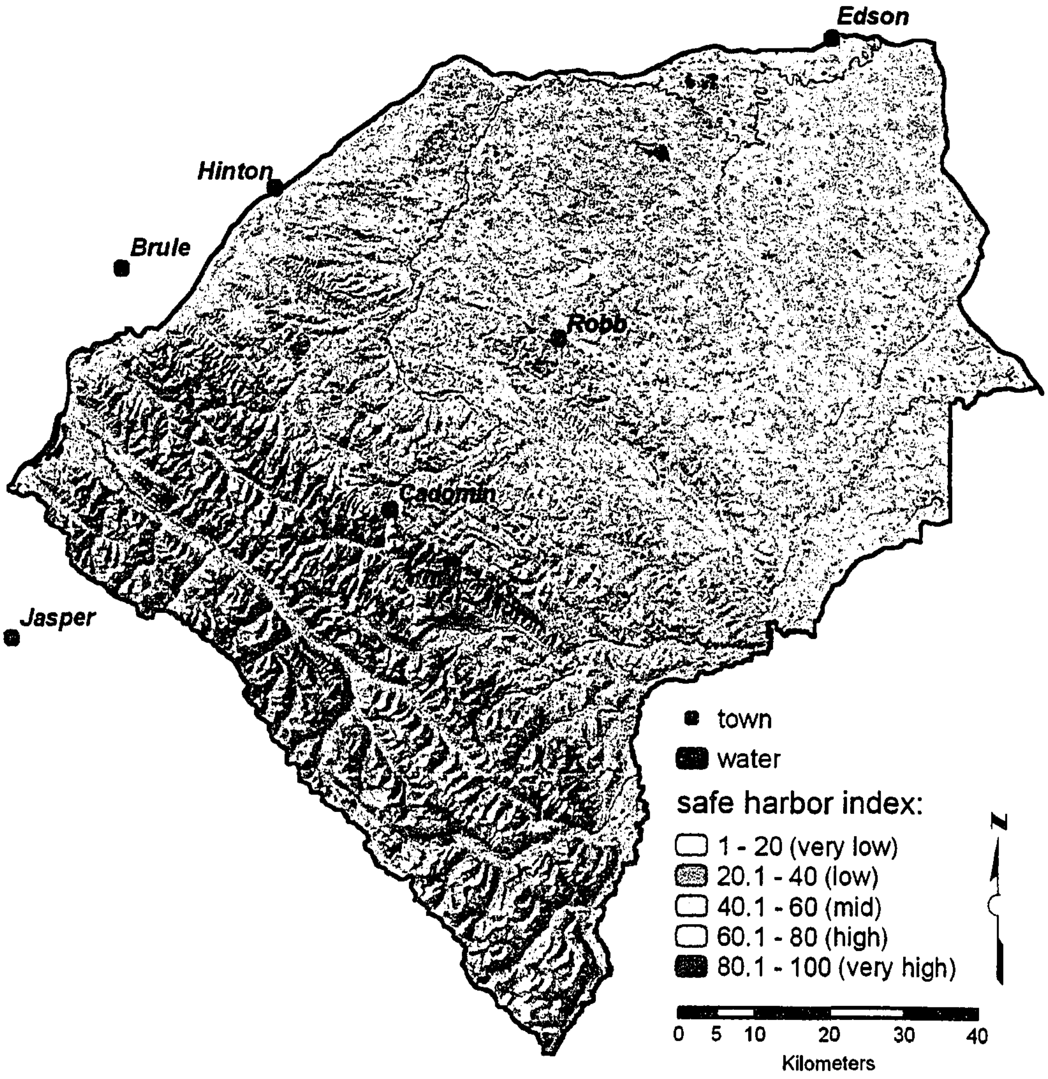

Figure 7-7. Index of safe harbor (SH_f) habitats for adult female grizzly bears during late hyperphagia in west-central Alberta, Canada. High and very high safe harbor values represent those habitats where animals are likely to occur and at low risk of mortality, hence the need for special protection.

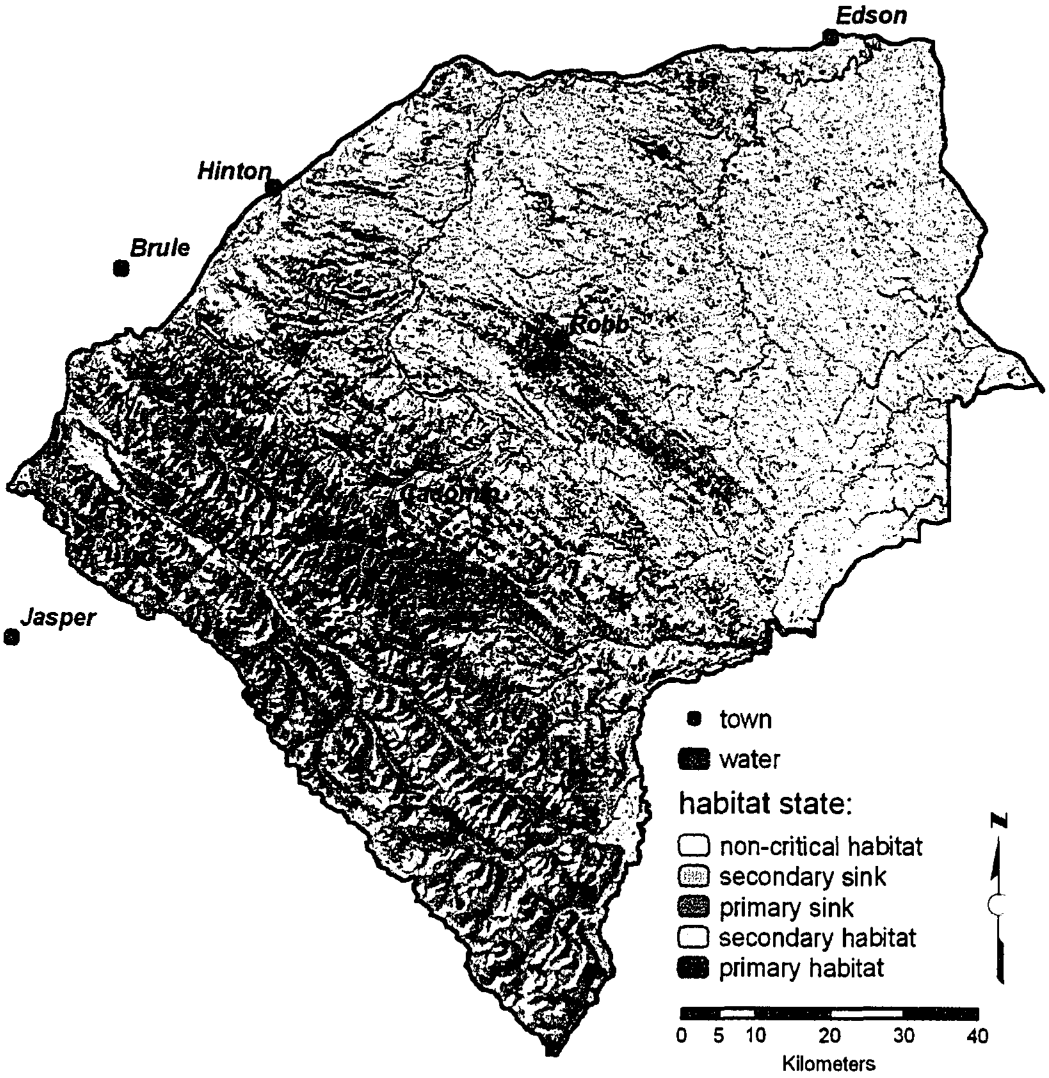

Figure 7-8. Hypothetical habitat states for west-central Alberta based on a 2-dimensional classification of habitat occupancy (H_f) and mortality risk (R_f) predictions. Primary sink relates closely to high-to-very high values of the attractive sink index, while primary habitat relates closely to high-to-very high values of the safe harbor index.

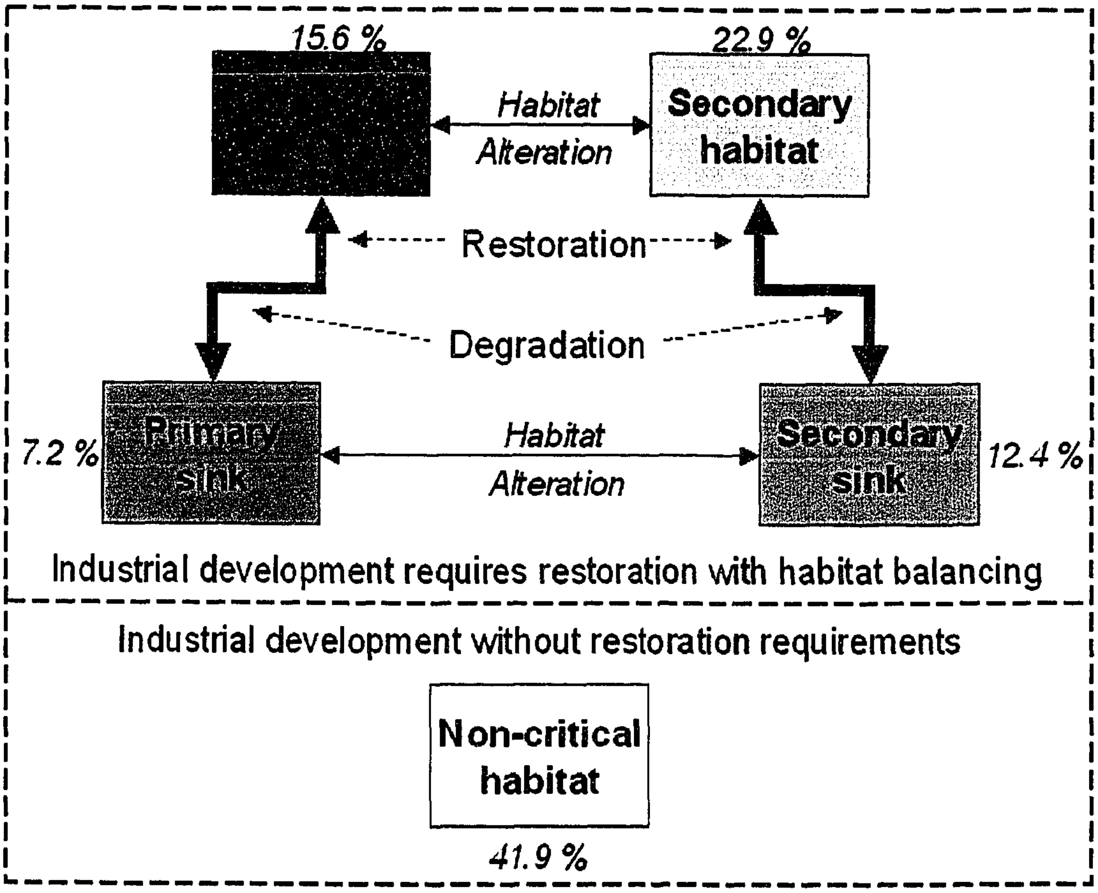

Figure 7-9. Schematic representation of habitat states on crown lands of west-central Alberta (with existing percentages for each state) depicting a suggested strategy for maintaining existing habitats and restoring sinks when degradation occurs. Non-critical habitats would be considered open for resource extraction without the need for restoration if those sites weren't adjacent to high quality habitats. Any alteration to secondary or primary habitats would have to be compensated by restoration of secondary or primary habitats. As well, some activities will alter habitat state composition through changes in habitat quality (habitat alteration).

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Chapter 8

A comparison of two-pass and natural disturbance-based forestry on grizzly bear population persistence in west-central Alberta, Canada

1. Introduction

Grizzly bear distribution and abundance have declined substantially in North America during the past century (McLellan, 1998; Mattson and Merrill, 2002). Low reproductive rates and low densities make grizzly bears vulnerable to population decline and slow their recovery (Russell et al., 1998; Purvis et al., 2000). Within Alberta, population trends have not been encouraging, with an approximate population on Provincial lands based on mortality records, an assumed 6% growth rate and 1988 habitat conditions of only 500 animals (Stenhouse et al., 2003). Although these estimates are admittedly crude, most would agree that continuing loss of habitats and more importantly, high rates of human-caused mortality (Benn, 1998; Benn and Herrero, 2002; Nielsen et al., 2004a), threaten the long-term persistence of grizzly bears in Alberta. Assessing industrial development effects on grizzly bear habitats and populations remains an important topic for conservation and management. Previous work by Nielsen et al. (2004a) depicted current grizzly bear habitats and pseudo-population states for a landscape in west-central Alberta that is at a relatively early stage of industrial development. With rapid industrial growth expected throughout Alberta (Schneider et al., 2003), including this region of Alberta, assessments of future grizzly bear habitats and populations are needed. This includes understanding risk of extinction or major population decline.

One approach for assessing risk of extinction is population viability analysis (PVA). Although there is no single method for conducting a PVA, the goal is often the same. That is, provide an assessment of extinction risk or persistence for a species at risk over time (Boyce, 1992). This process can be spatial (e.g., habitat-based PVA) or non-spatial in nature, with potential response variables including, time to extinction or quasi-extinction (a given, small number of individuals); probability that a population will persist after an arbitrary defined number of years; and various measures of habitat occupancy (Noon et al., 1999). The former 2 methods, however, require unbiased estimates of population counts or demographic rates. For the vast majority of species, such data are sparse at best making any statements of viability notoriously imprecise (Boyce, 1992). Confidence intervals for extinction, for instance, often overlap 0 and 1 shortly into the future, making their usefulness for predictions of actual extinction questionable (Ludwig, 1999; Fieberg and Ellner, 2000). Year-to-year variation in demographic data, often due to fluctuating food resources (Ostfeld and Keesing, 2000), common for grizzly bears (Pease and Mattson, 1999), make uncertainty around predictions even greater. For example, if one were to assume relatively small year-to-year variation in demographic processes, between 5 and 10 times as many years of count data would be required to estimate the probability of quasi-extinction with reasonable precision (Fiebert and Ellner, 2000). Following this rule of thumb, annual counts of Yellowstone grizzly bears since 1959, would only provide a reasonably accurate prediction of extinction risk for 9 years into the future (Morris and Doak, 2002). Gathering the necessary data to parameterize a quantitative PVA for accurate predictions therefore presents a 'catch-22' situation, where the amount of time required to collect necessary data may end up exceeding the time to extinction for some species at grave risk.

Given such limitations, many have argued instead for a more qualitative role for PVA where risk of extinction is ranked among management scenarios (Boyce, 1992; Beissinger and Westphal, 1998; Morris and Doak, 2002). In fact, ranks of population risk among management scenarios appear to be rather robust (McCarthy et al., 2003), although an adaptive management approach should be sought where various management strategies are implemented for spatially segregated populations (Noon et al., 1999). Using such an approach, PVA provides a supporting tool for management decisions, rather than a formal estimation of extinction risk (Possingham et al., 2002). As Lacy and Miller (2002) point out, analyses should strive to integrate human activities more directly into PVA models and ask questions such as, "What happens to the probability of population persistence (or some other measure of viability) *if* humans do not change in number, distribution, or activity patterns over time?"

Management models relying on a habitat-based PVA make the assumption that changes in the amount and distribution of habitat are driving population numbers (Noon et al., 1999). Although demographic rates can be associated with habitats and simulated through time (Akçakaya and Atwood, 1997), a much simpler approach is to simply associate animal densities directly to habitats and modify these as a function of predicted landscape change (Boyce and McDonald, 1999). This approach requires a habitat model like a resource selection function (RSF) and a baseline population estimate to formulate habitat-based density estimates, thereby allowing predictions of populations in space and/or time (Boyce and McDonald, 1999; Boyce and Waller, 2003). By comparing these habitat-based densities among various future scenarios, one can rank population risk. The primary advantage of such an approach is the predictive success of RSFs (Boyce et al., 2002), something that is likely to show much more predictive power than a demographic-based model.

In this paper, we follow this habitat-based PVA approach to help support management directions for grizzly bears in Alberta, Canada. Specifically, we compare how changes in forestry practices might affect grizzly bear populations by using a resource selection model, a risk of human-caused mortality model, a baseline population estimate, and future scenario modelling. Currently, Alberta follows a two-pass harvest design where clearcut harvest guidelines attempt to limit clearcut size, often forcing roads and clearcuts to be dispersed spatially, and human activity within harvest areas prolonged temporally. Stands adjacent to clearcuts within a harvest block remain un-harvested until a 3-meter green-up rule of harvested clearcuts (re-forestation) is reached. Recently, some have argued that a natural disturbance-based approach for forest harvesting should be considered with the aim of conserving biodiversity (Swanson and Franklin, 1992; Hunter, 1993; Bergeron et al., 1999). Often the emphasis is placed on the proportion of land disturbed and size of individual patches being harvested, attempting to emulate historic fires by often harvesting large blocks of forests. This has been referred to as natural disturbance-based forestry and contradicts the present forest guidelines by supporting very large clearcuts. Although Granström (2001) points out some flaws in following past disturbance regimes for current forestry, such an approach would presumably lower road densities and long-term activities thereby benefiting species such as grizzly bears that are sensitive to human access. The goal of this paper was to test differences among two-pass and natural disturbance-based forestry on grizzly bear habitat and persistence for a 100-year period into the future. More specifically, we were interested in tracking habitat indices, relative habitat states, and the number of potential and effective (free from human-caused mortality risk) adult female territories estimated through habitat-based densities and assessments of mortality risk.

2. Study Area

We studied grizzly bear habitat conditions and adult female territory numbers for a 9,752-km^2-study landscape over a 100-year period in west-central Alberta, Canada (53° 15′ N, 118° 30′ W, Figure 8-1). Contrasting land use and land cover zones dominated this region, with one area in the west consisting of protected mountainous terrain and the second area to the east characterized by rolling foothills widely used by resource industries. Mountainous land cover classes consisted of montane forests, conifer forests, sub-alpine forests, alpine meadows, and high elevation areas of rock, snow, and ice (Achuff, 1994; Franklin et al., 2001). In comparison to the protected mountains, the eastern foothills were characterized by a number of resource extraction activities, including forestry, oil and gas, and open pit coal mining. Large numbers of roads and seismic lines typify this landscape. Land cover for the foothill region includes conifer, mixed, and deciduous forests, areas of open and treed-bogs, small herbaceous meadows (including small agricultural fields in the far northeast), and areas of regenerating (fire and clearcut harvesting) forests (Achuff, 1994; Franklin et al., 2001). Climate within the area was intermediate, with an average summer and winter temperature of 11.5 C and –6.0 C respectively, and a normal annual precipitation of 538 mm (Beckingham et al., 1996). Temperature and precipitation were strongly influenced by elevation that ranged from 984 to 3,012 m. With a short growing season, lack of salmon and other high protein foods (Jacoby et al., 1999), these interior grizzly bear populations occur at relatively low densities (e.g., ≤ 4 animals/1000-km^2).

3. Methods

3.1. Future scenario modelling

We used the program PATCHWORKS (Spatial Planning Systems, Deep River, Ontario), a forestry model, to simulate two potential future landscapes in a GIS across a 100-year period at decade intervals. PATCHWORKS is a spatially explicit optimization model that has recently gained notice as a forest-planning tool by forest industries in Ontario and Alberta, Canada. The program is 3-dimensional in having a traditional 2-dimensional GIS framework (spatial coordinates) along with a third temporal dimension to track and simulate landscape change. PATCHWORKS is similar to a multiple-objective goal-programming model where a solution is found that maximizes the objective within a framework of constraints. PATCHWORKS uses information on forest yield within individual forest stands (polygons) to 'harvest' fiber, the primary objective, transport raw materials to a defined mill (node) along existing roads or build roads at a minimum cost to access inaccessible resources. To build the PATCHWORKS modelling framework, we used a non-spatial timber supply model, WOODSTOCK (Remsoft, Fredericton, New Brunswick), to estimate forest-level actions (proportion harvested) for each strata (forest class × age class). PATCHWORKS thereby spatially represented possible solutions for WOODSTOCK for each time period.

As previous habitat modelling for grizzly bears in the study region have relied on a remote sensing classification of land cover from Franklin et al. (2001), we used this same product to define operable (forest) and non-operable classes for model simulation (Table 8-1). In total, 5 operable forest classes, including closed conifer, open conifer, closed deciduous, open deciduous, and mixed forests, were defined. We combined stand age for each forest class using information from Alberta Vegetation Inventory (AVI) and fire history GIS maps from the Foothills Model Forest (FMF). For regenerating clearcuts, we used harvest data provided from forestry stakeholders to associated stand age. Along with information on compartment and forest management agreement (FMA), we merged stand age and forest class into a single shapefile that identified unique individual polygons. As PATCHWORKS only harvests individual polygons (i.e., the program cannot split a forest polygon into multiple subsequent polygons), homogenous areas that were too large for effective harvesting required finer-level separation. We divided all 'large' polygons into smaller stands using a 50 ha hexagon grid overlaid on the study area, where any polygon larger than 50 ha was subdivided into a unique polygon (even if surrounded by an identical stand type and age) along hexagon boundaries. For each unique forest age and stand class polygon, we estimated forest volume using average growth-yield curves by forest class (Figure 8-3). During each decadal time step, volumes in each polygon were modified to reflect the succession of reforested stands or the removal of forest volume from clearcut harvesting or senescence of old-growth stands. Once stands were harvested, they were reverted to the same original forest class. As well as disregarding potential compositional changes, we also did not consider 'natural' forest disturbances, such as fire, insects, wind-throw, ice storms, drought, or climate change, all of which have the potential to modify landscape structure and forest growth (i.e., Waring and Running, 1998). Although adding such complexity would provide more realism, it would constrain the modelling process and objectives. Current forest stakeholders in Alberta do not include natural forest disturbance within long-term forest planning, dealing with such events instead in an *ad hoc* manner.

Road development, within an existing coverage of roads, was based on a network of potential arcs occurring in ordinal and inter-ordinal directions using a 600 m grid (Figure 8-2). Potential roads were used to bridge gaps between existing roads and future harvest actions. We accounted for road operating costs for existing and potential roads by estimating haul, maintenance, and building costs (Table 8-2). In total, 4 resource stakeholders, each with a minimum of one mill (node), where considered. These included the three FMAs of Sundance, Weldwood, and Weyerhaeuser (Figure 8-1), as well as an oil and gas industry. Mill (node) locations included the towns of Hinton for Weldwood and Edson for Sundance, Weyerhaeuser, and the oil and gas industry (Figure 8-1). For each mill, a set volume of necessary resources (timber) was defined, with the program attempting to find those resources under minimal costs given defined parameters, targets, or constraints based on forestry guidelines and landbase characteristics.

By modifying model targets and constraints within PATCHWORKS, we were able to simulate 2 forestry scenarios of interest: (1) a two-pass forestry; and (2) a natural disturbance-based forestry (Table 8-3). In the former scenario, we minimized the number of large clearcuts (>100 ha) and very small clearcuts (<5 ha) by controlling ranges of patch sizes. This resulted in a range of clearcut sizes, striving for the 'small' clearcut targets, with 75% of clearcuts being 20 to 100 ha in size and 25% within the 5 to 20 ha range. Finally, we used compartment (management blocks provided by forestry companies) control (i.e., turning compartment access 'on' or 'off' in different time periods) to regulate when individual compartments were open for harvest, thus replicating a two-pass forest harvest design. For the natural disturbance scenario, we modified the target for clearcut size to minimize the number of patches under 250 ha and 'turned off' the compartment sequence. Compartment sequence needed to be removed from this scenario, as large clearcuts were only possible by extending their boundaries beyond existing compartment boundaries. It is important to realize that both forestry scenarios were passive in design, as PATCHWORKS seeks to meet criteria (attempts to optimize toward defined targets), but may deviate from those criteria (targets) if costs become too high. As well, PATCHWORKS is not a deterministic model and as such, model results from the same criteria (scenario) can vary by simulation.

As well as representing spatio-temporal changes in forest resources, we simulated changes in the oil and gas industry by establishing well pad polygons (approximating various current shapes) for each period according to current oil and gas trends. This was done in a more speculative manner where discoveries were considered to be random on Crown lands. Similar to forest modelling, roads were built to each well pad that became active to extract resources to the Edson oil and gas node. As the majority of well pads in the area are natural gas, we assumed gas sites to be in operation for two decades, decommissioned in the third decade and mitigated to a regenerating forest of the same original forest class in the fourth decade (B. Stelfox, personal communication). For both forestry scenarios, we maintained the same natural gas targets. Scenarios that further modify oil and gas activity would be fruitful exercises, but were not considered here. We focus instead on the two-pass and natural disturbance-based forestry, allowing for a semi-realistic process of oil and gas development to proceed in the 'background' in exactly the same manner for both forestry scenarios.

3.2. Adult female habitat model

To develop a habitat-based PVA, we required information on habitat affinities for local grizzly bears. We used a resource selection model for adult female grizzly bears from Nielsen (2005) to define habitats. As habitat selection was found to vary substantially among not only sex-age groups, but also seasons (Nielsen 2005), we chose a single season, in this case late hyperphagia, for representing grizzly bear habitat. Late hyperphagia, occurring between 16 August and 15 October, coincided with the ripening of numerous fruit-bearing species (Hamer and Herrero, 1987; Hamer et al., 1991; Nielsen et al., 2004b). Arguably, this period could be considered the most important season for local bear populations, as animals acquire a large majority of their calories necessary for survival and reproduction. In total, 5,172 radio-telemetry observations from 13 adult female animals were collected during this season from 1999 through 2002 (Nielsen, 2005). In addition to these model training data, Nielsen (2005) used an additional 1,201 radiotelemetry observations from 7 adult females during the same period in 2003 for model assessment. The specific habitat model describing the relative probability of occurrence for adult females during late hyperphagia took the exponential form following Manly et al. (2002) of,

$$w(\boldsymbol{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_{24} x_{24}) \qquad (8\text{-}1),$$

where $w(\boldsymbol{x})$ represented the relative probability of occurrence within any study area pixel (30 m × 30 m), β_1 the selection coefficient for x_1 representing the land cover category alpine/herbaceous, β_2 the selection coefficient for x_2 representing the land cover category for anthropogenic, and so on for all 24 categorical and continuous environmental predictor variables used to describe grizzly bear habitat (Tables 8-4 and 8-5). These 24 variables included 10 land cover categories, distance to nearest edge, a terrain-derived index of soil wetness, an index of terrain ruggedness, forest or regenerating forest age, global solar radiation within 3 land cover types (interactions), and the interactions of soil wetness with either edge distance or forest age. For the regenerating forest class, we considered all harvest polygons ≥60 years in age to once again be forests by converting each harvest polygon to its previous forest class. For those harvest polygons with unknown forest composition (i.e., those harvested prior to 2004), we used a majority filter, donut in shape, around each polygon (30 m [1 pixel width] in distance) to assign unknown stands to a forest type.

Map predictions were transformed ($Tw(\boldsymbol{x}) = w(\boldsymbol{x}) / (1+w(\boldsymbol{x}))$) and binned into 10 ordinal (quantile classification) habitat classes (Nielsen, 2005), ranging from a low relative probability of occurrence at 1 to a high relative probability of occurrence at 10. We refer to this habitat map as H_f. Previously, Nielsen (2005) found the H_f map to have significant fit and prediction with model training and testing data respectively. During late hyperphagia, adult females favored alpine/herbaceous, open conifer, and deciduous forests, while tending to avoid anthropogenic, regenerating forests, and non-vegetated areas. However, the primary factors governing habitat selection tended to be characterized by micro-site conditions (soil wetness, terrain ruggedness, solar radiation, etc.) and landscape configuration (e.g., distance to edge). For each new time step and scenario combination, we estimated the relative probability of occurrence, $w(\boldsymbol{x})$, transformed values of $w(\boldsymbol{x})$, and a H_f map using the original habitat bin thresholds from Nielsen (2005). Habitat maps based on binned values for each time step and scenario combination were used to estimate new habitat-based adult female densities.

3.3. Adult female habitat-based density estimates

Adult female habitat densities were estimated for the baseline (current) period by associating animal densities to habitat ranks using a habitat model and a baseline population estimate. In 1999, DNA mark-recapture efforts (Woods et al., 1999) were used to estimate the population of grizzly bears for a 5,351-km^2 area of the western portion of the given study. Using the mark-recapture data, Boulanger (2001) estimated a superpopulation; adjusting for closure and scaling for bear residency using the proportion of trapping sessions that collared animals were present on the sampling grid (Kenward et al., 1981). The superpopulation estimate in 2000 was 80 animals (14.95 animals/1000-km^2). Although large confidence intervals (95% C.I. of 53 to 145) surrounded this estimate, it was the only empirically based estimate available for the current population. The value also is close to that used for management purposes, as well as within the range of densities reported for interior grizzly bear populations elsewhere (Poole et al., 2001). Regardless of the accuracy, we grounded this population estimate to be our baseline condition from which to measure future trends. However, as we required a baseline population estimate for the entire study boundary, not just the 5,351-km^2 sub-region, we needed to make an estimate of the population for our entire study before proceeding with tracking population change. To estimate a new population, we needed to estimate animal densities within habitat bins for the 1999 DNA census area and extrapolate these density patterns to the remaining 4,401-km^2 region. Using the methods of Boyce and McDonald (1999) and Boyce and Waller (2003), we first defined bear habitat use, $U(\mathbf{x}_i)$, for the *i*th habitat bin as:

$$U(x_i) = w(x_i)A(x_i) \Big/ \sum_j w(x_j)A(x_j) \qquad (8\text{-}2),$$

where $w(x_i)$ is the bin midpoint from equation 8-1, $A(x_i)$ is the area in the respective habitat bins, and the summation is over the number of habitat bins, j. The number of bears in the ith habitat bin was estimated to be,

$$N_i = N \times U(x_i) \qquad (8\text{-}3),$$

where N is the population estimate of 80 for the reference area (1999 DNA census area) and $U(x_i)$ from equation 8-2 above. Habitat based densities for the reference area for each habitat bin were therefore defined as,

$$D(x_i) = N_i / A(x_i) \qquad (8\text{-}4),$$

where $D(x_i)$ was the density of bears in habitat bin i, N_i the population of bears in the same habitat bin, and $A(x_i)$ the area of that respective habitat bin. Assuming similar patterns of habitat use for the expanded region, we estimated the number of grizzly bears for the new study boundary using bear densities, $D(x_i)$, estimated in equation 8-4 and the following formula:

$$\hat{N}^* = \sum_j D(x_j)A'(x_j) \qquad (8\text{-}5),$$

where $\hat{N}^*$ is the new population estimate for grizzly bears in the entire study, summing the product of grizzly bear densities, $D(x_j)$, and the area of that habitat within the new boundary, $A'(x_j)$, among all habitat bins j. Although we now had a new population estimate, we were specifically interested in tracking adult females. As such, we used simple demographic proportions from Yellowstone to divide our population into an adult female-only estimate. Using Craighead et al. (1995), the adult female proportion was 23.5% of the population (Table 8-6). We therefore estimated the adult female population for the new study, $\hat{N}^*_f$, to be,

$$\hat{N}^*_f = \hat{N}^* \times 0.235 \qquad (8\text{-}6),$$

where $\hat{N}^*$ is the total number of grizzly bears for the study area. This estimated adult female population was considered our final baseline conditions for the entire study area for further comparison.

To estimate future adult female populations, we used the Patchworks results to estimate new habitat conditions (bins) using equation 8-1. By associating these values with equation 8-2 through 8-5 and using the baseline adult female population, $\hat{N}_f^{*}$ in equation 8-6 as the reference population, in place of N in equation 8-3, we estimated a new adult female population for each time step and scenario combination, as well as specific animal densities within habitats.

3.4. Mortality risk, territory allocation, and territory status

We developed a script, using ArcGIS 8.3 (ESRI, 2002), to allocate the estimated adult female population into individual territories for each time period and forestry scenario. For each scenario and time period, we used the estimated adult female density from equation 8-4 to distribute adult females into pixel-based densities for the entire study area. The GIS script summed pixel values, in a rectangular pattern, until a value of 1 was reached, representing an individual adult female territory. This was repeated until all pixels were assigned to a specific territory polygon. Given the irregular shape of the study area, however, it was necessary to iterate this procedure until the territory number equaled the expected population of adult females (sum of all pixels across the study area), as some irregular patterns along study boundary borders sometimes occurred preventing solutions that matched the expected number of territories.

Once territories were established as polygon features for each scenario and time period, we assessed the risk of human-caused mortality for each adult female grizzly bear territory using a mortality risk model from Nielsen et al. (2004a). The model, developed just south of the exiting study, described the distribution of grizzly bear mortalities based on a comparison of human-caused grizzly bear mortalities with random available locations using common landscape covariates that represented human encroachment and bear habitat. We used the model specific to adult animals, as the distribution of sub-adult mortalities were found to differ from that of other sex-age classes, while no variation in the spatial distribution of adult male and female mortalities were evident. Risk of human-caused mortality for adult grizzly bears was defined from Nielsen et al. (2004a) as,

$R_f = \exp(d0.415 + g0.503 + n0.592 + s1.023 + r{-}0.152 + e{-}11.738 + w{-}1.490 + a{-}2.901 + t{-}6.740)$ (8-7),

where R_f was an index of human-caused mortality risk for adult females based on the exponential form of 9 environmental covariate predictors. Environmental covariates included, deciduous forest (*d*), grassland and crop (*g*), non-vegetated areas (*n*), and shrub (*s*) landcover categories (0 or 1) with conifer forests the reference class; greenness (*r*), an index of vegetative productivity (White et al., 1997; Waring and Running, 1998) based on a tasseled-cap transformation of Landsat TM bands (Crist and Cicone, 1984); and distance to nearest edge of a habitat (*e*), water (*w*) or human access (*a*) feature measured in kilometers.

For each scenario, we generated the necessary variables in equation 8-7 from PATCHWORKS outputs to estimate R_f. We assumed, however, that greenness values were constant, as we did not have predictions for future greenness values. Regardless, the primary variable modifying R_f values was distance to human access, a variable derived from resulting road networks produced in the PATCHWORKS modelling process. Although the original model included hiking trails in human access features, we excluded these features for two primary reasons: (1) they were not modeled within PATCHWORKS; and (2) previous examinations of mortality risk extrapolations for the study area (Nielsen et al., 2004) indicated that the risk was potentially over-estimated for remote areas with isolated hiking trails in Jasper National Park. Predicted values of R_f were scaled and binned in a similar manner to that of $w(\boldsymbol{x})$, where the relative risk of mortality ranged from a low of 1 to a high of 10. We re-classified the 10 ordinal bins to a single low- or high-risk class, by assigning R_f values from 1 to 5 as low-risk and R_f values from 6 to 10 as high-risk following that of Nielsen et al. (2004). Using this risk classification, we estimated the proportion of high-risk within 90% kernel home ranges of radiocollared animals in a GIS. We used logistic regression to identify the threshold value of proportion risk at which bears were likely to die using the status of radiocollared animals as the dependent variable (0-alive, 1-dead) and the proportion of high-risk within 90% kernels and the sex of the individual (0-female; 1-male) as independent variables. We used sensitivity and specificity curves to identify the optimal (location of where both sensitivity and specificity are maximized) mid-point classification, or threshold, of either survival (0) or death (1) of female bears. We used the resulting threshold values for assessing whether territories established in future scenarios were effective (below threshold value) or non-effective (above threshold value). We compared the rank of effective or what might be considered source territories between the two scenarios for each time period as the basis of our habitat-based assessment of population viability. A cartographic model describing the modelling process (steps) is described in Figure 8-4. We assumed that the number of effective territories respresented a critical metric for long-term conservation of grizzly bears. We assumed that effective (source) adult female territories represented sites where animals were likely to survive, reproduce, and disperse offspring.

3.5. Tracking future habitat indices and relative habitat states

Finally, we tracked both attractive sink (AS_f) and safe harbor (SH_f) indices, first introduced in chapter 7, as well as the 5 relative habitat states of non-critical habitat, primary sink, secondary sink, primary habitat, and secondary habitat. Both the indices and relative habitat states were based on a 2-dimensional model composed of H_f (binned values of habitat occupancy from $w(\mathbf{x})$ in equation 8-1 and transformed as described above) and R_f (mortality risk from equation 8-7 above). For a more detailed description of the derivation of indices and relative habitat states, refer to chapter 7. For each time period and scenario, we estimated AS_f, SH_f, and the 5 relative habitat states to compare forestry scenarios, landscape compostion on Crown lands (outside of Jasper National Park and Whitehorse Widllands Provincial Park), and assess the spatial patterns of habitat conditions (Figure 8-4).

4. Results

4.1. Future landscapes

Outside of the protected non-operable management zones of Jasper National Park and adjacent Whitehorse Wildlands Provincial Park (static landscapes), scenario modelling resulted in broadly similar proportions for each land cover class, although forested stands tended to be less common and regenerating forests more common over time for the natural disturbance-based forestry scenario (Table 8-7). We suspect dissimilarities between two-pass and natural disturbance-based forestry were due to differences in spatial patterns of stand volume. Two-pass harvesting was better able to select patchy, high volume stands that were often small in size, while natural disturbance-based harvesting was 'forced' to harvest both high and low volume stands co-occurring in a mosaic of forest types meeting the large footprint (e.g., ~250 ha) criteria. Differences in spatial patterns of the land cover classes between two-pass and natural disturbance-based forestry were even more evident, again reflecting model constraints imposed by the two separate forestry scenarios of numerous, small clearcuts for two-pass forestry and few, large clearcuts for natural disturbance-based forestry (Figure 8-5).

Patterns of road development to access forest and natural gas resources appeared reasonable (Figure 8-5), although potentially over-estimated for the second half of next century because the program tended to favor building new roads rather than maintaining existing roads, hence saving maintenance costs. As we assumed no road closures, deactivations, or reclamations in Patchworks, final road densities and patterns may be liberal. Regardless, final road densities for two-pass and natural disturbance-based forestry at 100-years into the future were estimated at 1.16 and 1.39 km/km^2 respectively. From an initial landscape of 0.35 km/km^2, that is more than a 3-fold increase in roads.

4.2. Assessing habitat indices and relative habitat states

Natural disturbance-based forestry resulted in higher average landscape values of attractive sink (AS_f) habitat and lower average landscape values of safe harbor (SH_f) habitat when compared to two-pass forestry (Figure 8-6). In fact, natural disturbance-based forestry averaged 5.9% higher and 4.4% lower than two-pass forestry in AS_f and SH_f habitat scores respectively. Higher AS_f and lower SH_f habitats for natural disturbance-based forestry was a consequence of greater road development. Despite consistent differences among scenarios, trends for the future were rather similar with higher proportions of AS_f habitats and lower proportions of SH_f habitats through time. Total percent increase for AS_f habitats on Crown lands for the 100-year period was estimated at 85.2% and 95.3% for two-pass and natural disturbance-based forestry respectively. Total percent decline in SH_f habitats, on the other hand, was 21.5% for two-pass forestry and 25.8% for natural disturbance-based forestry. Despite differences among forestry scenarios, the general spatial pattern of AS_f (Figure 8-7) and SH_f (Figure 8-8) habitats were relatively comparable. Fragmentation of SH_f habitats and increasing prevalence of AS_f habitats through time was apparent and widespread to Crown lands. As Jasper National Park and Whitehorse Wildlands Provincial Park were considered non-operable (protected areas in the western and the southwestern portion of study area), little variation occurred here, since habitat changes only reflected the succession of existing forest stands.

Trends in the composition of relative habitat states on Crown lands supported trends in habitat indices. Non-critical habitats declined by 20% during forestry simulations, with little difference (–0.4% average difference for natural disturbance-based forestry compared with two-pass forestry) among forestry scenarios (Figure 8-10a). This suggests that both forestry activities were increasing habitat quality. Secondary and primary sink habitats, however, increased by 120.5% to 170.5% during 100-year simulations from current baseline conditions (Figure 8-10b and 8-10c). Although trends for both forestry scenarios proved relative similar, natural disturbance-based forestry averaged 4.7% and 10.6% higher in composition for secondary and primary sink habitats respectively, a consequence of higher road densities. In contrast to increasing sink habitats, primary and secondary habitats declined over time (Figure 8-10d and 8-10e). Secondary habitats declined most rapidly at 43.4% and 50.4% for two-pass and natural disturbance-based forestry respectively, while primary habitats declined by 11.6% (two-pass forestry) and 16.7% (natural disturbance-based forestry). Average differences among scenarios also showed greater differentiation for secondary habitats with a –8.6% difference for natural disturbance-based forestry when compared to two-pass forestry and a –4.2% difference for the same comparison of primary habitats.

4.3. Assessing mortality risk, animal density, and territory status

The grizzly bear territory-status model, contrasting alive (0) versus dead (1) bears based on high risk (e.g., $R_f > 5$) home range proportions and sex was significant overall (LR $\chi^2 = 10.78$, $p = 0.005$, d.f. = 29), fit the data well according to Hosmer and Lemeshow goodness-of-fit χ^2 test ($\hat{C} = 6.14$, $p = 0.631$), and had a significant parameter for the variable risk (Table 8-9). Model accuracy was also good based on receiver operator characteristic (ROC) area under the curve estimates (ROC AUC = 0.853). Specificity and sensitivity curves estimated an optimal cut-off probability of 0.3609, corresponding to a critical threshold value for proportion risk within female territories at 0.263. Using this threshold value, each simulated territory was classified as either effective (<26.3% risk) or non-effective (≥26.3% risk) during each time period and scenario combination.

Potential carrying capacity for adult female animals, estimated from habitat use patterns (Table 8-5), landscape changes, a baseline population estimate, and an assumed ratio of adult females, increased during the 100-year simulation by approximately 10% for both scenarios (Table 8-10; Figure 8-11). This suggests that from a purely habitat perspective, future forestry activities will benefit grizzly bears through increased habitat quality and consequently effecting potential carrying capacities. There were modest differences between forestry scenarios, with natural disturbance-based forestry predicting a slightly higher carrying capacity after 100 years of 33 animals, compared with 32.8 animals for two-pass forestry (Table 8-10). In fact, average percent difference among two-pass and natural disturbance-based forestry was only 0.6%. Our territory allocation model, using habitat-based animal densities on 30-m pixels and summing surrounding pixels until a single territory unit was achieved, resulted in various sized territory polygons reflecting landscape patterns of habitat quality. Small territories were found along the east slopes, particularly in the Whitehorse Wildlands Provincial Park, while larger territories were estimated in the lower foothills to the east. Patterns were reasonable with average model territory size (325-km^2) similar to average 90% kernel home range size (316-km^2). Residual territory units (areas smaller than a single territory) were left remaining, however, when population carrying capacity was larger than a whole interger (Figure 8-12).

Examinations of human-caused mortality risk (proportion of high risk) within individual territories revealed that current baseline conditions supported only 20 effective (secure) territories out of an available 29 potential territories (Table 8-10). Spatially, secure territories were highly correlated with protected parks in the west-southwest region, with a few territories considered to still be secure along park boundaries and the east-southeast study area border (Figure 8-12). Although both two-pass and natural disturbance-based forestry scenarios predicted a 10% increase in density and resulting potential carrying capacities (territories), assessments of risk within territories revealed a loss in effective territories (Table 8-10; Figure 8-11). More specifically, total number of effective territories declined from between –53.9% (two-pass forestry) to –66.7% (natural disturbance-based forestry) from current baseline conditions. Overall, natural disturbance-based forestry averaged 6% lower in total number of effective territories when compared with two-pass forestry. Irrespective of forestry scenario, locations of all projected effective (secure) territories, even by year 30, were all within or adjoining protected parks (Figure 8-12). Temporally, the loss of effective territories within Crown lands to the east of the parks occurred within the first 3 decades (Table 8-10).

5. Discussion

Future scenario modelling predicted similar landscape conditions for two-pass and natural disturbance-based forestry. Differences that were evident included higher road densities and higher clearcut composition for natural disturbance-based forestry compared with two-pass forestry. Road densities increased more than 3-fold, from an initial density of 0.35 km/km^2 to 1.16 and 1.39 km/km^2 for two-pass and natural disturbance-based forestry respectively. Ecologically, this represented 3 times the suggested threshold (maximum) road density (0.40–0.42 km/km^2) for maintaining grizzly bear security (Mattson, 1993; Craighead et al., 1995). Although total volume of timber resources harvested each period was by default defined to be the same, we found a greater harvest footprint in natural disturbance-based forestry. As a result of the larger footprint, a more extensive network of roads was required, hence the higher road densities observed. We suspect that greater clearcut composition in natural disturbance-based forestry was caused by spatial variation in timber composition and age (e.g., yield) at scales smaller than the average clearcut size in natural disturbance-based forestry. Large clearcuts in natural disturbance-based forestry required harvesting some areas that were less than optimal in yield, while two-pass forestry 'searched' for harvest units that were more optimal per unit area (e.g., lower within cutblock variation). Additional calibration of the PATCHWORKS model is needed to consider the temporary nature of in-block roads. This could ultimately cause decreases in road densities for natural disturbance-based forestry. Regardless of potential model inaccuracies, trends in road patterns and densities were consistent to even conservative compared with that of other forested landscapes with a history forest harvesting (Reed et al., 1996; Tinker et al., 1998). For instance, Reed et al. (1996) found 43 years of forest harvesting in a mountainous landscape of southern Wyoming resulted in an average road density of 2.52 km/km^2, about twice that of our prediction 100 years into the future. As we did not consider exploratory seismic lines as human-access features, however, total access density may have been under-estimated in the near term, but unlikely to be a factor in the future as most petroleum exploration is moving towards hand-cut, low-impact operations that are difficult if not impossible to use with motorized off-road vehicles.

When applying future scenario results to grizzly bear habitat indices, we found that grizzly bear habitat conditions degraded continually over the 100-year period, regardless of forest scenario. The attractive sink index, which highlighted high-quality habitats in risky environments (e.g., those areas in need of mitigation/restoration), increased considerably over the 100-year period, while the safe-harbor index, which highlighted high-quality habitats secure from human-caused mortality risk (e.g., those areas in need of protection), declined substantially. Because natural disturbance-based forestry had higher associated road densities, attractive sink values were slightly higher and safe-harbor values slightly lower than that of two-pass forestry. Examinations of relative habitat states revealed similar trends among forestry scenarios, although a 20% decline in non-critical habitats over the 100-year period suggested that forestry activities resulted in increases in habitat quality. This increase in potential habitat quality with on-going forestry is consistent with that of a habitat generalist and a disturbance-evolved species (Bengtsson et al., 2000), such as grizzly bears. Higher risk of human-caused mortality, however, far outweighed any gains in habitat quality, as primary and secondary habitats declined precipitously and primary and secondary sinks increased at even sharper rates. If habitat balancing of primary and secondary habitats was used as a standard for future management, as suggested by Nielsen (2005), significant restoration or modification of forestry practices would be required to maintain current grizzly bear habitat conditions.

Habitat-based adult female animal densities, potential territory number (carrying capacity), and territory status revealed similar trends to that of habitat indices and relative habitat states. Although potential territory number increased by 10% over the 100-year simulation, the number of effective (secure) territories declined by more than 50%. Remaining effective territories were all within or adjacent to protected mountainous parks. As most of the decline in effective territory number occurred within the first 3 decades, we suggest a rapid decline in effective (i.e., ability to survive, reproduce, and disperse young) adult female grizzly bears in the foothills of west-central Alberta, regardless of forest-management scenario. As results for habitat indices, relative habitat states, and effective territory conditions were similar among forestry scenarios, we do not see the utility of promoting natural disturbance-based forestry as a potential conservation strategy for grizzly bears. Given current attitudes towards grizzly bears and an open road policy, a co-existence between forestry and grizzly bears does not look promising. Undoubtably, it appears that Jasper National Park and Whitehorse Wildlands Provincial Park will provide source habitats for grizzly bear populations, with the foothills acting as sink habitats for any dispersing young animals. Reversing these trends in the foothills will require both an education programme for the public and hunters to reduce bear-human conflicts (Schirokauer and Boyd, 1998) and an aggressive road-management programme (gating, deactiviation, etc.). Removal of unnecessary roads should be considered (Switalski et al., 2004).

Although numerous population viability assessments for grizzly bears have been performed (Doak, 1995; Boyce et al., 2001; Weilgus, 2002; McLoughlin et al., 2003; Carroll et al., 2004; Johnson et al., in press), ours is the first assessment of grizzly bears for west-central Alberta. Furthermore, our approach largely differs from previous assessments as we rely solely on empirical habitat relationships, specifically habitat affinities (e.g., resource selection), animal densities, mortality risk, and territory status, rather than habitat-based demographic rates, such as that used in ALEX (Possingham and Davies, 1995), PATCH (Schumaker, 1998), or RAMAS GIS (Akçakaya, 1998) software. As Boyce (2002) points out, measuring habitat-specific demographic rates is a difficult and time-consuming process, something that is truly exceptional, especially for a long-lived species with low fecundity like grizzly bears. Even in Yellowstone where counts of grizzly bears have occurred since 1959 (Craighead et al., 1995), reasonably accurate predictions of extinction risk could currently only be estimated 9 years into the future (Fiebert and Ellner, 2000; Morris and Doak, 2002). Obviously, populations at dire risk of decline and therefore in need of conservation action cannot wait for a long period of demographic data collection. Waiting that long would be requisite to simply documenting the decline, rather than providing conservation suggestions, especially in the presence of obvious habitat degredation and population decline. Therefore, approaches that use existing knowledge of habitat ecology or assessments of probability of occurrence or abundance are needed (Boyce, 2002). Indeed, habitat ecology as a basis of a PVA, as opposed to demography, has shown to be a useful process (Foin and

Brenchley-Jackson, 1991) and even in more traditional demographic-based PVAs, habitat has emerged as the single most influential parameter for long-term population viability (Boyce et al., 1994). This suggests that there is no replacement to a detailed understanding of the habitat ecology of a species.

Our PVA approach further differs from previous PVA methods, in that habitat quality directly influenced territory size and hence carrying capacity. Most PVA models instead, assume territory size to be constant, regardless of habitat quality. For instance, PATCH (Schumaker, 1998) uses constant-sized hexagon territories to assess suitable territories. This is questionable for many species including grizzly bears, as the literature suggests that animal densities and home range size change as a function of habitat quality (McLoughlin and Ferguson, 2000; McLoughlin et al., 2000; Dahle and Swenson, 2003). Our approach to territory allocation used estimated habitat-based animal densities within pixels (30×30m) to define territory size (approximating 90% kernel home ranges) and placement. Thus, areas with higher habitat quality had higher densities of animals (smaller territories), while areas of poorer habitat quality resulted in lower animal densities (larger territories). However, our method of territory allocation was not without its limitations. Given the complexity of arranging different sized territories within a GIS, we were not able to use hexagons, the more biologically reasonable shape for animal territories. Instead, we used rectangular territory units, which aligned with one another much easier, and despite its generalized shape unlikely altered overall patterns population risk observed.

Finally, we consider our habitat-based PVA to be readily transparent compared with other software approaches that yield "black box" solutions. Our approach simplified the PVA process for grizzly bears down to two critical habitat dimensions (Naves et al., 2003), habitat occupancy and mortality risk, data which are frequently available for many grizzly bear populations. Using the occupancy model and a population estimate, we varied adult female animal densities among habitats, tracking those changes based on projected future landscape change (e.g., Boyce and McDonald, 1999). As we assumed grizzly bears occupied defined territories that varied as a function of habitat quality, our territory allocation model defined individual territory units allowing for assessements of mortality risk. Although these methods are straightforward, such approaches to assessing population risk assume that changes in habitat availability will not alter habitat selection, something that clearly cannot be assumed (Mysterud and Ims, 1998; Mysterud et al., 1999). Regardless, all PVA approaches that use habitat quality as the basis for distributing animals or vital rates assume that relationships will not change as a function of changing habitat availability. Examinations of functional responses in habitat use may therefore be required to assure consistency or introduce further model complexity.

6. Conclusion

Based on scenario models, grizzly bear populations in the foothills of west-central Alberta should be considered threatened. Neither two-pass forestry, nor natural disturbance-based forestry (on Crown lands) resulted in the persistence of effective adult female grizzly bear territories or necessary habitat conditions within the foothills during a 100-year simulation. Despite predicted gains in habitat quality and potential carrying capacity, road development (>3-fold increase) overwhelmed gains in habitat quality by increasing risk of human-caused mortality beyond that which we predict can be sustainable. Simulations suggest that only the large mountainous parks provided long-term suitable adult female grizzly bear territories, while effective (secure) grizzly bear territories on Crown lands were largely displaced within 30 years. Methods outlined in this paper, can be used for other species where a 2-dimensional habitat model well describes population conditions. In the presence of a population estimate, we suggest an approach that assesses population viability through calculation of habitat-based animal densities, potential territories, mortality risk, and ultimately territory status. When one lacks a population estimate, however, habitat indices and relative habitat states still provide useful information on local site (habitat) conditions. Finally, we suggest that our territory allocation and status model can be used for reserve design and/or restoration planning through examinations of spatial clustering of effective territories or by targeting non-effective territories in need of restoration.

Table 8-1. Summary of grizzly bear study area landbase used for future scenario modelling.

Landbase	Landcover class	Area (ha) FMA	Non-FMA	Total
Non-operable				
	Alpine/subalpine	169	37,310	37,479
	Herbaceous<1800m	1,902	3,618	5,520
	Shrub<1800m	3,318	1,568	4,886
	Wet open	61,162	4,035	65,197
	Wet treed	49,036	4,511	53,547
	Rock	4,081	104,304	108,385
	Snow	9	45,430	45,439
	Shadow	2	3,992	3,994
	Water	6,073	4,388	10,461
	Road/Rail line	20,250	3,190	23,440
	Pipeline	4,607	525	5,132
	Well site	63	0	63
	Urban	0	215	215
	Burn 0-3 years	850	0	850
	TOTAL	151,522	213,086	364,608
Potentially operable				
	Closed conifer	301,739	111,918	413,657
	Closed deciduous	23,601	5,355	28,956
	Mixed forest	59,349	8,270	67,619
	Open conifer	4,645	19,161	23,806
	Open deciduous	155	18	173
	Unknown strata	75,797	327	76,124
	TOTAL	465,286	145,049	610,335
	GRAND TOTAL	616,808	358,135	974,943

Table 8-2. Cost, ignoring inflation, of hauling, maintaining, and building existing and potential roads in the foothills of west-central Alberta.

Road type	Road class or location	Haul ($\$/m^3/km$)	Maintenance ($/km)	Building ($/km)
Existing roads				
	1	0.03	1,000	0
	1a	0.15	1,000	0
	2	0.04	1,000	0
	2a	0.20	1,500	0
	3	0.07	1,000	0
Potential roads				
	general	0.07	1,000	21,000
	slope > 30	0.09	1,000	42,000
	slope > 45	2.00	1,000	84,000

Table 8-3. Summary of objectives and constraints used to simulate two-pass or natural disturbance-based logging in Patchworks.

Scenario	Objectives and constraints
Two-pass logging	
	• Maximize total harvest volume
	• Even-flow total harvest volume
	• Maintain a minimum coniferous and deciduous primary growing stock
	• Congregate harvest activities into operational compartments
	• Encourage block sizes between 5 and 100 ha
	• Use compartment sequences from company plans
Natural disturbance-based logging	
	• Maximize total harvest volume
	• Even-flow total harvest volume
	• Maintain a minimum coniferous and deciduous primary growing stock
	• Congregate harvest activities into operational compartments
	• Encourage block sizes over 250 ha
	• No compartment sequence

Table 8-4. Remote sensing and GIS environmental predictor variables used for modelling the relative probability of occurrence for adult female grizzly bears during late hyperphagia in west-central Alberta, Canada.

Model variable	Code	Linear or Non-linear	Units/Scale	Data range / Area (km^2)
Land cover:				
alpine/herbaceous	alpine	category	n.a.	0 or 1 / (439)
anthropogenic	anthro	category	n.a.	0 or 1 / (381)
closed conifer	clscon	category	n.a.	0 or 1 / (3715)
deciduous forest	decid	category	n.a.	0 or 1 / (349)
mixed forest	mixed	category	n.a.	0 or 1 / (746)
non-vegetated	nonveg	category	n.a.	0 or 1 / (1689)
open-bog/shrub	opnbog	category	n.a.	0 or 1 / (810)
open conifer	opncon	category	n.a.	0 or 1 / (280)
regenerating forest	regen	category	n.a.	0 or 1 / (759)
treed-bog	treedbg	category	n.a.	0 or 1 / (585)
edge distance	edge	linear	100 m	0 - 35
compound topographic index	cti	non-linear	unitless	1.89 - 31.7
terrain ruggedness index	tri	non-linear	unitless	0 - 0.29
forest age	for-age	non-linear	10-yr age class	1 - 15
regenerating clearcut age	cut-age	non-linear	10-yr age class	1 - 5
solar radiation × alpine	solar×alpine	linear	kJ/m^2	17,133 - 91,836
solar radiation × clscon	solar×clscon	linear	kJ/m^2	21,698 - 91,835
solar radiation × regen	solar×regen	linear	kJ/m^2	57,110 - 91,831
cti × age class	cti×age	linear	unitless	0 - 402
cti × edge distance	cti×edge	linear	unitless	0 - 522

Table 8-5. Estimated habitat selection coefficients for adult female grizzly bears in west-central Alberta, Canada based estimates from Nielsen (2004). Robust standard errors and significance levels (*p*) were estimated from modified sandwich estimates of variance among animals with categorical contrasts from deviance coding.

Environmental covariate	Coefficient	Standard Error	*p*
alpine/herbaceous	0.218	0.941	0.817
anthropogenic	-0.114	0.344	0.740
closed conifer forest	2.530	0.703	<0.001
deciduous forest	1.366	0.309	<0.001
mixed forest	0.778	0.553	0.159
non-vegetated	0.510	0.445	0.252
open-bog/shrub	0.322	0.502	0.522
open conifer forest	1.909	0.348	<0.001
regenerating forest	-8.865	2.856	0.002
treed-bog	1.346	0.377	<0.001
edge distance	-0.302	0.061	<0.001
cti	0.107	0.049	0.029
†cti^2	-0.294	0.195	0.130
tri	34.009	7.564	<0.001
tri^2	-147.07	31.84	<0.001
for-age	-0.219	0.058	<0.001
†for-age^2	0.766	0.364	0.036
cut-age	-0.262	0.390	0.545
cut-age^2	0.097	0.075	0.197
§solar × clscon	-0.207	0.093	0.026
§solar × regen	0.934	0.355	0.009
§solar × alpine	0.166	0.123	0.180
†cti × age class	0.633	0.126	<0.001
cti × edge	0.017	0.005	<0.001

†estimated coefficients and standard errors reported at 100 times their actual value
§estimated coefficients and standard errors reported at 10,000 times their actual value

Table 8-6. Demographic sex-age class ratios used to characterize a population of grizzly bears (Craighead et al. 1995).

Sex-age class	% of population
cub (new born)	18.4
yearlings (1 yr old)	13.0
sub-adults (2–4 yrs old)	24.9
adult female (>4 yrs old)	23.5
adult male (>4 yrs old)	20.2
TOTAL	100

Table 8-7. Percent composition for each of the 10-land cover classes by decade for two-pass (TP) and natural disturbance-based (ND) forestry scenarios modeled in Patchworks.

Land cover	Baseline		10-yrs		20-yrs		30-yrs		40-yrs		50-yrs		60-yrs		70-yrs		80-yrs		90-yrs		100-yrs	
class	TP	ND	TP	ND	TP	ND	TP	ND	TP	ND	TP	ND	TP	ND	TP	ND	TP	ND	TP	ND	TP	ND
alpine/herbaceous	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1
anthropogenic	4.3	4.3	5.0	5.3	5.5	5.9	5.9	6.3	6.1	6.6	6.3	6.8	6.4	7.0	6.6	7.3	6.8	7.5	6.9	7.7	7.0	7.8
closed conifer	47.5	47.5	44.8	43.6	43.1	40.9	42.8	40.0	42.3	38.8	41.1	36.8	41.6	37.4	42.2	37.6	42.6	37.3	42.3	36.9	41.6	36.2
deciduous forest	3.7	3.7	3.6	3.6	3.5	3.3	3.6	3.2	3.6	3.2	3.6	3.1	3.5	3.0	3.5	3.0	3.3	3.1	3.3	3.1	3.2	3.0
mixed forest	8.7	8.7	8.3	8.1	8.0	7.5	7.9	7.0	7.9	6.7	7.6	6.2	7.6	6.1	7.3	5.9	7.3	5.9	7.0	5.7	7.0	5.7
non-vegetated	4.7	4.7	4.7	4.7	4.7	4.7	4.7	4.7	4.7	4.7	4.7	4.7	4.7	4.7	4.7	4.7	4.7	4.7	4.7	4.7	4.7	4.7
open-bog/shrub	9.5	9.5	9.4	9.4	9.3	9.3	9.3	9.3	9.3	9.2	9.2	9.2	9.2	9.2	9.2	9.2	9.2	9.1	9.1	9.1	9.1	9.1
open conifer	1.9	1.9	1.9	1.9	1.9	1.8	1.9	1.8	1.9	1.8	1.9	1.7	1.8	1.7	1.8	1.7	1.8	1.7	1.8	1.7	1.8	1.7
regenerating forest§	10.5	10.5	13.0	14.4	14.9	17.4	14.9	18.6	15.2	20.0	16.6	22.4	16.1	21.9	15.7	21.6	15.3	21.7	15.9	22.2	16.6	22.9
treed-bog	7.1	7.1	7.0	7.0	7.0	7.0	6.9	6.9	6.9	6.9	6.9	6.9	6.9	6.9	6.9	6.9	6.8	6.8	6.8	6.8	6.8	6.8

§: Regenerating forests were 'rolled' back into prior land cover forest classes at 60-years of age.

Table 8-8. Percent composition for each of 5 relative habitat states during baseline (current conditions), 50-year, and 100-year projections for two-pass (TP) and natural disturbance-based (ND) forestry scenarios modeled in Patchworks.

	Baseline	50-years		100-years	
Relative habitat state	TP/ND	TP	ND	TP	ND
Non-critical	43.5	35.7	36.1	34.6	34.4
Secondary sink	9.8	19.0	19.2	21.5	22.6
Primary sink	6.5	13.2	14.4	16.0	17.5
Secondary habitat	24.1	17.1	15.8	13.7	12.0
Primary habitat	16.1	15.1	14.5	14.3	13.5

Table 8-9. Parameters of the logistic regression model predicting the probability of a grizzly bear territory (90% kernel home range) as being classified as unsustainable based on the current status (dead = 1 or alive = 0) of radiotelemetry bears, proportion risk within a territory (risk) and the sex of the animal (male = 1, female = 0).

				95% Confidence Interval	
Variable	Coef.	S.E.	*p*	lower	upper
risk	7.984	3.473	0.022	1.177	14.791
male	1.714	0.936	0.067	-0.120	3.547
constant	-2.671	0.933	0.004	-4.499	-0.842

Table 8-10. Habitat-based adult female potential carrying capacity (*K*) based on projected landscape changes, a habitat use model, and base-line population densities. The number of contiguous simulated adult female territories using a territory allocation model in a GIS to assess territory status (effective or non-effective territory) is indicated in parentheses. Number and percent (in paratheses) of effective territories based on assessements of mortality risk within simulated territory units.

		Adult female carrying capacity		Number (%) of effective territories	
Year	Period	Two-pass	Natural disturbance	Two-pass	Natural disturbance
2004	0	29.8 (29)	29.8 (29)	20 (69.0%)	20 (69.0%)
2014	1	30.4 (30)	30.6 (30)	17 (56.7%)	16 (53.3%)
2024	2	31.2 (31)	31.3 (31)	16 (51.%)	14 (45.2%)
2034	3	31.5 (31)	31.5 (31)	15 (48.4%)	15 (48.4%)
2044	4	31.6 (31)	31.7 (31)	14 (45.2%)	13 (41.9%)
2054	5	32.2 (32)	32.4 (32)	13 (40.6%)	12 (37.5%)
2064	6	32.3 (32)	32.6 (32)	15 (46.9%)	12 (37.5%)
2074	7	32.5 (32)	32.8 (32)	13 (40.6%)	13 (40.6%)
2084	8	32.6 (32)	32.9 (32)	14 (43.8%)	13 (40.6%)
2094	9	32.7 (32)	32.9 (32)	13 (40.6%)	12 (37.5%)
2104	10	32.8 (32)	33.0 (33)	13 (40.6%)	14 (42.4%)

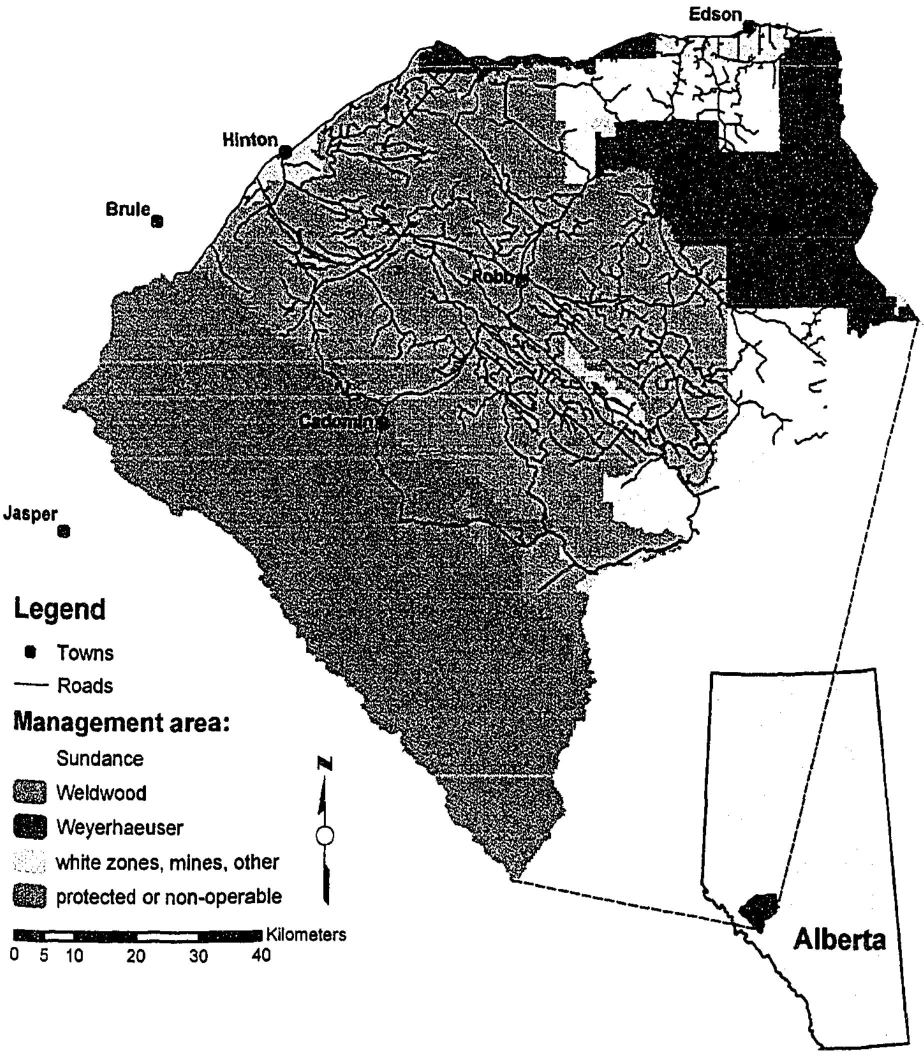

Figure 8-1. Study area map depicting towns, roads, management stakeholders or region.

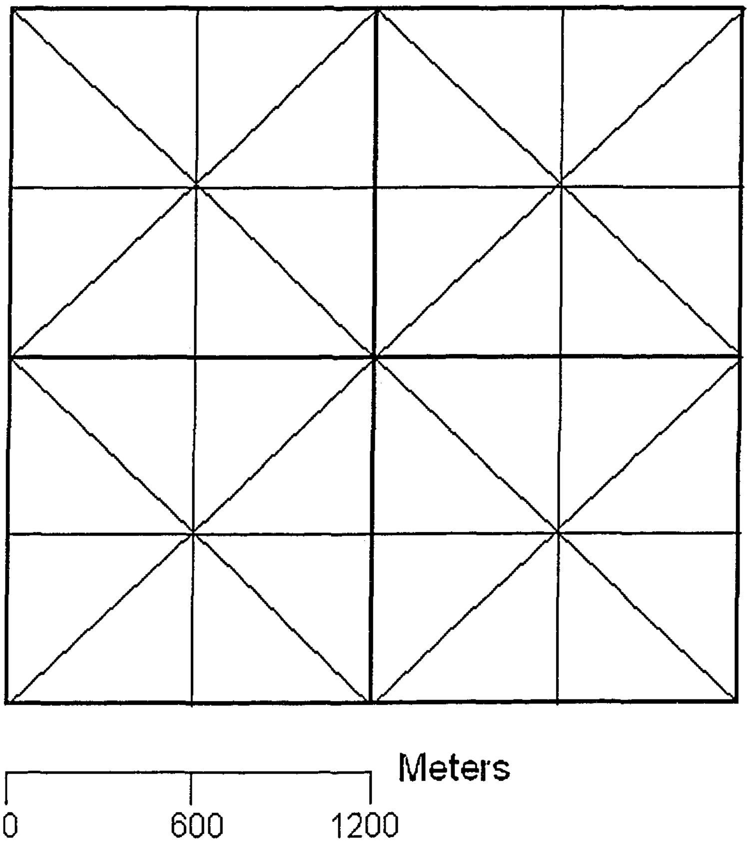

Figure 8-2. Schematic representation of potential road arcs used to describe new road features on a 600-meter grid with ordinal and inter-ordinal directions of movement within each grid cell.

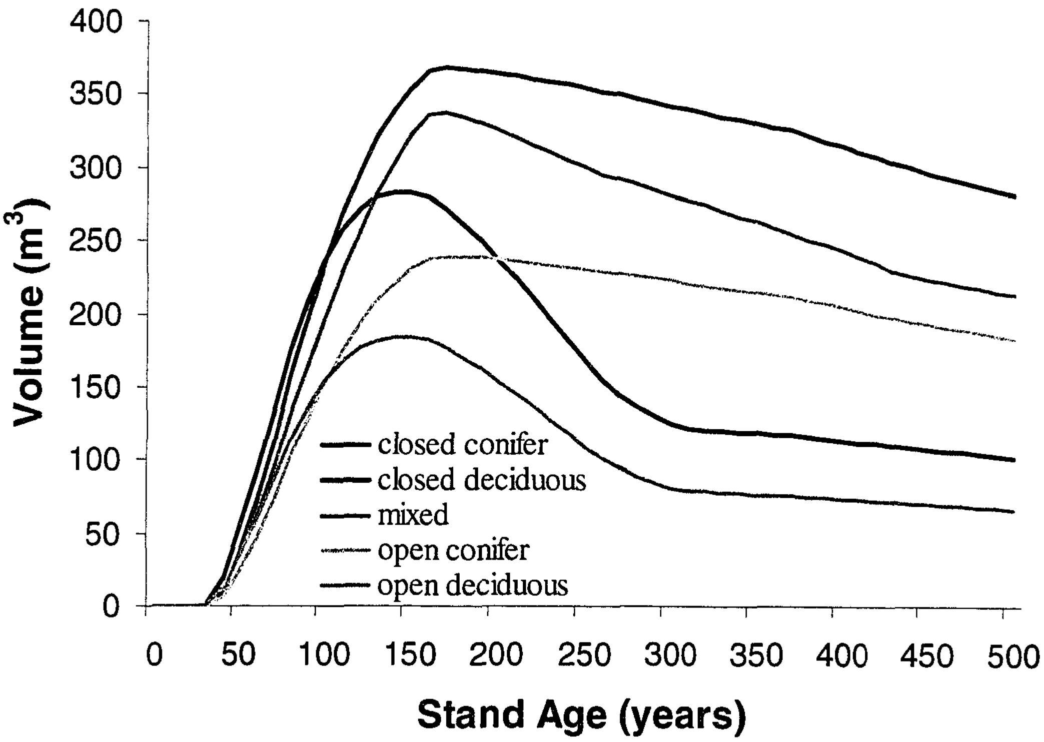

Figure 8-3. Growth-yield curves by forest class used for modelling forest succession in west-central Alberta, Canada using the forestry model WOODSTOCK.

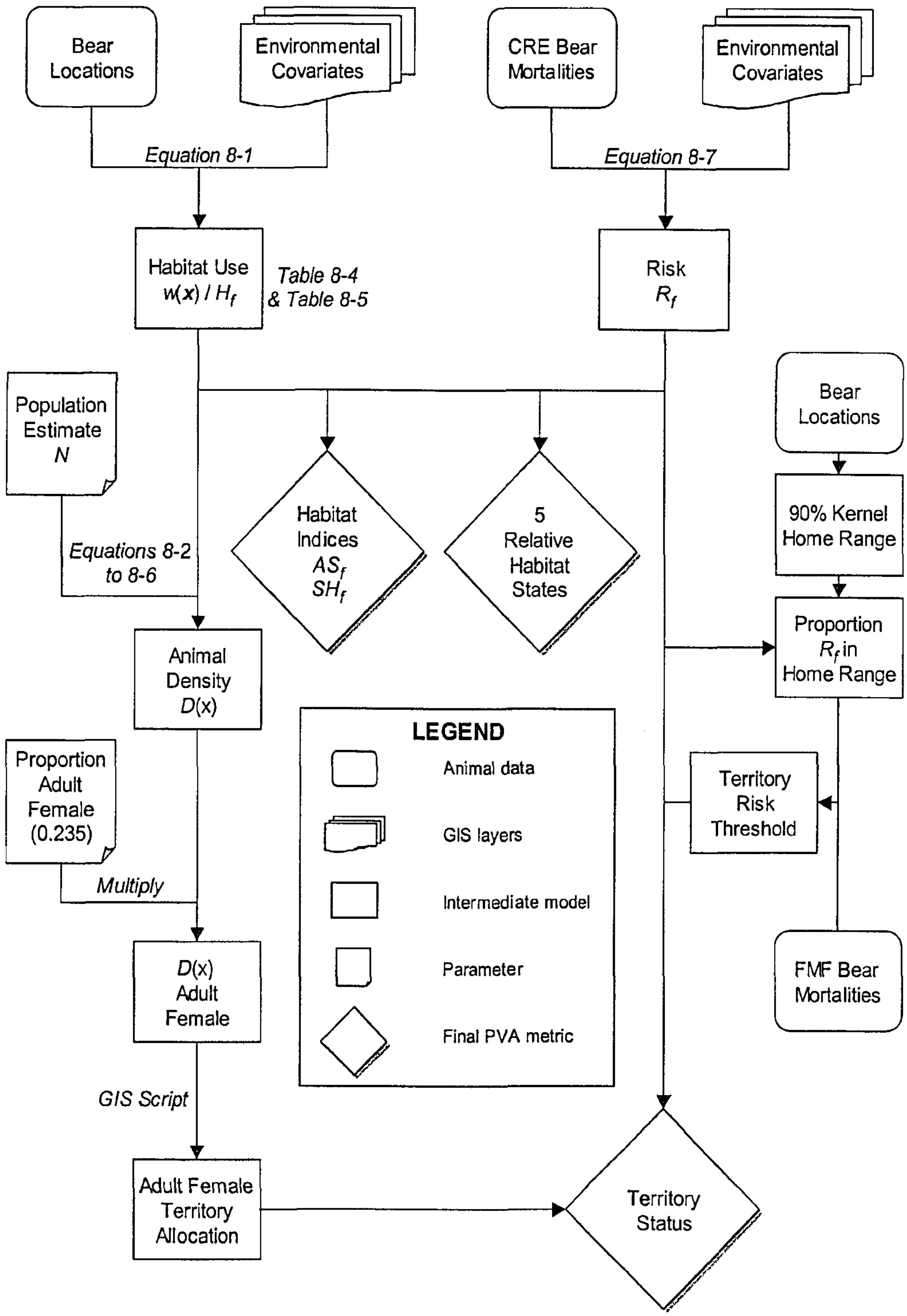

Figure 8-4. Cartographic model depicting population viability modelling for grizzly bears in west-central Alberta, Canada. The process was repeated for each scenario and time period combination.

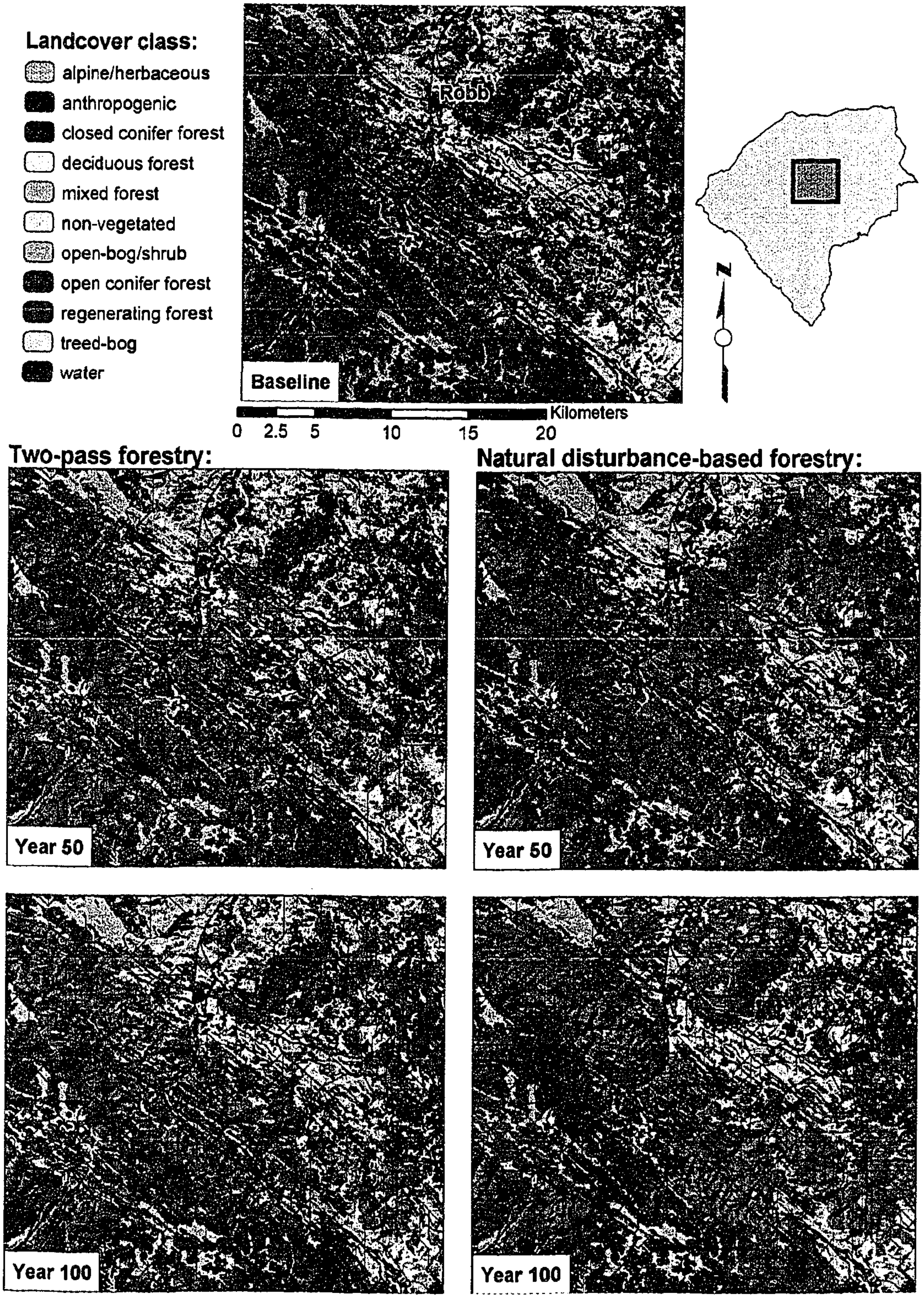

Figure 8-5. Baseline (current) and future (50 and 100 years) landscapes projected from the forestry model PATCHWORKS, depicting two-pass and natural disturbance-based forestry patterns.

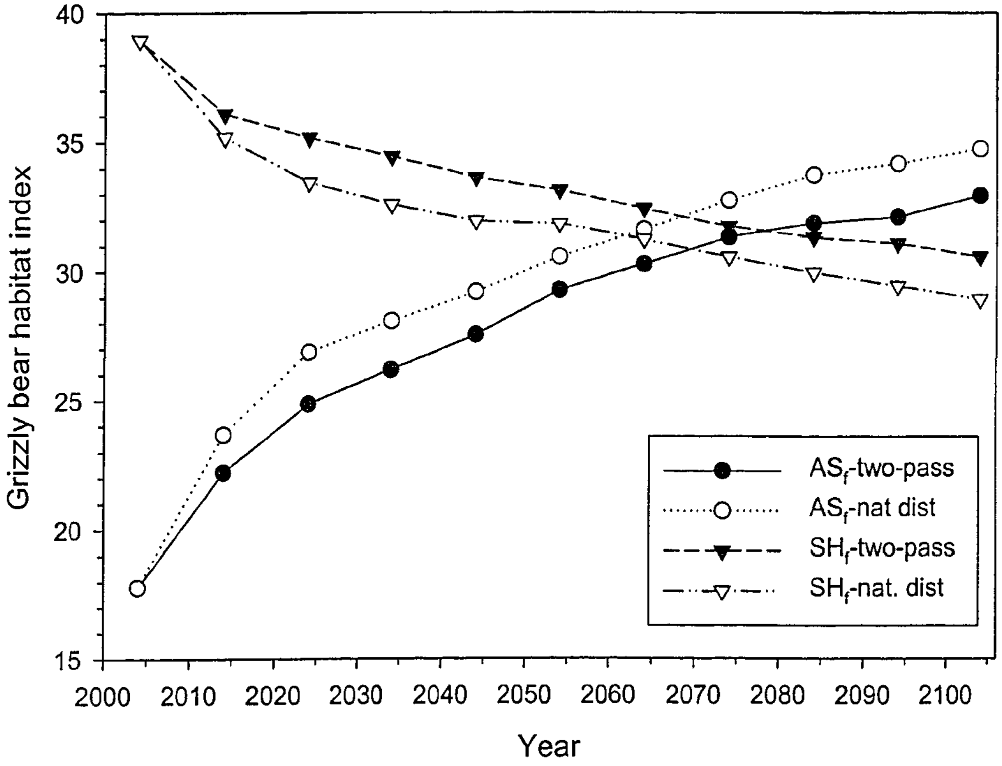

Figure 8-6. Mean operable (Crown lands) landscape values of attractive sink (*ASf*) and safe harbor (*SHf*) indices at 10-year intervals from 2004 (current) to 2104 (100-years).

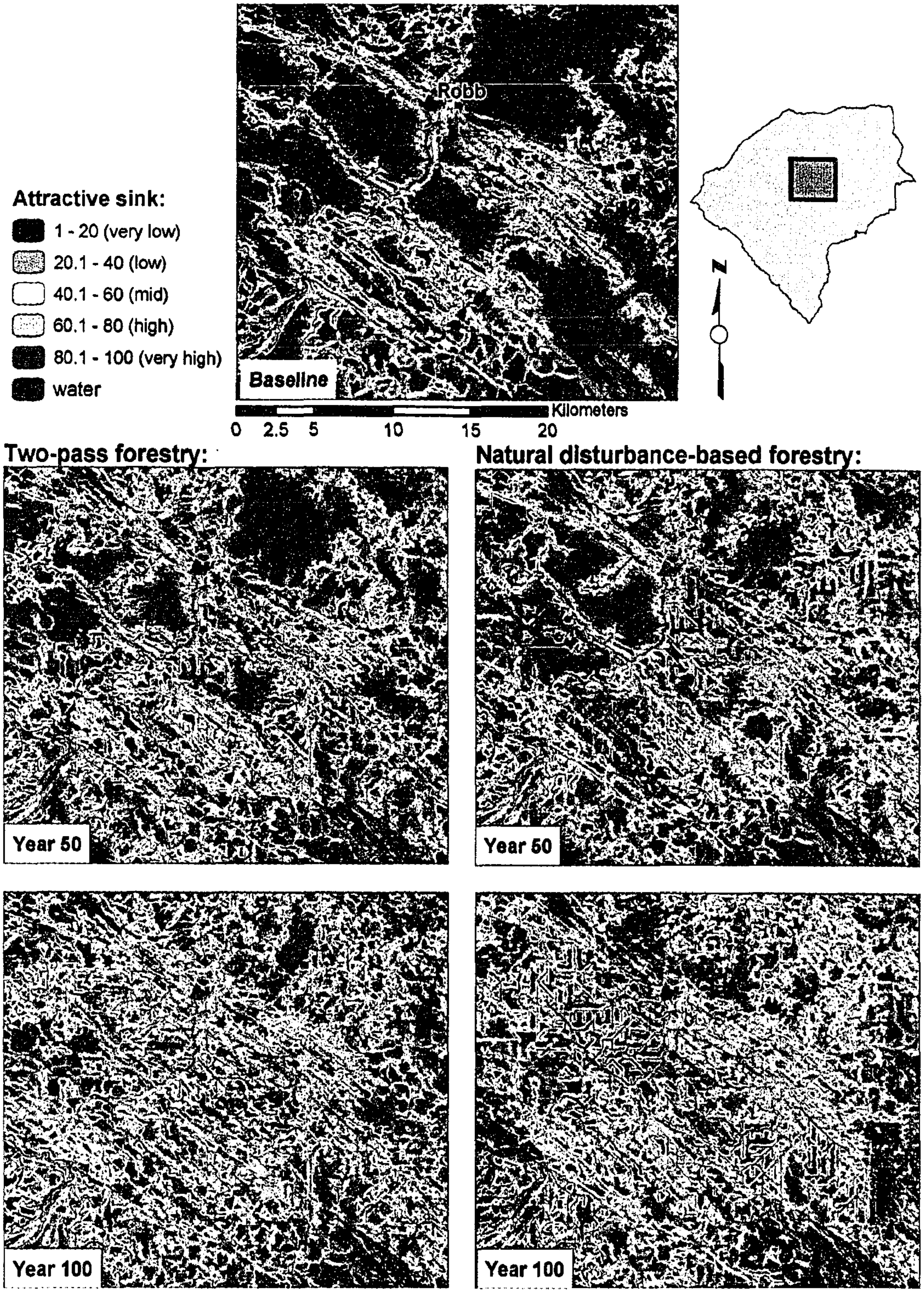

Figure 8-7. Baseline (current) and projected (50 and 100 years) attractive sink index based on PATCHWORKS outputs, the habitat occupancy model (H_f), and risk model (R_f) for two-pass and natural disturbance-based forestry scenarios.

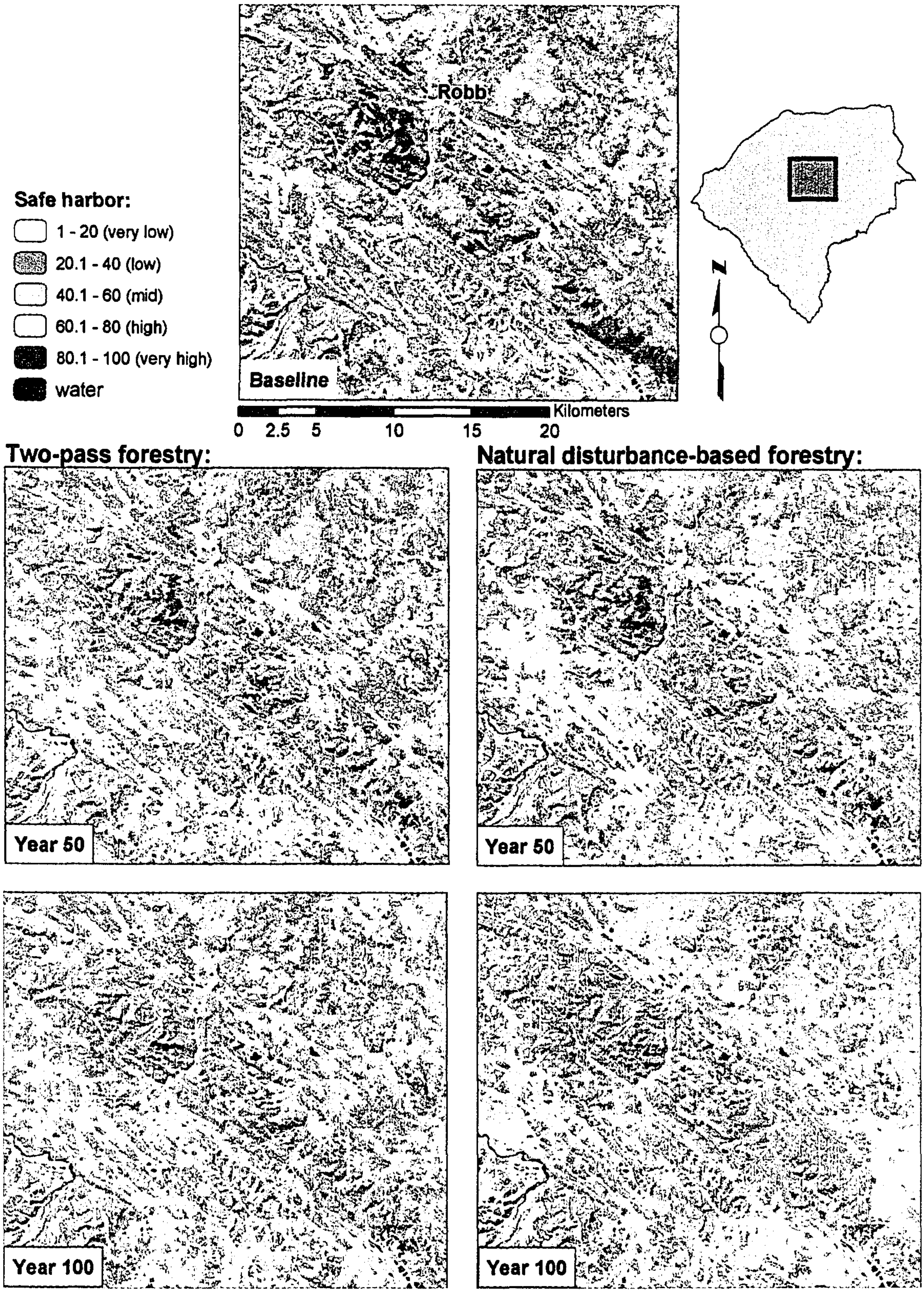

Figure 8-8. Baseline (current) and projected (50 and 100 years) safe harbor index based on PATCHWORKS outputs, the habitat occupancy model (H_f), and risk model (R_f) for two-pass and natural disturbance-based forestry scenarios.

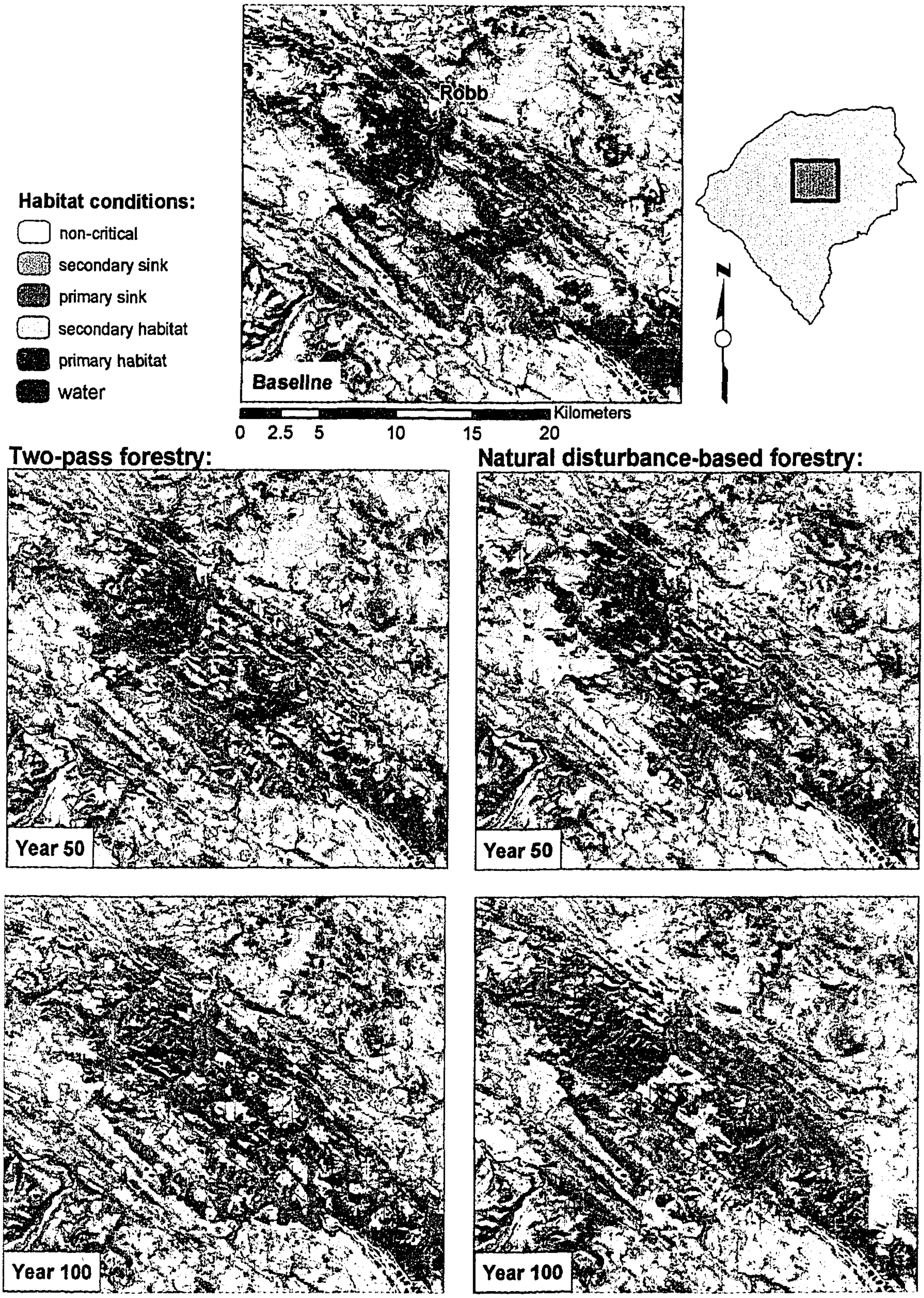

Figure 8-9. Baseline (current) and projected (50 and 100 years) relative habitat states based on PATCHWORKS outputs and a classification of the habitat occupancy (H_f) and the risk (R_f) models for two-pass and natural disturbance-based forestry scenarios.

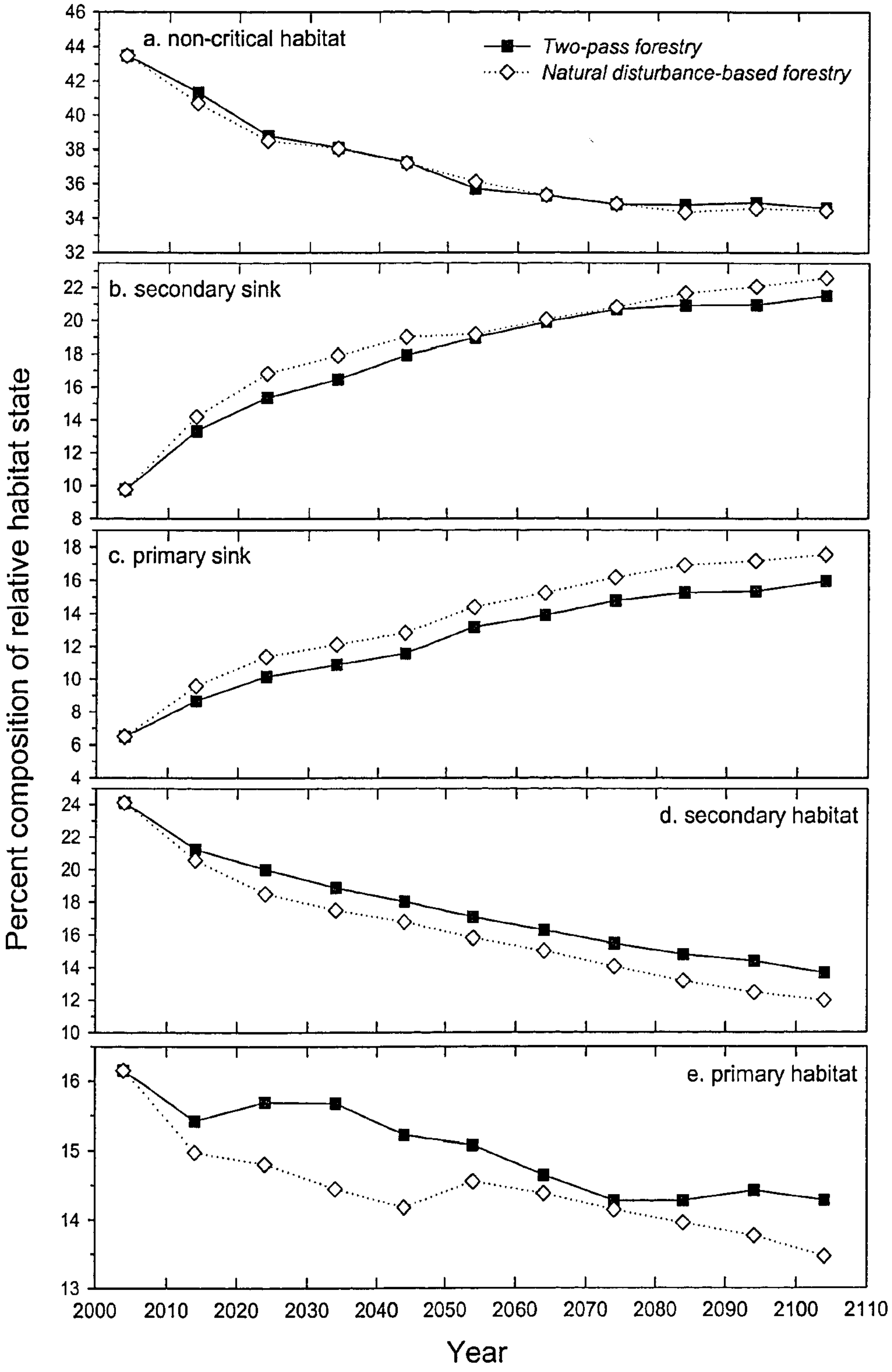

Figure 8-10. Trends (100-year period) in the composition of 5 relative habitat states on Crown lands for two scenarios (two-pass and natural disturbance-based forestry).

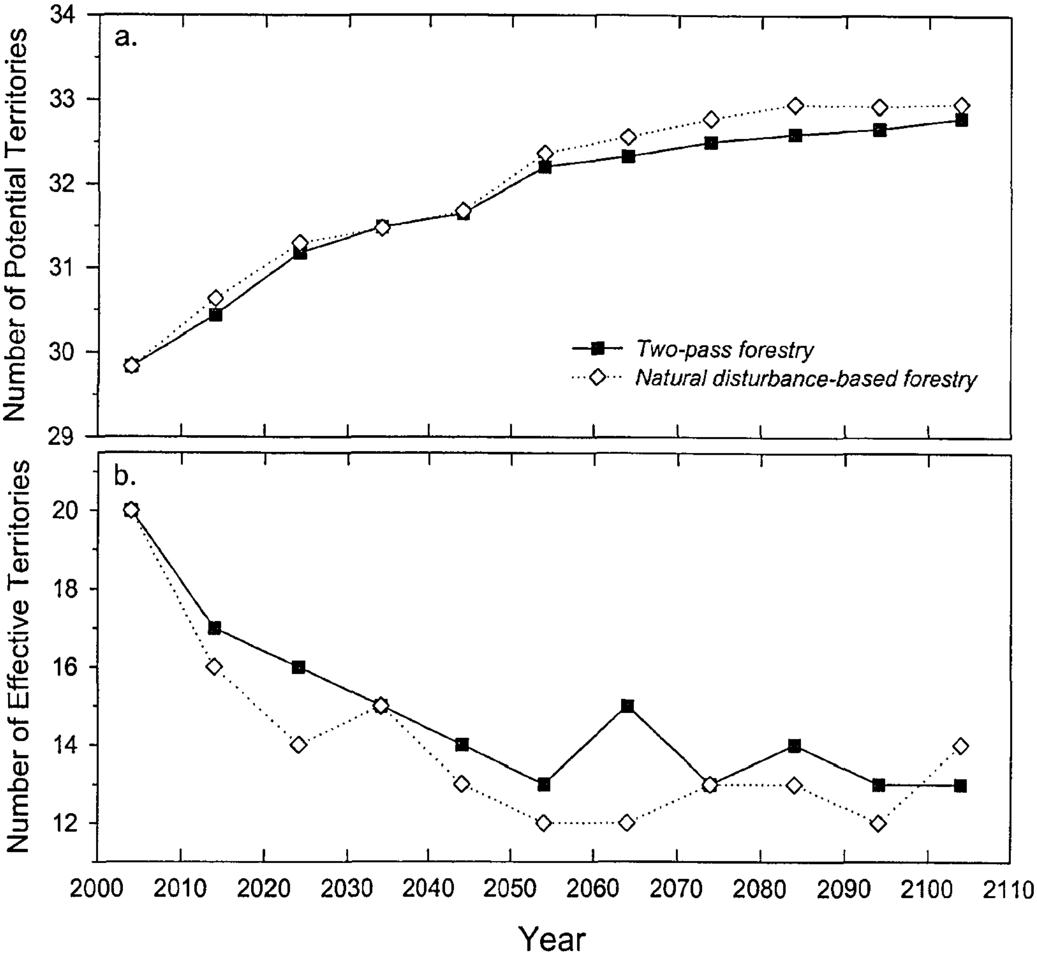

Figure 8-11. Estimated number of potential adult female territories (a.) and the number of effective (low risk of mortality) territories (b.) by decade for a 100-year simulation of two-pass and natural disturbance-based forestry.

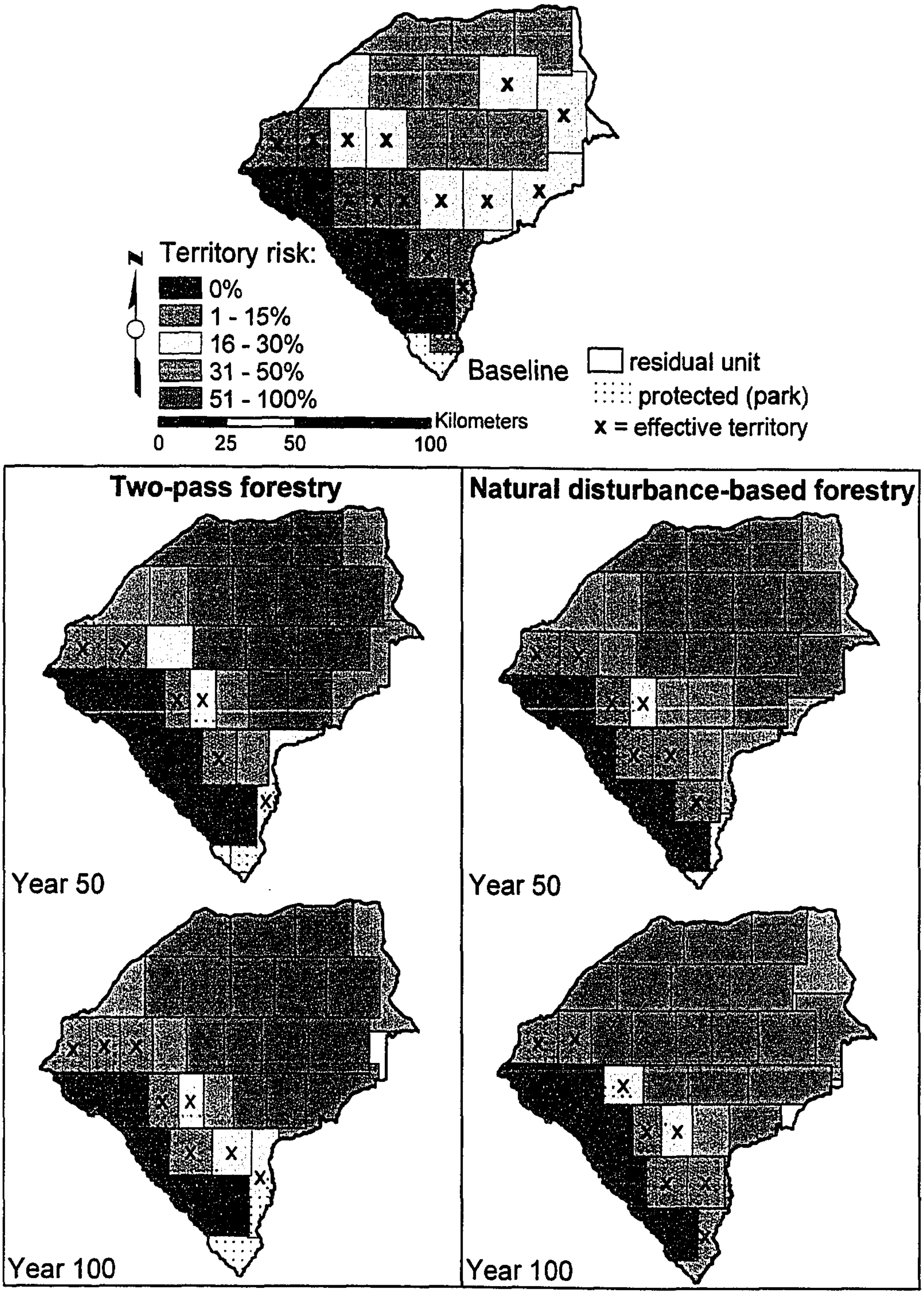

Figure 8-12. Territory risk (% of territory in high-risk condition) and status (x- effective [secure] territory; non-symbolized territories are considered non-effective) by year (baseline-current condition, year 50 and year 100) and forestry scenario (two-pass and natural disturbance-based forestry). Un-allocated regions of space too small to contain an individual territory are referred to as residual units. Major protected areas (Jasper National Park and Whitehorse Wildlands Provincial Park) are indicated by stippling.

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Chapter 9

Conclusion: Revisiting Leopold's 'Pig in the Parlor' 80 years later

In 1925, Aldo Leopold wrote a short note regarding the problem of extensive road building in wilderness areas to his colleagues at the U.S. Forest Service, which he entitled 'The Pig in the Parlor' (Flander and Callicott, 1991). Leopold wrote, "Roads and wilderness are merely a case of the pig in the parlor. We now recognize that the pig is all right—for bacon, which we all eat. But there no doubt was a time, soon after the discovery that many pigs meant much bacon, when our ancestors assumed that because the pig was so useful an institution he should be welcomed at all times and places. And I suppose that the first "enthusiast" who raised the question of limiting his distribution was construed to be uneconomic, visionary, and anti-pig." Conservation of grizzly bears and other large carnivores for that matter largely reflects the 'pig in the parlor' problem. Many conservationists have questioned the widescale fragmentation of our wildlands by roads, as science has documented the degredation that it causes to many ecosystem traits, often leading to population decline for sensitive species, such as grizzly bears. Yet, science has been largely ineffective in persuading landowners, managers, and the public of the importance roads and associated activities play in constraining the long-term conservation of species and ecosystems.

For this thesis, I examined the habitat ecology of grizzly bears in west-central Alberta. Undoubtably, I think the overriding conclusion of this work supports Leopold's root argument that roads threaten the health of the land, in our case grizzly bears (through increased risk of human-caused mortality). Because the foothills of the Rocky Mountains of Alberta are being developed at unprecedented rates (for coal, timber, and petroleum), it is unlikely that such development can co-exist with the current complement of species. Some will undoubtably decline or even disappear, while others will increase, and still others appear anew from elsewhere (perhaps exotics). Evidence strongly suggests that grizzly bears will be on the declining to disappearing end of this spectrum. In fact, recent population estimates place only 500 animals on Provincial lands (Stenhouse et al., 2003), much fewer that previously thought (Kansas, 2002). The logical question therefore becomes, how do we prevent grizzly bear populations from further decline? From a biological point of view, we know fairly well what needs to be done. On the proximate end, we need to substantially reduce mortality, specifically below 6% (Stenhouse et al., 2003). In the short term for Alberta, this will require that the limited-entry hunt be closed and that we work to prevent the development of 'problem' animals that often are re-located and effectively removed from the population. A total of 45 grizzly bear mortalities (18 from the limited entry spring bear hunt) were documented in 2003. Such high rates of mortality are unlikely to be sustainable in the long-term (Stenhouse et al., 2003). Of course the ultimate solution for grizzly bear conservation will be the recognition that habitat fragmentation through road development associated with resource extraction threatens the long-term viability of grizzly bear populations. Although grizzly bears prefer early-successional habitats often associated with human activities like forestry, many of these sites result in the formation of attractive sinks, where the animals lack the cues necessary to distinguish the substantial risk of occupying those sites (Delibes et al., 2001). Human attitudes towards grizzly bears in Alberta, which currently reflect pioneering attitudes, also will require substantial change and only education programmes (Schirokauer and Boyd, 1998) and time (human population cohort turnover) will likely help this effort. In short, although future study is always helpful, political and social change is required. Population viability analyses performed in this thesis support the need for substantial change, because few if any sites in the foothills will provide secure sources of habitat for adult female grizzly bears in as short of a period as 30 years.

Although these conclusions seem rather dismal, I believe that if Albertan's recognize the importance of maintaining such species (a decision they will ultimately have to decide, hopefully with biological input), there will be unprecedented opportunities for change and co-existence between people and bears. We need not have to look to the future to find such evidence, as Linnell et al. (2001) found favorable management policy (legislation) in the USA led to population increases in grizzly bears (see also Pyare et al. 2004), while European populations failed to show a relationship with human density suggesting that grizzly bears can persist even with relatively high human densities if attitudes are favourable (see also Mattson et al., 1996a; 1996b). However, this will not be without a price. Public sacrifices, such as reduced recreational access or more costly extraction of resources, likely will be required if substantial changes to grizzly bear habitats are desired. If Albertan's fail to consider the price tag worthy, grizzly bears may not be present for future generations to enjoy. Thus, despite the synthesis this thesis provides for a habitat-based conservation assessment of grizzly bears, it will ultimately be the political and social will of the people of Alberta deciding whether this information is put to use (Keiter and Locke, 1996; Blundell and Gullison, 2003).

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