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DEMOGRAPHY AND HABITAT SELECTION BY GRIZZLY BEARS (*Ursus arctos* L.) IN CENTRAL BRITISH COLUMBIA

by

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Dedication

Dedicated to D.A. Bears

Abstract

I conducted a radiotelemetry study of grizzly bears (*Ursus arctos* L.) near the Parsnip River, British Columbia, 1998-2003. Prior to this study there have been no scientific investigations of grizzly bears inhabiting BC's Arctic watershed. Further, the link between changes in the land base created by forestry activities and grizzly bear habitat selection was lacking. In this thesis, I examine and model factors that contribute to the 4-fold higher density of bears in a relatively pristine mountainous landscape than in an adjacent plateau that has been heavily harvested for timber. To determine genetic differentiation, migration, body weight and condition, reproductive parameters, annual survival rates, mortality, multi-scale habitat use, and den-site selection, I radiotracked up to 59 grizzly bears, visited bear-use locations, and used 15 loci microsatellite markers for 133 individuals. I used resource selection functions (RSF) to estimate the relative probability of use during foraging and denning seasons. DNA-based estimates of population size were used to apply new methods for linking populations to habitats by scaling RSF models to density.

In contrast with the findings of studies where grizzly bears fed upon salmon, I found that during the foraging season bears selected for early seral habitats created by forestry operations. Results suggest that plateau bears were not limited by available forage based on their heavier weight, superior condition, and high cub survival rate. Rather, 3 main factors contributed to low population density on the plateau: (1) no female, and limited male, migration of bears from the mountains; (2) increased human access via high road densities; and (3) use of areas where human-caused mortality was high. Forestry operations increased human access while creating early seral habitats, making these areas an “attractive sink” for bears. Habitat selection was scale dependent; results varied between mountain and plateau landscapes, males and females, and across scales. Management recommendations included restoration through road closures and reclamations on managed landscapes, and altering future timber harvest plans to minimize the need for permanent roads. Legal kills can be controlled through permits and restricting human-access; however, reducing illegal kills will require increased hunter education, access management, and law enforcement.

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This work benefited from the valuable feedback provided by my supervisor, Dr. M. S. Boyce, and my committee, Drs. C. Cassady St. Clair, F. Schmiegelow, and D. Seip. I thank them for their expertise and comments throughout the years. External examiners Drs. J. Swenson and A. Derocher provided valuable comments that improved this thesis. I also appreciate the thorough and thoughtful comments by D. Heard who provided a wealth of advise throughout the study. Fellow ACA-TEAM lab mates Dr. C. Johnson, J. Mao, Dr. S. Nielsen, Dr. C. Aldridge, and C. Shier provided interesting discussions and knowledge. In particular, I appreciate S. Czetwertynski for always being there and providing many laughs. Dr. D. Paetkau of Wildlife Genetics International, and Dr. M. Proctor, patiently discussed, reviewed, and helped with the genetic connectivity analyses. H. Beyer provided exemplary GIS expertise.

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CHAPTER 1
GENERAL INTRODUCTION

1. CONTEXT

Ecology has been defined to be the study to determine causes behind the distribution and abundance of organisms (Krebs 1985). In 1859, Darwin noted that organisms tended to be specialized in morphology and/or behaviour to the environments in which they are found. Today this observation persists and habitats have been defined as "places" (Begon et al. 1996) that provide an organism with the requirements to maintain a population. In present day society, few "places" exist outside of parks or protected areas where landscapes remain pristine and natural ecological processes are allowed to occur. Rather, habitat alteration either through direct loss or modification is becoming commonplace and is cited as the factor most identified with species extinction (Diamond 1989, Caughley 1994, Sih et al. 2000). The sub-boreal forest of British Columbia (BC) is no exception with escalating forestry operations being the primary means of habitat alteration. In these landscapes, natural fire cycles have been suppressed to protect the commercial value of timber (DeLong and Tanner 1996). Although there are many differences between wildfires and clearcutting (McRae et al. 2001), forest harvest may mimic fire processes by opening up the forest canopy allowing for vigorous understory growth and succession (Carleton and MacLellan 1994), which can be enhanced with proper site preparation (Bergeron et al. 1999). Unlike forest fires, however, timber extraction requires roads, ultimately facilitating human access, and increasing habitat loss and fragmentation, which in turn effects the distribution and abundance of flora and fauna (McRae et al. 2001). Increased human access into formerly undeveloped areas introduces risks associated with the new environment. Recent theories of habitat selection are focusing on the link between the selection of habitats and the risk of predation (Delibes et al. 2001, Battin 2004). The risk of predation has been found to influence decisions made by animals (Lima and Dill 1990), and experimental studies have shown that avoidance of predation risk can indeed alter habitat selection (Gilliam and Fraser 1987). In this study I examine the effects of timber harvesting on grizzly bear (*Ursus arctos* L.) habitat selection, distribution, and density in an 18,096-km^2 area in central-eastern BC.

1.1 Conservation Needs of Grizzly Bears

Grizzly bears inhabiting Canada face range restriction, annual kills that may be unsustainable, over-harvest of females (Banci 1991, Banci et al. 1994), and excessive human mortality rates affecting their population viability (Nielsen et al. 2004a, Mattson and Merrill 2002). Due to the history of declining and isolated grizzly bear populations (Mattson and Merrill 2002), their sensitivity to human activities (Banci et al. 1994, Nielsen et al. 2004a), and because they have extensive home range requirements, low reproductive rates, late weaning age, and delayed implantation, the Committee on the Status of Endangered Wildlife in Canada (2002) nationally lists grizzly bears as a species of special concern. In BC, grizzly bears are listed as vulnerable (blue-listed species) (Harper et al. 1994). Recently, the management of grizzly bears and their habitats has become a high profile conservation issue (Peek et al. 2003). Intense public concern regarding BC's grizzly management practices occurs at the international, national, provincial, and local level (Peek et al. 2003). In BC, the Forest and Range Practices Act requires that the needs of red and blue listed species be addressed during forest management activities (BC IWMS 2004). Forest companies that have, or are trying to obtain 3rd party environmental certification for their products, must implement acceptable practices to protect threatened and endangered species within their operating area (Canadian Standards Assoc. 2003, BC IWMS 2004). Consequently, there is a great need for reliable information on the habitat requirements of grizzly bears to facilitate improved forest and land management practices.

1.2 Why Study Grizzly Bears Surrounding the Parsnip River, BC?

Grizzly bear research projects in BC have focused on coastal areas (Hamilton 1987, Hamilton and Bunnell 1987) or the southeastern portion of the province, such as the Selkirk Mountains (Wielgus 1994, Wielgus and Bunnell 1994, 1995, 2000), the Flathead River Valley (McLellan 1989a,b; McLellan and Hovey 2001), the Columbia Mountains (Ramcharita 2000), and the southern BC-

US boarder (Proctor et al. 2002, 2004, 2005). However, grizzly bear population ecology and habitat selection had not been studied in the central and northern portions of the province. The location of the Parsnip Grizzly Bear Project (PGBP) provided a number of unique opportunities to better understand grizzly bear habitat requirements:

i. The study area ranged from wilderness mountain habitat (7,476 km^2) to plateau habitat (10,624 km^2) that had extensive road access and forest harvesting activities (Fig. 1-1). Prior to this study, little was known about the habitat use of grizzlies on the sub-boreal plateau;

ii. The majority of the study area was within the watershed draining northward to the Arctic (i.e., Arctic watershed) so bears did not have access to salmon; and,

iii. Aside from a few small provincial parks, the entire study area was within a 'working forest,' meaning there were no protected areas within or immediately adjacent to the study area that could potentially provide or maintain a source population of grizzly bears.

The recent development of a variety of research and inventory tools, including DNA population census (Woods et al. 1999) and Geographic Information Systems are now being used with advanced analysis techniques such as resource selection functions (RSF) (Manly et al. 2002). DNA fingerprinting techniques using 15 polymorphic genetic markers can identify individual bears and be used to evaluate migration, dispersal, and genetic differentiation (Proctor 2003). These new research and analysis techniques provide an opportunity to enhance our understanding of grizzly bear ecology and demography.

1.3 Defining the Study Area

The 18,096 km^2 study area boundary was defined based on movements of radiocollared male and female grizzly bears, 1998-2003, using a combination of GPS and VHF locations (n = 13,463 locations). I excluded 8 outlier locations that fell west of the western boundary; one subadult female and two male bears made extended movements to the Vanderhoof district and Fort St. James. I limited the western boundary because inclusion of these locations would have greatly increased the size of the plateau study area beyond that which was feasible to adequately monitor, trap, or conduct microsite habitat plots due to logistical and budget constraints. In addition, because I did not trap in the omitted area there was not a representative sample of bears using that area.

I used the plateau and mountain portions of the study area to determine availability at the study-wide scale. I believe the study area boundary was correctly chosen because: (1) movement by bears was limited between the mountains and the plateau (see Chapter 2), (2) grizzly bears have large home range sizes and bears were free to wander from south to north (see Fig. 2-1), and (3) available resources were similar within each mountain or plateau landscape but not across mountain and plateau landscapes. Further, by using the animals' locations to determine the boundary, I am confident that the entire study area was occupied by grizzly bears. Therefore, I addressed the primary considerations outlined by Manly et al. (2002:5) when using RSF designs for examining habitat selection, those are, "distribution of resource units, the scale of selection studied, what is truly available to the animals, and manpower and budget constraints for sampling." Further, I have devoted chapter 4 to the issue of how varying the extent of availability can influence habitat selection patterns by grizzly bears.

1.4 Radiocollared Sample, Trapping Techniques, and Potential Biases

A total of 59 grizzly bears were radiocollared between August 1997 and fall of 2002 (*n* [plateau] = 30, 19 females, 11 males; *n* [mountain] = 29, 18 females, 11 males). The University of Alberta's Animal Care Committee, following the Canadian Council on Animal Care guidelines and principles, approved bear handling procedures (protocol # 307204). There were 2 main capture periods for both landscapes: late April through beginning of June and September through October. Due to staggered entry and exit, sample sizes varied among years, and therefore, analysis techniques used in the subsequent chapters were dependent upon the questions asked and methods used. For example, although 59 bears were captured, and body condition was assessed for all 59 bears, only 28 of these bears had adequate sample sizes/locations obtained throughout the year to estimate a yearly home range, due to dropped collars, mortality, missing locations, etc. Further, when multi-year locations were used, 52 bears had adequate sizes to estimate a multi-year home range. In Chapter 5 on den-site selection, the number of study bears increases to 61 because I used the known den locations of 2 additional plateau bears captured by the Peace-Williston Compensation program. These bears were not used in any other portions of this thesis.

Every effort was made to ensure that a random sample of bears was obtained. Bears were captured using a combination of Aldrich foot snares placed at baited sites, aerial darting from helicopter, culvert traps, and free-ranged darting. In the mountains, the majority of bears were aerial darted from helicopter 24 (83%) because helicopters were the only efficient means of accessing this landscape due to the limited road network. However, we also placed snares in low-elevation forests in an attempt to catch mountain bears if they inhabited timbered landscapes. In forested areas, we were limited by where the helicopter could land. Because we were required to check snares daily, helicopters are costly, and the mountains were prone to volatile weather conditions during spring and fall trapping sessions, we were limited in our attempts to snare in low-elevation forests. Regardless, we placed considerable capture effort into snaring in the forested mountains and believe that snare sites were well distributed. Four bears were captured during snaring attempts (14%), while 1 (3%) was free-ranged at a snare site. Further, the number of grizzly bear hair samples obtained during the DNA population census also supports the high use of subalpine and alpine landscapes that I report in this thesis; grizzly bear hair was more often found in subalpine and alpine sites as compared with sites placed in low-elevation forests. Conversely, black bear hair was more often located in the lower elevation sites (Mowat et al. 2005). Therefore, although it is possible that my findings may over-represent use of alpine and subalpine habitats by mountain bears because the majority of radiocollared bears were darted from a helicopter, I believe that grizzly bears that inhabited the mountains truly selected for higher-elevation sites, rather than a bias in my radiocollared sample. Indeed, I recorded some of the study bears that lived in the mountains to use both lower elevation forests and alpine areas. Recaptures on the DNA study also support my conclusion that movements were smaller overall in the mountains as compared with the plateau (Mowat et al. 2005).

On the plateau, due to the forested sub-boreal spruce landscape, it was most effective to capture bears using ground snares. Further, due to the abundance of black bears, and conversely low number of grizzly bears (Mowat et al. 2005), it was most efficient to bait areas prior to setting snares to minimize incidental catch of black bears. Thus, snares were set on the plateau only when grizzly bear sign was detected. Baits were primarily beaver (*Castor canadensis*) carcasses, but moose (*Alces alces*) and horse (*Equus caballus*) also were used. We also monitored a decommissioned landfill area and again set snares when grizzly bear sign was detected. Furthermore, each spring all helicopter companies in Prince George were contacted to request immediate reporting of grizzly bear sightings. Notices also were posted in the surrounding area, aimed at pilots, forestry workers, and local residents, requesting that observations of grizzly bears be reported to the capture team. Facilitated by an extensive road network on the plateau, most bears were captured in snares (n = 19, 63%), followed by culvert traps (n = 7, 23%), and darting from a helicopter (n = 4, 13%). Helicopters were used to fly the plateau and search for aerial-darting opportunities; however, trees limited bear sightings as well as inhibited safe darting.

Despite intensive capture efforts surrounding the mountain and plateau boundary, few bears were captured in this area. From 1995-1998, the BC Ministry of Water, Land and Air Protection (MWLAP) implemented a diversionary feeding program east of the Parsnip River, adjacent to the plateau/mountain boundary, in an attempt to reduce predation on wild ungulates. During those years spring food for carnivores was supplemented by placing a total of 35,900 kg of bait (salmon, moose, cougar, black bear, deer, and beaver carcasses) in the plateau and mountain divide (Heard, White and Watts unpublished data). In 1998, we capitalized on those opportunities by flying baited areas, searching for aerial darting possibilities, and setting snares. In 1999, we baited areas ourselves and monitored them for signs of grizzly bears. Although other wildlife was sighted (e.g., wolves (*Canis lupus*), wolverine (*Gulo gulo*), and black bears) only 1 subadult male grizzly bear was darted during these baiting attempts. Early hunter harvest data obtained from MWLAP shows a number of bears were removed from areas surrounding the Parsnip River, and historical reports discuss heavy hunting of grizzly bears during the early-to-mid 1900s along this divide and in certain areas throughout the Parsnip plateau (Boudreau 1998). I noted that radiocollared bears that crossed this divide tended to do so quickly, and it appears that grizzly bears currently avoid this area.

A total of 25 bears were outfitted with 12 channel Televilt GPS-Simplex™ Global Positioning System (GPS) collars (Televilt/TVP Positioning AB, Lindesberg, Sweden) during captures or re-captures, between 1998-2002. Fourteen of those bears wore GPS collars for $\geq$1 year, and VHF collars for their remaining years, thereby yielding a mix of GPS and VHF data. Remaining bears were fitted with VHF (very high frequency) collars (Lotek, Newmarket, Ontario, Canada) (n = 20). Ear-tag transmitters were placed on captured offspring to evaluate dispersal (n = 9) and coupled on some adults with VHF or GPS collars. Despite the type of monitoring device, all bears were located by single engine fixed wing aircraft flights at the same frequency, that was, biweekly from 1998-2000, weekly in 2001-2002, and every 2 weeks in 2003.

Throughout this thesis I use data obtained from aerial flights, with the exception of determining the study area boundary and for location of den sites. I chose not to use the GPS data for habitat selection because I experienced a number of problems with GPS collar performance (Gau et al. 2004). Six GPS collars had catastrophic failures and could not be retrieved. Of the collars that I was able to retrieve, the mean fix rate was only 54% (SE = 4.2, n = 17; Gau et al. 2004). Fix rates also were lower for bears that lived in the forested plateau than those that lived in the mountains (Ciarniello et al. unpublished data). The highest fix rate was 87%, and was worn by a mountain female that largely ranged in the alpine meadow and shrub landcover types; the highest fix rate on the plateau was 67%, with the lowest fix rate being 9%. Many authors have concluded that vegetation (Moen et al. 1997, Belant and Follman 2002, Frair et al. 2004) and/or animal behaviour (Moen et al 1996, 2001; Obbard et al. 1998, Dussault et al. 1999) may affect the fix rate of GPS collars. Due to the unreliability of the GPS data, and the subsequent need to correct for bias introduced by behaviour and canopy closure, as well as mixing both VHF and GPS data, I chose to use only VHF data for habitat-selection analysis. Additional papers are being prepared that evaluate the bias in the GPS data.

I recognize that VHF telemetry data also contain biases. For example, flights must be flown during daylight hours, thereby being biased against activities that occur at night (Belant and Follmann 2002). This bias may over represent resting locations as compared with foraging locations, or vice versa, if behavioural activities regularly occur during specific times of the day. More importantly, it may affect the results of habitat use by bears for cutblocks (Nielsen et al. 2004b), roads, and human use areas (Gibeau et al. 2002) if that use occurs mainly during nocturnal periods with avoidance occurring diurnally. However, some studies report grizzly and black bears as being primarily diurnal or crepuscular (Garshelis and Pelton 1980, Bjarvall and Sandegren 1987, Rode et al. 2001). New research using GPS collars on grizzly bears in Alberta is showing that "bears were crossing roads more during daylight hours" than at night (G. Stenhouse, personal communication). In an attempt to minimize bias, animals were flown in different patterns to vary the time of day they were located, although flights always occurred between 0:700 and 19:00. However, to maximize crew safety and minimize the possibility of sever downdrafts, the mountains had to be flown when weather conditions allowed, and neither landscape could be flown during poor weather. Unlike GPS locations, however, VHF telemetry does not appear to be affected by canopy closure, which is an important consideration in habitat-selection studies, especially those focusing on forestry activities. Furthermore, because VHF locations were obtained without delay, I could immediately visit bear-use locations to determine the mechanism of their selection (i.e., traveling, resting, foraging, mortality, denning) and did not have to wait for the downloading of GPS-collar locations (Mech 1980, Schwartz and Arthur 1999).

2. THESIS OBJECTIVES

The Parsnip Grizzly Bear Project began in August 1997, and I began my thesis research in the spring of 1999. My primary objective was to determine the effects of forest harvest activities on grizzly bear demography and habitat selection in central British Columbia. Specifically, I was interested in determining the factors responsible for limiting the number of grizzly bears inhabiting the plateau landscape as compared to the adjacent mountainous landscape. In 2000, a DNA based population inventory of grizzly bears was conducted on a 6,144-km^2 (3,016 km^2 plateau, 3,128 km^2 mountains) area contained within the larger study area (Mowat et al. 2005) (Fig. 1-1). The study design employed 1 mark and 3 recaptures using an 8 × 8 km grid cell size (64 km^2), for a total of 96 cells and 384 sites. The estimates were 49 bears per 1,000 km^2 in the mountains (95% C.I. = 43-59; core corrected density), and 12 bears per 1,000 km^2 on the plateau (95% C.I. = 7-28, boundary strip corrected density) (Mowat et al. 2005). Recent statistical techniques allow RSF (Manly et al. 2002) to be linked to populations if reference areas exist where densities are known (Boyce and McDonald 1999). In this thesis, I use RSF and associated techniques to quantitatively examine what contributed to the differences in density found between the mountains and plateau landscapes. A secondary objective was to examine the effects of scale on grizzly bear habitat selection because different processes can operate at different scales (Johnson 1980, Addicott et al. 1987). The issue of scale and its effects on habitat selection studies has been argued to represent a unifying framework for ecological studies (Levin 1992, Guisan and Thuiller 2005).

3. THESIS ORGANIZATION

This thesis was written in paper format with the intention that each chapter be submitted for journal publication. My goal is that chapters 2-5 become co-authored publications with Dr. M. S. Boyce, Dr. D. Seip, and D. Heard; therefore, I have used ‘we/our’ throughout these chapters. Although each chapter is considered independent, they are related in the overall objective of contributing to understanding the population ecology and habitat selection of grizzly bears in the Arctic watershed of BC. In Chapter 2, I begin by examining the migration patterns, body condition, birth rate, and death rate of grizzly bears. The objective of this chapter was to gain an understanding of the mechanisms leading to the differences in density between landscapes before the application of statistical modeling techniques (see Lima and Zollner 1996). I was particularly interested in focusing on what limited bear density on the plateau. I used 15 loci microsatellite markers to assess migration between landscapes and examine whether I could detect genetic differences between bears that lived in the mountains and those that lived on the plateau. I compared the results of the genetic analysis with those obtained by VHF radiotelemetry monitoring of the movements of bears, 1998-2003. Next, I determined reproductive parameters for bears in each landscape to assess whether the difference in density might be related to cub production. Annual survival rates were calculated for sex and age specific groups of bears. I discuss and evaluate the relationships between the proximity of secondary logging roads and bear deaths that I noticed when investigating kill locations.

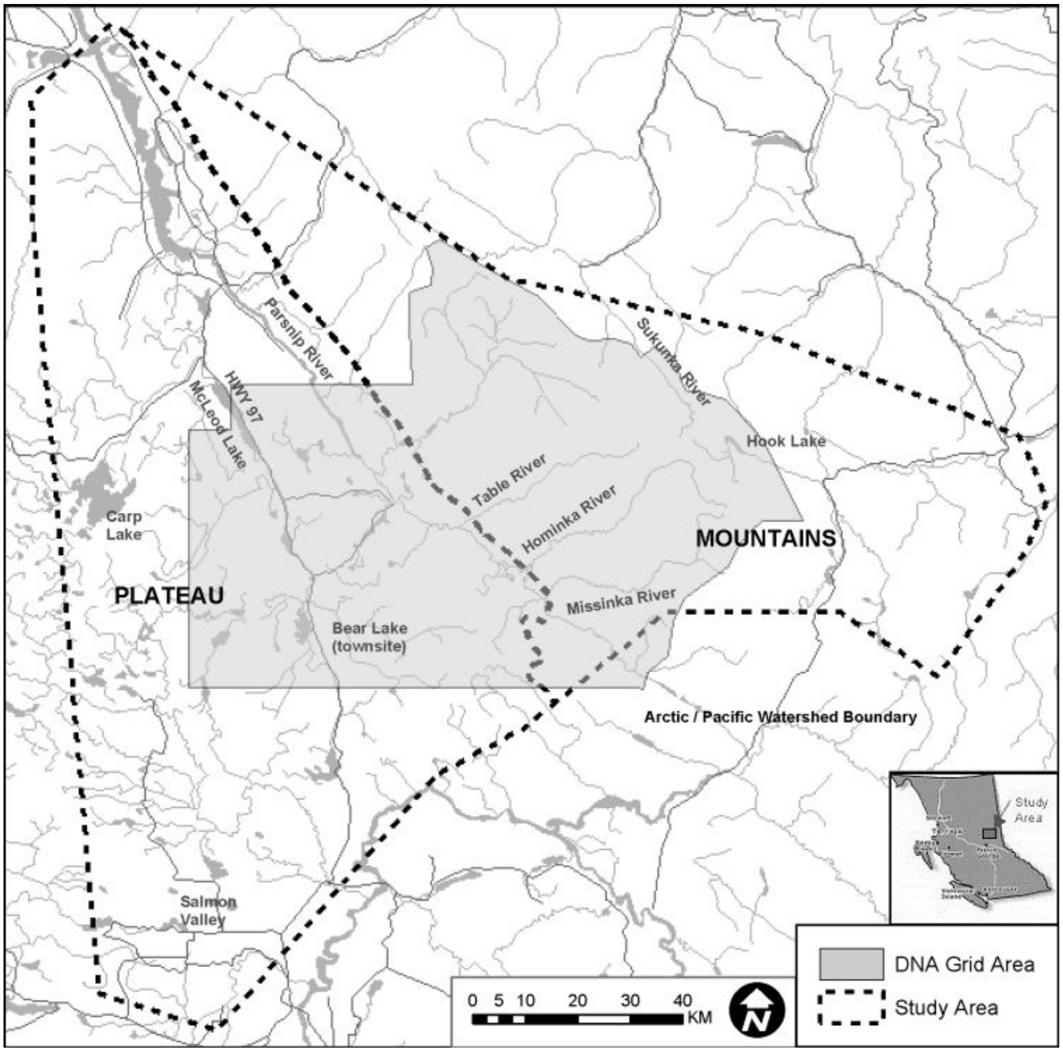
In the preceding chapter I concluded that bears that lived on the plateau were limited by human-caused mortality linked to access afforded by forestry activities rather than differences in habitat quality. Following from this, in Chapter 3, I examine the long-standing hypothesis that the abundance and distribution of organisms partly result from their selection of habitats (MacArthur and Pianka 1966, Charnov 1976) by modeling the relationship between habitats and grizzly bear density using mechanistic and/or statistical approaches to habitat selection (Manly et al. 2002). Selection occurs when a resource or landscape type is used disproportionately to its availability (Johnson 1980, Thomas and Taylor 1990). However, habitats that results in close contact between bears and humans often result in high bear mortality (Knight et al. 1988, McLellan 1989b, Mattson and Merrill 2002, Nielsen et al. 2004a) thereby acting as “ecological sinks” (Delibes et al. 2001) or “traps” (Schlaepfer et al. 2002, Kristan 2003, Battin 2004). In ecological trap situations, the assumption that density is a function of habitat quality or provides a fitness benefit (Garshelis 2000) may be misleading because human caused mortality may negatively affect population productivity (Mattson and Merrill 2002). To investigate whether differences in landcover type, roads, and/or mortality risk could account for the differences in bear density, the results of the DNA mark-recapture population census were linked to population density using RSF models (Boyce and McDonald 1999). Specifically, I used the mountain RSF model to predict habitat use, density, and number of bears on the plateau, and conversely the plateau RSF model to predict grizzly bear use, density, and number of bears in the mountains.

Chapter 4 evaluates the influence of scale and design on resource selection. Recent ecological studies have focused on the importance of addressing multi-scale habitat selection (Johnson 1980, Addicott et al. 1987, Orians and Wittenberger 1991, Anderson and Gutzwiller 1996, McLean et al. 1998). The hierarchical and nested patterns of habitat selection may make results scale sensitive (Guisan and Thuiller 2005). Thus, management actions based on only one scale of analysis may be limited in their scope. Although the influence of scale has been studied for a number of large ungulates (Schaefer and Messier 1995, Rettie and Messier 2000, Apps et al. 2001, Johnson et al. 2002, Boyce et al. 2003, Johnson et al. 2004b), it is largely lacking in studies examining the habitat selection of grizzly bears (McLoughlin et al. 2002, Johnson et al. 2004a, Nielsen et al. 2004b). Using RSF, and varying the extent of availability, I examined the effects on the habitat selection of grizzly bears inhabiting mountain and plateau landscapes. I estimated separate models for females and males using 3 extents: study-wide, home range, and a predetermined movement buffer. By applying different combinations of Johnson's (1980) 4 hierarchical orders of habitat selection with Manly et al.'s (2002) sampling designs for resource selection studies, I addressed both population level (i.e., where are the animals located on the landscape) and individual based (i.e., what are animals using within their home range) questions. Specifically, I employed 2 methods for evaluating the effects of scale on the RSF designs: first, I chose *a priori* 6 candidate models, estimated at each scale, and ranked them using Akaike Information Criteria (AIC); second, I examined changes in the model coefficients between the 3 scales within one of the candidate models (all-inclusive landcover). By comparing changes in the model coefficients derived from altering the study design and extent of available habitat I was able to evaluate whether habitat selection patterns by grizzly bears remained constant across the 3 spatial scales.

Chapters 2-4 focused on grizzly bear survival and habitat selection during the foraging season. In Chapter 5, I was interested in developing an understanding of the den site requirements of grizzly bears, focusing on whether bears inhabiting the plateau landscape exhibited a different pattern of den site selection, timing of den entry and exit, and denning structures compared with those inhabiting the mountainous landscape. Grizzly bears in northern latitudes may spend from 5 to 6.5 months each year in their den (Vroom et al. 1980, Judd et al. 1986, Van Daele et al. 1990, Friebe et al. 2001, Seryodkin et al. 2003), making den site selection an important activity affecting both survival and reproduction. Cubs are born in dens and disturbance of denning grizzly bears has been documented to reduce reproductive success of pregnant females (Swenson et al. 1997). I used RSF models to examine the relative probability of grizzly bear den-site occurrence. Further, I visited a subset of den sites to verify selection and record den attributes, such as stability of the structure. Gaining an understanding of the features grizzly bears select is important in a landscape that is subjected to increasing modification. Once we understand these processes, resource managers can better manage for those features within the landscape. This chapter has been published in the peer-reviewed journal, *Ursus* (Ciarniello et al. 2005).

In chapter 6, I link together the results of the previous 4 data chapters. The intention of this work was to provide a broad perspective on the ecology and survival of grizzly bears surrounding the Parsnip River, British Columbia, Canada. Before this study, management of grizzly bears heavily relied on the assumption that bears behaved similarly in their habitat-selection patterns and survival to coastal or southern interior grizzly bears. I offer management recommendations for the conservation of grizzly bears on timbered landscapes based on my research results. I hope this work highlights the special requirements of bears that inhabit non-salmon bearing portions of BC, especially because BC's sub-boreal forest lacks large areas where resource extraction activities are prohibited (i.e., source areas). The conservation of bears, particularly in a landscape that lacks the predictable supply of nutrition available to salmon feeding bears, requires a fundamental understanding of their habitat selection patterns as well as what limits their survival.

Figure 1-1. Study area map, including mountain and plateau boundary just east of the Parsnip River, British Columbia, Canada, 1998 to 2003. The mountain/plateau boundary (i.e., ecosection line) was delineated by the BC Ministry of Water, Land and Air Protection by following the mountain ridges. The DNA-based population census boundary is represented by the shaded box contained within the core of the larger study area and encompassed both mountain and plateau landscapes.



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CHAPTER 2
GRIZZLY BEAR POPULATION ECOLOGY: COMPARISON OF A WILDERNESS VERSUS HEAVILY ROADED LANDSCAPE

1. INTRODUCTION

The distribution and abundance of animal populations is determined in part by differences in birth rate, death rate, dispersal, immigration, and emigration across their range. Understanding demographic parameters, and the factors that influence them, can provide useful information for conservation and management (Caughley 1994). Devoid of human intervention, populations of large mammals can be expected to be near carrying capacity in stable systems (Fowler 1981). In those systems, density-dependent factors regulate the population and help ensure population persistence (Sinclair 1989, Boyce 1992, Sinclair 2003). Human modification of the landscape can alter natural processes such that density-independent factors limit population growth and abundance (Mattson and Merrill 2002, Laliberte and Ripple 2004).

We studied the population ecology of grizzly bears in central-eastern British Columbia. Within our study area, grizzly bear density was 4 times higher in a relatively pristine mountainous area than in an adjacent plateau that had been heavily modified by humans (Mowat et al. 2005). This paper compares population parameters and limiting factors apparently responsible for that difference. Because grizzly bears have high mortality rates near human activity (Nielsen et al. 2004, Mattson and Merrill 2004), grizzly bear conservation may be compromised by the rapidly expanding development of forest and mineral resources in western Canada. Small populations of grizzly bears are vulnerable to isolation and extirpation, which has already occurred in BC's southern interior (Hamilton et al. 2004). We are the first to report on demographic processes as they relate to the population dynamics of grizzly bears inhabiting the Arctic watershed of BC.

Research techniques using DNA fingerprinting permit analysis of the genetics of grizzly bears (Proctor et al. 2002, Proctor 2003). Proctor (2003) reported that human settlement and roads reduced dispersal of grizzly bears leading to spatially separated sub-populations. We documented the movement of grizzly bears between the mountains and plateau by monitoring radiocollared bears, and we quantified dispersal by comparing the genetics of bears from the mountains with those sampled on the plateau.

Reproductive parameters, including age of first reproduction, breeding interval, and litter size, are also important to understanding differences in density between areas. The age of first reproduction for female grizzly bears most commonly ranges from 5 to 7 years (McLellan 1989, Eberhardt et al. 1994, Hovey and McLellan 1996, Wielgus and Bunnell 2000), although 8 (McLellan 1994) and 10.3 years have been reported (Miller et al. 2003). Estimates of mean breeding interval have ranged from 2.6 to 4.6 years (Eberhardt et al. 1994, McLellan 1994, Hovey and McLellan 1996), and average litters sizes range from 1.4 (Wielgus and Bunnell 2000) to 2.2 (Wielgus and Bunnell 2000, Miller et al. 2003) to 2.6 cubs per female (McLellan 1989, 1994). The variance in reproductive parameters appears to be related to nutritional condition (Hilderbrand et al. 1999, Ben-David et al. 2004). Bears that have access to predictable meat supplies are larger (Hilderbrand et al. 1999, Miller et al. 2003, Ben-David et al. 2004) and body size has been linked to increased reproductive success (Blanchard 1987, Stringham 1990, Welch et al. 1997).

Understanding juvenile and adult survival is critical to conservation (Sinclair 2003). Cub-of-the-year survival ranges from 30-40% in their first year of life (Bunnell and Tait 1985). In Alaska, Miller et al. (2003) report annual survival of 34% for all ages of cubs in Denali and Katmai National Parks, as compared with 57% in Black Lake. He concluded cub survival was higher in hunted areas versus non-hunted areas (Miller et al. 2003). Cub survival ranged from 56-82% for 6 interior populations, and 45-72% for 3 coastal populations (McLellan 1994). For adult female grizzly bears, annual survival ranged from 90-97% in Alaska (Miller et al. 2003) to 95-96% for females in the southern Rocky Mountains (McLellan et al. 1999). Adult male survival ranged from 75-98% in Alaska (Miller et al. 2003) as compared with 84-89% in the southern Rocky Mountains (McLellan et al. 1999).

Range constriction due to human activities is the primary factor influencing grizzly bear mortality because it can result in loss of suitable habitat and increased human-caused mortality of bears (Servheen 1984, Mattson and Merrill 2002). Natural causes of cub mortality include infanticide by adult males (Swenson et al. 1997), adult females (Hessing and Aumiller 1994), or immigrant subadult males (Wielgus and Bunnell 1995, 2000), starvation (Knight et al. 1988), and accidental death (Nagy et al. 1989). For adult grizzly bears the major reported causes of mortality are the legal 'permitted' kill by hunters, followed by 'non-permitted' harvest including, illegal kills, livestock depredation, problem wildlife (McLellan 1990), and collisions with vehicles. In naturally regulated populations the survival of adult grizzly bears is high (McLellan 1990). Intra-specific killing may be important in naturally regulated populations (McLellan 1994), but in most grizzly bear populations, human-caused mortality is the primary cause of death for adults (McLellan 1990, Mattson and Merrill 2004, Nielsen et al. 2004). Human-induced mortality was cited as being the primary factor influencing grizzly bear population viability (Proctor 2003). Studies have reported that the magnitude of human-caused mortality for grizzly bears is related to the density of human settlements and roads (Mattson et al. 1987, Nagy et al. 1989, Mace et al. 1996, Nielsen et al. 2004).

We compared the demographic parameters of grizzly bears in the mountains and the adjacent plateau to determine the factors that were related to the difference in grizzly density. Our objectives were to determine: (1) immigration, emigration and dispersal of bears between the 2 areas; (2) reproductive parameters in the two areas; (3) age-specific mortality and its role in influencing the difference in population density; and, (4) identification of primary risk factors responsible for mortality. Developing an understanding of the primary limiting factors (see Sinclair 1989) for grizzly bears inhabiting 'working forests' will be crucial to the development of sound management practices for bears, especially outside of protected areas.

2. STUDY AREA

The study area comprised 18,096 km^2 and was located in central-eastern British Columbia, Canada (54°39'N, 122° 36'W), including the northern limits of the city of Prince George extending north past the town of Mackenzie. The ecosection line, as delineated by the BC Ministry of Water, Land, and Air Protection, was used to divide the study area into 2 major landscapes (Fig. 2-1).

1. Parsnip Plateau (hereafter plateau). The plateau landscape covered 10,624 km^2 of rolling hills and flat valleys in the sub-boreal spruce (SBS) biogeoclimatic zone (Meidinger et al. 1991). Climax forests in the wetter portion of the plateau were dominated by white spruce (*Picea glauca*), while lodgepole pine (*Pinus contorta*) occurred mainly in the dryer portions. Most plateau landcover types were a mix of white spruce and pine or spruce and subalpine fir (*Abies lasiocarpa*) associations. The plateau was modified by forestry activities, with approximately 12% of the area clearcut in a 20 year period (1970-1990) (DeLong and Tanner 1996). The majority of logging had taken place within the last 50 years, and resulted in a mosaic of cutblocks and successional stages. The plateau had a mean annual temperature of 2.6° C, with 72 cm rainfall and 300 cm snowfall (DeLong et al. 1993, 1994). Elevations ranged from 600 m to 1,650 m.
2. Hart Ranges of the Canadian Rocky Mountains (hereafter mountains). The mountains covered 7,472 km^2 and contained both east and west slopes of the Rockies. The primary forest type was SBS in the valley bottoms and Engelmann spruce – subalpine fir in the subalpine (Coupe et al. 1991). Valley bottoms were predominately a mix of white spruce and subalpine fir, while higher elevation habitats consisted of subalpine parkland dominated by subalpine fir. Subalpine grassland slopes were comprised of lush forb communities. The alpine-tundra zone, beginning at approximately 1,400 m, typically consisted of shrubs or krummholtz tree formations, and lush heath communities. Less than 1% of the study area was barren rock, alpine snow, or glacial ice. The mean annual

temperature was 0.3° C, with 154 cm rainfall, and 700 cm snowfall (DeLong et al. 1993, 1994). Elevations ranged from 720 m to 2,550 m.

Both mountain and plateau landscapes were within a 'working forest' with just a few small parks. Forestry was the predominant industry in the study area, and the plateau contained the majority of timber extraction activities. However, each year harvesting expanded further up the 4 main river valleys (Missinka, Hominka, Table and Anzac Rivers) leading deeper into mountainous areas. Other potential disturbances to grizzly bears included the towns of Bear Lake and Mackenzie, Highway 97, a railway line through the mountains for coal extraction, 3 sawmills, 2 logging camps, and various consumptive and non-consumptive recreational activities, such as hunting, fishing, snowmobiling and hiking.

3. METHODS

3.1 Bear Capture

Every effort was made to vary capture techniques to reduce the potential of a bias sample of bears towards animals of particular habitat associations that might be more vulnerable to some capture methods than others. Bears were captured from August 1997 through fall 2002 using a combination of Aldrich foot snares placed at baited sites, aerial darting from helicopter, culvert traps, and free-range darting. Each year there were 2 main capture periods for both landscapes: late April through beginning of June and September through October.

Despite considerable trapping effort, we captured few bears adjacent to the mountain/plateau boundary. From 1995-1998, the BC Ministry of Water, Land and Air Protection implemented a diversionary feeding program to reduce predation on wild ungulates (Heard, White and Watts unpublished data). During those years spring food for carnivores was supplemented by placing a total of 35,900 kg of bait (salmon, moose, cougar, black bear, deer and beaver carcasses) within the plateau and mountain divide. In 1998, we capitalized on the placement of 3,900 kg of bait by flying baited areas, searching for aerial darting opportunities, and setting snares. In 1999, we again set and monitored a number of bait stations along the divide.

The University of Alberta's Animal Care Committee, following the Canadian Council on Animal Care guidelines and principles, approved bear handling procedures. Bears were immobilized using Telazol (tiletamine HCL/zolazepam HCL) at a dosage of 8 mg/kg administered using the Palmer Cap-Chur Inc. system (Powder Springs, GA). Ketamine was used as a top-up drug when necessary at a dosage of 2 mg/kg. While immobilized chest girth was measured and bears were assessed for their reproductive status (Jonkel 1993). Pinching the layer of fat surrounding the bears' ribs and flanks was used to assess body condition. Bears were assigned a condition based on the thickness of their fat layer with excellent representing a very thick fat layer and poor representing very thin or no fat layer. Bears <4 years of age were placed into the subadult and juvenile category, whereas adults were bears ≥4 years of age as long as they were not accompanied by their mother. Biological samples collected from each bear included blood for serum and DNA analyses and hair for DNA analysis. A first premolar tooth was extracted for age determination (Mattson's Laboratory, Milltown, Montana). Weights were taken where possible. If a weight was not possible (e.g., steep mountain slopes), the chest girth/weight relationship outlined in Jonkel (1993) was used to estimate bear weight. We found that Jonkel's method provided a good fit when compared with our known bear weights (Fig. 2-2). Statistical comparisons of capture weight between groups was calculated using a Mann-Whitney *U*-test with a significance level of $\alpha<0.05$.

3.2 Monitoring and Home Range

Bears were outfitted with a combination of 12 channel Televilt GPS-Simplex^{TM} Global Positioning System (GPS) collars (Televilt/TVP Positioning AB, Lindesberg, Sweden) or VHF (very high frequency) collars (Lotek, Newmarket, Ontario, Canada) and/or ear tag transmitters. Despite the type of monitoring device, bears were monitored from capture until their death, lost/failed collar, or through denning using a single engine fixed-wing aircraft and occasionally a helicopter. Monitoring occurred biweekly from 1998 to 2000, weekly in 2001 and 2002, and every 2 weeks in 2003, dependent upon weather conditions and aircraft availability. Due to the low fix rate of GPS collars (Gau et al. 2004), we have used only the aerial locations to calculate home range size. All aerial telemetry locations were collected during daylight hours. Substantial effort was directed at obtaining accurate low elevation aerial locations and/or visual observation of the bear. Universal Transverse Mercator (UTM) coordinates were taken with a hand-held 12 Channel Global Positioning System unit. Locations were mapped and verified on 1:50,000 topographic maps. For study animals with >10 locations that spanned throughout the year, multi-year (1998-2003) 100% Minimum Convex Polygons were constructed using the program Animal Movement (Hooge and Eichenlaub 1997). We recognize that 10 locations may be too few to accurately estimate an animal's home range size (Boulanger and White 1990, Arthur and Schwartz 1999); thus, we caution the reader that home range sizes may be underestimated for some animals. Statistical comparisons between home range size and landscape were calculated using a Mann-Whitney *U*-test with a significance level of $\alpha<0.05$.

After 2 consecutive mortality signals, we visited locations to determine the cause of death. Natural deaths refer to any deaths where humans or their activities were not the direct primary cause. Non-permitted kills refer to bears shot without a legal license, including poaching and species misidentification.

3.3 Reproduction

Bears were assessed annually for reproductive status during capture events and at den emergence. If a visual observation of the bear was obtained during monitoring the activity of the bear (e.g., resting, moving, feeding, etc.), the number of animals present, along with an estimate of their age class (cub-of-the-year (COY), yearling, two-year old, subadult, adult) were recorded. We only used known-aged litters to estimate an average inter-birth interval. Because we did not capture any female bears in the mountains <7 years of age, reproductive status was determined for bears ≥7 years of age. Statistical comparisons between reproductive status and landscape were calculated using a Mann-Whitney *U*-test with a significance level of $\alpha<0.05$.

3.4 Population discreteness

To evaluate dispersal and migration, genetic analysis was conducted on hair root samples gathered during a DNA-based population census grid in 2000 (see Mowat et al. 2005) and at bear captures. For multiply captured bears, only the first capture location was used. We define dispersal as the separation of dependent offspring from their mother and subsequent establishment their own home range. Migration was used to refer to movement back and forth between areas. DNA finger printing using 15 polymorphic genetic markers was used to identify individual bears (D. Paetkau, Wildlife Genetics International, Nelson, British Columbia, Paetkau et al. 1998). Genetic differentiation was calculated using 15-locus microsatellite genotypes and a calculation of F_{ST} (Wright 1965) between the mountains and plateau using the program GenePop v3.4 (Raymond and Rousset 1995). GenePop uses a weighted analysis of variance to examine genetic distance between two groups. To verify that the groups were displaying sufficient random mating and that markers were operating independently, we checked to make sure they met the assumptions of Hardy-Weinberg and linkage disequilibria respectively. Both tests were conducted using GenePop v3.4. Because these comparisons may lack independence we lowered our type I error rate by employing a conservative approach to the alpha values (Sokal and Rohlf 2000). Using the Dunn-Šidák method we adjusted critical values for the experiment wise error rate; the adjusted alpha for our Hardy-Weinburg was 0.003, and 0.00024 for linkage disequilibria (Sokal and Rohlf 2000:239). Our results met the assumptions of Hardy-Weinberg equilibrium (1 of 15, $P = 0.0007$) and linkage disequilibria (4 of 210 loci combinations, $P = 0.00014$, $P = 0.0000$, $P = 0.0000$, $P = 0.0000$), meaning we were able to continue with the genetic analysis.

GeneClass2 (Piry et al. 2004) was used further to detect and verify first-generation migrants. GeneClass2 examines the probability and likelihood that each individual belongs to either the mountain or plateau landscape. The software verifies the test by simulating a distribution of 1,000 individuals. The adjusted alpha for acceptance of an individual as a migrant was 0.0038.

For bears identified as migrants we examined all potential parent-offspring relationships with 0 or 1 mismatching loci using the program CERVUS (Marshall et al. 1998). We were not interested in identifying the correct mother and father, but rather the landscape to which the potential parents were assigned. CERVUS makes use of likelihood-ratio tests to assign parentage to a specific individual and generates a likelihood of parentage for each candidate parent, based on Mendelian inheritance, the probability of a genotyping error, and the probability of sampling the true parent (Slate et al. 2000).

3.5 Survival

Survival rates, $\hat{S}_t$, for radiocollared grizzly bears were estimated using a staggered entry Kaplan-Meier design following Pollock et al. (1989):

$$\hat{S}_t = \prod_{i=1}^{n} \left[1 - \left(\frac{d_i}{r_i} \right) \right] \tag{1}$$

where *n* refers to the number of times bears were checked, while d_i is the number of deaths, and r_i is the number of bears at risk recorded at time *i*. Greenwood's (1926) formula was used to estimate the variance for survival rates:

$$\mathrm{var}(\hat{S}_t) = \hat{S}_t^2 \left[\sum_{i=1}^{n} \left(\frac{d_i}{r_i(r_i - d_i)} \right) \right] \tag{2}$$

Precise dates when a bear went off-line were known for collars removed during trapping, dropped collars, limited-entry hunts, or problem wildlife. We lost contact with 6 bears due to what we believed to be catastrophic failure of the GPS transmitters; two of these bears were sighted wearing their failed collars. We used the last known location as the date missing bears went off-line. Our results may be conservative because it is possible that some of the missing bears were killed and the transmitter destroyed. For bears that died during aerial tracking, or dropped their collars between flights, the midpoint between the flight before and the mortality-emitted flight was used as the bear's off-line or death date as long as that time frame was $\leq$14 days. We censored the known deaths of 4 male bears (3 subadults and 1 young adult; 3 legal hunts and 1 problem wildlife) because we lost contact with them for periods ranging from 8 months to 1.5 years. For bears that dropped their collars in their den sites the mean den emergence date was used as the off-line date (Ciarniello et al. 2005). All such dens were investigated so we knew the bear had lived through the denning period.

3.6 Risk of Mortality

A logistic discriminant function (Seber 1984:308-317) was estimated to contrast the distribution of grizzly bear mortality locations (1) with radiotelemetry locations where kills were not recorded (0), for mountain and plateau landscapes using the log-linear equation:

$$m(\mathbf{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 \ldots \beta_p x_p) \qquad (3)$$

where the relative probability of mortality, $m(\mathbf{x})$, was influenced by coefficients, β_i , for each covariate, x_i, for $i = 1,2,\ldots p$, estimated using logistic regression (Nielsen et al. 2004).

Mortality locations were obtained by combining the 11 recorded deaths during our study with 150 permitted and non-permitted (i.e., poaching, collision with vehicles, problem wildlife) kill locations acquired from the BC Ministry of Water, Land, and Air Protection Compulsory Inspections Databases, 1990 to 2003. Hunters are required to report their location data with accuracy of only 1 km. For the plateau, we compared 972 use locations representing 32 bears (18 females, 14 males) with 106 mortality locations. For the mountains, we compared 1,527 locations on 30 bears (19 females, 11 males) with 55 mortality locations. By comparing bear use with bear mortality we were able to examine the riskiest places for bears while taking into account that bears may select to be there (Nielsen et al. 2004).

Model covariates included the predominant forest cover types of alpine, black spruce (*P. mariana*), spruce species, true firs, Douglas fir (*Pseudotsuga menziessi* var. *glauca*), pine, mixed wood, shrubs, swamps, meadows, and anthropogenic landscapes (i.e., urban) obtained from forest cover maps (FCM; BC Ministry of Forests, Prince George, BC). Urban typing on the plateau included the outlying human settlements around Mackenzie and McLeod Lake, the McLeod Lake first nations reserve, the Bear Lake townsite, and some southern agricultural areas approaching the city of Prince George. In the mountains, areas that were not available to be harvested, such as the right-of-way surrounding the railway, were classified as urban; however, because those areas had low or no human use they were not the same as those areas typed urban on the plateau. Elevation above sea level, slope, and aspect data were obtained from digital elevation maps built from terrain resources inventory maps (TRIM2; BC Ministry of Water, Land, and Air Protection, Victoria, Canada). Greenness provides an index of the amount of lush green biomass and was calculated for four satellite images using ERDAS® Imagine (Atlanta, Georgia, USA) at a 30 m pixel resolution. High greenness values indicate lush green vegetation while non-vegetated areas have very low greenness values (Mace et al. 1999).

For each landscape we ranked 7 *a priori* candidate models and used Akaike Information Criteria for small sample sizes (AIC_c) to determine the most parsimonious model (Tables 2-1 and 2-2; Burnham and Anderson 1998, Anderson et al. 2000). Secure habitats for grizzly bears are often cited as roadless areas containing a juxtaposition of forest types and successional stages (Mattson et al. 1987, McLellan and Shackleton 1989; Mace et al. 1996, Gibeau et al. 2002). Conversely, areas that provide close contact between humans and bears also provide high human-caused bear mortality (Mattson and Merrill 2002, Nielsen et al. 2004), and selection patterns by bears have been altered due to the presence of roads and trails (Mattson et al. 1987, McLellan and Shackleton 1989, Mace et al. 1996). Based on the aforementioned research, we chose sets of covariates that we deemed as contributing to the probability of grizzly bear mortality (Tables 2-1 and 2-2). We present the best model as determined by the normalized Akaike weights (AIC_w). We considered significant coefficients to be those with confidence intervals that did not overlap 0. A Spearman's rank correlation obtained using 5-fold cross validation was used to assess the internal consistency of the model

(Boyce et al. 2002). Model estimates were then interfaced with GIS to create maps of relative probability of mortality risk to grizzly bear across each landscape.

3.7 Road Information

Locations gathered from the ground, air, or compulsory inspection database were used to query a straight-line distance to the nearest road using ArcGIS® 8.3 (Environmental Systems Research Institute, Redlands, California, USA). We amalgamated road network layers obtained from Forest Cover Maps (BC Ministry of Forests, Prince George, BC), with those provided by Canadian Forest Products (Canfor) East, Canfor West, The Pas Lumber, and Slocan Forest Products Ltd. (Prince George, BC, Canada). Road networks were visually verified by crosschecking Landsat 5 TM images obtained from Spatial Mapping (on behalf of Canadian Forest Products Ltd. and the BC Ministry of Forests). Roads were classified into 3 categories: highway, primary logging road, or secondary/decommissioned logging road. Highway refers to the 2-lane paved Highway 97 North. Primary logging roads were main arteries that serviced a number of cutblocks. Secondary logging roads spurred off primary logging roads and were used to access cutblocks. We noticed inconsistencies in the GIS databases with respect to the status of the road and our knowledge of the landscape. Specifically, we lumped decommissioned roads with secondary roads because actual ground access could not be accurately assessed through GIS.

4. RESULTS

Grizzly bears captured included 18 mountain and 19 plateau females, and 11 mountain and 11 plateau males, for a total of 59. The mean age at first capture for female bears that lived in the mountains was 12 years, with a range of 7-22 years (SE = 0.96, n = 18). Thus, all female bears captured in the mountains were adults. For female bears captured on the plateau the mean age at first capture was 7 years, with a range of 1-18 years (SE = 1.28, n = 18). For male bears, the mean capture age in both landscapes was 5 years (SE [mountains] = 1.29, range 1-16, n = 11, SE [plateau] = 1.54, range 1-17, n =11).

4.1 Movements of Collared Bears

From 1998-2003, we gathered 2,475 locations on female bears ($\bar{x}$ = 75/bear, SE = 8.4, range 14-175) and 549 locations on male bears ($\bar{x}$ = 31/bear, SE = 5.3, range 13-109). We monitored 1 adult female that moved a straight-line distance of 40.5 km from the plateau to the mountains for denning (Fig. 2-1). She was the only radiocollared female to move between these 2 landscapes, and the family group returned to the plateau upon den emergence (Ciarniello et al. 2005). Two adult males traveled between the landscapes, and 3 subadult males dispersed from the mountains to the plateau (Fig. 2-3). On the plateau, both male and female bears crossed Highway 97 and the Parsnip River (Figs. 2-1 and 2-3). There did not appear to be any barriers to movement within the study area and bears were free to range between the mountains and the plateau; however, all but the 6 mentioned bears remained in their landscape of capture (Fig. 2-1 and 2-3).

Omitting tagged offspring with family groups, females that resided in the mountains had significantly smaller home range sizes than females that resided on the plateau (Fig. 2-1; $P < 0.001$, n [mountain] = 50 home ranges, $\bar{x}$ = 57 km^2, SE = 7, n [locations] = 1,598; n [plateau] = 13 home ranges, $\bar{x}$ = 446 km^2, SE = 120, n [locations] = 877). Mountain males also had smaller home range sizes than plateau males (Fig. 2-3; $P = 0.009$, n [mountain] = 8, $\bar{x}$ = 423 km^2, SE = 108, n [locations] = 270; n [plateau] = 8, $\bar{x}$ = 1,759 km^2, SE = 492, n [locations] = 279).

4.2 Population discreteness

Bears that were captured in the mountains were genetically distinguishable from bears captured on the plateau ($F_{ST} = 0.0174$, n [mountain females] = 67, n [mountain males] = 34, n [plateau females] = 16, n [plateau males] = 16). Movement between the mountains and the plateau was rare and when it occurred it was most frequent from the mountains to the plateau, consistent with our telemetry results.

Four animals (3 males and 1 female, $n = 32$) caught at a plateau DNA site were most similar genetically to mountain bears (Fig. 2-4). Two of those bears were radiocollared subadult males trapped on the plateau, whereas 1 was an unknown male and 1 an unknown female. The female was 500 times, 2 males were 1,000 times, and 1 male was 10,000 times more likely to have been born in the mountains than the plateau. All potential mothers and fathers for 2 of the 3 males were assigned to the mountains suggesting they had dispersed from the mountains to the plateau. The remaining male had all potential mothers assigned to the mountains but 1 of 3 potential fathers assigned to the plateau, again suggesting he had dispersed from the mountains to the plateau. For the female, all potential mothers assigned to the plateau and all potential fathers assigned to the mountains. Likely, the female was born to a plateau mother with a migrating mountain father, and therefore she was not a true migrant.

Using GeneClass2 only 1 of the subadult radiocollared males was identified to be a statistically significant mountain to plateau migrant ($P = 0.001$, likelihood ratio 3.851), whereas the other radiocollared male was close to significant ($P = 0.006$, likelihood ratio 2.889) but above our adjusted alpha value. The remaining male and female bears, with potentially mixed DNA, were not significantly different from random although their likelihood ratios were higher than other plateau bears ($P = 0.013$ and 0.014, likelihood ratio 2.695 and 2.536, respectively). Using this analysis we also detected one male caught in the mountains that strongly assigned to the plateau ($P = 0.000$, likelihood 3.639, $n = 101$). GeneClass2 assigned all mountain females to the mountains. Overall, the results indicate little movement of bears between the mountains and plateau.

4.3 Reproduction

If we examine the reproductive status of plateau bears with offspring, regardless of the age of the mother, female bears on the plateau were more often accompanied by offspring than mountain bears (Table 2-3, $P = 0.01$). However, since we did not catch any mountain bears <7 years of age, when we omit mothers on the plateau that were <7 years of age, there was no significant difference in reproductive status between landscapes (Table 2-3, $P = 0.058$). Litter sizes were similar between landscapes. Mountain bears averaged 1.93 cubs per litter (SE = 0.14, range = 1-3, $n = 13$), whereas bears that lived on the plateau averaged 2.0 cubs per litter (SE = 0.31, range = 1-3, $n = 7$).

We were able to determine the age of 1st reproduction for 3 female plateau bears: 1 at 4 years, and 2 at 5 years ($\bar{x}$ = 4.3 years). We also monitored a plateau female from 5-8 years of age that was not accompanied by cubs. This female had pink teats, which may indicate that she had not previously produced cubs. Thus, although potential primiparity for plateau bears was 4 years, our limited data indicate the average age of first reproduction was somewhat higher, possibly ≥7 years.

We monitored 1 mountain female for 5 consecutive years that was not accompanied by cubs (age 8-12), and another mountain female for 7 consecutive years prior to producing cubs (age 9-15). Thus it appears that the age of first reproduction is later for mountain females, possibly as late as 9± years. In both landscapes, the oldest females to produce cubs were 21 years of age.

4.4 Inter-birth Interval

We monitored only 2 females that had more than one litter. A plateau female had 3 COYs at 18 years of age and 1 COY at 21 years, an inter-birth interval of 3 years. This female successfully separated from her 1998 litter before birthing her following cub. A mountain female had a 4-year inter-birth interval, however, late in the fall she lost her first litter and was not accompanied by cubs again for 4 years. The 2 mountain females that had litters monitored from birth were in the company of their young for 4 years, resulting in a minimum 5-year inter-birth interval. One of these females dropped her collar, while the remaining female did not have cubs the following 3 years, making her inter-birth interval a minimum of 8 years. Our limited data indicate that conservatively plateau bears had a 3-year inter-birth interval, while the mountains had a 5 to 6-year inter-birth interval.

4.5 Independence

We recorded age of independence of offspring from their mothers for 11 family groups (*n* [mountains] = 7, *n* [plateau] = 4). In the mountains, we monitored 2 family groups, representing 5 offspring, from birth over the next 4 years. One of those female's offspring became independent at the end of September at 3.75 years of age, while the other female dropped her collar still in the company of her 3.75-year-old offspring also during the last week of September. Five mountain family groups had offspring whose age we estimated at the time of capture based on their size. We believe these offspring were ≥ 3 years of age when they became independent.

In the plateau, we had 1 known age family group that separated from her 3 cubs when they were 2 years of age. We also captured a subadult male on the plateau estimated through cementum aging to be 3 to 4 years old. This bear and his sibling became independent from their radiocollared mother the following year, between 4 and 5 years of age. Only 1 plateau bear became independent as a yearling when his mother was killed. He lived until 3 years of age when he was legally shot >100 km from his natal home range while foraging in a cutblock.

4.6 Capture Condition

Adult female plateau bears were heavier in the spring ($\bar{x}$ = 42 kg) and fall ($\bar{x}$ = 50 kg) than adult mountain bears (Fig. 2-5, spring n [mountain] = 16, n [plateau] = 5, $P = 0.02$). Spring captured adult male plateau bears were also heavier than adult male bears that inhabited the mountains ($\bar{x}$ = 140 kg, spring n [mountain] = 5, n [plateau] = 4, $P = 0.05$). There was no significant difference between subadult/juvenile spring capture weights (n [mountain] = 4, n [plateau] = 5, $P = 0.62$). We also assessed condition at capture to calculate whether the weight differences also translated into better body condition overall (Table 2-4). Regardless of the season, no female mountain bears were assessed as being in excellent condition, while only 3 (17%) were in good condition. The majority of female mountain bears were assigned 'poor' condition (n =14, 78%). Conversely, the majority of plateau females were in excellent (23.5 %) and good (47%) condition, while only 2 (12%) were in poor condition.

Difference in condition among male bears were less pronounced than females, however, overall mountain males were again in poorer condition (n = 6 of 11, 55%) than plateau males (n = 3 of 10, 30%, Table 2-4). However, each landscape had 2 male bears in excellent condition. We attribute some of the similarities in male condition to our placing bears in either landscape based solely on their capture location. For female bears, the capture location adequately reflected the landscape where they lived because movement between the landscapes occurred only on 1 occasion. However, the 2 mountain males in excellent condition were very large adults, 1 of whom was known to travel between the 2 landscapes while the other dropped his collar too early to determine his movement patterns. Therefore for these adult males their capture location does not necessarily reflect the landscape where they acquired their large body size. One of the 2 large adult males in excellent condition remained on the plateau, while the other occasionally traveled to mountain ridges.

4.7 Adult and Subadult Survival

Kaplan-Meier annual survival rates were 0.97 for mountain bears as compared to 0.79 for plateau bears (number at risk $\bar{n}$ [mountain] = 59, range 52-73, SE = 0.02; number at risk $\bar{n}$ [plateau] = 36, range 30-44, SE = 0.06) (Table 2-5). By age-class, adult female bears that lived in the mountains had a 0.96 survival rate, as compared to 0.92 for adult plateau females (number at risk $\bar{n}$ [mountain] = 50, range 45-58; number at risk $\bar{n}$ [plateau] = 11, range 9-15). Subadult plateau females, however, had a 0.77 survival rate ($\bar{n}$ = 14, range 11-17). We were unable to estimate survival for subadult mountain females because all mountain females captured were ≥ 7 years. The 3 adult males captured on the plateau survived until they dropped their collars ($\varphi = 1.00$). However, subadult males had a 0.62 survival rate and few survived to become adults ($\bar{n} = 9$, range 4-12). Survival rates were high for mountain males ($\varphi = 1.00$, $n = 8$).

4.8 Cub Survival

No COYs were recorded to have died on the plateau, however, 63% of COYs born in the mountains did not survive to be yearlings (Table 2-6). We investigated a location of a radiocollared male that lived in the mountains and found a consumed COY. We do not know whether this male killed the COY but he was seen together with an assumed female on the subsequent flight.

4.9 Mortality Descriptions and Time of Year

We recorded the death of 3 radiocollared adult mountain bears (Table 2-7). The 2 natural deaths were adult females (7 and 21 years). Two COYs accompanied the 21-year-old female, while the 7-year-old female was alone. A large adult male that traveled between the landscapes killed the lone female. The cause of death of the other female is less certain, but she was either killed by the same adult male, or died from unknown natural causes and was scavenged by the male. The legal hunting death was a 7-year-old male that was shot while feeding in a mountain cut-block.

On the plateau 12 radiocollared bears died (5 females, 7 males; Table 2-7). We were unable to accurately attribute the cause of death for 2 plateau bears: (1) a subadult male's collar and ear tags were returned into the Conservation Officer Service and the carcass was reported but we could not locate it on ground investigation, and (2) an adult female accompanied by 2 yearlings that may have been hit on the highway or died in defence of her yearlings, however, her carcass had been consumed. All known deaths on the plateau were human-caused (n = 10). Of the 5 females killed, 1 was an adult (7 years), while 4 were subadults ($\bar{x}$ [age] = 3, range 1-4 years). All 7 of the plateau males that died were subadult bears ($\bar{x}$ [age] = 3). Four of the 5 non-permitted bears killed were not reported to authorities (3 females, 1 male).

4.10 Mortality Risk

Eight of the 15 bear deaths occurred during fall and all fall deaths were on the plateau (Fig. 2-6). Three of the 5 non-permitted kills occurred in the fall and were associated with hunter-killed moose carcasses, while a grouse hunter shot 1 bear as problem wildlife, and a rancher shot 1 bear in defense of life or property. The unclassified bear death where the carcass was reported but not located also occurred in the fall and was a suspicious death. Permitted hunters killed the remaining 2 bears. The spring season was the next highest for human-caused deaths. Of the 3 bears that died on the plateau 1 was mistaken for black bear, 1 was shot and left, and 1 was killed by a permitted hunter. A permitted hunter also shot a mountain bear. No bears were documented to have died during the winter denning period. There were no known natural deaths on the plateau.

Omitting the 2 natural deaths, 6 of the 9 bears shot within the study area were within 100 m of a secondary or decommissioned logging road, 1 was shot on a primary logging road, 1 was 340 m from the highway although the exact cause of her death could not be determined, and 1 was the unknown carcass location which was reported to have occurred along a decommissioned road.

Four bears died outside the study area: 2 were shot by permitted hunters from a secondary logging road, 1 was shot by a grouse hunter while walking along a decommissioned road, and 1 was shot on a ranch. Therefore, all 12 non-natural bear deaths occurred within 400 m of a road; only the 2 natural deaths were >500 m from a road (622 m and 9.7 km, respectively). The average distance one could be from any type of road on the plateau was 529 m (SE = 5.1 m, SD = 748 m, range 0 to 7.3 km). In the mountains, the average distance from any type of road was 3.2 km (SE = 25.6 m, SD = 3.1 km, range 0 to 18.8 km).

Using the Province's database we found a 1.9-fold difference in the number of grizzly bears killed on the plateau (n = 98) versus the mountains (n = 52). Although the plateau area was larger (10,624 km^2 versus 7,472 km^2) the density of bears was 4-fold higher in the mountains. Again, bears that lived on the plateau had the highest number of deaths recorded closest to decommissioned or secondary logging roads (n = 84), followed by primary logging roads (n = 8), and the highway (n = 6). Similar to the plateau, the majority of mountain bears in the Province's database had the highest number of deaths recorded closest to secondary and decommissioned logging roads (n = 43), followed by primary logging roads (n = 8), and the highway (n = 1).

4.11 Modeling Mortality

Grizzly bears on the plateau were 12 times more likely to die in urban areas, followed by 3 times for pine-dominated stands, than their reference category of spruce landcover (Table 2-8, Fig. 2-7). Conversely, bears were least likely to die in shrub-dominated habitat. For the remaining landscape types confidence intervals overlapped 0, suggesting poor precision. Grizzly bear mortalities also were more likely in areas with low greenness scores (i.e., less productive vegetative habitat).

Using the Province's database to assess risk of human-caused mortality on the plateau, we were unable to detect whether grizzly bear kills were associated with closer distance to roads because confidence intervals for all road types overlapped 0. We attribute this to the low use of habitats adjacent to the Highway by plateau bears, occurring on only 17 of 972 occasions compared with 6 deaths. Similarly, 8 grizzly bear died closest to primary logging roads with use occurring on just 99 occasions. Bears were more frequently located closest to decommissioned and secondary logging roads (n = 856 of 972) but so were bear deaths (n = 84). The Spearman's Rank correlation for the plateau model was 0.52 ($P = 0.1$), indicating that this model had overall low internal predictive consistency.

RSF revealed that grizzly bears that lived in the mountains were more likely to die at lower elevations, in areas of low greenness scores, and closer to secondary and decommissioned roads (Table 2-9, Fig. 2-8). The five-fold cross validation provided a mean Spearman's Rank correlation of 0.68 indicating that the mountain risk model had good internal predictive capability and predictions were non-random ($P < 0.05$).

5. DISCUSSION

Population genetics suggests minimal mixing between mountain and plateau bears, consistent with movements recorded during our 6 years of radiotracking. The degree of genetic differentiation in the Parsnip does not suggest complete isolation between the mountains and plateau but suggests a much lower level of connectivity than expected (D. Paetkau, Wildlife Genetics International, pers. comm.; Proctor 2003). Our results are similar to the Purcell Mountains (F_{ST} score of 0.024) as compared to the Rocky Mountains (F_{ST} score of 0.035) (Proctor 2003). In the Purcell Mountains, human-settled valleys limited genetic exchange by reducing male movement and there was "no evidence of female movement" (Proctor 2003:25). In our study area, the partitioning of the genetic structure resulted in a slight population sub-structure; thus, we did not identify 2 distinct populations but also we could not conclude that there was 1 continuous population. We considered the following explanations on why mountain and plateau bears did not mix: (1) cultural learning tradition, i.e., mountain bears teach their offspring how to live in mountains; (2) matriarchal female social structure (Støen et al. 2005); (3) inverse density dependence dispersal (Swenson et al. 1998); (4) mortality is higher for dispersers (Proctor 2003); and/or, (5) a combination of the aforementioned.

We could find only one study where long-distance dispersal by female bears was attributed to increased density: density of black bears (*U. americanus*) became so high that 2 adult females dispersed off of Long Island, Washington (Taylor 1994). For grizzly bears, female dispersal has been reported for expanding populations in Scandinavia before they reached carrying capacity (Swenson et al. 1998). Recent methods using mtDNA lineages revealed that some females in Scandinavia were in matrilinear assemblages whereas others dispersed, established a home range in the new area, and then began to form matrilinear assemblages (Støen et al. 2005). However, in most North American studies females establish a home range close to their mothers, whereas males are more likely to disperse greater distances before establishing home ranges (Blanchard and Knight 1991, Mace and Waller 1998, McLellan and Hovey 2001, Proctor et al. 2004). Consequently, in stable or declining populations there appears to be limited potential for the number of breeding females to be strongly influenced by dispersal. Rather, subadult male dispersal has been cited as one of the main mechanisms regulating grizzly bear populations in North America (McLellan 1994). We did not record any female dispersal between landscapes. Rather, we found male sex bias dispersal from the mountains to the plateau and some adult male migration between the landscapes. Male sex-biased dispersal and kin-relatedness have the ability to influence social organization (Støen et al. 2005). The overlapping home ranges of female bears, especially in the mountains, may support evidence for the matriarchal female social structure (Støen et al. 2005), leading to little female dispersal. Støen et al. (2005) claim that habitats with sufficient resources may allow for the formation of matrilinear assemblages with competition over resources determining whether female dispersal occurs.

We also recorded significantly larger home range sizes for bears that lived on the plateau as compared with those in the mountains. It has been found that as food abundance increases home range size decreases (Ims 1987, Schoen 1990, Tufto et al. 1996), suggesting that habitat quality was more concentrated in the mountains than on the plateau. We suggest that the large home range size of plateau bears may be attributed to more dispersed forage items on the plateau. Bears in the mountains can access a variety of different habitats within a small area because of altitudinal variation in habitat types, whereas bears on the plateau may have to move further to locate the same variety of habitats. Similarly, bears on the plateau might have expanded their movements in search of moose carcasses or hunting opportunities. Bears on the plateau were found to feed on moose, and some bears were shot in association with hunter-killed moose carcasses, however, neither was recorded for bears in the mountains. An alternate explanation may be attributed to the inferior condition of female bears in the mountains. It is possible that smaller body weights and poor condition of female bears in the mountains meant that they did not have the nutritional condition to conduct long search times if those searches did not result in locating high quality forage items. Finally, home range size may simply be a reflection of the difference in densities (Nagy and Haroldson 1990). Therefore, because plateau bears were at a lower density than mountain bears there should be less competition for resources allowing plateau bears to expand their home range. Home range size is also influenced by the number of telemetry locations with a higher number of locations providing more accurate estimates (White and Garrott 1990, Seamen et al. 1999). We do not believe we were missing a lot of extended movements made between flights by mountain bears because bears were flown at the same frequency.

Since there appeared to be minimal movement between the mountains and the plateau, we investigated whether the 4-fold difference in density was primarily due to differences in reproductive parameters and/or mortality rates within the two areas. As populations approach carrying capacity ecological theory suggests reduced survivorship, recruitment, and/or dispersal must occur (Caughley 1977). Parameters most likely to be reduced with increased bear density are the production and survival of cubs (Taylor 1994). Conversely those vital rates should be higher in areas with bear densities far below carrying capacity

(Garshelis 1994). Cubs-of-the-year born to mountain females had high mortality. The cause of COY mortality is unknown but may have been due to poor nutrition or intraspecific killing. Intraspecific killing of cubs has often been reported for bears (Taylor 1994, Wielgus and Bunnell 1995, Swenson et al. 1997), and we located one cub that was probably killed by a male grizzly. Also, 1 adult mountain female's death was attributed to intraspecific killing, while the other was possibly due to intraspecific killing. For density dependence to regulate a population one or more vital rates must decrease with increasing density (Sinclair 1989). For bears those vital rates are normally intraspecific killing and/or dispersal (McLellan 1994:15). Results suggest that the mountain bear population was primarily regulated by natural limiting factors, including poorer nutrition and probably increased intraspecific killing.

Unlike the mountains where grizzly bears were more likely to die of natural causes, human-caused mortality was the only documented source of bear deaths on the plateau. Adult and subadult bears on the plateau had a 7 times greater chance of dying than those in the mountains. Based on body size and condition, the density of bears that lived on the plateau appeared to be below what would be expected on the basis of available food resources. The low survival rates of the plateau bear population suggest that it was limited by human-caused mortality.

Grizzly bear population growth rates are sensitive to adult female survival (Knight and Eberhardt 1985, McLellan et al. 1999, Boyce et al. 2001, McLoughlin et al. 2003). Survival for adult female bears that lived in the mountains were similar to those reported in the southern Rocky Mountains (McLellan et al. 1999, adult female 0.95-0.96). Plateau females, however, had lower survival than mountain counterparts. Furthermore, survival for subadult females that lived on the plateau was low. Non-reported kills also were higher for females than males. In 5 years of intensive trapping we captured only 3 males that lived on the plateau ≥ 7 years of age; the majority of subadult males did not appear to survive to become adults. Similar to our findings, Miller (1990*a*) found that subadult and adult males became rare when hunting pressure was increased in a heavily hunted area of Alaska.

The pattern of bear mortality was consistent between the Province's database and our sample of study animals; more plateau bears died than mountain bears despite the lower density of plateau animals. Further, the majority of grizzly bear deaths occurred closest to secondary/decommissioned logging roads as compared with primary logging roads or highways. However, by employing a logistic discriminant analysis that contrasted bear mortality locations with bear-use locations, we were able to document that urban areas were riskier places for grizzly bears on the plateau than roads. We attribute this to the infrequent bear use of urban areas; however, when bears used those areas they experienced high mortality rates. Indeed, the mortality analysis confirmed that areas with high human activity are the riskiest places for bears to inhabit, a finding that is consistent with other grizzly bear mortality studies (Mattson and Merrill 2002, Nielsen et al. 2004).

High mortality risk areas that have the potential to reduce or eliminate populations have been termed "attractive sinks" (Delibes et al. 2001) or "ecological traps" (Battin 2004). In these situations, animals are attracted to areas of poor-quality habitats, e.g., bears selecting areas with low greenness scores such as urban environments or bears selecting high quality foraging habitats that also have a high risk of mortality. Attraction of animals to poor quality habitat can have serious population-level consequences and may result in extirpation (i.e., ecological trap) (Kristan 2003). Kristan (2003:457) writes that "preferential use of poor habitat elevates extinction risk" making ecological traps more detrimental to population persistence than source-sink dynamics.

In addition to the lethal removal of bears from urban areas, we believe that the low use by bears of habitats surrounding highways and primary logging roads might also reflect learned displacement by some bears from ecological traps, causing them to seek out areas with lower human use, such as those adjacent to secondary/decommissioned logging roads. In an experimental study with treefrogs (*Hyla chrysoscelis*) and fish predators, it was found that some habitats adjacent to areas with high predation become “guilty by association” (Resetarits 2005:484). In these situations, animals’ actively avoid suitable habitats because they perceive them as unsuitable (Resetarits 2005). We believe that this avoidance behaviour might be an additional factor in determining the distribution of animals on the landscape. Similarly, with our radiocollared sample, the number of bears dying in close proximity to secondary and decommissioned logging roads was over four times that of highways or primary logging roads; however, because of the higher bear use (i.e., less displacement) surrounding secondary logging roads we were unable to detect selection for or against secondary roads when employing a logistic discriminant analysis. Certainly the high removal of bears from backcountry areas reduces the local density of the bear population, and may ultimately represent a risk to the population.

In our study area human use of the backcountry landscape was unpredictable; plateau bear deaths coincided with the timing of hunting for other game species, such as moose. Hunting for moose begins 10 September and ends 5 November, averaging about 10,000 hunter days on the study area. The majority of moose hunting corresponds with the rut, occurring in our study area from late September to mid-October. This late-fall period corresponded with the majority of bear deaths, and all bears killed in the fall were on the plateau. Some bears appeared to be attracted to hunter kills during the fall hyperphagia period, making them vulnerable to being shot. Other bears appeared to be wary of human activity and remained in difficult to access backcountry areas; when human use of a landscape is unpredictable it becomes difficult for these bears to develop risk-avoidance strategies necessary to avoid conflicts with humans (Herrero 1985, Jope 1985, McLellan and Shackleton 1989, Mace et al. 1996). For wary bears, this results in reducing bear density in areas where habitat still exists to support them.

Excluding COYs, the primary source of bear mortality occurred from humans killing bears without a permit. Our findings support the hypothesis of Mattson et al. (1996) that grizzly bear deaths were dependent upon the type and frequency of contact between bears and humans; the number of people carrying firearms on the plateau landscape increased substantially in the fall. The density of bears on the plateau was affected by bears being shot and habitat alteration (i.e., urban areas). Our results are consistent with those reported in Alaska, where a heavily hunted portion of Susitna drainage contained half the density of grizzly bears of an adjacent lightly hunted area (Miller 1990*b*).

To access timber, forestry activities create roads, which in turn facilitates human access. This access allows for a myriad of human activities further into formerly pristine habitats, bringing humans and bears into closer contact. Each year forestry activities made their way further up the major river valleys leading from the plateau into the mountains. Because most study bears died near secondary logging roads, we conclude that access leads to high human-caused bear mortality. We predict bear mortality will increase in the mountains if roads are built there without any access management process in place. Indeed, we documented 1 mountain male shot while feeding in a mountain cutblock, and mortality modelling for the mountain landscape tended to identify similar risk factors to the plateau, such as closer distances to roads and lower greenness scores. We also documented genetic differentiation and male sex-biased dispersal. Based on the lack of female dispersal between landscapes we do not believe that female dispersal from the mountains will buffer the high mortality rates on the plateau.

5.1 Management Implications

The road access created by industrial activities within interior BC grizzly bear habitat appears to be a greater threat to the bears than the direct habitat change caused by those activities. We believe that society wants to maintain grizzly bears but it is not clear what density most people would find acceptable. From our data it appears that grizzly bear survival would likely be higher if harvesting activities were carried out with fewer permanent roads. To sustain grizzly bears on industrial forest landscapes we recommend the following:

i. Coordinate access planning to minimise the amount and duration of active roads. Specifically, logging plans should minimize the need for permanent roads, thereby providing a perpetual supply of large ‘roadless’ areas on the landscape.

ii. Limit unauthorised use of roads by regulations or physical barriers.

iii. Conduct effective and immediate deactivation of all unnecessary roads, especially for passage by 4x4 and all terrain vehicles.

iv. Provide adequate enforcement to reduce grizzly poaching.

v. Increase hunter education to ensure that hunters understand that it is not acceptable to kill a grizzly if it takes your game. Hunter education courses should include a component on how to reduce human-bear conflicts while hunting in grizzly bear country.

Table 2-1. Rank of 7 resource selection function candidate models indicating the relative risk of mortality for grizzly bears inhabiting the plateau landscape of the Parsnip River study area, British Columbia, Canada. Models were estimated by comparing mortality locations with non-mortality locations.

Rank	Candidate model variables	AIC_c	ΔAIC_c	$AIC_c w$
1	Rds- distance to highway, primary logging, secondary/decommissioned Predominate forest cover types (withheld Spruce) Greenness	623.75	0	1.00
2	Rds- distance to highway, primary logging, secondary/decommissioned Greenness Elevation	666.67	42.92	4.78E-^{10}
3	Rds- distance to highway, primary logging, secondary/decommissioned Stand age (categorical)	669.01	45.26	1.49E-^{10}
4	Rds- distance to highway, primary logging, secondary/decommissioned Greenness	669.98	46.24	9.11E-^{11}
5	Rds- distance to highway, primary logging, secondary/decommissioned Stand age (continuous)	680.72	56.97	4.26E-^{13}
6	Rds- distance to highway, primary logging, secondary/decommissioned	680.77	57.02	4.15E-^{13}
7	Distance to cutblock Greenness	683.08	59.34	1.3E-^{13}

Table 2-2. Rank of 7 resource selection function candidate models indicating the relative risk of mortality for grizzly bears inhabiting the mountain landscape of the Parsnip River study area, British Columbia, Canada. Models were estimated by comparing mortality locations with non-mortality locations.

Rank	Candidate model variables	AIC_c	ΔAIC_c	$AIC_c w$
1	Rds- Distance to primary logging, secondary/decommissioned Greenness Elevation	361.84	0	1.00
2	Rds- Distance to primary logging, secondary/decommissioned Predominant forest cover types (withheld spruce) Greenness	372.86	11.02	4.02E^{-03}
3	Rds- Distance to primary logging, secondary/decommissioned Elevation	383.05	21.21	2.46E-^{05}
4	Rds- Distance to primary logging, secondary/decommissioned Stand age	395.97	34.13	3.86E-^{08}
5	Rds- Distance to primary logging, secondary/decommissioned Greenness	398.95	37.11	8.69E-^{09}
6	Elevation	399.72	37.88	5.92E-^{09}
7	Rds- Distance to primary logging, secondary/decommissioned	419.26	57.42	3.39E-^{13}

Table 2-3. Reproductive status at den emergence for female grizzly bears by mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada, for all sample years (1997-2003). Bears monitored for multiple years were assessed each spring for their reproductive status and have been treated as independent.

Group	Mountains (%)	Plateau (%)	
	mothers	mothers	mothers
	≥7 year only	all ages	≥7 year only
Adult female producing COYs	21	24	17
Adult females with offspring >COYs	30	55	57
Lone females	49	21	26
		$P = 0.010$	$P = 0.058$

Table 2-4. Frequency distribution of the condition of 59 grizzly bears at the time of initial capture for mountain and plateau landscapes of the Parsnip River study area for all sample years (1997-2002). Only the first capture event for each animal was used. All summer captures occurred after 31-August.

	Mountain				Plateau				
Group	Excellent	Good	Fair	Poor	Excellent	Good	Fair	Poor	No comment
Females - Spring		2	1	13		5	1	2	
Females - Summer					1		1		1
Females - Fall		1		1	3	3	1		1
Females - Total	**0**	**3**	**1**	**14**	**4**	**8**	**3**	**2**	**2**
[1]Males - Spring	2	1	1	6	2	2	1	3	1
Males - Summer						1	1		
Males - Fall		1							
Males - Total	**2**	**2**	**1**	**6**	**2**	**3**	**2**	**3**	**1**
Total	**2**	**5**	**2**	**20**	**6**	**11**	**5**	**5**	**3**

Table 2-5. Staggered entry Kaplan-Meier annual survival estimates by groups for grizzly bears in mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada, for all sample years combined (1997-2003). Four male bears that died were not used in these estimates due to the length of time between last contact and their death (>14 days).

Group	Annual Survival Rate	SE	CV	L95%CL	U95%CL	*n*	*n* dying	*n* censored
Plateau – females (all ages)	0.82	0.07	0.09	0.68	0.96	18	5	0
Mountain – females (>7 years)	0.96	0.02	0.03	0.92	1.00	18	2	0
Plateau - females >7 years	0.92	0.08	0.09	0.76	1.00	8	1	0
Plateau - females <7 years	0.77	0.10	0.13	0.57	0.97	10	4	0
Plateau – males (all ages)	0.66	0.14	0.22	0.38	0.94	14	4	3 males
Mountain – males (all ages)	1.00					8	0	1 male
Plateau – males >7 years	1.00	0.00				3	0	0
Plateau – males <7 years	0.62	0.16	0.25	0.31	0.92	11	4	3 males
Mountains and Plateau (all bears)	0.895	0.03	0.03	0.84	0.95	58	11	4 males
Plateau – all males & females	0.79	0.06	0.08	0.66	0.91	32	9	3 males
Mountain – all males & females	0.97	0.02	0.02	0.93	1.00	26	2	1 male

Table 2-6. Grizzly bear cub survival by mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada, for all sample years (1997-2003). Mothers that lost radiocollars while in the company of young and have been omitted. Bears monitored for multiple years were treated independently.

	Mountain					Plateau				
Age class	*n* family groups	*n* cubs	Survived	Died	% Dying	*n* family groups	*n* cubs	Survived	Died	% Dying
COYs	10	19	7	12	63	6	13	13	0	0
Yearlings -known	4	8	6	2	25	6	14	10	4	29
2 yrs. old -known	3	7	6	1	14	1	3	3	1	33
3 yrs. old -known	1	2	2	0	0	0				n/a
1 or 2 yrs. old	0				n/a	1	2	2	0	0
2 or 3 yrs. old	5	6	6	0	0	2	4	4	0	0
3 or 4 yrs. old	1	1	1	0	0	1	2	2	0	0
4 or 5 yrs. old	0				n/a	1	2	2	0	0
TOTAL	24	43	28	15		18	40	36	5	

Table 2-7. Causes of mortality for radiocollared grizzly bears by mountain and plateau landscapes surrounding the Parsnip River study area, British Columbia, Canada, 1998-2003.

Cause	Mountains	Plateau
Natural	2 (67%)	0
Human caused – permitted	1 (33%)	3 (33%)
Human caused – not permitted	0	5 (42%)
Human caused – problem wildlife	0	2 (17%)
Unknown	0	2 (17%)
Total	3	12

Table 2-8. Resource selection function model indicating the relative risk of grizzly bear mortality in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1990–2003, (n = 106).

Variables	$ß$	S.E.	L95%CL	U95%CL	AIC_c	$AIC_c\Delta$	AIC_cw
Greenness	-0.026	0.013	-0.051	$-3.10E^{-04}$	623.75	0.00	0.58
Mixed wood	-0.330	0.419	-1.151	0.491			
True firs	0.298	0.438	-0.560	1.156			
Pine	1.137	0.265	0.617	1.657			
Shrub	-2.257	1.023	-4.261	-0.253			
Swamp	0.308	0.565	-0.799	1.415			
Urban	2.494	0.494	1.525	3.462			
Distance to highway	$-2.1E^{-05}$	$2.2E^{-05}$	$-6.5E^{-05}$	$2.34E^{-05}$			
Dist. to primary logging road	$-1.1E^{-04}$	$7.1E^{-05}$	$-2.5E^{-04}$	$2.97E^{-05}$			
Dist. to secondary & decommissioned logging roads	$1.2E^{-04}$	$2.0E^{-04}$	$-2.7E^{-04}$	$5.12E^{-04}$			

Table 2-9. Resource selection function model indicating the relative risk of grizzly bear mortality in the mountain landscape of the Parsnip River study area, British Columbia, Canada, 1990–2003, (n = 55).

Variables	β	S.E.	L95%CL	U95%CL	AIC_c	$AIC_c\Delta$	AIC_cw
Greenness	-0.054	0.012	-0.078	-0.030	361.84	0.00	1.00
Elevation	-0.004	0.001	-0.006	-0.003			
Dist. to primary logging road	$5.90E^{-06}$	$3.1E^{-05}$	$-5.4E^{-05}$	$6.57E^{-05}$			
Dist. to secondary & decommissioned logging roads	$-2.5E^{-04}$	$7.1E^{-05}$	$-3.9E^{-04}$	$-1.11E^{-04}$			

Figure 2-1. Study area for monitoring grizzly bear survival, including mountain and plateau boundary just east of the Parsnip River, British Columbia, Canada, 1998 to 2003. The DNA based population census boundary is represented by the shaded box contained within the core of the larger study area and encompassed both mountain and plateau landscapes. The polygons represent 100% MCPs for female bears for all sample years combined (1998-2003).

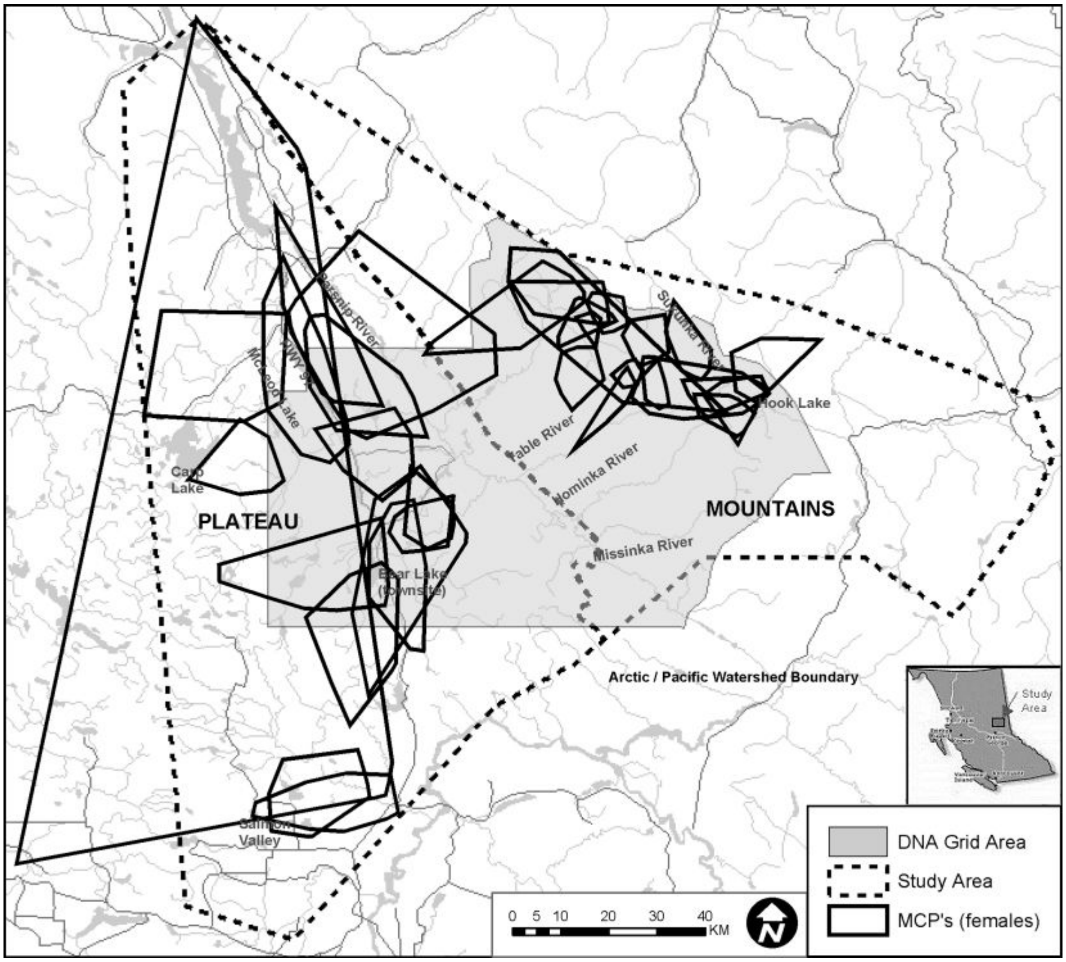


Figure 2-2. Relationship between chest girth and body weight using known bear weights for grizzly bears (*n* = 28) in the Parsnip River study area, British Columbia, Canada, 1997-2002, compared with Jonkel's (1993) estimated chest girth-weight relationship.

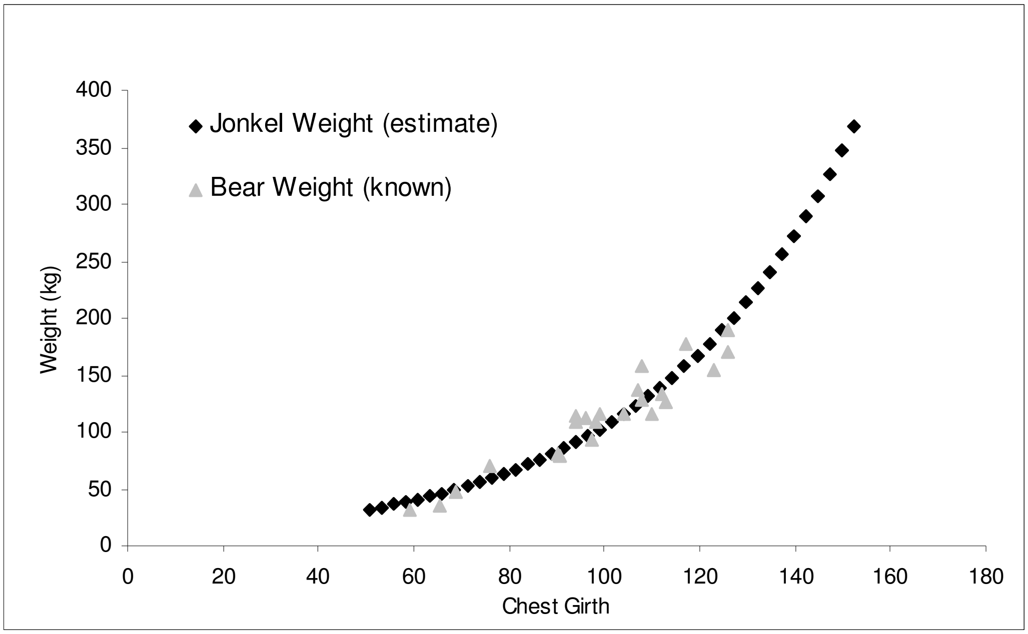


Figure 2-3. 100% minimum convex polygons for male grizzly bears in the Parsnip River study area, British Columbia, Canada, for all sample years combined (1998-2003). The dashed line indicates the boundary between the mountain and plateau landscapes.

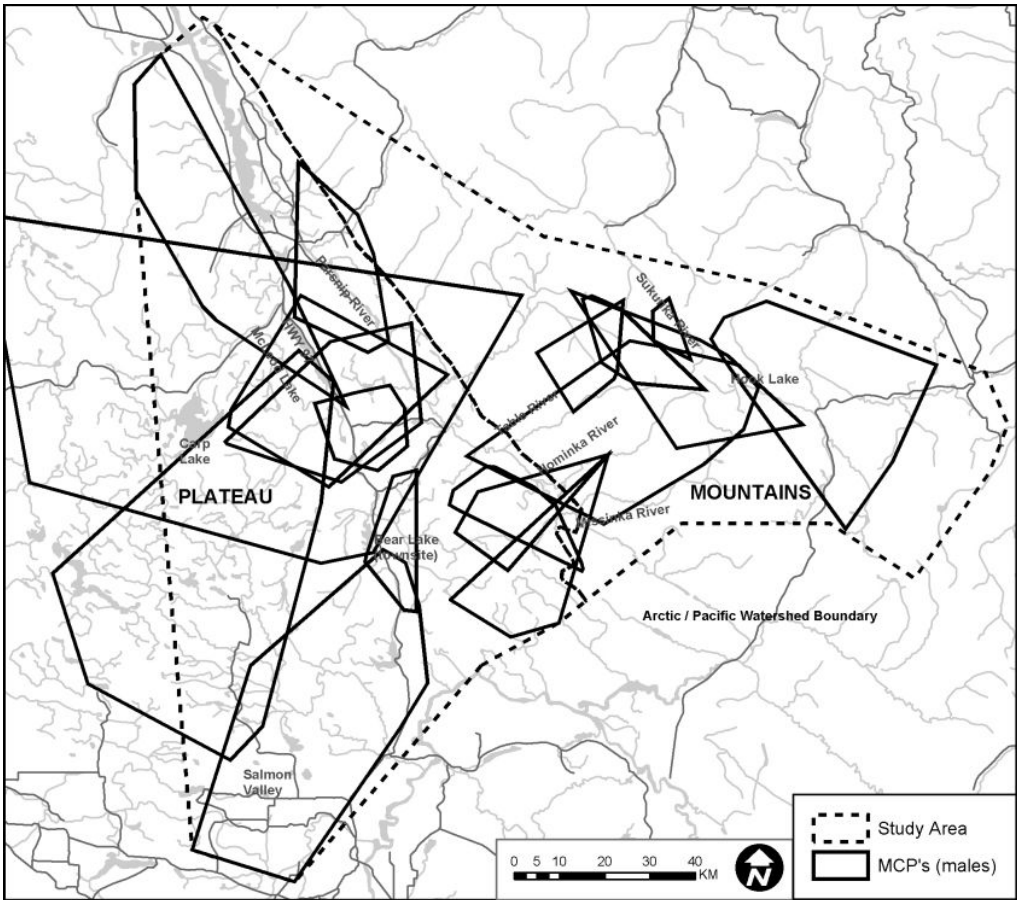


Figure 2-4. Population assignments of grizzly bears in the Hart Ranges of the Rocky Mountains (*n* = 101) versus the Parsnip Plateau (*n* = 32), British Columbia, Canada. Axes are the log of the probabilities of assignment to each population. Four bears, 1 female and 3 males, caught on the plateau were between 500 and 10,000 times more genetically similar to the mountains than the plateau.

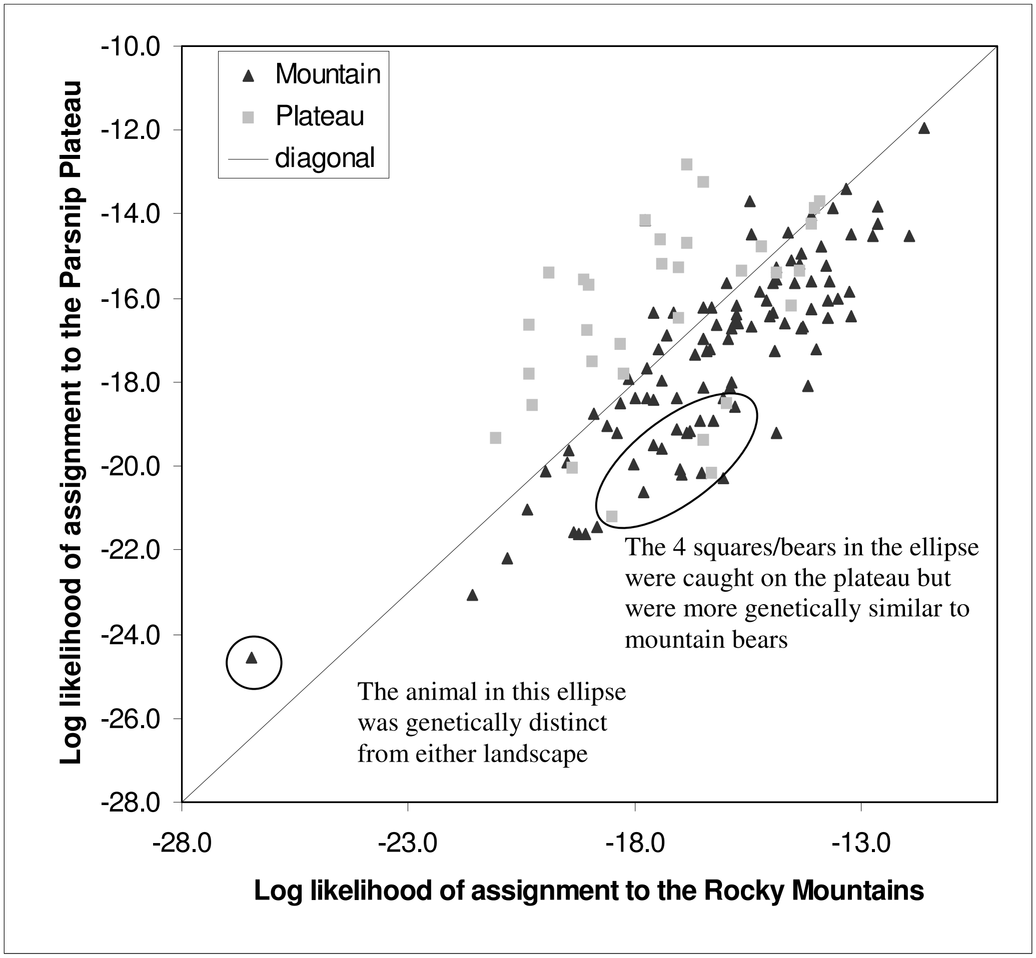


Figure 2-5. Comparisons of mean initial capture weights by age classes for grizzly bears in mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada, for all sample years (1997-2002). Only the first capture event for each animal was used. Subadults and juveniles were bears <4 years of age. Adults were bears $\geq$4 years of age as long as they were not accompanied by their mother. Spring captures occurred from late April-beginning June. Fall captures occurred September-mid-October. Differences were calculated in kilograms between the same groups in each landscape.

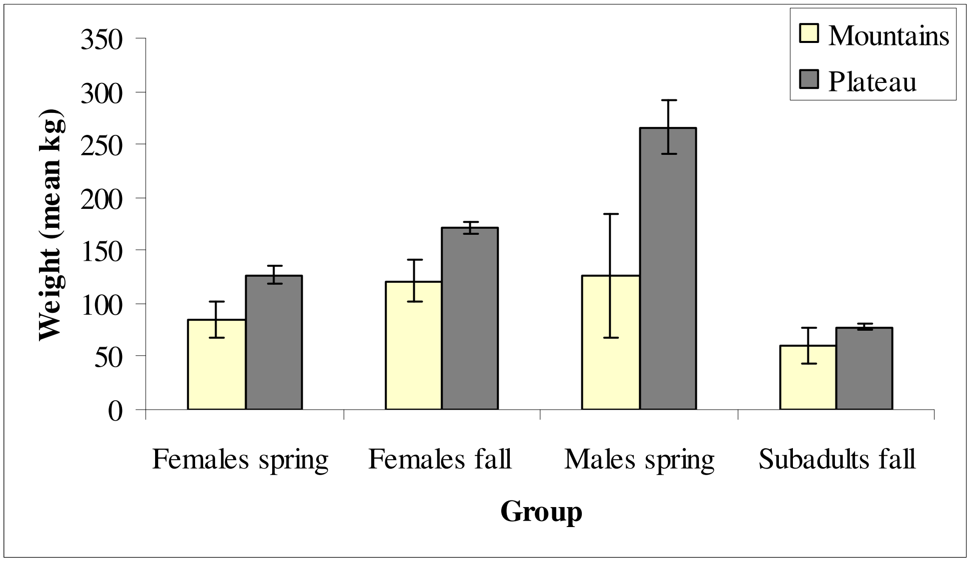


Figure 2-6. Frequency of 15 grizzly bear deaths by 2-week period in the Parsnip River study area, British Columbia, Canada, for all sample years (1998 to 2003) for grizzly bears in mountain and plateau landscapes. We defined spring as being from den emergence to 14-July, summer from 15-July to 20-September, and fall from 21-September to den entry. Arrows indicate the placement of the 2 natural and 1 unknown death.

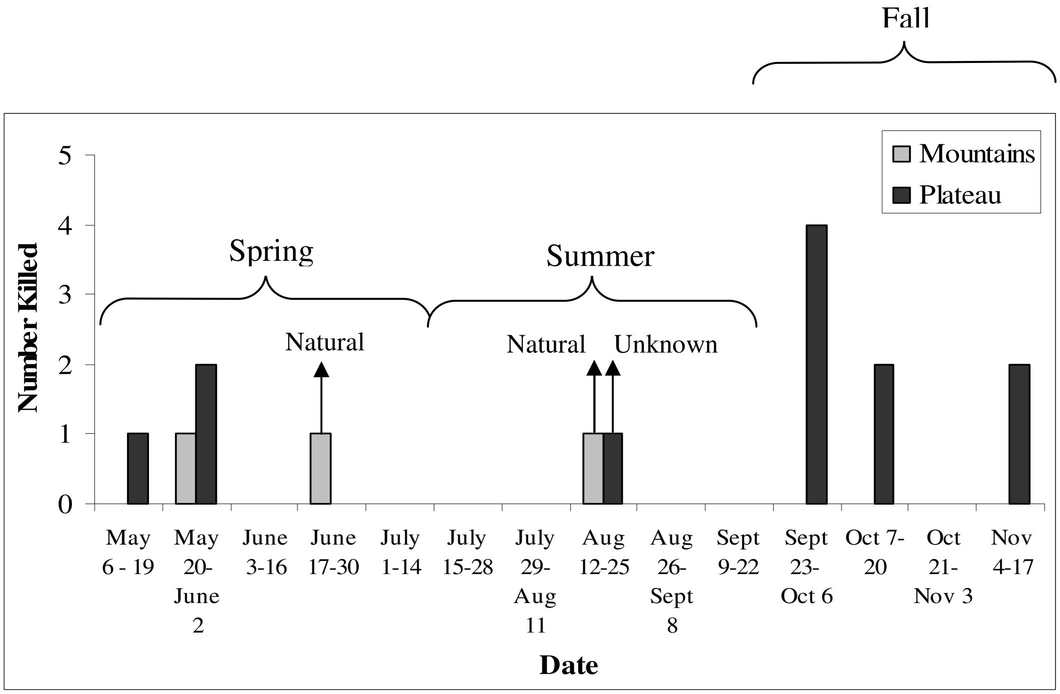


Figure 2-7. Relative risk of human-caused mortality for grizzly bears inhabiting the plateau landscape of the Parsnip River study area, British Columbia, Canada, calculated using the BC government's compulsory inspection database, 1990-2003 (*n* = 98). Orange areas represent an increased relative probability of risk (greater RSF values).

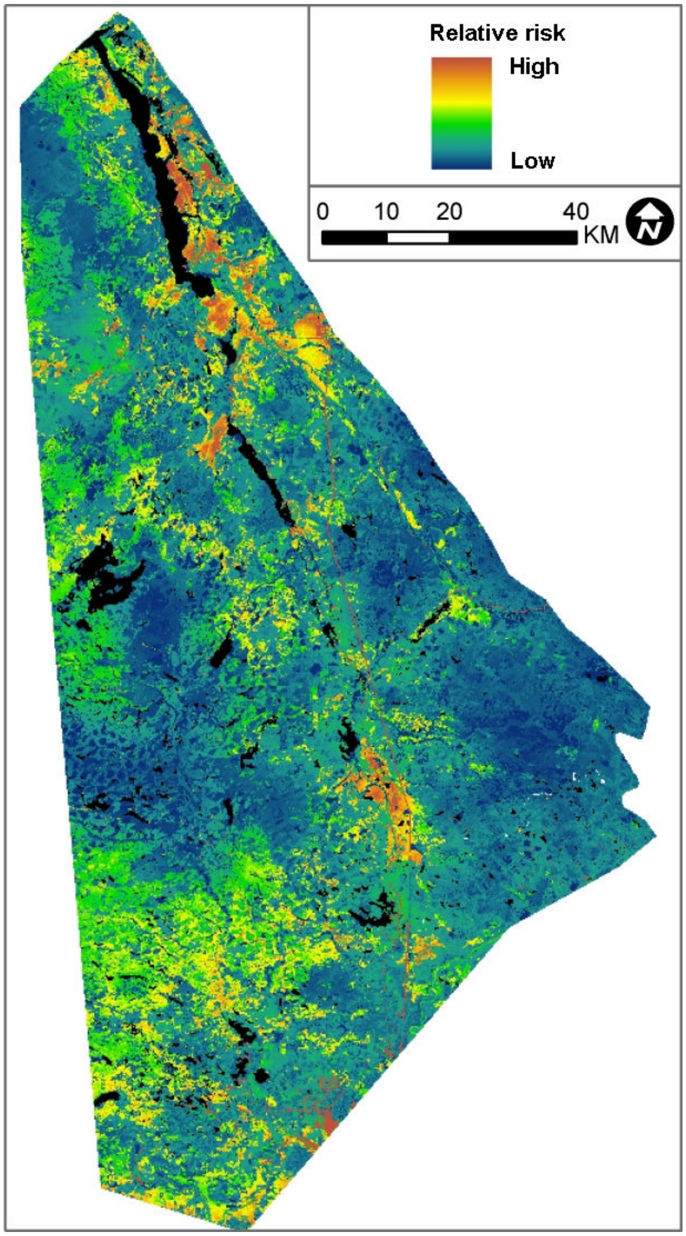
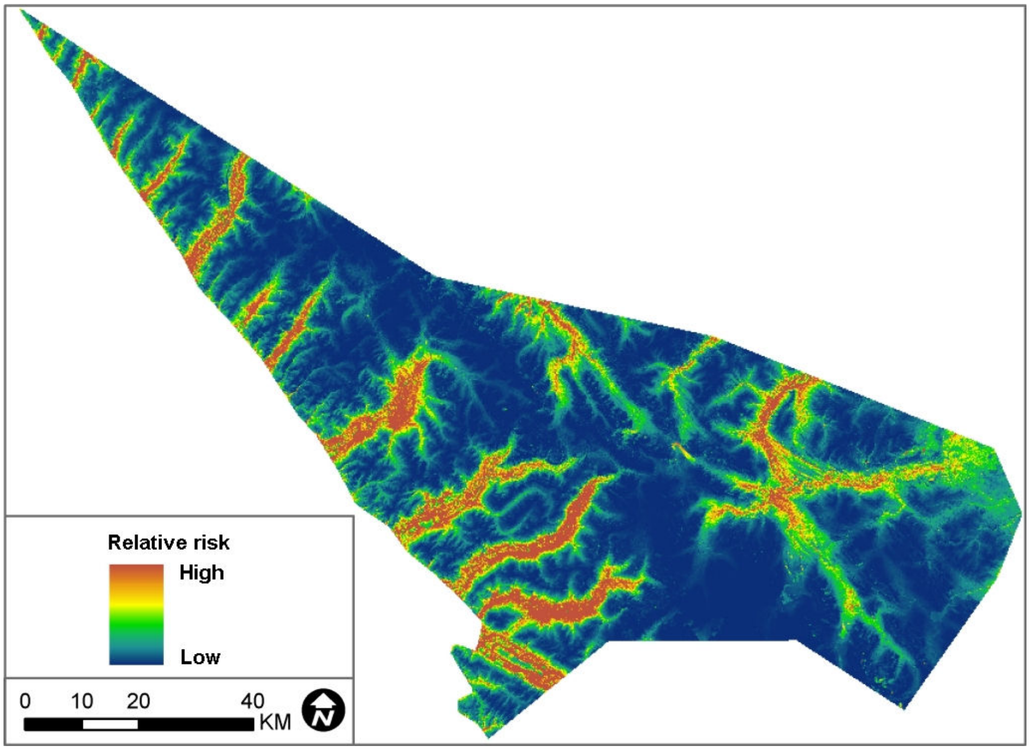


Figure 2-8. Relative risk of human-caused mortality for grizzly bears inhabiting the mountain landscape of the Parsnip River study area, British Columbia, Canada, calculated using the BC government's compulsory inspection database, 1990-2003 (*n* = 52). Orange areas represent an increased relative probability of risk (greater RSF values).



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CHAPTER 3
COMPONENTS OF GRIZZLY BEAR HABITAT SELECTION: DENSITY, HABITATS, ROADS, AND MORTALITY RISK

1. INTRODUCTION

Landscapes contain temporal and spatial variation among and within habitat patches (Southwood 1977), and habitat selection has a direct impact on population density and behaviour (Rosenzweig 1981). The abundance and distribution of organisms, or in reference to one species, population structure, partly result from their preference for certain habitat types. Frequently, the spatial distribution of foods has been used to explain the spatial distribution and dynamics of animals (MacArthur and Pianka 1966, Charnov 1976). In theory, an animal living in a patchy environment should seek to optimize its foraging strategy by choosing richer patches over poorer patches (Charnov 1976). Therefore, animal populations are expected to have a higher density in richer patches. Also, the risk of predation has been found to influence decisions made by animals (Lima and Dill 1990, Donovan and Thompson 2001), and experimental studies have shown that avoidance of predation risk can alter habitat selection (Gilliam and Fraser 1987, Abrahams and Dill 1989, Resetarits 2005).

In our study area, a relatively pristine mountainous landscape contained 4 times the density of grizzly bears as an adjacent plateau landscape that was heavily harvested for timber (Mowat et al. 2005). The distribution of foods (Mace et al. 1996, Mace et al. 1999, McLellan and Hovey 2001) and/or human-caused mortalities (Mattson and Merrill 2002, Nielsen et al. 2004) are recognized as primary determinants of the abundance of grizzly bears. High quality habitats close to areas of human use are often areas of high bear mortality (Knight et al. 1988, McLellan 1989, Mattson and Merrill 2002, Nielsen et al. 2004) thereby negatively affecting population productivity (Mattson and Merrill 2002). Further, areas of low quality habitat that attract individuals may also be low in both survival and/or recruitment ultimately acting as local population sinks, or "ecological traps" (Delibes et al. 2001, Kristan 2003). Consequently, individual occurrence and abundance are not necessarily related to habitat quality (Hobbs and Hanley 1990, Kristan 2003).

We found that grizzly bears that lived on the plateau were significantly heavier and in better condition than bears that lived in the mountains (Ciarniello chpt. 2). In areas with high food availability, particularly meat items, bears tend to have increased reproductive success, larger body mass, and a higher population density (Hilderbrand et al. 1999). In our study area, we observed significantly larger body masses and better condition in our low-density area (i.e., the plateau). We concluded that the density of bears on the plateau was limited by human-caused mortality linked to access afforded by forestry activities rather than differences in habitat quality (Ciarniello chpt 2). In this paper, we evaluate this conclusion using 2 methods: (1) examining the foods consumed by bears that lived in the mountains compared with those that lived on the plateau to investigate whether bears on the plateau were limited by available forage; and, (2) modeling the relationship between habitats and population structure using mechanistic and/or statistical approaches to habitat selection.

Recent modeling techniques in habitat selection focus on establishing a link between habitats and population structure (Rosenweig and Abramsky 1997, Boyce and McDonald 1999, Manly et al. 2002, Boyce and Waller 2003). Population dynamics are determined in part by how resources are distributed. Similarly, where to forage, what forage to use, and the density of competitors can contribute to which individuals compete both through inter- and intraspecific competition. Thus, habitat structure and population structure collectively drive evolutionary patterns making them key to understanding population dynamics (Schlaepfer et al. 2002).

Habitats for grizzly bears can be modeled statistically using resource selection functions (RSF; Manly et al. 2002) facilitated by applications of geographical information systems (GIS; Mace et al. 1996, 1999). Although these models are simply statistical descriptions of use of the landscape, if reference areas exist where densities are known, RSF models can be linked to populations (Boyce and McDonald 1999). Furthermore, using radiotelemetry to study use of habitats by individual grizzly bears, we can distinguish variation in resource use among individuals, which can be important at the population level (see Sutherland

1996, White 2000). By combining the results of the DNA mark-recapture census with habitat based density-modeling techniques we are able to distribute density across the landscape based on RSF scores. In particular, the habitat based density modeling was used to evaluate whether the difference in densities was attributed to differences in habitat, roads, and/or the risk of human-caused mortality. We believe that such a link between habitat and population models is a powerful approach for anticipating the consequences of human activities on grizzly bears.

2. STUDY AREA

The 18,096-km^2 study area was centered along the Parsnip River, in central-eastern British Columbia, Canada (54°39'N, 122° 36'W) (Fig. 3-1). The ecosection line, as delineated by the BC Ministry of Water, Land and Air Protection (Victoria, BC), represents a topographic division between a plateau (10,624 km^2) that contained rolling hills and flat valleys, and the west and east slopes of the Hart Ranges of the Rocky Mountains (7,472 km^2). Elevations ranged from 600-1,650 m in the plateau, and 720-2550 m in the mountains. The plateau was warmer and had less precipitation than the mountains ($\bar{x}$ = 2.6° C, 72 cm rainfall, 300 cm snowfall versus $\bar{x}$ = 0.3° C, 154 cm rainfall, 700 cm snowfall (DeLong et al. 1993, 1994).

The sub-boreal spruce (SBS) biogeoclimatic zone dominated the plateau and some lower-elevation areas in the mountains (e.g., along major rivers). Most forests on the plateau were a mix of white spruce (*Picea glauca*), pine (*Pinus contorta*), and subalpine fir (*Abies lasiocarpa*). Black spruce (*Picea mariana*) bogs occurred in lower elevation wet areas. Interior Douglas fir (*Pseudotsuga menziesii*) occurred in small portions on the plateau and lower elevation mountain valley bottoms. Aspen (*Populus tremuloides*), cottonwood (*Populus balsamifera*), and paper birch (*Betula papyrifera*) were present within these forests, especially along riparian areas and in areas recently disturbed by logging or fires.

The Engelmann spruce – subalpine fir zone occurred above the SBS and dominated in the mountainous portion of the study area. Higher elevation mountain habitats consisted of subalpine parkland predominantly comprised of subalpine fir and Engelmann spruce (*P. engelmannii*). Subalpine meadows supported forbs such as glacier lily (*Erythronium grandiflorum*), Indian helabore (*Veratrum viride*), and arrow-leaved groundsel (*Senecio triangularis*). Large burns within the mountains had abundant huckleberries (*Vaccinium membranaceum*), blueberries (*Vaccinium myrtilloides*), and Canadian buffalo-berry (*Shepherdia canadensis*). The alpine-tundra biogeoclimatic zone began at approximately 1,400 m and typically consisted of small shrubs or krummholtz, heath communities. Barren rock or alpine snow and ice at elevations over 2,400 m were <1% of the study area.

The study area was heavily harvested for timber and logging was expanding in 4 main river valleys (Missinka, Hominka, Table, and Anzac Rivers) leading from the plateau into mountainous areas. On the plateau, the majority of logging had taken place within the last 50 years, resulting in a mosaic of forest habitats in various successional stages. There were 2 resource-based towns, 3 backcountry-logging camps, 2 sawmills, and an extensive network of forestry roads. A 2-lane paved highway bisected the plateau portion of the study area. In the mountains, the only permanent disturbances to bears were a railway line for coal extraction that extended onto the plateau and road networks expanding up the low-elevation valleys. Recreational activities occurred in both landscapes, including hunting, fishing, snowmobiling, and hiking. The majority of the study area was within the Arctic watershed where bears do not have access to salmon runs. There were two provincial parks within the study area but they were small relative to the size of grizzly bear home ranges.

3. METHODS

3.1 Bear Capture

Grizzly bears were captured using aerial darting, leg snares, or culvert traps and fitted with VHF collars (Very High Frequency, Lotek Inc., Aurora, Ontario), GPS collars (Global Positioning System, Televilt Ltd., Lindesberg, Sweeden), and/or ear tag transmitters between August 1997 and spring 2003. Bears were immobilized with Telazol (tiletamine HCL/zolazepam HCL) at a dosage of 8 mg/kg. Ketamine was used as a top-up drug when necessary at a dosage of 2 mg/kg. A first premolar tooth was extracted for age determination (Mattson's Laboratory, Milltown, Montana). Hair was taken from the shoulder of captured bears for stable isotope analysis. The University of Alberta's Animal Care Committee, following the Canadian Council on Animal Care guidelines and principles, approved bear handling procedures.

3.2 Radiotelemetry

Fourteen bears wore GPS collars for 1or 2 years and VHF collars for the remaining years, thereby having a mix of GPS and VHF data. We did not use the GPS data in the following analyses due to the low fix rate of our GPS collars (Gau et al. 2004) as well as the mixing of VHF and GPS data on some bears. The high failure rate of GPS data was attributed to behavioural activity (i.e., low fix rates when bears were resting), vegetation cover (i.e., fix rates were lower in denser canopies), and battery failure (Ciarniello unpublished data). We recognize that VHF locations also contain bias. For example, locations must be gathered during daylight, thereby being biased against activities that occur at night (Belant and Follmann 2002). Unlike GPS locations, however, VHF telemetry should not be affected by canopy closure, which is an important consideration in habitat selection studies.

Despite the type of monitoring device bears were monitored during May through October at a frequency of twice per week in 1998-2002, once per week in 2001-2002, and once every 2 weeks in 2003 by fixed-wing aircraft. Some aerial locations were obtained from a helicopter. Only low-level locations in which we were confident of the position of the animal were used in analyses. Once the bear was located, Universal Transverse Mercator (UTM) coordinates were taken with a hand-held GPS unit. Locations east of the ecosection line, as delineated by the BC Ministry of Water, Land and Air Protection, were classified as mountain, while locations on the west side were referred to as plateau.

A Polaroid photograph was taken of each bear location. A dot was placed on the photograph marking the location of the bear and a north arrow was provided. The photo was used to identify the location for subsequent microsite habitat investigations.

3.3 Microsite Habitat Investigations

We visited a random sample of bear locations to gain an understanding of the mechanisms of bear use. Site investigations were performed after the bear was known to have left the area and were normally, with the exception of actively fed on carcasses or den sites, less than 7 days old. The centre of a 10 x 10 (100 m^2) plot focused on what we determined to be the primary activity after we were confident that criteria, such as visual location, telemetry reliability, age of the sign, scat, hair, and/or tracks had been met. Because microsite habitat investigations relied on the radiotelemetry data (one point in time) we were limited in our ability to determine the primary activity (e.g., we were unable to watch bears and devise an activity budget). Therefore, rather than using time as a determination of primary activity we defined the primary activity to be the activity with the most bear sign. Bear activities were classified into: foraging (i.e., ants, berries, carcass/meat, cambium, digging for roots, digging for rodents, grazing vegetation, non-natural attractants, or bees/wasps), traveling, mortality of the bear, resting, rub trees, den site, other, or unknown. Statistical comparisons between foods consumed by bears inhabiting the mountains or plateau used Chi-squared tests with significance at $\alpha < 0.05$.

3.4 Stable Isotopes

Stable isotope analysis was used to quantify the relative amount of meat and/or ants in mountain and plateau bear diets. We determined stable nitrogen isotope ratios for grizzly bear guard hairs obtained from barbed-wire strands set around DNA lure sites (Mowat at al. 2005), live captured bears, dropped collars, and den sites. Methods for stable isotope analyses followed Hobson et al. (2000). Hair was cleaned using repeated rinses of a 2:1 chloroform:methanol solution and then air dried for $\geq$24 hours. Approximately 1mg of each sample was sent to the Stable Isotope Facility at University of California at Davis. Nitrogen results represent the deviation in parts per thousand between the 15N/14N ratio in the sample relative to the same ratio in an albumin standard (Hobson et al. 2000). We present stable isotope results in δ notation, as the per mil (parts per thousand) $^{15}N/^{14}N$ ratio of sample to atmospheric nitrogen where:

$$\delta^{15}N = [(^{15}N/^{14}N_{sample}/^{15}N/^{14}N_{standard}) - 1] \times 1000 \qquad (1)$$

3.5 Geographic Information System Data

We selected a set of predictor variables from GIS data that represented habitats believed to characterize selection by grizzly bears (Table 3-1). If correlations between predictor variables were <0.7 we concluded that collinearity was not a problem (Sokal and Rohlf 2000). Correlations >0.7 were not included in the same model.

Terrain resources inventory maps (TRIM2; BC Ministry of Water, Land, and Air Protection, Victoria, Canada) were used to build digital elevation maps (DEM) to obtain elevation, slope, aspect, and hillshade data. Forest cover maps (FCM; BC Ministry of Forests, Prince George, BC) were used to obtain the predominant forest stand and/or landcover type, and stand age. Road networks were built by amalgamating FCM with layers obtained from the major forestry operators within the study area: Canadian Forest Products (Canfor) East, Canfor West, the Pas Lumber, and Slocan Forest Products Ltd., in Prince George, British Columbia, Canada. Raster layers (i.e., DEM, slope, aspect, hillshade, and distance to roads) had a resolution of 25 m. The forestry data (e.g., age, height, forest type) were based on vector GIS layers that were rasterized, also with a resolution of 25m.

Greenness is the second component of the standard "tasseled cap" transformation for Landsat 5 TM satellite data (White et al. 1997) and was calculated for four satellite images using ERDAS® Imagine (Atlanta, Georgia, USA) at a 30 m pixel resolution. Greenness is an index of the amount of green herbaceous phytomass (Mace et al. 1999). Lush green vegetation has high greenness values, sparse or senesced vegetation has lower greenness values, and non-vegetated areas have very low greenness values (Mace et al. 1999).

The mortality risk layer was built by assessing the relationship between grizzly bear morality locations (1), and non-kill locations (0) using logistic regression (see Ciarniello chpt 2). Separate mortality models were estimated for mountain and plateau landscapes (Ciarniello chpt 2). Values were scaled 0-1; with the closer to 1 the more secure the area from the risk of human-caused bear mortality. We then applied the values back to each mountain and plateau landscape to form a layer reflecting the relative probability of human-caused grizzly bear mortality across the study area.

3.6 Resource Selection Functions

Resource selection functions reflecting the relative probability of use for the foraging season were estimated using logistic regression. To capture the primary foraging season, we removed UTM radiotelemetry coordinates when each bear moved to <1 km of its den site for fall and spring. We employed a variation on Design 2 (Manly et al. 2002), third-order selection (Johnson 1980) at the landscape scale because the study area extent was occupied by grizzly bears. With this design, data from individual animals were pooled and GIS attributes were calculated for each bear location (i.e., used units). By pooling data we are assuming that habitat availability was fairly static among years. Availability was by landscape at the population level (Manly et al. 2002). The following log-linear equation was assumed to characterize the influence of covariates on relative use, $w(\mathbf{x})$:

$$w(\mathbf{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 \ldots \beta_p x_p) \qquad (2)$$

where β_i are selection coefficients for each covariate, x_i, for $i = 1,2,\ldots p$, estimated using logistic regression. Bear locations were the used sites, assigned a value of 1, while to characterize availability, 36,192 randomly generated sites were assigned 0 (1 location/500m^2, 14,944 in mountains and 21,248 in plateau). Random points were generated using the program HawthsTools (Beyer 2004) for ArcGIS® 8.3 (Environmental Systems Research Institute, Redlands, California, USA). Models were estimated using Stata 7.0 (Stata Corporation, Texas, USA).

We put forward a set of 5 candidate models that we deemed biologically relevant to grizzly bear habitat use (Burnham and Anderson 1998, Anderson et al. 2000). Model selection was based on Akaike Information Criteria (AIC; Burnham and Anderson 1998). However, to examine whether the lower density of plateau bears was a function of the different landscape attributes we needed the same coefficients in both the plateau and mountain models. Therefore, to make the models comparable we did not necessarily choose the individual model with the lowest AIC score (the most parsimonious model) but rather the best models in which each variable occurred within both landscapes. Normalized Akaike weights (AIC_w) were used to evaluate whether a candidate model was the best model (Anderson et al. 2000). Models with ΔAIC values <2.0 are comparable (Burnham and Anderson 1998). Coefficients with confidence intervals that did not overlap 0 were considered to be statistically significant.

The internal predictive capability of the chosen models were assessed using a Spearman's Rank correlation based on 5-fold cross validation (Boyce et al. 2002). In this procedure, an RSF model was estimated using a random draw of 80% of the data and this model was used to predict the frequency of occurrence in the withheld 20% using 10 RSF bins; the process was repeated 5 times replacing the withheld 20% and removing the next 20% (Boyce et al. 2002). A model that has strong internal predictive capabilities will have a higher number of locations in bins with the highest RSF scores. The highest-ranked mountain and plateau models were interfaced with GIS to create maps of relative probability of grizzly bear use across each landscape.

3.7 Habitat-Based Density Modeling

RSF has been used to link populations to habitats (Boyce and McDonald 1999, Boyce and Waller 2003). We examined density among habitats in the mountain and plateau populations using a method outlined by Boyce and McDonald (1999). First, we calculated an RSF score for each use and random landscape location. Using the random locations we then binned the landscape into 10% increments providing a gradation from the poorest to the most highly selected habitats. Calculations were performed using the square root transformation of $w(\mathbf{x})$ to obtain RSF values that were proportional to probability of use (Keating and Cherry 2004, Johnson et al. 2006). Binned RSF scores were scaled (i.e., 0-1) for each landscape by dividing by the maximum RSF value. Then we calculated the relative use:

$$U(x_i) = \frac{w(x_i)A(x_i)}{\sum_j w(x_j)A(x_j)} \tag{3}$$

where $w(x_i)$ is the bin midpoint RSF value, and $A(x_i)$ is area for the i-th habitat variable, x_i.

Population densities for the mountains and the plateau were obtained from a DNA-based population estimate from spring 2000 at 49 bears/km^2 ((95% C.I. = 43-59) in the mountains and 12 bears/km^2 (95% C.I. = 7-28) in the plateau (Mowat et al. 2005). We estimated the density of animals, $D(\boldsymbol{x})$, by the i-th habitat type using:

$$D(x_i) = \frac{N \cdot U(x_i)}{A(x_i)} \tag{4}$$

Here the density of bears in the mountains or the plateau, N, is divided by the area of relative use, $A(x_i)$, characterized by the respective habitat model. We then used the model for bear habitat selection in the mountains to see how well we could predict densities of bears on the plateau. Conversely, we estimated bear densities that we would expect in the mountains based on the RSF model estimated for the plateau. We individually examined the effects of landcover type, risk of mortality, and primary and secondary logging roads on predicted density of bears in the mountains versus the plateau while holding all other variables constant. To do this we used the coefficients for the variable(s) in question and exchanged them between landscapes. Using the above methods, we recalculated RSF values and density each time a variable was exchanged. Thus, the Boyce and McDonald (1999) method was used to distribute density across the landscape based on RSF scores. Our methods are similar to Manly et al.'s (2002:181-191) galaxiid fish (*Galaxias vulgaris*) and brown trout (*Salmo trutta*) example where they used the known used units for galaxiid fish to predict their presence in streams where competition with trout made their abundance low or absent.

4. RESULTS

We monitored 24 bears that lived in the mountains (17 females, 7 males) and 30 bears that lived on the plateau (17 female, 13 male), resulting in 1,527 locations in the mountains (1,281 female, 246 male) and 972 locations on the plateau (726 female, 246 male).

4.1 Habitat Investigations and Stable Isotope Analysis

We visited 21% of randomly selected bear locations ($n = 534$) to conduct microsite habitat investigations ($n = 202$ mountain, $n = 332$ plateau). Bear foraging was the primary activity identified at 381 of the 534 (71%) sites visited. Grazing on grasses (Poaceae) and forbs was an activity common to both mountain and plateau bears ($\chi^2 = 0.069$, $P > 0.05$). However, bears that lived on the plateau foraged more on berries than bears that lived in the mountains ($\chi^2 = 7.31$, $P < 0.05$). Furthermore, bears that lived on the plateau scavenged or killed more large game ($\chi^2 = 11.72$, $P < 0.05$), and fed on more ants ($\chi^2 = 10.15$, $P < 0.05$) than bears that lived in the mountains. Twenty-seven carcass sites of apparent prey were investigated on the plateau; the majority were moose (*Alces alces*), although black bears (*U. americanus*), domestic cattle, and beavers (*Castor canadensis*) also were recorded. We recorded only one carcass in the mountains, which was a grizzly bear cub-of-the-year believed to have been killed by a radiocollared adult male. On one occasion a mountain bear was believed to be excavating a caribou (*Rangifer tarandus*) carcass from an avalanche path in spring. However, we were not able to access this site due to terrain limitations. Bears that lived in the mountains appeared to obtain the majority of their meat by digging for rodents, which we did not record for bears living on the plateau. We never detected bears eating fish, in part because they were primarily in the Artic watershed and did not have access to any major spawning runs of salmon. From stable isotope analysis we found that the proportion of meat and/or ants was 20-40% in the diet of plateau bears ($n = 14$ females & 10 males, $\bar{x}$ $\delta^{15}N = 5.2\ ^{o}/_{oo}$), as opposed to 2-4% in the diet of bears that lived in the mountains ($n = 66$ females & 17 males, $\bar{x}$

$\delta^{15}N = 3.4^{o}/_{oo}$). Mountain bears dug for roots and bulbs of plants more than plateau bears ($\chi^2 = 43.28$, $P < 0.05$).

4.2 Resource Selection Functions

We present the final RSF predicting the relative probability of grizzly occurrence by landscape (Tables 3-2, 3-3). Of the 5 candidate models examined, this model ranked first in the mountains and second on the plateau. The ΔAIC value for first and second-ranked plateau models was 0.32, indicating that the support for both models was similar (Burnham and Anderson 2002). In the mountains the second-ranked model had an ΔAIC of 3.06, therefore, we chose the first-ranked mountain model.

In the mountains, 10 of the 12 variables measured have confidence intervals that do not include 0, suggesting that those parameters are good predictors of mountain bear use of the landscape (Table 3-2, Fig. 3-2). The 5-fold cross validation provided a mean Spearman's rank correlation of 0.94 ($P < 0.002$), indicating that this model had high internal consistency. On the plateau, 7 of the 12 variables measured have confidence intervals that do not include 0 (Table 3-3, Fig. 3-3). The plateau model also had excellent internal consistency with a Spearman's rank correlation of 0.93 ($P < 0.002$). Although both models did an excellent job of predicting spatial patterns in the probability of use by grizzly bears, overall, more of the covariates contributed significantly to the mountain RSF model than the plateau RSF model.

Mountain bears avoided all forested landcover types relative to the withheld categories (see Table 3-1). Confidence intervals for pine and shrub landcover included 0, suggesting poor inference for those parameter estimates. The probability of detecting selection for the remaining landcover types decreases because to make the models comparable we withheld alpine, which was common within the mountains and highly used by mountain bears. However, to swap the models to examine the effects of habitat covariates on density we had to exclude alpine because we did not have any bear use of the small area of alpine on the plateau. On the plateau, we were able to detect selection by bears for spruce and shrub landscapes. There was no detectable selection for or against true firs, mixed wood, or pine dominated forests by plateau bears.

Common to bears in both areas was selection for open canopies, higher greenness scores, and southwest facing aspects. Southwest aspects are snow free earlier, and remain snow free longer than cooler aspects, which influences food availability in northern environments. Bears in the mountains also avoided landscapes where the risk of mortality was highest. A negative risk value is interpreted as a high risk of mortality in areas with high RSF values (i.e., selected habitats). Bears that lived on the plateau had a higher risk of mortality than those that lived in the mountains.

Interestingly, road coefficients were opposite between the mountain and plateau models. Bears in the mountains were a greater distance than random points from highways and secondary logging roads. However, mountain bears were located closer to primary logging roads. Primary logging roads in the mountains had very little traffic due to their distance from town. In addition, in the mountains some watersheds were largely helicopter logged. In helicopter logging operations logs are transported from the block to primary logging roads using helicopters. Thus, due to the nature of logging in the mountains, there were more primary logging roads than secondary roads.

On the plateau, more bears were located closer to the highway than random. We do not believe that the selection for areas closer to the highway was a true road effect but rather a product of bear use of a pipeline and power-line corridor that paralleled the highway. Those corridors were among the first areas to make available new growth in the spring providing good foraging conditions for bears. Furthermore, there was an increased density of bears as one moved from west to east across the study area, which was confirmed during the DNA population estimate (Mowat et al. 2005). We could not detect selection for or against secondary/decommissioned logging roads. The lack of detectable selection may have been a product of the amount of these road types in the plateau landscape; the average distance from a secondary road on the plateau was

558 m ($\bar{x}$ [highway] = 13.46 km; $\bar{x}$ [primary] = 3.17 km). Plateau bears avoided logging traffic associated with primary logging roads.

4.3 Habitat-Based Density Modeling

In both landscapes there were more bears in bins where the RSF values approached 1 (Fig. 3-4, 3-5), meaning that bears in both areas had the same underlying selection patterns for higher-quality habitats. However, even though the mountains and plateau were adjacent, when we recalculated square-root RSF values using the mountain model with the plateau data (and vice versa), and then compared those results with the observed square-root RSF values obtained using the mountain data and model (and vice versa), we found poor predictive capability between landscapes (Fig. 3-6, 3-7). We attribute these patterns to the fact that the available landcover types, amount of primary and secondary/decommissioned roads, and risk of human-caused mortality were dissimilar between areas. To clarify the role that differences in these covariates played between the mountains and plateau, we examined how grizzly bear density would be expected to change if we applied the observed values in the mountains in the plateau RSF model (Table 3-4).

For the plateau, all predicted densities fell within the confidence interval outlined in Mowat et al. (2005) (12 bears/km^2, 95% C.I. = 7-28) (Table 3-4); however, the CI represents a large range in density. We estimated changes in population size by comparing our estimated *N* with the observed *N* obtained from the DNA mark-recapture estimate adjusted for study area size (*N* = 127). The only predictor variable to reduce the number of bears on the plateau was the available landcover types. We predicted a decrease of 9 bears on the plateau (i.e., observed density of 127 bears in plateau study area minus estimated landcover density of 118 bears) when we applied the landcover data from the mountains into the plateau RSF model. Because we held all other variables constant, this suggests that the effect of habitat alone cannot account for the difference in the number of grizzly bears between the mountains and the plateau. Conversely, the plateau population increased by 34 bears when the effects of primary and secondary logging roads were made similar to the mountains, i.e., if plateau bears avoided secondary logging roads similar to mountain bears, we would expect 34 more bears on the plateau landscape. If the risk of mortality were similar to what we observed in the mountains we estimate an increase of 49 bears on the plateau (Table 3-4). Lastly, we examined the effect of switching the values for all model variables. If bears on the plateau had similar patterns of selection to mountain bears, we expect that the population of bears on the plateau would increase 1.75 times ($N = 223$ individuals estimated) the observed population.

We also performed the analysis in reverse, i.e., using data from the plateau in the mountain RSF model. We found a converse result with a predicted decrease in the number of grizzly bears when the mountain model was applied on the plateau landscape (Table 3-4). Our predicted densities for bears in the mountains when subjected to a plateau landscape were well below the confidence intervals outlined in Mowat et al. (2005) (49 bears/km^2, C.I. = 43-59; Table 3-4). Our lowest density was obtained by switching the risk of human-caused mortality. We predicted a decrease to 4-bears/1,000 km^2 ($N = 31$ bears) if the risk of human-caused mortality was similar to what we observed in the plateau. Similarly, differences in primary and secondary logging roads, and landcover type, provided predicted densities of 5-bears/1,000 km^2. Applying the mountain bear model to the plateau landscape also limited the number of bears on the plateau from the observed 363 bears to 42 bears (Table 3-4).

5. DISCUSSION

The location of the Parsnip Grizzly Bear Study provided a number of opportunities to better understand the density of grizzly bears as it relates to habitat, roads, and risk of mortality. In particular, the study area ranged from a wilderness mountain landscape with minimal human disturbance to a plateau landscape with extensive road access and forest-harvesting activities. Compared with other DNA-based population estimates in interior British Columbia, grizzly bear density in the mountains was high (McLellan 1989, Hovey and McLellan 1996), but density on the plateau was low (Mowat and Strobeck 2000).

Habitat selection is best understood if we attempt to understand the mechanisms of the selection (Lima and Zollner 1996). Higher-quality habitats often are assumed to be linked to increased fitness in the animals that occupy them, generally resulting in higher densities of animals (Garshelis 2000). The availability of foods does not appear to be limiting the density of bears on the plateau. Differences in foraging items occurred between the areas with plateau bears consuming more high-calorie foods, such as meat and berries. Indeed, plateau bears ate up to 10 times the amount of meat/ants as mountain bears, likely allowing them to be heavier and in better condition (Ciarniello chpt. 2). Bigger bears and access to meat has been shown to be correlated with population density in grizzly bear populations (Hilderbrand et al. 1999). Thus, we might expect that the density of bears to be the same as or higher on the plateau than in the mountains. Rather, we found that bears on the plateau were at low density relative to the types of high calorie foods they consumed. We examined the link between bear density and landscape structure by investigating the predictions from RSF models when we applied habitat values from one landscape to the other. We found no evidence that the 4-fold difference in bear density between the mountains and the plateau could be attributed to differences in the respective landcover types. Indeed, based on differences in landcover alone we predicted a reduction in the current number of bears on the plateau.

Our results point to the importance of roads, and associated risk of mortality, on bear density between the mountains and the plateau, although the magnitude of response does not account for the entire 4-fold difference. We would expect the density of bears to increase on the plateau if the human-caused mortality rate should decrease but we do not know whether the density of bears would be the same as or higher than in the mountains. Clearly the extensive road network on the plateau subjected bears there to higher risk of human-induced mortality than in the mountains by providing access for human activities (Ciarniello et al. chpt. 2).

We found that switching all model coefficients between areas had the greatest effect on predicted plateau bear density. We believe that the extensive secondary and decommissioned road network (i.e., low-human-use roads) on the plateau, combined with the high risk of mortality in these areas (Ciarniello chpt. 2), made the backcountry of the plateau an "attractive sink" (Delibes et al. 2001) or "ecological trap" (Schlaepfer et al. 2002). Bears in our study area lacked salmon (i.e., Arctic watershed) and instead bears that lived on the plateau relied on foods found in early seral stands, particularly forbs, ants, and berries. During the last 50 years since fire suppression was implemented, the majority of these early seral stands on the plateau have been created by forestry operations. In the RSF analysis, selection for early seral stands is reflected in part by the selection for higher greenness scores and open canopies. The regenerating vegetation in cutblocks had high greenness scores, and bears were attracted to these areas. Because of fire suppression and forestry practices, logged areas now provide most of the early seral vegetation important to bears. Forestry operations also have been responsible for an increased number of roads on the landscape, which, in turn, has lead to increased human access, contact with bears, and human-caused bear mortality (Ciarniello Chpt. 2).

High levels of human use may displace bears from high quality habitats (e.g., TransCanada Highway, Gibeau et al. 2002), and numerous studies have observed avoidance of roads by bears (Mattson et al. 1987, McLellan and Shackleton 1988, Kasworm and Manley 1990, Mace et al. 1996). Bears on the plateau appear to have been displaced from using areas near primary logging roads due to the high volume of logging traffic. However, predictable, or low levels of human use may allow bears to habituate (Herrero 1985, Jope 1985, McLellan and Shackleton 1989, Mace et al. 1996). In our study area, however, human use of the backcountry road network appeared to be low to none. During spring, those areas were difficult to access due to snow and soil conditions, and during summer most people remained close to primary logging roads for camping or berry picking. However, during the fall hunting season hunters often preferred difficult to access backcountry areas on the plateau. Therefore, although RSF models predicted a high relative probability of occurrence in early seral areas, and forestry operations provided attractive early seral habitat for bears, they also allowed for increased human access.

Unlike plateau bears, mountain bears primarily foraged in high elevation open alpine and subalpine bowls in a landscape far less affected by humans. The attraction by mountain bears to high-elevation sites provided a natural separation between bears and humans, resulting in significantly lower human-caused mortality. During the study, there were few secondary logging roads in the mountains. The distance from town, and late melting of snow on roads in spring, greatly limited human use of even primary logging roads in the mountains except when logging was occurring. Therefore, during our study bears in the mountains were at a lower risk of mortality when foraging adjacent to primary logging roads, which we believe contributed to their increased relative probability of use.

The severely predicted decrease in the relative probability of occurrence of grizzly bears in the mountains when subjected to a plateau landscape was likely due to 3 factors: 1) difference in the distribution and characteristics of roads in the mountains; 2) opposite road effects; and, 3) extrapolation to a landscape with a different suite of available resources. Due to opposite effects of roads on bears in mountain and plateau landscapes when the model coefficients from the plateau RSF were applied to the mountain landscape the predicted number of mountain bears declined. Each year harvesting activities occurred further into the mountains. Over time, bears in the mountains were subjected to the risks associated with a plateau landscape. If mountain bears continue to use the landscape as modelled (e.g., selecting for closer distances to primary logging roads), we predict a decline in their population if human access and illegal hunting is not properly managed. The predicted decline in the number of mountain bears is in part attributed to their lacking the learned cues necessary to survive in a high-mortality risk landscape (Schlaepfer et al. 2002). Naïve individuals tend to lack the appropriate risk-avoidance cues and maladaptive habitat selection patterns can occur (Kristan 2003). As a result, the risk of extinction is elevated in areas where animals, especially naïve ones, are attracted to ecological traps (Schlaepfer et al. 2002, Kristan 2003). Mountain bears were born and raised in a landscape with a low risk of human-caused mortality, and during our study more closely resembled a naturally regulated population (Ciarniello chpt. 2).

Our results also suggest that caution should be applied when extrapolating RSF results to different areas. Unlike Manly et al. (2002:187) where the presence of galaxiid fish were predicted "very well" at sites where trout were present, we predicted drastically different RSF models in our adjacent areas (Fig. 3-6, 3-7), even though both of our models had excellent internal predictive capability and were proportional to the probability of use. Such extrapolations have been completed for grizzly bears in the Bitterroot, where the authors stated confidence in their predicted number of bears because RSF models have been shown to accurately predict animal distribution (Boyce and Waller 2003). From our results, we suggest that extrapolation of RSF models into areas with a different suite of available resources may be highly misleading. For example, our predicted number of bears obtained from applying the plateau values to the mountains was affected by the lack of grizzly bear use of the small portion of alpine habitat that existed on the plateau landscape. In such instances, the results from the mountain landscape should accurately predict the number of bears on the plateau because bears on the plateau did not use the alpine and a coefficient was not estimated. However, when using the plateau model to predict the number of grizzly bears in the mountains, omitting a highly used landcover type (i.e., alpine) by mountain bears likely underestimated the results. We believe that had grizzly bears on the plateau used alpine areas, and we were able to provide a reasonable estimate of the alpine beta coefficient, we would have predicted a higher number of bears for the mountain landscape.

Our results also show that caution must be applied to the interpretation of RSF models so as to recognize high-quality habitats that might be acting as attractive sinks. If such dynamics are not recognized, conservation initiatives may be maladaptive or even harmful to population persistence (Johnson et al. 2004). For example, if we had not previously examined the ratio of use to mortalities, as well as the location of mortalities, we might have improperly interpreted the results by suggesting that increasing the number of roads (e.g., highways on the plateau or primary logging roads in the mountains) on the landscape would result in an increase in grizzly bears. If caution is applied during extrapolations, proper application of the link between habitat and density provides a useful tool for examining and quantifying the effects of human activities on grizzly bears.

5.1 Management Implications

Each year, new roads were expanding further into the mountain ranges for timber harvests and also for oil and gas exploration. Similar to Mace et al. (1999), we recommend a reduction in active road density. Increased human access may result in increased grizzly bear mortality; thus, access management plans that reduce active road density should be implemented. Management techniques can influence the extent and location of human impacts by implementing strict access management plans. For example, an indirect management technique may be to remove a bridge prohibiting access past the obstruction. If our current system of forestry management continues, and several logging roads remain accessible to the public after the timber has been extracted, the number of bears will decline. The results of the habitat-based density modeling suggest that simply providing habitat is not enough to sustain grizzly bear populations at their current numbers. For grizzly bears to remain viable outside of protect areas, we must maintain places secure from the risk of human-caused bear mortality across each landscape.

Table 3-1. Description of variables from geographic information system layers used to select candidate models for grizzly bears in the mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada (1998-2003).

Variable	Type		Description
Primary landcover categories used in modeling:	*Categorical* % Landscape		*Leading landcover type*
	Mtn	Plt	
True firs	34	10	Stands dominated by subalpine fir
Pine	7	27	Stands dominated by lodgepole pine
Spruce	30	35	Stands dominated by Spruce species
Mixed wood	2	13	Stands dominated by cottonwood, aspen, and/or common paper birch
Shrub	3	6	Areas with no or few trees and large expanse of shrubs, most frequently occurred adjacent to swamps and rivers
Withheld landcover categories:			
Alpine	23	0.1	Dynamic, high elevation, largely forb and/or shrub dominated parkland or krummholz subalpine fir
Black spruce	1	2	Stands dominated by black spruce
Douglas Fir	0.05	1	Stands dominated by Douglas fir
Meadow	0.05	2	Large, open forb dominated areas
Rock/bare ground	0.2	0.03	Typically high elevation mountain tops
Swamp	0.5	3	Water table above ground surface
Anthropogenic	0.2	1	Areas of human settlement or regular maintenance, such as along the railway line. Excludes harvested areas
Topographic features:			
Crown closure	Linear		Relative amount of gaps in a forest stand in 10% increments from closed/dense (100%) to open (0%)
Elevation	Linear		Elevation above sea level
Forest height	Linear		Height of the forest in meters
Greenness	Linear		Calibrated greenness values
Hillshade	Linear		Combination of slope and aspect to measure solar insulation as it varies with topography (azimuth: 225, sunangle: 45). Negative

		coefficients indicate selection for cooler, northeast aspects, while positive coefficients reflect selection for warmer southwest aspects.
Risk layer (human influenced risk of mortality only)	Scaled 0-1	Evaluates the relative probability of grizzly bear mortality risk by landscape (see Ciarniello chpt. 2)
Road	Linear	Straight-line distance to the nearest road in meters
Stand age	Categorical	Early seral 0-45 years including shrub, meadow, non-commercial and non-productive brush, swamps, and alpine. Young forest 46-99 years. Old forest 100+ years.

Table 3-2. Resource selection function model coefficients, standard errors, and 95% confidence limits indicating the relative probability of grizzly bear occurrence in the mountain landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003. Bold and italicized variables had confidence intervals that did not include 0.

Variables	β	SE	L95%CL	U95%CL	*AIC*	*AICw*	*ΔAIC*
Crown closure	-0.018	0.003	-0.023	-0.012	7275.52	0.82	0.00
Greenness	0.035	0.002	0.032	0.039			
Hillshade	0.004	0.001	0.002	0.005			
True firs	-0.341	0.117	-0.570	-0.113			
Spruce	-0.960	0.137	-1.228	-0.691			
Pine	-0.347	0.287	-0.909	0.215			
Mixed wood	-1.066	0.541	-2.125	-0.006			
Shrub	-0.079	0.176	-0.425	0.267			
Distance to highway	$7.66E^{-05}$	$3.75E^{-06}$	$6.92E^{-05}$	$8.39E^{-05}$			
Dist. to primary logging road	$-1.48E^{-04}$	$7.20E^{-06}$	$-1.62E^{-04}$	$-1.34E^{-04}$			
Dist. secondary logging road	$1.56E\text{-}^{04}$	$1.24E^{-05}$	$1.32E^{-04}$	$1.80E^{-04}$			
Risk of mortality	-21.108	3.507	-27.983	-14.234			

Table 3-3. Resource selection function model coefficients, standard errors, and 95% confidence limits indicating the relative probability of grizzly bear occurrence in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003. Bold and italicized variables had confidence intervals that did not include 0.

Variables	β	SE	L95%CL	U95%CL	*AIC*	*AICw*	*ΔAIC*
Crown closure	-0.008	0.002	-0.011	-0.004	7464.54	0.46	0.32
Greenness	0.015	0.004	0.008	0.022			
Hillshade	0.005	0.002	0.002	0.008			
True firs	0.074	0.175	-0.269	0.416			
Spruce	0.617	0.137	0.349	0.885			
Pine	-0.049	0.156	-0.356	0.257			
Mixed wood	0.206	0.160	-0.107	0.519			
Shrub	1.071	0.160	0.758	1.384			
Distance to highway	$-8.14E^{-05}$	$5.23E^{-06}$	$-9.16E^{-05}$	$-7.11E^{-05}$			
Dist. to primary logging road	$2.08E^{-05}$	$1.56E^{-05}$	$9.85E^{-06}$	$5.15E^{-05}$			
Dist. to secondary logging road	$-2.84E^{-05}$	$5.59E^{-05}$	$-1.38E^{-04}$	$8.11E^{-05}$			
Risk of mortality	-3.875	2.663	-9.095	1.345			

Table 3-4. Recalculating grizzly bear density using habitat-based density modeling techniques. Population sizes, (*N*), were calculated by swapping the RSF model coefficients in Table 3-2 with those in Table 3-3, and vice versa, for the Parsnip River study area, British Columbia, Canada, 1998–2003. Observed grizzly bear density was obtained from a DNA mark-recapture population census at 12 bears per1,000 km^2 on the plateau and 49 bears per 1,000 km^2 in the mountains adjusted for study area size. Except where indicated by confidence intervals, numbers in brackets represent density in 1,000 km^2.

	Subpopulation Size	
Model covariate	Mountains	Plateau
Landcover type	36 (5)	118 (11)
Primary and secondary roads	34 (5)	161 (15)
Risk of mortality	31 (4)	176 (17)
Entire model	42 (6)	223 (21)
Observed density (*N*)	363	127
Observed density per 1,000 km^2	49 (CI 43-59)	12 (CI 7-28)

Figure 3-1. Study area for determining grizzly bear habitat use and density, including mountain and plateau boundary line just east of the Parsnip River, British Columbia, Canada, 1998 to 2003. The shaded box contained within the core of the larger study area represents the DNA based population census boundary and encompassed mountain and plateau landscapes.

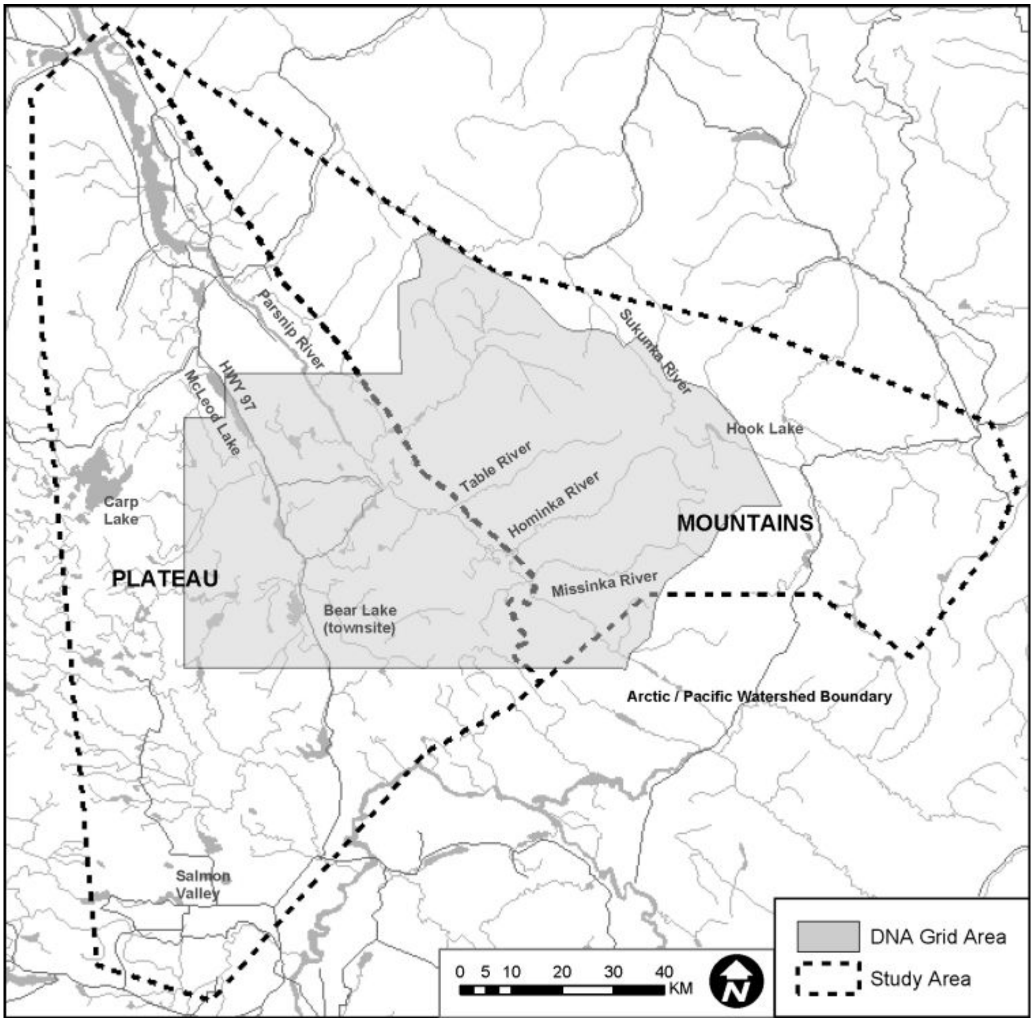


Figure 3-2. Relative probability of grizzly bear occurrence in the mountain landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003. Orange areas represent an increased relative probability of use (greater RSF values).

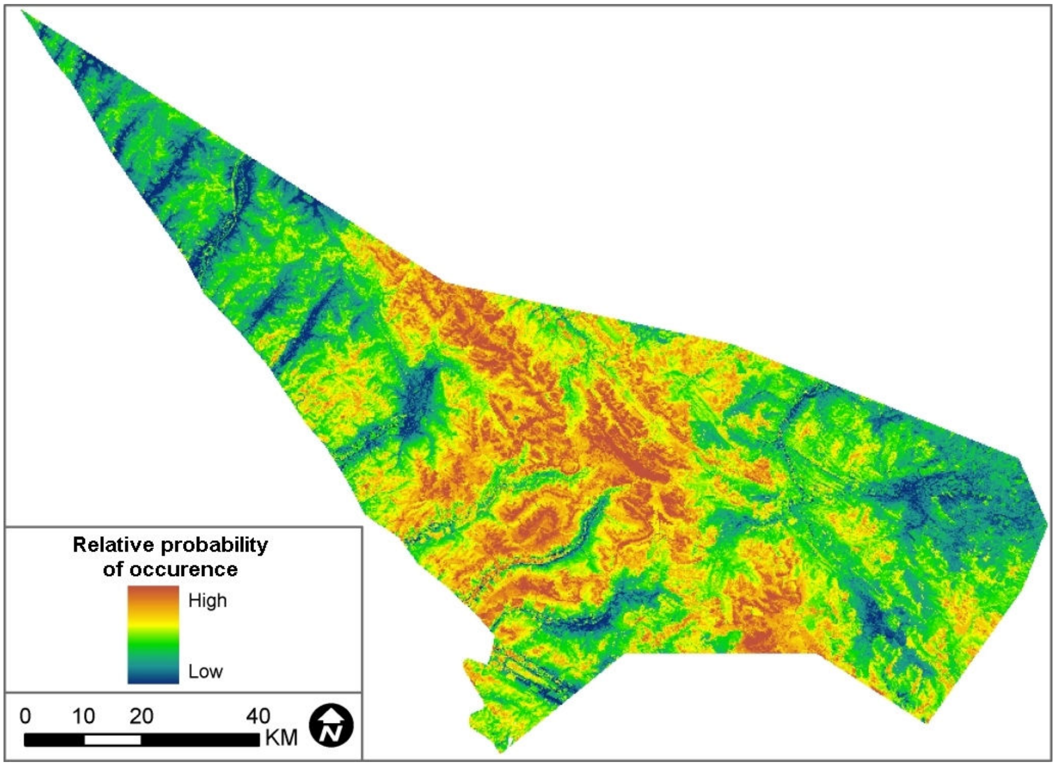


Figure 3-3. Relative probability of grizzly bear occurrence in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003. Orange areas represent an increased relative probability of use (greater RSF values).

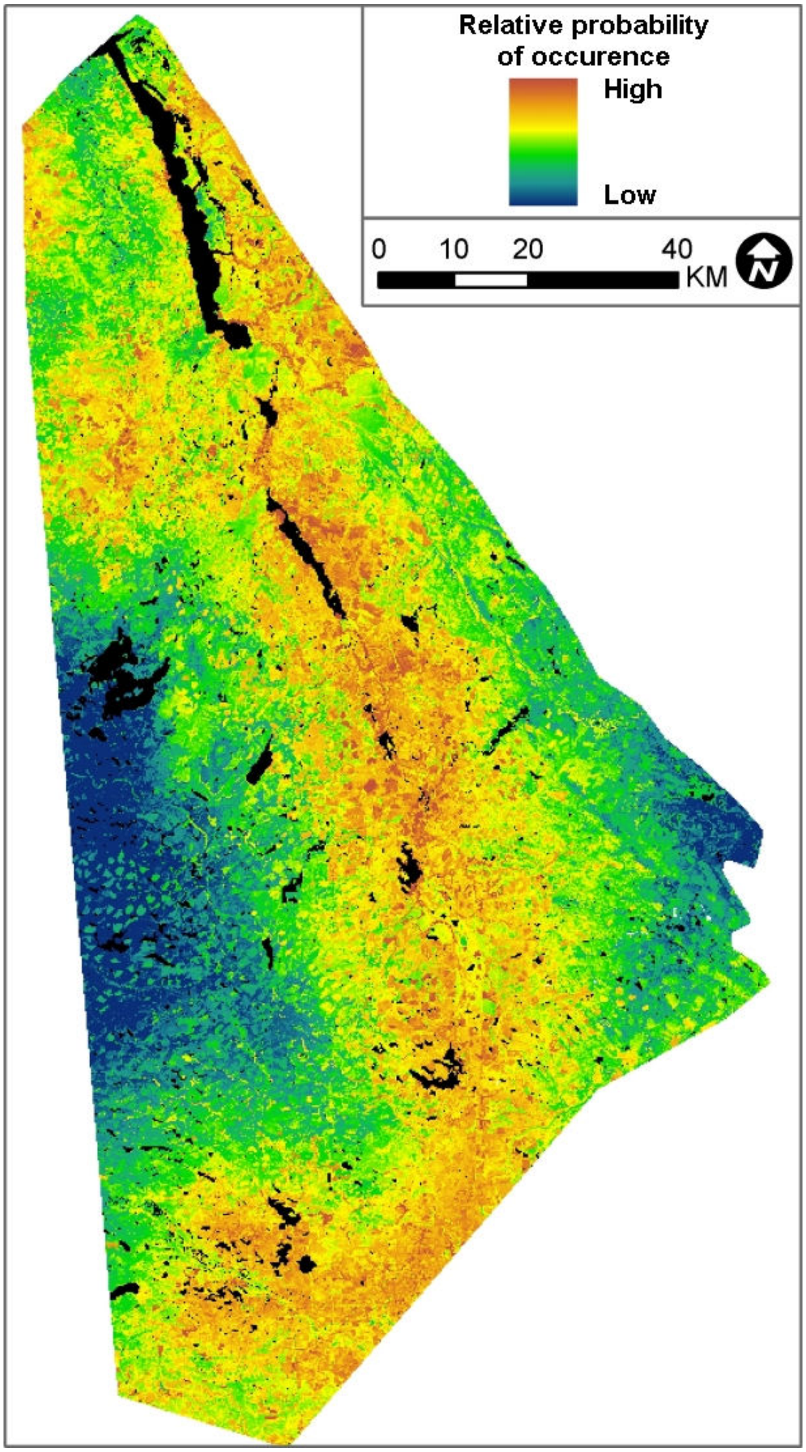


Figure 3-4. Distribution of the number of grizzly bears in each of the 10 landscape bins for the mountain landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003. RSF values are based on the bin mid-points.

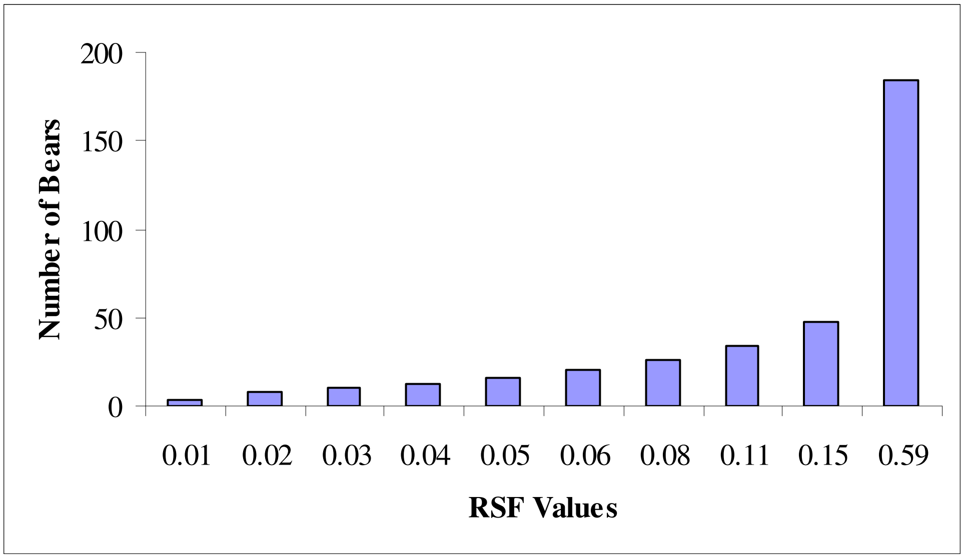


Figure 3-5. Distribution of the number of grizzly bears in each of the 10 landscape bins for the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003. RSF values are based on the bin mid-points.

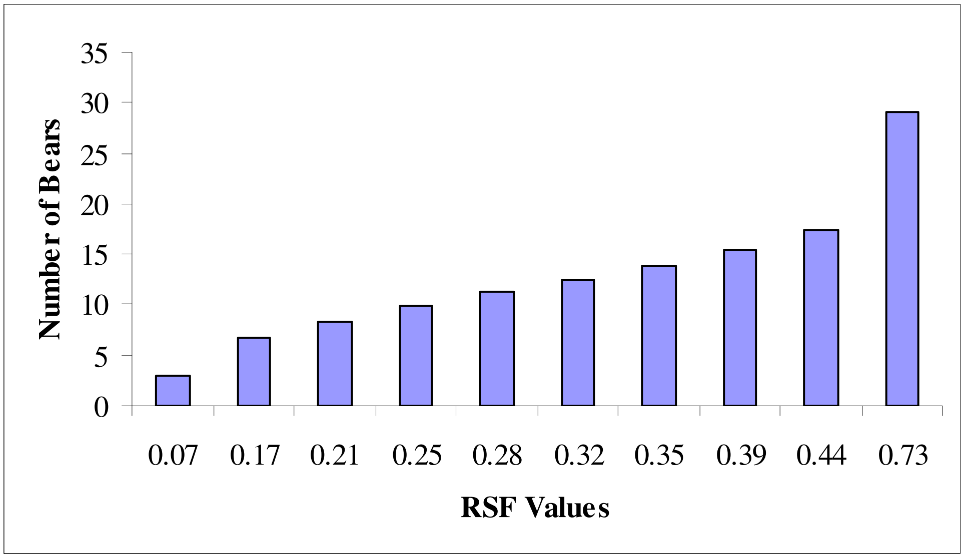


Figure 3-6. Correlation between each RSF point predicted in the plateau landscape versus the RSF scores predicted using the mountain model with the plateau data for the Parsnip River study area, British Columbia, Canada, 1998-2003. Axes are the square root of the predicted RSF value.

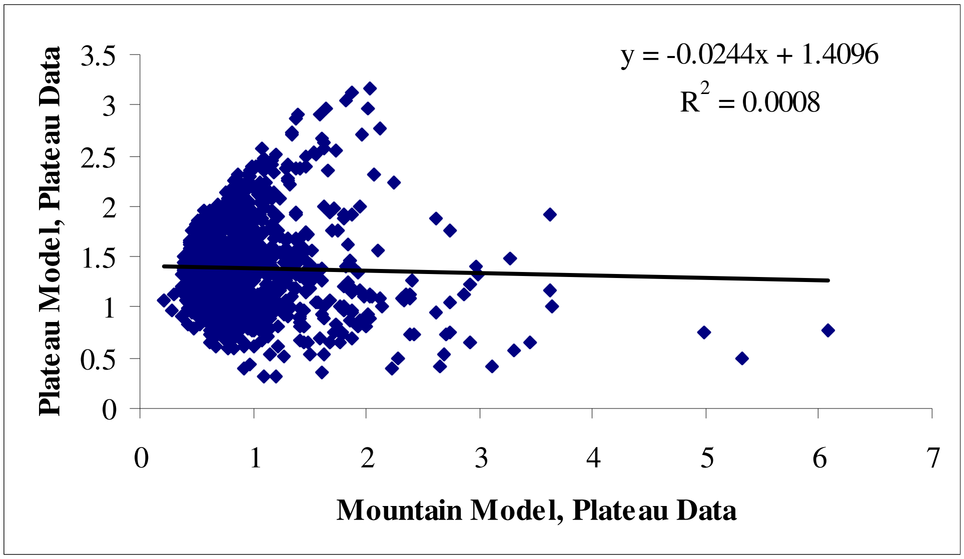
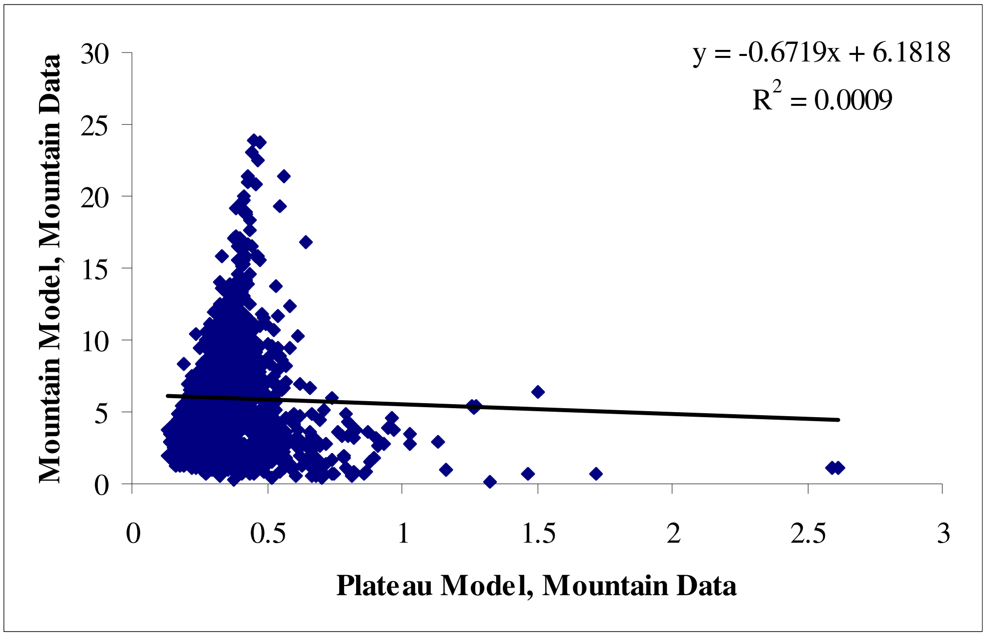


Figure 3-7. Correlation between each RSF point predicted in the mountain landscape versus the RSF scores predicted using the plateau model with the mountain data for the Parsnip River study area, British Columbia, Canada, 1998-2003. Axes are the square root of the predicted RSF value.



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CHAPTER 4
SCALE DEPENDENT HABITAT SELECTION BY GRIZZLY BEARS

1. INTRODUCTION

The importance of scale, especially when drawing conservation and biological inferences from the results of habitat selection studies, is becoming forefront in ecological literature (Johnson 1980, Addicott et al. 1987, McLean et al. 1998, Orians and Wittenberger 1991, Levin 1992, Anderson and Gutzwiller 1996). This is because different processes can operate at different scales and what may appear important at one scale may have little relevance at another scale, making results scale sensitive (Guisan and Thuiller 2005). Johnson (1980) suggested that habitat selection is a hierarchical process in which relationships may change along a continuum of spatial scale; an argument subsequently supported by a number of authors (Orians and Wittenberger 1991, Aebischer et al. 1993, Boyce et al. 2003). Because varying the extent of available habitat can provide diverse results (Johnson 1980, Garshelis 2000, Guisan and Thuiller 2005), some authors claim that conclusions are valid only within the spatial scale examined (Kotliar and Wiens 1990, Lord and Norton 1990). Thus, the applicability of management actions derived from examining only one scale may be limited to that scale. Research that focuses on the conservation of wildlife and their habitat requires an understanding of how scale affects animal behaviour and distribution (Addicott et al. 1987, Weins 1989). Accordingly, habitat selection studies should be scale dependent (Addicott et al. 1987, Boyce 2006).

Scale is composed of two main components: grain and extent. Grain refers to the finest spatial resolution that could measured, whereas extent refers to the vastness of the landscape covered (Turner et al. 2001). Varying either of these components of scale can change the apparent magnitude of selection by the animal (Johnson 1980, O'Neil 1989, Boyce 2006), and individuals of the same species may respond to processes at different scales (Mysterud and Ims 1998). It has been argued that a minimum of 3 scales should be examined in ecological studies because selection is constrained by the level above and clarified at the level below (O'Neill 1989). Thus, scales are nested within each other, and when availability changes so might the way in which the organism perceives the landscape (Johnson 1980).

This paper compares the habitat selection of grizzly bears in central-eastern British Columbia (BC) by altering the extent of available habitat employing 3 different designs. The effects of scale on habitat selection have been studied for other large mammals, such as elk (*Cervus canadensis*, Boyce et al. 2003), muskoxen (*Ovibos moschatus*; Schaefer and Messier 1995), and caribou (*Rangifer tarandus*; Rettie and Messier 2000, Apps et al. 2001, Johnson et al. 2002, Johnson et al. 2004b). However, for grizzly bears, most studies of habitat selection have employed only a single scale of analysis (Servheen 1983, Waller and Mace 1997, McLellan and Hovey 2001) or focused on the possible segregation between males and females (Wielgus and Bunnell 1994, 1995, Waller and Mace 1997). Only 3 studies have addressed the effects of scale on selection patterns of grizzly bears (McLoughlin et al. 2002, Johnson et al. 2004a, Nielsen et al. 2004). All of these studies concluded that scale-dependent habitat selection did indeed occur. Nielsen et al. (2004) examined 3 seasons of selection at 2 scales but focused solely on the selection of clearcuts with data pooled for males and females. Johnson et al. (2004a) focused on the effects of scale on multi-species habitat selection (i.e., grizzly bears, wolves and caribou) concentrating on the spatial variation of resources. McLouglin et al. (2002) examined the selection of the home range on the landscape (study-area extent), and selection within the home range, for males and females; results were limited to univariate analysis using selection ratios.

Johnson (1980) proposed 4 hierarchical orders of habitat selection: the geographic range of a species (1st order), selection of a home range (2nd order), selection of patches of resources within the home range (3rd order), and selection of food items within the patch (4th order). These scales of resource selection can be combined with Manly et al.'s (2002) sampling designs for resource selection studies. In design I (Manly et al. 2002) individual animals are not identified, measurements are made at the population level, and use and availability are censused for the entire study area. In design II, individual animals are identified, use is quantified for each individual, and availability is measured at the population level. In design III, individual animals are identified, and use and availability are sampled for each individual. Combining Johnson's (1980) 2nd order selection with Manly et al.'s (2002) design I, we are able to ask broad population level questions, such as, 'where are the animals located on the landscape?' By constricting the scale of availability, we can ask more specific questions, such as 'what are animals using within their home range?' (3rd order, design III). Further, by employing different combination of scale with design we are able to investigate whether the patterns of habitat use depended on the availability of resources (Mysterud and Ims 1998).

We estimated separate resource selection functions (RSF) for female and male grizzly bears inhabiting mountain and plateau landscapes. By comparing changes in model coefficients from various study designs and extents of available habitat we are able to evaluate whether habitat selection patterns by grizzly bears remained constant across 3 spatial scales. We hypothesized that the magnitude and/or direction of selection will vary according to the hierarchy of scales examined. Further, we expected that the study-wide extent design would be the least explanatory for female grizzly bear habitat selection because the methods require blending second and third order scales. Our primary objective was to determine if there was one appropriate scale to mitigate the effects of forestry management operations on grizzly bears or if management actions would best be served at multiple scales (Hobbs 2003). From an applied resource management perspective, we were interested in whether the factors responsible for limiting the abundance of grizzly bears varied at multiple spatial scales.

2. STUDY AREA

The 18,096 km^2 study area was located within the 'working forest' in central-eastern BC, Canada (54°39'N, 122° 36'W) (Fig. 4-1). Forestry operations were the predominant industry, and aside from small provincial parks there were no protected areas. Each year, timber harvesting expanded from the plateau up the main river valleys (Missinka, Hominka, Table and Anzac Rivers) into the relatively pristine mountainous landscape.

The Parsnip Plateau comprised 10,624 km^2 of the study area, incorporating the northern limits of the city of Prince George and extending north past the town of Mackenzie. The rolling hills of the plateau were primarily in the sub-boreal spruce (SBS) zone, with elevations ranging from 600 m to 1,650 m. Climax forests of lodgepole pine (*Pinus contorta*) dominated dryer areas; white spruce (*Picea glauca*) was predominant on wetter sites, while black spruce (*Picea mariana*) bogs occurred in hydric sites. Mesic sites often consisted of spruce and subalpine fir (*Abies lasiocarpa*) associations. Small patches of alpine, subalpine fir climax forests, as well as interior Douglas fir (*Pseudotsuga menziesii*) remained. The plateau was heavily modified by forestry activities with the majority of logging occurring since the 1950s, resulting in a mosaic of successional stages (DeLong and Tanner 1996). The plateau had a mean annual temperature of 2.6° C, with 72 cm rainfall and 300 cm snowfall (DeLong et al. 1993, 1994).

We used the BC Ministry of Environment's ecosection line to divide the plateau from the Hart Ranges of the Canadian Rocky Mountains. The mountain area covered 7,472 km^2, with elevations ranging from 720 m to 2,550 m. Lower elevation valley bottoms leading from the mountains into the plateau were SBS, above which the predominant forest type was Engelmann spruce (*Picea engelmannii*) – subalpine fir associations, followed by the alpine-tundra zone (1,400 m+). The alpine consisted of shrubs or krummholtz tree formations, and lush heath communities. Subalpine grassland slopes were comprised of glacier lily (*Erythronium grandiflorum*), Indian helabore (*Veratrum viride*), and arrow-leaved groundsel (*Senecio triangularis*). Less than 1% of the study area was barren rock, alpine snow, or glacial ice. Mean annual temperature was 0.3° C, with 154 cm rainfall, and 700 cm snowfall (DeLong et al. 1993, 1994).

3. METHODS

3.1 Bear Capture and Monitoring

Grizzly bears were captured between August 1997 and spring 2003, using aerial darting, leg snares, or culvert traps. The University of Alberta's Animal Care Committee, following the Canadian Council on Animal Care guidelines and principles, approved bear handling procedures (protocol #307204). Bears were immobilized with Telazol (tiletamine HCL/zolazepam HCL) at a dosage of 8 mg/kg. Ketamine was used as a top-up drug when necessary at a dosage of 2 mg/kg. Captured bears were fitted with VHF collars (Very High Frequency, Lotek Inc., Aurora, Ontario), GPS collars (Global Positioning System, Televilt Ltd., Lindesberg, Sweden), and/or ear tag transmitters. Due to the high failure rate of GPS collars (Gau et al. 2004), and therefore the subsequent need to correct for bias introduced by both vegetation cover (Moen et al. 1997, Belant and Follman 2002, Frair et al. 2004) and/or animal behaviour (Moen et al 1996, 2001; Obbard et al. 1998, Dussault et al. 1999), we have used only the VHF locations for the scale dependent habitat selection analysis.

Regardless of the type of monitoring device, bears were monitored biweekly from 1998 to 2000, weekly in 2001 and 2002, and a minimum of every 2 weeks in 2003, using a fixed wing aircraft (normally Cessna 185). All aerial telemetry locations were collected during daylight hours. Universal Transverse Mercator (UTM) coordinates were taken with a hand-held 12 Channel Garmin® GPS unit. Locations were mapped and verified on 1:50,000 topographic maps. Multi-year (1998-2003) 100% minimum convex polygons were constructed using the program Animal Movement (Hooge and Eichenlaub 1997) for study animals with >10 locations that spanned the entire year. Home range size may be underestimated when <60 locations per animal are used to calculate the home range (Boulanger and White 1990, Arthur and Schwartz 1999). Comparisons of GPS and VHF telemetry obtained on the same animals have shown that VHF home ranges are normally underestimates of the actual home range size (Arthur and Schwartz 1999). We used multi-year locations and 100% MCPs in an attempt to achieve the largest home range area for our home range scale; however, we caution the reader that the home range of some animals may under represent its true size.

3.2 Scales of Analysis

We examined the use of 3 different methodologies to examine different scales of analysis. For all scales we removed locations when each bear moved to <1 km of its den site for fall and spring, because attributes for den site selection are different from those during the primary foraging season (Ciarniello et al. 2005). We also removed all locations (i.e., random and use) that fell within lakes and rivers. GIS attributes were calculated for the remaining used (i.e., bear location) and random locations. Separate models were calculated for males and females. For all designs, the following log-linear equation was assumed to characterize the influence of covariates on relative use, $w(\mathbf{x})$:

$$w(\mathbf{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 \ldots \beta_p x_p) \qquad (1)$$

where β_i are selection coefficients were estimated using logistic regression for each of p covariates, x_i, for $i = 1,2,\ldots p$ (Johnson et al. 2006). Bear telemetry locations were the used sites (1), and randomly generated locations were the available sites (0). Random locations were generated using the program HawthsTools (Beyer 2004) for ArcGIS® 8.3 (Environmental Systems Research Institute, Redlands, California, USA). Models were estimated using Stata 7.0 (Stata Corporation, Texas, USA).

***3.2.1** Scale and Design A - RSF Study-wide Level Design.*--In this population-level design we were interested in examining reasons for the locations of bears on the landscape. To answer this question we must draw availability from an area larger than the individual home range (Boyce 2006). We compared characteristics of areas used by bears versus available areas drawn throughout the mountain or plateau study area (i.e., population level). Although individual animals were radiocollared, they were not identified in the model; therefore, we employed a Design 1 (Manly et al. 2002), 2nd and 3rd -order selection (Johnson 1980) at the landscape scale. Because some of the random locations fell within the home range of each animal we spanned both of Johnson's (1980) 2nd and 3rd order scales. To control for variation, bear locations were weighted for equal sample sizes among animals. Random locations were sampled at an intensity of 1 location/500m^2 (i.e., 14,944 in mountains and 21,248 in plateau). Because we used animal locations to determine the boundary of the study area we are confident that the study area extent was occupied by grizzly bears. Population level designs require pooling data from individual animals; thus, we assume that habitat availability was fairly static among years.

3.2.2 *Scale and Design B - RSF Home Range Scale Design.*--Given that bears selected their home ranges within the larger landscape, in this home-range scale design we were interested in examining what bears were selecting within their home range and whether this differed from the selection of their home range on the landscape. Therefore, availability was limited and drawn only from within each bears' home range (Design 3, Manly et al. 2002). By limiting our available points to within home range we are employing a 3rd-order study design (Johnson 1980). We used conditional logistic regression by pairing the random points to each bears' use points (Compton et al. 2002), thereby controlling for variation amongst individuals by treating each bear as a fixed effect. The random sample intensity remained the same as in Design 1, at 1 location/500m^2 (n [females] = 4,360, n [males] = 7,626).

3.2.3 *Scale and Design C - RSF Buffered Home Range Scale Design.*--In this design we vary the extent of available habitat by drawing availability within a fixed buffer size surrounding each use location. Buffer sizes were determined by plotting the average distance moved between telemetry locations as long as those locations were $\leq$7 days apart (Fig. 4-2). By plotting the distance moved between all consecutive locations, we believed that locations that were $\leq$7 days apart were more representative of animals' immediate decisions than those that were $\geq$7 days apart. We chose a buffer size that incorporated a minimum of 80% of bear locations in each landscape because the majority of bears will have what is available for them within this distance (Boyce et al. 2003, Boyce 2006). This buffer size was 6 km for bears that lived in the mountains and 11 km for bears that lived on the plateau (Fig. 4-2). Because we buffered locations that fell on the boundary, a portion of the available habitat may be drawn from outside the home range. Therefore, while mostly 3rd order, this design also incorporates some 2nd order properties (Johnson 1980). We again used conditional logistic regression to compare for variation amongst individuals (Compton et al. 2002). However, in this design, we paired 10 randomly generated points with each use point.

3.3 Geographic Information System Data

We used Terrain resources inventory maps (TRIM2; BC Ministry of Water, Land, and Air Protection, Victoria, Canada) to build digital elevation maps (DEM) to obtain elevation, slope, aspect, and hillshade data. Forest cover maps (FCM; BC Ministry of Forests, Prince George, BC) were used to obtain the predominant forest stand and/or landcover type, as well as stand age. Road networks were built by amalgamating FCM with layers obtained from the major forestry operators within the study area: Canadian Forest Products (Canfor) East, Canfor West, the Pas Lumber, and Slocan Forest Products Ltd., in Prince George, British Columbia, Canada. GIS layers were visually crosschecked with Landsat™ imagery. Raster layers (i.e., DEM, slope, aspect, hillshade, and distance to roads) had a resolution of 25 m. The forestry data (e.g. age, height, forest type) were based on vector GIS layers that were rasterized, also with a resolution of 25m. For all categorical variables (e.g., landcover) selection for, or against, the remaining covariates is in relation to the withheld categories (see Table 4-1).

3.4 Model Selection and Validation

We used 2 methods for evaluating the effects of scale on our RSF designs: (1) comparisons between the rank of 6 candidate models, and (2) comparisons within 1 candidate model. In method 1, based on the variables in Table 4-1, we chose *a priori* 6 candidate models that we deemed biologically relevant to grizzly bear habitat use (Burnham and Anderson 1998, Anderson et al. 2000) (Table 4-2). Inclusion of variables in the candidate set of models was based on field knowledge and published research on grizzly bear habitat selection (Servheen 1983, Wielgus and Bunnell 1995, Waller and Mace 1997, McLellan and Hovey

2001, Nielsen et al. 2004). Grizzly bears have been shown to prefer habitats that contain a juxtaposition of forest structural stages (i.e., seral stages) (Herrero 1972, Waller and Mace 1997, McLellan and Hovey 2001, Nielsen et al. 2004). As such, we put forward a model (i.e., seral model) containing the set of covariates most strongly influenced by forest structural stage: stand age and greenness. Older age stands and non-vegetated areas have low greenness values, while early seral stands containing lush vegetation have high greenness values (Mace et al. 1999). Conversely, grizzly bears have been shown to avoid human use areas (Gibeau et al. 2002), and habitat selection patterns have been altered due to the presence of roads and trails (Mattson et al. 1987, McLellan and Shackleton 1989; Mace et al. 1996). Because high-quality habitats are generally roadless areas that also contain a juxtaposition of early-seral forests, then the opposite should be true for areas of high mortality risk. Thus, we also put forward a model that contained a set of covariates that we deemed as 'risky' places to the survival of grizzly bears (i.e., risk model, Table 4-2). We included stand age in the risk model because it can affect the amount of security cover available to bears. We also considered a model based on a set of covariates that reflect the landscape's terrain (i.e., terrain model). The mountains contained steep-sided slopes and rocky mountain peaks, therefore, terrain may influence decisions by bears that lived in the mountains. Finally, because there was a higher density of bears in our study area in the wetter predominant forest types (e.g., spruce) versus the drier predominant forest types (e.g., pine) (Mowat et al. 2005), we examined the effects of predominant landcover type on grizzly bear habitat selection (i.e., landcover model). Lastly, we investigated whether a mix of the above mentioned covariates offered a more complete examination of habitat selection (i.e., the 'all-inclusive' models). Due to collinearity between the predominant landcover type and stand age, we built separate 'all-inclusive' models for these sets of covariates. Model variables were chosen based on their applicability to mountain or plateau landscapes. For example, we withheld the variable alpine from the plateau vegetation model because there was no use by bears of alpine on the plateau and only small patches (0.1%) existed.

Collinearity was examined between all predictor variables. We assumed that collinearity was not a concern if correlations between predictor variables were <0.6. If correlations between predictor variables were $\geq$0.6 they were not included in the same model. Within each scale of analysis we rank these 6 candidate models based on Akaike Information Criteria (AIC) to identify the most parsimonious model (Burnham and Anderson 1998). Because male bears had small sample sizes for candidate models with $\geq$7 variables (i.e., n/K <40), final model selection for male bears was based on AIC_c difference for small samples (Burnham and Anderson 1998). The closer the normalized Akaike weights (AIC_w) to 1, the better the model (Anderson et al. 2000). Models were considered comparable if ΔAIC values were <2.0 (Burnham and Anderson 1998). Significant coefficients were those with confidence intervals that did not overlap 0 (Anderson et al. 2000).

In our second method, we examined the effects of scale by selecting 1 model and comparing the coefficients across the 3 scales. In this method, the number of random locations varied between designs, therefore, we could not use AIC score to rank models. Rather, to account for the difference in sampling intensity, we used 5-fold cross validation to compare the internal consistency of each model using a Spearman's Rank correlation (r_s) between predicted and observed frequencies (Boyce et al. 2002). Data were drawn at random and divided into 5 groups. Using random drawings of 80% of the data, 5 models are constructed. RSF predictions from these models were contrasted with the frequency of the withheld data (20%) distributed across 10 RSF bins (Boyce et al. 2002). A higher number of locations in bins where RSF scores approach 1 indicate a highly internally consistent model. Rank correlations across the 5 models were then averaged ($\bar{r}_s$). Estimates for the top-ranked mountain and plateau models were interfaced with GIS to create maps of relative probability of grizzly bear use across each landscape.

4. RESULTS

We gathered 2,005 non-denning season locations on 33 female bears (*n* [mountains] = 1,275 locations on 17 bears; *n* [plateau] = 730 locations on 16 bears), and 487 locations on 18 male bears (*n* [mountain] = 237 locations on 6 bears; *n* [plateau] = 250 locations on 12 bears).

4.1 Rank of the 6 candidate models using resource selection functions

For male bears, patterns of habitat selection were dependent upon the scale of availability but for female bears each scale estimated the same top-ranked model (Tables 4-3, 4-4). At the study-wide and home-range spatial extents, male bears that resided in the mountains had the greatest response to models that contained set of covariates based on the structural stage of the forest, suggesting that prime foraging areas (i.e., early seral stages) were sought out by mountain males (Table 4-3). When the extent of availability was restricted to a buffer, the terrain model ranked 1st for mountain males. The terrain model did not include any human-use variables, suggesting that small-scale habitat selection decisions by mountain males were based more on the natural surrounding topography than was reflected by patterns of use seen at the larger scales.

For male bears that resided on the plateau each scale estimated a different top ranked model, meaning that habitat selection strongly varied according to the extent of availability (Table 4-3). At the study-wide extent, male bears from the plateau selected a number of the dominant landcover types, areas where the risk of mortality by humans was high, and against secondary logging roads. Interestingly, when availability was restricted to selection within the home range there was no detectable selection for or against areas with a high risk of mortality, although they continued to avoid primary logging roads. The ΔAIC_c value for the mortality risk and all-inclusive seral models was <2.0, suggesting support for these models was comparable (Burnham and Anderson 1998). In the all-inclusive seral model, male plateau bears selected for early seral age stands (i.e., 0-40 years) at the study-wide extent but there was no detectable selection for or against these stands at the home range and buffer extents. At the buffer scale, the landcover based models ranked highest, although the risk and terrain models also had $\Delta AIC_c<2$. The commonality across these models was selection for landcover dominated by shrubs while avoiding primary logging roads.

Unlike males, female bears inhabiting mountain and plateau landscapes had the same model estimated first at each scale (Table 4-3). Thus, we recorded differences in habitat selection between males and females. For females residing in both landscapes the all-inclusive landcover model ranked 1st at all scales, while the all-inclusive seral model ranked second. Across all scales, females on the plateau selected for early seral stands, which reflects in part a selection for early seral cutblocks. The ΔAIC values for these models were >2, suggesting the all-inclusive landcover model was the most parsimonious for female habitat selection. For females that lived on the plateau, the mortality risk based model ranked 3rd for all scales of analysis, whereas the seral model ranked 3rd across all scales for females that lived in the mountains; plateau females responded more to mortality risk factors than mountain females. Unlike the plateau, in the mountains the risk of mortality from human causes was low. The terrain and landcover based models consistently were the lowest-ranked models for female bears, suggesting that female habitat selection was based on more than simply the dominant forest type or topography. At the study-wide scale, the distribution of female bears was least well explained by the more-simplified terrain-based model.

4.2 Resource selection function results for one candidate model at 3 scales

We chose the all-landcover model to examine how scale affects the same RSF design because it ranked 1st most consistently based on AIC (Table 4-4). For all bears, selection varied based on the extent of available habitat, although some variables (e.g., greenness) were consistently selected or avoided across scales. Based on 5-fold cross validation, we could not discern one extent that was consistently better than another; rather support for a model was dependent upon the bears' sex as well as landscape.

***4.2.1** Mountain males.*--For mountain males, selection for alpine habitats was strongest at the study-wide scale ($\beta = 1.75$), decreased as availability was restricted to the home range ($\beta = 0.72$), and had no detectable selection or avoidance at the smallest scale (Table 4-5, Fig. 4-3). Spruce dominated forests were selected for throughout the study area and reflected the distribution of these forests on the landscape; alpine occurred at higher elevations, while spruce forests primarily occurred at lower elevations. Therefore, there was selection for these landcover types at the broadest scale but significant avoidance of spruce when availability was restricted (Fig. 4-3). Consistent across scales was selection for green vegetation (i.e., higher greenness scores); the magnitude of which was slightly stronger at the population level but similar at the home range and buffer extents. At the population and home-range scales, male mountain bears were found closer to primary and secondary/decommissioned logging roads than random. We suggest that this was due to males using these roads for travel as well as the foraging opportunities on early seral vegetation associated with roadside clearing. We observed males along difficult-to-access secondary/decommissioned logging roads on a number of occasions, or foraging adjacent to roadways in early-seral-age cutblocks. When availability was restricted to a buffer, we could not detect selection for or against primary or secondary/decommissioned logging roads by male bears that lived in the mountains. Overall support was highest for the study-wide model with high internal consistency ($\bar{r}_s = 0.833$). Although the internal consistency decreased with the extent it remained moderately high ($\bar{r}_s$ [home range] = 0.802; $\bar{r}_s$ [buffer] = 0.749) across scales (Fig. 4-4).

4.2.2 *Plateau males*--At the study wide extent the inclusion of shrubs, spruce, and true fir landcover types was important to the distribution of plateau male bears on the landscape (Table 4-6). The magnitude and significance of selection for landcover types decreased once the home range was established and availability was restricted to what bears were selecting within their home range. The selection for shrub-dominated areas was the only consistent pattern across scales although the magnitude decreased being strongest for the study-wide extent followed by the buffer and home range extents. Thus, plateau males selected resource units with shrubs when selecting their home range, and included the presence of shrubs in their immediate decisions (buffer scale) (Fig. 4-5). The early seral stage of shrub habitats are known to provide a number of foraging opportunities for plateau bears both with increased early seral vegetation and also the opportunity of encountering moose (Ciarniello chpt 3). Furthermore, shrub landscapes likely provide added security cover in a landscape with a high risk of human mortality (i.e., the plateau). Males that resided on the plateau were the only subset of bears to select for risky landscapes, although selection was only significant at the study area wide extent. Plateau males also had the highest mortality rates (Ciarniello chpt 2). We found that male study bears that did not avoid risky places were often removed through management actions or human conflicts (Ciarniello chpt 2).

Male bears that lived on the plateau were located closer to the highway than random although this was likely an artifact of a power line that paralleled the highway corridor that had earlier spring green-up. In addition, a DNA grid conducted in 2000 revealed that the number of bears increased as one moved eastward across the plateau (Mowat et al. 2005). At all scales, plateau males avoided primary logging roads and the magnitude of the avoidance was similar across scales. Although we often located bears close to secondary and decommissioned logging roads, modeling revealed that use was not significantly different than random. Overall support was highest for the study-wide model with moderate internal consistency ($\bar{r}_s = 0.635$, $\alpha = 0.05$). Although the buffer model had the next highest internal consistency ($\bar{r}_s$ [buffer] = 0.386), followed by the home range extent ($\bar{r}_s$ [home range] = 0.262), these models had low internal predictive capabilities and were not statistically significant (Fig. 4-6). However, the low internal predictive success of the buffer and home range models was not surprising given that the all-inclusive landcover model was not the top-ranked model for plateau males at these scales (Table 4-4).

4.2.3 *Mountain Females.*--Study-wide patterns of selection for female bears that resided in the mountains showed strong selection for alpine landscapes ($\beta = 3.651$), followed by shrubs ($\beta = 2.604$), and high elevation true firs ($\beta = 2.446$) (Table 4-7, Fig. 4-7). However, selection of these forest cover types was largely scale dependent; covariates that were selected for at the study area wide scale may be avoided at the home range and buffer extents (Fig. 4-3). While roughly 23% of the mountainous landscape was alpine habitat, 43% was found to occur within the home range of mountain females. Thus, although mountain females highly selected alpine and shrub landcover types when establishing their home range, they showed random use when extent was restricted to the home range and buffer scales. Similarly, although they selected spruce and true firs while establishing their home range, they avoided them when selecting forest types within their home range. Consistent across scales was selection for higher greenness scores and warmer aspects. These 2 covariates are surrogates for bear foods by representing lush green vegetation and early seral stages.

Mountain females selected against human-risk areas when establishing their home range. However, this may reflect in part a bias in our radiocollared sample because some bears had low to no human-influenced mortality risk factors within their home range. Thus, when availability was restricted to the home range and buffer extents there was no detectable selection for or against risky areas. Unlike plateau bears, mountain females selected for closer distances than random to primary logging roads at the study-wide extent and further distances from secondary logging roads across all scales. In the mountains, human use of primary logging roads was low due to their distance from settlements, making foraging adjacent to this road type much less risky than on the plateau. Further, primary roads tended to bisect low elevation riparian areas from higher habitats. Thus, mountain bears with roads in their home range were required to cross these areas if selecting lower elevations in spring.

Across all scales, the all-inclusive landcover model had excellent internal consistency and was statistically significant. Overall support was highest for the buffer scale ($\bar{r}_s = 0.970$, $\alpha = <0.002$), suggesting that the immediate landscape offered the most important factors in mountain female habitat selection; this was followed closely by the study-wide model ($\bar{r}_s = 0.963$), and the home range extent model ($\bar{r}_s = 0.934$).

4.2.4 *Plateau females.*--Black spruce ($\beta = 1.189$) and shrub ($\beta = 1.290$) landscapes were selected by female plateau bears at all spatial scales, however, the magnitude of selection was scale dependant (Table 4-8, Figs. 4-3, 4-8).

Approximately 6% of the plateau landscape contained shrubs, whereas shrubs comprised 12% of the home range of plateau females. We located females in the shrub landscapes of the plateau on 88 of 730 locations, ranking it as the 4th highest use of the 10-landcover types. Although plateau females were located in pine forests on 98 occasions, pine forests comprised 27% of the plateau landscapes. Female plateau bears strongly avoided pine forests. Because pine was a withheld landcover type, selection for the remaining forest types increases.

Across scales, females on the plateau were distributed closer to highways; because we never located bears on the side of the highway, and seldom located them close to the highway, we believe this was an artifact of spring use of a power-line corridor that paralleled the highway as well as the increased number of bears as one moved from the western boundary eastwards, and not true selection. Within their home range female bears were located closer to secondary logging roads than random. However, when the extent of available habitat was restricted to an immediate buffer, confidence intervals overlapped 0, suggesting that selection for secondary roads may actually reflect the large number of this road type on the plateau landscape making these roads difficult for bears to avoid.

At the study-wide and home-range extents, the all-inclusive landcover model had excellent internal predictive capability. Overall support was highest for the study-wide scale ($\bar{r}_s = 0.944$, $\alpha = <0.002$), followed by the home range extent ($\bar{r}_s = 0.802$). Interestingly, the buffer scale had only moderate internal predictive capability ($\bar{r}_s = 0.656$), suggesting that plateau females made decisions regarding habitat use on a larger scale than their immediate surroundings.

5. DISCUSSION

In this paper we examined the effects of altering spatial extent as it relates to the habitat selection of grizzly bears. Our results support the hypothesis that grizzly bear habitat selection is scale dependent; results varied between mountain and plateau landscapes, males and females, and across scales. Within sexes, however, there were patterns of selection for some variables that remained consistent across scales. We could not discern one ‘best’ scale for management that predicted across all bears; rather, results were landscape and sex-specific.

Initially, we assumed that the study-wide extent design would be the least predictive scale, especially for females, because the large available area may be unrealistic for the animal; selection tends to be merged in the process of drawing the random landscape locations from the extent of the study area as well as within the home range (i.e., 2nd and 3rd order). Using 5-fold cross validation, we rejected this hypothesis; the study area extent was the most predictive scale for female bears that lived on the plateau and for male bears in both landscapes. Further, for mountain females the buffer scale design had only marginally better internal predictive capabilities than the study-wide design. Our analysis, however, was limited by the attributes measured, and resolution of, our GIS layers; had we been able to more finely measure grain by including, for example, forage items, we anticipate more dramatic variation across scales. Similarly, differences among scales are difficult to discern in areas where the vegetation is uniformly distributed across the landscape or that have little topographic relief (Schaefer and Messier 1995).

By ranking models, we found that patterns of selection changed depending on the scale of availability for males but not for females. Between scales the greatest amount of variation occurred with male bears that lived on the plateau. We attribute this in part to the considerable home range sizes of plateau males, reaching as large as 4,361 km^2 ($\bar{x}$ = 1,759 km^2, Ciarniello chpt. 2), therefore the likelihood of all landscape types being represented within the home range was greater (i.e., less variance). Alternatively, mountain females had the smallest range of variation between designs, likely because they have the smallest home range sizes ($\bar{x}$ = 57 km^2, Ciarniello chpt. 2). The larger home range size of plateau males allowed them to encompass more attributes of the larger landscape; thus, when availability was restricted, selection was easier to discern between large and small scales. However, all of the variation between scales by male bears cannot be explained by the differences in home range sizes because plateau females also showed consistent patterns of selection across scales and they had similar home range sizes to mountain males ($\bar{x}$ [plateau females] = 446 km^2, $\bar{x}$ [mountain males] = 443 km^2, Ciarniello chpt. 2). Behaviour has been claimed to affect the scale of selection when examining the distribution of eggs by treefrogs (*Hyla chrysoscelis*) in response to fish predators (Resetarits 2005). Many authors claim that the risk of mortality contains a behavioural component that contributes to explaining the distribution and abundance of organisms (Lima and Dill 1990, Sutherland 1996, Fryxell and Lundberg 1998, Lima 2002, Hebblewhite et al. 2005). We believe that our results also contain a behavioural component explained in part by differences in the type and/or magnitude of male and female habitat selection patterns.

We found that female grizzly bears exhibited different selection patterns than males, a result that in part supports segregation in habitat selection between sexes. Intraspecific predation on cubs and females has been suggested to limit grizzly bears (McLellan 1994, McLoughlin et al. 2002) and alter habitat selection (Wielgus and Bunnell 1994, 1995), thereby displacing females into other habitats (Weilgus and Bunnell 1995, Ben-David et al. 2004). Waller and Mace (1997), and McLoughlin et al. (2002), found that females did not avoid males when selecting their home range on the larger landscape, but rather avoidance was strongest at the smaller scales. We suggest that avoidance may be more difficult to detect at larger scales because larger scales reflect more broad level selection patterns; for example, when selecting their home range on the landscape all bears may try to encompass some large patches of trees or shrubs for security. However, if we were able to differentiate the spatial location of the patch, we may better detect avoidance at larger scales. Thus, at smaller scales it is easier to detect avoidance simply due to the finer selection patterns. For our results, we suggest that the prominent selection for high elevation alpine, true firs, and shrub landscapes at the study-wide extent by females that lived in the mountains may be interpreted as segregation from mountain males, even though mountain males also were selecting alpine landscapes but to a much lesser degree. Interestingly, both sexes were selecting for higher greenness values and warmer aspects at a similar magnitude, suggesting that the underlying patterns of selection for lush, green vegetation remains the same for both males and females. For the plateau, sexual segregation was not as obvious as in the mountains. The main difference between males and females that lived on the plateau was that males entered human-risk areas. I believe that for plateau males the pressure to attain large body sizes was greater than the chance of being killed; males were willing to risk being killed in an attempt to become dominant. Dominant individuals of many species tend to achieve a greater energy intake (Metcalfe 1986) by having priority over food resources (Monaghan and Metcalfe 1985, Stahl et al. 2001). Therefore, the difference between males and females on the plateau does not necessarily reflect sexual segregation, but rather may simply reflect behavioural differences between the sexes; males are more likely to enter risky environments than females (Herrero 1985).

In our second method we examined changes in RSF model coefficients within one model and found that by altering the extent of available habitat both the direction and magnitude of some coefficients varied. Boyce et al. (2003) also found changes in the direction and magnitude of RSF coefficients when examining habitat use at four scales by elk. They stated that smaller extents can be expected to have smaller β values due to a restriction in the range of variance over smaller landscapes. For grizzly bear habitat selection, smaller scales generally resulted in smaller β values, although for some variables selection was stronger at smaller scales. From a behavioural prospective, Rettie and Messier (2000) claim that for caribou, selection and avoidance at larger scales indicate factors most responsible for limiting fitness, while smaller scales reflect less important limiting factors. We found this to be consistent with our results for male bears that lived on the plateau; plateau males selected for areas with a high risk of human caused mortality at the study-wide extent likely limiting the number of males on the plateau. From a study design perspective, we propose that if behavioural choice is the factor motivating grizzly bear landscape selection, the matched-case-control designs should best reflect this choice, regardless of model rank, because each bear is closely matched to the available points.

We found the selection of habitats to be dependent upon availability on the landscape making some patterns of selection vary across scales (Mysterud and Ims 1998, Guisan and Thuiller 2005). Thus, our ability to detect selection was influenced by the spatial heterogeneity within, and between, mountain and plateau landscapes. For example, alpine and spruce forests were highly sought out by mountain females at the study-wide extent, but we could not detect selection for or against alpine within the home range or buffer extents, while spruce forests were significantly avoided at the home range extent. Indeed, the β coefficients indicate strong selection for alpine and spruce forests at the study-wide extent; these landscapes were important to females that lived in the mountains. However, if we had only examined the home range scale, we may have erroneously concluded that female mountain bears avoided spruce landscapes, and that there was no discernable selection for or against alpine areas. Thus, contrary to Van Horn (2002), we found that relevant ecological influences that occur at smaller scales may not be able to be discerned if RSF is built on too large a scale. Van Horn (2002) claimed that a problem exists if the extent is too small to capture a gradient. Rather, we found that large-scale patterns may overwhelm smaller scale patterns. Specifically, selection of resources by individual bears might be obfuscated by large-scale variation in the availability of various foods, for example. As a result, we show support for examining 3 scales of analysis as argued by O'Neill (1989); alpine landscapes were constrained at the study-wide extent and explained at the buffer extent. On the plateau, alpine landscapes were limited to very small patches and we did not record any female use of alpine landscapes by plateau bears. Therefore, we could not model alpine landscapes for plateau bears, again making selection dependent on availability as suggested by Mysterud and Ims (1998).

We recognize that both spatial and temporal scales are important considerations for habitat selection studies (Orians and Wittenberger 1991) and that our study only examined a subset of possible extents (Boyce 2006). Grizzly bears have been shown to alter selection based on season (McLellan and Hovey 2001, Nielsen et al. 2004) and inclusion of season into our models likely would alter the results. For example, we were unable to investigate the effects that the spring breeding season had on male habitat selection. Males are known to travel widely while breeding and it is possible that the differences between males and females may be partly explained by these extended movements. However, we were limited by the sample size afforded by VHF telemetry when applied to multi-variable analysis. Similarly, we were limited by daytime aerial telemetry; grizzly bears have been argued to display different diurnal and nocturnal patterns of selection (Schwartz and Arthur 1999, Gibeau et al. 2002, Nielsen et al. 2004). However, others studies have shown that grizzly and black bears were primarily diurnal or crepuscular (Garshelis and Pelton 1980, Bjarvall and Sandegren 1987, Rode et al. 2001). New research using GPS collars on grizzly bears in the foothills of Alberta is showing that "bears were crossing roads more during daylight hours" than at night (G. Stenhouse, personal communications). Therefore, for broad-scale forestry planning time of day may be less important than managing for the suite of resources within the home range. These questions would, however, be relevant when managing the movements of grizzly bears surrounding human-use areas for the purpose of avoiding human-bear conflicts, since bears may use human use areas mainly during nocturnal periods with avoidance occurring diurnally (Gibeau et al. 2002). Regardless, our results show strong differences in habitat-selection patterns based on the scale examined. Indeed, where sufficient sample sizes are available (e.g., GPS-telemetry studies), we believe it would be prudent to devise temporal and seasonal models for grizzly bears to reflect differences in RSF models.

5.1 Management implications

Our results differed based on the scale examined, suggesting that scale indeed acts in a hierarchy distinguishing broad-level population questions from more fine-scale activity patterns for grizzly bears. Selection by bears also varied across mountain and plateau landscapes, suggesting that caution should be applied when extrapolating results to new systems, especially if those systems contain a different suite of resources. Generally, when predicting patterns of habitat use it is prudent to examine selection across multiple scales (O'Neill 1989).

The “best” scale depends upon the management question (Boyce et al. 2003, Hobbs 2003, Boyce 2006); if the objective is to examine the effects of forestry operations across the landscape then the study-wide extent will reflect the broad distribution of grizzly bears throughout the area. Because random locations are drawn from the larger study area as well as within the home range, this larger scale allows one to answer more general questions relating to selection by grizzly bears for certain landscape features. However, when management questions become more specific, such as ‘what are the most important attributes to manage for within each stand-level patch’, then it is best to limit availability to the home range, or even buffer, extents. Further, if management is interested in planning for the more immediate habitat selection of bears, for example, to limit the conflict between humans and bears by offering bears the heterogeneity of resources they require within their average movement distances, the extent should be limited to a buffer.

We found that we were limited by the variables measured, and the grain of our GIS layers, especially when attempting to examine fine-scale questions, such as those relating to specific forage items. GIS layers were made for commercial forestry operations and as such some attributes that might be biologically relevant to grizzly bear habitat selection have not been recorded. If questions relating to specific forage items, or time spent within patches, are the management goal then studies must be designed to answer these questions, for example using GPS collars with frequent locations coupled with ground investigation plots and botanically detailed GIS layers. Currently, the management of a number of wildlife species in British Columbia (e.g., caribou, Johnson et al. 2002, 2004) are based upon the results of selections studies derived from attributes queried on GIS layers obtained from government agencies or forest companies. As such, these agencies and companies should consider the management of wildlife when establishing GIS layers.

Table 4-1. Description of variables from geographic information system layers used to select candidate models for grizzly bears in the mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada (1998–2003).

Variable	Type		Description
Primary Landcover Categories	Categorical		Leading landcover type.
	% Landscape		
	Mtn	Plt	
Alpine	23	0.1	Dynamic, high elevation, largely forb and/or shrub dominated parkland or krummholz subalpine fir.
Anthropogenic	0.2	1	Areas of human settlement or regular maintenance, such as along the railway line. Excludes harvested areas.
Black spruce	1	2	Stands dominated by black spruce.
Douglas Fir	0.05	1	Stands dominated by Douglas fir.
Meadow	0.05	2	Large, open forb dominated areas.
Mixed wood	2	13	Stands dominated by cottonwood, aspen, and/or common paper birch.
Pine	7	27	Stands dominated by lodgepole pine.
Rock/bare ground	0.2	0.03	Typically high elevation mountain tops.
Shrub	3	6	Areas with no or few trees and large expanse of shrubs, most frequently occurred adjacent to swamps and rivers.
Spruce	30	35	Stands dominated by spruce species other than black spruce.
Swamp	0.5	3	Water table above ground surface.
True firs	34	10	Stands dominated by subalpine fir.
Topographic Features:			
Elevation	Linear		Elevation above sea level.
Forest height	Linear		Height of the forest in meters. Mountains 0-43 m, Plateau 0-50 m.
Greenness	Linear		Calibrated greenness values related to the amount of green biomass. Lush green vegetation has high greenness values, sparse or senesced vegetation has lower greenness values, and non-vegetated areas have very low greenness values. Pixel resolution 30 m.

Hillshade	Linear	Combination of slope and aspect to measure solar insulation as it varies with topography (azimuth: 225, sun angle: 45). Negative coefficients indicate selection for cooler, northeast aspects, while positive coefficients reflect selection for warmer southwest aspects.
Risk layer (human influenced risk of mortality only)	Linear	Evaluates the relative probability of grizzly bear mortality risk by landscape. Built by assessing the relationship between grizzly bear morality locations (1), and non-kill locations (0) using logistic regression (see Ciarniello chpt 2). The closer to 1, the greater the risk of mortality.
Road – Distance to Highway, Primary Logging road, or secondary/decommissioned logging road	Linear	Straight-line distance to the nearest Highway, primary, or secondary logging road in meters. Highway refers to the 2-lane paved Highway 97 North. Primary logging roads were main arteries that serviced a number of blocks. Secondary and decommissioned logging roads spurred off primary logging roads and were used to access the blocks.
Stand Age	Categorical	Early seral 0-45 years including shrub, meadow, non-commercial brush, non-productive brush, swamps, and alpine. Young forest 46-99 years. Old forest 100+ years.

Table 4-2. Six *a priori* candidate models for grizzly bear habitat selection in the mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada. Separate all-inclusive models were built for landcover classes and stand age due to collinearity.

Model no.	Model Name	Landscape	Model Structure
1	Landcover model	Mountains	Alpine + true firs + spruce + shrub
		Plateau	True firs + spruce + mixed wood + black spruce + shrub
2	Risk Model	Mountains	Dist. primary logging road + dist. secondary logging road + risk + stand age
		Plateau	Dist. Highway + dist. primary logging road + dist. secondary logging road + risk + stand age
3	Seral model	Both	Stand age + greenness
4	Terrain model	Mountains	Forest height + hillshade + elevation
		Plateau	Forest height + hillshade
5	All-inclusive landcover	Mountains	Landcover model + greenness + hillshade + risk + primary road + secondary road
		Plateau	Landcover model + greenness + hillshade + risk + highway + primary road + secondary road
6	All-inclusive seral	Mountains	Stand age + greenness + hillshade + risk + primary road + secondary road
		Plateau	Stand age + greenness + hillshade + risk + highway + primary road + secondary road

Table 4-3. Resource selection function candidate model ranks for male and female grizzly bear habitat selection in the mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada. Bold and italicized numbers had ΔAICc values <2.0.

Extent →	Study-wide				Home range				Buffer			
Model	Mtns Male	Plateau Male	Mtns Female	Plateau Female	Mtns Male	Plateau Male	Mtns Female	Plateau Female	Mtns Male	Plateau Male	Mtns Female	Plateau Female
Landcover model	6	2	5	4	6	5	6	4	6	***1***	6	4
Risky Model	4	4	4	3	3	***1***	5	3	5	***4***	5	3
Seral model	2	5	3	5	2	6	3	5	3	5	3	6
Terrain model	5	6	6	6	4	4	4	6	1	***3***	4	5
All-inclusive landcover	3	1	1	1	5	3	1	1	4	***2***	1	1
All-inclusive seral	1	3	2	2	1	***2***	2	2	2	6	2	2

Table 4-4. Topped ranked resource selection function model assessed using Akaike information criteria for male and female grizzly bear habitat selection in the mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada, 1998-2003.

		Mountains		Plateau	
Design	Extent	Male	Female	Female	Male
A	Study-wide	All-seral	All-landcover	All-landcover	All-landcover
B	Home range	All-seral	All-landcover	All-landcover	Risky
C	Buffer	Terrain model	All-landcover	All-landcover	Landcover

Table 4-5. Resource selection functions at three spatial scales for male grizzly bear habitat selection in the mountains landscape of the Parsnip River study area, British Columbia, Canada, 1998-2003. Bold and italicized numbers had confidence intervals that did not include 0.

Scale →	Study-wide		Home range		Buffer	
Covariate	β	SE	β	SE	β	SE
Alpine	***1.745***	0.289	***0.720***	0.287	-0.042	0.304
Shrub	-0.041	0.514	0.113	0.477	-0.266	0.508
Spruce	***0.730***	0.321	0.107	0.280	***-0.823***	0.296
True firs	***0.711***	0.284	0.405	0.282	-0.352	0.301
Greenness	***0.049***	0.006	***0.027***	0.005	***0.029***	0.005
Hillshade	0.003	0.002	0.002	0.001	***0.004***	0.001
Risk	-7.210	4.193	-6.875	5.266	-0.734	5.707
Distance primary road	***-6.34E^{-05}***	1.90E^{-05}	***-4.37E^{-05}***	1.63E^{-05}	1.90E^{-05}	1.75E^{-05}
Distance secondary road	***-7.54E^{-05}***	3.61E^{-05}	***-9.02E^{-05}***	4.04E^{-05}	-6.02E^{-05}	3.99E^{-05}
k-fold ($\bar{r}_s$)	0.833		0.802		0.749	

Table 4-6. Resource selection functions at three spatial scales for male grizzly bear habitat selection in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998-2003. Bold and italicized numbers had confidence intervals that did not include 0.

Scale ⟶	Study-wide		Home range		Buffer	
Covariate	β	SE	β	SE	β	SE
Black spruce	0.385	0.621	0.462	0.603	0.431	0.632
Mixed wood	0.230	0.270	0.316	0.258	0.238	0.266
Shrub	***1.486***	0.258	***0.781***	0.260	***0.956***	0.272
Spruce	***0.815***	0.194	0.323	0.196	0.241	0.199
True firs	***0.723***	0.256	0.281	0.257	0.115	0.260
Greenness	***0.021***	0.007	0.005	0.007	0.011	0.007
Hillshade	0.006	0.004	0.005	0.003	0.003	0.003
Risk	***6.599***	2.587	2.956	4.095	3.301	4.046
Distance highway	***-3.17E^{-05}***	8.69E^{-06}	***-4.18E^{-05}***	1.25E^{-05}	***-2.42E^{-05}***	1.08E^{-05}
Distance primary road	***7.26E^{-05}***	2.49E^{-05}	***8.15E^{-05}***	3.00E^{-05}	***7.20E^{-05}***	2.95E^{-05}
Distance secondary road	-1.86E^{-05}	8.55E^{-05}	-5.47E^{-07}	1.06E^{-04}	-4.16E^{-05}	1.03E^{-04}
k-fold ($\bar{r}_s$)	0.635		0.262		0.386	

Table 4-7. Resource selection functions at three spatial scales for female grizzly bear habitat selection in the mountain landscape of the Parsnip River study area, British Columbia, Canada, 1998-2003. Bold and italicized numbers had confidence intervals that did not include 0.

Scale →	Study-wide		Home range		Buffer	
Covariate	β	SE	β	SE	β	SE
Alpine	***3.651***	0.425	-0.430	0.471	0.018	0.407
Shrub	***2.604***	0.455	-0.070	0.501	0.301	0.441
Spruce	***1.743***	0.435	***-1.765***	0.475	***-1.312***	0.419
True firs	***2.446***	0.423	***-1.050***	0.470	-0.569	0.409
Greenness	***0.043***	0.002	***0.027***	0.002	***0.031***	0.002
Hillshade	***0.004***	0.001	***0.004***	0.001	***0.003***	0.001
Risk	***-13.206***	5.027	-3.547	6.131	$1.39E^{-38}$	$1.74E^{-38}$
Distance primary road	***-9.21E***$^{-05}$	$8.19E^{-06}$	$-1.11E^{-05}$	$1.31E^{-05}$	$1.71E^{-06}$	$1.08E^{-05}$
Distance secondary road	***1.87E***$^{-04}$	$1.41E^{-05}$	***1.55E***$^{-04}$	$2.18E^{-05}$	***8.17E***$^{-05}$	$1.73E^{-05}$
k-fold ($\bar{r}_s$)	0.963		0.934		0.970	

Table 4-8. Resource selection functions at three spatial scales for female grizzly bear habitat selection in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998-2003. Bold and italicized numbers had confidence intervals that did not include 0.

Scale →	Study-wide		Home range		Buffer	
Covariate	β	SE	β	SE	β	SE
Black spruce	***1.189***	0.303	***0.978***	0.280	***1.034***	0.289
Mixed wood	0.230	0.163	0.115	0.150	0.112	0.148
Shrub	***1.290***	0.180	***0.938***	0.164	***0.878***	0.164
Spruce	***0.708***	0.128	***0.318***	0.121	***0.342***	0.120
True firs	-0.021	0.187	0.041	0.176	0.013	0.178
Greenness	***0.023***	0.004	***0.016***	0.004	***0.014***	0.004
Hillshade	***0.006***	0.002	0.004	0.002	***0.006***	0.002
Risk	-0.089	3.094	-2.708	3.426	-1.336	3.210
Distance highway	***-7.96E^{-05}***	6.32E^{-06}	***-4.66E^{-05}***	9.91E^{-06}	***-3.72E^{-05}***	8.50E^{-06}
Distance primary road	2.55E^{-05}	2.22E^{-05}	3.93E^{-05}	2.50E^{-05}	2.47E^{-05}	2.34E^{-05}
Distance secondary road	-1.37E^{-04}	8.96E^{-05}	***-1.47E^{-04}***	6.77E^{-05}	-9.61E^{-05}	6.68E^{-05}
k-fold ($\bar{r}_s$)	0.944		0.802		0.656	

Figure 4-1. Study area for grizzly bear habitat selection, including mountain and plateau boundary just east of the Parsnip River, British Columbia, Canada, 1998-2003.

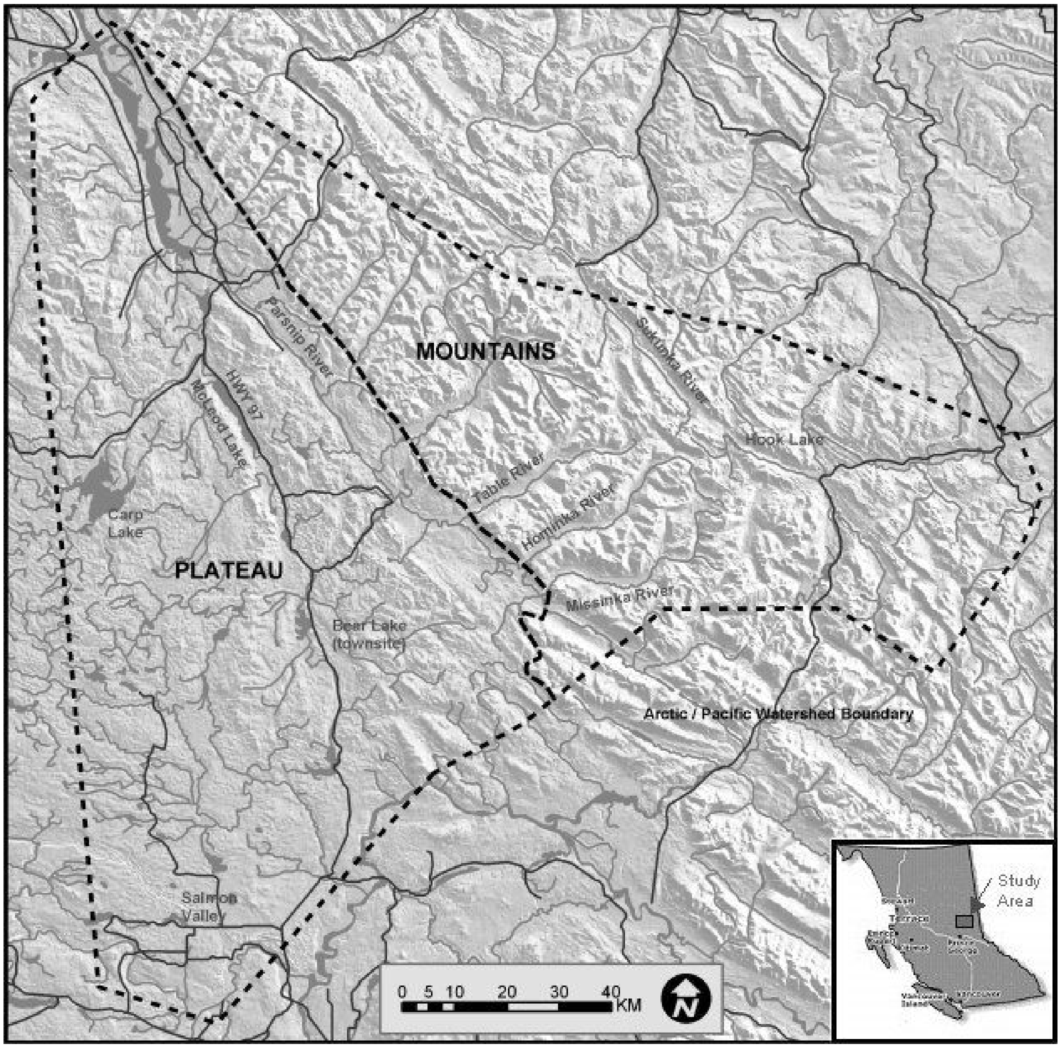


Figure 4-2. Distance moved by grizzly bears between radiotelemetry locations ≤7 days apart in the mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada, 1998-2003. The distance that incorporated 80% of grizzly bear movements was used as the buffer size for the 3rd order RSF design.

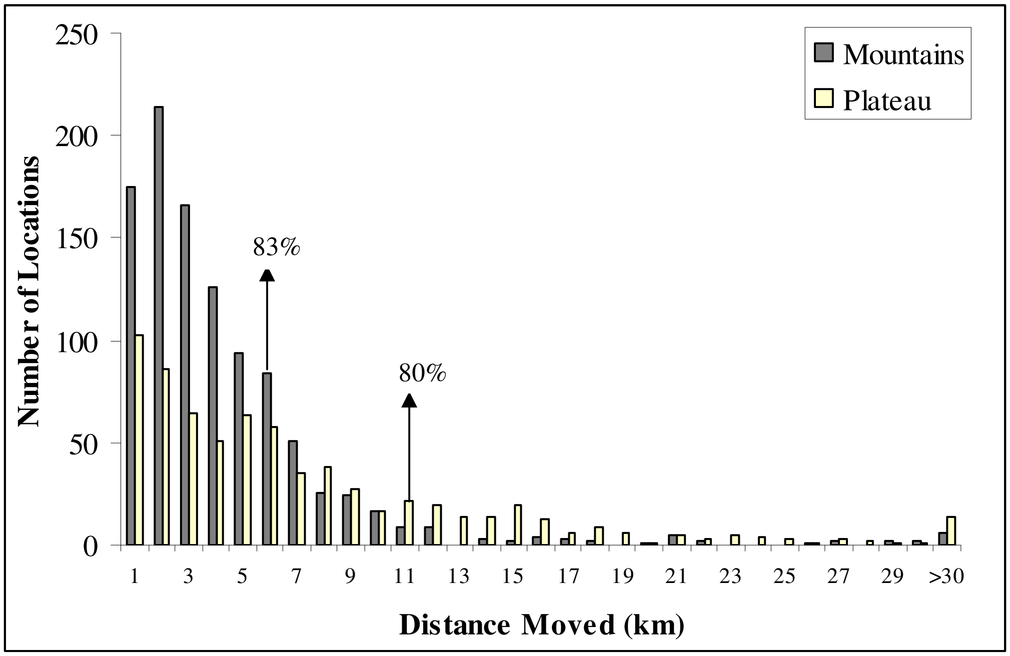
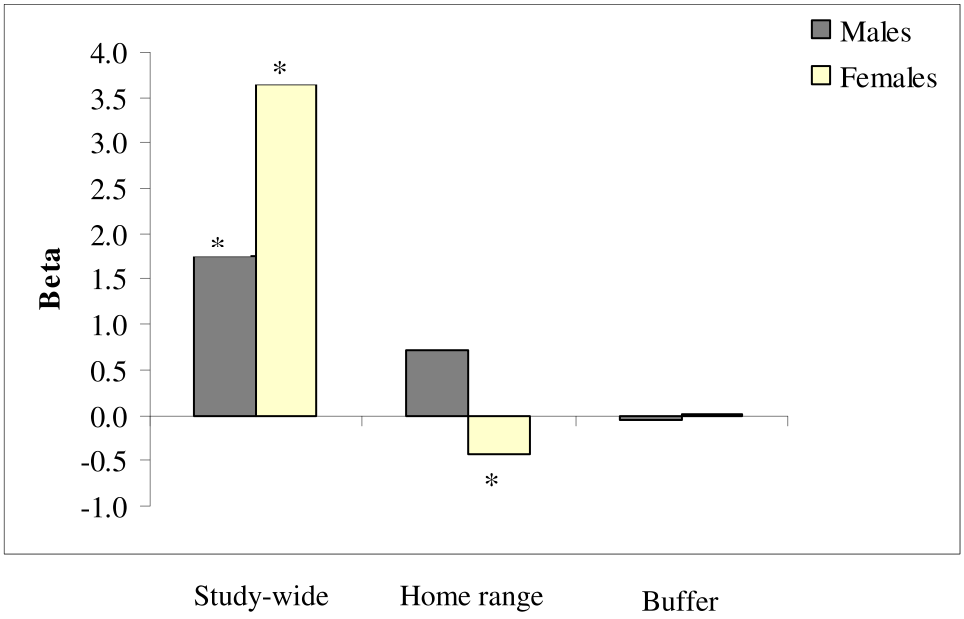


Figure 4-3. Resource selection function coefficients for male and female grizzly bears in the mountainous landscape of the Parsnip River study area, British Columbia, Canada, 1998-2003, using a) alpine landscapes, and b) spruce forests at three spatial scales. The * indicates that the β is significantly different from 0 based on a Wald statistic ($P < 0.05$).

a) alpine landscapes



b) Spruce forests

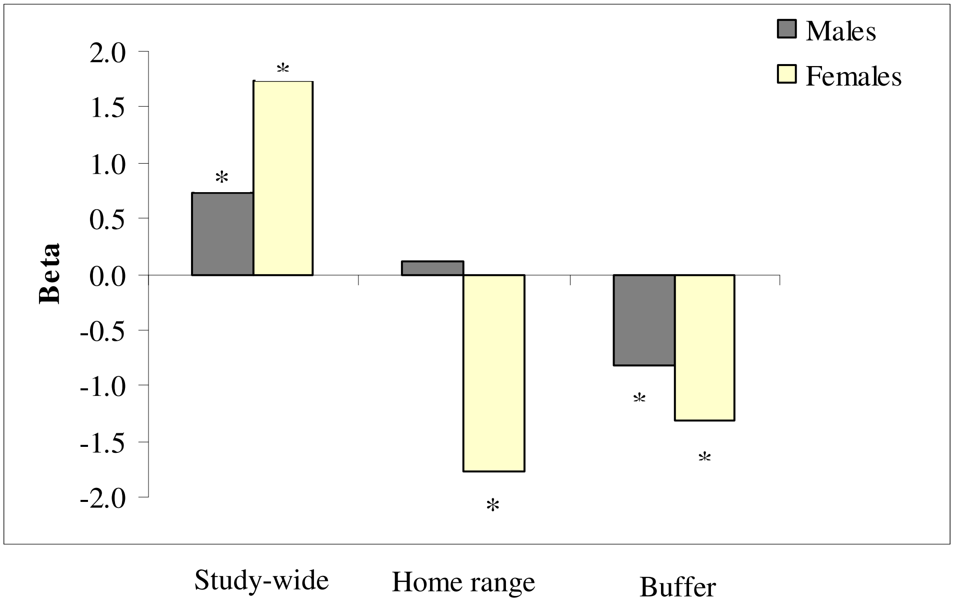


Figure 4-4. Relative probability of occurrence of male grizzly bears in the mountain landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003, based on a) study-wide extent, b) home range extent, and c) buffer extent. Orange areas represent an increased probability of occurrence (greater RSF values).

a) Study-wide extent

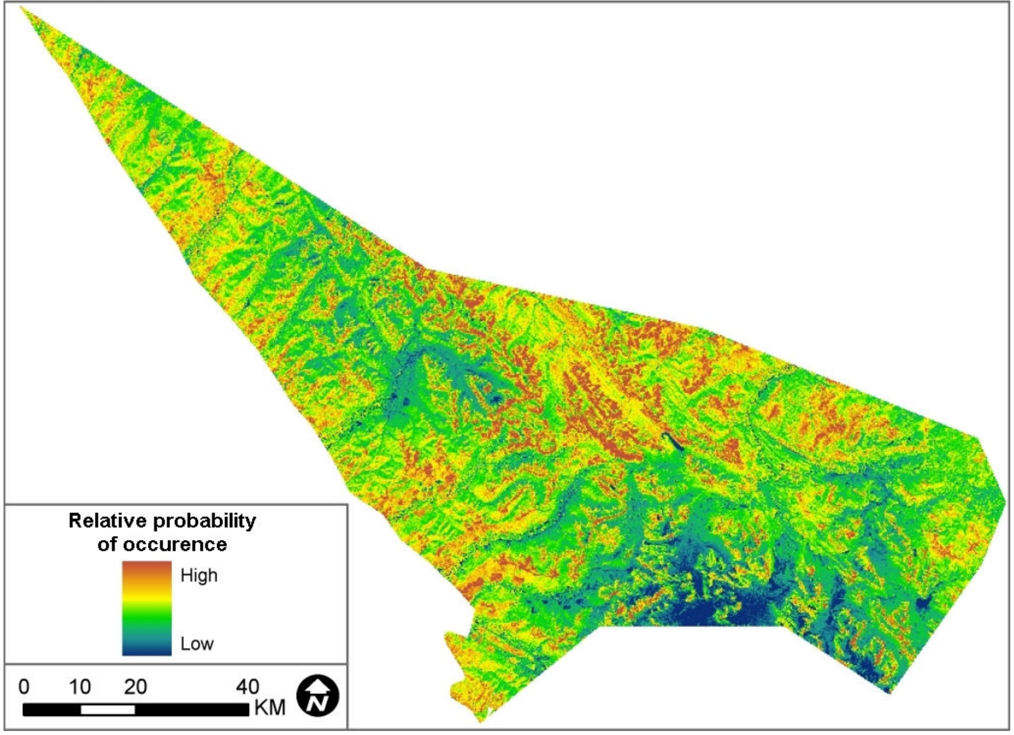


Figure 4-4b. Relative probability of occurrence of male grizzly bears in the mountain landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003, based on a) study-wide extent, b) home range extent, and c) buffer extent. Orange areas represent an increased probability of occurrence (greater RSF values).

b) Home range extent

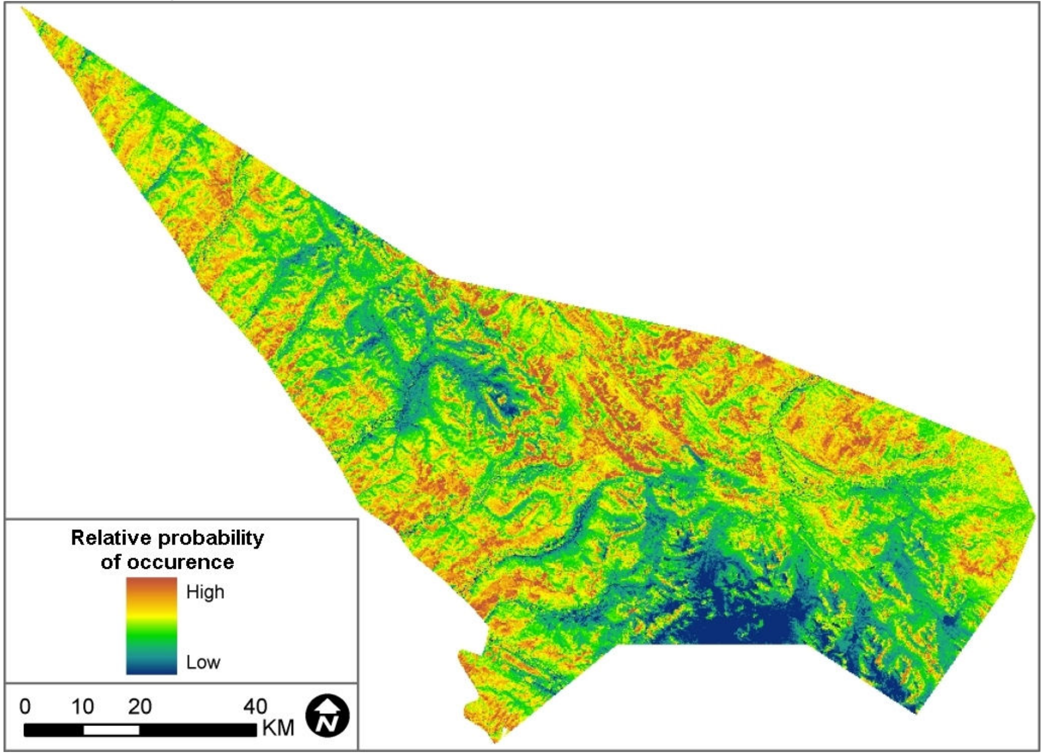


Figure 4-4c. Relative probability of occurrence of male grizzly bears in the mountain landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003, based on a) study-wide extent, b) home range extent, and c) buffer extent. Orange areas represent an increased probability of occurrence (greater RSF values).

c) Buffer extent

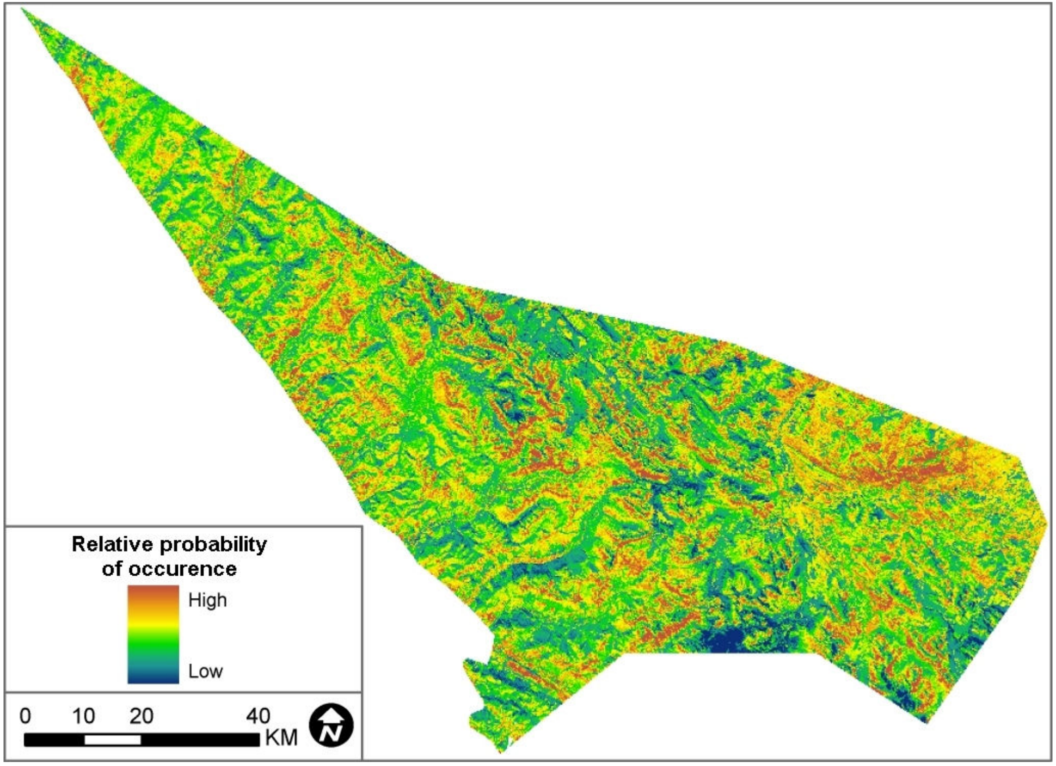


Figure 4-5. Resource selection function coefficients for male and female grizzly bears in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998-2003, using shrub-dominated landscapes at three spatial scales. All β's are significantly different from 0 based on a Wald statistic ($P < 0.05$).

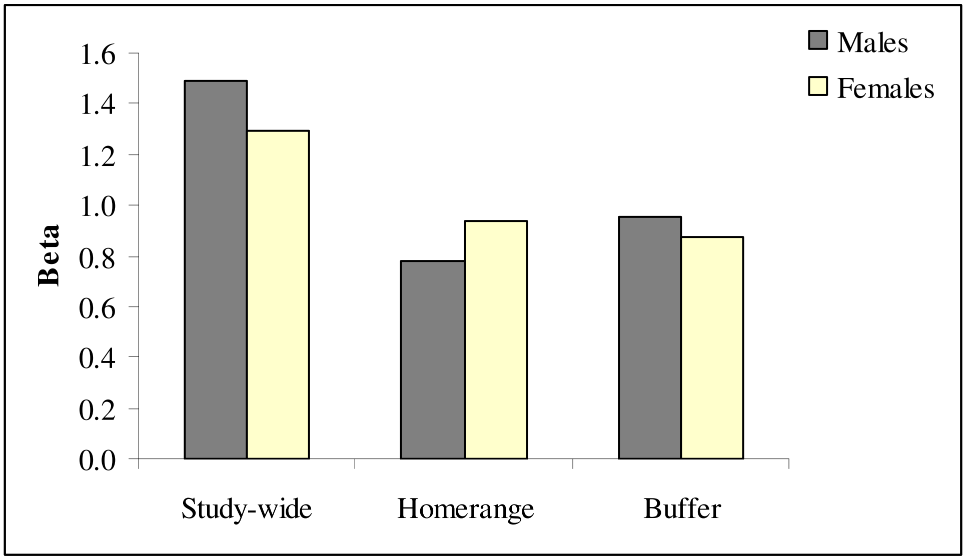


Figure 4-6. Relative probability of occurrence of male grizzly bears in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003, based on a) study-wide extent, b) home range extent, and c) buffer extent. Orange areas represent an increased probability of occurrence (greater RSF values).

a) Study-wide extent

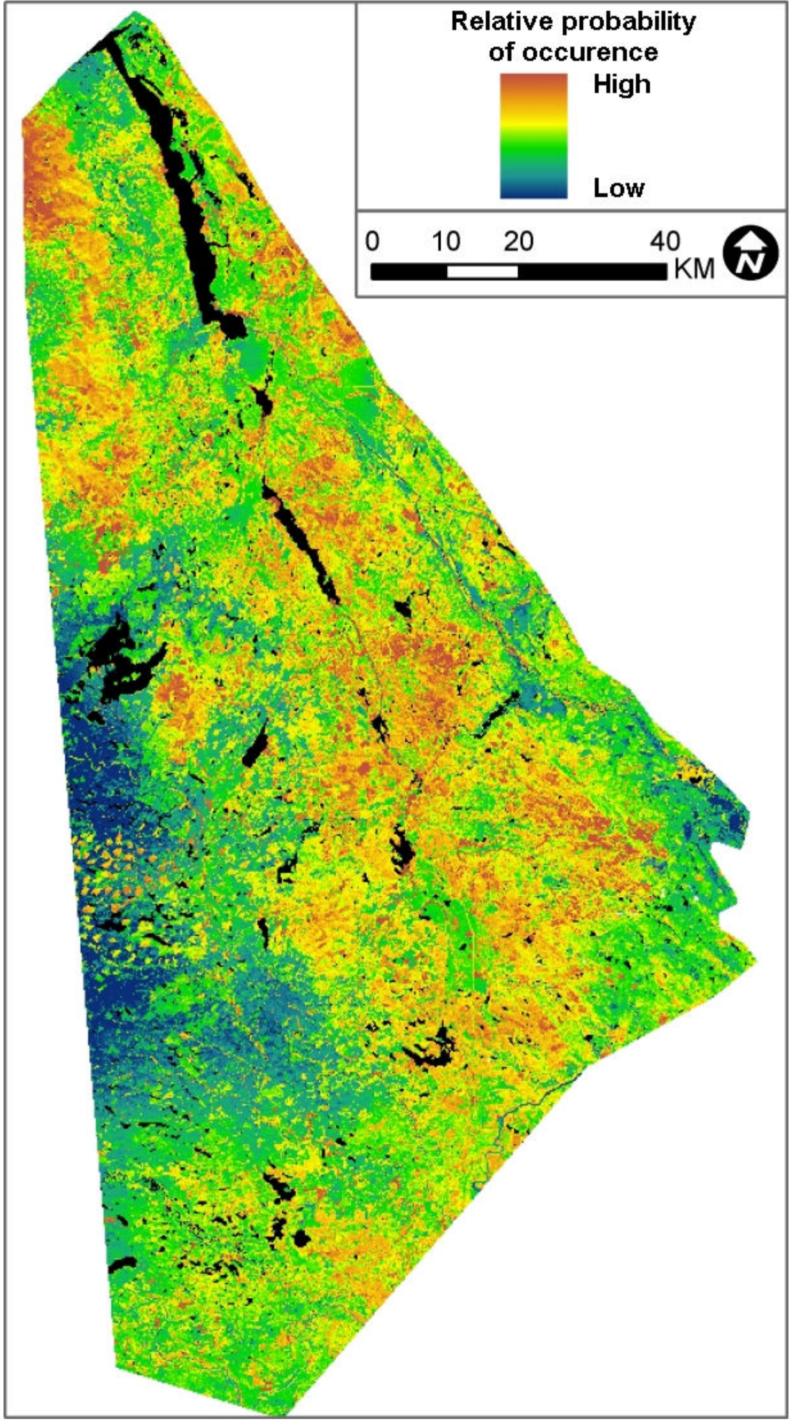


Figure 4-6b. Relative probability of occurrence of male grizzly bears in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003, based on a) study-wide extent, b) home range extent, and c) buffer extent. Orange areas represent an increased probability of occurrence (greater RSF values).

b) Home range extent

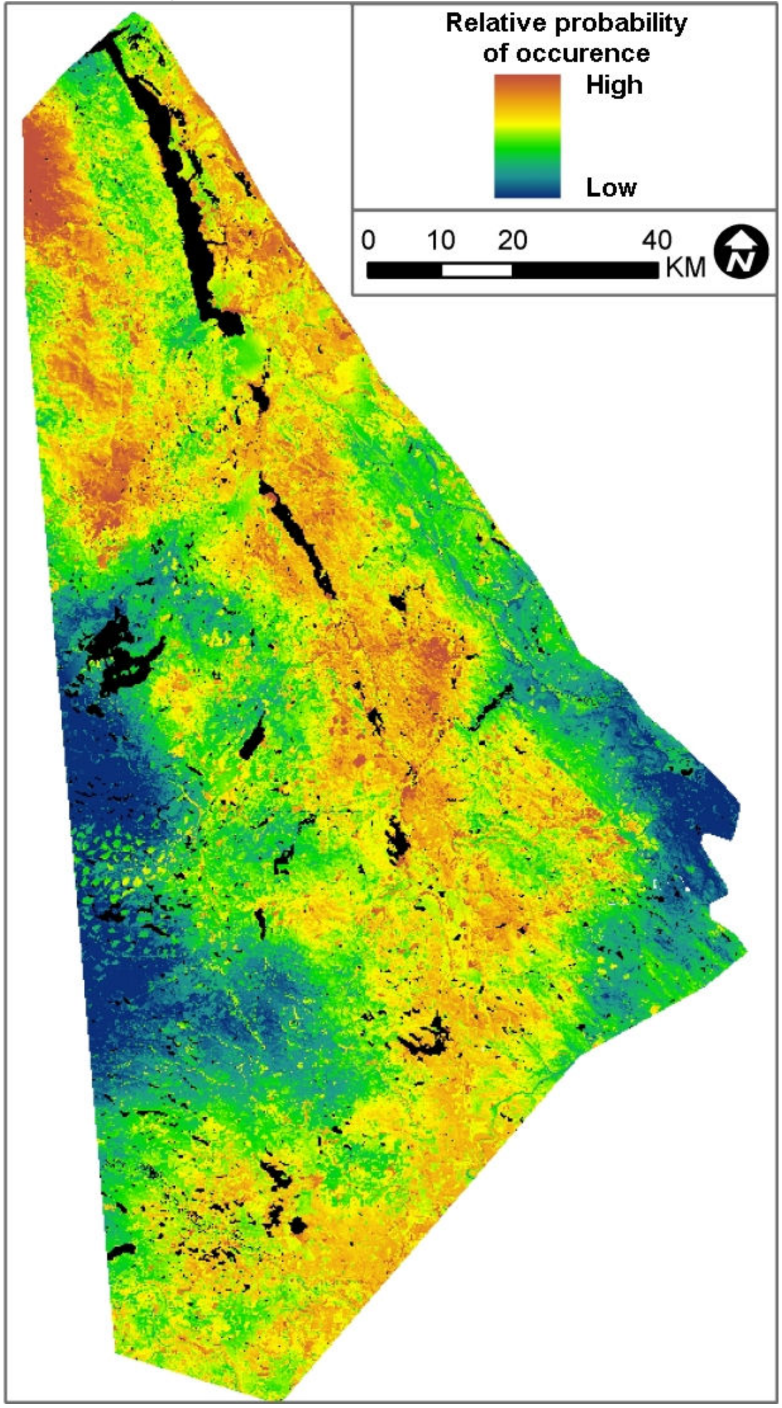


Figure 4-6c. Relative probability of occurrence of male grizzly bears in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003, based on a) study-wide extent, b) home range extent, and c) buffer extent. Orange areas represent an increased probability of occurrence (greater RSF values).

c) Buffer extent

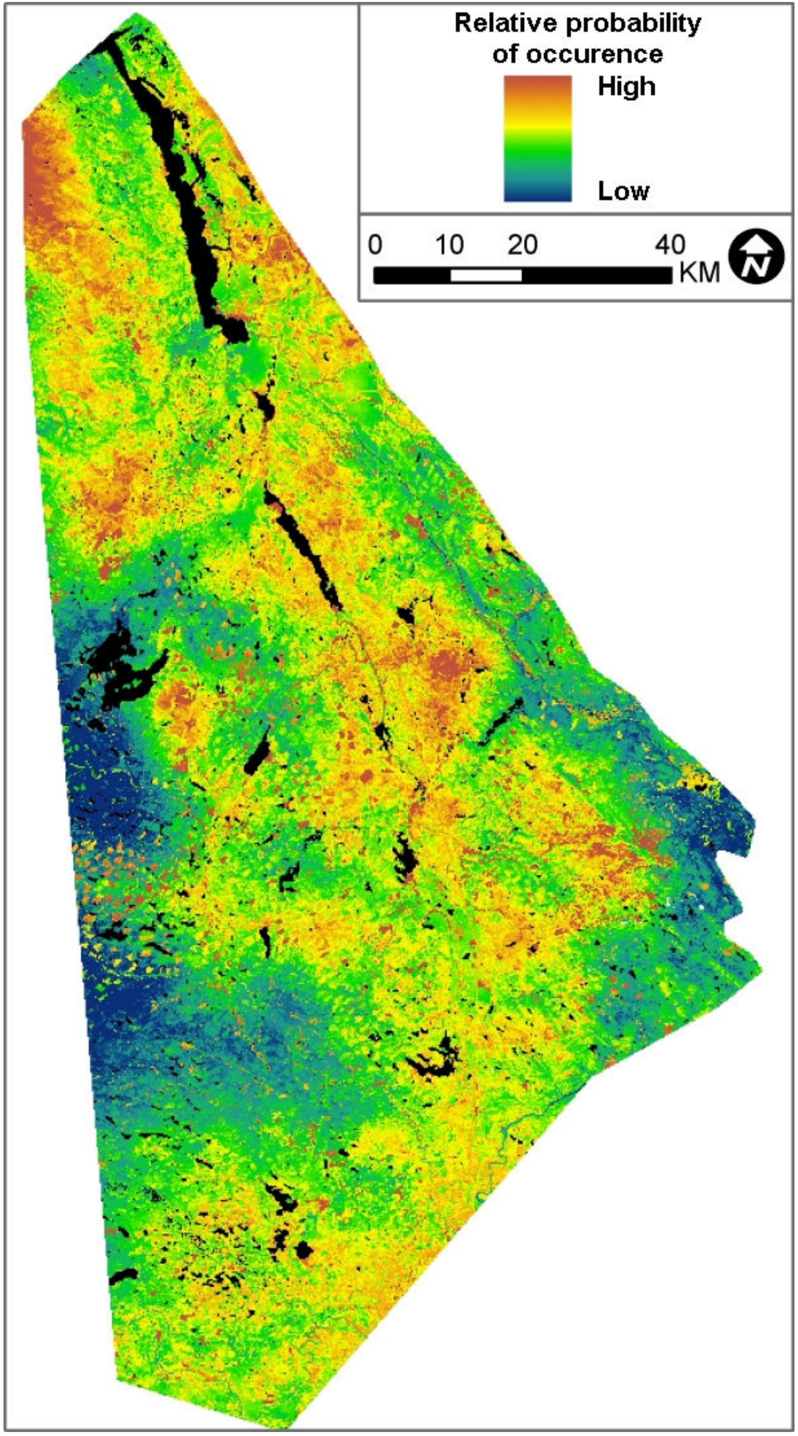


Figure 4-7. Relative probability of occurrence of female grizzly bears in the mountain landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003, based on a) study-wide extent, b) home range extent, and c) buffer extent. Orange areas represent an increased probability of occurrence (greater RSF values).

a) Study-wide extent

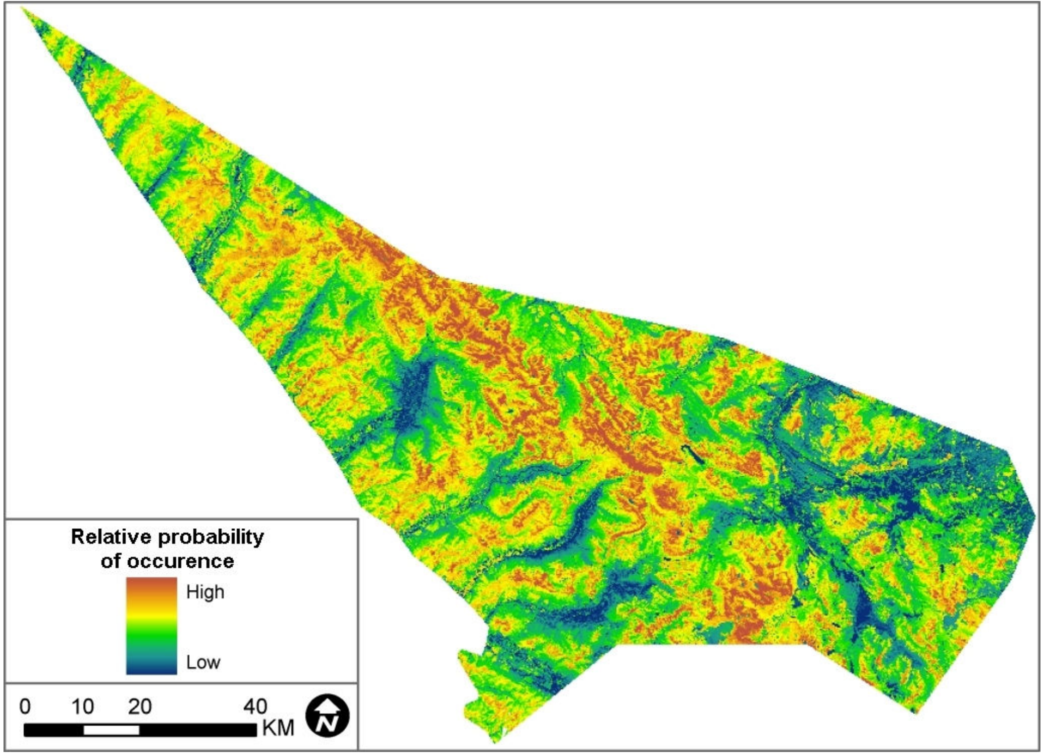


Figure 4-7b. Relative probability of occurrence of female grizzly bears in the mountain landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003, based on a) study-wide extent, b) home range extent, and c) buffer extent. Orange areas represent an increased probability of occurrence (greater RSF values).

b) Home range extent

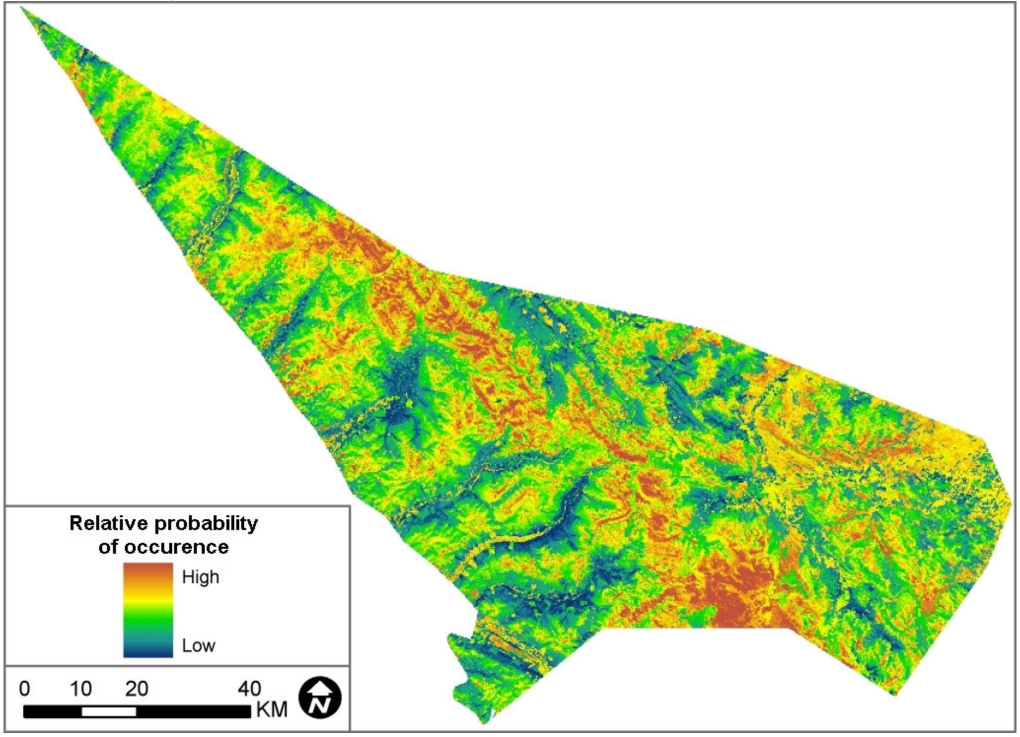


Figure 4-7c. Relative probability of occurrence of female grizzly bears in the mountain landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003, based on a) study-wide extent, b) home range extent, and c) buffer extent. Orange areas represent an increased probability of occurrence (greater RSF values).

c) Buffer extent

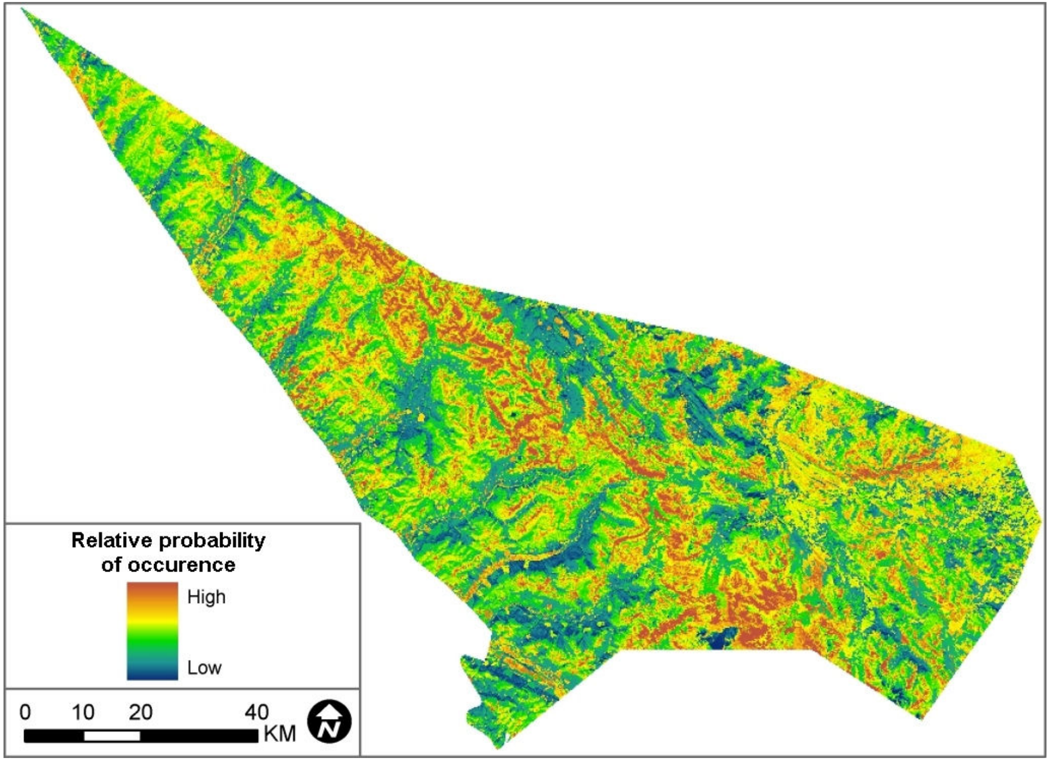


Figure 4-8. Relative probability of occurrence of female grizzly bears in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003, based on a) study-wide extent, b) home range extent, and c) buffer extent. Orange areas represent an increased probability of occurrence (greater RSF values).

a) Study-wide extent

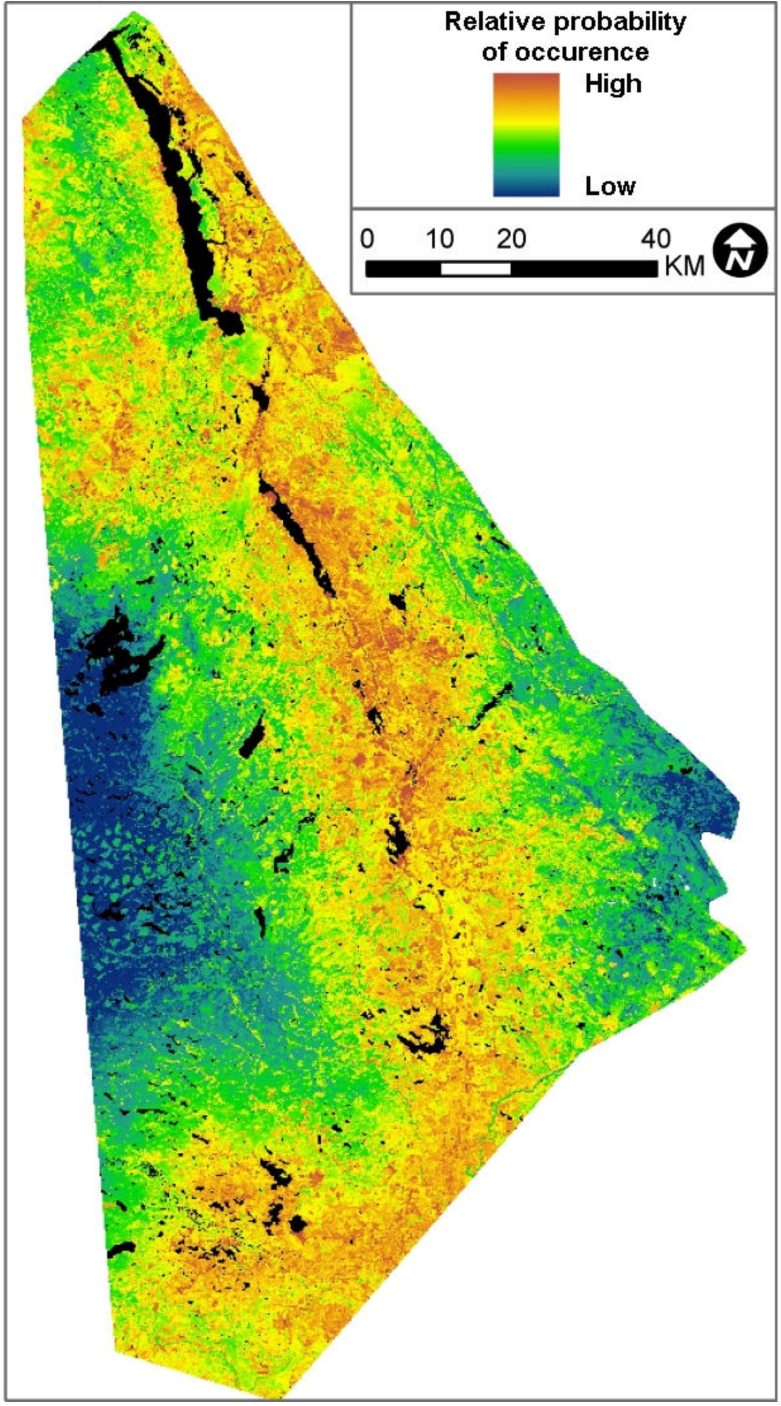


Figure 4-8b. Relative probability of occurrence of female grizzly bears in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003, based on a) study-wide extent, b) home range extent, and c) buffer extent. Orange areas represent an increased probability of occurrence (greater RSF values).

b) Home range extent

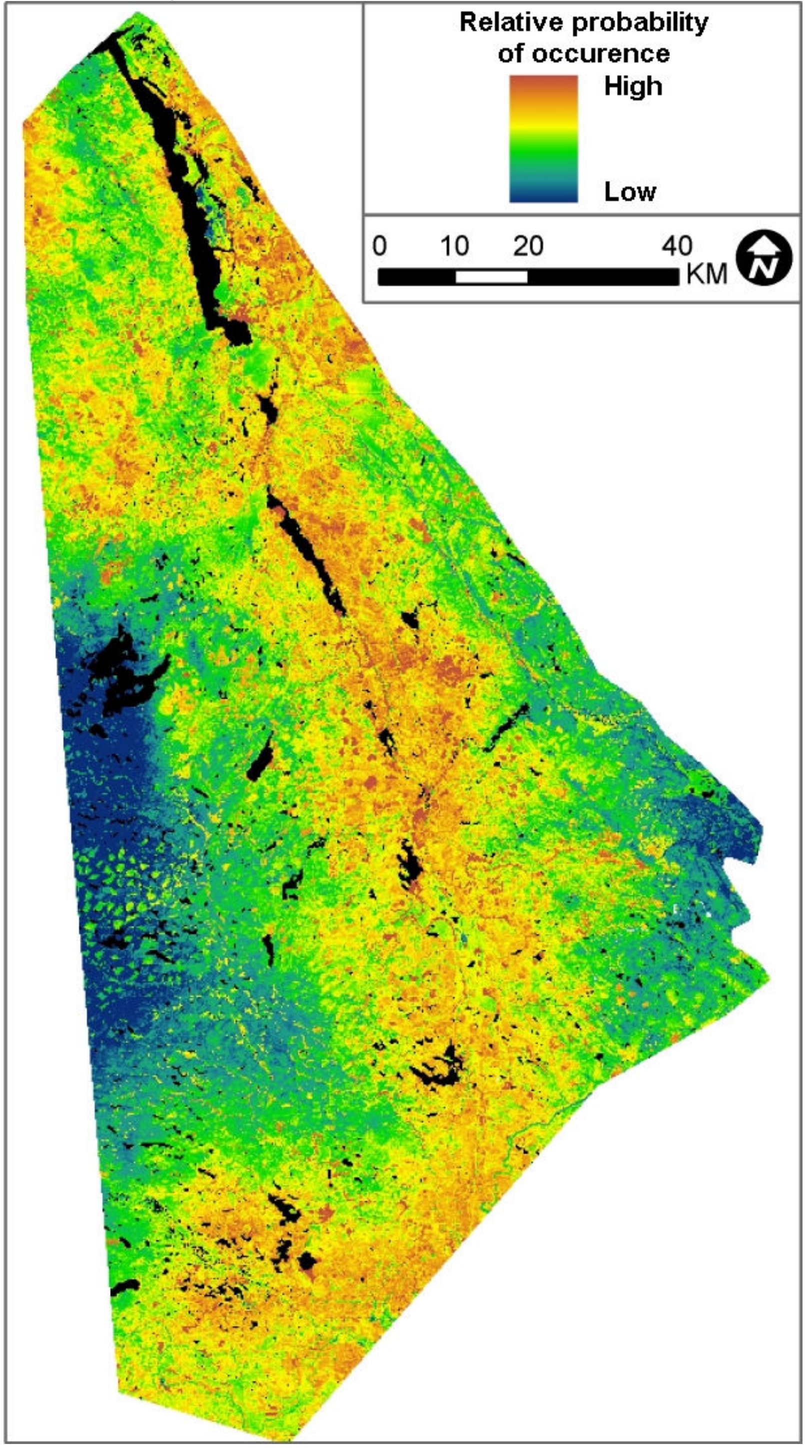
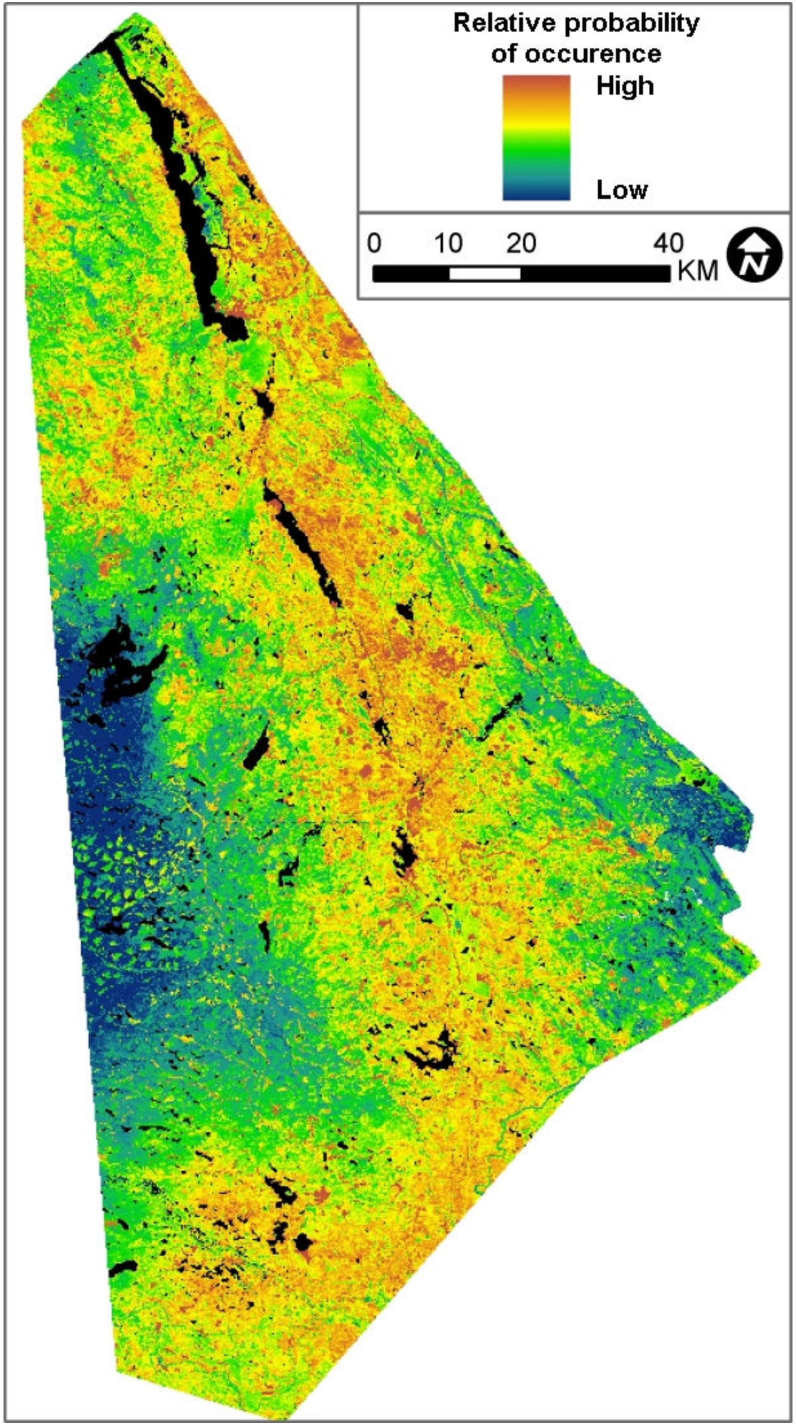


Figure 4-8c. Relative probability of occurrence of female grizzly bears in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003, based on a) study-wide extent, b) home range extent, and c) buffer extent. Orange areas represent an increased probability of occurrence (greater RSF values).

c) Buffer extent



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CHAPTER 5
DENNING BEHAVIOR AND DEN SITE SELECTION OF GRIZZLY BEARS ALONG THE PARSNIP RIVER, BRITISH COLUMBIA, CANADA[1]

1. INTRODUCTION

Grizzly bears (*Ursus arctos*) inhabiting northern latitudes may spend 5 to 6.5 months each year in a den (Vroom et al. 1980, Judd et al. 1986, Van Daele et al. 1990, Friebe et al. 2001, Seryodkin et al. 2003). During denning, bears do not eat, urinate, or defecate and must rely on fat reserves attained during the non-denning period (Hellgren 1998). Dens are constructed or selected to provide thermal insulation (Vroom et al. 1980) and security cover (Seryodkin et al. 2003) for denning bears and birthing sites for pregnant females (Swenson et al. 1997). Understanding the den site requirements of grizzly bears is fundamental in a landscape that is subject to increasing modification. Resource extraction activities may remove denning habitats and facilitate human access and disturbance through road construction. Disturbance of hibernating grizzly bears has been documented to reduce reproductive success of pregnant females (Swenson et al. 1997), and den abandonment has been linked to a greater probability of death for dependent offspring (i.e., cubs and yearlings; Linnell et al. 2000). If we understand what den structures bears select, resource managers can better manage for those features when developing sustainable forest harvest plans.

Grizzly bear den site selection varies by region (Vroom et al. 1980). The denning ecology of grizzly bears in the Arctic watershed of central British Columbia (BC) has not been studied previously. This area contains mountain and plateau landscapes, and it is believed that grizzly bears in the area may behave similarly to other interior BC bears by denning within mountain habitat, traveling to plateau or flatland areas upon den emergence, and moving back to the mountains during berry season, where they remain to den (McLellan and Hovey 2001). We investigated whether grizzly bears inhabiting the plateau landscape in central BC exhibited a different pattern of den site selection, timing of den entry

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[1] This chapter was published in the peer-reviewed journal *Ursus* (2005, 16:47-58) by Ciarniello, L. M., M. S. Boyce, D. C. Heard, and D. R. Seip. Reprinted with permission from Dr. Rich Harris, Editor, *Ursus*.

and exit, and denning structures compared with those inhabiting the mountainous landscape.

2. STUDY AREA

The study site, approximately 18,096 km^2, was contained within a 'working forest' in central-eastern British Columbia (54°39'N, 122° 36'W) and was delineated by using a composite minimum convex polygon (MCP) of bear locations collected during the study, omitting 8 outlier locations on the western boundary (Fig. 5-1). The Hart Range of the Central Canadian Rocky Mountains comprised 7,472 km^2 of the study area. The mountainous landscape was relatively pristine, although most low-elevation valleys contained logged areas of varying sizes. Unlike other areas of the Rocky Mountains, most of the landscape in the Hart Range was largely open alpine–parkland habitat. The highest peak was 2,500 m, and <1% of the area contained glacial rock and ice. Mountain valleys consisted of subalpine fir (*Abies lasiocarpa*) and spruce (*Picea glauca* × *P. engelmannii*) with less lodgepole pine (*Pinus contorta*) than the plateau. The proportion of subalpine fir became progressively greater with increasing elevation. The area above treeline was primarily alpine parkland and typically consisted of small shrubs or krummholz form trees, shrub–forb–sedge (*Carex* spp.) meadows, and wide avalanche chutes.

The rolling hills and flat valleys of the plateau comprised 10,624 km^2 and have been used for timber harvest since about 1960. In the wetter portion east of Highway 97, the old growth forests of the plateau were comprised of white spruce (*P. glauca*) and spruce–fir (*A. lasiocarpa)* associations. There also were small remnants of Douglas-fir (*Pseudotsuga menziesii*) on southern aspects with coarse soils. In the drier area west of Highway 97, climax forests were largely lodgepole pine. Only small patches of high-elevation, subalpine fir occurred on the plateau. The plateau was warmer and drier than the mountains with a mean annual temperature of 2.6 °C and 72 cm of rainfall compared with the mountains (0.3 °C and 154 cm of rainfall; DeLong et al. 1993, 1994). The mountains also received over twice the mean annual snowfall (700 cm) than the plateau areas (300 cm; DeLong et al. 1993, 1994).

3. METHODS

3.1 Radiotelemetry

From August 1997 to fall 2002, 61 bears were captured (27 mountains, 34 plateau; 22 males, 39 females) using aerial darting, leg snares, or culvert traps. Twenty-five bears were fitted with collars equipped with a global positioning system (GPS; Televilt, Lindesberg, Sweden), whereas 36 received VHF (very high frequency) collars (Lotek, Newmarket, Ontario, Canada). Bear ages were estimated using cementum annuli of an upper premolar (Mattson's Laboratory, Milltown, Montana, USA). Female bears were classified into 4 categories based on age and reproductive status: (1) females that entered the den pregnant and emerged from denning with cubs of the year (cubs, hereafter), (2) females with young that entered the den with offspring passing their first through fourth birth date while denned, (3) lone females ≥4 years of age and not in the company of offspring (presumably not pregnant on den entry), and (4) subadult females ≤3 years of age and not in the company of their mother. Female categorization followed Friebe et al. (2001); however, we used ≥4 years as our age of transition from subadult to adult rather than 3 years. We classified age based on site-specific knowledge of reproduction (e.g., 2 4-year-old females produced cubs whereas 2 other 4-year-olds denned with their mother) and independence of young from their mothers. Males were classified as subadult (≤3) or adult (≥4 years).

Bears were monitored from April to December using aerial VHF and GPS telemetry to determine timing of den entry and exit and the habitat characteristics of den sites. Dens were relocated and verified by helicopter in late February. Universal Transverse Mercator (UTM) coordinates were obtained using a hand-held 12 channel Garmin® GPS unit (average horizontal displacement error = 5 m). We sampled the habitat characteristics for the exact den location (single pixel).

3.2 Duration of denning

Arrival at the denning area in fall was defined as when bears moved to ≤1 km of that winters' den site. The arrival date was calculated as the mid-point between the date bears were first located at the den site and the date of the prior location (Van Daele et al. 1990, Davis 1996, Friebe et al. 2001). If the prior location was >14 days earlier, we did not calculate a den area arrival date (Haroldson et al. 2002). We used 14 days between flights because it allowed for a break during volatile weather conditions, which occurred frequently during late fall and early spring.

Den entry dates were calculated as the mid-point between the date when no fresh sign of bear activity was visible at the den site (Judd et al. 1986) and the date of the previous location. Den emergence date was calculated as the mid-point between the date of first evidence of bear activity and the date of the previous location with no bear sign if that location was ≤14 days (Haroldson et al. 2002). The number of days between the den entry and emergence dates was the denning duration.

Where applicable, dates recorded by the GPS-collars were used. GPS locations were taken sufficiently frequently (i.e., 4–6 per day or 4 every other day) that the specific dates of bear arrival in the den area, denning, and emergence could be determined. Statistical comparisons between denning duration and distance between consecutive den sites for the mountains and plateau were calculated using the Mann-Whitney *U*-test. Analysis of variance (ANOVA) was used to determine whether bear denning differed by reproductive status, age or location.

3.3 Den investigations

After bears exited dens we visited den sites to record den type (excavated, cave, nest) and stabilizing material (root mass, rock, soil). Sites were accessed using a helicopter as well as ground transportation to reduce bias associated with sampling bears that denned close to roads. We used the ground investigations to gain an understanding of fine-scale attributes associated with den sites that cannot be obtained from the geographic information system (GIS) database. The GIS databases were designed to depict attributes important to commercial logging operations, which were not necessarily attributes most biologically relevant to bears.

3.4 GIS data

Digital elevation maps (DEM) were built from terrain resources inventory maps (TRIM2; BC Ministry of Water, Land, and Air Protection, Victoria, Canada) and were used to obtain elevation, slope, and aspect for bear den sites and random locations. Forest cover maps (FCM) and road networks were obtained from the BC Ministry of Forests, Canadian Forest Products (Canfor) East, Canfor West, the Pas Lumber, and Slocan Forest Products Limited in Prince George, British Columbia, Canada. These map layers were used to obtain land-cover type, stand age, and distance to roads. All raster layers (DEM, slope, aspect, hillshade, distance to roads, forest age) had a resolution (pixel size) of 25 m.

***3.4.1** Land-cover types.*--Locations that occurred within forested polygons were categorically classified using the leading tree species (mixed wood, true firs, Douglas-fir, spruce, or pine). Locations that occurred in non-forested polygons were classified into alpine, shrub, swamp, meadow, rock–bare ground, or anthropogenic categories based on the vegetation described in the forest cover database.

***3.4.2** Stand age and related classifications.*--Forest cover maps provided ages for all commercial forest types, which we classified into 3 categories: early seral (<45 years), young forest (46–99 years), and old forest (≥100 years). Early seral comprised herb and shrub–herb stages with an open coniferous canopy that facilitated vigorous growth in the understory. Young forests generally were dense, closed canopy coniferous forests with reduced understory, whereas old forests were self-thinning with canopy gaps that facilitated vigorous understory growth (B.C. Ministry of Forests 1998).

We were limited by the GIS database because habitats of non-commercial value (i.e., alpine, meadows, swamps, and urban) did not contain age information. Therefore, if an age class was not assigned we examined the non-productive and non-commercial descriptors to gain information regarding those land-cover types. From those descriptors, we classified shrub, meadow, non-commercial brush, non-productive brush, and swamps into the early seral age class. We considered alpine as a unique age class due to its unique dynamic features. In the plateau, settlements and some agricultural areas were classified in the GIS database as urban. However, in the mountains some forests and right-of-ways surrounding the railway and mines also were classified as urban because they were not available to be harvested, distinguishing those areas from the urban areas on the plateau. Therefore, we added an anthropogenic (human influence) category to distinguish these areas from the urban land-cover classes.

3.4.3 *Forest height.*--Forest height in meters was highly correlated with stand age, so these variables could not be used in the same model.

3.4.4 *Hillshade*.--Hillshade measured solar insulation as it varied with topography. Hillshade was estimated by a combination of slope and aspect data from the DEM, which was used to estimate the average amount of shade during the course of the year at any pixel. Warm southwest facing (225°) slopes of 45° received the greatest hillshade values, whereas cooler northeastern slopes corresponded to the lowest hillshade values.

3.4.5 *Distance to the nearest road.*--Road network data from FCM, TRIM, Canfor East, Canfor West, the Pas Lumber, and Slocan Forests Products Limited were combined and used to determine the Euclidean distance to the nearest road. The majority of roads within the study area were logging roads, but a 2-lane paved highway bisected the plateau.

3.5 Resource selection functions

Because den sites have little or no variation (that is, there are single or few observations for each animal) we used a special case of Design I studies (Manly et al. 1993:7, Manly et al. 2002). In our design, individual animals were identified and attributes of resource units such as den sites were quantified. Because the entire study area contained grizzly bears and a few radiocollared animals traveled between the 2 landscapes, we assumed that bears were free to explore either mountain or plateau landscapes. Thus, availability was measured for each landscape at the population level (Manly et al. 1993, 2002) by generating random locations using Hawth'sTools (Beyer 2004) for ArcGIS® 8.3 (Environmental Systems Research Institute, Redlands, California, USA) at 1 location/km^2 (7,472 in mountains and 10,624 in plateau). Characteristics of the den site and random locations were compared assuming the following log-linear model:

$$w(\mathbf{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 \ldots \beta_p x_p), \qquad (1)$$

where the $\beta_i s$ are selection coefficients for a vector **x** of covariates (habitat and terrain variables), x_i, for $i = 1, 2, \ldots p$, estimated using logistic regression. We assumed that habitat availability was fairly static among years, so we pooled the data. Models were estimated using Stata 7.0 (Stata Corporation, College Station, Texas, USA).

By definition, RSF is proportional to the probability of use of a resource unit and, as such, the intercept, β_0, is not used (Manly et al. 1993, 2002). To construct the likelihood, we conditioned on the realized samples and computed the relative probability of being used and a value proportional to the probability that the unit is in the available sample, given a unit is in the tested or available sample, respectively. Therefore, from the way the likelihood is constructed, a small number of used samples compared with a large number of random samples does not present a problem. Non-intercept coefficients and standard errors are not affected because they stabilize after a sufficient number of available locations are included (T. McDonald, Western EcoSystems Technology, Cheyenne, Wyoming, USA, personal communication, 2004). In this design we could not estimate the sampling fractions.

We followed the information theoretic approach of Burnham and Anderson (1998) and Anderson et al. (2000) and determined a set of candidate models that we deemed biologically relevant. Final model selection was based on Akaike information criteria difference for small samples (AIC$_c$; Burnham and Anderson 1998); the model with the lowest AIC$_c$ score represents the most parsimonious model. The probability that candidate models are the best models is provided by the normalized Akaike weights (AIC$_{cw}$) (Anderson et al. 2000).

Significant coefficients were those whose 95% confidence intervals did not include 0. The parameter estimates of the highest-ranked model were used to calculate and map the relative probability of occurrence of grizzly bear dens across the study area. We used 5-fold cross validation to assess the predictive capability of the top-ranked model (Boyce et al. 2002). For each of the 5 iterations, 20% of the data were retained and the frequency of these test data were compared against predictions from models constructed using the remaining 80% within 10 RSF bins (Boyce et al. 2002). We used Spearman's rank correlation to test whether the number of locations increased in bins with greater RSF scores as a measure of the predictive capability of the model.

4. RESULTS

We located 86 den sites (68 female, 9 male, 9 unidentified). Seventy-seven dens were used by 41 radiocollared bears (34 females, 7 males). The 9 animals of unidentified gender were associated with den sites we encountered incidentally. Den sites of 19 radiocollared bears (18 females, 1 male, 55 den sites) were used for >1 year.

Twenty-nine (33.7%) and 57 (72.3%) of the den sites occurred in the plateau and mountain portions of the study area, respectively. On the plateau, female bears (*n* = 16) occupied 24 dens; males (*n* = 2) used 2 dens. Sibling pairs (male–male, male–unknown, and female–female) occupied the remaining 3 plateau den sites. In the mountainous landscape, female bears (*n* = 17) occupied 42 dens; males (*n* = 4) used 6 dens. The 9 dens encountered incidentally were all in the mountains. Average age of bears denning on the plateau was 7.5 years (*n* = 28, range 1–22) compared with 12.0 years (*n* = 48, range 3–20) for bears denning in the mountains.

4.1 Timing of denning events

4.1.1 *Den area arrival and entry.*--Female bears in the mountains arrived at their den areas on 14 October, 12 days earlier than plateau bears (26 Oct); subadults arrived 24 days earlier (14 Nov; Table 5-1). The 2 bears that moved from the plateau to the mountains had similar arrival dates to plateau bears (10 Nov).

Female bears in the mountains spent an average of 10 days in the vicinity of their den sites prior to denning (n = 20), with a mean entry date of 23 October (n = 28). Female bears that lived on the plateau spent 11 days (n = 15) at their den sites prior to denning and entered their dens 17 days later than mountain females (9 Nov, n = 17). Subadult bears on the plateau averaged 10 days (n = 7) at their den sites prior to denning. The 2 male bears in the mountains used the den area an average of 14 days prior to denning.

4.1.2 *Den emergence.*--We determined only a mean den emergence date for female plateau bears for 2 of the 5 years. Conservatively, the mean date of emergence for bears that lived on the plateau was 24 April (range 4 Apr to 1 May), whereas bears that lived in the mountains emerged 11 May (range 27 Apr to 27 May; Table 5-1). The bears that moved from the plateau to the mountains to den had emergence dates more similar to plateau bears (8 Apr).

Mountain females averaged 8.5 days ≤1 km of their den sites after emergence (n = 33, range 0–29 days), whereas plateau females averaged 6 days (n = 11 females, range 0–11 days). By group, mountain females with cubs averaged 11 days (n = 9) within 1 km of their den site, whereas plateau females with cubs averaged 8 days (n = 3). Mountain females with young averaged 10.5 days (n = 9) within 1 km of the den compared with 6 days for plateau females with young (n = 3); lone mountain females averaged 6 days (n = 15) and lone plateau females averaged 5 days (n = 5). We only had data on 1 plateau male that remained within 1 km of his den site for 3 days after emergence, whereas males that lived in the mountains averaged 6 days (n = 4, range = 3–10 days).

4.1.3 *Duration of denning.*--Adult female bears that lived in the mountains spent >1 month longer in their dens than those that lived on the plateau (Table 5-2). Denning duration varied by landscape (n [plateau] = 10, n [mountain] = 22; $P < 0.001$) but not by year (n [plateau] = 10 $P = 0.068$, n [mountain] = 22; n [year] = 5; $P = 0.321$). Pregnant females on the plateau had a longer denning duration than lone females (n [plateau pregnant] = 3; n [plateau lone] = 4; $P = 0.025$; n [mountain pregnant] = 6; n [mountain lone] = 9; $P = 0.443$). In both landscapes, there was no statistical difference in denning duration between pregnant females and females with young, although pregnant females spent 12 (plateau) and 13 (mountains) days longer in their den sites. Male bears and subadults had the shortest duration of denning (Table 5-2). ANOVA revealed that neither age (F = 1.245, 10,11 df, P = 0.279) nor reproductive status (F = 1.304, 2,19 df, P = 0.296) was associated with denning duration for mountain females. However, when considered together, both age (F = 4.984; 9,1 df, P = 0.045) and reproductive status (F = 6.823, 2,8 df, P = 0.035) influenced denning duration for plateau bears. On 22 occasions bears emerged before the first spring flight (13 plateau and 9 mountain bears).

4.2 Den area fidelity

Only 2 bears (1 female with young, 1 male) moved outside their core home range to den. Both bears lived primarily on the plateau, denned in the mountains, and returned to the plateau the subsequent spring.

For 19 bears (12 mountain, 7 plateau), we had den locations for >1 consecutive year. The mean distance between subsequently used den sites was 2.4 km for mountain females (n = 11 bears, n = 36 dens, SE = 0.45 km, range = 0–9 km) and 5.1 km for plateau females (n = 7 bears, n = 16 dens, SE = 1.4 km, range = 1.2–11.7 km; n = 32; P = 0.068). One 3-year-old male in the mountain area had den locations 12 and 44 km apart, respectively.

4.3 Types of den structures

We visited 39 of the 86 den sites (45%): 19 mountain den sites (33%) and 20 plateau sites (69%). Most dens were excavated into the sides of slopes (74% mountains, 90% plateau; Table 5-3). In the mountains, bears also used natural caves for den sites (5%). Natural cave sites likely were underrepresented in the mountains because many were on slopes too steep to safely access. We did not find any natural caves on the plateau, although 1 excavated den site had rocks as the stabilizing material, forming a durable, cave-like structure.

Rocks (47%, n = 9) were the primary stabilizing structure for dens in the mountains, followed by roots (37%, n = 7), a combination of roots and rocks (11%, n = 2), and roots, rocks, and clay soil (5%, n = 1). Roots (80%, n = 16) were the primary stabilizing material for dens on the plateau, followed by no stabilizing material (10%, $n = 2$), rock (5%, $n = 1$), and root and soil combination (5%, $n = 1$).

4.4 Forest stand structure at investigated den sites

Investigated dens in the mountains were primarily located in the alpine ($n = 14$, 74%), followed by the upper reaches of the Engelmann spruce–subalpine fir habitat ($n = 5$, 26%) (Table 5-4). Only small patches of alpine habitat existed on the plateau. Ninety percent of den sites investigated on the plateau were in forest stands ≥45 years, with 50% occurring in stands >100 years of age (Table 5-4). All forest stands contained tall trees. We also noted that the 2 dens in early seral stands were located under the roots of large stumps or deciduous trees that remained in the stand.

4.5 Den re-use

Eleven of the 36 (30.5%) dens for which a determination could be made showed signs of previous use, whereas 25 (69%) dens were made during the year of investigation (Table 5-3). Re-use for 3 sites was undetermined because the chamber or tunnel had largely collapsed. Den re-use in the mountains was 50% ($n = 8/16$), compared with 15% ($n = 3/20$) on the plateau. All dens with durable or permanent structures ($n = 7$; caves, tree cavity, excavated rock) were used by grizzly bears during >1 winter. Re-use of excavated dens was much less likely. Only 2 bears re-used a den they were known to have used before.

4.6 Resource selection analysis

We present 5 of 10 ecologically plausible RSF models examining the relative probability of grizzly bear den site occurrence by landscape (Tables 5-5, 5-6). Alpine and true firs (Engelmann spruce and sub-alpine fir) were the best predictors of grizzly bear den site occurrence for the mountain landscape (Table 5-5, model 1, Fig. 5-2). The 5-fold cross validation provided a mean Spearman's Rank correlation of 0.792 ($P = 0.01$), indicating that this model had excellent predictive capability and predictions were statistically significant. The ΔAIC_c values for the top 4 models in the mountain landscape were <2.0, indicating that the support for models 1–4 was similar (Burnham and Anderson 1998). The commonality between those models was selection for alpine or true fir habitat types that had lower forest heights and occurred at mid-high elevations. The parameter estimate for elevation-squared revealed there was an optimum mid-elevation range for den site placement (Table 5-5, model 3). We documented no dens in the low elevation sub-boreal spruce forests, early seral habitats, or anthropogenic areas, preventing us from modeling these features. An interaction between alpine and hillshade was used to test whether alpine den sites tended to be on mesic northeast (i.e., negative coefficient) slopes. However, confidence intervals for hillshade and the alpine–hillshade interaction included 0, suggesting poor inference for those parameter estimates. Model 5 was the model with the least parsimony, as shown by its high AIC_c score, low AIC_c weight, and $\Delta AIC_c > 2$.

In the plateau, models 1–3 were similar (i.e., $\Delta AIC_c < 2$, Table 5-6, Fig. 5-3). The commonality between those models was the selection for higher forest heights for den site placement. The 5-fold cross validation provided a mean Spearman's Rank correlation of 0.527 ($P = 0.1$), indicating that the top-ranked model had low predictive capability. The negative hillshade value indicated selection for cooler northeast aspects; however, the confidence intervals included 0, suggesting poor inference. Selection for higher elevations was minor for bears that lived on the plateau likely because the relief was not as great as within the mountains (model 2). The fourth ranked model revealed that grizzly bears selected den sites in stands with taller trees that were away from roads; although the ΔAIC_c places less importance on this model, it is important from a management perspective. Forest stand type ranked as the least parsimonious model (model 5). Grizzly bears selected spruce forests over pine; however, for the remaining stand types confidence intervals overlapped 0. We documented no dens in black spruce, shrubs, meadows, swamps, rock–bare ground, or anthropogenic landscapes.

5. DISCUSSION

There were notable differences in the timing of denning and the land-cover type of den sites selected by bears that lived in the mountains and those that lived on the plateau. Bears that lived in the mountains arrived earlier at denning areas and had a longer denning duration. We found that average denning dates varied between the 2 landscapes but not among years. Pregnant females had the longest denning duration, whereas subadult plateau bears and adult males had the shortest denning duration. These findings are consistent with brown bears in central Sweden (Friebe et al. 2001), Admiralty and Chichagof Islands, Alaska (Schoen et al. 1987), and the Greater Yellowstone Ecosystem (Haroldson et al. 2002), but dissimilar to Russia, where no intraspecific differences were detected (Seryodkin et al. 2003). Similar to our findings, pregnant females were found to den first on Kodiak Island (Van Daele et al. 1990), in the Mission Mountains of Montana (Servheen and Klaver 1983), and in Yellowstone (Judd et al. 1986, Haroldson et al. 2002). However, in the Swan Mountains of Montana, females with young were found to den first (Mace and Waller 1997).

Van Daele et al. (1990) reported similar patterns of den entry and emergence dates between bear populations that lived within 70 km of each other on Kodiak Island, Alaska; entry and emergence also were separated by 2 to 3 weeks for females that lived in the southwestern portion. The authors hypothesized that the difference in denning behavior was attributed to varying food availability across the study area. Similarly, American black bears (*U. americanus*) in the warmer Kenai Peninsula of Alaska denned 2 weeks earlier and emerged later than those in the colder climate of the Susitna River (Schwartz et al. 1987), although these authors attributed the difference to weather and physical condition. There is general agreement that denning behavior may be triggered by a reduction in availability of forage items (Servheen and Klaver 1983, Schoen et al. 1987, Haroldson et al. 2002) and the reproductive status of individuals (Van Daele et al. 1990, Mace and Waller 1997). We believe those triggers also existed in our study area: the mountains were subjected to harsher weather conditions than the plateau, resulting in a shorter growing season. The longer duration of denning, earlier arrival at den site areas, and greater den-area fidelity resulted in a shorter non-denning period for mountain bears. A shorter non-denning period implies an overall reduction in the time available for foraging in the mountains compared with the plateau.

Most grizzly bears denned in their respective mountain or plateau areas. Only 2 bears denned outside their core home range, moving from the plateau to the mountains to select a den site. The first was a family unit (GF35 and her two 4-year-old offspring) that moved 40.5 km from the plateau to the mountains to den. This observation also was the only evidence of a female moving between landscapes in any season. The other observation was a large adult male that primarily resided on the plateau. Some large adult males have been known to travel between the 2 landscapes (Ciarniello et al. 2003). Grizzly bears, however, readily adapt physiologically to their environment; for example, in areas with late salmon (*Oncorhynchus* spp.) runs in Alaska, some male grizzly bears did not enter a den (Van Daele et al. 1990). Unlike resident mountain bears, these 2 migrating plateau bears had entrance and emergence dates more similar to plateau bears and immediately traveled to the plateau for early foraging opportunities. All other bears were located in the vicinity of their den sites at some point during the non-denning period. Friebe et al. (2001) also found that most bears denned within their core home range and visited their denning areas during the non-denning season. They suggested that bears may select their denning area during the non-denning season (Friebe et al. 2001).

Bears primarily excavated dens into the sides of slopes, and dens excavated by grizzly bears have been reported often (Vroom et al. 1980, Van Daele et al. 1990, Seryodkin et al. 2003). However, bears that lived in the mountains also used natural cave dens. We believe caves are important den sites for mountain grizzly bears, and especially important as natal den sites. We also noted bears using caves during the non-denning period. Natural caves likely provide cool places to bed during the non-denning season, while offering added security in alpine landscapes. Mountain cave dens were associated with (1) extensive clumps of bear hair deposited at various times, (2) >1 bear (as evidenced by mixed DNA samples), and (3) some worn rock structures, suggesting long-term use by a number of different bears. The use of cave dens also was reported for brown bears in Trentino, Italy and, similar to our findings, dens often were located on steep slopes difficult for people to access (Groff et al. 1998). The authors suggested that selection for steep slopes likely reflects selection for increased security (Groff et al. 1998). A study in Banff National Park also reported the use of cave dens, although the authors focused on excavated dens (Vroom et al. 1980). Bears on Admiralty Island, Alaska, denned in cave dens but those dens were considered "atypical" (Schoen et al. 1987:299).

All of the natural cave dens showed signs of re-use, as did the tree cavity and the excavated cave den. The only unstable den with evidence of previous use was an excavated den site associated with 1 other successful den and 1 attempt. Because the 3 dens were 1–2 m apart, we believe the bear had fidelity toward the denning area rather than the den site. In a synthesis paper on bear denning, Linnell et al. (2000) cited similar results with low re-use of excavated or ground dens and a greater frequency of re-use of natural caves and tree cavities. Some authors have suggested that high den re-use is positively correlated with low den availability (Lindzey and Meslow 1976, Schwartz et al. 1987, Linnell et al. 2000). Mace and Waller (1997) suggested that denning habitat is limited when bears travel extensively outside their normal home ranges to den. In our study the commonality between dens that were re-used was related to the stability of the den structure. We believe that den sites likely were not limited in either landscape. Bears often used pre-existing stable dens when available or otherwise excavated dens that usually were used only once.

Bears selected different land-cover features for denning depending on the landscape they occupied. We suggest that plateau bears selected older forests to avoid human disturbances prevalent in the early seral forests and open areas (e.g., disturbance by hunters and forestry workers in the fall). Moose (*Alces alces*) hunting season ended 5 November, but most hunting occurred in the plateau portion of the study area between 10 and 25 October (about 10,000 hunter days), corresponding with bears arriving at their denning areas (Table 5-1). The only measure of disturbance in the model was distance to the nearest road. Plateau bears selected for areas away from roads, which likely was correlated with selection for older forests where road densities were lower. On the plateau, all hunters accessed the area by truck or all-terrain vehicle, so there was extensive use of the entire road network. Linnell et al. (2000) indicated that grizzly bears avoided human activity areas, including roads and industrial activity, for den-site selection; bears selected distances of 1–2 km from those areas. Those authors also suggested that grizzly bears may tolerate human activity and noise during denning if the disturbance is >1 km from the den site; however, if regular visits by humans occurred early in the denning season, bears often abandoned their den sites (Linnell et al. 2000). Swenson et al. (1996 in Linnell et al. 2000) found that brown bears selected den sites >3 km from villages and >1 km from roads. Disruption during the denning period has been documented to decrease reproductive success of brown bears (Swenson et al. 1997, Linnell et al. 2000) and increase winter weight loss of black bears (Goodrich and Berger 1994). Thus, frequent disruptions in early seral areas may cause some bears to avoid those areas when selecting a den site. Due to the lack of site-specific human use data, we were unable to include a disturbance variable into our plateau model, which could have improved the predictive capacity. In the alpine portion of the mountains, there were no roads and few hunters. Hunters accessed those areas on foot after flying in or by hiking or horseback from the roads in commercial forests at lower elevations. Disturbance of mountain bears by humans was limited due to the inaccessibility of the terrain, especially during winter. Also, selection by bears for higher elevation alpine habitat provided a natural separation between low elevation valley bottom forestry operations and den site placement. Therefore, environmental variables provided excellent predictive capability in the mountain portion of the study area.

5.1 Management implications

The Parsnip River area is subject to modifications due to resource extraction and recreational use. Roads are required for timber harvest and, once established, often provide recreational access into backcountry areas. Resource managers need information on the requirements of grizzly bears to preserve denning habitat and to minimize disruption to hibernating bears during winter logging operations.

The habitat map for plateau den sites (Fig. 5-3) shows a low relative probability of use of clear-cut areas and early seral stands. For den sites on the plateau, management should focus on maintaining some large tracts of forest in old-growth and reducing the density of open roads within and adjacent to those stands to limit disturbance. Swenson et al. (1997) suggested that human activity should be avoided within 100–1,000 m of active den sites. Disturbance of hibernating bears due to winter logging operations has been shown to result in a greater probability of mortality of grizzly bear offspring (Swenson et al. 1997). Thus, several large patches of mature forest should be maintained within every 300–400 km^2 area, an area equivalent to the mean annual home range of plateau females (Ciarniello et al. 2003). Five plateau den sites were located on the west side of McLeod Lake. We identified this area as an important denning habitat for plateau bears; as such, this area would be a good candidate area for an old-growth reserve.

We also observed plateau grizzly bears denning in young forest stands if large trees were present within the stand. Also, many plateau dens were excavated into slopes adjacent to riparian areas. Consequently, within forest harvest areas, retention of large trees within riparian areas and retention of wildlife tree patches within cut areas should promote stand-level diversity, thereby enhancing the future value of those stands for grizzly denning habitat in regenerating forests.

In the mountain area, impacts on denning habitat areas were relatively low. However, recent mining and oil and gas developments may affect alpine denning habitat and mountainous alpine areas are experiencing increasing levels of winter disturbance from motorized backcountry recreation, including snowmobiles, snowcat skiing, and helicopter skiing. The expansion of forest road networks contributes to increased winter access to alpine areas. Managing the level of winter access and disturbance in alpine areas may not only be important for grizzly denning habitat, but also for other wildlife such as caribou (*Rangifer tarandus*), mountain goats (*Oreamnos americanus*), and wolverine (*Gulo gulo*).

Table 5-1. Median fall arrival date to <1 km of a known den site location, median den entry date, and median emergence date for grizzly bears in the mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada (1998–2003). Den emergence dates were not calculated for bears that emerged before the first survey flight in any given year.

		Den arrival		Den entry		Den emergence			
Landscape	Group	Median	*n*	Median	*n*	Median	Range	*n*	Number of bears emerged prior to 1st spring flight
Mountain	females	14 Oct	25	23 Oct	28	11 May	27 Apr–27 May	32	6 (5 >27 Apr and 1 >30 Apr)
	males	8 Nov	2	23 Nov	2	5 May	24 Apr–18 May	3	2 (1 >13 Apr and 1 >27 Apr)
	migrators[a]	10 Nov	2	23 Nov	2	8 Apr		1	1 (>13 Apr)
	subadults	21 Oct	1		0	28 May		1	0
Plateau	females	26 Oct	16	9 Nov	17	24 Apr	4 Apr–1 May	10	7 (5 >27 Apr and 2 >30 Apr)
	males		0		0	27 Apr		1	0
	subadults	14 Nov	8	20 Nov	7	15 Apr	8–24 Apr	3	0

[a] Migrators were bears that lived primarily on the plateau but denned in the mountains.

Table 5-2. Mean denning duration for grizzly bears in the mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada, 1998–2003. Differences were calculated in days between the same groups in each landscape. Approximate number of months spent in the den site was calculated using an average 30 days per month.

	Mountain				Plateau				
Group	Denning duration	Range	*n*	Months	Denning duration	Range	*n*	Months	Difference (days)
All adult females	200	136–221	22	6.7	164	141–186	10	5.5	36
Pregnant females	206	191–221	6	6.8	177	169–186	3	5.9	29
Females with young	193	136–207	7	6.4	165	141–184	3	5.5	28
Females with young (minus plateau migrators[a])	202	194–207	6	6.7	165	141–184	3	5.5	37[b]
Lone females	202	193–220	9	6.7	154	146–159	4	5.1	48
Male	152	n/a	1	5.1	n/a	n/a	0	n/a	n/a
Subadults	n/a	n/a	0	n/a	153	139–166	3	5.1	n/a

[a] Migrators were bears that lived primarily on the plateau but traveled to the mountains to den.

[b] Thirty-seven days represents the difference between resident mountain bears with young versus resident plateau bears with young.

Table 5-3. Type of den and den re-use for 39 den sites used by grizzly bears in the mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada, 1998–2003.

	Mountains				Plateau			
Den type	Dens	%	Dens re-used	%	Dens	%	Dens re-used	%
Excavated	14	74	3	27	17	85	1	6
Excavated rock	0				1	5	1	100
Natural cave	5	26	5	100	0			
Tree cavity	0				1	5	1	100
Ground nest	0				1	5	0	
Unknown	0		3		0			
Total	19	100	8	42	20	100	3	15

Table 5-4. Forest age at 39 den sites used by grizzly bears in the mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada, 1998–2003.

	Mountains				Plateau			
Den type	Alpine	>100	45–99 yr	≤45 yr	Alpine	>100	45–99 yr	≤45 yr
Excavated	10	4				8	8	1
Excavated rock						1		
Natural cave	4	1						
Tree cavity						1		
Ground nest								1
Mean (%)	74	26	0	0	0	50	40	10

Table 5-5. Resource selection function (RSF) candidate models indicating the relative probability of grizzly bear den site (*n* = 57) occurrence in the mountain landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003. Model 1, with the lowest AIC$_c$ score, represents the best model based on the combination of precision and parsimony.

Rank	Variables	β	SE	95%CI	AIC$_c$	ΔAIC$_c$	AIC$_c$*w*
Model 1	Alpine	5.216	1.472	2.330–8.101	588.12	0.00	0.38
	True firs	1.513	0.770	0.004–3.021			
	Hillshade	0.006	0.007	-0.007–0.020			
	Alpine x hillshade	-0.012	0.007	-0.026–0.003			
Model 2	Alpine	3.248	0.727	1.824–4.672	588.52	0.40	0.31
	True firs	1.509	0.769	0.002–3.017			
	Hillshade	-0.004	0.002	-0.008–-$6.6E^{-05}$			
Model 3	Forest height	-0.135	0.024	-0.183–-0.087	589.63	1.52	0.18
	Elevation	0.036	0.010	0.016–0.056			
	Elevation squared	-$1.2E^{-05}$	$3.45E^{-06}$	-$1.9E^{-05}$ –-$5.65E^{-06}$			
Model 4	Alpine	3.350	0.724	1.932–4.769	590.07	1.95	0.14
	True firs	1.520	0.769	0.012–3.028			
Model 5	Alpine	3.245	0.732	1.811–4.679	591.44	3.32	0.07
	True firs	1.482	0.770	-0.027–2.992			
	Distance to nearest road	$3.85E^{-05}$	$3.86E^{-05}$	-$3.7E^{-05}$ –$1.14E^{-04}$			

Table 5-6. Resource selection function (RSF) candidate models indicating the relative probability of grizzly bear den site (n = 29) occurrence in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003. Model 1, with the lowest AIC_c score, represents the best model based on the combination of precision and parsimony.

Rank	Variables	β	SE	95%CI	AIC_c	ΔAIC_c	AIC_cw
Model 1	Forest height	0.051	0.020	0.012–0.090	396.33	0.00	0.35
	Hillshade	-0.015	0.008	$-0.031–3.77E^{-04}$			
Model 2	Forest height	0.053	0.020	0.013–0.093	396.73	0.40	0.29
	Elevation	0.002	0.001	$-1.89E^{-04}–0.004$			
Model 3	Forest height	0.051	0.020	0.012–0.089	397.04	0.71	0.25
Model 4	Forest height x distance to nearest road	$1.86E^{-05}$	$6.18E^{-06}$	$6.51E^{-06}–3.07E^{-05}$	398.66	2.33	0.11
Model 5	Mixed wood	0.460	0.764	-1.038–1.958	407.46	11.13	0.00
	True firs	1.050	0.708	-0.337–2.438			
	Spruce	1.206	0.556	0.115–2.296			
	Douglas-fir	1.852	1.122	-0.348–4.051			

Figure 5-1. Study area to determine denning habitat of grizzly bears in mountain and plateau areas, British Columbia, Canada, 1998–2003.

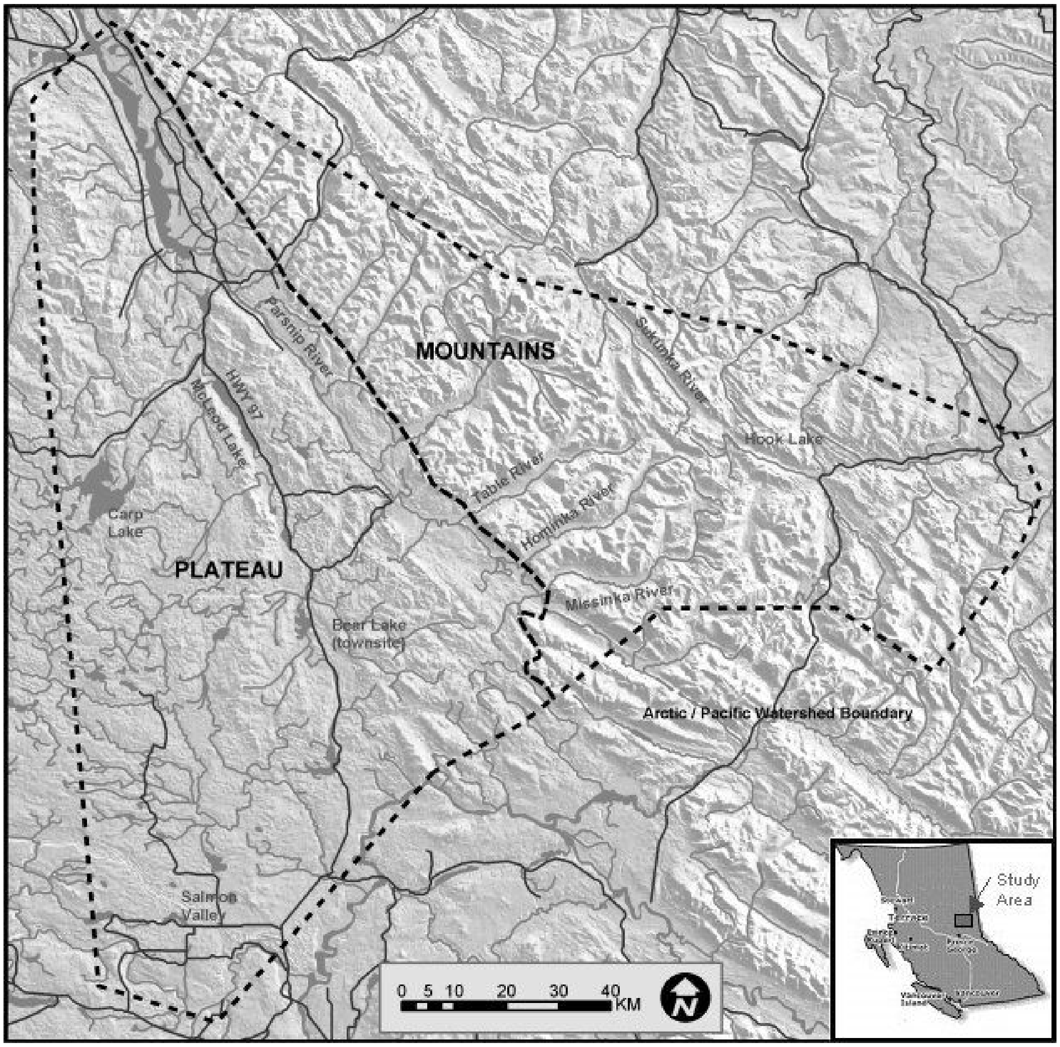

Figure 5-2. Relative probability of grizzly bear den site occurrence in the mountain landscape, British Columbia, Canada, 1998–2003. Darker areas represent an increased probability of den site occurrence (greater RSF values).

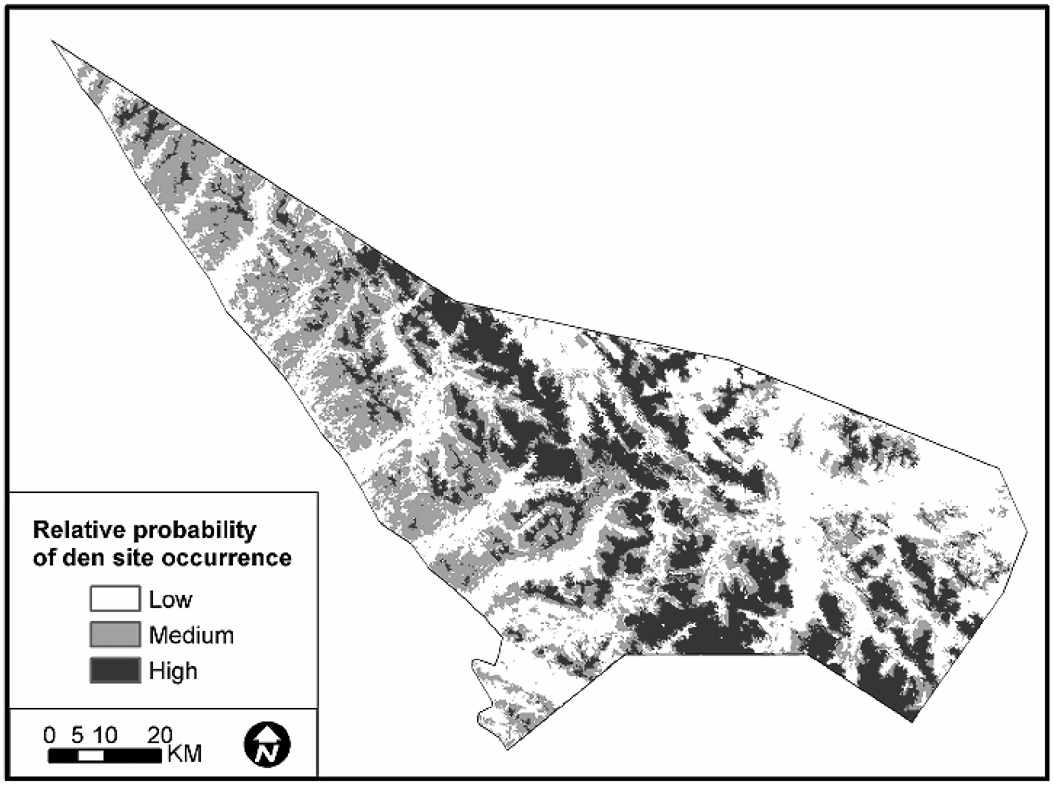

Figure 5-3. Relative probability of grizzly bear den site occurrence in the plateau landscape, British Columbia, Canada, 1998–2003. Darker areas represent an increased probability of den site occurrence (greater RSF values).

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CHAPTER 6
GENERAL CONCLUSIONS: IMPLICATIONS FOR GRIZZLY BEAR CONSERVATION IN TIMBERED LANDSCAPES

1. INTRODUCTION

The Parsnip River area in British Columbia, Canada, provides important habitats for grizzly bears. The location of the study area provided a unique opportunity to examine differences between grizzly bears that inhabited a relatively pristine mountainous landscape as compared with an adjacent plateau that was heavily harvested for timber. Increasing human modification of both landscapes will affect the quality of grizzly bear habitat. In this thesis I was interested in the effects of timber harvesting activities on grizzly bear habitat selection, distribution, and density. Before my thesis project the BC government managed on the assumption that grizzly bears that inhabited the Arctic watershed of BC behaved similarly to other studied populations in BC, that is, they denned in the mountainous landscape, upon emergence traveled to lowland valleys to capitalize on earlier foraging opportunities, and during berry season returned back to higher elevations where they remained until denning (McLellan and Hovey 2001). Accordingly, grizzly bears surrounding the Parsnip River were managed as one unit with similar management strategies and hunting quotas between the mountain and plateau landscapes. Through radiotracking bears, investigating bear use locations, employing genetic analysis techniques, and modeling habitat selection I found that bears inhabiting the Arctic watershed of BC were dissimilar to their coastal and southern counterparts. After obtaining the results of the DNA-based population estimate, I focused on identifying the population parameters and limiting factors responsible for the 4-fold difference in density between these adjacent landscapes. In particular, I was interested in what limited the bear population on the plateau and whether habitat-selection patterns by bears that inhabited the plateau landscape had been altered by the risk of human-caused mortality (Gilliam and Fraser 1987, Delibes et al. 2001). Further, I examined whether grizzly bear selection patterns were scale sensitive (Guisan and Thuiller

2005) because it has been argued that conclusions may only be valid within the scale examined (Kotliar and Wiens 1990, Lord and Norton 1990).

2. TYING TOGETHER THE RESEARCH RESULTS

Through microsite habitat investigations, stable isotope analysis, and habitat-selection modeling, I found that grizzly bears foraged extensively in early seral stands. For example, across all 3 scales females on the plateau selected for young stands (i.e., 0-40 year), while plateau males selected for these stands at the study-wide extent. Before human-caused changes to the landscape, early seral vegetation on the plateau was largely created by wildfires. Historically, throughout the study area the dominant stand-replacing disturbance was wildfires. The disturbance cycle on the western portion of the plateau was about 100-125 years (DeLong 1998, 2002). Climatic conditions become wetter further east towards the mountains and the plateau forests in that area had a historic stand replacing disturbance interval of 200-250 years (DeLong 1998, 2002). The dominant disturbance patch size in the drier western plateau was >1000 ha (70%), and most of those were >10,000 ha (DeLong 1998). On the eastern plateau, the most common disturbance patch size was between 100-1000 ha (45%), with 40% being >1,000 ha. These large patch sizes resulted in extensive tracts of young forests with patches of mature and old forest (i.e., fire skips). It is estimated that 20-50% of the forests on the western plateau were <40 years of age, with only 6-12% >250 years of age (DeLong 1998). In the wetter eastern plateau, 13-31% of the forest were estimated to be <40 years of age, with 26-39% >250 years. The majority of the forests on the eastern plateau (54-72%) ranged between 41-100 years of age (DeLong 1998). These frequent and extensive natural fire cycles have likely contributed to the distribution and abundance of sub-boreal forest organisms. Because central-interior bears lack the predictable supply of nutrition available to coastal salmon-feeding bears they are strongly tied to the land base; historically, central-interior bears have coexisted with these large scale disturbances, having to rely on early seral foraging opportunities because of the abundant forage. Bears on the plateau were also found to feed on moose adults and calves (*Alces alces*). Moose is also a species that selects early seral stages and increase their numbers due to disturbance (Franzmann and Schwartz 1997, Rempel et al. 1997).

In the mountains, the average wildfire cycle was estimated to be 900 years (DeLong 1998, 2002), although the frequency increases towards the plateau to the west, and the boreal foothills to the east. Consequently, the mountain forests were naturally dominated by old growth stands, with 74-80% being >250 years. Only 3-7% of the forested area was estimated to be <40 years of age (DeLong 1998). However, snow accumulations, temperature, and avalanches in the upper elevations of the mountain landscape maintained vegetation perpetually in the grass-forb or shrub stage, providing different early seral foraging opportunities than the plateau. The size of stand-destroying wildfires was smaller in the mountains than on the plateau, probably due to the wetter conditions. The dominant disturbance patch size was in the range of 100-1000 ha (60% of the mountainous landscape), with only 10% being >1,000, while 30% was <100 ha (DeLong 1998).

Grizzly bears that inhabited the mountainous landscape also selected for early seral stands, however, these stands were largely high-elevation alpine slopes and lush forb meadows. The selection by mountain bears for higher-elevation habitats provided a natural separation between humans and bears. In the mountains grizzly bears foraged largely in open alpine and sub-alpine landscapes. Each year, logging was making its way into the mountainous landscape from the plateau introducing new risks to bears that lived in the mountains. Indeed, one of the mountain males was shot while foraging in an early seral cutblock. For mountain bears the risk of mortality as a result of recent industrial activity may be more problematic than for plateau bears because they were not raised in a risky environment and habitat selection under those conditions may be naïve or maladaptive (Kristan 2003). Thus, if parental rearing does indeed shape habitat-selection patterns (Davis and Stamps 2004, Haughland and Larsen 2004, Nielsen 2005) then mountain bears might lack learned responses from their mother necessary to avoid areas with a high risk of mortality by humans. The high mortality of plateau bears likely shows that time has not been sufficient for adaptations to appear (Schlaepfer et al. 2002) in a long-lived species like a grizzly bear over such a short distance; however, differences in learning from parental rearing are likely. Kristan (2003) claims that ecological traps are more detrimental to population persistence than source-sinks because the risk of extinction is elevated due to the species' preference for poor habitats. I predict human-caused bear mortality will increase considerably in the mountains if roads are built there without strict access-management plans.

Although no human-identified barriers appeared to exist between landscapes, gene flow and movement of bears was limited. Using 15 loci microsatellite markers for 133 bears, I was able to detect genetic differences between bears captured in the mountains as compared with those captured on the plateau; the plateau and mountain grizzly bear populations were somewhat discrete. Indeed, during the study the mountains did not act as a source population for plateau grizzly bears, and dispersal was biased towards subadult males. This finding, I believe, has significant ramifications for BC's grizzly bear management strategies. If the mountains were acting as a source population for plateau grizzly bears, then harvest of plateau bears may be compensated by dispersal from the mountains to the plateau. However, the study area did not contain any source areas (protected or otherwise), and movement between the landscapes by female bears was limited, being recorded on only one occasion when a plateau female denned in the mountainous landscape and returned to the plateau upon emergence.

For bears, greater nutritional condition has been linked to larger body size, increased reproductive parameters, and higher population densities (Blanchard 1987, Hilderbrand et al.1999, Ben-David et al. 2004). I found that adult plateau bears were heavier (P [females spring] = 0.02, P [males spring] = 0.05) and in better condition than adult mountain bears. Litter sizes were similar between landscapes ($\bar{x}$ 1.93 mountains, $\bar{x}$ = 2.0 plateau cubs per litter) but inter-birth interval was longer in the mountains (5-6 years versus 3 years). Because of their large body size and similar reproductive rates, I concluded that industrial activity did not appear to have negative effects on reproductive parameters of grizzly bears on the plateau. Thus, over the long-term plateau bears should attain similar or higher densities to mountain bears, however, their densities were ¼ that of mountain bears. I explored 2 main reasons for these density differences: 1) bears on the plateau were limited by mortality; and/or 2) differences in habitats were regulating the plateau population.

I found that bears residing on the plateau were subjected to higher risk of human-caused mortality than bears that resided in the mountains. All deaths on the plateau in which the cause could be determined were attributed to humans (n = 10 of 12) as compared with 1 out of 3 in the mountains. Non-permitted kills were the primary cause of plateau bear deaths. I also found that plateau bears had a much lower annual survival than mountain bears (φ = 0.79 ±SE 0.06 versus 0.97 ±SE 0.02, respectively). Bear deaths were most frequent in fall and coincided with people hunting other species, such as moose. Because some hunters used the secondary and decommissioned road networks to access backcountry areas in anticipation of ungulate game, and also because use by bears was higher closer to these road types, plateau bears died closer to secondary and decommissioned logging roads than any other road type. RSF models revealed that female bears that lived on the plateau were selecting for closer distances to secondary and decommissioned logging roads within their home range. This selection was likely a result of their attraction to early seral habitats where for the majority of the foraging season human use was low. Since the suppression of forest fires, early seral habitats have been created through forestry activities; however, timber extraction has also imposed a heavily roaded landscape. As a result, humans and bears were afforded closer contact, ultimately resulting in a number of bear deaths. In most areas the decommissioning of logging roads was not sufficient to prohibit the passing of all-terrain vehicles. The high number of bear deaths I recorded adjacent to these road types resulted in reducing the number of bears in areas where habitats still exists to support them. Further, using logistic discriminant analysis of a BC grizzly bear mortality database, I found that another factor that contributed to the low density of bears on the plateau was the high number of bears removed from "urban" areas. Based on the deaths of study animals, I estimated a 21% annual mortality rate for plateau bears. I do not believe the plateau bear population can sustain such a high mortality rate and therefore probably declined during the study. Because female dispersal from the mountains to the plateau was low, I do not believe dispersal or migration will be sufficient to offset the high mortality on the plateau.

Using RSF-based density modeling I also examined whether differences in habitat could be responsible for the differences in density. In theory, the selection of habitats has been related to the distribution of food items, ultimately affecting population density and the spatial distribution of animals (MacArthur and Pianka 1966, Charnov 1976). Therefore, I began by examining the contribution of meat versus vegetation in bears' diets using site visits and stable isotope analysis. I found that plateau bears ate significantly more high-quality food items, such as meat and berries, leading me to suggest that food limitation was not responsible for the differences in densities. Further, in my earlier work (chapter 2), I reported that adult bears that lived on the plateau were significantly heavier and were in better condition than mountain bears, also suggesting that it was unlikely that the quantity of these food items were limiting on the plateau.

Recent theories in habitat selection focus on the avoidance of human activities, and the risk of predation, altering habitat selection thereby altering population structure (Gilliam and Fraser 1987, Lima and Dill 1990). To examine the link between the number of bears and landscape structure, I first used RSF to estimate the relative probability of use by landscape for 54 radiocollared grizzly bears (*n* [mountain] = 24, *n* [plateau] = 30). Next, independent estimates of bear population size from a DNA study (Mowat et al. 2005) allowed me to apply RSF methods for linking populations to habitats by scaling RSF models to population density (Boyce and McDonald 1999). Thus, I used habitat-based density modeling (Boyce and McDonald 1999) to investigate the predictions from RSF models when I applied values from one landscape to the other. Specifically, to evaluate whether differences in landcover type, roads, or mortality risk could account for the differences in bear density I used the mountain RSF model to predict habitat use and number of bears on the plateau, and conversely I used the plateau RSF model to predict grizzly bear use and number of bears in the mountains. I predicted an increase of 34-96 bears on the plateau when switching models for the risk of mortality, the distance to roads, or all model coefficients. Further, when only constricting landcover type variables and then applying this model to the plateau, the model predicted that the plateau population would be 9 bears lower than was observed, leading me to suggest that differences in habitats were not responsible for the density differences between landscapes. Large reductions in the population of mountain bears were predicted when I subjected them to a model based on habitat selection by grizzly bears on a plateau landscape, likely because of: 1) differences in road distribution and characteristics of road types in the mountains versus the plateau; 2) opposite road effects with mountain bears selecting for closer distances to primary roads, while plateau bears avoided this road type; and, 3) problems associated with extrapolation to a landscape with a different suite of available resources. Therefore, caution should be applied to the extrapolation and interpretation of RSF models.

Using RSF, and varying the extent of availability, I also examined the effects of scale on the habitat selection of grizzly bears during the foraging season using 3 spatial extents: study-wide, home range, and a predetermined movement buffer. I employed 2 methods for evaluating the effects of scale on the RSF design. First, I chose *a priori* 6 candidate models and ranked them using Akaike Information Criteria. For female bears inhabiting both the mountain and plateau landscapes, a model that contained a full suite of covariates focusing on the dominant landcover types, human-influenced mortality risk, distance to roads, and greenness ranked 1st at each scale. For male bears that resided in the mountains, models based on forest succession (i.e., stand age and greenness) ranked highest at the study-wide and home-range extents, while models that contained covariates based on terrain features (e.g., elevation and forest height) ranked highest at the buffer extent. For male bears on the plateau, each scale estimated a different highest-ranked model. Thus, using method 1, patterns of habitat selection changed scales for male bears but not for females. My results may be explained in part by the differences in behaviour between males and females. Male bears may displace females, sometimes into sub-optimal habitats (Weilgus and Bunnell 1995, Ben-David et al. 2004) and/or be more likely to take risks than females (Herrero 1985). I found that differences in habitat use occurred between males and females in both the mountains and the plateau, a result I attributed to the differences in behaviour between sexes. Behavioural decisions associated with the risk of mortality may also alter habitat selection and help explain species' abundance and distribution (Fryxell and Lundberg 1998, Lima 2002, Hebblewhite et al. 2005), thereby affecting the scale of selection (Resetarits 2005).

I used a second method to further explore scale and its effect on habitat selection by examining the differences among the 3 scales in model coefficients for one of the candidate models. I found that both the magnitude and direction of model coefficients were dependent upon the scale examined; results varied between landscapes, scales, and sexes. Greenness, reflecting lush green vegetation, was a strong predictor of female bears in both landscapes and males that lived in the mountains. Male bears on the plateau were the only subset of animals to select for areas that exposed them to a high risk of mortality by humans. This finding supports my earlier chapters where I recorded a low annual survival rate of subadult plateau males ($\varphi = 0.62$ ±SE 0.16), and captured few adult plateau males despite intensive trapping efforts. In many species, the dominant individual has priority over food resources (Appleby 1980, Monaghan and Metcalfe 1985, Stahl et al. 2001), thereby achieving a greater energy intake (Metcalfe 1986). Bears too interact with each other in a hierarchy with dominant bears ruling prime feeding areas (Herrero 1983, Stringham 1983, Gende and Quinn 2004), and breeding more females in areas where these males remain to control immigrating non-sire males (Weilgus and Bunnell 1995, Swenson et al. 1997). I believe that for plateau males the pressure to become big was greater than the chance of being killed; males were willing to risk being killed in an attempt to attain large body sizes and become dominant. Indeed, although few large adult males remained on the plateau landscape, those that did had the highest survival rates ($\varphi = 1.00$, $n = 3$). Therefore, my results support the hypothesis that grizzly bear habitat selection was scale dependent, patterns of habitat selection changed with different scales, and to a lesser extent sexual segregation may have occurred between males and females. Further, I found that the selection of resources can be dependent on the availability of a particular type of resource on the landscape (Mysterud and Ims 1998). Thus, my ability to detect selection was influenced by the spatial heterogenity within, and between, mountain and plateau landscapes. As a result, I could not identify one ‘best’ scale of analysis (Hobbs 2003, Boyce 2006), making the appropriate scale dependent upon the management question (Boyce et al. 2003, Hobbs 2003, Boyce 2006). For example, more general broad-level questions, such as those relating to the broad distribution of bears across the landscape, would be best addressed using the study-wide extent because random locations are drawn from a much larger area than the home range. More specific management questions, such as those focusing on attributes within a patch, will be best addressed using a more restricted scale, such as the home range or buffer extents.

Lastly, I examined denning behavior and den-site selection of grizzly bears (n [plateau] = 34, [mountain] = 27) to see whether patterns were different between mountain and plateau landscapes and if den site were in places used by bears during the foraging season. Adult females residing in the mountainous landscape arrived earlier to their denning areas (14 Oct versus 26 Oct), entered dens earlier (23 Oct versus 9 Nov), and emerged later (11 May versus 24 Apr) than plateau females, spending on average 36 days longer in their dens (200 days versus 164 days). In part, then, the larger body sizes of plateau bears may also be explained by having a longer foraging season than mountain bears. Dens used in consecutive years by mountain females tended to be in closer proximity to one another ($\bar{x}$ = 2.4 km) than those of plateau females ($\bar{x}$ = 5.1 km). Dens in the mountains were excavated into steeply sloping ground (74%), or natural caves (5%), using rocks as the primary stabilizing structure (47%). RSF revealed that mountain bears selected dens in alpine habitats at mid-to-upper elevations. Plateau bears mainly excavated dens under the base of trees (90%), where roots stabilized material (80%). These dens primarily were located in older-aged forest stands ranging from 45–99 years (40%) or >100 years (50%); RSFs further revealed that grizzly bears on the plateau selected stands with tall trees. Therefore, although bears on the plateau selected early seral stands for foraging, they selected mature and old growth stands for their den sites, while avoiding early seral habitats. Also unlike the foraging season, plateau dens were located away from roads, possibly to avoid disturbance and because older trees were farther from roads. Therefore, bears that lived on the plateau required a juxtaposition of forest structural stages to adequately provide for their life requisites.

3. IMPLICATIONS FOR FORESTRY MANAGEMENT

Forestry practices alter the natural landscape, and for interior grizzly bears the concern is primarily through the removal of canopy cover, the creation of monocultures and/or even age stands, and the creation of roads to access blocks. The removal of trees reduces security cover for bears but also increases forage production. Selection for harvested areas by bears is contrary to other published results in coastal and southern BC (Hamilton and Bunnell 1987, McLellan and Hovey 2001) and Montana (Zager et al. 1983); however, it has been recently reported for bears inhabiting foothill forests of Alberta (Nielsen et al. 2004). Further, in the Selkirk mountains, Weilgus and Vernier (2003) reported use in proportion to availability for clearcut areas.

Currently, in the boreal forest, fires are aggressively suppressed to protect the commercial value of timber and human habitations. Consequently, the creation of early seral habitat by fire has been replaced by the removal of canopy closure afforded by forestry activities. During the foraging season bears inhabiting the plateau portion of the Parsnip River selected for the early seral vegetation that today is largely provided by timber harvests. In the "working forest," outside of ecological reserves and parks, the challenge is how to manage the land-base to maintain forest characteristics that are selected for by bears while minimizing their risk of human-caused mortality. Based on my research results I put forward the following recommendations for the conservation of grizzly bears on managed landscapes:

The high rate of grizzly bear mortality in areas with roads necessitates special efforts to reduce that limiting factor. The first priority for management should be to separate humans from bears, which requires limiting human access into harvested blocks. Potential solutions include:

1. *Decommission and Reclamation*: reclaim roads immediately after harvesting or planting by removing bridges and/or placing some of the remaining debris on the road. Many people recreate on ATVs, therefore it is prudent that the decommissioning be at a level to also prevent use by ATVs.

2. *Plan future roads to minimize active road density*: plan the scheduling and pattern of harvest within an area to minimize the active road density over time. Potential solutions include:
    i. Concentrate timber harvest in portions of a watershed and then deactivate roads and stay out of that area for an extended period.
    ii. Plan roads with access control points.
    iii. Establish no-harvest reserves. Areas with very high grizzly densities and low timber values should be considered for no roads or harvesting. The headwaters of many of the mountain drainages meet these criteria.

3. *Reduce road density*: specifically, reduce on-block (i.e., secondary) roads, especially in the mountains; harvesting systems that do not require on-block roads can be used (i.e., helicopter, skyline). On-block roads are those that spur off of primary logging roads and are used to access harvested blocks.

4. *Access management*: control human access using indirect and direct management techniques:

  i. Physical deactivation of all unnecessary roads.
  ii. Remove unnecessary bridges.
  iii. Gates and barriers.
  iv. Close roads by regulation
  v. Limit the use of mechanized transportation within zones identified as having a high relative probability of use by grizzly bears.

Plan the blocks depending on whether one wants to encourage or discourage grizzly bear use. These management actions are only recommended in areas where the decommissioning of the road network is absolutely not possible:

By examining the selection patterns of bears, foraging opportunities may be encouraged in some areas and discouraged in others areas. This would be achieved through managing for structures based on what grizzly bears select or avoid. For example, treating blocks to remove the berry-producing shrubs, and/or placing blocks closer to primary logging roads. In these areas, management should focus on discouraging use by bears so that these areas do not act as attractive sinks for bears.

Place core security areas for female bears throughout the landscape and in these areas actively encourage the use of regenerating blocks by grizzly bears. All roads in these areas must be made inaccessible to motorized human use:

Rather than treating blocks to reduce shrubs and encourage the growth of commercial trees, I recommend leaving some blocks to encourage grizzly bear foraging:

  i. Allow natural regeneration of berry-producing shrubs.

ii. Leave debris in blocks to increase opportunities for bears to forage on ants. Coarse woody debris also harbours small mammals that can be attractive to bears.

iii. Leave retention patches throughout the block: Retention patches in blocks can serve a number of purposes by providing: 1) security cover for bears, especially females with young, 2) foraging opportunities further from the edge of the block, 3) bedding opportunities for bears; and, 4) maintaining mesic to hydric sites which allows for feeding opportunities on cow-parsnip (*Heracleum lanatum*), fern fiddle heads (e.g., *Athyrium filix-femina*), and other rich soil plants. Planning should capitalized on the natural attributes of the stand by retaining alder swales interspersed with large trees and retaining patches close to the forest edge, which would allow an animal to travel from the forest, into the retention patch, and forage between the two patches.

Actively pursue opportunities for increased education:

Hunter education courses should be modified to stress that shooting grizzly bears when hunting for ungulates and other species should only occur in life-threatening situations. Also, grizzly/black bear identification training to reduce legal deaths due to misidentification.

Support and/or finance increased law enforcement:

The high number of bears shot without a license necessitates increased enforcement to reduce poaching, especially during the moose-hunting season. Increased fines for poaching bears should reflect the serious nature of this offence to the overall bear population.

Reduce or eliminate the limited-entry hunt of plateau bears:

I recommend being proactive in management and limiting the harvest of mountain bears (Peek et al. 2003) while prohibiting the harvest of bears on the plateau. Bears have low reproductive rates, large area requirements, and are sensitive to over harvest (Weilgus et al. 2001). Recovery efforts (e.g., Yellowstone National Park) take decades to achieve making it prudent to manage bears proactively rather than reactively.

Establish an old-growth reserve(s) to protect prime den-site areas:

I found a low relative probability of use of clear-cut areas and early seral stands for grizzly bear den sites. Therefore, I recommend maintaining some large tracts of forest in old growth and reducing the density of open roads within and adjacent to those stands to limit disturbance. Within forest harvest areas, retention of large trees within riparian areas, and retention of wildlife tree patches within cut areas, should promote stand-level diversity, thereby enhancing the future value of those stands for grizzly denning habitat in regenerating forests.

4. FINAL THOUGHTS

Throughout this thesis I have recommended management strategies that embody the principles of ecosystem management (Grumbine 1994). The rationale of an ecosystem management approach is that if forests are managed to closely resemble natural forests, most native species that are adapted to those forests will be maintained. Alternatively, the more that managed forests deviate from the natural forest condition the greater the probability that the abundance of native species will be significantly changed, and some species may be eliminated. From a forest harvest perspective, the maintenance of ecological processes requires an understanding of the natural forests landscape and stand-level attributes. Forest harvesting creates young and mature timber stands, thereby limiting the amount of old growth on the landscape and altering the natural age class distribution (McRae et al. 2001). Forest age class should be examined in an historical perspective to determine the disturbance regime of natural processes such as fire intervals and average fire patch size for the landscape. For example, coastal landscapes have a much less frequent fire regime than interior landscapes. Thus, the natural abundance of old growth habitat would be less in interior areas and greater in the wet coastal landscapes. Bears learn how to exploit certain foods that are present on the natural landscape, and this knowledge appears to be passed on to their cubs. Thus, differences in habitat selection patterns between coastal, central interior, and southern interior areas should be expected.

Ecosystem management employs the theories of landscape ecology by examining how the patterns and structure of the landscape ultimately affects the abundance and distribution of organisms (Grumbine 1994). Landscape ecology principles state that both spatial and temporal scale must be considered in management decisions (Grumbine 1994). From an ecosystem management perspective, temporal scale refers to the long-term consequences of our management decisions and influences evolutionary and ecological processes. An important consideration regarding temporal scale is that mimicking the juxtaposition of seral stages on the landscape may take years or decades and is not bound by political timelines or boundaries.

I believe that the challenge to conserving bears surrounding the Parsnip River lies not only with government and resource extraction companies but also with the public. The study area was contained within a working forest. Provincial legal mandates for wildlife residing within working landscapes focus on ensuring naturally self-sustaining populations but I believe the goals are unclear and conservation measures are lacking; for example, does a self-sustaining population require 10, 20, 100 individuals? Would simply maintaining the mountain subpopulation meet this mandate? Ultimately, I believe that society must decide whether or not it wants to balance the demands of consumerism with the requirements of wildlife. Indeed, the 3rd party environmental certification that some forest companies are striving to achieve for their products, and that was largely responsible for this study, was a result of the requirement implemented by a select few of the lumber distribution companies as a direct result of consumer requests. Thus, the ability to conserve species such as the grizzly bear outside of protected areas may be largely influenced by decisions made by the public.

In 2002, due to the ongoing findings of this study, the BC government altered the boundaries for grizzly bear management units to follow the mountain drainage, allowing them to manage based on mountain and plateau landscapes. Limited-entry hunt quotas were modified to reflect the difference in densities, specifically being reduced on the plateau although at the time of writing the limited-entry hunt remains open. Regardless of the current initiatives, I believe that it may be impossible to sustain grizzly bears on managed forest landscapes if we are unable to control the excessive level of human-caused mortality associated with uncontrolled road access. The inability to control this limiting factor compromises the government's obligations to protect environmental values, and the ability of the forest industry to conduct sustainable forest management.

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