UNIVERSITY OF CALGARY

# Evaluating the ecological consequences of human land-use on grizzly bears in southwest Yukon, Canada

by

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## Abstract

This study investigated the effects of human land-use on grizzly bear (*Ursus arctos* L.) habitat and populations in the Kluane region of southwest Yukon, Canada. Previous studies in the region identify grizzlies as the species most at risk from cumulative impacts of human activity. The goals of this project were to: 1) identify the effects of cumulative human activities on grizzly habitat and populations; and 2) provide recommendations on human-use management with respect to the conservation of grizzlies and their habitat. Thus, I investigated three aspects of bear ecology and synthesized them to examine the influence of human-activities on bears. First, I examined the appropriateness of using Tasselled Cap Transformation variables for representing the distribution of bear forage. Tasselled Cap layers correlated with aggregate measures of forage abundance, provided continuous variables for linear occupancy estimation models, and were more cost-effective to produce than land cover classifications. I then tested the influence of conspecific distribution on habitat selection by grizzly bear sex/age cohorts. Family groups segregated from other cohorts, in part, to avoid intra-specific aggression and to protect cubs. Segregation also occurred because of differential response by each cohort to the distribution of human activity, and the distribution of forage. I next examined the temporal trends and spatial characteristics of grizzly bear mortality in Kluane. While efforts reduced the frequency of occurrences and management-related mortalities, there was a substantial lag between the management efforts and the decline of human bear interactions and human-caused bear mortalities. Increased human activity in the region may have negated the positive effects of landfill closures. Finally, to examine the influence habitat and mortality models had on grizzly bear productivity and survival, I compared the explanatory power of empirical habitat models based on grizzly bear telemetry relocations or forage availability against expert-opinion models. I used the best model, established by model selection criteria, for explaining reproductive and survival rates to predict population status for grizzly bears in Kluane. Survival and productivity of grizzly bears decreased on the periphery of the protected area adjacent to the highways. While productivity in the areas adjacent to the highways was relatively high, mortality was also high. These areas, therefore, were acting like attractive sinks. Reducing human-caused mortality on the Park periphery and developing a transboundary management strategy will be necessary to conserve grizzly bears in Kluane.

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Dedication

*born this year,*

*for Evan Narayan Pearson Maraj, his siblings to come, his friends to be, his life ahead*

*our efforts to preserve wild things and wild places are for his generation*

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# Chapter One: Introduction

## BACKGROUND

Habitat loss and fragmentation, habitat alteration, and high rates of direct human-caused mortality are pressing issues for conservation of wildlife, and are often attributable to poor planning and incompatible land-use management. To prevent these threats from resulting in loss of species, parcels of land have been set aside by various agencies as parks or protected areas. These areas are managed primarily for conservation. However, pressures to develop protected areas and adjacent lands for recreation have often resulted in degradation or decimation of wildlife rich areas (Banff Bow Valley Study 1996, Woodroffe and Ginsberg 1998). Additionally, the management of these protected areas is complex because the borders that separate them from the surrounding land-use matrix usually do not follow habitat use boundaries for species, and land-use plans from the various surrounding agencies are often incongruous with land-use plans for protected areas. This can considerably reduce the effectiveness of protected areas for conserving wildlife populations and habitat (Banff Bow Valley Study 1996, Clark et al. 1996, Woodroffe and Ginsberg 1998).

Large carnivores have an ecological role that makes them useful focal species for evaluating the effectiveness of protected areas (Gibeau et al. 1996, Noss et al. 1996, Paquet et al. 1996). Landscapes that sustain viable populations of carnivores are often ones where natural vegetation predominates, where native species can still be found, and where historical ecological processes still operate (Noss et al. 1996, Carroll et al. 2001). As an apex predator, grizzly bears are one of the first species to be lost from an area as a result of land development activities (Noss et al. 1996, Woodroffe 2000). Grizzly bears (*Ursus arctos* L.) are particularly sensitive to the impacts of human activities because generally they have relatively few young, range over large areas, and occur at low population densities (Gibeau et al. 1996, Mattson et al. 1996b, Paquet et al. 1996, Russell et al. 1998, Purvis et al. 2000). Consequently, large carnivores have been considered indicators of the health or integrity of an ecosystem. They are also prone to direct conflict with people. The combination of these biological traits interacting with people's affinity to develop and use grizzly bear habitat usually results in compromised wildlife populations and habitat (Banff Bow Valley Study 1996, Woodroffe 2000, Mattson and Merrill 2002).

In 1976, in an effort to protect grizzly bears and other wildlife species, the Canadian federal government designated a portion of the southwest Yukon as a national park. This region, designated as Kluane National Park and Reserve (KNPR), adjoined Glacier Bay National Park in the Alaska Panhandle, Wrangell-St. Elias National Park in Alaska, and later Tatshenshini-Alsek Park in British Columbia to form the world's largest international protected area and World Heritage Site. Since then, the area has been described as one of the last remaining strongholds for grizzly bear populations in North America (Herrero et al. 1993). KNPR has been described as an important grizzly bear 'source' population for the surrounding area (Jingfors 1990). Grizzlies have shown regional movements south into Tatshenshini-Alsek Park, east into the Aishihik region and north in the Kluane Wildlife Sanctuary. In the first two years of the most recent grizzly bear population study in KNPR (McCann 1998), 21% and 36% of the tracked bears made out-of-park movements (McCann 1998). Hence, KNPR serves an important ecological role for the surrounding area (Jingfors 1990, Hegmann 1995).

While the bear population in KNPR is thought to act like a source population, previous studies in the region single out grizzly bears as the species most at risk of being affected by cumulative impacts (Hegmann 1995). Increased town site development in communities neighbouring the Park, mining, hunting, forestry and agriculture pressure outside of the Park, landfills in nearby towns that attract carnivores, and increased air traffic are all potential threats to the ecological integrity of KNPR (Hegmann 1995, Danby and Slocombe 2005). Further, although the Park area is over 22 000 km$^2$, only 18% is vegetated (Environment Canada 1987). The vegetated portion of the Park is a thin belt, confined on the west by the St. Elias Icefields (the largest non-polar icefield in the world) and on the east by the Alaska and Haines Highways. The distance between the highways and the icefield is approximately 55 km at its widest and averages 35 km (Environment Canada 1987). The dimensions of the greenbelt cannot easily contain the multi-annual home range of a female grizzly (McCann 1998), so bears are highly reliant on the surrounding area to meet part their life requisites. However, when bears have made out-of-park movements they were subject to various sources of direct mortality – principally hunting and management controls. Rates of mortality have been high, exceeding the growth rate for the population (McCann 1998, Yukon Territorial Government 2003).

## RESEARCH GOALS AND OBJECTIVES

The grizzly bear is an important indicator of wilderness integrity and is an umbrella species representing the health of an ecosystem (Noss et al. 1996, Paquet et al. 1996). Agencies have largely relied on protected areas to maintain viable grizzly bear populations. However, in face of growing demands to provide recreation opportunities for visitors and economic opportunities for locals, there is an increasing encroachment on grizzly bear habitat near and within protected areas (Hegmann 1995, Gibeau 2000, Mattson and Merrill 2002, Mueller et al. 2004). The research undertaken for this dissertation provided the basis for developing a decision framework for managing human influences on grizzly bear populations in KNPR and surrounding area.

The goals of this project were to:

1. Assess the cumulative effects of human activities on grizzly bear habitat and populations; and
2. Provide recommendations on human-use management with respect to the conservation of grizzly bears and grizzly bear habitat.

These goals were met through the following objectives:

1. Evaluate the influence of habitat features on grizzly bear distribution. Habitat features important for grizzly bears were identified by a) creating explanatory models for bear forage distribution, and b) developing explanatory models for bear occupancy patterns. I also created expert-opinion models for comparison purposes.

2. Evaluate the impacts of human land-uses on the spatial distribution of human-bear conflicts and grizzly bear mortality. I mapped 23 years of occurrences and mortality locations for grizzly bears killed in the Kluane Region. (I considered occurrences as a reported interaction between grizzly bears and people, which did not result in the death of a bear. Management agencies usually consider bear mortalities as a specific type of occurrence where a bear was killed as an outcome; however, for these analyses I consider mortalities separate from occurrences. Mortalities included dead bears and bears translocated so far that they could be considered removed from the population.) An explanatory model was developed to assess mortality risk relative to human land-use patterns.

3. Develop a modeling framework to support decision-making about various human land-use options related to grizzly bears and their habitats. Once habitat, human land-use and mortality models were developed, I combined the models into a framework. This framework included changes in grizzly bear demography as an important management variable. The modeling framework can be used to evaluate the effects of alternative future scenarios of human activities in the region.

## STUDY AREA

The study area (60°00' – 61°20'05"N, 137°00'30" – 141°00'W; Figure 1-1) encompassed KNPR, and Kluane Wildlife Sanctuary, portions of the neighbouring public and private lands, Yukon Territory, Canada and a small, northern portion of Tatshenshini-Alsek Park in British Columbia, Canada (herein referred to as the protected area complex). This area skirts the Wrangell-St. Elias Mountains and Icefield; the highest mountain range in Canada and the largest non-polar icefield in the world. Numerous large glaciers protrude into the vegetated zone of the Park. KNPR is 22 013 km$^2$, but only approximately 4000 km$^2$ of this is vegetated. The remainder is rock and icefield. The focus of this study was on the greenbelt bordering the icefield region. Exact study area boundaries vary among the chapters in this dissertation because data availability varied for each analysis. The study area boundaries for each analysis are depicted and further clarified in each chapter.

There are major altitudinal differences throughout the region, ranging between 600 m and 5950 m. As a consequence, the climate is highly varied. There is a maritime influence in the southern portion of the study area and average temperatures are 12°C in summer and -3°C in winter. There is a rain shadow effect of mountains in the north and the average temperature is 10°C in summer and -8°C in winter. Annual precipitation is less than 100 mm in some areas and up to 700 mm in other areas (Environment Canada 1987).

The greenbelt contains three major vegetation zones. The montane zone, which ranges up to 1100 m on deposited moraines, stream terraces and alluvium, contains boreal forest characterized by white spruce (*Picea glauca*) with balsam poplar (*Populus balsamifera*) and trembling aspen (*P. tremuloides*), and an understory of buffaloberry (*Shepherdia canadensis*), dwarf birch (*Betula glandulosa*), red bearberry (*Arctostaphylus rubra*), and hypnum moss (*Hypnum imponens*). The subalpine zone (1100 – 1400 m) is dominated by willows such as grey-leaf willow (*Salix glauca*) and Barclay's willow (*S. barclayi*), with some meadows of fescue grasses (*Festuca* spp.). Alpine tundra (1600 – 2000 m) is

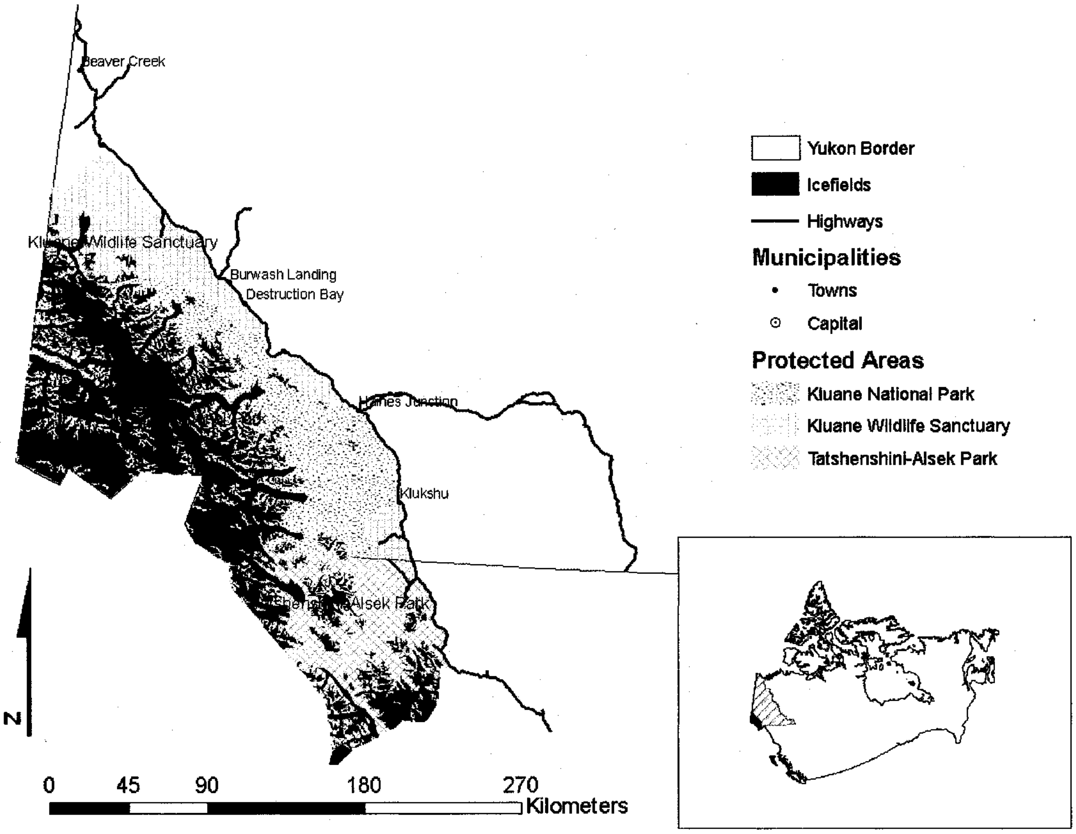

Figure 1-1. Study area. Kluane National Park and Reserve, the Kluane Wildlife Sanctuary, and a portion of Tatshenshini-Alsek Park (protected area complex) were part of the study area. The study area also included the public and private adjacent to the protected area complex.

characterized by lichens and low shrubs such as Arctic Willow (*S. arctica*), crowberry (*Empetrum nigrum*) and White Mountain avens (*Dryas integrifolia*; Douglas 1974, Krebs and Boonstra 2001).

Human land-use in the area is dominated by recreation, habitation, and mining. The Alaska and Haines Highway bound the protected area complex on the east. The distance between the highways and the icefield is approximately 55 km at the widest point and averages 35 km (Environment Canada 1987). Both highways are major points of entry and exit for traffic into and out of Alaska. Approximately 175 000 and 36 500 vehicles per year travel the Alaska and Haines Highways, respectively (Yukon Territorial Government 2004). Four towns are situated along the highways and consequently border the Park and Wildlife Sanctuary: Haines Junction, Destruction Bay, Burwash Landing, and Beaver Creek. There are several small, summer-use aboriginal villages that are on the border of the Wildlife Sanctuary, including Shaw'she and Klukshu. There are also numerous rural residential dwellings, summer homes and other infrastructure along both highways. The region is jointly managed through various co-management agreements among federal, territorial and aboriginal governments.

## LOGIC OF INQUIRY

In light of the pressures to develop in and around parks and protected areas, an essential approach to promoting effective wildlife conservation is identifying which landscape features are inherently attractive to wildlife and how that attraction is modified by the presence of humans (Clark et al. 1996, Nielsen 2005). Expert opinion models, such as habitat effectiveness and security area models, are relatively inexpensive approaches for identifying important habitat and estimating the impacts of human land-use on grizzly bear habitat throughout North America (USDA Forest Service 1990, Purves and Doering 1998, Gibeau 2000). Habitat effectiveness is an estimate of the percentage of habitat that is available to bears after subtracting habitat alienated as a result of human influence (Gibeau et al. 1996). Security areas are habitat patches large enough to allow grizzly bears to forage and meet their daily energetic requirements without encountering humans (Gibeau et al. 1996). However, these models have been criticized for not performing as well as empirical habitat models (Nielsen et al. 2003, Stenhouse et al. 2003), and because of lack of statistical rigor, they are viewed as unreliable.

Resource selection function modeling (Manly et al. 2002), which frequently uses logistical regression, is a more statistically robust approach than expert-opinion methods for examining the distribution of wildlife in relation to landscape characteristics. The distribution of most organisms relates to the distribution of patches of habitat. Patches occur at different scales and are encompassed by a landscape matrix in which the species is absent or occurs at much lower densities (Paquet et al.1996, Boyce et al. 2003). Disturbance by humans can displace organisms from preferred or frequently used habitat patches (Paquet et al. 1996, Woodroffe 2000). Disturbances may include concentrations of people in space and time, the physical alteration of an area, or some combinations of these effects (Paquet et al. 1996). To predict how alterations to habitat affect the status of species in a given area, it is necessary to identify what constitutes "essential habitat" and what constitutes a "disturbance". The occurrence of an organism can be statistically correlated with the attributes of landscape features. When a habitat is used disproportionately to its availability, habitat is said to be "selected" (Manly et al. 2002). The premise of this method is that the organism of interest will be located most frequently in high quality patches and least frequently in disturbed and sub-optimal habitats.

Statistical habitat modeling requires measures of availability for the resources used by a species. Resources of interest are commonly difficult to directly measure, so proxies are used (Heglund 2002). Land cover classifications are often used to represent forage availability, and biomass of forage in a given cover class is estimated (Mattson and Despain 1985). However, development of a land cover classification layer is costly and time consuming, and the information represented can be spatially coarse. The Tasselled Cap Transformation provides an alternative to land cover classifications (Mace et al. 1999). Greenness values represent the absorption of red light by chlorophyll and the reflectance of infrared radiation by water-filled leaf cells. This index is correlated with photosynthesis, and because photosynthesis occurs in the green parts of plant material, the greenness index is used to estimate the amount of vegetation in an area (Crist and Kauth 1986). Greenness indices derived from Tasselled Cap Transformation of Landsat imagery have a demonstrated positive linear relationship with the occurrence of grizzly bears in other regions of North America (Mace et al. 1999, Ciarniello et al. 2002, Stevens 2002). Presumably, lush vegetation in very green areas may represent a greater abundance or quality of bear foods; however, the relationship between greenness and forage productivity has not been evaluated. This is a key oversight in utilization of this variable because bears often do not consume the photosynthesizing parts of plants and there is not necessarily correlation between phytomass and roots, flowers or berries (Edge et al. 1990). Thus, in Chapter 2 of this dissertation, I examined the relationship between greenness derived from Tasselled Cap Transformation of Landsat imagery and grizzly bear forage availability. I evaluated whether greenness was a better explanatory variable for forage abundance than land cover classes and I evaluated the effect that seasonal timing of satellite images may have on the correlation between greenness and forage abundance.

Accurate maps of species distribution are fundamental for understanding the ramifications of human land-use on populations. Most statistically based habitat models are concerned with how resource distribution affects animal distribution (Garshelis 2000). Models also can incorporate human activities to examine their influence on resource and animal distribution. However, grizzly bear occupancy patterns are affected not only by the distribution of resource and human activity, but by other bears (Mattson et al. 1987). Smaller and less competitive individuals may be supplanted from key habitats by dominant individuals (Hornocker 1962, Wielgus and Bunnell 2002). Females with young may avoid lone adults, which may kill non-sire offspring. Previous habitat modeling studies omit conspecific distributions as a variable for explaining habitat selection, and therefore, may produce models that are poor for predicting habitat use patterns when resources are scarce (Egbert and Stokes 1986). Competition for resources can exacerbate the impacts of human activity. If habitat use patterns are a function of avoidance of conspecifics, alterations to habitat could push adult males and lone adult female grizzly bears into regions where family groups find refuge, thereby increasing competition for resources or rates of infanticide (Ben-David et al. 2004). Cub survival may suffer as a consequence and the productivity of the population would subsequently decline (Wielgus and Bunnell 2000). Habitat models that do not incorporate cascading competitive interactions may only show habitat deterioration where lone adults subsist but will not indicate effects on family groups.

In Chapter 3, I created habitat models that used the distribution of higher status cohorts as an explanatory variable to assess if there is conspecific avoidance in habitat selection. Higher status cohorts are a demographic group that has better access to resources than another group because of differences in size, age, or reproductive status. I used telemetry relocation data for 68 individuals (30 males, 38 females), spanning 1989 to 2004, inclusive. Separate models were developed for each of two feeding periods. The best models for each cohort were used in subsequent analyses.

Grizzly bear survival is often limited by human-caused mortality. In fact, human-caused mortality may be more likely than habitat loss to cause extirpation of a grizzly bear population (Nielsen 1975, Mattson and Merrill 2002, Ross 2002). Even when there is an adequate supply of high quality habitat, populations can still decline if harvest rates, management kills, road kills, poaching or other forms of direct mortality are cumulatively unsustainable. For instance, Merrill and Mattson (2003) found three extensive areas in the Yellowstone region that were suitable for but unoccupied by grizzly bears. The surrounding landscape matrix became fragmented, disconnecting these areas from the surrounding bear populations. Bears were then likely extirpated from these areas because of high rates of human-caused mortality. A key undertaking for reducing human-caused bear mortality is to identify the factors that lead to mortality. Intensity (Benn and Herrero 2002, Nielsen et al. 2004a) and potential lethality (Merrill and Mattson 2003) of human activities are key factors associated with the spatial locations and rates of mortality.

Causes of bear mortality in the Kluane Region are similar to elsewhere in North America (McCann 1998); human-caused mortality far outweighs natural mortality (Craighead et al. 1988, Carr 1989, McLellan 1990, Dood and Pac 1993, Gunson 1995, Gibeau et al. 1996; McCann 1998). Managers in the Kluane Region have implemented a number of mitigation measures to reduce human-caused bear mortality. Landfills have been enclosed with electric fencing, education programs developed, and attempts have been made to spatially redistribute recreational activities to reduce human-bear conflicts. In Chapter 4, I evaluated the effectiveness of these management actions in reducing the frequency of negative human-bear encounters and bear mortality. I examined the trends in occurrences and mortalities from 1983 to 2004. I also examined the spatial distribution of mortalities and identify spatial factors associated with mortalities.

For a habitat model to be useful (Boyce and McDonald 1999, Naves et al. 2003) it is necessary to show differential survival or differential reproductive success resulting from an animal's habitat selection choice. There are three avenues for habitat selection to be addressed (Bleich et al. 1997, Naves et al. 2003): 1) distribution patterns of animals within the habitat mosaic (i.e., habitat use), 2) the short-term proximate reasons for these choices, and 3) the long-term ultimate consequences of these decisions (Boyce and McDonald 1999). Modeling the distribution of forage, relocation data and kill sites provides insights into the latter two. Long-term influences are most often measured as population change or viability. A central question deals with how alterations to the landscape affect the viability of populations and how well habitat models relate to population change. Models based solely on habitat attributes cannot consistently and accurately estimate species' population responses (Mitchell and Powell 2003). However, if habitat models are specific to demographic features such as births or deaths, changes in the availability of resources that affect these processes, represented by spatial predictors of resource distribution, may correlate with population responses (Naves et al. 2003). That is, as factors that increase bear productivity or survival become prevalent, productivity and survival rates for bears should concurrently increase (McLellan 1994). In Chapter 5 I evaluated this concept by assessing the effectiveness of occupancy and mortality risk models for explaining productivity and survival rates. I appraised empirical habitat models, forage distribution models and expert-opinion models with respect to explaining reproductive and annual adult survival rates. Empirical habitat models described the relative probability distributions for family groups, all adult females, adult males and mortality locations. Expert-opinion models included habitat effectiveness and security models.

Though Chapters 2 to 4 addressed independent aspects of grizzly bear ecology, they provide the modules that together were used to develop an index of the impact of human activity on demographic features of the Kluane grizzly bear population – the end product of this thesis. The logic of inquiry followed in this dissertation, including general statistical methodology, used to arrive at this index is illustrated in Figure 1-2. In Chapter 2, habitat modeling covariates were selected for representing forage availability, considering the Tasselled Cap Transformation over use of traditional land cover classifications. Using the Tasselled Cap Transformation and other thematic layers, in combination with grizzly bear relocation data, I developed habitat selection models in Chapter 3. Mortality risk models were developed in Chapter 4 using thematic layers in combination with grizzly bear mortality location data. Forage availability, habitat effectiveness and security area models were developed in Chapter 5. The output of these five models (habitat selection, mortality, forage availability, habitat effectiveness, and security area) then became thematic layers for explanatory modeling of habitat-specific productivity and survival rates for grizzly bears in Kluane. The explanatory models for habitat-related productivity and survival rates were then used to predict productivity and survival rates in bear management units (BMUs) throughout the study area. BMUs aerially encompassed enough area of a watershed to support the multi-annual home range of a female grizzly bear. Population status for each BMU, or the index for impact of human activities on the bear population, was assigned using source-like, refuge-like, attractive sink-like, and sink-like categorizations outlined by Naves et al. (2003).

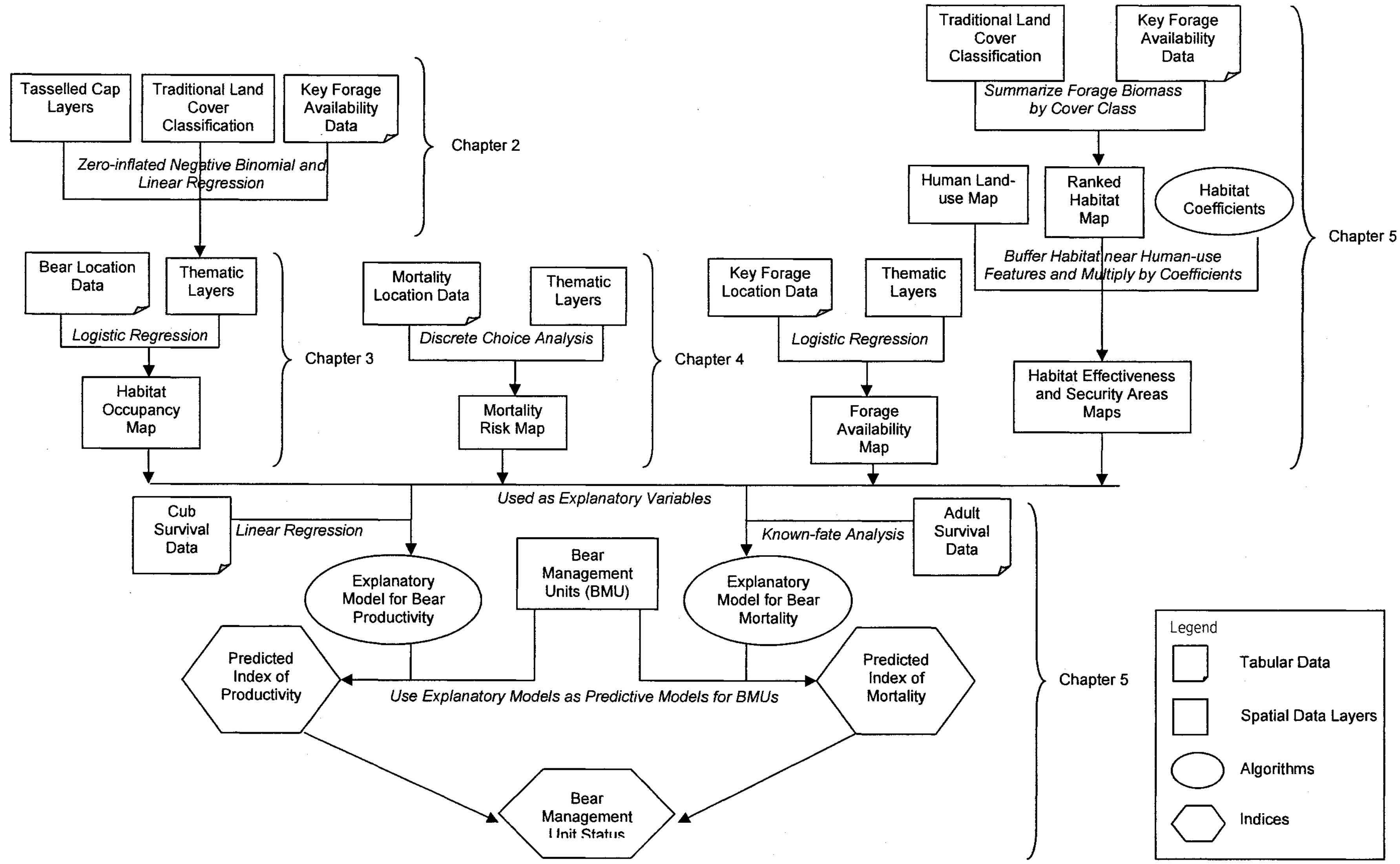

Figure 1-2. Flowchart illustrating logic of inquiry, linkages between Chapters 2 to 5, and general statistical methods (*italicized*) used for each step.

# Chapter Two: The ecology of greenness: Evaluation of Tasselled Cap Transformation variables for modeling grizzly bear habitat

## INTRODUCTION

Habitat maps are fundamental for wildlife conservation activities. Conventional habitat maps for grizzly bears (*Ursus arctos* L.) use land cover classifications to represent forage abundance and other habitat attributes presumed to be important for the species (Kansas and Riddell 1995, McCormick 1999). Land cover classes typically are derived by using ground-based information to classify spectral values from digital satellite images, in combination with interpretation of terrain attributes. The vegetative community and substrate character of a landscape generally are categorized into nominal data classes. To create a grizzly bear habitat map, classes are ranked according to the estimated abundance of certain bear forage species, or the frequency of bear relocation data is compiled by cover class (Despain 1986, Kansas and Riddell 1995, McCormick 1999).

Using a land cover classification that describes vegetation community assemblages to model species-habitat relationships can be problematic for a number of reasons. The relationship of cover classes to forage abundance or quality can be imprecise and complex (Diehl 1984, Carr et al. 2002, Fertig and Reiners 2002). Sometimes unexpected associations occur between cover classes and wildlife species occurrence. Establishing whether or not the relationship is ecologically meaningful may be difficult, particularly when mechanisms influencing distribution patterns are not evident. Ground-truthing and validation of land cover classifications is costly and time consuming. Additionally, the accuracy of land cover classifications is often poor (e.g., < 60% of pixels correctly identified; Congalton 1991) and improving the accuracy of a classification can significantly increase the cost of a project.

An alternative approach to traditional land cover classification involves creating a habitat map using Tasselled Cap Transformation of satellite imagery

(Manley et al. 1992, Mace et al. 1999). Unlike land cover classifications, which provide nominal data, the Tasselled Cap Transformation creates data that are continuous. This remote-sensing approach to habitat modeling avoids the often-prohibitive expense of ground-based habitat assessments. Some satellite platform sensors record reflected energy bands representing the visible, near-infrared, middle-infrared, and thermal infrared regions of the electromagnetic spectrum. The Tasselled Cap Transformation uses information from these bands to produce three orthogonal planes of data: greenness, wetness and brightness (Crist and Cicone 1986).

Greenness is a contrast between near-infrared and visible reflectance, and is thus a measure of the presence and density of green vegetation. Simultaneous high near-infrared and low red reflectance typically characterizes green areas. The greater the difference between near-infrared and red reflectance, the greater the index and the more green vegetation is present. Wetness is a contrast between middle-infrared and visible plus near-infrared reflectance, providing a measure of soil moisture content and vegetation health or density. Brightness is a measure of overall reflectance (e.g., differentiating light from dark soils or bright from dark vegetation; Crist and Kauth 1986), and is most highly indicative of varying incident light. Mathematically, the Tasselled Cap dimensions are the sum of the visible bands from satellite imagery weighted by the eigenvectors of the first three principal components developed for a study area with varying soil cover and vegetation (Crist and Cicone 1986). If the satellite images are collected under similar climatic conditions and scene types are similar (e.g., primarily vegetated) to the image for which the transformation was developed, the same weightings can apply across scenes (Ezra et al. 1984).

Among the Tasselled Cap variables, greenness has most commonly been used to predict grizzly bear habitat use within home ranges and at the landscape scale (Mace et al. 1996, Mace et al. 1999, Gibeau 2000, Nielsen et al. 2002, Stevens 2002, Apps et al. 2004). The relationship between the probable presence of grizzly bears and high greenness values has been demonstrated in disparate ecosystems including the Northern Continental Divide in northern

Montana (Mace et al. 1999), the Eastern Slopes of Alberta (Gibeau 2000, Stevens 2002), the Western Slopes of British Columbia (Stevens 2002, Apps et al. 2004), the Yellowhead region of Alberta (Nielsen et al. 2002), and the Parsnip Region in northern British Columbia (Ciarniello et al. 2002).

Although greenness is correlated with total photosynthesizing biomass (Crist et al. 1983), the nature of the positive relationship between greenness and the probability of grizzly bear presence is poorly understood. Bears exhibit preferences for specific forage species (Mattson et al. 1991, MacHutchon and Wellwood 2003) and show a high preference for certain non-photosynthetic parts of plants such as berries, flowers and roots. The mass of these parts may be strongly influenced by soil type, wind dispersal, or the availability of pollinators, and is not detectable as phytomass represented by greenness (Edge et al. 1990). The seasonal timing of satellite images may further obfuscate any relationship between greenness and forage abundance. Greenness values peak in mid-summer, when berries begin to ripen. Toward the fall, leaves senesce, greenness diminishes, but berry abundance does not change. Additionally, each forage species may have a different rate of green-up and senescence; therefore, determining which forage species are being represented by greenness values at various times of year is difficult.

The possible reasons for association between bear habitat use and greenness have not been explicitly explored. The objective of this study was to determine if Tasselled Cap data correlated with bear forage abundance. I compared the efficacy of Tasselled Cap and land cover classification models for predicting bear food occurrence, and also considered greenness as an interaction term with land cover class to specify within-class variation. I evaluated the relationship that Tasselled Cap data had to total bear forage abundance and the abundance of specific bear forage species. I then evaluated how the seasonal timing affected the efficacy of Tasselled Cap Transformed Landsat 5 TM imagery (30-m resolution; summer and fall) for explaining variation in grizzly bear forage distribution in the Kluane Region of southwest Yukon. Examining the relationship between Tasselled Cap data and forage abundance facilitates informed use of the greenness variable for bear habitat modeling.

## STUDY AREA

Between 1989 and 2004, 68 grizzly bears were captured and fitted with radio-tracking collars. Relocations (VHF) were obtained for all bears. I used a 100% minimum convex polygon (MCP) for all grizzly bear aerial telemetry locations (McCann 1998) to establish a study area frame. The area encompassed an 18 260-km$^2$ region in the southwest Yukon (Figure 2-1).

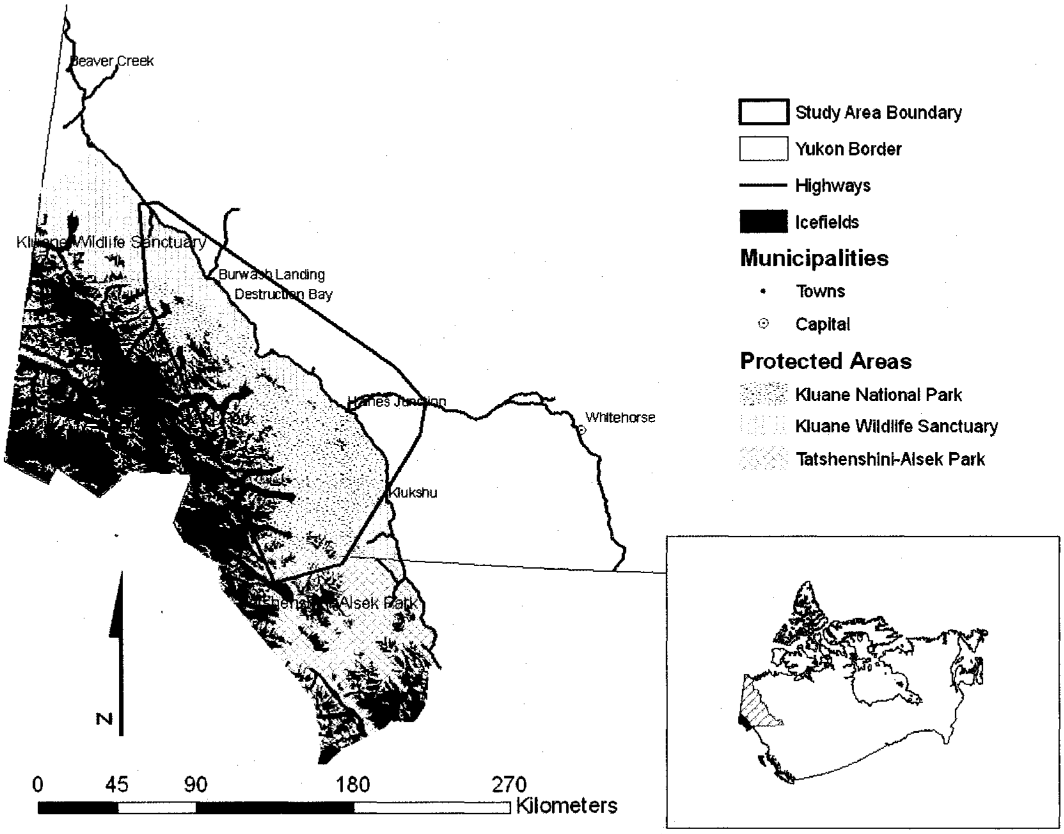

Figure 2-1. The study area in the Kluane Region, southwest Yukon, Canada for evaluating the relationship of Tasselled Cap variables to grizzly bear forage abundance.

## METHODS

### Vegetation Sampling

To measure bear forage abundance, I would have ideally sampled a random set of points across the study area. Unfortunately the study area was relatively inaccessible, all sampling was done by foot, and it would have been cost prohibitive to reach all the random points by helicopter. Therefore, to capture the variability of the landscape and variability among sample sites, while maximizing sampling efficiency, I opted to use a line transect method to sample all accessible valleys. Line transects allow for efficient systematic sampling of an area, while enabling the surveyor to capture information on gradients that may be present (Krebs 1999). I ran transects through large, homogenous polygons (i.e., greater than 200 m in diameter or width) for 10 pre-defined cover classes (Table 2-1). I visually classified areas into the pre-defined cover classes while on-site. Transects followed gradients in slope, elevation, or distance from water. I surveyed a variety of aspects. The start point for each transect was selected randomly. I located transect lines in every valley accessible by foot within Kluane National Park and Reserve (KNPR), and covered as many vegetation types within each valley as possible (Table 2-2). Where time permitted, I sampled areas outside of the Park. Vegetation sampling was conducted in 2000, 2001 and 2002.

Transect length varied with polygon size. Most transects equalled or exceeded 500 m, but some were shorter if polygons were small. Along each transect, I sampled bear forage abundance within 1-m x 1-m plots spaced at 25-m intervals. I sampled 1486 plots on 64 transect lines. To increase sample size, 65 additional plots were placed randomly within polygons for vegetation types that were under-represented by line transect sampling. Hence 1551 plots were sampled in total. I recorded the percent cover of 22 plant species commonly consumed by bears in the Kluane Region (McCann 1998, McCormick 1999;

Table 2-1. Pre-defined cover classes and class descriptions used for field sampling and satellite image classification.

| **Vegetation Class** | **Description** |
|---|---|
| ice_snow | ≥50% of cover was made up of ice or snow. |
| water | ≥80% of cover was clear or turbid water. |
| scree_talus | ≥50% of the cover was composed of rock, scree and/or talus, and vegetation made up <20% of the cover. |
| gravel_alluvial | Sparsely vegetated sites that were composed of >50% gravel or alluvium, associated with hydrological features. |
| disturbed | ≥25% of cover was disturbed by anthropogenic causes. |
| spruce forest | >75% of the canopy cover composed of spruce forest. |
| deciduous forest | Poplar forest with a canopy >3 meters in height with grass and/or sedge understory. >75% of the canopy cover composed of deciduous species. |
| shrub | Wood vegetation, with majority of the canopy <3 meters in height. |
| alpine_grass | Herbaceous areas predominantly comprised of graminoids and sedges. Little to no water present. |
| wetland | >20% of the bed is emergent. |

Table 2-2. Number of vegetation plots sampled for each of the pre-defined cover classes for each area in the Kluane Region. Bear forage abundance was sampled within 1-m x 1-m plots spaced at 25-m intervals along transect lines. 1486 plots were sampled among 64 transect lines. Sixty-five additional plots were placed randomly within polygons for vegetation types that were under-represented by line transect sampling. Transect lines were located in every valley accessible by foot, and covered as many vegetation types within each valley as possible.

| | **Vegetation Class** | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Valley** | **ice/snow** | **water (shoreline)** | **scree/talus** | **gravel/ alluvium** | **disturbed (human)** | **spruce forest** | **deciduous forest** | **shrub** | **alpine/grass** | **wetland** | **Total** |
| Alsek | | | | | | | | | | 9 | 9 |
| Auriol | | | | | 1 | 1 | | 4 | 17 | | 23 |
| Bates Lake | | 2 | 6 | 2 | | 2 | 5 | 1 | 5 | | 23 |
| Burwash Uplands | 6 | | 12 | | | | | 10 | 59 | | 87 |
| Congdon | | | | | | 12 | | 1 | | | 13 |
| Deceoli | | | | | | | | 17 | 17 | | 34 |
| Dezadeash | | | | | 3 | | 4 | | | | 7 |
| Donjek | | 1 | | | | 10 | | 65 | 30 | 1 | 107 |
| Dalton Post | | | | | 6 | | 1 | | | | 7 |
| Duke River | | | 16 | 3 | 2 | 4 | 11 | 41 | 10 | | 87 |
| Highway Corridor | | | | | | 68 | 62 | 14 | | | 144 |
| Jarvis River | | | | | | | 17 | 17 | 4 | | 38 |
| Kathleen Lake | | | | | | 1 | 1 | | | | 2 |
| Kathleen Lake North | | 4 | 2 | | | | 3 | 23 | | | 32 |
| Kathleen Lake South | | 20 | 25 | 2 | | 59 | 32 | 33 | 5 | | 176 |
| Kaskawulsh | | | 4 | 6 | | 1 | | 1 | 2 | | 14 |
| Mush Lake | | | | | | | 11 | 10 | | 1 | 22 |
| Onion Lake | | 14 | 1 | | | 11 | 14 | 41 | 64 | | 145 |
| Pipeline Corridor | | | | | 23 | 17 | 19 | 4 | | | 63 |
| Slims East | | | 72 | 26 | | 96 | | 8 | 5 | 2 | 209 |
| Slims (Delta and Sheep Mountain) | | | 10 | 10 | 2 | | | 4 | 4 | | 30 |
| Slims West | | 7 | 94 | 34 | | 23 | 5 | 39 | 71 | 1 | 274 |
| Tatshenshini | | | | | | | | 5 | | | 5 |
| **Total** | 6 | 48 | 242 | 83 | 37 | 305 | 185 | 338 | 293 | 14 | 1551 |

Table 2-3). All berries of fruiting species were collected, separated into ripe, unripe, and over-wintered berries, then counted and weighed to the nearest half-gram. I counted and weighed berries on site with a Pesola spring scale. Sampling was done from mid-June to late July, the time of year when most berries are developed but not ripe. This reduced bias that may have resulted from ripe berries being consumed by birds and other species. I recorded the height of vegetation and measured percent cover within pre-defined height classes; hence, total cover could exceed 100%. For *Hedysarum alpinum*, bears only consume the tuberous portion of the plant, so I assumed a positive linear correlation between percent leaf cover and the tuber mass (McCormick 1999). I recorded the location of each plot using a handheld Global Positioning System (GPS) unit.

### Explanatory Variables

Tasselled Cap effectiveness and comparability depends upon good quality cloud-free Landsat satellite images. Two sets of four Landsat 5 TM scenes covering the study area were acquired on the 27th and 28th of July 1996, and the 6th and 8th of September 1996 (path 61/rows 17 and 18; path 63/rows 16 and 17; RADARSAT International Inc). These were the most recent cloud-free TM scenes available for the study area during the peak of the growing season and the peak of fall color change. Peak timing was determined from changes in the normalized difference vegetation index (NDVI) from Advanced Very High Resolution Radiometer (AVHRR) imagery (1-km resolution) freely available through the Alaska Geospatial Data Clearinghouse (http://agdc.usgs.gov/). No cloud-free springtime Landsat (mid-May to mid-July) images were available for the study area. I included all bands in the analysis except the thermal band (band 6; see Appendix 1 for band wavelengths). To remove distortions and calibrate the images for ease of use, each scene was corrected for possible radiometric effects by using known spectral properties of pseudo-invariant reflectance targets

Table 2-3. Bears foods for which percent cover, number of berries, and berry biomass were assessed.

| **Species** **(Latin name)** | **Species** **(common name)** | **Response variable** | | |
|---|---|---|---|---|
| | | cover | berry abundance | berry weight |
| *Astragalus* spp. L. | Milk Vetch | x | | |
| *Arctostaphylos uva-ursi* L. Spreng. | Kinnikinnick | x | x | x |
| *Carex* spp. L. | Sedge | x | | |
| *Elaeagnus commutata* Bernh. ex Rydb. | Silverberry, Wolfberry | x | x | x |
| *Empetrum nigrum* L. | Crowberry | x | x | x |
| *Equisetum arvense* L. | Horsetail | x | | |
| Grass spp. | Grass | x | | |
| *Hedysarum alpinum* L. | Bear root, Sweet Vetch | x | | |
| *Oxytropis campestris* L. DC. | Locoweed | x | | |
| *Shepherdia canadensis* L. Nutt. | Buffaloberry, Soapberry | x | x | x |
| *Arctostaphylos rubra* (Rehd. & Wilson) Fern. | Bearberry | x | x | x |
| *Epilobium angustifolium* L. | Fireweed | x | | |
| *Epilobium latifolium* L. | River Beauty | x | | |
| *Eriophorum* spp. L. | Cottongrass | x | | |
| *Heracleum lanatum* Michx. | Cow-parsnip | x | | |
| *Ribes* spp. L. | Currant | x | x | x |
| *Rosa acicularis* Lindl. | Prickly Rose | x | x | x |
| *Salix* spp. L. (excludes *S. reticulata* L. and *S. arctica* Pallas) | Willow (excludes Net-veined and Arctic Willow) | x | | |
| *Vaccinium caespitosum* Michx. | Dwarf blueberry | x | x | x |
| *Vaccinium uliginosum* L. | Bog Blueberry | x | x | x |
| *Vaccinium vitis-idaea* L. | Low-bush Cranberry | x | x | x |
| *Vibrunum edule* Michx. Raf. | High-bush Cranberry | x | x | x |

such as spruce forest and deep lakes (Richter 1990) using standard pre-processing. Atmospheric effects were not visually apparent; therefore, no atmospheric corrections were applied to the images. Images were orthorectified using a 30-m resolution digital elevation model (DEM), re-projected to an Albers projection using nearest neighbour analysis, and mosaiced (Suitor 2003).

I performed a Tasselled Cap Transformation on the 6 visible and infrared bands to derive brightness, greenness, and wetness using the transformation algorithms reported by Crist and Cicone (1986) for Landsat 5 TM imagery:

$$\text{Brightness} = \begin{aligned}&(0.2909 \text{ x Band 1}) + (0.2493 \text{ x Band 2}) + (0.4806 \text{ x Band 3})\\ &+ (0.5568 \text{ x Band 4}) + (0.4438 \text{ x Band 5}) + (0.1706 \text{ x Band 7})\end{aligned}$$

Equation 2-1

$$\text{Greenness} = \begin{aligned}&(- 0.2728 \text{ x Band 1}) - (0.2174 \text{ x Band 2}) - (0.5508 \text{ x Band 3})\\ &+ (0.7221 \text{ x Band 4}) + (0.0733 \text{ x Band 5}) - (0.1648 \text{ x Band 7})\end{aligned}$$

Equation 2-2

$$\text{Wetness} = \begin{aligned}&(0.1446 \text{ x Band 1}) + (0.1761 \text{ x Band 2}) + (0.3322 \text{ x Band 3})\\ &+ (0.3396 \text{ x Band 4}) - (0.6210 \text{ x Band 5}) - (0.4186 \text{ x Band 7})\end{aligned}$$

Equation 2-3

Tasselled Cap values were output to three 16-bit channels.

A 12-class land cover classification for the Kluane Region was developed by Gleig et al. (2005). The 12 cover classes were cloud, shadow (from cloud and topography), human disturbance, ice and permanent snow, water, alluvium and gravel, scree and talus, spruce forest, deciduous forest, shrub, alpine and low elevation grassland, and wetland (Table 2-2). The portion of the study area covered by cloud and shadow was exceedingly small (i.e., 0.02% and 0.45%, respectively) and no vegetation plots were located in areas classified as cloud or shadow; therefore, cloud and shadow classes were excluded from the analysis.

Slope and elevation were derived from a 30-m DEM. I used the Solar Analyst Extension 1.0 (Fu and Rich 1999) for ArcView 3.2 (ESRI 2000) to generate the daily potential direct solar radiation (WH/m$^2$) from the 30-m DEM. I calculated total direct solar radiation for the entire year for 32 zenith divisions at 60° latitude. I measured distance of each plot to the nearest water body using digital hydrology maps at the 1:50 000 scale from the National Topographic Database (Natural Resources Canada 1999). Excluding wetlands, I considered any hydrological feature that was active year round.

### Evaluating Data Biases

I used chi-squared and likelihood ratio tests (g-tests) to evaluate sampling bias in the data. I generated 10 000 random locations within the study area boundary using the Animal Movements extension for ArcView (Hooge and Eichenlaub 2000) random point generator and the uniform distribution option. Frequency distributions of elevation classes (600-m interval classes), slope classes (15°-interval slope classes), and vegetation classes (10 classes) for random locations were used to determine expected values, given random sampling. The observed values were generated from the variable frequency classes for the sampled plots. I performed chi-squared tests for heterogeneity for each variable to determine which classes were sampled disproportionately. I used two-sample t-tests to compare summer and fall brightness, greenness and wetness and direct solar radiation ($\alpha = 0.05$) between 1551 random locations (randomly sub-sampled from the 10 000 locations) and the surveyed locations.

### Modeling Forage Availability

I developed models relating explanatory variables to three response variables representing bear forage abundance: the total cover of all bear foods, the total number of berries for all bear foods, and the total wet-weight of berries for all bear foods. I also considered models for four primary bear foods: *H. alpinum*, *Oxytropis campestris*, *Shepherdia canadensis*, and *Empetrum nigrum*. *H. alpinum* and *O. campestris* were the most prevalent herbaceous species, by volume, in scats, while *S. canadensis* and *E. nigrum* were the most prevalent berry species (McCann 1998). I pooled ripe and unripe berries together for total berry number and biomass. Information on over-wintered berries was potentially subject to bias as I could not determine how many had been consumed prior to sampling or what proportion of the previous year's production was being sampled; therefore, I excluded over-wintered berries from analyses.

I considered five groups of explanatory variables for each response variable. The first two groups were comprised of the variables brightness, greenness and wetness for summer (group 1) and fall (group 2). The third group comprised the land cover class variables (group 3) and the fourth and fifth grouping contained interaction variables for greenness and vegetated land cover classes (alluvium and gravel, spruce forest, deciduous forest, shrub, alpine, grassland, and wetland) for summer (group 4) and fall (group 5). Slope, elevation, direct solar radiation and distance to riparian area were included in each of the five groups, and hence, are referred to as standard variables. I included a quadratic term for modeling the relationship of bear forage to solar radiation, suspecting that areas with high amounts of direct radiation would be too arid to support abundant bear forage, while areas with low amounts of direct solar radiation would have less photosynthetic capability than areas with intermediate values. I coded the 10 cover classes as dummy variables for analysis. I ran separate analyses for summer and fall Tasselled Cap values. Prior to building the models, I tested the explanatory variables for collinearity using Pearson correlation ($r$), tolerance, and variance inflation function (VIF) diagnostics. All correlations greater than 0.6, or tolerance scores of 0.1 or less or individual VIF scores > 10 were judged to be collinear and not included in the model structure.

Bear foods were patchily distributed (Jalkotzy et al. 1999, Nielsen et al. 2004b) and sampled plots often did not have any bear foods. This produced response variable distributions that were inflated with zeros. I applied the Box-Cox transformation ($\lambda = 0.4$) to the response variable, total percent cover of forage, to make the residuals of regressions more homoskedastic and closer to a normal distribution (Box and Cox 1964). The Box-Cox transformation ($\tau$) of the response variable Y, given the Box-Cox parameter, $\lambda \geq 0$, is defined as:

$$\tau(Y;\lambda) = \begin{cases} (Y^{\lambda}-1)/\lambda & \text{if } \lambda \neq 0, \\ \ln(Y) & \text{if } \lambda = 0 \end{cases}$$

Equation 2-4

The transformed values for total percent cover were then used in a multiple linear regression.

I considered all nested subsets of each group of explanatory variables and used a model selection approach, calculating the corresponding Akaike Information Criterion (AIC) score for linear regression. Each model was ranked using its $\Delta$AIC score where:

Equation 2-5

$$\Delta AIC = AIC_i\text{-}\min AIC;$$

where $AIC_i$ is the AIC score for model i; and
minAIC is the minimum AIC score across all models.

I considered models with a $\Delta$AIC between 0 and 2 to have strong support, models with a $\Delta$AIC between 2 and 10 to have less support and models with a $\Delta$AIC greater than 10 to have no support (Anderson et al. 2001, Burnham and Anderson 2002).

I calculated Akaike weights (w) for each model, where:

$$w = \frac{\exp(-0.5 \times \Delta AIC)}{\sum \exp(-0.5 \times \Delta AIC)}$$

Equation 2-6

I obtained estimates of variable importance (I) by summing Akaike weights across all models in which a variable was present (Burnham and Anderson 2002). The larger the summed Akaike weight, the more important the variable. To calculate the relative importance for each variable, all explanatory variables must have equal representation among the models. This is best accomplished by running all possible models for all possible combinations of variables. However, generation of such a data set with dummy variables would have resulted in over 2 billion models to consider. This was computationally impossible; therefore, I selected the variables present in the 10 highest ranked models. I used those variables to run analyses of all possible models. I then used those models to calculate variable importance.

Of the 1551 plots, 1329 did not contain berries. In those plots that did, the number of berries ranged from 1 to 1463. To examine the relationship between number of berries and the explanatory variables, I used Voung's statistic to establish whether the functional form was best described by a Poisson or zero-inflated model (Long and Freese 2003). The analysis revealed that the data would be best fit to a zero-inflated model. I then used a likelihood ratio test on the parameter $\alpha$ to determine if a zero-inflated Poisson or zero-inflated negative binomial model was appropriate. The analysis suggested that the zero-inflated negative binomial model was most appropriate for the analysis (Johnson and Kotz 1969).

I developed zero-inflated models in three steps. The first step modeled membership in one of two latent groups, one group with the outcome of "zero" and the other with the outcome of "not zero". Next, the probability of the count associated with the "not zero" group was estimated. Finally, a model was developed for the observed probabilities as a mixture of the probabilities for the two groups. To model the membership probabilities for the latent groups, I converted the data on the number of berries to presence-absence data, coding plots with berries as "1" and plots without berries as "0". I used this data to run all possible logistic regressions using the nested subsets of the Tasselled Cap, land cover and interaction models. I ranked the models using AIC and selected the best models to develop the mixed probabilities for the two latent groups. However, the best logistic model always encapsulated variables derived from either fall or summer images. Rather than use the best equation across all models, and consequently developing mixed-probability models with summer and fall image data, I considered a set of summer and a set of fall models using the best logistic regression equation for the corresponding images. This also allowed me to investigate the relationship of response variables to summer versus fall Tasselled Cap variables. It was not feasible to run all possible models for the second and third steps in the zero-inflated modeling process; therefore, keeping variable balance in mind, I selected a set of 20 likely models. I calculated variable importance based on this subset of models.

The berry weight data contained a high number of zeros; therefore, I performed a Box-Cox transformation on berry weights ($\lambda = -4.4$). The transformed values were used in a multiple linear regression. Again, I considered all nested subsets of each model and calculated the corresponding AIC score for linear regression, ranked the models, then calculated variable importance based on all possible models for the subset of variables in the 10 highest ranked models.

Sampling plots were located spatially proximal to each other. This could create issues with spatial autocorrelation, where, without making adjustments to test statistics, one would detect significance more frequently than one should (Type I error; Lennon 2000). However, autocorrelation among sample plots was not an issue for my analyses because my comparisons were relative, examining only variable importance and relative measures of model performance. Estimates of the model parameters and the log-likelihoods are unaffected by autocorrelation (Lennon 2000).

## RESULTS

### Tests of Data Bias

Sampling over-represented elevations between 600 – 1200 m, and under-represented elevations between 1800 – 2400 m (Table 2-4). I found a slight deviation from expected in the 31 – 45 degree slope category, indicating under-

Table 2-4. $\chi^2$ and g-test results testing representativeness of the vegetation plot data against availability of landscape characteristics. Categories for each variable were grouped to determine which categories were represented disproportionate to expectation. Grouping "a" includes all categories for that variable and provides the overall $\chi^2$ and g-test value (g). Categories with similar letter codes, within the variable of interest, were considered together. Corresponding $\chi^2$ test statistic, $P$-values ($P$) and degrees of freedom (df) are presented for each grouping. Variables in a grouping with a $P$-value > 0.05 were considered homogenous. Variable classes that were sampled disproportionate to availability are highlighted in grey.

| Variable/category | Grouping | Group | $\chi^2$ | $P$ | df | g | $P$ | df |
|---|---|---|---|---|---|---|---|---|
| *Elevation* | | | | | | | | |
| 0 – 600 m | a, b, c, d | a | 36.35 | < 0.0001 | 5 | 46.24 | < 0.0001 | 5 |
| 600 – 1200 m | a, c | b | 6.51 | 0.1 – 0.05 | 3 | | | |
| 1200 – 1800 m | a, b, c, d | c | 23.99 | < 0.0001 | 4 | | | |
| 1800 – 2400 m | a, d | d | 19.05 | < 0.0001 | 4 | | | |
| 2400 – 3000 m | a, b, c, d | | | | | | | |
| >3000 m | a, b, c, d | | | | | | | |
| *Slope* | | | | | | | | |
| 0 – 15 degrees | a,b | a | 16.53 | < 0.005 | 4 | 21.36 | < 0.005 | 5 |
| 16 – 30 degrees | a,b | b | 6.96 | 0.25 – 0.1 | 3 | | | |
| 31 – 45 degrees | a | | | | | | | |
| 46 – 60 degrees | a,b | | | | | | | |
| 61 – 75 degrees | a,b | | | | | | | |
| *Vegetation class* | | | | | | | | |
| ice_snow | a,c | a | 42.22 | < 0.001 | 10 | 40.42 | < 0.001 | 10 |
| water | a,b,c,d | b | 42.22 | 0.25 – 0.1 | 8 | | | |
| shadow | a,b,c,d | c | 24.77 | < 0.005 | 9 | | | |
| scree_talus | a,b,c,d | d | 42.22 | < 0.001 | 9 | | | |
| gravel_alluvium | a,b,c,d | | | | | | | |
| disturbed | a,b,d | | | | | | | |
| spruce forest | a,b,c,d | | | | | | | |
| deciduous forest | a,b,c,d | | | | | | | |
| shrub | a,b,c,d | | | | | | | |
| alpine_grass | a,b,c,d | | | | | | | |
| wetland | a,b,c,d | | | | | | | |

representation (Table 2-4). I also under-sampled ice and permanent snow cover classes and disturbed areas. All other land cover classes were represented proportional to availability on the landscape (Table 2-4).

Greenness values were higher in sampled plots than in random plots ($t = 10.1582$, $P < 0.0001$, df = 3100 for summer greenness; $t = 13.1201$, $P < 0.0001$, df = 3100 for fall greenness). Conversely, brightness and wetness values were significantly lower than available ($t = -4.9725$, $P < 0.0001$, df = 3100 for summer brightness; $t = -11.5046$, $P < 0.0001$, df = 3100 for fall brightness; $t = -9.2990$, $P < 0.0001$, df = 3100 for summer wetness; $t = -11.0305$, $P < 0.0001$, df = 3100 for fall wetness). Sampled plots also occurred in regions with less direct solar radiation than prevalent in the study area ($t = -6.3967$, $P < 0.001$, df = 3100).

## Forage Availability Models

*Percent cover.*--Models incorporating peak summer Tasselled Cap variables were the best for explaining the variation in bear forage cover (Table 2-5). All models with a $\Delta$AIC of 2 or less contained the three summer Tasselled Cap variables, slope, elevation, distance to riparian area, and direct solar radiation. The top 134 models all contained summer greenness. No other variable was this consistently represented in the top models. Models containing land cover classification ranked higher than models with interaction terms, but the data did not strongly support use of these models. The top two models within the land cover class subset of models (group 3) performed slightly better than the models with fall Tasselled Cap covariates (group 2; Table 2-5).

I used all the variables contained within the top 10 models for examining variable importance. Peak summer greenness was the most influential variable for discriminating plots with high amounts of bear forage cover (Table 2-6). Brightness and wetness were the next most important variables, while elevation and solar radiation were the least important.

*Number of berries.*--I used a logistic regression model to differentiate plots with and without berries. I ran all possible models for each nested group of variables. Models with the fall brightness, greenness and wetness ranked as the five highest (Table 2-7). Models with the summer Tasselled Cap variables were the next most supported models. Generally, models that included an interaction term between fall greenness and vegetation classes performed better than models with just land cover classes. I used the top ranked fall model as my inflator for a set of fall-based zero-inflated negative binomial models. Similarly, I used the top ranked summer model for a set of summer-based zero-inflated

Table 2-5. Top 10 models for total percent cover of bear foods (*n* = 1551). Box-Cox transformed values ($\lambda = 0.4$) for total percent cover were regressed against summer and fall Tasselled Cap, land cover class, Tasselled Cap and land cover interaction variables, slope, elevation, solar radiation and distance to water (standard variables). The "s" in front of the Tasselled Cap variables signifies summer imagery. Root mean square error (RMSE), AIC and ΔAIC scores and weights are shown for each model. Weights (w) are calculated for the top 10 models in the variable subset. k is the number of parameters estimated for the model. The intercept and RMSE are included in k.

| Model | k | RMSE | AIC | ΔAIC | w |
|---|---|---|---|---|---|
| -slope+elevation-solar+dist_riparian+sgreen+swet+sbright | 9 | 27.37 | 10273.69 | 0.00 | 0.5681521 |
| -slope+elevation+solar-solar$^2$+dist_riparian+sgreen+swet+sbright | 10 | 27.37 | 10274.73 | 1.59 | 0.3377781 |
| -slope+elevation+dist_riparian+sgreen+swet+sbright | 8 | 27.41 | 10277.30 | 4.16 | 0.0934465 |
| -slope+solar-solar$^2$+dist_riparian+sgreen+swet+sbright | 9 | 27.51 | 10289.43 | 16.29 | 0.0002171 |
| elevation+solar-solar$^2$+dist_riparian+sgreen+swet+sbright | 9 | 27.51 | 10289.56 | 16.42 | 0.0002034 |
| -slope-solar+dist_riparian+sgreen+swet+sbright | 8 | 27.52 | 10289.72 | 16.58 | 0.0001878 |
| solar-solar$^2$+dist_riparian+sgreen+swet+sbright | 8 | 27.58 | 10296.11 | 22.97 | 0.0000077 |
| -slope+dist_riparian+sgreen+swet+sbright | 7 | 27.59 | 10296.41 | 23.27 | 0.0000066 |
| -slope+elevation-solar+sgreen+swet+sbright | 8 | 27.63 | 10301.62 | 28.48 | 0.0000005 |
| -slope+elevation+solar-solar$^2$+sgreen+swet+sbright | 9 | 27.64 | 10303.22 | 30.08 | 0.0000002 |

Table 2-6. Variable importance (I) and rankings for the variables contained within the top 10 models for predicting total cover of 22 bear food species. Variable importance is derived by summing the AIC-derived weight of every model containing the variable within a subset of models. The "s" before the Tasselled Cap variables indicates that summer imagery variables were used.

| Variable | I | Rank |
|---|---|---|
| slope | 0.99988 | 5 |
| elevation | 0.99958 | 6 |
| solar | 0.51853 | 7 |
| dist_riparian | 1.00000 | 4 |
| sgreen | 1.00000 | 1 |
| swet | 1.00000 | 3 |
| sbright | 1.00000 | 2 |

Table 2-7. Top 10 models for predicting the presence and absence of berries (*n* = 1551). All possible logistic regressions were run using the nested subsets of the Tasselled Cap, land cover and interaction explanatory variables. The "f" in front of the Tasselled Cap variables signifies fall imagery and the "s" signifies summer imagery. Log-likelihoods (LL), AIC and ΔAIC scores and weights are shown for each model. Weights (w) are calculated based on the 10 models presented here. k is the number of parameters estimated for the model and includes the intercept.

| Model | k | LL | AIC | ΔAIC | w |
|---|---|---|---|---|---|
| slope+fgreen+fwet | 4 | -610.17 | 1228.33 | 0.00 | 0.14771 |
| slope+fgreen+fwet-fbright | 5 | -609.24 | 1228.48 | 0.15 | 0.13704 |
| slope+fgreen-fbright | 4 | -610.30 | 1228.61 | 0.28 | 0.12842 |
| slope-elevation+fgreen-fbright | 5 | -609.43 | 1228.85 | 0.52 | 0.11390 |
| slope+sgreen+swet | 4 | -610.48 | 1228.94 | 0.61 | 0.10889 |
| slope-elevation+sgreen+swet | 5 | -609.67 | 1229.34 | 1.01 | 0.08915 |
| slope+fgreen+fwet+solar-solar$^2$ | 6 | -608.85 | 1229.70 | 1.37 | 0.07446 |
| slope-elevation+fgreen-fbright+solar-solar$^2$ | 7 | -607.94 | 1229.88 | 1.55 | 0.06806 |
| slope+fgreen-fbright+solar-solar$^2$ | 6 | -608.96 | 1229.92 | 1.59 | 0.06671 |
| slope+fgreen+fwet-solar | 5 | -609.98 | 1229.95 | 1.62 | 0.06571 |

negative binomial models. Slope, wetness and greenness were included as covariates in both top models.

As expected, because the top presence-absence model used fall Tasselled Cap covariates, the top performing fall count models had lower AIC scores than the top summer models. The regressors for the best fall count model were slope, elevation, distance to water and solar radiation (Table 2-8). The next best model included fall Tasselled Cap covariates in the count model. There was only moderate support for models containing land cover classes, with the exception of one model using alpine class and containing all other classes in the reference category. This model had strong support. The best summer models followed a similar pattern, though brightness as opposed to slope, greenness, or wetness was included in the second best model (Table 2-8).

Elevation was the most important variable in the summer model subset (Table 2-9). Distance from water, solar radiation, and slope ranked next highest, respectively. Land cover classes were not as influential as Tasselled Cap variables but were more influential than interaction variables. Variable importance calculations for fall models indicated that, like the summer models, elevation, followed by distance from water then amount of solar radiation, were the most important variables for explaining the abundance of berries (Table 2-9). Brightness was the fourth ranked variable, and was more important than wetness and greenness. Interaction variables were the least important covariates. Land cover classes ranked between the Tasselled Cap and standard variables and the interaction variable. Alpine and grassy areas were the most influential cover classes.

*Berry biomass.*--The top two models for explaining variation in berry biomass included fall greenness and wetness and did not include any land cover classes or interaction terms (Table 2-10). All models with a $\Delta$AIC of 2 or less contained slope and either fall or summer greenness and wetness (Table 2-10). All models with a $\Delta$AIC of 8 or less contained either summer or fall greenness. There were two models that had moderate support and included land

Table 2-8. Top models for explaining variation in berry abundance ($n$ = 1551). Count data for berries were regressed against summer and fall Tasselled Cap, land cover class, Tasselled Cap and land cover interaction variables, slope, elevation, solar radiation and distance to water (standard variables) using zero-inflated negative binomial regression. Logistic regression was used to model the probability of berries being present in a plot. The equation used for logistic regression is in brackets beside the season headings. The other models estimate the probability of the count of berries. The "f" in front of the Tasselled Cap variables signifies fall imagery and the "s" signifies summer imagery. Combining the two models in a zero-inflated modeling framework produces a mixture of the probabilities. Log-likelihoods (LL), AIC and $\Delta$AIC scores and weights (w) are shown for each combination of models. Weights were calculated based on all models that were run within the variable set. k is the number of parameters estimated for the model and includes an intercept for the logistic regression equation, an intercept for the count model, and a dispersion parameter ($\alpha$).

***Summer (-slope-sgreen-swet)***

| **Model** | k | LL | AIC | $\Delta$AIC | w |
|---|---|---|---|---|---|
| slope+elevation+solar-solar$^2$+dist_riparian+sgreen+swet-sbright | 14 | -1679.57 | 3381.13 | 0.00 | 0.26342 |
| slope+elevation+solar-solar$^2$+dist_riparian | 11 | -1679.80 | 3381.60 | 0.47 | 0.20867 |
| sgreen-swet+sbright | 9 | -1684.01 | 3382.02 | 0.89 | 0.16847 |
| slope+sgreen-swet | 9 | -1684.39 | 3382.78 | 1.65 | 0.11521 |
| elevation+solar-solar$^2$+dist_riparian-sbright | 11 | -1677.78 | 3383.55 | 2.42 | 0.07848 |
| slope | 7 | -1685.30 | 3384.61 | 3.48 | 0.04633 |
| elevation | 7 | -1685.33 | 3384.67 | 3.54 | 0.04492 |
| dist_riparian | 7 | -1685.75 | 3385.51 | 4.38 | 0.02954 |
| solar-solar$^2$ | 8 | -1683.99 | 3385.97 | 4.84 | 0.02343 |
| sgreen | 7 | -1686.07 | 3386.13 | 5.00 | 0.02158 |

***Fall (-slope-fgreen-fwet)***

| **Model** | k | LL | AIC | $\Delta$AIC | w |
|---|---|---|---|---|---|
| slope+elevation+solar-solar$^2$+dist_riparian+fgreen-fwet-fbright | 14 | -1678.22 | 3378.43 | 0.00 | 0.17587 |
| slope+elevation+solar-solar$^2$+dist_riparian | 11 | -1675.26 | 3378.52 | 0.09 | 0.16813 |
| fgreen-fwet-fbright | 9 | -1678.44 | 3378.87 | 0.44 | 0.14128 |
| slope+fgreen-fwet | 9 | -1682.52 | 3379.03 | 0.60 | 0.13016 |
| elevation+solar-solar$^2$+dist_riparian+fbright | 11 | -1682.59 | 3379.17 | 0.74 | 0.12136 |
| slope | 7 | -1682.89 | 3379.78 | 1.35 | 0.08946 |
| elevation | 7 | -1680.98 | 3379.96 | 1.53 | 0.08184 |
| dist_riparian | 7 | -1681.93 | 3381.85 | 3.42 | 0.03181 |
| solar | 7 | -1683.98 | 3381.96 | 3.53 | 0.03014 |
| fgreen | 7 | -1683.99 | 3381.97 | 3.54 | 0.02999 |

Table 2-9. Variable importance (I) and rankings for the fall and summer count models for predicting total number of berries for 22 bear food species. Variable importance is derived by summing the AIC-derived weight of every model containing the variable within a subset of models. The "f" before the Tasselled Cap variables indicates that fall imagery variables were used and an "s" indicates that summer imagery was used.

| ***Summer*** | | | ***Fall*** | | |
|---|---|---|---|---|---|
| **Variable** | I | **Rank** | **Variable** | I | **Rank** |
| slope | 0.28698 | 4 | slope | 0.32236 | 6 |
| elevation | 0.57074 | 1 | elevation | 0.51206 | 1 |
| solar | 0.44548 | 3 | solar | 0.40986 | 3 |
| dist_riparian | 0.46127 | 2 | riparian | 0.41872 | 2 |
| green | 0.15933 | 6 | green | 0.30591 | 7 |
| wet | 0.09165 | 8 | wet | 0.33522 | 5 |
| bright | 0.24453 | 5 | bright | 0.34911 | 4 |
| water | 0.05008 | 11 | water | 0.03232 | 13 |
| scree_talus | 0.07469 | 9 | scree_talus | 0.03851 | 10 |
| gravel_alluvium | 0.03603 | 15 | gravel_alluvium | 0.02708 | 15 |
| disturbed | 0.07428 | 10 | disturbed | 0.04365 | 9 |
| spruce forest | 0.04311 | 12 | spruce forest | 0.03376 | 11 |
| deciduous forest | 0.04116 | 14 | deciduous forest | 0.03249 | 12 |
| shrub | 0.04127 | 13 | shrub | 0.03215 | 14 |
| alpine_grass | 0.12117 | 7 | alpine_grass | 0.09858 | 8 |
| sgreen x gravel_alluvium | 0.02060 | 20 | fgreen x gravel_alluvium | 0.01291 | 20 |
| sgreen x spruce forest | 0.02307 | 16 | fgreen x spruce forest | 0.01650 | 16 |
| sgreen x deciduous forest | 0.02119 | 19 | fgreen x deciduous forest | 0.01407 | 19 |
| sgreen x shrub | 0.02187 | 17 | fgreen x shrub | 0.01514 | 17 |
| sgreen x alpine_grass | 0.02139 | 18 | fgreen x alpine_grass | 0.01417 | 18 |

Table 2-10. Top 10 models predicting berry biomass ($n$ = 1551). Box-Cox transformed values ($\lambda$ = -4.4) for total percent cover were regressed against summer and fall Tasselled Cap, land cover class, Tasselled Cap and land cover interaction variables, slope, elevation, solar radiation and distance to water (standard variables). The "f" in front of the Tasselled Cap variables signifies fall imagery and the "s" signifies summer imagery. Root mean square error (RMSE), AIC and $\Delta$AIC scores and weights are shown for each model. Weights (w) are calculated based on the 10 models presented here. k is the number of parameters estimated for the model and includes the intercept and RMSE.

| **Model** | k | RMSE | AIC | ΔAIC | w |
|---|---|---|---|---|---|
| slope+fgreen+fwet | 5 | 0.24 | -4440.94 | 0.00 | 0.20847 |
| slope-elevation+fgreen+fwet | 6 | 0.24 | -4439.94 | 1.00 | 0.12645 |
| slope+sgreen+swet | 5 | 0.24 | -4439.79 | 1.15 | 0.11731 |
| slope-elevation+sgreen+swet | 6 | 0.24 | -4439.74 | 1.20 | 0.11441 |
| slope+fgreen+fwet-fbright | 6 | 0.24 | -4439.18 | 1.76 | 0.08647 |
| slope-dist_riparian+fgreen+fwet | 6 | 0.24 | -4439.16 | 1.78 | 0.08561 |
| slope-solar+fgreen+fwet | 6 | 0.24 | -4439.06 | 1.88 | 0.08144 |
| slope+solar-solar$^2$+fgreen+fwet | 7 | 0.24 | -4438.83 | 2.11 | 0.07259 |
| slope-elevation+fgreen+fwet-fbright | 7 | 0.24 | -4438.23 | 2.71 | 0.05378 |
| slope-elevation+solar-solar$^2$+fgreen+fwet | 8 | 0.24 | -4438.22 | 2.72 | 0.05351 |

cover classes as explanatory variables. Generally, models with fall Tasselled Cap values performed best among model subsets. Models with peak summer greenness and wetness performed better than models with cover classes. Models containing interaction terms performed poorly, though some fall interaction models performed slightly better than the summer interaction models.

To examine variable importance, I again used all variables contained within the top 10 models to run all possible regression models. This included all standard variables, the fall Tasselled Cap variables, and summer greenness and wetness. Slope was the most influential variable for explaining berry biomass (Table 2-11). Fall greenness and summer greenness were the next most important variables, followed by summer wetness and then fall wetness. Areas with high berry biomass were steep, hydric and associated with high vegetative biomass. Solar radiation and brightness were the least important variables for explaining the weight of berries.

### Species-specific Models

*H. alpinum.*--While the Tasselled Cap variables were important variables for explaining variation in overall bear forage availability, individual species cover for *H. alpinum* was better explained by cover class models combined with information on slope, elevation, distance to riparian areas, and amount of solar radiation (Table 2-12). Summer Tasselled Cap models were better than fall model for explaining variation in the percent cover of *H. alpinum* – particularly models with summer greenness and land cover class interaction terms.

Elevation and distance to riparian areas were the most important variables for predicting percent cover of *H. alpinum* (Table 2-13). Solar radiation was the next highest ranked variable. Shrub was the most influential cover class. *H. alpinum* had a positive association with that cover class. Wetland and deciduous habitats were the least influential variable in explaining the variation in percent cover of the species (Table 2-13).

Table 2-11. Variable importance (I) and rankings for the variables contained with in the top 10 models for predicting berry biomass of 22 bear food species. Variable importance is derived by summing the AIC-derived weight of every model containing the variable within a subset of models. The "f" before the Tasselled Cap variables indicates that fall imagery variables were used, and the "s" indicates that summer imagery was used.

| Variable | I | Rank |
|---|---|---|
| slope | 0.83109 | 1 |
| elevation | 0.54593 | 6 |
| solar | 0.36846 | 8 |
| dist_riparian | 0.43578 | 7 |
| fwet | 0.59440 | 5 |
| fgreen | 0.63562 | 2 |
| fbright | 0.34253 | 9 |
| swet | 0.59881 | 4 |
| sgreen | 0.62897 | 3 |

Table 2-12. Top 10 models predicting *H. alpinum* cover ($n$ = 1551). Box-Cox transformed values ($\lambda = 0.4$) for total percent cover were regressed against summer and fall Tasselled Cap, land cover class, Tasselled Cap and land cover interaction variables, slope, elevation, solar radiation and distance to water (standard variables). The "s" in front of the Tasselled Cap variables signifies summer imagery. Root mean square error (RMSE), AIC and ΔAIC scores and weights are shown for each model. Weights (w) are calculated for the top 10 models in the variable subset. k is the number of parameters estimated for the model. The intercept and RMSE are included in k.

| Model | k | RMSE | AIC | ΔAIC | w |
|---|---|---|---|---|---|
| elevation+solar-solar$^2$+dist_riparian+water+scree_talus+gravel_alluvium+disturbed+spruce+deciduous+shrub +alpine_grass+wetland | 15 | 0.13 | -6304.46 | 0.00 | 0.55696 |
| -slope+elevation+solar-solar$^2$+dist_riparian+water+scree_talus+gravel_alluvium+disturbed+spruce+deciduous+shrub +alpine_grass+wetland | 16 | 0.13 | -6302.77 | 1.69 | 0.23925 |
| elevation+solar-solar$^2$+dist_riparian+water+scree_talus+gravel_alluvium+spruce+deciduous+shrub+alpine_grass +wetland | 14 | 0.13 | -6300.07 | 4.39 | 0.06203 |
| -slope+elevation+solar-solar$^2$+dist_riparian+water+scree_talus+gravel_alluvium+spruce+deciduous+shrub +alpine_grass+wetland | 15 | 0.13 | -6298.68 | 5.78 | 0.03096 |
| elevation+solar-solar$^2$+dist_riparian+water+scree_talus+gravel_alluvium+spruce+deciduous+shrub+alpine_grass | 13 | 0.13 | -6298.49 | 5.97 | 0.02815 |
| elevation+solar-solar$^2$+dist_riparian+water+scree_talus+gravel_alluvium-disturbed+shrub | 11 | 0.13 | -6298.26 | 6.20 | 0.02510 |
| elevation+solar-solar$^2$+dist_riparian+water+scree_talus+gravel_alluvium-disturbed+shrub-alpine_grass | 12 | 0.13 | -6297.30 | 7.16 | 0.01553 |
| elevation+solar-solar$^2$+dist_riparian+water+gravel_alluvium-disturbed+shrub-alpine_grass | 11 | 0.13 | -6297.24 | 7.22 | 0.01507 |
| elevation+solar-solar$^2$+dist_riparian+water+scree_talus+gravel_alluvium-disturbed+spruce+shrub | 12 | 0.13 | -6297.05 | 7.41 | 0.01371 |
| -slope+elevation+solar-solar$^2$+dist_riparian+water+scree_talus+gravel_alluvium+spruce+deciduous+shrub+alpine_grass | 14 | 0.13 | -6296.99 | 7.47 | 0.01330 |

Table 2-13. Variable importance (I) and rankings for the variables contained with in the top 10 models for predicting total cover of *H. alpinum*. Variable importance is derived by summing the AIC-derived weight of every model containing the variable within a subset of models.

| **Variable** | I | **Rank** |
|---|---|---|
| slope | 0.31010 | 13 |
| elevation | 1.00000 | 1 |
| solar | 0.99880 | 3 |
| dist_riparian | 1.00000 | 1 |
| water | 0.89377 | 6 |
| scree_talus | 0.85569 | 7 |
| gravel_alluvium | 0.98438 | 5 |
| disturbed | 0.82863 | 8 |
| spruce forest | 0.76853 | 10 |
| deciduous forest | 0.75801 | 11 |
| shrub | 0.99700 | 4 |
| alpine_grass | 0.78747 | 9 |
| wetland | 0.69573 | 12 |

*O. campestris.*--Like *H. alpinum*, variation in *O. campestris* abundance was best explained by land cover class models combined with the standard covariates (Table 2-14). Again, models with peak summer Tasselled Cap values and with summer greenness and cover class interaction terms performed better than their fall counterparts for discerning variation in percent cover, and Tasselled Cap models performing better than the interaction models within the season of comparison. However, $\Delta$AIC scores indicated no support for models that excluded cover class as a variable (Table 2-14).

Slope was the most important variable for explaining the variation in percent of *O. campestris* cover (Table 2-15). Scree and talus habitats and spruce habitats were the next most important explanatory variable and *O. campestris* had a positive association with both cover classes. Gravel and alluvial and shrub habitats were the least influential variable for explaining variation in the percent cover of the species (Table 2-15).

*S. canadensis.*--Land cover classification-based models outperformed all other models for explaining variation in percent of *S. canadensis* cover (Table 2-16). This species was positively associated with shrub and deciduous cover classes. Generally, summer imagery models were slightly better than fall imagery models and interaction models performed worse than Tasselled Cap models. Elevation and slope were the most important variables for predicting *S. canadensis* cover (Table 2-17). Deciduous, shrub and gravel or alluvium cover classes were the next most important variables.

Among the models for differentiating *S. canadensis* berry presence and absence showed that interaction models between peak summer greenness and land cover class were best (Table 2-18). Among models that used fall imagery, models that considered the Tasselled Cap variables (group 2) outperformed models with interaction variables (group 5). The top model in the fall Tasselled Cap subset had a $\Delta$AIC of less than two when compared to the top model among all subsets. Land cover class and fall greenness interaction models performed the worst among all model subsets. As would be expected, fall count models also

Table 2-14. Top 10 models predicting *O. campestris* cover (*n* = 1551). Box-Cox transformed values ($\lambda = 0.4$) for total percent cover were regressed against summer and fall Tasselled Cap, land cover class, Tasselled Cap and land cover interaction variables, slope, elevation, solar radiation and distance to water (standard variables). The "s" in front of the Tasselled Cap variables signifies summer imagery. Root mean square error (RMSE), AIC and ΔAIC scores and weights are shown for each model. Weights (w) are calculated for the top 10 models in the variable subset. k is the number of parameters estimated for the model. The intercept and RMSE are included in k.

| Model | k | RMSE | AIC | ΔAIC | w |
|---|---|---|---|---|---|
| -slope-elevation-water+scree_talus+disturbed+spruce | 8 | 0.29 | -3915.64 | 0.00 | 0.16986 |
| -slope-elevation-water+scree_talus+spruce | 7 | 0.29 | -3915.03 | 0.61 | 0.12521 |
| -slope-water+scree_talus+disturbed+spruce | 7 | 0.29 | -3914.96 | 0.68 | 0.12091 |
| -slope-elevation-water+scree_talus+disturbed+spruce-wetland | 9 | 0.29 | -3914.52 | 1.12 | 0.09703 |
| -slope-elevation-solar+solar$^2$-water+scree_talus+disturbed+spruce | 10 | 0.29 | -3914.43 | 1.21 | 0.09276 |
| -slope-elevation-dist_riparian-water+scree_talus+disturbed+spruce | 9 | 0.29 | -3914.30 | 1.34 | 0.08692 |
| -slope-solar+solar$^2$-water+scree_talus+disturbed+spruce | 9 | 0.29 | -3914.24 | 1.40 | 0.08435 |
| -slope-elevation-water+scree_talus+spruce-wetland | 8 | 0.29 | -3914.04 | 1.60 | 0.07633 |
| -slope-elevation-solar+solar$^2$-water+scree_talus+spruce | 9 | 0.29 | -3913.97 | 1.67 | 0.07370 |
| -slope-dist_riparian-water+scree_talus+disturbed+spruce | 8 | 0.29 | -3913.95 | 1.69 | 0.07297 |

Table 2-15. Variable importance (I) and rankings for the variables contained with in the top 10 models for predicting total cover of *O. campestris*. Variable importance is derived by summing the AIC-derived weight of every model containing the variable within a subset of models.

| Variable | I | Rank |
|---|---|---|
| slope | 1.00000 | 1 |
| elevation | 0.56281 | 6 |
| solar | 0.43030 | 7 |
| dist_riparian | 0.34293 | 9 |
| water | 0.81071 | 4 |
| scree_talus | 0.96063 | 2 |
| gravel_alluvium | 0.32204 | 13 |
| disturbed | 0.59281 | 5 |
| spruce forest | 0.94743 | 3 |
| deciduous forest | 0.33440 | 11 |
| shrub | 0.33104 | 12 |
| alpine_grass | 0.33588 | 10 |
| wetland | 0.37399 | 8 |

Table 2-16. Top 10 models predicting *S. canadensis* cover ($n$ = 1551). Box-Cox transformed values ($\lambda$ = 0.4) for total percent cover were regressed against summer and fall Tasselled Cap, land cover class, Tasselled Cap and land cover interaction variables, slope, elevation, solar radiation and distance to water (standard variables). The "s" in front of the Tasselled Cap variables signifies summer imagery. Root mean square error (RMSE), AIC and ΔAIC scores and weights are shown for each model. Weights (w) are calculated for the top 10 models in the variable subset. k is the number of parameters estimated for the model. The intercept and RMSE are included in k.

| Model | k | RMSE | AIC | ΔAIC | w |
|---|---|---|---|---|---|
| slope-elevation+solar+deciduous+shrub | 7 | 0.26 | -4162.03 | 0.00 | 0.15205 |
| slope-elevation+solar+water+deciduous+shrub | 8 | 0.26 | -4161.74 | 0.29 | 0.13153 |
| slope-elevation+solar-gravel_alluvium+deciduous+shrub | 8 | 0.26 | -4161.42 | 0.61 | 0.11208 |
| slope-elevation+solar+deciduous+shrub-wetland | 8 | 0.26 | -4161.33 | 0.70 | 0.10715 |
| slope-elevation+solar+water+deciduous+shrub-wetland | 9 | 0.26 | -4160.92 | 1.11 | 0.08729 |
| slope-elevation+deciduous+shrub | 6 | 0.27 | -4160.91 | 1.12 | 0.08685 |
| slope-elevation+solar-gravel_alluvium+deciduous+shrub-wetland | 9 | 0.26 | -4160.88 | 1.15 | 0.08556 |
| slope-elevation+solar+water-gravel_alluvium+deciduous+shrub | 9 | 0.26 | -4160.84 | 1.19 | 0.08387 |
| slope-elevation+solar+scree_talus+deciduous+shrub | 8 | 0.26 | -4160.67 | 1.36 | 0.07703 |
| slope-elevation+solar+water+scree_talus+deciduous+shrub | 9 | 0.26 | -4160.66 | 1.37 | 0.07665 |

Table 2-17. Variable importance (I) and rankings for the variables contained within the top 10 models for predicting total cover of *S. canadensis*. Variable importance is derived by summing the AIC-derived weight of every model containing the variable within a subset of models.

| Variable | I | Rank |
|---|---|---|
| slope | 0.99882 | 2 |
| elevation | 0.99999 | 1 |
| solar | 0.47143 | 6 |
| dist_riparian | 0.32144 | 10 |
| water | 0.40948 | 8 |
| scree_talus | 0.31489 | 11 |
| gravel_alluvium | 0.48151 | 5 |
| disturbed | 0.27861 | 13 |
| spruce forest | 0.36482 | 9 |
| deciduous forest | 0.99840 | 3 |
| shrub | 0.68291 | 4 |
| alpine_grass | 0.31175 | 12 |
| wetland | 0.43732 | 7 |

Table 2-18. Top 10 models to predict presence and absence of *S. canadensis* berries ($n$ = 1551). All possible logistic regressions were run using the nested subsets of the Tasselled Cap, land cover and interaction explanatory variables. The "s" in front of the Tasselled Cap variables signifies summer imagery. Log-likelihoods (LL), AIC and ΔAIC scores and weights are shown for each model. Weights (w) are calculated based on the 10 models presented here. k is the number of parameters estimated for the model and includes the intercept.

| **Model** | k | LL | AIC | ΔAIC | w |
|---|---|---|---|---|---|
| slope-elevation+sgreen_alluvium+sgreen_spruce-sgreen_deciduous-sgreen_alpine | 7 | -166.95 | 347.91 | 0.00 | 0.21676 |
| slope-elevation+sgreen_alluvium+sgreen_spuce-sgreen_deciduous | 6 | -168.17 | 348.33 | 0.43 | 0.17544 |
| slope-elevation-dist_riparian+sgreen_alluvium+sgreen_spruce-sgreen_decduous-sgreen_alpine | 8 | -166.91 | 349.81 | 1.91 | 0.08350 |
| slope-elevation+solar+sgreen_alluvium+sgreen_spruce-sgreen_deciduous-sgreen_alpine | 8 | -166.92 | 349.83 | 1.93 | 0.08296 |
| slope-elevation+sgreen_alluvium+sgreen_spruce-sgreen_deciduous-sgreen_alpine+sgreen_wetland | 8 | -166.93 | 349.85 | 1.95 | 0.08205 |
| slope-elevation+sgreen_alluvium+sgreen_spruce-sgreen_deciduous+sgreen_shrub-sgreen_alpine | 8 | -166.93 | 349.85 | 1.95 | 0.08193 |
| slope-elevation+sgreen_spruce-sgreen_deciduous-sgreen_alpine | 6 | -168.99 | 349.98 | 2.08 | 0.07696 |
| slope-elevation-dist_riparian+sgreen_alluvium+sgreen_spruce-sgreen_deciduous | 7 | -168.11 | 350.22 | 2.32 | 0.06812 |
| slope-elevation+sgreen_alluvium+sgreen_spruce-sgreen_deciduous+sgreen_wetland | 7 | -168.14 | 350.27 | 2.37 | 0.06658 |
| slope-elevation+sgreen_alluvium+sgreen_spruce-sgreen_deciduous+sgreen_shrub | 7 | -168.15 | 350.29 | 2.39 | 0.06575 |

performed better than summer models at explaining variation in berry count data (Table 2-19). Land cover classification models, without standard variables were the highest ranked models. In the fall variable subset, spruce forests were the most influential variable for explaining variation in berry abundance (Table 2-20). Interestingly, in the summer model subset, greenness was the most important variable for explaining variation in berry abundance, and the top ranked model included Tasselled Cap variables and interaction terms.

Variation in *S. canadensis* berry mass was best explained by summer imagery interaction models (Table 2-21). Land cover classification models were the next best set of models, but the $\Delta$AIC for those models was out of the range of support. The interaction term between summer greenness and the deciduous cover class was the most important explanatory variable for variation in *S. canadensis* berry mass (Table 2-22). This covariate was selected against, indicating that deciduous areas with high greenness values were less likely than the reference class to have higher berry biomass. Elevation and slope were the next most important explanatory variables. Greenness by wetlands and distance from riparian area were the least influential variables.

*E. nigrum.--A*s with the other species, models with land cover classes explained variation in *E. nigrum* cover better than other models (Table 2-23). There was also strong support for the top ranking fall models. Summer and all interaction models performed very poorly. Direct solar radiation and elevation were the strongest explanatory variables for variation in *E. nigrum* cover (Table 2-24). Scree and talus and alluvium or gravel cover classes, which were negatively associated with *E. nigrum* cover, were the next most influential explanatory variables. Wetland cover class and distance to riparian areas were the least influential variables.

Presence and absence of *E. nigrum* berries was best differentiated by models with peak summer Tasselled Cap values (Table 2-25). I used that model to look at a set of summer related models. Models that used fall imagery were the next highest ranked, but the $\Delta$AIC between the top fall Tasselled Cap model

Table 2-19. Top models for explaining variation in berry abundance of *S. canadensis* ($n$ = 1551). Count data for berries were regressed against summer and fall Tasselled Cap, land cover class, Tasselled Cap and land cover interaction variables, slope, elevation, solar radiation and distance to water (standard variables) using zero-inflated negative binomial regression. Logistic regression was used to model the probability of berries being present in a plot. The equation used for logistic regression is in brackets beside the season headings. The other models estimate the probability of the count of berries. The "f" in front of the Tasselled Cap variables signifies fall imagery and the "s" signifies summer imagery. Combining the two models in a zero-inflated modeling framework produces a mixture of the probabilities. Log-likelihoods (LL), AIC and ΔAIC scores and weights (w) are shown for each combination of models. Weights were calculated based on all models that were run within the variable set. k is the number of parameters estimated for the model and includes an intercept for the logistic regression equation, an intercept for the count model, and a dispersion parameter ($\alpha$).

**Summer (-slope+elevation-sgreen_alluvium-sgreen_spruce+sgreen_deciduous+sgreen_alpine)**

| Model | k | LL | AIC | ΔAIC | w |
|---|---|---|---|---|---|
| sgreen-swet-sbright+sgreen_alluvium-sgreen_spruce-sgreen_deciduous-sgreen_shrub-sgreen_alpine | 17 | -370.67 | 769.33 | 0.00 | 0.61829 |
| spruce | 10 | -379.11 | 772.22 | 2.90 | 0.14556 |
| -alluvium+spruce+deciduous-shrub+alpine | 14 | -375.13 | 772.26 | 2.94 | 0.14282 |
| spruce+deciduous-shrub+alpine | 13 | -377.46 | 774.91 | 5.59 | 0.03793 |
| water+scree-alluvium-disturbed+spruce+deciduous+shrub+alpine | 17 | -374.43 | 776.85 | 7.53 | 0.01436 |
| sgreen_alluvium-sgreen_spruce-sgreen_deciduous+sgreen_shrub-sgreen_alpine+water+scree-alluvium-disturbed+spruce+deciduous+shrub-alpine | 22 | -369.52 | 777.03 | 7.71 | 0.01314 |
| sgreen_alluvium-sgreen_spruce-sgreen_alpine | 12 | -379.85 | 777.70 | 8.38 | 0.00940 |
| -sgreen_spruce | 10 | -382.27 | 778.53 | 9.21 | 0.00620 |
| -alluvium | 10 | -382.27 | 778.54 | 9.22 | 0.00617 |
| sgreen_alluvium | 10 | -382.27 | 778.54 | 9.22 | 0.00617 |

**Fall (-slope-fwet-fgreen)**

| Model | k | LL | AIC | ΔAIC | w |
|---|---|---|---|---|---|
| spruce | 7 | -375.95 | 765.89 | 0.00 | 0.63691 |
| spruce+deciduous-shrub+alpine | 10 | -374.29 | 768.58 | 2.70 | 0.16579 |
| -alluvium+spruce+deciduous-shrub+alpine | 11 | -373.77 | 769.53 | 3.65 | 0.10319 |
| -fgreen_spruce | 7 | -379.09 | 772.18 | 6.30 | 0.02735 |
| -shrub | 7 | -379.23 | 772.45 | 6.57 | 0.02395 |
| water+scree-alluvium-disturbed+spruce+deciduous+shrub+alpine | 14 | -373.06 | 774.12 | 8.24 | 0.01035 |
| elevation+solar+dist_riparian-fbright | 10 | -376.16 | 774.32 | 8.44 | 0.00937 |
| solar | 7 | -379.30 | 774.60 | 8.72 | 0.00815 |
| fgreen_alluvium-fgreen_spruce-fgreen_deciduous+fgreen_shrub-fgreen_alpine+water+scree-alluvium-disturbed+spruce+deciduous+shrub+alpine | 19 | -368.34 | 774.67 | 8.79 | 0.00787 |
| -slope+elevation-solar-dist_riparian | 10 | -376.44 | 774.87 | 8.99 | 0.00712 |

Table 2-20. Variable importance (I) and rankings for the summer and fall count models for predicting total number of berries for *S. canadensis*. Variable importance is derived by summing the AIC-derived weight of every model containing the variable within a subset of models. The “f” before the Tasselled Cap variables indicates that fall imagery variables were used and an “s” indicates that summer imagery was used.

| ***Summer*** | | | ***Fall*** | | |
|---|---|---|---|---|---|
| **Variable** | I | **Rank** | **Variable** | I | **Rank** |
| slope | 0.00405 | 20 | slope | 0.01265 | 19 |
| elevation | 0.00579 | 18 | elevation | 0.02038 | 12 |
| solar | 0.00666 | 17 | solar | 0.02389 | 11 |
| dist_riparian | 0.00537 | 19 | dist_riparian | 0.01876 | 14 |
| green | 0.64227 | 1 | green | 0.06218 | 6 |
| wet | 0.60490 | 7 | wet | 0.00840 | 20 |
| bright | 0.60278 | 8 | bright | 0.01340 | 17 |
| water | 0.03375 | 16 | water | 0.02449 | 10 |
| scree_talus | 0.03412 | 15 | scree_talus | 0.02722 | 8 |
| gravel_alluvium | 0.17688 | 13 | gravel_alluvium | 0.11943 | 5 |
| disturbed | 0.03414 | 14 | disturbed | 0.02645 | 9 |
| spruce forest | 0.34660 | 9 | spruce forest | 0.85851 | 1 |
| deciduous forest | 0.20624 | 11 | deciduous forest | 0.27051 | 3 |
| shrub | 0.21058 | 10 | shrub | 0.28999 | 2 |
| alpine_grass | 0.20620 | 12 | alpine_grass | 0.27030 | 4 |
| sgreen x gravel_alluvium | 0.62880 | 3 | fgreen x gravel_alluvium | 0.01932 | 13 |
| sgreen x spruce forest | 0.62882 | 2 | fgreen x spruce forest | 0.04057 | 7 |
| sgreen x deciduous forest | 0.61464 | 6 | fgreen x deciduous forest | 0.01270 | 18 |
| sgreen x shrub | 0.61492 | 5 | fgreen x shrub | 0.01406 | 16 |
| sgreen x alpine_grass | 0.62343 | 4 | fgreen x alpine_grass | 0.01776 | 15 |

Table 2-21. Top 10 models predicting *S. canadensis* berry biomass ($n$ = 1551). Box-Cox transformed values ($\lambda$ = -4.4) for total percent cover were regressed against summer and fall Tasselled Cap, land cover class, Tasselled Cap and land cover interaction variables, slope, elevation, solar radiation and distance to water (standard variables). The "f" in front of the Tasselled Cap variables signifies fall imagery and the "s" signifies summer imagery. Root mean square error (RMSE), AIC and ΔAIC scores and weights are shown for each model. Weights (w) are calculated based on the 10 models presented here. k is the number of parameters estimated for the model and includes the intercept and RMSE.

| Model | k | RMSE | AIC | ΔAIC | w |
|---|---|---|---|---|---|
| slope-elevation+sgreen_alluvium+sgreen_spruce-sgreen_deciduous-sgreen_alpine | 8 | 0.02 | -12237.85 | 0.00 | 0.18697 |
| slope-elevation+sgreen_alluvium+sgreen_spruce-sgreen_deciduous | 7 | 0.02 | -12237.44 | 0.41 | 0.15232 |
| slope-elevation+sgreen_spruce-sgreen_deciduous-sgreen_alpine | 7 | 0.02 | -12237.12 | 0.73 | 0.12980 |
| slope-elevation+sgreen_spruce-sgreen_deciduous | 6 | 0.02 | -12236.82 | 1.03 | 0.11172 |
| slope-elevation+sgreen_alluvium+sgreen_spruce-sgreen_deciduous+sgreen_shrub-sgreen_alpine | 9 | 0.02 | -12236.10 | 1.75 | 0.07795 |
| slope-elevation-dist_riparian+sgreen_alluvium+sgreen_spruce-sgreen_deciduous-sgreen_alpine | 9 | 0.02 | -12236.01 | 1.84 | 0.07452 |
| slope-elevation+sgreen_alluvium+sgreen_spruce-sgreen_deciduous-sgreen_alpine+sgreen_wetland | 9 | 0.02 | -12235.93 | 1.92 | 0.07159 |
| slope-elevation+solar+sgreen_alluvium+sgreen_spruce-sgreen_deciduous-sgreen_alpine | 9 | 0.02 | -12235.86 | 1.99 | 0.06913 |
| slope-elevation-dist_riparian+sgreen_alluvium+sgreen_spruce-sgreen_deciduous | 8 | 0.02 | -12235.68 | 2.17 | 0.06318 |
| slope-elevation+sgreen_alluvium+sgreen_spruce-sgreen_deciduous+sgreen_shrub | 8 | 0.02 | -12235.67 | 2.18 | 0.06287 |

Table 2-22. Variable importance (I) and rankings for the variables contained with in the top 10 models for predicting *S. canadensis* berry biomass. Variable importance is derived by summing the AIC-derived weight of every model containing the variable within a subset of models. The “s” before the Tasselled Cap variables indicates that summer imagery variables were used.

| Variable | I | Rank |
|---|---|---|
| slope | 0.99480 | 3 |
| elevation | 0.99630 | 2 |
| solar | 0.28968 | 8 |
| dist_riparian | 0.28084 | 9 |
| sgreen_alluvium | 0.58215 | 5 |
| sgreen_spruce | 0.90274 | 4 |
| sgreen_deciduous | 0.99971 | 1 |
| sgreen_shrub | 0.29570 | 7 |
| sgreen_alpine | 0.54357 | 6 |
| sgreen_wetland | 0.27688 | 10 |

Table 2-23. Top 10 models predicting *E. nigrum* cover ($n$ = 1551). Box-Cox transformed values ($\lambda$ = 0.4) for total percent cover were regressed against summer and fall Tasselled Cap, land cover class, Tasselled Cap and land cover interaction variables, slope, elevation, solar radiation and distance to water (standard variables). Root mean square error (RMSE), AIC and ΔAIC scores and weights are shown for each model. Weights (w) are calculated for the top 10 models in the variable subset. k is the number of parameters estimated for the model. The intercept and RMSE are included in k.

| Model | k | RMSE | AIC | ΔAIC | w |
|---|---|---|---|---|---|
| -elevation-solar+solar$^2$+water+spruce+deciduous+shrub+alpine_grass | 10 | 0.23 | -4575.96 | 0.00 | 0.12445 |
| slope-elevation-solar+solar$^2$+spruce+shrub+alpine_grass-gravel_alluvium-scree_talus | 11 | 0.23 | -4575.92 | 0.04 | 0.12198 |
| slope-elevation-solar+solar$^2$+spruce+deciduous+water+shrub+alpine_grass | 11 | 0.23 | -4575.92 | 0.04 | 0.12198 |
| -elevation-solar+solar$^2$-scree_talus-gravel_alluvium-disturbed-deciduous | 9 | 0.23 | -4575.65 | 0.31 | 0.10658 |
| -elevation-solar+solar$^2$-scree_talus-gravel_alluvium+spruce+shrub+alpine_grass | 10 | 0.23 | -4575.65 | 0.31 | 0.10658 |
| slope-elevation-solar+solar$^2$-scree_talus-gravel_alluvium-disturbed-deciduous | 10 | 0.23 | -4575.32 | 0.64 | 0.09037 |
| slope-elevation-solar+solar$^2$-scree_talus-gravel_alluvium-deciduous+alpine_grass | 10 | 0.23 | -4575.23 | 0.73 | 0.08639 |
| slope-elevation-solar+solar$^2$-scree_talus-gravel_alluvium+spruce+alpine_grass | 10 | 0.23 | -4575.14 | 0.82 | 0.08259 |
| slope-elevation-solar+solar$^2$-scree_talus-gravel_alluvium-deciduous | 9 | 0.23 | -4575.10 | 0.86 | 0.08096 |
| slope-elevation-solar+solar$^2$-scree_talus-gravel_alluvium-disturbed-deciduous+alpine_grass | 11 | 0.23 | -4575.03 | 0.93 | 0.07817 |

Table 2-24. Variable importance (I) and rankings for the variables contained with in the top 10 models for predicting total cover of *E. nigrum*. Variable importance is derived by summing the AIC-derived weight of every model containing the variable within a subset of models.

| Variable | I | Rank |
|---|---|---|
| slope | 0.61082 | 6 |
| elevation | 0.95769 | 2 |
| solar | 0.96849 | 1 |
| dist_riparian | 0.27236 | 13 |
| water | 0.36185 | 11 |
| scree_talus | 0.81789 | 3 |
| gravel_alluvium | 0.76100 | 4 |
| disturbed | 0.40921 | 10 |
| spruce forest | 0.60318 | 7 |
| deciduous forest | 0.55642 | 8 |
| shrub | 0.53712 | 9 |
| alpine_grass | 0.68604 | 5 |
| wetland | 0.30059 | 12 |

Table 2-25. Top 10 models to predict presence and absence of *E. nigrum* berries ($n$ = 1551). All possible logistic regressions were run using the nested subsets of the Tasselled Cap, land cover and interaction explanatory variables. The "s" in front of the Tasselled Cap variables signifies summer imagery. Log-likelihoods (LL), AIC and ΔAIC scores and weights are shown for each model. Weights (w) are calculated based on the 10 models presented here. k is the number of parameters estimated for the model and includes the intercept.

| Model | k | LL | AIC | ΔAIC | w |
|---|---|---|---|---|---|
| slope+sgreen-sbright | 4 | -235.93 | 479.85 | 0.00 | 0.19527 |
| -solar+sgreen-sbright | 4 | -236.41 | 480.81 | 0.96 | 0.12101 |
| slope-dist_riparian+sgreen-sbright | 5 | -235.48 | 480.96 | 1.11 | 0.11215 |
| slope-solar+sgreen-sbright | 5 | -235.52 | 481.03 | 1.19 | 0.10813 |
| slope+sgreen+swet-sbright | 5 | -235.53 | 481.06 | 1.22 | 0.10642 |
| -solar-dist_riparian+sgreen-sbright | 5 | -235.71 | 481.41 | 1.56 | 0.08951 |
| slope+elevation+sgreen-sbright | 5 | -235.89 | 481.77 | 1.92 | 0.07492 |
| slope-solar-dist_riparian+sgreen-sbright | 6 | -234.89 | 481.77 | 1.92 | 0.07477 |
| -solar+sgreen+swet-sbright | 5 | -236.10 | 482.19 | 2.34 | 0.06070 |
| elevation-solar+sgreen-sbright | 5 | -236.16 | 482.31 | 2.46 | 0.05716 |

and the top model was substantial (> 10), indicating that there was no support for these models. Similar to the count models for overall berry abundance, the regressors for the best summer and fall count model were slope, elevation, distance to riparian area and solar radiation (Table 2-26). The summer count models were better than the fall models. There was no support for models containing land cover classes. Tasselled Cap variables ranked higher than land cover class variables for variable influence, as did interaction variables (Table 2-27). Standard variables were the most important explanatory variables across summer and fall models.

Variation in *E. nigrum* berry biomass was best explained by the summer Tasselled Cap models (Table 2-28). Fall Tasselled Cap models were the next best set of models, with only moderate support. All other model subsets had little support. Variation in berry biomass was best explained by summer wetness values, followed by brightness and then wetness (Table 2-29). Elevation and distance to riparian area were least influential for explaining variation in berry biomass for this species.

## DISCUSSION

Areas in this study that were not intensively sampled for forage availability had a low expected frequency of use by bears. Information from telemetry data collected in the study area showed that bears were seldom found above 1900 m elevation and only 11% of relocations were on slopes greater than 35 degrees (McCann 1997). Previous research in the Kluane Region has also shown that forage availability is poor in very high elevation or steep areas, and areas of predominantly rock and ice cover (McCormick 1999). Therefore, inclusion of such areas in my analyses was unwarranted. These areas also had very low greenness values, consistent with my findings that greenness and bear forage abundance were positively correlated.

Table 2-26. Top models for explaining *E. nigrum* berry abundance ($n$ = 1551). Count data for berries were regressed against summer and fall Tasselled Cap, land cover class, Tasselled Cap and land cover interaction variables, slope, elevation, solar radiation and distance to water (standard variables) using zero-inflated negative binomial regression. Logistic regression was used to model the probability of berries being present in a plot. The equation used for logistic regression is in brackets beside the season headings. The other models estimate the probability of the count of berries. The "f" in front of the Tasselled Cap variables signifies fall imagery and the "s" signifies summer imagery. Combining the two models in a zero-inflated modeling framework produces a mixture of the probabilities. Log-likelihoods (LL), AIC and ΔAIC scores and weights (w) are shown for each combination of models. Weights were calculated based on all models that were run within the variable set. k is the number of parameters estimated for the model and includes an intercept for the logistic regression equation, an intercept for the count model, and a dispersion parameter ($\alpha$).

***Summer (-slope-sgreen+sbright)***

| **Model** | k | LL | AIC | ΔAIC | w |
|---|---|---|---|---|---|
| -slope+elevation-solar+solar$^2$+dist_riparian | 11 | -546.98 | 1115.95 | 0.00 | 0.62575 |
| -slope+elevation-solar+solar$^2$-dist_riparian+sgreen+swet+sbright | 14 | -545.16 | 1118.32 | 2.38 | 0.19077 |
| elevation | 7 | -553.06 | 1120.12 | 4.17 | 0.07780 |
| elevation+solar-solar$^2$+dist_riparian-sbright | 11 | -549.10 | 1120.21 | 4.26 | 0.07442 |
| sbright | 7 | -555.03 | 1124.05 | 8.11 | 0.01088 |
| -swet | 7 | -555.23 | 1124.46 | 8.52 | 0.00888 |
| solar-solar$^2$ | 8 | -555.09 | 1126.18 | 10.24 | 0.00375 |
| sgreen_alpine | 7 | -556.45 | 1126.90 | 10.95 | 0.00263 |
| sgreen | 7 | -556.46 | 1126.91 | 10.97 | 0.00260 |
| sgreen-swet+sbright | 9 | -554.48 | 1126.95 | 11.01 | 0.00256 |

***Fall (-slope+elevation+fwet-fgreen+fbright+dist_riparian)***

| **Model** | k | LL | AIC | ΔAIC | w |
|---|---|---|---|---|---|
| -slope+elevation-solarsolar$^2$+dist_riparian | 14 | -551.66 | 1125.31 | 0.00 | 0.68427 |
| elevation+solar-solar$^2$+dist_riparian-fbright | 14 | -553.38 | 1128.76 | 3.45 | 0.12196 |
| elevation | 10 | -557.88 | 1129.76 | 4.46 | 0.07388 |
| slope+elevation+solar-solar$^2$+dist_riparian-fgreen+fwet+fbright | 17 | -550.97 | 1129.94 | 4.63 | 0.06780 |
| -fwet | 10 | -559.34 | 1132.68 | 7.37 | 0.01720 |
| fbright | 10 | -559.58 | 1133.15 | 7.84 | 0.01362 |
| fgreen | 10 | -560.22 | 1134.44 | 9.13 | 0.00715 |
| fgreen-fwet-fbright | 12 | -558.55 | 1135.10 | 9.79 | 0.00514 |
| slope+fgreen-fwet | 12 | -558.62 | 1135.23 | 9.93 | 0.00480 |
| fgreen_alluvium+fgreen_spruce+fgreen_deciduous+fgreen_shrub+ fgreen_alpine | 14 | -556.75 | 1135.49 | 10.18 | 0.00422 |

Table 2-27. Variable importance (I) and rankings for the summer and fall count models for predicting total number of berries for *E. nigrum*. Variable importance is derived by summing the AIC-derived weight of every model containing the variable within a subset of models. The "f" before the Tasselled Cap variables indicates that fall imagery variables were used and an "s" indicates that summer imagery was used.

| ***Summer*** | | | ***Fall*** | | |
|---|---|---|---|---|---|
| **Variable** | **I** | **Rank** | **Variable** | **I** | **Rank** |
| slope | 0.80114 | 4 | slope | 0.73699 | 4 |
| elevation | 0.94760 | 1 | elevation | 0.92206 | 1 |
| solar | 0.87517 | 2 | solar | 0.85370 | 2 |
| dist_riparian | 0.87273 | 3 | dist_riparian | 0.85151 | 3 |
| green | 0.20367 | 6 | green | 0.09922 | 6 |
| wet | 0.20077 | 7 | wet | 0.09608 | 7 |
| bright | 0.27372 | 5 | bright | 0.20614 | 5 |
| water | 0.00174 | 17 | water | 0.00173 | 17 |
| scree_talus | 0.00359 | 13 | scree_talus | 0.00319 | 13 |
| gravel_alluvium | 0.00156 | 18 | gravel_alluvium | 0.00168 | 19 |
| disturbed | 0.00203 | 16 | disturbed | 0.00194 | 16 |
| spruce forest | 0.00269 | 14 | spruce forest | 0.00291 | 14 |
| deciduous forest | 0.00149 | 20 | deciduous forest | 0.00165 | 20 |
| shrub | 0.00153 | 19 | shrub | 0.00170 | 18 |
| alpine_grass | 0.00267 | 15 | alpine_grass | 0.00259 | 15 |
| sgreen x gravel_alluvium | 0.00427 | 11 | fgreen x gravel_alluvium | 0.00886 | 11 |
| sgreen x spruce forest | 0.00421 | 12 | fgreen x spruce forest | 0.00884 | 12 |
| sgreen x deciduous forest | 0.00484 | 10 | fgreen x deciduous forest | 0.00992 | 9 |
| sgreen x shrub | 0.00496 | 9 | fgreen x shrub | 0.00990 | 10 |
| sgreen x alpine_grass | 0.00617 | 8 | fgreen x alpine_grass | 0.01146 | 8 |

Table 2-28. Top 10 models predicting *E. nigrum* berry biomass ($n$ = 1551). Box-Cox transformed values ($\lambda$ = -4.4) for total percent cover were regressed against summer and fall Tasselled Cap, land cover class, Tasselled Cap and land cover interaction variables, slope, elevation, solar radiation and distance to water (standard variables). The "s" in front of the Tasselled Cap variables signifies summer imagery. Root mean square error (RMSE), AIC and ΔAIC scores and weights are shown for each model. Weights (w) are calculated based on the 10 models presented here. k is the number of parameters estimated for the model and includes the intercept and RMSE.

| **Model** | **k** | **RMSE** | **AIC** | **ΔAIC** | **w** |
|---|---|---|---|---|---|
| slope-solar+swet+sgreen-sbright | 7 | 0.04 | -10689.96 | 0.00 | 0.18233 |
| -solar+solar$^2$+swet+sgreen-sbright | 7 | 0.04 | -10689.04 | 0.92 | 0.11510 |
| slope-solar+swet-sbright | 6 | 0.04 | -10688.76 | 1.20 | 0.10006 |
| -solar+swet+sgreen-sbright | 6 | 0.04 | -10688.71 | 1.25 | 0.09759 |
| slope-solar+swet+sgreen | 6 | 0.04 | -10688.64 | 1.32 | 0.09424 |
| slope-solar-dist_riparian+swet+sgreen-sbright | 8 | 0.04 | -10688.56 | 1.40 | 0.09054 |
| -solar+swet+sgreen | 5 | 0.04 | -10688.50 | 1.46 | 0.08787 |
| slope+elevation+swet+sgreen-sbright-solar | 8 | 0.04 | -10688.31 | 1.65 | 0.07990 |
| slope-solar+solar$^2$+swet+sgreen-sbright | 8 | 0.04 | -10688.24 | 1.72 | 0.07716 |
| slope+swet-sbright | 5 | 0.04 | -10688.19 | 1.77 | 0.07525 |

Table 2-29. Variable importance (I) and rankings for the variables contained with in the top 10 models for predicting *E. nigrum* berry biomass. Variable importance is derived by summing the AIC-derived weight of every model containing the variable within a subset of models. The "s" before the Tasselled Cap variables indicates that summer imagery variables were used.

| Variable | I | Rank |
|---|---|---|
| slope | 0.62428 | 5 |
| elevation | 0.33969 | 6 |
| solar | 0.63498 | 4 |
| dist_riparian | 0.32717 | 7 |
| swet | 0.96411 | 1 |
| sgreen | 0.72254 | 3 |
| sbright | 0.75325 | 2 |

Traditional grizzly bear habitat mapping techniques predict assemblages of preferred forage species associated with specific land cover classes, and then index the cover classes according to seasonal forage value (Kansas and Riddell 1995, McCormick 1999). Land cover classes have been demonstrated as important for predicting forage occurrence in other regions of North America (Mattson and Despain 1985, Mattson et al. 1998, Nielsen et al. 2003). However, previous studies did not predict forage abundance, only the presence of forage species, and, they did not evaluate Tasselled Cap variables as potential predictors (Nielsen et al. 2003). I compared the utility of Tasselled Cap variables and land cover classes in predicting bear food abundance. Land cover classes were better than Tasselled Cap variables for predicting the percent cover of individual forage species. However, where the abundance of forage was measured for individual species by the number or weight of berries, Tasselled Cap, or greenness and cover class interaction variables, out-performed the land cover classification. Tasselled Cap variables were also better explanatory variables than land cover classes for all measures of aggregate forage species abundance. Though stratifying land cover classes by greenness might improve resolution for predicting forage abundance, there was little support for models that considered an interaction between cover class and greenness.

There are two probable reasons why Tasselled Cap variables performed better than land cover classes. First, bear foods are associated with many cover classes. *S. canadensis*, for instance, can be found in alluvium, shrub and spruce cover classes (Viereck and Little 1972) and *H. alpinum* can occur in spruce, alpine and shrub habitats (Densmore and Holmes 1987). Land cover classes may predict individual forage species occurrence, but no cover class relates well to aggregate forage availability. Habitat models in which bears select specific cover classes reflect the influence of an individual forage species on bear distribution, rather than overall forage abundance. Second, the Tasselled Cap Transformation for Landsat imagery provides a more heterogeneous and detailed representation of forage distribution than possible with conventional land cover classification. For 8-bit data, 256 values (or more values for 16-bit and 32-bit data) are assigned on a continuous scale to the pixels comprising a satellite image. Land cover data is nominal and cover classes are typically coded as dummy variables for regression modeling. A regression model built with 256 cover classes would likely have high parameter uncertainty, and cover classes would need to be aggregated to reduce the number of variables in the model. By aggregating cover classes, fine scale information on vegetation is lost and data become more generalized. Hence, where an adjacent group of pixels might be represented as spruce forest by a land cover classification, the Tasselled Cap Transformation may reveal that a few pixels within the group have more phytomass than their neighbours.

Tasselled Cap variables provide more direct information than land cover classes on the mechanisms that relate leaf area (greenness) to production of roots, flowers and berries. The relationship between root volume and photosynthetic biomass is complex (Reich et al. 1998), but the two have a general positive correlation (Davies and Zhang 1991). Increased nutrient availability promotes simultaneous leaf and root growth (Davies and Zhang 1991, Ericsson 1995). Land cover classes typically do not provide information on plant vigour, especially as it varies across years. Leaf area and flower or berry production does not always have a general positive correlation because some plant species invest in sexual reproduction only when extra resources are available, whereas others vary vegetative growth but maintain relatively constant sexual reproductive effort (Pitelka et al. 1980). In the latter circumstance, land cover classes may be useful for predicting berry abundance; however, for the former case, Tasselled Cap data can provide insight into water and nutrient availability at a relatively fine scale. Land cover classes often only provide relatively broad scale information on nutrient and moisture availability.

I detected a relationship of bear food abundance measured in 2000, 2001, and 2002 to satellite images recorded in 1996, indicating robustness in the relationship. However, phenological changes between fall and summer produced substantial differences in the explanatory power of Tasselled Cap Transformation variables. Summer Tasselled Cap variables best predicted the total cover of bear foods. In the summer images plants are leafed out to their maximum and greenness is directly measuring the total forage cover. Fall Tasselled Cap variables were the best explanatory variables for total berry abundance and biomass, indicating that berry production may be strongly tied to soil characteristics. Plants need water, minerals, and nitrogen from soil, in addition to light and carbon dioxide, to grow. In combining these elements, plants produce a number of hormones (e.g., auxin, gibberellins, and cytokinins) that regulate flower production and fruiting. The ability of a plant to utilize available light and carbon dioxide is tied to leaf area, while the availability of water, minerals and nitrogen is associated with the substrate. Soils that are rich in nitrogen and minerals tend to be darker or more textured and have low brightness values (Zheng and Schreier 1988). For many forage species the availability of water, minerals and nitrogen may be more limiting for flower or fruit production than the availability of light and carbon dioxide. Differences in soil texture, represented by brightness, were more apparent in fall images.

For models that used Tasselled Cap variables from fall images, brightness was a better predictor of forage availability than greenness. During peak summer, greenness signatures vary widely across the landscape. When plants fully leaf-out, the reflectance from the soils below the leaf area is minimized. As plants senesce, the chlorophyll breaks down and the variation in greenness diminishes (Crist and Kauth 1986). Leaves also lose water, but as plants senesce, they shrivel and expose the soil below – which may or may not contain moisture (Jensen 1996). The signature for wetness becomes somewhat ambiguous. As signatures for greenness and wetness diminish and become homogenous, brightness becomes the predominant signature across the landscape and hence the most important predictor of forage productivity.

While Tasselled Cap data is better than land cover classifications for explaining variation in grizzly bear forage abundance, land cover classifications may still have utility in describing other aspects of grizzly bear life history. Moose, a food source for bears during the calving season, for instance, may be closely associated with wetlands, sub-alpine regions or closed canopy riparian areas (Geist and Francis 1999). Ants and other insects can comprise a significant portion of the bear diet, but are not necessarily associated with lush vegetation. There are other cautions when using Tasselled Cap Transformation variables for habitat modeling. Land cover classifications may be easier to use than Tasselled Cap variables for investigating the relationship between landscape pattern and bear habitat use. For example, in examining the influence of inter-patch distances on bear distribution one needs to be able to define a "patch" (e.g., Linke 2003). A continuous variable like greenness does not lend well to patch definition. Also, Beck et al. (1990) discuss problems in applying greenness measures globally, noting that the correlation between greenness and the amount of biomass can be affected by plant structure and significant accumulation of senescent plant material (such as in grasslands, and akin to some alpine and coastal graminoid vegetation types). In some ecosystems, such as coastal environments, greenness may be saturated. That is, increasing phytomass would not increase the greenness because values are as high as they can be, and additional leaves are not exposed to the sensor (Hales et al. 2004).

Using measures of aggregate forage abundance for appraisal, Tasselled Cap layers were better explanatory variables than land cover classes; however, use of aggregate measures obfuscates seasonal patterns of forage availability. Seasonal nuances of forage availability affect distribution patterns of bears (e.g., Waller and Mace 1997, Theberge 2002, Nielsen et al. 2003). By considering aggregate measures of forage availability, equal importance is given to all forage species, and there is presumed equal availability to and selection by bears. Yet, fecal analysis shows that bears in Kluane strongly select for only a few forage species variant on the time within the active period (McCann 1998).

Optimally, forage abundance should be represented directly (Nielsen et al. 2003). Maps representing forage availability might be generated using land cover classifications, as land cover classes were better explanatory variables for individual forage species distribution by percent cover. Slope, elevation, distances from hydrological features, and solar radiation were consistently comparable or better than Tasselled Cap or land cover variables for explaining the distribution of forage on the landscape. Land cover classes, combined with these standard variables may be used to develop predicted probability distributions of the primary forage species, weighted by their seasonal importance in diet. Probability maps for primary forage species are easier to relate to bear ecology than proxy variables for forage availability such as land cover classes and Tasselled Cap data. Tasselled Cap layers may then be reserved for use in areas where there is little or no information that may lead to development of predictive models based on primary forage species distribution.

A final consideration with use of Tasselled Cap data is that the generic application of these indices, to date, has not allowed for comparability of patterns of grizzly bear habitat selection among study areas. Coefficients used for derivation of Tasselled Cap layers are specific to the satellite sensor and to whether the values of the image being transformed are digital numbers, radiance or reflectance (Huang et al. 2001, Huang et al. 2002). Steps to pre-processes images are often not described in habitat studies. Without such information one may not know if the correct coefficients have been applied and whether the output values from the Tasselled Cap analysis are relative or absolute. Products where raw digital numbers are converted to surface radiance, and radiance data are then converted to reflectance improves inter-scene comparability by removing illumination effects (Lillesand and Kiefer 2000).

## CONCLUSIONS

When selecting variables for modeling habitats, researchers try to relate the life history requirements of an organism to environmental variables that have adaptive significance (Heglund 2002). Land cover classifications are often used as proxies for forage abundance. However, the relationship of total forage abundance to a specific cover class is complex. While researchers have tried to ascribe forage values to cover classes, these models typically do not predict bear distribution very well (Nielsen et al. 2003). General descriptors such as land cover class may only represent correlative factors for species occurrence. If correlative factors only moderately relate to causative factors, the predictive utility of the variable is less than ideal.

The Tasselled Cap Transformation offers an interesting approach for habitat modeling, where the link between forage availability and habitat use can be explicitly interpreted. Greenness directly provides information about percent cover of photosynthesizing biomass, including forage species. In addition the Tasselled Cap data represent overall vegetative bear food abundance better than land cover classes because they relay information on forage production such as the ability of plants in an area to photosynthesize, and acquire water, minerals and nitrogen – elements essential for flower and berry production.

Though Tasselled Cap data are better than land cover data for representing overall forage abundance, the limitations of such data are important to consider when developing explanatory models for bear habitat use. For instance, the choice of which Tasselled Cap variables to use and the timing of a satellite image can have a significant effect on the explanatory strength of habitat models. Researchers typically use only greenness to model bear habitat relationships, regardless of the time of year that their images represent. Notably, in mountainous regions it may be difficult to obtain a seasonal cross-section of cloud-free images during the period when bears are active. For researchers who cannot explore the relationship between imagery timing and bear habitat relationships, I recommend that all three Tasselled Cap variables be considered for modeling bear habitat.

# Chapter Three: Effects of conspecifics on habitat selection by grizzly bears in the southwest Yukon, Canada

## INTRODUCTION

Sexual segregation, conventionally defined as the differential use of space (and often habitat and forage) by the sexes outside of the mating season (Bowyer and Kie 2004), is a phenomenon that occurs across many mammalian species (Wielgus and Bunnell 1995, Bleich et al. 1997, Conradt et al. 2001, Lin and Batzli 2001). Despite its prevalence, sexual segregation in carnivore species such as grizzly bears (*Ursus arctos* L.), has received little attention. Given the importance of habitat models for bear conservation and the influence sexual segregation may have on habitat use, understanding mechanisms of segregation in grizzly bears is non-trivial. For instance, if habitat models generalize use across sexes, but human activities alter habitats that are particularly important to females, impacts to cub productivity maybe underestimated.

Numerous hypotheses have been proposed to explain sexual segregation in mammals (Bleich et al. 1997, Ruckstuhl and Neuhaus 2005); however, only two are relevant for solitary, sexually dimorphic species like grizzly bears. For bears, sexual segregation may be driven by: 1) physiological differences in nutritional requirements, and/or 2) size and reproductive status-related needs to avoid predation or conspecific aggression (Weilgus and Bunnell 1995, Bleich et al. 1997, Ruckstuhl and Neuhaus 2005). These hypotheses are premised on the principle that individual fitness increases through segregation (e.g., Morgantini and Hudson 1981, Bleich et al. 1997), and recognize that male grizzly bears are larger than females. The hypotheses are not mutually-exclusive.

Nutrition-related segregation may have evolved to increase the reproductive success (number of fertilized ova, number of young born, or number of cubs surviving to disperse) of individuals. For instance, superior adipose tissue reserves in females may enhance the likelihood of blastocyst implantation (Rogers 1976, Ramsay and Stirling 1988, Tsubota et al. 1990, Samson and Hout

1995, Harlow et al. 2002). The amount of adipose tissue is also linked to the quantity and quality of milk for nursing cubs, and hence, cub growth and survival (Atkinson and Ramsay 1995, Samson and Huot 1995). Therefore, females might select foods that maximize accumulation of adipose tissue reserves. On the other hand, males confer a reproductive advantage by being socially dominant (Zuckerman 1932, Kodric-Brown and Brown 1984, Dewsbury 1982, Bellemain et al. 2006), and social dominance is correlated with body size or lean muscle mass (Kovach and Powell 2003). Muscle mass is most efficiently accreted by consumption of meat (McNab 1963, Hilderbrand et al. 1999). Meat protein may also enable male bears to meet the power requirements of large muscle mass (Muñoz-Garcia and Williams 2005). Consequently, males, more than females, may prefer habitats where proteinaceous foods are abundant (Mattson 2000). Segregation of males and females into protein-rich and fat-rich habitat types, respectively, would be pronounced when feeding activity intensified during hyperphagia.

In northern interior areas, such as the Kluane Region in southwest Yukon, Canada (Figure 3-1), sporophytes (e.g., *Equisetum arvense*), ants (e.g., *Myrmica* spp.), salmon (*Onchyrinkus* spp.), moose (*Alces alces*), and ground squirrels (*Spermophilus parryii plesius*) provide some fat and/or protein, but none of these foods are abundant. Instead, bears must rely on fat- and protein-poor over-wintered and ripe berries as a major food source. Bears that are primarily frugivorous have to consume excess fruit relative to their energy needs to meet minimum-protein requirements, and though inefficient, they may be able to convert the excess energy to fat (Rode et al. 2001). If males and females can meet their physiological needs by feeding on berries, and there is a scarcity of other food sources, habitat selection would converge; both sexes would select for areas with high berry productivity.

Alternative to nutrition-based hypotheses, sexual segregation may be a response to resource competition or avoidance of energetically costly aggressive encounters (Berger 1991, Bleich et al. 1997, Lin and Batzil 2001). Those that obtain the best habitats are often the larger individuals of the species or those

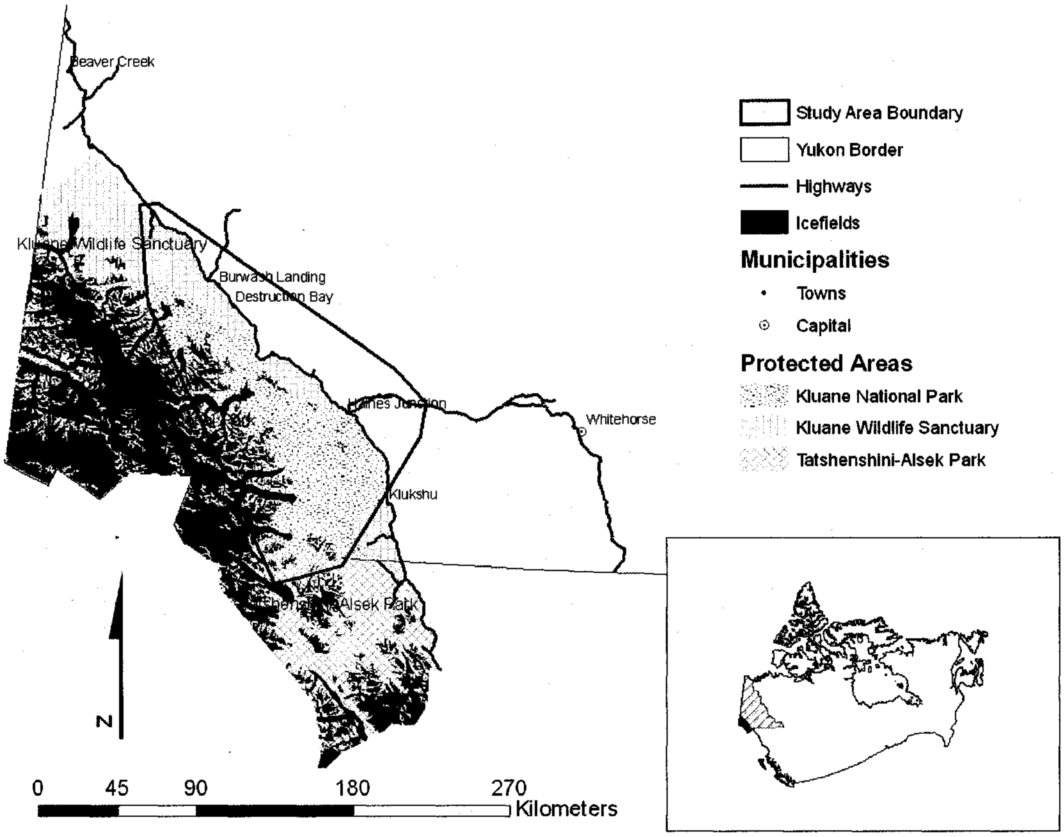

Figure 3-1. The study area in the Kluane Region, southwest Yukon Territory, Canada for modeling bear habitat relationships.

individuals not caring for young (Hrdy and Haufater 1984, Berger 1991). Weaker or encumbered individuals – often females with young or subadults – are relegated to marginal habitats (Appleby 1980). These individuals might maximize energy gains by selecting for the best habitats with the lowest probability of encountering dominant individuals (Cowlishaw 1997, Kie 1999, Barten et al. 2001, Ben-David et al. 2004).

Sexual segregation also may be a response to sexually selected infanticide pressures. Male grizzly bears, like males of other ursids (Hansson and Thomassen 1983, Larsen 1985, Taylor et al. 1985, Derocher and Wiig 1999), will kill and eat dependent cubs (Wielgus and Bunnell 1995, Swenson et al. 1997, Wielgus and Bunnell 2000). In the southwest Yukon there is high human-caused bear mortality adjacent to Kluane National Park and Reserve (KNPR; Yukon Territorial Government 2003) and the resulting mortality sink (McCann 1998) may act as a conduit for non-sire males (or females) to influx into the area (Hessing 1994, Weilgus and Bunnell 2000). If non-sire males are more likely than sire males to kill cubs (Swenson et al. 1997), and there is an influx of non-sire males into the region, females with cubs may respond to infanticide pressures by selecting habitats to minimize interactions with males. If competition or infanticide promotes sexual segregation, differences in habitat use would be most pronounced after den emergence. Cubs are small and family groups have poor mobility. In the spring, subadults are also small relative to adults, and if size is a factor relating to dominance, they are less competitive.

Effects of nutritional needs or avoidance of conspecifics on habitat selection may be obfuscated by the effects of human activity. Depending on the type, intensity and timing of human activity, and on the wariness of the bear, they will avoid areas (Mace et al. 1996, Gibeau et al. 2002, Graves 2002) where human activities are not predictable (Nadeau 1987, Bader 1989, Olson and Gilbert 1994). Bears often avoid locations where human activities are common, such as roads, by a sufficient distance so they will not be disturbed (Mattson et al.1987, McLellan and Shackleton 1988, McLellan 1990). Bears can become conditioned to predictable human activities, and may use areas close to development (Archibald et al. 1987, Bader 1989). Family groups will sometimes use habitats near human developments because these areas offer security from other bears (McLellan and Shackleton 1988).

Researchers who have investigated sexual segregation in grizzly bears most commonly used radio-tracking data (Millspaugh et al. 1998) only to describe differences in habitat use among sex/age cohorts (e.g., Wielgus and Bunnell 1995, McLoughlin et al. 2002, Nielsen et al. 2002). While these studies speculate on the causes of sexual segregation, they often do not directly explore the mechanisms for differential habitat use. Mechanisms might be better elucidated than by simply describing differences in habitat selection if 1) variables used in habitat modeling were chosen specifically to test hypothesized causes of sexual selection, and 2) the relative importance of these variables in driving habitat selection was considered for each sex/age cohort.

I investigated sexual segregation for grizzlies in the Kluane Region by developing a set of seasonal explanatory models for bear occupancy that incorporated conspecific distributions as an independent variable. When sexual segregation results in one demographic group having better access to resources than another group, individuals with the advantage can be said to have a higher status (Morse 1974). To investigate the relative influence of one or more cohorts on the occurrence of other individuals I included the distribution of higher status groups as a covariate in the models for lower status groups. I assumed that adult males were the most dominant status group, and most likely to influence the distribution of other individuals in the population (Weilgus and Bunnell 2000, Gende and Quinn 2004). Lone adult females were assumed to be the next highest status group and, along with adult males, likely to influence family group and subadult distribution. Family groups also were assumed to affect the distribution of subadults (Hornocker 1962, McCullough 1981, Stringham 1983, McLoughlin et al. 2002). Subadults were assumed to be the lowest status group and were not likely to have much general influence on other individuals in the population.

The importance of conspecific distribution on habitat use by lower status individuals was examined relative to the importance of the forage productivity and human activity variables. Considering full models for the distribution of each cohort during phenological periods, I predicted that: 1) if differential food requirements primarily drive habitat selection, variables relating to forage productivity and quality should be the most important drivers of distribution of grizzly bear cohorts. Unlike some ecosystems, fat-rich and protein-rich food resources are not widely available in Kluane; therefore, all cohorts should select for areas with similar forage species; and 2) if competition or infanticide risk primarily drives habitat segregation of cohorts, the distribution of higher status groups and/or the distribution of secure habitat should strongly influence the distribution of lower status groups. Family groups and subadults, though preferring similar foraging areas as lone adults, would use habitats that had a low risk of interaction with higher status cohorts. The effects of human activity can mask the effects of nutritional or avoidance-based segregation on habitat selection (Mattson et al. 1987). If the intensity of human activity was too high for bears to tolerate, they may have occupied areas remote from roads and other developments. I anticipated that the relatively mobile lone adults occupied areas closer to developments than family groups.

## METHODS

### Grizzly Bear Use Data and Study Area

Between 1989 and 2004, 68 individuals (30 males, 38 females; Table 3-1) were captured using either aerial darting or culvert traps, and were fitted with VHF, satellite or GPS collars. Radio-relocations (VHF) were obtained for all bears; however, because of the differences in bias associated with relocations, I excluded satellite and GPS collar data from these analyses. Of the 68 individuals captured, 64 were initially captured within KNPR, two were initially captured in the Kluane Wildlife Sanctuary, and two were initially captured at the Haines Junction landfill.

Collared bears were monitored once per week or as often as weather permitted using fixed-wing aircraft. Aerial VHF relocations totalled 3941 and ranged between 26 relocations and 593 relocations in any year. During aerial relocations the bear number, collar frequency, date, time, and habitat type were recorded. Flying schedules were strongly influenced by the tendency for winds to increase in velocity during the day, and by the availability of aircraft and local weather forecasts. Consequently, the temporal distribution of relocations is strongly biased towards mid-day with 75% of all relocations obtained between 1100 and 1600 hours. I used a 100% minimum convex polygon (MCP) for all grizzly bear aerial telemetry locations (McCann 1998) to establish a study area

Table 3-1. Identification, gender (M = male, F = female), age at collaring, multi-annual 100% minimum convex polygon home range size (km$^2$), year the bear was collared, and year the bear exited the study. Between 1989 and 2004, 68 individuals (30 males, 38 females) were captured and collared.

| Bear ID | Gender | Age at collaring | MCP (km$^2$) | Year collared | Exit year |
|---|---|---|---|---|---|
| KNP01 | M | unknown-adult | 1482 | 1989 | 1991 |
| KNP02 | M | 17 | 6 | 1989 | 1989 |
| KNP03 | M | unknown-adult | 341 | 1989 | 1990 |
| KNP04 | F | 9 | 231 | 1989 | 1993 |
| KNP05 | F | 6 | 605 | 1991 | 1991 |
| KNP06 | F | 11 | 383 | 1991 | 1998 |
| KNP07 | M | 5 | 1330 | 1991 | 1992 |
| KNP08 | M | 16 | 61 | 1991 | 1991 |
| KNP09 | M | 22 | 1747 | 1991 | 1995 |
| KNP10 | M | 8 | 940 | 1991 | 1992 |
| KNP11 | F | 4 | 310 | 1991 | 1998 |
| KNP12 | F | 19 | 457 | 1989 | 1992 |
| KNP14 | F | 9 | 99 | 1991 | 1992 |
| KNP15 | F | 10 | 2 | 1991 | 1992 |
| KNP16 | M | 3 | 631 | 1992 | 1993 |
| KNP17 | F | 11 | 84 | 1992 | 1992 |
| KNP18 | F | 6 | 197 | 1992 | 2003 |
| KNP19 | M | 15 | 1385 | 1992 | 1995 |
| KNP20 | M | 14 | 1346 | 1992 | 1993 |
| KNP21 | F | 13 | 154 | 1992 | 1993 |
| KNP23 | F | 12 | 216 | 1992 | 1994 |
| KNP24 | F | 9 | 236 | 1992 | 1997 |
| KNP25 | F | 3 | 52 | 1992 | 1993 |
| KNP26 | M | 15 | 833 | 1992 | 1993 |
| KNP27 | F | 5 | 174 | 1992 | 2003 |
| KNP28 | M | 3 | 260 | 1992 | 1993 |
| KNP29 | M | 10 | 602 | 1992 | 1994 |
| KNP30 | M | 3 | 445 | 1992 | 1993 |
| KNP31 | M | 8 | 392 | 1992 | 1995 |
| KNP32 | F | 5 | 564 | 1992 | 1999 |
| KNP33 | F | 14 | 277 | 1992 | 1994 |
| KNP34 | M | 10 | 932 | 1992 | 1997 |
| KNP35 | M | 6 | 478 | 1992 | 1993 |
| KNP36 | F | 10 | 1667 | 1992 | 2000 |
| KNP37 | M | 3 | 0 | 1992 | 1993 |
| KNP38 | F | 3 | 707 | 1993 | 2003 |
| KNP39 | F | 3 | 199 | 1993 | 1995 |
| KNP40 | M | 6 | 2843 | 1993 | 1997 |
| KNP41 | M | 19 | 522 | 1993 | 1995 |
| KNP42 | F | 15 | 223 | 1993 | 1997 |
| KNP43 | F | 17 | 161 | 1993 | 1997 |
| KNP44 | F | 23 | 232 | 1993 | 1998 |
| KNP45 | F | 13 | 238 | 1993 | 1997 |
| KNP46 | F | 11 | 228 | 1993 | 1995 |
| KNP47 | F | 4 | 255 | 1993 | 1994 |
| KNP48 | M | 10 | 957 | 1993 | 1997 |
| KNP49 | M | 2 | 2000 | 1994 | 2002 |
| KNP50 | F | 7 | 212 | 1994 | 1997 |
| KNP51 | M | 4 | 2221 | 1994 | 1996 |
| KNP52 | M | 4 | 381 | 1994 | 1997 |
| KNP53 | F | 1 | 26 | 1994 | 1995 |
| KNP54 | M | 4 | 2454 | 1994 | 1997 |
| KNP55 | M | 9 | 1648 | 1995 | 1996 |
| KNP56 | F | 7 | 128 | 1995 | 1996 |
| KNP57 | F | 6 | 1056 | 1995 | 2004 |
| KNP58 | M | 2 | 530 | 1995 | 1997 |
| KNP59 | F | 5 | 334 | 1995 | 1999 |
| KNP60 | M | 17 | 41 | 1995 | 1996 |
| KNP61 | M | 6 | 218 | 1996 | 1997 |
| KNP62 | F | 7 | 727 | 1996 | 2004 |
| KNP63 | F | 3 | 258 | 1997 | 2000 |
| KNP64 | F | 4 | 176 | 1998 | 2000 |
| KNP65 | F | 2 | 158 | 1998 | 2000 |
| KNP66 | F | 17 | 100 | 2000 | 2003 |
| KNP67 | F | 9 | 93 | 2002 | 2004 |
| KNP68 | M | 7 | 43 | 2002 | 2003 |
| KNP69 | F | 5 | 374 | 2002 | 2004 |
| KNP70 | F | 5 | 97 | 2002 | 2003 |

frame. The area encompassed an 18 260-km$^2$ region in the southwest Yukon (Figure 3-1).

To account for variation in habitat use through time, I stratified grizzly bear location data into two seasons based on food habits and selection patterns for the region. McCann (1998) identified four dietary switches, defining five feeding seasons. The first feeding season became evident about May 15 and was dominated by sporophytes. Sporophytes were dominant in the diet until approximately June 14, when *Oxytropis* spp. became the predominant species. *Oxytropis* spp. were typically only predominant in the grizzly bear diet for one week (ending about June 21), then bears returned to feeding predominantly on sporophytes (June 22 to July 21). The two seasons that bracketed the *Oxytropis* season were not unique from each other. The season where *Oxytropis* species were predominant was too short to subdivide telemetry locations into adequate-sized samples for modeling a relative probability distribution. Consequently, I pooled relocation data for these three feeding seasons together into one feeding period. This feeding period coincided with increased leaf-out leading to peak greenness and hereafter is referred to as the green-up period.

The fourth feeding season identified by McCann (1998) was predominated by berries and extended from July 22 to the end of September. This feeding period coincided with the start of senescence and hereafter is referenced as the green-down or senescence period. In early October locations were likely to be associated with denning activity. Similarly, relocations prior to May 15 were likely related to den emergence. I did not have enough telemetry data for analyses on habitat selection during these two 'shoulder' time periods.

To examine the variation in habitat selection due to status groups I broke relocation data into locations for adult males, lone adult females, family groups and subadults. I classified an individual as an adult if it was five years or older. All other individuals were considered subadults. Though there can be behavioural differences in habitat selection between male and female subadults, there were not enough locations to separate these groups (Hosmer and Lemeshow 2001).

Consequently, I pooled together locations within each feeding period for all subadults. I considered any female accompanied by young-of-year or young-of-last year as a family group. If a female lost her young at some point throughout the survey, her relocations were then analyzed as lone adult female locations. The numbers of locations for each status group, by feeding season, are detailed in Tables 3-2a – h.

## Explanatory Variables

I selected explanatory variables based on a review of other grizzly bear studies (Servheen 1983, Darling and Zager 1987, Waller and Mace 1997, McLellan and Hovey 2001a, McLoughlin et al. 2002, Theberge 2002), correspondence to the habitat selection phenomenon being modeled, and ease with which the variable could be measured. Variables related to forage productivity, security from humans, terrain, and conspecific distribution (i.e., the relative probability distribution for a cohort).

I performed a Tasselled Cap Transformation (Crist and Cicone 1986) on 8-bit peak summer Landsat 5 TM images to obtain brightness, greenness and wetness values. I used raw scores to model habitat relationships. High greenness values indicated areas of high vegetative biomass, while low values represented de-vegetated areas. Brightness values corresponded to soil reflectance changes. High values typically corresponded to areas with exposed bare rock. Wetness corresponded to the amount of substrate moisture and water in plant cells. Permanent snow and areas with dense and lush vegetation had high wetness values, while steep and well drained substrates had low wetness values. Both high and low areas of substrate moisture were unlikely to contain habitat features attractive to bears; therefore, I included a quadratic term for wetness in the habitat models.

Table 3-2a. Number of relocations per year for adult male bears in the green-up period.

| **Bear ID** | **Year** | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **1989** | **1990** | **1991** | **1992** | **1993** | **1994** | **1995** | **1996** | **1997** | **1998** | **1999** | **2000** | **2001** | **2002** | **2003** | **2004** | **Total for bear** |
| KNP01 | 6 | 4 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 11 |
| KNP02 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| KNP03 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 |
| KNP07 | 0 | 0 | 2 | 14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 16 |
| KNP08 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| KNP09 | 0 | 0 | 1 | 2 | 8 | 7 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 23 |
| KNP10 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 |
| KNP19 | 0 | 0 | 0 | 6 | 0 | 8 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 |
| KNP20 | 0 | 0 | 0 | 6 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 |
| KNP26 | 0 | 0 | 0 | 3 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 |
| KNP29 | 0 | 0 | 0 | 2 | 7 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 16 |
| KNP31 | 0 | 0 | 0 | 0 | 7 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 13 |
| KNP34 | 0 | 0 | 0 | 0 | 3 | 7 | 6 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 21 |
| KNP35 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 |
| KNP40 | 0 | 0 | 0 | 0 | 9 | 6 | 7 | 6 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 30 |
| KNP41 | 0 | 0 | 0 | 0 | 0 | 11 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 19 |
| KNP48 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 6 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 16 |
| KNP49 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 6 | 9 | 8 | 2 | 1 | 0 | 0 | 32 |
| KNP51 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 14 |
| KNP52 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 7 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 21 |
| KNP54 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 6 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 18 |
| KNP55 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 17 |
| KNP61 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 |
| KNP68 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 3 |
| **Total for year** | 14 | 4 | 5 | 41 | 49 | 60 | 64 | 52 | 23 | 6 | 9 | 8 | 2 | 3 | 1 | 0 | 341 |

Table 3-2b. Number of relocations per year for lone adult female bears in the green-up period.

| Bear ID | Year | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | Total for bear |
| KNP04 | 0 | 0 | 0 | 11 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 17 |
| KNP05 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 |
| KNP06 | 0 | 0 | 3 | 6 | 11 | 0 | 0 | 8 | 9 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 43 |
| KNP11 | 0 | 0 | 0 | 9 | 7 | 9 | 7 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 37 |
| KNP12 | 0 | 3 | 5 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 |
| KNP14 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 |
| KNP15 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 |
| KNP17 | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 |
| KNP18 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 6 | 14 | 4 | 1 | 4 | 4 | 0 | 0 | 0 | 38 |
| KNP21 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 |
| KNP23 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 |
| KNP24 | 0 | 0 | 0 | 0 | 9 | 0 | 6 | 7 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 23 |
| KNP27 | 0 | 0 | 0 | 5 | 8 | 11 | 7 | 6 | 7 | 0 | 0 | 3 | 4 | 0 | 0 | 0 | 51 |
| KNP32 | 0 | 0 | 0 | 0 | 6 | 8 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 21 |
| KNP33 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 |
| KNP36 | 0 | 0 | 0 | 0 | 8 | 10 | 8 | 7 | 7 | 5 | 3 | 1 | 0 | 0 | 0 | 0 | 49 |
| KNP38 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 6 | 8 | 5 | 4 | 3 | 3 | 0 | 0 | 0 | 39 |
| KNP39 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| KNP42 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 |
| KNP43 | 0 | 0 | 0 | 0 | 0 | 12 | 7 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 26 |
| KNP44 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 14 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 18 |
| KNP45 | 0 | 0 | 0 | 0 | 0 | 7 | 7 | 6 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 26 |
| KNP46 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 |
| KNP47 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 |
| KNP50 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 |
| KNP56 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 |
| KNP57 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 3 | 0 | 4 | 2 | 0 | 2 | 18 |
| KNP59 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 9 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 20 |
| KNP62 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 4 | 0 | 0 | 4 | 0 | 0 | 2 | 22 |
| KNP63 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 3 | 0 | 0 | 0 | 0 | 5 |
| KNP64 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 6 |
| KNP66 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 8 | 0 | 0 | 10 |
| KNP67 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 |
| KNP69 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 1 | 7 |
| KNP70 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 |
| **Total for year** | | 3 | 13 | 71 | 62 | 73 | 59 | 88 | 90 | 38 | 16 | 17 | 21 | 18 | 3 | 5 | 577 |

Table 3-2c. Number of relocations per year for family groups in the green-up period.

| Bear ID | Year | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | Total for bear |
| KNP04 | 0 | 5 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 13 |
| KNP06 | 0 | 0 | 0 | 0 | 0 | 10 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| KNP11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 8 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| KNP12 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 11 |
| KNP14 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 |
| KNP18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 4 | 0 | 0 | 3 | 3 | 0 | 19 |
| KNP21 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 14 |
| KNP23 | 0 | 0 | 0 | 0 | 10 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 17 |
| KNP24 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 2 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 22 |
| KNP27 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 5 | 4 | 0 | 0 | 3 | 2 | 0 | 8 |
| KNP32 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 8 | 0 | 5 | 1 | 0 | 0 | 0 | 0 | 0 | 4 |
| KNP33 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 |
| KNP38 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 17 |
| KNP42 | 0 | 0 | 0 | 0 | 0 | 10 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 |
| KNP43 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 28 |
| KNP44 | 0 | 0 | 0 | 0 | 0 | 11 | 7 | 0 | 9 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 9 |
| KNP46 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 |
| KNP50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 21 |
| KNP57 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 7 | 0 | 0 | 4 | 0 | 0 | 2 | 0 | 5 |
| KNP59 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 17 |
| KNP62 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 4 | 0 | 2 | 1 | 0 | 10 |
| KNP67 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 4 |
| KNP69 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| **Total for year** | | 5 | 6 | 5 | 20 | 48 | 38 | 27 | 39 | 15 | 17 | 8 | 1 | 9 | 13 | 2 | 253 |

Table 3-2d. Number of relocations per year for subadults in the green-up period.

| Bear ID | Year | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | Total for bear |
| KNP16 | 0 | 0 | 0 | 5 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 |
| KNP25 | 0 | 0 | 0 | 5 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 13 |
| KNP28 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| KNP30 | 0 | 0 | 0 | 2 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 |
| KNP38 | 0 | 0 | 0 | 0 | 9 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 19 |
| KNP39 | 0 | 0 | 0 | 0 | 7 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 18 |
| KNP49 | 0 | 0 | 0 | 0 | 0 | 7 | 7 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 19 |
| KNP53 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 |
| KNP58 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 |
| KNP63 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 10 |
| KNP64 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 4 |
| KNP65 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 2 | 2 | 0 | 0 | 0 | 0 | 10 |
| **Total for year** | 0 | 0 | 0 | 14 | 33 | 28 | 13 | 12 | 4 | 17 | 2 | 2 | 0 | 0 | 0 | 0 | 125 |

Table 3-2e. Number of relocations per year for adult males in the green-down period.

| Bear ID | Year | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | Total for bear |
| KNP01 | 9 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 13 |
| KNP03 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 11 |
| KNP07 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| KNP08 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| KNP09 | 0 | 0 | 5 | 5 | 8 | 9 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 33 |
| KNP10 | 0 | 0 | 12 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 19 |
| KNP19 | 0 | 0 | 0 | 1 | 4 | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 |
| KNP20 | 0 | 0 | 0 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 13 |
| KNP26 | 0 | 0 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 |
| KNP29 | 0 | 0 | 0 | 10 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 21 |
| KNP31 | 0 | 0 | 0 | 5 | 7 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 |
| KNP34 | 0 | 0 | 0 | 3 | 7 | 5 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 18 |
| KNP35 | 0 | 0 | 0 | 5 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 13 |
| KNP40 | 0 | 0 | 0 | 0 | 8 | 0 | 8 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 24 |
| KNP41 | 0 | 0 | 0 | 0 | 8 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 11 |
| KNP48 | 0 | 0 | 0 | 0 | 5 | 10 | 12 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 33 |
| KNP49 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 3 | 0 | 3 | 1 | 1 | 0 | 0 | 18 |
| KNP51 | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 14 |
| KNP52 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 7 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 22 |
| KNP54 | 0 | 0 | 0 | 0 | 0 | 0 | 13 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 24 |
| KNP55 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 |
| KNP60 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 |
| KNP61 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 18 |
| KNP68 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 |
| **Total for year** | 20 | 4 | 20 | 62 | 66 | 38 | 78 | 51 | 25 | 3 | 0 | 3 | 1 | 2 | 1 | 0 | 374 |

Table 3-2f. Number of relocations per year for lone adult females in the green-down period.

| Bear ID | Year | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | Total for bear |
| KNP04 | 10 | 0 | 0 | 14 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 25 |
| KNP06 | 0 | 0 | 6 | 13 | 10 | 0 | 0 | 10 | 8 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 49 |
| KNP11 | 0 | 0 | 0 | 14 | 10 | 9 | 7 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50 |
| KNP12 | 0 | 3 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 11 |
| KNP14 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| KNP15 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| KNP17 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| KNP18 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 7 | 11 | 3 | 5 | 5 | 2 | 0 | 0 | 0 | 41 |
| KNP21 | 0 | 0 | 0 | 11 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 13 |
| KNP23 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 |
| KNP24 | 0 | 0 | 0 | 0 | 1 | 0 | 9 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 17 |
| KNP27 | 0 | 0 | 0 | 11 | 11 | 13 | 8 | 10 | 11 | 0 | 3 | 3 | 2 | 0 | 0 | 0 | 72 |
| KNP32 | 0 | 0 | 0 | 10 | 9 | 13 | 9 | 6 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 56 |
| KNP33 | 0 | 0 | 0 | 4 | 9 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 16 |
| KNP36 | 0 | 0 | 0 | 0 | 9 | 12 | 9 | 8 | 13 | 4 | 2 | 1 | 0 | 0 | 0 | 0 | 58 |
| KNP38 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 8 | 12 | 4 | 3 | 4 | 1 | 0 | 0 | 0 | 42 |
| KNP42 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 8 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 29 |
| KNP43 | 0 | 0 | 0 | 0 | 0 | 9 | 9 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 27 |
| KNP44 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 7 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 15 |
| KNP45 | 0 | 0 | 0 | 0 | 6 | 9 | 10 | 8 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 38 |
| KNP46 | 0 | 0 | 0 | 0 | 7 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 16 |
| KNP47 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 |
| KNP50 | 0 | 0 | 0 | 0 | 0 | 7 | 1 | 0 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 19 |
| KNP56 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 |
| KNP57 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 5 | 1 | 0 | 3 | 2 | 3 | 2 | 24 |
| KNP59 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 7 | 8 | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 29 |
| KNP62 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 17 | 11 | 3 | 0 | 0 | 2 | 0 | 0 | 1 | 34 |
| KNP63 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 3 | 0 | 0 | 0 | 0 | 5 |
| KNP64 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 |
| KNP66 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 1 | 0 | 6 |
| KNP67 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 4 |
| KNP69 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 2 | 4 | 11 |
| KNP70 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 1 | 0 | 5 |
| **Total for year** | 10 | 3 | 19 | 98 | 92 | 91 | 97 | 122 | 110 | 25 | 19 | 18 | 12 | 17 | 7 | 7 | 747 |

Table 3-2g. Number of relocations per year for family groups in the green-down period.

| Bear ID | Year | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | Total for bear |
| KNP04 | 0 | 6 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 |
| KNP06 | 0 | 0 | 0 | 0 | 0 | 10 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 19 |
| KNP11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 |
| KNP12 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| KNP18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 3 | 0 | 5 |
| KNP21 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 |
| KNP23 | 0 | 0 | 0 | 0 | 14 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 |
| KNP24 | 0 | 0 | 0 | 14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 14 |
| KNP27 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 0 | 0 | 2 | 1 | 0 | 8 |
| KNP32 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 5 |
| KNP33 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 |
| KNP36 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| KNP38 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 3 | 0 | 5 |
| KNP42 | 0 | 0 | 0 | 0 | 0 | 11 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 22 |
| KNP43 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 16 |
| KNP44 | 0 | 0 | 0 | 0 | 0 | 11 | 9 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 29 |
| KNP46 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 |
| KNP50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 |
| KNP57 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 9 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 21 |
| KNP59 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| KNP62 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 4 | 0 | 2 | 5 | 0 | 14 |
| KNP67 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 3 |
| **Total for year** | 1 | 6 | 9 | 17 | 29 | 38 | 38 | 16 | 38 | 6 | 7 | 7 | 0 | 8 | 14 | 1 | 235 |

Table 3-2h. Number of relocations per year for subadults in the green-down period.

| Bear ID | Year | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1989 | 1991 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | Total for bear |
| KNP11 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 |
| KNP16 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 |
| KNP25 | 0 | 0 | 0 | 15 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 16 |
| KNP28 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 |
| KNP30 | 0 | 0 | 0 | 11 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 17 |
| KNP38 | 0 | 0 | 0 | 0 | 9 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 22 |
| KNP39 | 0 | 0 | 0 | 0 | 9 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 18 |
| KNP47 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 |
| KNP49 | 0 | 0 | 0 | 0 | 0 | 9 | 10 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 30 |
| KNP51 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 |
| KNP52 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 |
| KNP53 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 |
| KNP54 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| KNP58 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 13 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 26 |
| KNP63 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 12 |
| KNP64 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| KNP65 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 3 | 0 | 0 | 0 | 0 | 7 |
| Total for year | 0 | 0 | 7 | 44 | 35 | 54 | 20 | 24 | 11 | 10 | 1 | 3 | 0 | 0 | 0 | 0 | 209 |

Grizzly bear forage species may be more abundant in areas with high vegetative diversity than in homogenous areas (Schleyer 1983). A 12-class land cover classification for the Kluane Region was developed by Gleig et al. (2005). Classes included cloud, shadow, human disturbance, ice and permanent snow, water, alluvium and gravel, scree and talus, spruce forest, deciduous forest, shrub, alpine and grassland, and wetland. Only 0.02% and 0.45%, respectively, of the four classified scenes were in the cloud and shadow classes; therefore, error associated with misclassification of these areas was considered negligible. I calculated Shannon's index of diversity (H; Turner 1989) using the vegetation classification and Pattern Analysis in Idrisi Kilimanjaro (Clark Labs 2003).

I used the Solar Analyst Extension 1.0 (Fu and Rich 1999) for ArcView 3.2 (ESRI 2000) to generate the daily potential direct solar radiation (WH/m$^2$) from a 30-m digital elevation model (DEM). The total direct daily radiation was calculated for the active period (April 1 to November 15) for bears in the Kluane Region. I included a quadratic term, suspecting that areas with high amounts of direct radiation would be too arid to abundantly support bear foods, while areas with low amounts of direct solar radiation would have less photosynthetic capability than areas with intermediate values.

Distance to hiding cover was generated from the land cover classification. I reclassified spruce forest, deciduous forest, and shrub classes as cover. All other classes were reclassified as non-cover. I generated a distance surface for cover, incremented in 30-m intervals, using the DISTANCE command in Idrisi Kilimanjaro (Clark Labs 2003).

Infrastructure density was calculated using three vector layers identifying all known sources of human activity. Vector layers represented: 1) linear features such as roads and trails, 2) point features such as buildings, cabins, campsites, and points of recreation, and 3) polygon features such as airstrips. Information for the layers was obtained from the National Topographic Database (NTDB; NRCAN 1999), data collected by local government agencies, and manually collected data (i.e., collect by visiting the feature and using a hand-held GPS unit to record its spatial location). Each vector layer was rasterized at 30-m resolution. Any cell containing a human use feature was given a value of one. I summed the value for each cell across the three raster layers. The resulting layer represented the total the number of human-use features per cell (i.e., 0 to 3), where cells containing more than one human use feature had values of 2 or 3. I used a moving window, sized to represent the average daily movements of female grizzly bears, to tally the values of all 30-m cells. I assumed, because of similarities in home range size, that the daily movement rate for bears in the Kluane Region was similar to the 9-$\text{km}^2$ movement rate for female grizzly bears in Central Rocky Ecosystem of Alberta (Gibeau 2000). The sum value within the window was assigned to the center cell.

Terrain ruggedness (TRI) describes the variability in topography using a ruggedness index at a specified scale for a moving window. Terrain ruggedness was derived using an adaptation from Nellemann and Cameron (1996) for use in a geographic information system (GIS) environment using 30-m pixel resolution for a 300-m moving window. The terrain ruggedness index is defined as:

$$\mathrm{TRI} = \frac{\text{Average Slope} * \mathrm{AV}}{\text{Average Slope} + \mathrm{AV}} \qquad \text{Equation 3-1}$$

Where Average Slope is the average slope in degrees calculated in the moving window and where AV is the Aspect Variability, calculated using the formula:

$$\mathrm{AV} = \left( \frac{\mathrm{n}}{\mathrm{nmax}} \right) * 100 \qquad \text{Equation 3-2}$$

Where n is the number of different aspects classes in the moving window and nmax is maximum number of aspect classes in the study area. AV is the algorithm for Relative Richness developed as a landscape metric by Turner (1989). For AV, 361 inter-classes were used including a 'no aspect' class for slopes under five degrees. Based on findings from previous studies (Theberge 2002), I suspected non-linear selection of terrain ruggedness; therefore, I included a quadratic term in the habitat models.

I obtained digital hydrology maps from the 1:50 000 scale digital National Topographic Database (Natural Resources Canada 1999). I classified hydrological features into two classes: water bodies and streams. Water bodies were defined as any hydrological feature (excluding wetlands) that was greater than or equal to 20 m between banks. Streams were defined as any linear hydrological feature smaller than 20 m between banks. All hydrological features were active year round, except in drought years.

Once a relative probability distribution map was developed for a status group (see the section on model building and evaluation below), I used it as an explanatory variable for lower status groups. The order in which the probability layers were developed and then subsequently used was based on the potential for a cohort to influence habitat selection in other cohorts. I presumed the order of status, from highest status to lowest status was: adult males, lone adult females, family groups, and then subadults. I suspected that lower status groups would avoid areas where there was a high probability of encountering individuals from higher status groups. However, areas with a low probability of higher status group occurrence were likely to be areas with a very low probability of any status group occurring. Therefore, I used a quadratic term when treating the relative probability values for each status group as a covariate.

## Model Building and Evaluation

I used logistic regression to model third-order (Johnson 1980) habitat selection by grizzly bears. My methods followed a “design III” approach, in which use of resource units by individual bears is evaluated relative to the availability of those units for each animal (Manly et al. 2002)[1]. This method used telemetry

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[1] See Johnson et al. (2006) for counter arguments to Keating and Cherry’s (2004) discussion on limitations of use-availability study designs.

locations for each grizzly bear cohort, and a number of random co-ordinates to model the relative probability of occurrence of grizzly bears as a function of a set of explanatory variables. I generated 1000 random locations within each 100% minimum convex polygon (MCP), created for individual bears in the Animal Movements extension for ArcView (Hooge and Eichenlaub 2000). The random points for each bear were pooled to represent availability for the population. I extracted the value of each explanatory variable for each telemetry and random location. I did not use error circles (a uniform distribution of error) around each point location because they may decrease the strength of selection for variables far below what the animal is actually selecting (Visscher 2006).

The model took the following structure:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_i x_i) \qquad \text{Equation 3-3}$$

Where $w(x)$ was the habitat selection function and $\beta_i$ were the selection coefficients based on explanatory variables, $x_i$ (Manly et al. 2002). Prior to building the models, I tested the explanatory variables for collinearity using Pearson correlation ($r$), tolerance, and variance inflation function (VIF) diagnostics. All correlations greater than 0.6, or tolerance scores of 0.1 or less and individual VIF scores > 10 were assumed to be collinear and not included in the model structure. The probability distributions for the cohorts were collinear with each other and other explanatory variables; therefore, I considered a base model for each cohort by season stratum comprised of all explanatory variables, but excluding information on the distribution of other cohorts. I also considered models that separately incorporated the distribution of each higher status group (excluding variables that were collinear with the distribution of the higher status group). Specifically, for lone adult females I considered the base model with a model incorporating adult male distribution (the second model). For family groups I considered the base model, a model incorporating adult male distribution and a model incorporating lone adult female distribution (the third model). For subadults, I considered the base model and three models incorporating the distribution of adult males, lone adult females, or family groups (the fourth model). I ran the logistic regression in SAS 9.1 (SAS 2004) using the APLR macro (Moore 2000) for all possible nested subset models for each cohort and season. I was interested in examining patterns of habitat use associated with each variable; therefore, I used the model average function in APLR to generate coefficients and standard errors for each β-value.

To examine variable importance within each cohort by season model subset, models were ranked using $\mathrm{AIC_c}$ scores (Burnham and Anderson 2002). I transformed the $\mathrm{AIC_c}$ scores into Akaike weights. Estimates of variable importance for each model subset can be obtained by summing Akaike weights across all models in which a variable occurred (Burnham and Anderson 2002). The larger the summed Akaike weight, the more important the variable.

I used the model with the best $\mathrm{AIC_c}$ score to generate seasonal relative probability surfaces for each cohort. I transformed the $w(x)$ values from Equation 3 for each model to a value between 0 and 1 using:

$$\mathrm{T}w(x) = \frac{w(x)}{1 + w(x)} \qquad \text{Equation 3-4}$$

I used the quantile classification function in the Spatial Analyst extension of ArcGIS 9.0 (ESRI 2004) to bin the logit values into 10 ordinal classes. On the ordinal scale a value of 1 represented a relatively low probability of grizzly bear occurrence, while a value of 10 represented a relatively high probability of occurrence.

To evaluate the models, I divided data from each feeding season and each cohort into two groups following a k-fold partitioning design (Fielding and Bell 1997). The first group was used as the model training data and represented a random 80% sub-sample of telemetry and availability point data. The second group was comprised of the remaining 20% of used points and was employed to assess model fit (Hosmer and Lemeshow 2001, Boyce et al. 2002). I repeated this procedure five times so that all points were used to train the model four times and all used points were employed once to assess the model fit. Each time the area-adjusted frequency of bear occurrence within a given bin was matched against the corresponding rank of the bin and Spearman's rank correlation ($r_s$) was calculated (Boyce et al. 2002). The correlation coefficient was averaged across the five repetitions. If the averaged $r_s$ value was 1, the frequency of bear occurrence and the habitat rank had a perfect positive correlation. Values between 1 and 0.5 were considered to have a strong positive correlation, while coefficients between 0.5 and 0 were considered to represent a weak correlation. Negative coefficients were conversely interpreted. A value of 0 indicated no relationship.

I examined the differences in mean use for each variable among cohorts for each phenological season using a one-way ANOVA in SPSS 13 (SPSS Inc. 2005). Data were normally distributed. Levene's test ($\alpha < 0.05$) showed unequal variances among cohorts; therefore, I calculated Welch's $F$-statistic ($\alpha < 0.05$). Welch's $F$-statistic also accounts for unequal sample sizes. I used Games-Howell tests ($\alpha < 0.05$) for post-hoc comparisons among cohorts.

## RESULTS

### Green-up Models

*Adult Males.*--During the green-up period adult male bears selected habitats in areas with low soil and plant moisture (wetness) and close to cover (Table 3-3a). There was a strong positive correlation of habitat ranks and the proportion of telemetry locations occurring within each rank (Table 3-4). Wetness was also the most important explanatory variable for adult male distribution during green-up (Table 3-5a). Human infrastructure density, distance to cover and terrain ruggedness were the next most influential variables. Adult males avoided areas with a high or low density of human infrastructure, more often occupying habitats with a mid-range of values. Distance to streams, distance to water, and vegetative diversity were the least influential variables.

*Lone Adult Females.*--Lone adult females selected areas that had high values of greenness (Table 3-3b). They selected habitats with intermediate probabilities of encountering an adult male (Table 3-3b). The base and second models showed selection for habitats close to cover and water bodies. Validation of both models indicated strong positive correlation between habitat ranks and lone adult female grizzly bear locations (Table 3-4).

Within a nested subset for the base model, distance to water bodies, greenness and distance to cover were substantially more influential than other explanatory variables (Table 3-5a). Terrain ruggedness was moderately influential. Most other variables had very little influence on lone adult female distribution. Within the nested subset for the second model, distance to water was again the most influential variable, followed by the linear variable for distribution of adult males (positive selection), the linear variable for human infrastructure density (negative selection), then the quadratic term for the adult male distribution (negative selection). Diversity, brightness, the amount of direct solar radiation and the distance to streams were the least influential variables.

*Family Groups.*--Family groups selected areas with high values of brightness and vegetative diversity (Table 3-3c). Family groups also selected habitats close to cover, away from streams and with high values of terrain ruggedness. They used habitats with intermediate probabilities of encountering adult males, and bimodal high or low probabilities of encountering lone adult females. Validation of the models indicated a good fit between family group occurrence and explained habitat value (Table 3-4).

Regardless of which model I considered, terrain ruggedness was the most influential variable on family group distribution (Table 3-5a). Distance to cover, distance to streams and greenness also appeared to be important explanatory variables. Unlike lone adult females, the distance to water bodies had little relative influence on family group distribution. The distribution of other adult cohorts was moderately important in explaining family group distribution. The positive linear variable for adult male distribution was more important than the negative quadratic term, indicating stronger selection for than avoidance of habitats with males. Similarly, the positive quadratic term for lone adult female distribution was more influential than the negative linear term. Human infrastructure density was not relatively influential in the base and third model subset, and was moderately influential in the second model subset.

*Subadults.*--During the green-up period, subadult bears selected habitats with high and low values of direct solar radiation, and intermediate values of human infrastructure density (Table 3-3d). The fourth model suggested that subadults avoided streams but used areas with high vegetative diversity. They also used areas with intermediate relative probability of lone adult occurrence, and low relative probability of family group occurrence. Correlation between habitat rank and subadult occurrence was poor for all four models (Table 3-4).

Direct solar radiation was the most influential variable on subadult distribution (Table 3-5a). Depending on the model subset, diversity, human infrastructure density, and the distribution of adult males also strongly influenced subadult distribution. Brightness, distance to streams and distance to water bodies were consistently the least important explanatory variables across all four models.

### Green-down (Senescence) Models

*Adult Males.*--During the green-down period, adult males selected areas with high vegetative diversity (Table 3-3a). They selected locations close to streams and water bodies, and sites with intermediate amounts of direct solar radiation. As with the green-up period, they also selected areas with an intermediate density of human infrastructure. Model validation indicated a strong relationship between habitat ranks and adult male occurrence (Table 3-4). Density of infrastructure was the most important variable influencing adult male distribution during the green-down period (Table 3-5b). Distance to streams and distance to water bodies were also very influential on adult male occurrence. Distance to cover, wetness and greenness were the least influential variables for explaining adult male occurrence during the green-down period.

*Lone Adult Females.*--The base model suggested that lone adult females selected locations with high greenness values and low wetness values (Table 3-3b). They also selected areas close to streams and water bodies. The second model showed that lone adult females used areas close to cover. Unlike the green-up period, lone adult females did not appear to avoid habitats where adult males were likely to occur. Model validation results were strongly positive (Table 3-4).

In the nested subset for the base model, the distance to streams and water bodies were most important variable explaining adult female distribution (Table 3-5b). Wetness, and distance to streams and water bodies were highly influential variables across models. Greenness was also highly influential relative to other variables in the base model subset. Diversity had little relative influence in both model sets. Distribution of males and human infrastructure density were also not very influential relative to other variables in the nest subset for the second model.

*Family Groups.*--Family groups used areas with low surface moisture and higher values of vegetative diversity (Table 3-3c). They used areas close to streams, intermediate values of terrain ruggedness, and human infrastructure density. Family groups also selected for habitats with high probability of encountering lone adults. Model validation revealed a good correlation between habitat rank and family group occurrence (Table 3-4).

Distance to streams, substrate moisture, distance to water, and terrain ruggedness were the most important variables influencing family group occurrence (Table 3-5b). Lone adult female distribution was the most important variable explaining family group distribution in the third model subset. Solar radiation and human infrastructure density were the least important variables in the base variable subset, but were relatively more influential in the other subset analyses. There were no variables that consistently ranked low across all model subsets.

*Subadults.*--During the green-down period, subadult distribution was negatively correlated with wetness (Table 3-3d). Subadults used areas with high vegetative diversity, close to cover, and close to streams. They selected areas within an intermediate range of human infrastructure density, and intermediate relative probabilities of encountering lone adults or family groups. There was a good correlation between model prediction and subadult occurrence (Table 3-4).

Infrastructure density, diversity, and distance to streams were the three most important variables explaining subadult distribution in the green-down period (Table 3-5b). The distribution of conspecifics was moderately influential. Distance to water, terrain ruggedness, and greenness were consistently ranked low across all models.

Table 3-3a. Model-averaged seasonal habitat coefficients and standard errors (SE) for adult male grizzly bear models in the green-up and green-down periods. Logistic regression was used to model third-order habitat selection by grizzly bears. Methods followed a “design III” approach, in which use of resource units by individual bears is evaluated relative to the availability of those units for each animal. Models were considered that separately incorporated the distribution of each higher status group. A base model (*B*) only was considered for adult males.

| **Green-up Variable** | **Coefficient** | SE | **Green-down Variable** | **Coefficient** | SE |
|---|---|---|---|---|---|
| *Model: B* | | | | | |
| greenness | 0.00594476 | 0.00335763 | greenness | 0.00403641 | 0.00288266 |
| brightness | 0.00289468 | 0.00288421 | brightness | 0.00615723 | 0.00253083 |
| wetness | -0.02195522 | 0.00653922 | wetness | -0.00664864 | 0.00501025 |
| wetness$^2$ | -0.00121234 | 0.00031121 | wetness$^2$ | -0.00051578 | 0.00017204 |
| diversity | 0.00002871 | 0.00065904 | diversity | 0.00123680 | 0.00062818 |
| cover | -0.00352941 | 0.00132775 | cover | -0.00142711 | 0.00106746 |
| streams | -0.00009465 | 0.00129822 | streams | -0.00066178 | 0.00014799 |
| water | 0.00002539 | 0.00004346 | water | -0.00016765 | 0.00004858 |
| [†]solar | 4.89E-7 | 3.80E-6 | solar | 9.42E-6 | 7.75E-6 |
| solar$^2$ | -3.12E-12 | 2.92E-12 | solar$^2$ | -1.08E-11 | 7.96E-12 |
| terrain | 0.00574698 | 0.04479621 | terrain | -0.04173178 | 0.02686806 |
| terrain$^2$ | -0.00278871 | 0.00126037 | terrain$^2$ | -0.00285426 | 0.00134033 |
| human | 0.00361367 | 0.00119287 | human | 0.00761619 | 0.00096954 |
| human$^2$ | -7.18E-6 | 2.78E-6 | human$^2$ | -0.00001086 | 2.11E-6 |

[†] “E-x” indicates that the value before the E is multiplied by $10^{-x}$ where x is the value following the E.

Table 3-3b. Model-averaged habitat coefficients and standard errors (SE) for lone adult female grizzly bear models in the green-up and green-down periods. Logistic regression was used to model third-order habitat selection by grizzly bears. Methods followed a "design III" approach, in which use of resource units by individual bears is evaluated relative to the availability of those units for each animal. Models were considered that separately incorporated the distribution of each higher status group. For lone adult females the base model (*B*) and a model incorporating adult male distribution was considered.

| **Green-up Variable** | **Coefficient** | SE | **Green-down Variable** | **Coefficient** | SE |
|---|---|---|---|---|---|
| *Model: B* | | | | | |
| greenness | 0.01056772 | 0.00223981 | greenness | 0.00850718 | 0.00179410 |
| brightness | -0.00001088 | 0.00170159 | brightness | 0.00442356 | 0.00181333 |
| wetness | -0.00377025 | 0.00284082 | wetness | -0.01751734 | 0.00417204 |
| [†]wetness$^2$ | -5.98E-6 | 0.00003870 | wetness$^2$ | -0.00068748 | 0.00014911 |
| diversity | 0.00042923 | 0.00050375 | diversity | 0.00069653 | 0.00044324 |
| cover | -0.00212541 | 0.00086961 | cover | -0.00050182 | 0.00073073 |
| streams | -0.00007335 | 0.00009862 | streams | -0.00073942 | 0.00010920 |
| water | -0.00020440 | 0.00003819 | water | -0.00019369 | 0.00003328 |
| solar | -3.64E-7 | 1.46E-6 | solar | 3.62E-6 | 3.45E-6 |
| solar$^2$ | 5.65E-13 | 1.47E-12 | solar$^2$ | -2.97E-12 | 3.85E-12 |
| terrain | 0.01930640 | 0.01448280 | terrain | 0.00921897 | 0.02039617 |
| terrain$^2$ | 0.00084636 | 0.00077317 | terrain$^2$ | 0.00117672 | 0.00067486 |
| human | -0.00035015 | 0.00059256 | human | 0.00149762 | 0.00089784 |
| human$^2$ | -9.66E-7 | 1.35E-6 | human$^2$ | -2.74E-6 | 1.95E-6 |
| *Model: B + adult male distribution* | | | | | |
| brightness | -0.00025874 | 0.00177401 | brightness | 0.00299450 | 0.00182980 |
| wetness | 0.00288659 | 0.00306932 | wetness | -0.01762467 | 0.00398075 |
| wetness$^2$ | 8.50E-6 | 0.00002990 | wetness$^2$ | -0.00057873 | 0.00015807 |
| diversity | 0.00037361 | 0.00050304 | diversity | 0.00039730 | 0.00046415 |
| streams | -0.00004652 | 0.00009966 | cover | -0.00150576 | 0.00066446 |
| water | -0.00021621 | 0.00003828 | streams | -0.00055271 | 0.00012687 |
| solar | 0.00080786 | 0.22949985 | water | -0.00014665 | 0.00003799 |
| solar$^2$ | 0.02061598 | 0.01655041 | solar | 0.20752523 | 0.15633454 |
| terrain | 0.03688995 | 0.02318430 | solar$^2$ | 0.01356543 | 0.02040918 |
| terrain$^2$ | 0.00224241 | 0.00093626 | terrain | 0.03018936 | 0.01703948 |
| human | -0.00214641 | 0.00112116 | terrain$^2$ | 0.00154610 | 0.00083684 |
| human$^2$ | 3.28E-6 | 2.27E-6 | human | 0.00016247 | 0.00072315 |
| males | 7.99854058 | 2.26699299 | human$^2$ | -6.07E-7 | 1.38E-6 |
| males$^2$ | -8.01280002 | 3.49321279 | males | 1.72600411 | 1.47868452 |
| | | | males$^2$ | 1.47516857 | 0.92424476 |

[†] "E-x" indicates that the value before the E is multiplied by $10^{-x}$ where x is the value following the E.

Table 3-3c. Model-averaged seasonal habitat coefficients and standard errors (SE) for family group models in the green-up and green-down periods. Logistic regression was used to model third-order habitat selection by grizzly bears. Methods followed a "design III" approach, in which use of resource units by individual bears is evaluated relative to the availability of those units for each animal. Models were considered that separately incorporated the distribution of each higher status group. For family groups the base model (*B*), a model incorporating adult male distribution and a model incorporating lone adult female distribution were considered.

| **Green-up Variable** | **Coefficient** | SE | **Green-down Variable** | **Coefficient** | SE |
|---|---|---|---|---|---|
| *Model: B* | | | | | |
| greenness | 0.00698220 | 0.00317079 | greenness | 0.00482305 | 0.00353500 |
| brightness | 0.00542790 | 0.00224912 | brightness | 0.00448165 | 0.00321231 |
| wetness | -0.00481703 | 0.00369055 | wetness | -0.02599149 | 0.00810860 |
| wetness$^2$ | -0.00005317 | 0.00004089 | wetness$^2$ | -0.00111582 | 0.00032986 |
| diversity | 0.00122066 | 0.00075138 | diversity | 0.00154062 | 0.00078602 |
| cover | -0.00231557 | 0.00119146 | cover | -0.00186471 | 0.00128400 |
| streams | 0.00024617 | 0.00012300 | streams | -0.00084541 | 0.00020159 |
| water | 0.00004632 | 0.00004583 | water | -0.00016869 | 0.00005639 |
| solar | -0.02625711 | 0.14246075 | solar | -1.24E-6 | 1.82E-6 |
| solar$^2$ | -0.00245830 | 0.01455924 | solar$^2$ | -1.04E-12 | 1.96E-12 |
| terrain | 0.11329760 | 0.03698396 | terrain | 0.13315394 | 0.05934033 |
| terrain$^2$ | -0.00190093 | 0.00238922 | terrain$^2$ | -0.00518183 | 0.00248062 |
| human | -0.00174543 | 0.00142107 | human | -0.00060760 | 0.00144947 |
| [†]human$^2$ | 3.07E-6 | 2.32E-6 | human$^2$ | -4.55E-6 | 3.85E-6 |
| *Model B + adult male distribution* | | | | | |
| brightness | 0.00559107 | 0.00221039 | brightness | 0.00327410 | 0.00348253 |
| wetness | -0.00340853 | 0.00374212 | wetness | -0.02455650 | 0.00796256 |
| wetness$^2$ | -0.00004355 | 0.00003563 | wetness$^2$ | -0.00097499 | 0.00036228 |
| diversity | 0.00121852 | 0.00074985 | diversity | 0.00131980 | 0.00084225 |
| streams | 0.00026033 | 0.00012374 | cover | -0.00189444 | 0.00121596 |
| water | 0.00003782 | 0.00004580 | streams | -0.00068800 | 0.00026199 |
| solar | 0.01180060 | 0.15762234 | water | -0.00013839 | 0.00006955 |
| solar$^2$ | 0.00746284 | 0.01541313 | solar | -0.48081891 | 0.59627584 |
| terrain | 0.12443711 | 0.03045986 | solar$^2$ | 0.04182654 | 0.07171452 |
| terrain$^2$ | -0.00090612 | 0.00253867 | terrain | 0.12521190 | 0.05800439 |
| human | -0.00363271 | 0.00160874 | terrain$^2$ | -0.00466818 | 0.00261352 |
| human$^2$ | 6.13E-6 | 2.11E-6 | human | -0.00206767 | 0.00172882 |
| male | 5.21620519 | 2.66776350 | human$^2$ | -4.61E-6 | 4.77E-6 |
| male$^2$ | -6.95774597 | 5.98758518 | male | 2.72144576 | 3.16601327 |
| | | | male$^2$ | 1.30708819 | 2.52849956 |
| *Model B + adult female distribution* | | | | | |
| brightness | 0.00447993 | 0.00188701 | brightness | 0.00043784 | 0.00287251 |
| diversity | 0.00121911 | 0.00074973 | diversity | 0.00085190 | 0.00079902 |
| cover | -0.00092875 | 0.00128573 | cover | -0.00073386 | 0.00116625 |
| streams | 0.00024755 | 0.00012381 | streams | -0.00014667 | 0.00025917 |
| water | 0.00018521 | 0.00006353 | water | 0.00004737 | 0.00006786 |
| solar | -0.03939976 | 0.14431623 | solar | -0.53586533 | 0.42158770 |
| solar$^2$ | 0.00006088 | 0.01497835 | solar$^2$ | 0.03059342 | 0.05753316 |
| terrain | 0.10701214 | 0.04544140 | terrain | 0.10530142 | 0.05775246 |
| terrain$^2$ | -0.00247061 | 0.00226322 | terrain$^2$ | -0.00447239 | 0.00253341 |
| human | -0.00148433 | 0.00139630 | human | -0.00193174 | 0.00124671 |
| human$^2$ | 2.88E-6 | 2.08E-6 | human$^2$ | -4.90E-6 | 4.71E-6 |
| female | -2.15906149 | 6.54568123 | female | 0.00983171 | 4.02263454 |
| female$^2$ | 4.71553067 | 2.9235249 | female$^2$ | 4.93203698 | 1.35519926 |

[†] "E-x" indicates that the value before the E is multiplied by $10^{-x}$ where x is the value following the E.

Table 3-3d. Model-averaged seasonal habitat coefficients and standard errors (SE) for subadult grizzly bear models in the green-up and green-down periods. Logistic regression was used to model third-order habitat selection by grizzly bears. Methods followed a "design III" approach, in which use of resource units by individual bears is evaluated relative to the availability of those units for each animal. Models were considered that separately incorporated the distribution of each higher status group. For subadults, I considered the base model (*B*) and three models incorporating the distribution of adult males, lone adult females, or family groups.

| **Green-up Variable** | **Coefficient** | SE | **Green-down Variable** | **Coefficient** | SE |
|---|---|---|---|---|---|
| *Model: B* | | | | | |
| greenness | 0.00217077 | 0.00442544 | greenness | 0.00095102 | 0.00392666 |
| brightness | 0.00166540 | 0.00382560 | brightness | 0.00207663 | 0.00293419 |
| wetness | -0.00276491 | 0.00581860 | wetness | -0.01051286 | 0.00445914 |
| wetness$^2$ | -0.00008259 | 0.00007101 | wetness$^2$ | -0.00003126 | 0.00008014 |
| diversity | 0.00188351 | 0.00105622 | diversity | 0.00227365 | 0.00082899 |
| cover | -0.00150088 | 0.00149668 | cover | -0.00247260 | 0.00123512 |
| streams | 0.00019041 | 0.00017838 | streams | -0.00039530 | 0.00017734 |
| water | 0.00007156 | 0.00006683 | water | -0.00004345 | 0.00005349 |
| $^{\dagger}$solar | -7.49E-6 | 5.39E-6 | solar | -1.88E-6 | 3.06E-6 |
| solar$^2$ | 6.27E-12 | 6.60E-12 | solar$^2$ | 1.54E-12 | 3.33E-12 |
| terrain | 0.02872706 | 0.06386175 | terrain | -0.01210840 | 0.02300935 |
| terrain$^2$ | -0.00299706 | 0.00242190 | terrain$^2$ | -0.00006794 | 0.01224594 |
| human | 0.00203336 | 0.00292905 | human | 0.00676711 | 0.00141111 |
| human$^2$ | -8.70E-6 | 7.85E-6 | human$^2$ | -0.00001105 | 3.44E-6 |
| *Model: B + adult male distribution* | | | | | |
| brightness | 0.00187872 | 0.00364131 | brightness | 0.00553060 | 0.00388189 |
| wetness | 0.00103087 | 0.00655980 | wetness | -0.01021928 | 0.00481439 |
| wetness$^2$ | -0.00005611 | 0.00006701 | wetness$^2$ | -0.00021762 | 0.00018920 |
| diversity | 0.00177536 | 0.00105976 | diversity | 0.00279199 | 0.00089816 |
| streams | 0.00023416 | 0.00018185 | cover | -0.00354535 | 0.00136240 |
| water | 0.00007510 | 0.00006637 | streams | -0.00069702 | 0.00025664 |
| solar | -0.87735066 | 0.57565387 | water | -0.00013465 | 0.00007302 |
| solar$^2$ | 0.08276764 | 0.06382851 | solar | 0.17480557 | 0.53423477 |
| terrain | 0.01335758 | 0.05231420 | solar$^2$ | -0.03984889 | 0.05215054 |
| terrain$^2$ | -0.00218713 | 0.00220298 | terrain | -0.03215042 | 0.03021903 |
| human | 0.00130812 | 0.00306839 | terrain$^2$ | -0.00192974 | 0.00160592 |
| human$^2$ | -8.26E-6 | 7.06E-6 | human | 0.00963882 | 0.00233295 |
| male | 5.09908147 | 3.80799295 | human$^2$ | -0.00001527 | 4.45E-6 |
| male$^2$ | -7.60987854 | 7.89053972 | male | 5.97411518 | 4.56928363 |
| | | | male$^2$ | -5.98853954 | 3.88453040 |
| *Model: B + adult female distribution* | | | | | |
| brightness | 0.00001442 | 0.00315654 | brightness | 0.00264927 | 0.00272992 |
| diversity | 0.00183602 | 0.00105834 | diversity | 0.00230548 | 0.00083150 |
| cover | -0.00037819 | 0.00190465 | cover | -0.00220427 | 0.00123231 |
| streams | 0.00019036 | 0.00018123 | streams | -0.00041916 | 0.00020124 |
| water | 0.00015255 | 0.00008764 | water | -0.00003504 | 0.00005792 |
| solar | -0.87935667 | 0.58820865 | solar | -0.22680527 | 0.37568485 |
| solar$^2$ | 0.07909613 | 0.06534907 | solar$^2$ | 0.02405707 | 0.03810862 |
| terrain | 0.01175410 | 0.06016206 | terrain | -0.01024094 | 0.02314454 |
| terrain$^2$ | -0.00291398 | 0.00208143 | terrain$^2$ | -0.00003313 | 0.00120354 |
| human | 0.00203433 | 0.00291297 | human | 0.00665805 | 0.00143592 |
| human$^2$ | -8.55E-6 | 7.93E-6 | human$^2$ | -0.00001073 | 3.46E-6 |
| female | -3.28150701 | 6.92630948 | female | 2.07199364 | 2.03108160 |
| female$^2$ | 4.13908901 | 4.11154608 | female$^2$ | -1.07652387 | 2.24709908 |

$^{\dagger}$"E-x" indicates that the value before the E is multiplied by $10^{-x}$ where x is the value following the E.

Table 3-3d. Continued.

| **Green-up Variable** | **Coefficient** | **SE** | **Green-down Variable** | **Coefficient** | **SE** |
|---|---|---|---|---|---|
| *Model: B + family group distribution* | | | | | |
| greenness | 0.00434067 | 0.00409354 | brightness | 0.00278400 | 0.00251907 |
| brightness | 0.00130158 | 0.00388344 | diversity | 0.00231533 | 0.00082766 |
| diversity | 0.00202130 | 0.00106388 | cover | -0.00216604 | 0.00121699 |
| streams | 0.00019616 | 0.00017941 | streams | -0.00040496 | 0.00019214 |
| water | 0.00004517 | 0.00006593 | water | -0.00003585 | 0.00005469 |
| solar | -0.41719249 | 0.29446112 | solar | -0.18397482 | 0.34802597 |
| solar$^2$ | 0.01273984 | 0.04990223 | solar$^2$ | 0.02188649 | 0.03483330 |
| human | 0.00196109 | 0.00292941 | terrain | -0.01554885 | 0.02586867 |
| human$^2$ | -8.40159E-6 | 7.75131E-6 | terrain$^2$ | 0.00004892 | 0.00135808 |
| family | -0.62769337 | 2.78276551 | human | 0.00674496 | 0.00142397 |
| family$^2$ | -0.20472671 | 1.92175196 | human$^2$ | -0.00001057 | 3.47E-6 |
| | | | family | 4.60242740 | 5.52993117 |
| | | | family$^2$ | -1.99927984 | 4.54324589 |

[†]"E-x" indicates that the value before the E is multiplied by $10^{-x}$ where x is the value following the E.

Table 3-4. Model validation results using k-fold cross validation. The correlation coefficient was averaged across the five repetitions. An averaged $r_s$ value of 1 indicated a perfect positive correlation. Values between 1 and 0.5 were considered to have a strong positive correlation, while coefficients between 0.5 and 0 were considered to represent a weak correlation. Negative coefficients were conversely interpreted. A value of 0 indicated no relationship. *B* refers to the base model, or variables from the base model that were too highly correlated with the relative probability value to be included in the model.

| **Model** | | **Number of bears** | **Number of locations** | **Spearman's rank ($r_s$)** |
|---|---|---|---|---|
| **Green-up** | | | | |
| | males | | | |
| | *B* | 24 | 341 | 0.850 |
| | females | | | |
| | *B* | 35 | 577 | 0.858 |
| | *B + males* | | | 0.846 |
| | family | | | |
| | *B* | 23 | 253 | 0.868 |
| | *B + males* | | | 0.831 |
| | *B + females* | | | 0.882 |
| | subadults | | | |
| | *B* | 12 | 125 | 0.376 |
| | *B + males* | | | 0.482 |
| | *B + females* | | | 0.474 |
| | *B + family* | | | 0.305 |
| **Green-down** | | | | |
| | males | | | |
| | *B* | 24 | 374 | 0.854 |
| | females | | | |
| | *B* | 33 | 747 | 0.894 |
| | *B + males* | | | 0.912 |
| | family | | | |
| | *B* | 22 | 235 | 0.865 |
| | *B + males* | | | 0.851 |
| | *B + females* | | | 0.796 |
| | subadults | | | |
| | *B* | 17 | 209 | 0.781 |
| | *B + males* | | | 0.649 |
| | *B + females* | | | 0.681 |
| | *B + family* | | | 0.681 |

Table 3-5a. Variable importance (I) and rankings for each subset of models for each cohort during the green-up period. Variable importance is derived by summing the $AIC_c$-derived weight of every model containing the variable within a subset of models. The top three variables are bolded.

| | ***Model: B*** | | |
|---|---|---|---|
| | Variable | I | Rank |
| males | greenness | 0.65 | 7 |
| | brightness | 0.39 | 11 |
| | **wetness** | **0.99** | **2** |
| | **wetness$^2$** | **1.00** | **1** |
| | diversity | 0.27 | 14 |
| | cover | 0.94 | 5 |
| | streams | 0.33 | 12 |
| | water | 0.30 | 13 |
| | solar | 0.52 | 9 |
| | solar$^2$ | 0.64 | 8 |
| | terrain | 0.42 | 10 |
| | terrain$^2$ | 0.86 | 6 |
| | **human** | **0.96** | **3** |
| | human$^2$ | 0.95 | 4 |

| | ***Model: B*** | | | ***Model: B + males*** | | |
|---|---|---|---|---|---|---|
| | Variable | I | Rank | Variable | I | Rank |
| females | **greenness** | **1.00** | **2** | greenness | -- | -- |
| | brightness | 0.28 | 14 | brightness | 0.28 | 14 |
| | wetness | 0.48 | 6 | wetness | 0.37 | 10 |
| | wetness$^2$ | 0.28 | 12 | wetness$^2$ | 0.29 | 13 |
| | diversity | 0.35 | 8 | diversity | 0.33 | 11 |
| | **cover** | **0.89** | **3** | cover | -- | -- |
| | streams | 0.33 | 10 | streams | 0.29 | 12 |
| | **water** | **1.00** | **1** | **water** | **1.00** | **1** |
| | solar | 0.28 | 13 | solar | 0.52 | 9 |
| | solar$^2$ | 0.29 | 11 | solar$^2$ | 0.66 | 6 |
| | terrain | 0.57 | 4 | terrain | 0.54 | 8 |
| | terrain$^2$ | 0.53 | 5 | terrain$^2$ | 0.67 | 5 |
| | human | 0.34 | 9 | **human** | **0.88** | **3** |
| | human$^2$ | 0.35 | 7 | human$^2$ | 0.58 | 7 |
| | cohort | -- | -- | **males** | **1.00** | **2** |
| | cohort$^2$ | -- | -- | males$^2$ | 0.85 | 4 |

Table 3-5a. Continued.

| | ***Model: B*** | | | ***Model: B + males*** | | | ***Model: B + females*** | | |
|---|---|---|---|---|---|---|---|---|---|
| | Variable | I | Rank | Variable | I | Rank | Variable | I | Rank |
| families | **greenness** | **0.80** | **3** | greenness | -- | -- | greenness | -- | -- |
| | **brightness** | **0.89** | **2** | **brightness** | **0.90** | **3** | **brightness** | **0.86** | **1** |
| | wetness | 0.51 | 8 | wetness | 0.41 | 10 | wetness | -- | -- |
| | wetness$^2$ | 0.55 | 7 | wetness$^2$ | 0.52 | 9 | wetness$^2$ | -- | -- |
| | diversity | 0.58 | 6 | diversity | 0.58 | 7 | diversity | 0.49 | 6 |
| | cover | 0.73 | 4 | cover | -- | -- | cover | 0.29 | 11 |
| | streams | 0.71 | 5 | streams | 0.75 | 6 | streams | 0.60 | 5 |
| | water | 0.38 | 12 | water | 0.34 | 11 | **water** | **0.83** | **3** |
| | solar | 0.30 | 13 | solar | 0.32 | 14 | solar | 0.25 | 12 |
| | solar$^2$ | 0.30 | 14 | solar$^2$ | 0.33 | 12 | solar$^2$ | 0.25 | 13 |
| | **terrain** | **0.98** | **1** | **terrain** | **0.98** | **1** | **terrain** | **0.84** | **2** |
| | terrain$^2$ | 0.39 | 11 | terrain$^2$ | 0.32 | 13 | terrain$^2$ | 0.39 | 8 |
| | human | 0.49 | 9 | human | 0.83 | 4 | human | 0.36 | 10 |
| | human$^2$ | 0.46 | 10 | human$^2$ | 0.78 | 5 | human$^2$ | 0.39 | 9 |
| | cohort | -- | -- | **males** | **0.96** | **2** | females | 0.42 | 7 |
| | cohort$^2$ | -- | -- | males$^2$ | 0.56 | 8 | females$^2$ | 0.69 | 4 |

| | ***Model: B*** | | | ***Model: B + males*** | | | ***Model: B + females*** | | | ***Model: B + families*** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Variable | I | Rank | Variable | I | Rank | Variable | I | Rank | Variable | I | Rank |
| subadults | greenness | 0.32 | 13 | greenness | -- | -- | greenness | -- | -- | greenness | 0.37 | 10 |
| | brightness | 0.32 | 14 | brightness | 0.31 | 13 | brightness | 0.28 | 13 | brightness | 0.31 | 12 |
| | wetness | 0.35 | 12 | wetness | 0.31 | 14 | wetness | -- | -- | wetness | 0.32 | 11 |
| | wetness$^2$ | 0.53 | 6 | wetness$^2$ | 0.39 | 11 | wetness$^2$ | -- | -- | wetness$^2$ | 0.52 | 4 |
| | **diversity** | **0.64** | **2** | diversity | 0.60 | 4 | diversity | 0.62 | 5 | **diversity** | **0.69** | **2** |
| | cover | 0.39 | 11 | cover | -- | -- | cover | 0.32 | 12 | cover | -- | -- |
| | streams | 0.39 | 10 | streams | 0.45 | 7 | streams | 0.39 | 11 | streams | 0.40 | 9 |
| | water | 0.40 | 9 | water | 0.41 | 9 | **water** | **0.65** | **3** | water | 0.31 | 13 |
| | **solar** | **0.85** | **1** | **solar** | **0.88** | **1** | **solar** | **0.88** | **1** | **solar** | **0.74** | **1** |
| | **solar$^2$** | **0.63** | **3** | **solar$^2$** | **0.70** | **3** | **solar$^2$** | **0.69** | **2** | solar$^2$ | 0.51 | 5 |
| | terrain | 0.43 | 7 | terrain | 0.35 | 12 | terrain | 0.42 | 9 | terrain | -- | -- |
| | terrain$^2$ | 0.61 | 4 | terrain$^2$ | 0.44 | 8 | terrain$^2$ | 0.64 | 4 | terrain$^2$ | -- | -- |
| | human | 0.42 | 8 | human | 0.40 | 10 | human | 0.41 | 10 | human | 0.42 | 8 |
| | human$^2$ | 0.59 | 5 | human$^2$ | 0.59 | 5 | human$^2$ | 0.55 | 7 | **human$^2$** | **0.56** | **3** |
| | cohort | -- | -- | **males** | **0.76** | **2** | females | 0.49 | 8 | family | 0.48 | 6 |
| | cohort$^2$ | -- | -- | males$^2$ | 0.56 | 6 | females$^2$ | 0.60 | 6 | family$^2$ | 0.47 | 7 |

Table 3-5b. Variable importance (I) and rankings for each subset of models for each cohort during the green-down period. Variable importance is derived by summing the AIC$_c$-derived weight of every model containing the variable within a subset of models. The top three variables are bolded.

| | **Model: *B*** | | |
|---|---|---|---|
| | Variable | I | Rank |
| males | greenness | 0.51 | 12 |
| | brightness | 0.85 | 7 |
| | wetness | 0.48 | 14 |
| | wetness$^2$ | 0.99 | 5 |
| | diversity | 0.72 | 8 |
| | cover | 0.50 | 13 |
| | **streams** | **1.00** | **3** |
| | water | 1.00 | 4 |
| | solar | 0.72 | 9 |
| | solar$^2$ | 0.86 | 6 |
| | terrain | 0.54 | 11 |
| | terrain$^2$ | 0.66 | 10 |
| | **human** | **1.00** | **1** |
| | **human$^2$** | **1.00** | **2** |

| | **Model: *B*** | | | **Model: *B* + males** | | |
|---|---|---|---|---|---|---|
| | Variable | I | Rank | variable | I | Rank |
| females | greenness | 1.00 | 5 | greenness | -- | -- |
| | brightness | 0.87 | 6 | brightness | 0.58 | 10 |
| | wetness | 1.00 | 4 | **wetness** | **1.00** | **1** |
| | **wetness$^2$** | **1.00** | **3** | **wetness$^2$** | **1.00** | **3** |
| | diversity | 0.56 | 12 | diversity | 0.35 | 13 |
| | cover | 0.32 | 14 | cover | 0.85 | 5 |
| | **streams** | **1.00** | **1** | **streams** | **1.00** | **2** |
| | **water** | **1.00** | **2** | water | 1.00 | 4 |
| | solar | 0.67 | 9 | solar | 0.61 | 6 |
| | solar$^2$ | 0.56 | 11 | solar$^2$ | 0.56 | 11 |
| | terrain | 0.47 | 13 | terrain | 0.59 | 9 |
| | terrain$^2$ | 0.68 | 8 | terrain$^2$ | 0.60 | 8 |
| | human | 0.76 | 7 | human | 0.30 | 14 |
| | human$^2$ | 0.61 | 10 | human$^2$ | 0.30 | 15 |
| | cohort | -- | -- | males | 0.54 | 12 |
| | cohort$^2$ | -- | -- | males$^2$ | 0.61 | 7 |

Table 3-5b. Continued.

families

| **Model: *B*** | | | **Model: *B* + males** | | | **Model: *B* + females** | | |
|---|---|---|---|---|---|---|---|---|
| Variable | I | Rank | Variable | I | Rank | Variable | I | Rank |
| greenness | 0.50 | 10 | greenness | -- | -- | greenness | -- | -- |
| brightness | 0.50 | 11 | brightness | 0.39 | 15 | brightness | 0.28 | 13 |
| **wetness** | **0.99** | **3** | **wetness** | **0.99** | **1** | wetness | -- | -- |
| **wetness$^2$** | **1.00** | **2** | **wetness$^2$** | **0.97** | **3** | wetness$^2$ | -- | -- |
| diversity | 0.71 | 7 | diversity | 0.57 | 8 | diversity | 0.39 | 8 |
| cover | 0.54 | 8 | cover | 0.58 | 7 | cover | 0.32 | 11 |
| **streams** | **1.00** | **1** | streams | 0.92 | 4 | streams | 0.31 | 12 |
| water | 0.98 | 4 | water | 0.73 | 5 | water | 0.33 | 10 |
| solar | 0.47 | 12 | solar | 0.45 | 13 | **solar** | **0.79** | **3** |
| solar$^2$ | 0.46 | 13 | solar$^2$ | 0.44 | 14 | solar$^2$ | 0.56 | 6 |
| terrain | 0.97 | 5 | **terrain** | **0.98** | **2** | **terrain** | **0.85** | **2** |
| terrain$^2$ | 0.84 | 6 | terrain$^2$ | 0.72 | 6 | terrain$^2$ | 0.75 | 4 |
| human | 0.38 | 14 | human | 0.54 | 9 | human | 0.59 | 5 |
| human$^2$ | 0.52 | 9 | human$^2$ | 0.49 | 10 | human$^2$ | 0.50 | 7 |
| cohort | -- | -- | males | 0.45 | 11 | females | 0.36 | 9 |
| cohort$^2$ | -- | -- | males$^2$ | 0.45 | 12 | **females$^2$** | **0.92** | **1** |

subadults

| **Model: *B*** | | | **Model: *B* + males** | | | **Model: *B* + females** | | | **Model: *B* + families** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Variable | I | Rank | Variable | I | Rank | Variable | I | Rank | Variable | I | Rank |
| greenness | 0.31 | 12 | greenness | -- | -- | greenness | -- | -- | greenness | -- | -- |
| brightness | 0.33 | 8 | brightness | 0.55 | 10 | brightness | 0.39 | 8 | brightness | 0.41 | 8 |
| wetness | 0.88 | 4 | wetness | 0.78 | 7 | wetness | -- | -- | wetness | -- | -- |
| wetness$^2$ | 0.32 | 10 | wetness$^2$ | 0.52 | 12 | wetness$^2$ | -- | -- | wetness$^2$ | -- | -- |
| **diversity** | **0.94** | **3** | **diversity** | **0.98** | **3** | **diversity** | **0.94** | **3** | **diversity** | **0.95** | **3** |
| cover | 0.76 | 6 | cover | 0.94 | 5 | cover | 0.68 | 5 | cover | 0.67 | 5 |
| streams | 0.85 | 5 | streams | 0.97 | 4 | streams | 0.77 | 4 | streams | 0.79 | 4 |
| water | 0.34 | 7 | water | 0.72 | 8 | water | 0.32 | 11 | water | 0.32 | 11 |
| solar | 0.32 | 9 | solar | 0.43 | 15 | solar | 0.32 | 10 | solar | 0.32 | 12 |
| solar$^2$ | 0.31 | 13 | solar$^2$ | 0.48 | 14 | solar$^2$ | 0.32 | 9 | solar$^2$ | 0.32 | 10 |
| terrain | 0.31 | 11 | terrain | 0.49 | 13 | terrain | 0.30 | 12 | terrain | 0.33 | 9 |
| terrain$^2$ | 0.30 | 14 | terrain$^2$ | 0.52 | 11 | terrain$^2$ | 0.29 | 13 | terrain$^2$ | 0.30 | 13 |
| **human** | **1.00** | **1** | **human** | **1.00** | **1** | **human** | **1.00** | **1** | **human** | **1.00** | **1** |
| **human$^2$** | **1.00** | **2** | **human$^2$** | **1.00** | **2** | **human$^2$** | **1.00** | **2** | **human$^2$** | **1.00** | **2** |
| cohort | -- | -- | males | 0.65 | 9 | females | 0.53 | 6 | family | 0.53 | 6 |
| cohort$^2$ | -- | -- | males$^2$ | 0.85 | 6 | females$^2$ | 0.43 | 7 | family$^2$ | 0.46 | 7 |

## Comparison of Demographic Groups

During the green-up period, lone adult females and family groups were more strongly influenced than other cohorts by phytomass distribution (Table 3-3b). Adult males were more strongly influenced by human infrastructure density compared to other cohorts. Diversity indices did not vary among cohorts either (Table 3-6). Adult males and lone adult females were found closest to cover in the green-up period, while family groups and subadults were similar in distance from cover. There were no significant differences among cohorts for distance to cover during the green-down period (Table 3-6).

During the green-up period, there was a successive increase in use of rugged terrain, corresponding to status (Table 3-6). Adult males used the least rugged habitats, followed by lone adult females and then family groups. Subadults used habitats with a similar mean value of terrain ruggedness as lone adult females. The standard error for terrain ruggedness values for family groups was smaller than for the other cohorts, indicating that habitat use by family groups was constrained to a tighter range of values for terrain ruggedness (Table 3-6). Family groups exhibited the strongest selection among cohorts for rugged terrain (Figure 3-2).

The pattern of selection for terrain ruggedness did not change between feeding seasons (Table 3-6). Subadults were, again, found in habitats with a similar mean value of terrain ruggedness to lone adult females (Table 3-6). While males used habitats that were slightly lower in ruggedness values than in the green-up period, values for lone adult females and subadults did not change. Terrain ruggedness values for family groups decreased, but were still higher than values for males and lone females.

During green-up, adult males occurred in locations with the highest density of infrastructure (Figure 3-3a). All other cohorts occupied areas with similar infrastructure density (Table 3-6). In the green-down period, males still occupied locations with higher human infrastructure density than for other cohorts (Figure 3-3b), but there were significant differences among other cohorts.

Table 3-6. Mean, standard errors (SE) for each cohort within each season, Welch's $F$-statistic and $P$-values for each phenological season (green-up df = 3, $n$ = 1295 and green-down df = 3, $n$ = 1545). Differences among groups (grp) were determined in post-hoc comparison. Groups that were not significantly different from each other have same letter coding.

| Variable | Green-up<br>Males |  |  | Females |  |  | Family |  |  | Subadult |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | mean | SE | grp | mean | SE | grp | mean | SE | grp | mean | SE | grp | Welch's $F$-statistic | $P$ |
| greenness | -1.02 | 1.13 | A | -1.77 | 0.96 | A | -9.82 | 1.78 | B | -9.56 | 2.25 | B | 9.204 | 0.000 |
| brightness | 107.83 | 1.41 | A | 110.68 | 1.28 | A | 121.51 | 2.30 | B | 109.41 | 2.53 | A | 8.769 | 0.000 |
| wetness | -1.44 | 0.59 | A | -0.34 | 0.69 | A | -1.65 | 1.40 | A | 2.00 | 1.70 | A | 1.551 | 0.201 |
| diversity | 101.50 | 4.38 | A | 101.99 | 3.53 | A | 102.66 | 5.24 | A | 108.10 | 7.66 | A | 0.202 | 0.895 |
| cover | 28.17 | 2.98 | A | 35.01 | 2.50 | A | 52.68 | 4.07 | B | 47.05 | 5.80 | B | 9.048 | 0.000 |
| streams | 468 | 25 | A | 485 | 18 | A | 593 | 33 | B | 569 | 46 | AB | 4.261 | 0.006 |
| water | 1704 | 79 | AC | 1527 | 55 | A | 2370 | 96 | B | 2006 | 148 | BC | 20.594 | 0.000 |
| solar | 496261 | 4343 | AB | 505398 | 4011 | A | 510702 | 7763 | A | 475540 | 10599 | B | 3.227 | 0.022 |
| terrain | 0.0799 | 0.0029 | A | 0.0948 | 0.0024 | B | 0.1291 | 0.0033 | C | 0.0959 | 0.0051 | B | 42.530 | 0.000 |
| human | 71.63 | 6.24 | A | 46.43 | 3.98 | B | 29.63 | 5.43 | B | 42.91 | 7.11 | B | 8.680 | 0.000 |
| ‡male_gu | 0.37 | 0.01 | A | 0.35 | 0.00 | B | 0.29 | 0.01 | C | 0.32 | 0.01 | BC | 21.5635.397 | 0.000 |
| female_gu | 0.86 | 0.00 | A | 0.86 | 0.00 | A | 0.79 | 0.01 | B | 0.81 | 0.01 | B | 19.6812.612 | 0.000 |
| family_gu | 0.86 | 0.00 | A | 0.86 | 0.00 | A | 0.85 | 0.01 | A | 0.85 | 0.01 | A | 3.0536.432 | 0.029 |

| Variable | Green-down<br>Males |  |  | Females |  |  | Family |  |  | Subadult |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | mean | SE | grp | mean | SE | grp | mean | SE | grp | mean | SE | grp | Welch's $F$-statistic | $P$ |
| greenness | -4.66 | 1.00 | AB | -2.58 | 0.73 | A | -3.53 | 1.30 | AB | -6.99 | 1.42 | B | 2.872 | 0.036 |
| brightness | 107.77 | 1.36 | A | 115.83 | 0.99 | B | 114.52 | 1.65 | B | 112.19 | 2.07 | A | 7.990 | 0.000 |
| wetness | -0.79 | 0.67 | A | -3.67 | 0.47 | B | -3.31 | 0.79 | AB | -2.22 | 1.18 | AB | 4.362 | 0.005 |
| diversity | 111.37 | 4.30 | A | 105.36 | 3.03 | A | 111.26 | 5.45 | A | 115.66 | 5.83 | A | 1.073 | 0.360 |
| cover | 35.99 | 3.09 | A | 42.22 | 2.29 | A | 39.81 | 4.18 | A | 40.15 | 4.48 | A | 0.875 | 0.454 |
| streams | 380 | 21 | A | 379 | 13 | A | 367 | 23 | A | 432 | 25 | A | 1.459 | 0.225 |
| water | 1256 | 70 | A | 1570 | 48 | B | 1694 | 91 | B | 1690 | 102 | B | 7.210 | 0.000 |
| solar | 496256 | 3283 | A | 519248 | 3204 | B | 498245 | 6680 | A | 504136 | 6782 | AB | 9.047 | 0.000 |
| terrain | 0.0623 | 0.0027 | A | 0.0952 | 0.0021 | B | 0.1056 | 0.0034 | C | 0.0870 | 0.0042 | B | 42.066 | 0.000 |
| human | 112.11 | 7.06 | A | 54.43 | 3.77 | B | 34.51 | 4.77 | C | 83.23 | 8.27 | D | 30.932 | 0.000 |
| ‡male_gd | 0.37 | 0.01 | A | 0.35 | 0.00 | B | 0.35 | 0.01 | B | 0.34 | 0.01 | B | 7.645 | 0.004 |
| female_gd | 0.87 | 0.00 | A | 0.86 | 0.00 | A | 0.86 | 0.01 | AB | 0.84 | 0.01 | B | 4.545 | 0.000 |
| family_gd | 0.85 | 0.00 | A | 0.86 | 0.00 | B | 0.86 | 0.00 | B | 0.84 | 0.00 | A | 8.779 | 0.000 |

‡ gu = green-up, gd = green-down

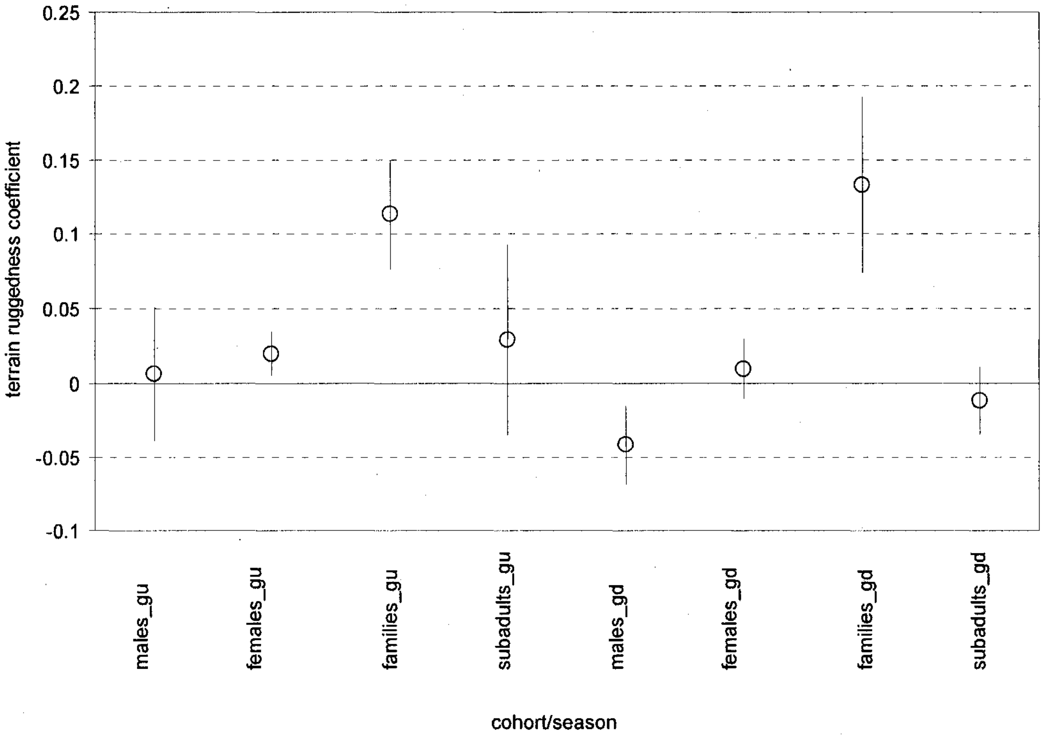

Figure 3-2. Estimated coefficients and confidence intervals for terrain ruggedness base models for each cohort in each feeding season (gu = green-up, gd = green-down). Circles (O) indicate the value for the coefficients. Bars indicate the 95% confidence interval for the coefficient estimate.

Subadults occupied areas with the next highest values, followed by lone adult females, then family groups (Table 3-6).

When compared to lone adult females and subadults in the green-up, family groups occupied habitats that had a lower mean relative probability for adult male presence. In the green-down period; however, all three cohorts used habitats with similar relative probability for adult male presence (Table 3-6). In comparison to other cohorts, family groups occupied habitats with significantly lower relative probability of encountering lone adult females. In the green-up period, relative probability of encountering a lone adult female was similar for adult males and family groups (Table 3-6).

## DISCUSSION

Though wetness was the most influential variable on male habitat selection during the green-up period, the effect did not represent selection for areas productive in forage. Analyses in Chapter 2 showed that forage productivity in Kluane was positively correlated with wetness, but males selected for dry-mesic or xeric habitats. In fact, in most models for all cohorts, high wetness was selected against. The analyses in Chapter 2, however, excluded glaciated and snow covered areas, and wetness values were constrained to the low end of those available in the landscape window for analyses in this chapter. Therefore, the inconsistency between the coefficients is probably because two different scales of effect were being modeled for wetness. Within the low end of the range of wetness values, males may select for moist-mesic areas – an effect that is not detectable within linear modeling constraints over a wider range of wetness values. Given that greenness (perhaps the most important variable for predicting forage productivity; Chapter 2) and distance to riparian areas were ranked under infrastructure density and distance to cover, it is unlikely that forage productivity was the primary influencing variable for habitat selection, and selection for dry areas probably represents use of areas where snow cover first disappeared.

Infrastructure density was the primary variable affecting adult male habitat selection during the active period; males occupied habitats with intermediate values. Selection for these areas probably reflects decisions to maximize food intake (especially given secondary selection for habitats with productive forage) while minimizing mortality risk (Frid and Dill 2002). Where infrastructure density was low (e.g., subalpine and alpine), forage productivity, reckoned by greenness values, also appeared to be low. Bears would not preferentially forage where they had to regularly expend more energy than they were procuring by obtaining food (Gendre et al. 2004). Conversely, developments were often in valley bottoms, which were more abundant with bear foods than elsewhere (McCormick 1999). Areas with increased human activities cause increased disturbance for bears as they forage or rest. Bears heighten vigilance, simultaneously reducing food consumption and increasing energy expenditure (White et al. 1999, Pitts 2001). Increased intensity of human activities also increases mortality risk to bears (Nielsen et al. 2004a). Therefore, bears may avoid developed areas by a sufficient distance so they will not be disturbed (Mattson et al.1987, McLellan and Shackleton 1988, McLellan 1990).

Males and other cohorts used habitats near developments concurrently with use of areas close to cover. When human activity is present, bears have been observed to forage closer to cover than when human activity is restricted (Gunther 1990), suggesting that although edge habitats may be rich in key bear foods (Hamer and Herrero 1987, Hamer et al. 1991, Mattson 1997), security also appears to be an important primary function of cover (Gunther 1990, Theberge 2002). In some regions bears have been found to select for edge habitats even when the areas are depauperate of critical foods (Nielson 2004). The relationship between human activity and cover requirements for bears in Kluane was consistent with bears using edges for security. Like the bears that Gunther (1990) observed, I found adult males and lone adult females, which occurred in areas with high values of infrastructure density, were closer to cover than family groups and subadults, which occurred in areas with low values of infrastructure density. For cohorts that showed an increased use of habitats with human activity in the green-down period, I observed a commensurate decrease in the average distance to cover.

Forage productivity variables such as greenness in the green-up and distance to streams and water bodies in the green-down were secondary selection mechanisms for males. Greenness was a better indicator than distance to riparian areas of overall forage productivity and an important predictor for abundance of legumes – key forage species during the green-up. Distance to riparian areas was a better predictor of the number of berries than greenness, and berries were more important forage in the green-down (McCann 1998).

Segregation between adult males and lone adult females appeared to be primarily driven by differential nutritional requirements rather than conspecific avoidance. Females used side slopes in the green-up period (Figure 3-3c); but distance to water and greenness were primary habitat selection variables. Similarly, in the green-down, variables relating to forage productivity, like distance to riparian areas and solar radiation, were more important than security-related variables such as terrain ruggedness or distance to cover. Though the relative probability distribution of males was the second most influential variable in the pertinent green-up model, the selection coefficient for the linear term was positive and likely reflects overlap in habitat use when males sought females during the mating season (Mace and Waller 1997b). The probability distribution of males in the green-down period was not as influential on lone adult female distribution as during the green-up period.

Lone adult females consistently occupied habitats with lower infrastructure densities, and further from developments (Figure 3-3d), than the habitats occupied by adult males. This pattern was contrary to findings in areas like the Flathead region of British Columbia (McLellan 1990) and Yellowstone National Park (Mattson et al. 1987), but consistent with findings in northwestern Montana (Zager 1980) and Jasper National Park (Russell et al. 1979). In the Flathead and Yellowstone, females, more so than males, used habitats closer to developments, presumably because the displacement of adult males by humans provided refuge for females to forage (McLellan 1990). However, valleys in the Flathead and Yellowstone were expansive and high quality forage was distributed throughout the lowland areas. Like Northwestern Montana and Jasper, Kluane's high quality forage was largely constrained within narrow valleys. Most human activities also occurred in the narrow valleys. Where space was confined, males may have been distributed closer to developments than they would have been in more expansive areas. Females may have been pushed further from developments and onto steeper slopes by the secondary effects of competition from adult males. The constriction of space between developments and adult males' range for foraging may have meant that females (and family groups) could not occupy habitats on the human-activity side of a core area for adult male distribution. Additionally, in Kluane, areas closed to developments had a relatively high rate of human-caused bear mortality.

Analyses to examine segregation between family groups and higher status cohorts produced mixed results. Specific hypotheses used by Bleich et al. (1997) to test the predation hypothesis were: 1) females will inhabit areas with more rugged terrain, and 2) females will inhabit areas with lower predator abundance (or in the case of grizzly bears, probability of encountering conspecifics). Family groups in Kluane used significantly more rugged habitat throughout the active period (Figure 3-3e, Figure 3-3f) than used by other cohorts and terrain ruggedness was the primary habitat selection variable in both feeding periods. However, probability of a family group encountering a conspecific was lower than for other cohorts only in the green-up, and in both feeding periods forage productivity variables were more influential on habitat selection than were conspecific distributions.

Irrespective of the mixed results, conspecific avoidance was probably the primary factor affecting segregation of family groups from other cohorts in both feeding periods. I suspected that family groups used a mix of real time information on the contemporaneous location of conspecifics, and generalized probabilistic information based on experience to avoid potentially aggressive encounters. However, rugged areas had lower bear food abundance compared to other habitat types (Douglas 1974, McCormick 1999; see Chapter 2). Relative to lush valley bottoms bears probably needed to make significant energy investments in rugged habitats to obtain adequate forage, forgoing foraging efficiency. Given distinctive use of rugged areas by family groups but not other cohorts, these areas were probably used primarily as security habitat for raising cubs (Pearson 1975, Stemlock 1981, Darling 1987). Rather than use probabilistic information on conspecific distribution to guide decisions on habitat selection, family groups may have manifested avoidance by selecting for landscape features, such as rugged areas, which females learned through experience provides security.

Subadult habitat selection patterns during the green-up period (Figure 3-3g) were difficult to interpret. Habitat selection in the green-down period was strongly influenced by human land-use (Figure 3-3h). In the green-up period, areas with high and low amounts of solar radiation were most important to subadults; however, bipartite selection of this variable appeared spurious. High forage abundance was associated with intermediate values of radiation. Areas with high solar radiation were high elevation, south facing aspects and may have been areas of early snow melt or areas close to dens; but, areas with low radiation were high elevation north facing aspects and had no known advantage for foraging or security. Diversity was the next most important variable during the green-up. Diverse areas in Kluane were edge habitats that probably had high foraging value (Schleyer 1983), but exclusive use of these areas by subadults and no other cohort suggests that unique resources were being utilized. However, other variables that relate to forage productivity were not highly ranked, and there is no information on forage availability in edge habitats in Kluane, so it is not possible to identify these resources. Anomalous patterns of habitat selection during hypophagia probably reflect differential response to human activity, foraging opportunities, and habitat selection uncertainty while dispersing. The irregularity of results is further corroborated by poor model fit. Selection patterns represent only a few individuals. 'Use' points for subadult green-up models were 45% comprised of three individuals, and 49% comprised of data from only two years. Habitat selection patterns were also obfuscated by pooling of males and females. Females are philopatric so they may select habitats closer to their mother, while males disperse further (Proctor 2003, Nielsen 2005). Separating data on males from that for females might show more interpretable patterns of habitat use.

Lone adult and subadult grizzly bear distribution was most affected by forage availability and human activity patterns. Family groups appeared to be most influenced by conspecifics and selected areas that provided security. However, there were two major limitations to my interpretations. First, I examined the response of each status group to the probability of encountering another bear, generalized at the population-level, within a home range and at a small patch size (30 m). I did not consider other scales of habitat selection in these analyses. A response to distribution of conspecifics may be detectable at higher orders of habitat selection, such as within the range of a daily foraging bout and at the home range-level (Theberge 2002, McLoughlin et al. 2002). Second, my data did not represent crepuscular or nocturnal activity by bears, when human activity is reduced over the landscape. Night fall acts like cover for bears and might mitigate the effects of human activity (McLellan 1990, Olson et al. 1997). This may create temporal refugia and allow family groups to use areas that would otherwise only be used by adult males (Olson et al. 1994). I also did not examine the effect of changing resource availability on habitat selection patterns. The effects of resource competition may be more visible when resources are scarce. Pearson (1975) found that the rugged areas in Kluane were used more by low status cohorts in years when there was berry crop failure. If I looked only at years when there was berry crop failure, thereby removing statistical 'noise' related to high abundance of food resources, I may have seen strong displacement effects by higher status cohorts (Mysterud and Ims 1998).

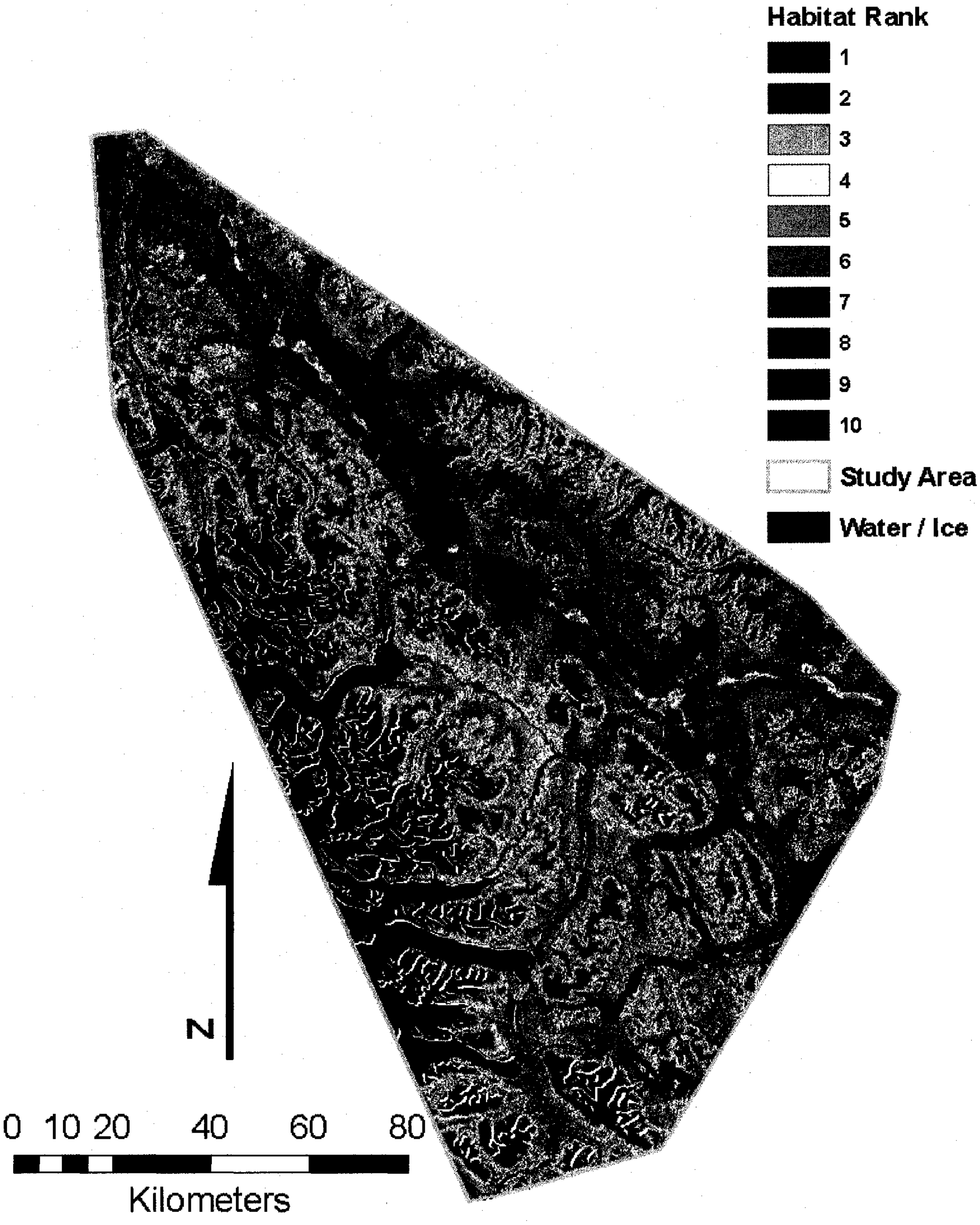

Figure 3-3a. Ranked adult male grizzly bear habitat map for the Kluane Region during the green-up period. A value of 1 represents low quality habitat. A value of 10 represents high quality habitat.

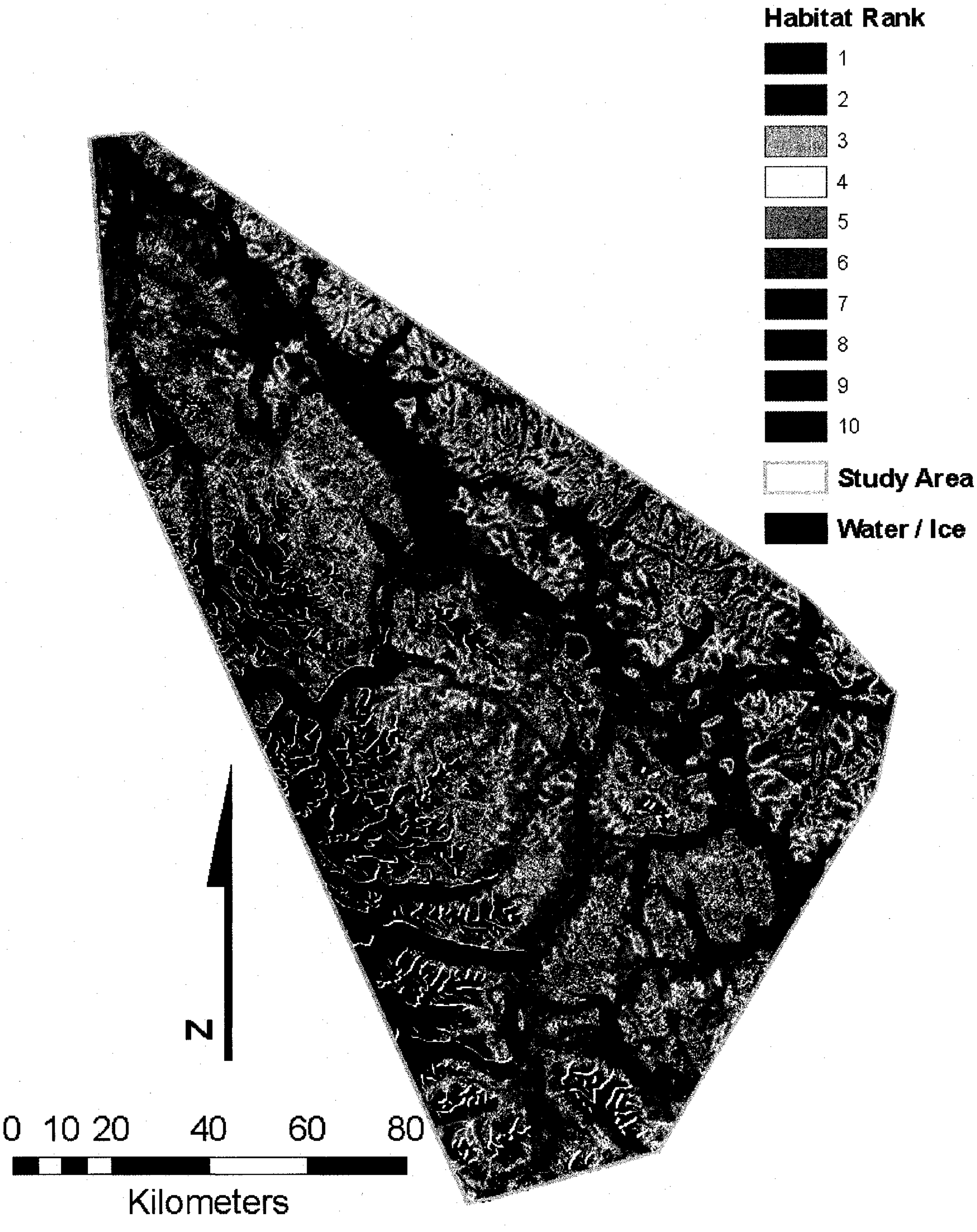

Figure 3-3b. Ranked adult male grizzly bear habitat map for the Kluane Region during the green-down period. A value of 1 represents low quality habitat. A value of 10 represents high quality habitat.

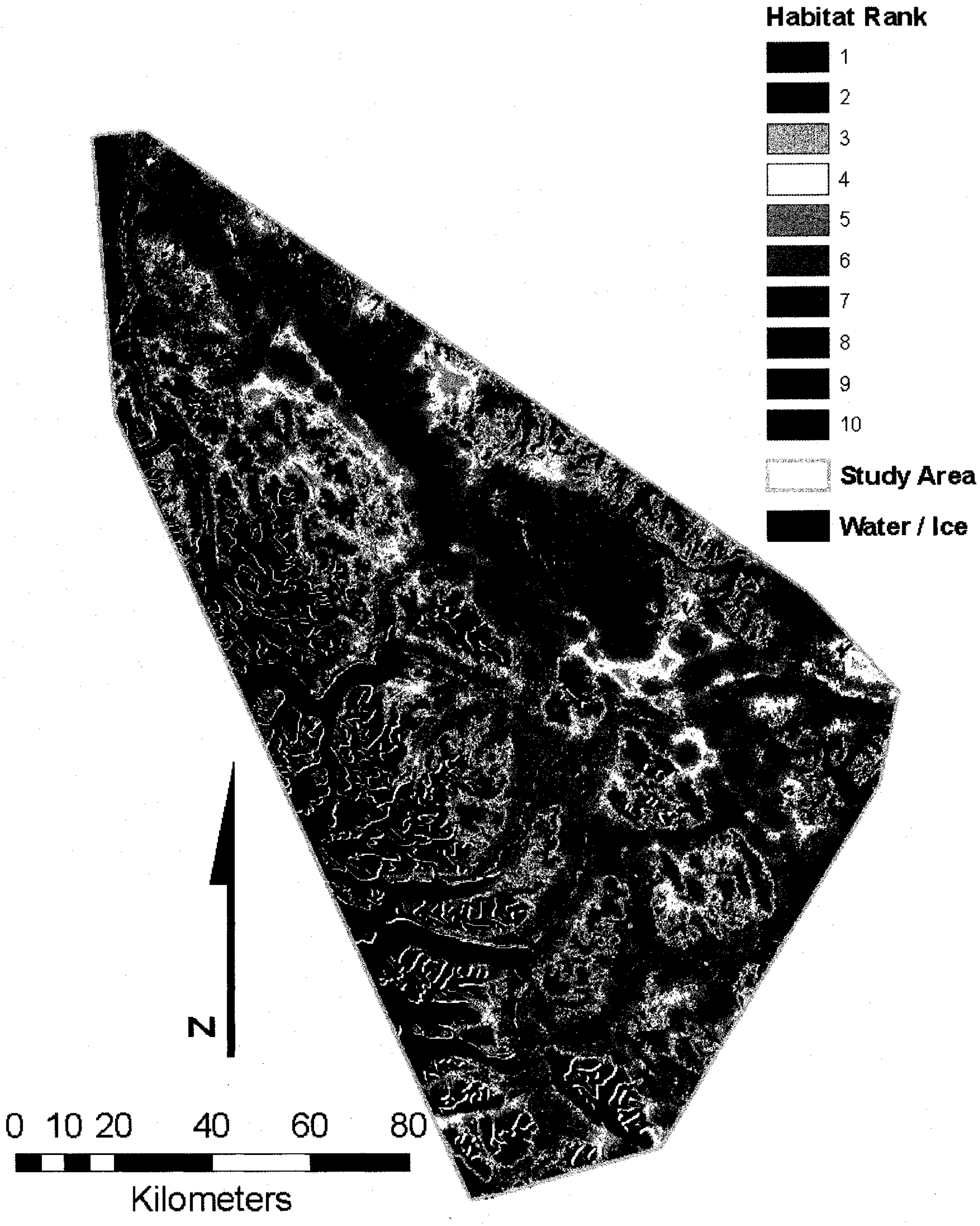

Figure 3-3c. Ranked lone adult female grizzly bear habitat map for the Kluane Region during the green-up period. A value of 1 represents low quality habitat. A value of 10 represents high quality habitat.

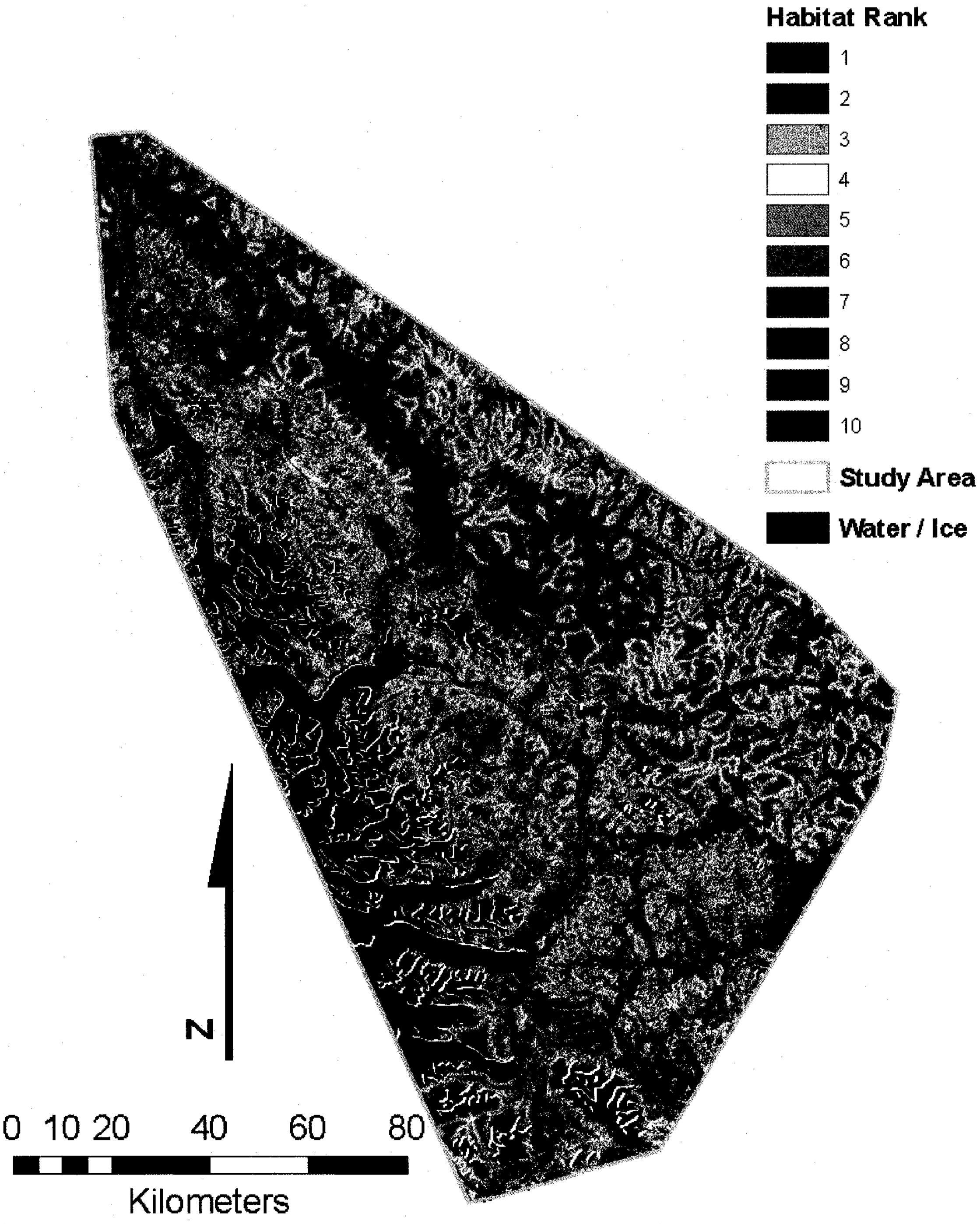

Figure 3-3d. Ranked lone adult female grizzly bear habitat map for the Kluane Region during the green-down period. A value of 1 represents low quality habitat. A value of 10 represents high quality habitat.

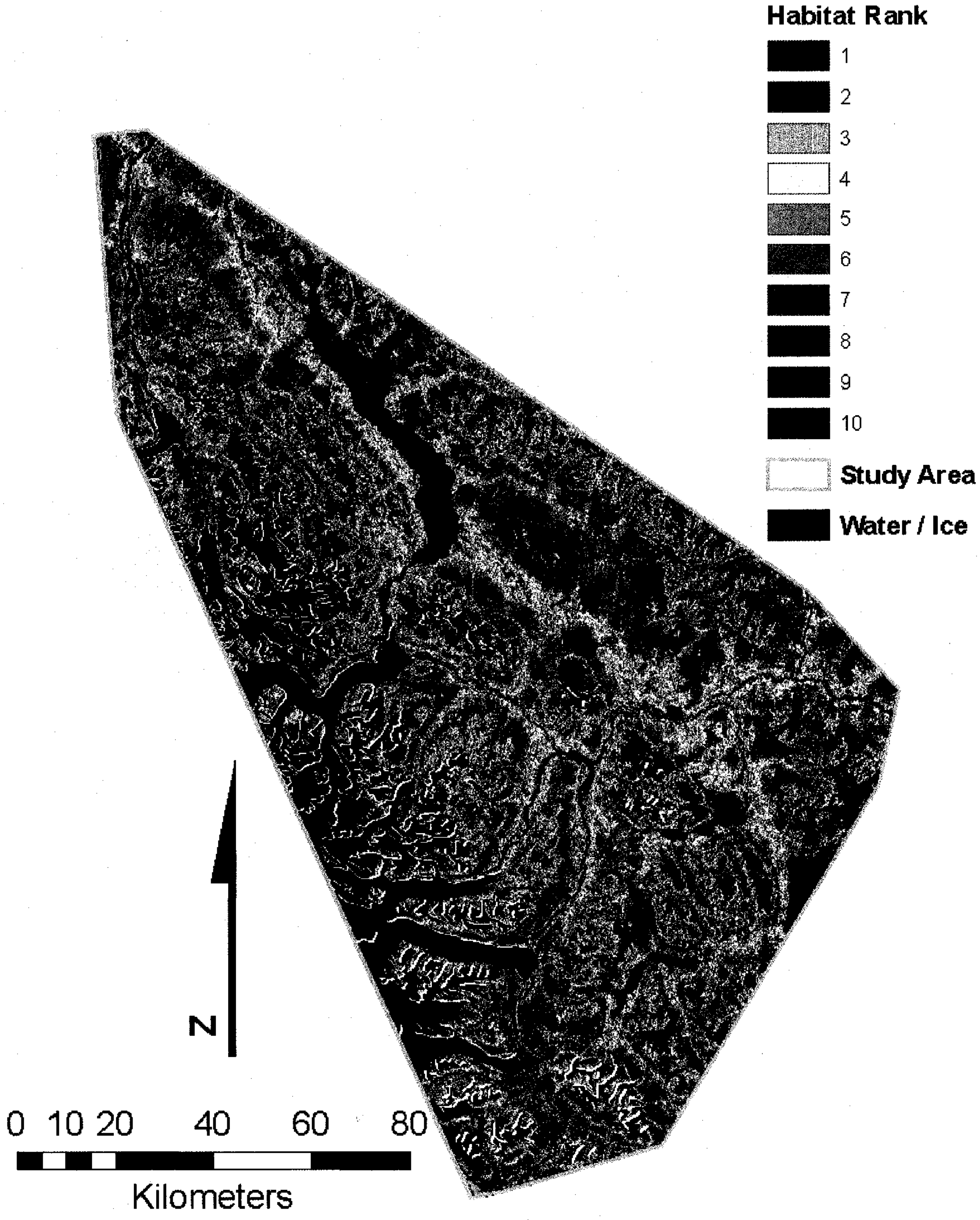

Figure 3-3e. Ranked family group grizzly bear habitat map for the Kluane Region during the green-up period. A value of 1 represents low quality habitat. A value of 10 represents high quality habitat.

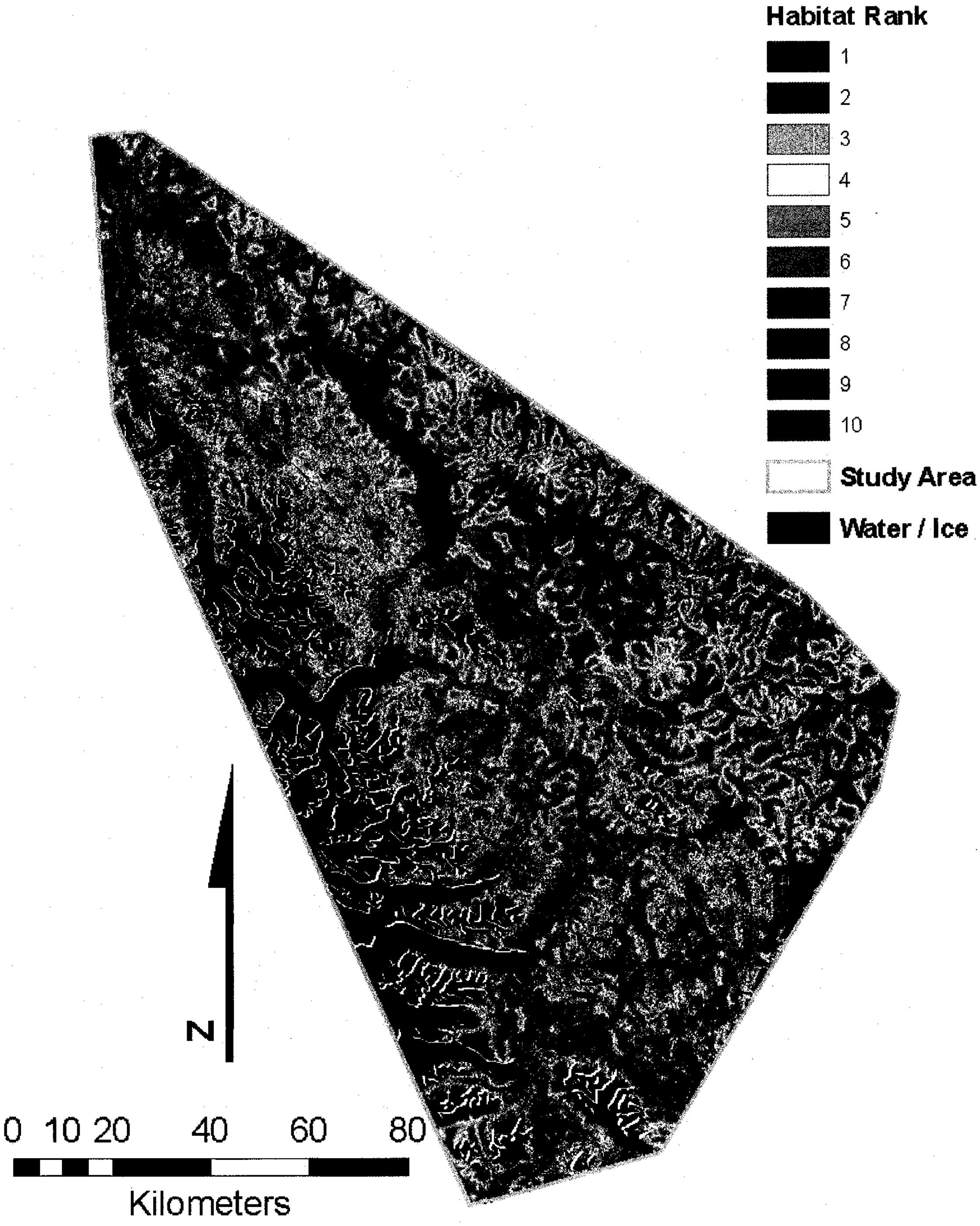

Figure 3-3f. Ranked family group grizzly bear habitat map for the Kluane Region during the green-down period. A value of 1 represents low quality habitat. A value of 10 represents high quality habitat.

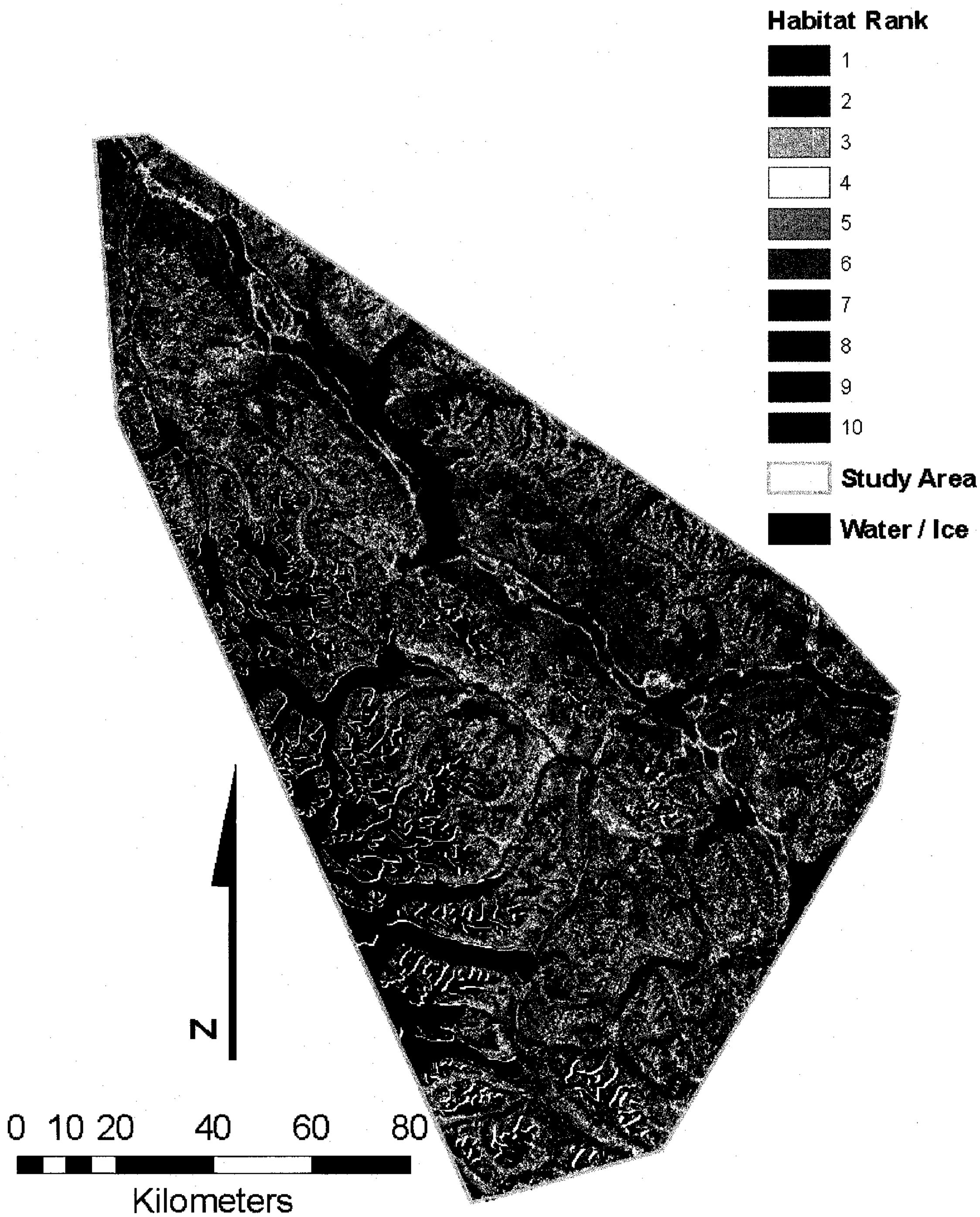

Figure 3-3g. Ranked subadult grizzly bear habitat map for the Kluane Region during the green-up period. A value of 1 represents low quality habitat. A value of 10 represents high quality habitat.

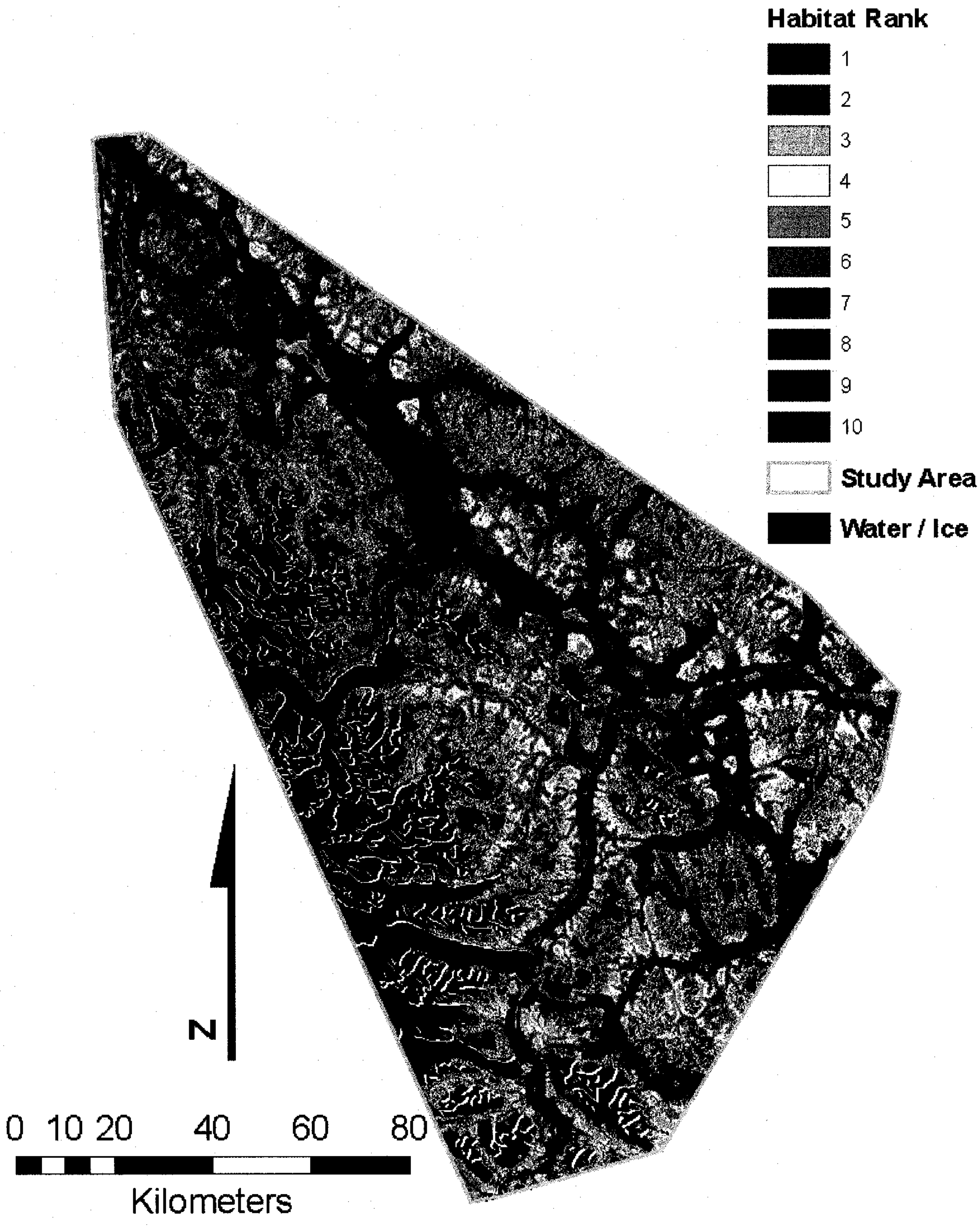

Figure 3-3h. Ranked subadult grizzly bear habitat map for the Kluane Region during the green-down period. A value of 1 represents low quality habitat. A value of 10 represents high quality habitat.

## CONCLUSIONS AND IMPLICATIONS

Three factors influence grizzly bear distribution: 1) the distribution of forage, 2) the distribution of human activity, and 3) the distribution of other bears. Seasonal patterns of habitat use for all status groups in Kluane followed patterns of habitat use reported by other studies in northern and interior mountainous areas (Curatolo and Moore 1975, Pearson 1975, Reynold and Hechtel 1980, Murie 1981, Stemlock 1981, Hamer 1985, Mattson et al. 1987, Mace and Waller 1997a, McLoughlin et al. 2002, Nielsen 2005), but these studies focused on the influence of forage distribution and human activity, and did not explicitly investigate the influence of conspecific distribution on habitat use patterns of lower status groups. This is the first study to incorporated conspecific distributions as a covariate in habitat models. By incorporating conspecific distribution as an explanatory variable it was apparent that, although competition or infanticide risk did not always appear to drive segregation, all lower status cohorts showed some avoidance of higher status individuals.

This study substantiates three major implications for habitat selection studies. First, my findings reinforce the importance of developing separate habitat models for each cohort. Where the impacts of human activities are being considered on a population, understanding the distribution of each cohort helps researchers understand which cohorts are most likely to be impacted so the effects of human activity on population change can be more accurately estimated. For example, if an area that is key habitat for family groups but not adult males is developed for human use, the productivity of the population will be impacted.

Second, studies sometimes pool relocation data for lone adult females with that for family groups. However, where pooling of data is necessary, in some circumstances it may be more appropriate to pool lone adult female with adult male data, rather than family group data. For many variables (e.g., ten variables during the green-up and five variables during the green-down) there was no significant difference in mean selection values between lone adult females and adult males, and during the green-up, lone adult females selected similar habitats as males (i.e., with a relatively high probability of adult male occupancy).

Last, competition for resources or infanticide could exacerbate the impacts of human activity on bear populations. Alterations to habitats used by adult males and lone adult females could push them into regions where family groups refuge. If segregation is a function of avoidance of conspecifics, and family groups occupy poor quality habitats to avoid conspecifics, they could be pushed into increasingly marginal habitats. Alternatively, if family groups had nowhere to move, competition for resources and rates of infanticide would increase. Cub survival may suffer as a consequence and the productivity of the population could decline. These effects can be accounted for by incorporating conspecific distribution as an explicit factor in habitat models.

# Chapter Four: Trends and patterns in human-bear interactions and human-caused grizzly bear mortality in the southwest Yukon, Canada

## INTRODUCTION

Over the last century grizzly bear populations have experienced a rapid decline throughout most of North America (Servheen 1999, Mattson and Merrill 2002, Ross 2002). Grizzly bears were eliminated from 98% of their original range in the contiguous United States between 1850 and 1970 (Mattson and Merrill 2002). While range contraction was less pronounced in Canada, the last individuals of the prairie grizzly bear population disappeared from the Cypress Hills area of Saskatchewan and Alberta around 1900 (Nielsen 1975, Ross 2002). Historically, grizzly bear mortality and extirpation has been linked with human land-use (Storer and Tevis 1955, Noble 1972, Nielsen 1975, Young and Beyers 1980, McCrory and Herrero 1982, Brown 1985). In North America and globally the extirpation of grizzly bear populations is the result of direct human-caused mortality, and conversion of natural habitat to agricultural, residential, and urban land-use (Horejsi 1989).

The historical association between human land-use and grizzly bear mortality prevails (McLellan and Shackleton 1988, Mattson et al. 1996a, Gibeau et al. 1996). Mortality, especially of adult females, is the primary factor limiting most grizzly bear populations (Knight and Eberhardt 1985, Knight et al. 1988). Human-caused mortality has significantly influenced both grizzly bear demography and population exchange even in the most pristine grizzly bear habitat, sometimes resulting in effective population isolation (Lodé 2000). While acceptable harvest mortality rates (Bunnell and Tait 1980, Harris 1984) have been identified by North American management agencies, the risk of mortality posed to bears by other human activities is not easily measured and can be substantial (Doak 1995, McLellan et al. 1999).

Human-caused mortality, particularly in systems that allow hunting, can account for more than 75% of all grizzly bear mortality (McLellan et al. 1999). Mortality data from the Kluane Region are similar to those found elsewhere in North America (McCann 1998). They show that human-caused mortality far outweighs natural mortality (Craighead et al. 1988, Carr 1989, McLellan 1990, Dood and Pac 1993, Gunson 1995, Gibeau et al. 1996; McCann 1998). The rate of bear mortality due to management actions in Kluane is equivalent to the harvest rate (McCann 1998), and the combined mortality rate often exceeds the annual prescribed mortality rate for the population (Yukon Territorial Government 2003). Pearson (1975) predicted that without intervention, the high mortality rate for grizzly bears in Kluane would cause population decline.

Management agencies are aware of the need to reduce non-hunting, human-caused grizzly bear mortality (Ciarniello 1997, Wood and Hengeveld 2001, Schwartz et al. 2003). Agencies are striving to reduce attractants for bears by closing and electrifying landfills (Follman and Hechtel 1990, Mattson et al. 1992, Benn 1998), and using bear-proof garbage and food storage facilities in front-country settings (Davis et al. 2002). Anthropogenic food sources such as drying meat or unattended camp food, gardens, bird feeders, or livestock have been implicated as causes of bear mortality (Gunther et al. 2004). Public education programs have been used to target people who may create these attractants (Jingfors 1995, Ciarniello 1997). Access management is a key factor influencing human-caused bear mortality (McLellan and Shackleton 1988, Nielsen et al. 2004a). Even in protected areas, such as national parks, rates of mortality associated with roads and trails are high (Benn and Herrero 2002). Consequently, some agencies are developing access management plans (Mace 2004, Parks Canada 2004). Agencies are also increasingly reluctant to lethally remove bears that get into conflicts with humans, opting for aversive conditioning instead (McCarthy and Seavoy 1994, Jingfors 1995, Treves and Karanth 2003, Gore 2004).

Given numerous potential causes of bear mortalities, managers need to direct efforts efficiently and proactively. Developing explanatory and predictive spatial models for areas of high mortality risk to bears can help managers clearly see priority areas for management actions and evaluate the consequences of proposed developments on human-caused bear mortality (Nielsen et al. 2004a). Maps depicting high risk areas for bear mortality can be used to identify potential mortality sink areas (Naves et al. 2003, Wilson et al. 2005), or contribute to a spatially explicit habitat-based population viability analysis (Boyce 2002). Spatial models of bear mortality are also necessary for evaluating the effectiveness of management actions. For instance, where bear-attractants have been closely managed but trend analyses show no decrease in the frequency of mortalities, new problem areas may have developed. Spatial models are an indispensable tool for identifying these new areas (Wilson 2003).

In 1989 the Yukon Territorial Government began a program to reduce human-bear interactions and associated bear mortality (Figure 4-1). Landfills in the Kluane Region were either closed or electric fencing was erected around the site to act as a deterrent for bears to enter the area. Similarly, Parks Canada began a program to reduce human-bear conflicts in Kluane National Park and Reserve (KNPR; Figure 4-1), starting with the introduction of bear-proof food canisters for backpackers on the Slims River trails in 1988, then the Alsek River Valley and the Cottonwood Trails in 1996. Human-use restrictions were placed in problem areas throughout the Park in 1998 and 1999 when hikers were required to camp at designated campsites and a minimum backcountry user group size recommendation was put in place in for the Sheep-Bullion Plateau. Efforts were made by both agencies to monitor bear movements and to educate the public. However, there has been no assessment of how effective management actions were in reducing human-bear interactions.

In this chapter I describe the trends and analyse the spatial distribution of human-bear encounters and grizzly bear mortality in the Kluane Region in the southwest Yukon, Canada. I examined changes in the annual frequency of grizzly bear occurrences and mortalities in conjunction with landfill closures or electrification, and other management actions. Occurrences and mortalities were treated as two subsets of human-bear interactions; occurrences were human-

| Year | Management action |
|---|---|
| 1980 | |
| 1981 | |
| 1982 | |
| 1983 | |
| 1984 | |
| 1985 | |
| 1986 | |
| 1987 | |
| 1988 | Food canisters required by backpackers on the Slims River trails |
| 1989 | Congdon Creek landfill closed |
| 1990 | |
| 1991 | Dezadeash landfill closed |
| 1992 | Haines Junction landfill electrified |
| 1993 | |
| 1994 | |
| 1995 | Old Burwash landfill closed |
| 1996 | Alsek River food storage recommendations |
| 1997 | Pine Valley landfill closed |
| 1998 | Designated campsites and group size recommendations on Sheep Bullion Plateau |
| 1999 | Designated campsites on the Cottonwood Trail; Kloo Lake landfill closed |
| 2000 | |
| 2001 | Parks Canada begins showing safety in bear country video to hikers |
| 2002 | Food storage lockers introduced at Kathleen Lake; Blanchard, Canyon and Champagne landfills electrified |
| 2003 | |
| 2004 | |

Figure 4-1. A timeline for selected management activities undertaken by Parks Canada and the Yukon Territorial Government to reduce human-bear conflicts in the Kluane Region, Southwest Yukon, Canada.

bear interactions that did not result in lethal removal of a bear from the population, and mortalities were the result of human-bear interactions where a bear was killed. I examined the spatial characteristics of human-grizzly bear interactions and human-caused mortality, and developed explanatory models for the Kluane Region. My objectives were to evaluate the efficacy of management actions for reducing human-bear interactions and to identify reasons why management actions were not successful. Management actions should have reduced the frequency of human-bear interactions and bear mortality, shifted human-bear conflicts and bear mortality away from key management areas, or reduced the aerial extent over which human-bear interactions occur.

## STUDY AREA

Two study area boundaries were used. Both boundaries encompassed KNPR and the Kluane Wildlife Sanctuary (herein referred to as the protected area complex), and portions of the neighbouring public and private lands in the southwest Yukon (Figure 4-2). The first study area boundary was used to examine temporal trends. This boundary extended at least 40 km out from the protected area complex, into the public and private lands, and included the full extent of all Yukon Territorial Government game management units that intersected the 40-km line. Forty kilometres was use to represent the maximum radial distance for a male bear with an established home range to travel and interact with grizzly bears within the protected area complex.

The second boundary extended another 40 km outside of the first boundary and used the full extent of spatial information available for the outfitting concessions adjacent to the protected area complex. I used this extended study area boundary to encompass as many mapped locations of human-bear interactions and incidents of bear mortality as possible. I assumed that spatial characteristics of human-bear interactions and bear mortality sites within the 40-km zone outside the protected area complex did not differ from locations another 40 km away.

KNPR is jointly managed by Parks Canada and First Nations. The Kluane Wildlife Sanctuary is jointly managed by the Yukon Territorial Government and First Nations and is comprised of three areas: the Klutlan Glacier and Burwash

Uplands area to the north, the Jarvis River area just northwest of Haines Junction, and the Tatshenshini River area to the south. These three parcels roughly total 4000 km$^2$. Only subsistence hunting by local First Nations is permitted in the Park or the Sanctuary. Some resource extraction activities, such as mining, may take place in the Sanctuary, but not in the Park. Human activity in the protected area complex is primarily recreation. Human land-use outside the protected area is dominated by habitation, recreation and mining.

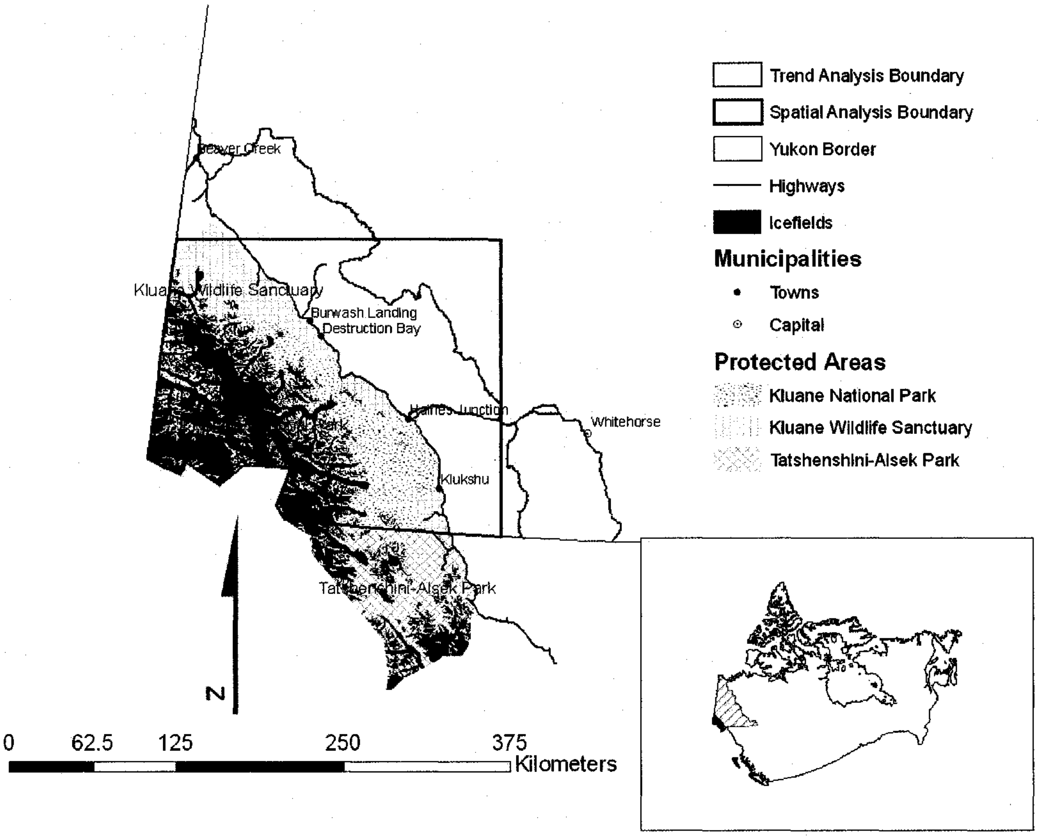

Figure 4-2. The study area boundaries for analyses of mortality and occurrence data. A boundary using all Yukon Territorial Government game management zones intersecting a 40-km radius from the protected area complex were included in trend analyses. Spatial analyses included all occurrence and mortality points within the total extent of available GIS data for the Kluane Region.

## METHODS

### Occurrence and Mortality Database

I created a database for 'occurrences' and grizzly bear mortalities in the Kluane Region. I considered occurrences as an interaction between grizzly bears and people, which did not result in the death of a bear. Management agencies usually consider bear mortalities as a specific type of occurrence where a bear was killed as an outcome; however, for these analyses I consider mortalities separate from occurrences. Mortalities included dead bears and bears translocated so far that they could be considered removed from the population. Legal hunter kills were also included in the mortality data set. Non-hunt mortalities included management-related kills (translocations were considered management related kills), defence kills, accidental kills and poaching.

Between 1983 and 2004 the Yukon Territorial Government and KNPR tracked occurrences, mortalities and translocations through problem wildlife and year end reports. After 1986, Parks Canada tracked most occurrences and mortalities through their observation data reporting system. Occurrence reports before 1983 were not available from the Yukon Territorial Government. Though I reviewed occurrences for Parks Canada back to 1980, the completeness of reporting was suspect prior to 1983. From 1980 to 2004 the Yukon Territorial Government tracked hunting mortality and some non-hunt mortality through the Yukon Biological Submission process.

I excluded records where human-bear interactions were clearly benign, e.g., where a person saw a bear, but the bear was unaware of the person's presence. Occurrences where a bear was seen repeatedly on private property or in close proximity to habitation or a human-use area were retained in the data set. Occurrences were included if a bear was aware of the presence of the human observer and was displaced, ignored the observer, approached or made contact with the observer (MacHutchon and Wellwood 2002). I also included occurrences where no human was present but it was obvious that a bear entered a camp, vehicle, or facility and property was damaged. Often there were several incidents associated with one bear, leading up to the bear being killed. I included the occurrences associated with these mortalities in the occurrence database if the bear was not killed within the following six days or at the same location some time shortly after the initial occurrence. Otherwise, occurrences were not considered independent of the mortality, and the location of the first occurrence associated with that bear was used as the kill site.

Mortalities were classified as hunt or non-hunt. Hunting mortality included kills by resident (including First Nation harvest) and non-resident hunters. Non-hunting mortality included kills by management agency personnel, those by a member of the public in defence of life or property, accidental kills (e.g., vehicle collisions), and poaching. Defence kills for which the public member later opted to use a harvest tag were considered as non-hunting mortality.

For each occurrence and mortality I attempted to acquire information on the date and time of the incident, the sex of the bear, the location and associated accuracy, and names of an associated manager, complainant or hunter. Where accurate locations (i.e., within 100 m) could not be obtained directly from reports or databases, a manager (e.g., a conservation officer or Park warden), the complainant, or the hunter (or alternately the guide or outfitter) was interviewed in-person or by telephone to obtain detailed geographical information for the location of the incident. Contact information of complainants or hunters was obtained from hunter registration certificates, the occurrence report or phonebooks. University of Calgary Ethics Committee approval was obtained before conducting any interviews (Appendix 2). When possible, I returned to the site of the incident and obtained a location using a handheld GPS unit. When it was not feasible to obtain a GPS fix, UTM coordinates were taken from a National Topographic System (NTS) map sheet.

I used Pearson's correlation coefficient ($r$) to examine correlations among occurrence and mortality frequencies. Values between 1 and 0.5 were considered to have a strong positive correlation, while coefficients between 0.5

and 0 were considered to represent a weak correlation. Negative coefficients were conversely interpreted. A value of 0 indicated no relationship.

## Trend Analyses

I examined trends in occurrences and mortalities between 1983 and 2004 ($n$ = 22 years), inclusive. I considered only incidents within the Park and the Sanctuary and within a 40-km radius of the protected area complex, within the Yukon Territory. I subdivided analyses for occurrences by jurisdiction: within the protected area complex, outside the protected area, and total occurrences in the study area. Mortality trends were analyzed for management-related, defence of life and property, non-hunting, and hunting mortality kill-types. Non-hunting mortality included management-related, defence kills, accidental kills and poaching.

I modeled the trends for occurrences and bear mortality for each category using five functional forms: linear, quadratic, cubic, bent-cable and piecewise (Figure 4-3). I elected to fit the bent-cable and piecewise functions because I suspected that management changes such as closure or electrification of landfills, required use of bear canisters on certain trails in the Park, and changes to public education and awareness programs may have caused directional changes in trend. Quadratic or cubic models would capture this change, but are constrained by requirements for symmetry in the functional form. The bent-cable comprises two straight lines joined smoothly by a quadratic bend in the middle. As the domain of the bend shrinks, the model approaches piecewise regression (also known as broken stick or break-point modeling) with an abrupt threshold. Therefore, piecewise regression is a special case of bent-cable regression, and is useful for systems that may suffer a 'shock'. Fitting a piecewise regression requires an *a priori* abruptness assumption, which can be obtained from the bent-cable regression. The estimated bend point, or $\theta$ parameter, from the bent-cable regression was used as the break point year for the piecewise regression. This method allowed the data to estimate the break point, rather than have the modeller arbitrarily chose one (Chui 2002). Bent-cable models were estimated using non-linear least squares regression and a macro developed by Lindstrom (2000; Appendix 3) for S-Plus 6 (Insightful Corporation 2001). All other models were estimated using linear regression. Models were ranked using $\Delta AIC_c$ where:

$$\Delta AIC_c = AIC_{c,i} - \min AIC_c; \qquad \text{Equation 4-1}$$

where $AIC_{c,i}$ is the $AIC_c$ score for model i; and
$\min AIC_c$ is the minimum $AIC_c$ score across all models.

I considered models with a $\Delta AIC_c$ between 0 and 2 to have strong support. I considered models with a $\Delta AIC_c$ between 2 and 10 to have less support and models with a $\Delta AIC_c$ greater than 10 to have virtually no support (Anderson et al. 2001, Burnham and Anderson 2002).

I evaluated factors that might affect changes in the frequency of occurrences in each jurisdiction and the frequencies of bear deaths by mortality type, including three correlates of human activity and four correlates of bear forage productivity. Correlates of human activity included the number of open landfills that were not surrounded with electric fencing, the amount of vehicle traffic in the area, and the amount of backcountry visitation. Correlates of bear forage productivity included the start of the growing season, a rough index of growing season length, the mean temperature and precipitation for May.

I obtained information on the number of open landfills from regional land-use managers and conservation officers. Electric fencing was used to enclose landfills. When a bear tried to cross the fence a shock was delivered to the bear, deterring it from entering the site (Follman and Hechtel 1990). Use of electric fencing around landfills began in 1989. By 2002 most landfills were enclosed by electric fencing or had been closed down completely (Figure 4-1). In 2003 and 2004 two of 18 (legal and illegal) landfills that existed over the 22-year period remained open and unfenced. All landfills opened after 1989 were enclosed

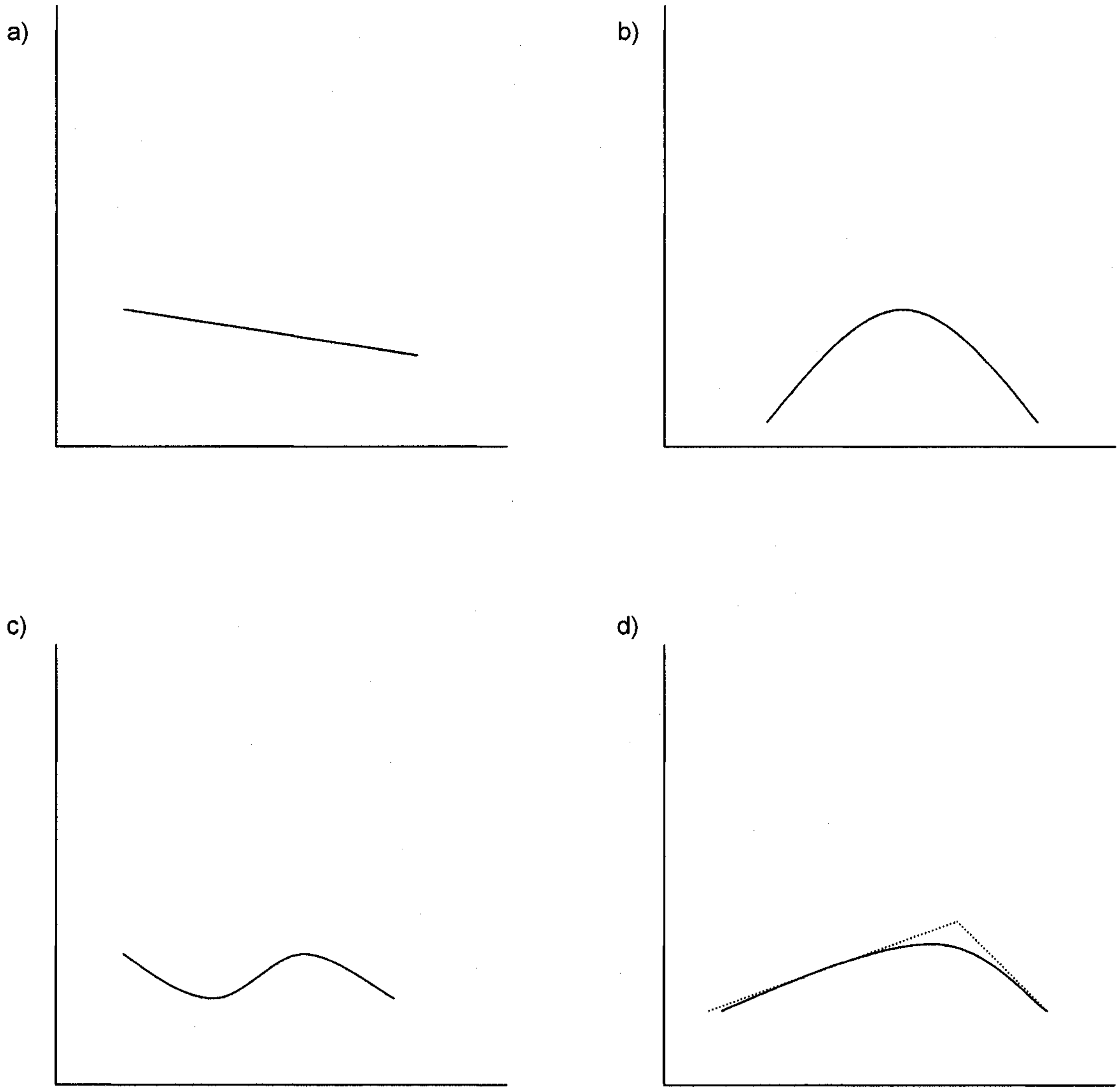

Figure 4-3. Functional forms for a) linear, b) quadratic, c) cubic, d) bent-cable (solid line) and piecewise (dotted line) regression. Trends for occurrences and mortalities were fit to these five functional forms.

with electric fencing. In 1992 the largest landfill in the Kluane area, the Haines Junction landfill, was electrified. Therefore, 1989, 1992, and 2002 were important dates for understanding changes in trends of mortalities and occurrences.

Vehicle count data were obtained from the Champagne traffic counter set up by the Yukon Territorial Government approximately 75 km east of Haines Junction on the Alaska Highway (Yukon Territorial Government 2004). Data from this counter were missing for 1984 to 1986, and had to be interpolated by averaging annual change in vehicle traffic from all surrounding traffic counters and adding that value to the previous year's value from the Champaign counter. I used a count of the average annual daily number of vehicles as a general index of human activity in the Haines Junction area, encompassing community population growth and tourism.

All overnight visitors to KNPR are required to register. Registration information was used to calculate the number of person nights for backcountry use in the Park for each year, calculated as the number of people in a party, multiplied by the number of nights they spent in the backcountry. I did not include overnight use by mountaineers in the annual totals. While statistics were only available for visitors using the Park, I considered the information reflective of backcountry activity in the entire Kluane Region.

Weather data for the Kluane Region were collected by Environment Canada and the Yukon Territorial Government at five weather stations including, two in Haines Junction, one at Dezadeash, one at Otter Falls and one at Burwash Landing (Environment Canada 2004). Weather data were not continuous for an entire summer in a given year for any station, and had to be pieced together. I used information from the Haines Junction stations when it was available. Otherwise, in order of priority, I used information from the Dezadeash station, the Otter Falls station or the Burwash Station. The incompleteness of the data for any given station meant that ideal indicators such as the number of growing degree days (McMaster and Wilhem 1997) and the timing of the first frost could not be determined every year. Weather data were complete enough to obtain growing season start dates, growing season length, and total precipitation and mean average temperature for May. Therefore, I used theses four values as indicators of berry productivity (Edey 1977). The start of the growing season was designated as 10 days after the first Julian calendar day where the daily average temperature was 5°C. I considered the number of days between the start of the growing season and the first killing frost (-2.2°C) as a proxy for the growing season length. May is a crucial month for determining *Shepherdia canadensis* berry productivity (Noble 1985, Hamer 1996, Knight 1999), a staple food for grizzly bears (McCann 1998); therefore, I considered the total amount of precipitation and the mean average temperature for that month as explanatory variables for human-bear interactions trends.

All explanatory variables were used in a linear regression to assess potential correlates with the number of occurrences and mortalities. While data on occurrences and mortalities were count data, data were normally distributed. Hence, I could use multiple linear regression. I generated all possible linear regression models using PROC REG in SAS 9.0 (SAS Institute 2004). I calculated $AIC_c$ scores and Akaike weights (w) for each model, where:

$$w = \frac{\exp(-0.5 \times \Delta AIC_c)}{\sum \exp(-0.5 \times \Delta AIC_c)} \qquad \text{Equation 4-1}$$

Estimates of variable importance (I) were obtained by summing Akaike weights across all models in which a variable is present (Burnham and Anderson 2002). The larger the summed Akaike weight, the more important the variable.

## Spatial Characteristics of Occurrences and Mortality

*Explanatory models for occurrences and mortality distribution.*--I generated seven GIS layers relevant to the spatial distribution of occurrences and mortalities: elevation, distance to water, infrastructure density, distance to primary roads, distance to other linear features, and distance to landfills. I developed a weighted average relative probability map for grizzly bear habitat use by taking the eight habitat selection maps reported in Chapter 3, weighing the values contained within each map by the proportion of the population that was represented by that demographic group (19.5% subadult, 32.8% lone adult female, 7.5% family groups, and 40.2% adult males; McCann 1998) and averaging the relative probabilities of occurrence to create one map.

Elevation was derived from a 30-m digital elevation model (DEM). I obtained digital hydrology maps at the 1:50 000 scale from the National Topographic Database (NRCAN 1999). Excluding wetlands, I considered any hydrological feature that was active year round. I calculated the distance of each occurrence or mortality location to the nearest hydrological feature.

I calculated infrastructure density using three vector layers representing known human infrastructure and activity. The three vector layers were developed using National Topographic Database (NTDB) information (NRCAN 1999), supplemental data collected by government agencies, and manually collected data (i.e., collected by visiting the feature and using a hand-held GPS unit to record its spatial location). The three vector layers were created representing: 1) linear features such as roads and trails, 2) point features such as buildings, cabins, campsites, points of recreation, and damns, and 3) polygon features such as airstrips. I rasterized each vector layer to a 30-m resolution. Any cell containing a human-use feature was given a value of 1. I summed the value for each cell across the three raster layers. The resulting layer represented the number of human-use features per cell (i.e., 0 to 3), where cells containing more than one human use feature had values of 2 or 3. I then used a moving window, representing the average daily movements of female grizzly bears, to tally the values of all 30-m cells. I assumed, because of similarities in home range size, that the daily movement rate for bears in the Kluane Region was similar to the 9-km$^2$ movement rate for grizzly bears in Central Rocky Ecosystem of Alberta (Gibeau 2000). The resulting value was ascribed to the center cell in the window.

I used Idrisi Kilimanjaro (Clark Labs 2003) to generate a distance surface for linear features, separating highways or primary roads from other linear features. Data for highways and other linear features were obtained from the National Topographic Database, or were manually digitized using a handheld GPS unit. Other linear features included secondary or unpaved roads, trails, transmission lines and pipeline corridors. I rasterized the distance surface to a 30-m resolution.

The number of landfills that were open and unfenced with electric fencing changed substantially between 1980 and 2004, making it difficult to estimate the distance to landfill using one succinct GIS layer. Rather, I developed landscape windows for each time period when the configuration of open or unfenced landfills changed. Occurrences and mortalities could then be matched to the appropriate window. A landfill was considered to not have any potential influence on bear occurrences or mortalities in the second year after it was electrified or closed. That is, I assumed a 1-year lag in occurrences and mortalities after closure or electrification.

I generated 100 random locations within a radius of a specified length for each occurrence or mortality location. The radius around each point was conditional on the gender of the bear. I used 9 km for females, representing the radial distance of the maximum annual female home range. If the bear was a male, I used 27 km, representing the radius of the maximum male annual home range. If the gender was unknown I used a 27-km radius (McCann 1998). All random locations were associated with the occurrence or mortality location using a unique identifier. Information for each explanatory variable was extracted from the appropriate GIS layers for each occurrence, mortality and random location.

Prior to building the models, I tested the explanatory variables for collinearity using Pearson correlation, tolerance, and variance inflation function (VIF) diagnostics. All correlations greater than 0.7, or tolerance scores of 0.1 or less and individual VIF scores > 10 were assumed to be collinear and not included in the model.

I used a discrete choice model to explore the relationship between occurrences or mortalities and the explanatory variables[2]. Discrete choice models accounted for the changing distribution of open landfills by fitting a model to the location of occurrences and mortalities while keeping the availability of landscape characteristics unique to each occurrence or mortality location. The discrete choice model was estimated by maximizing the multinomial logit likelihood (Manly et al. 2002) using the logistic regression routine (PROC LOGISTIC) in SAS 9.0 (SAS Institute 2004) with the STRATA command to identify the choice set (Kuhfeld 2005). The stratified PROC LOGISTIC does not allow for calculation of all possible models and is therefore prohibitive for calculating variable importance. Consequently, I opted to use full models ($\alpha$ = 0.05) and standardized estimates of coefficients for comparisons.

To evaluate the discrete choice models, I used the quantile classification function in the Spatial Analyst extension of ArcGIS 9.0 (ESRI 2004) to bin the logit values from the discrete choice model into 10 ordinal classes. A value of 1 represented a relatively low probability of an occurrence or mortality, while a value of 10 represented a relatively high probability of an occurrence or mortality. For each analysis, I divided data into two groups using a k-fold partitioning design (Fielding and Bell 1997). The first group was used for model training and represented a random 80% sub-sample of mortalities or occurrences and availability point data. The second group was comprised of the remaining 20% of mortalities or occurrences and was employed to assess model fit (Hosmer and Lemeshow 2001, Boyce et al. 2002). I repeated this procedure five times so that all points were used to train the model four times and all mortalities or occurrences were employed once to asses the model fit. Each time the area-adjusted frequency of occurrences or mortalities within a given bin was matched against the corresponding rank of the bin and calculated Spearman's rank correlation ($r_s$; Boyce et al. 2002). The correlation coefficient was averaged across the five repetitions. If the averaged $r_s$ value was 1, the frequency of

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[2] See Lancaster and Imbens (1996) for discussion of contaimination issues (Keating and Cherry 2004). Results of this method are acceptable if contamination levels are not high (>20%).

occurrences or mortalities and the rank had a perfect positive correlation. Values between 1 and 0.5 were considered to have a strong positive correlation, while coefficients between 0.5 and 0 were considered to represent a weak correlation. Negative coefficients were conversely interpreted. A value of 0 indicated no relationship.

*Occurrence and mortality hot spots.*--Hot spot analysis was used to elucidate high human-bear interaction zones, and identify if, rather than reduce the frequency of human-bear interactions, management actions caused them to shift to a new location or reduced the aerial extent over which they occurred. I examined the spatial clustering of occurrences and non-hunt mortalities within specified time periods. Time periods corresponded to: 1) the electrification of the Haines Junction landfill, accounting for a 1-year lag in bear behavioural responses, and 2) break points determined by the bent-cable models in the trend analyses for occurrences and non-hunt mortalities. The lag year for electrification of the Haines Junction landfill and the break point for non-hunt mortalities were the same year, so there were only two time periods to consider for this analysis: 1980 to 1993 and 1994 to 2004. A break point occurred for the frequency of occurrences in 1997; therefore, data were stratified into the periods 1980 to 1993, 1994 to 1997, and 1998 to 2004.

I used a scan-type clustering algorithm developed by Block (1995) to delineate hot spots for bear occurrences and mortalities. This procedure is available in CrimeStat III (Levine 2004) through the spatial and temporal analysis of crime (STAC) routine. STAC repeatedly lays circles over a grid and the number of points within each circle is counted. It shares similar properties with other scan routines (Openshaw et al. 1987, Kuldorff and Nagarwalla 1995), but differs in that overlapping clusters are combined into larger clusters until there are no longer any overlapping circles. Hence, STAC clusters can be of differing sizes. The routine, therefore, combines some elements of partitioning clustering (the search circles) with hierarchical clustering (the aggregating of smaller clusters into larger clusters). I used a 2-km search radius and defined a cluster as a minimum of five occurrences or three mortalities. I ran 100 simulations using the STAC algorithm to identify hot spots. CrimeStat III automatically generates a display of the clusters as an ArcView 3.x shape file.

I visually compared changes in the location and size of hot spots. I used a two-sample t-test assuming unequal variances ($\alpha = 0.05$) to evaluate the average change in hot spot size among time periods. While I compared the difference in the sizes of occurrence hot spots among time periods, unequal samples sizes among time periods may have biased hot spots sizes. Time periods with fewer years of data, and hence fewer occurrence locations, were likely to have smaller hot spots than time periods with more occurrence locations. The numbers of years of data in the time periods used to delineate hot spots for mortalities were roughly equal; therefore, analyses to compare hot spot sizes for mortalities were less likely to be subject to this problem.

I used Ripley's K to examine changes in the spatial dispersion of occurrences and mortalities. The expected value of L(d), the linearized form of the K-test statistics, is d, the distance. The confidence interval, or envelope, for the expected L(d) is generated by examining the specified number of permutations of randomly generated patterns of N points over the entire study area. If for any distance, the observed L(d) falls above or below the expected L(d) the null hypothesis of complete spatial randomness (CSR; or the null hypothesis of expected L(d) is equal to observed L(d)) can be rejected at an appropriate level of significance ($\alpha = 0.05$). An observed L(d) below the envelope indicates that the points are dispersed at that distance, whereas an observed L(d) above the envelope indicates clustering. I calculated the observed L(d) using the Ripley's K analysis module available in CrimeStat III (Levine 2004). I ran 100 simulations to generate an envelope for random point distribution, using a rectangular border correction

## RESULTS

There were 441 reported occurrences and 133 known kills from 1980 to 2004. I obtained accurate spatial information on over 97% of reported occurrences, 90% of non-hunt mortality locations, and 34% of hunt-related locations. Table 4-1 shows an annual breakdown of the total number of occurrences and mortalities for which information was obtained.

I used Pearson's correlation coefficient to examine the relationships among frequencies for occurrences and mortalities. There was moderate positive correlation between frequency of occurrences in the protected area and the frequency of management kills. All other independent response variables showed only weak correlations (Table 4-2). Notably, the relationship between the frequency of hunt-related mortality and occurrences or management kills was negative (Table 4-2).

### Trends in Occurrences

The piecewise functional form best fit the trend for occurrences inside and outside the protected areas (Table 4-3). Occurrences inside the protected area complex increased from 1983 to 1999, then decreased three times as fast from 2000 to 2004. Occurrences outside the protected area gradually increased from 1983 to 1997, then rapidly declined. Concordantly, the piecewise model best fit the trend for total occurrences, increasing until 1997, and then decreasing (Table 4-3).

The frequency of occurrences inside the protected area was positively correlated with backcountry visitation and vehicle traffic, but negatively associated with the number of open landfills (Table 4-4). These were also the three most influential explanatory variables (Table 4-5). Overnight visitation was the most important variable, present in nine of the top 10 models. The berry

Table 4-1. Annual number of occurrences and mortalities used for trend and spatial analyses. Total non-hunt kills include management kills, public kills, accidental kills and poaching.

| | Occurrences | | | | | Mortalities | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Trend | | | Spatial | | Trend | | | | Spatial | | | |
| Year | Total | Inside protected area | Outside protected area | Inside protected area | Outside protected area | Total non-hunt | Management kills | Public kills | Hunt | Total non-hunt | Management kills | Public kills | Hunt |
| 1980 | na | na | na | 0 | 0 | na | na | na | na | 3 | 0 | 3 | 5 |
| 1981 | na | na | na | 3 | 0 | na | na | na | na | 3 | 2 | 0 | 2 |
| 1982 | na | na | na | 2 | 0 | na | na | na | na | 1 | 1 | 0 | 1 |
| 1983 | 5 | 4 | 1 | 4 | 1 | 3 | 0 | 0 | 10 | 0 | 0 | 0 | 1 |
| 1984 | 9 | 4 | 5 | 4 | 3 | 6 | 0 | 5 | 17 | 5 | 0 | 4 | 4 |
| 1985 | 20 | 16 | 4 | 16 | 3 | 4 | 2 | 2 | 14 | 5 | 4 | 1 | 2 |
| 1986 | 9 | 6 | 3 | 6 | 3 | 7 | 2 | 5 | 8 | 7 | 2 | 5 | 5 |
| 1987 | 18 | 15 | 3 | 15 | 2 | 10 | 4 | 6 | 13 | 8 | 4 | 4 | 2 |
| 1988 | 13 | 7 | 6 | 7 | 5 | 5 | 1 | 3 | 13 | 4 | 0 | 2 | 5 |
| 1989 | 17 | 10 | 7 | 10 | 7 | 10 | 4 | 5 | 8 | 9 | 4 | 4 | 4 |
| 1990 | 15 | 15 | 0 | 14 | 1 | 5 | 1 | 2 | 10 | 5 | 1 | 2 | 2 |
| 1991 | 6 | 6 | 0 | 5 | 0 | 3 | 1 | 0 | 0 | 4 | 1 | 0 | 1 |
| 1992 | 24 | 21 | 3 | 21 | 3 | 7 | 3 | 3 | 1 | 6 | 3 | 2 | 4 |
| 1993 | 22 | 15 | 7 | 15 | 7 | 11 | 6 | 3 | 1 | 10 | 5 | 3 | 0 |
| 1994 | 28 | 17 | 11 | 17 | 7 | 4 | 2 | 1 | 1 | 3 | 2 | 1 | 0 |
| 1995 | 26 | 20 | 6 | 20 | 6 | 10 | 4 | 6 | 2 | 8 | 4 | 4 | 0 |
| 1996 | 39 | 22 | 17 | 22 | 16 | 7 | 4 | 3 | 8 | 7 | 3 | 4 | 1 |
| 1997 | 32 | 20 | 12 | 20 | 10 | 5 | 1 | 3 | 5 | 6 | 2 | 3 | 1 |
| 1998 | 26 | 17 | 9 | 17 | 8 | 9 | 1 | 5 | 9 | 5 | 1 | 4 | 1 |
| 1999 | 31 | 24 | 7 | 24 | 6 | 7 | 2 | 3 | 12 | 5 | 1 | 2 | 2 |
| 2000 | 33 | 24 | 9 | 24 | 9 | 8 | 6 | 2 | 11 | 7 | 6 | 1 | 2 |
| 2001 | 16 | 14 | 2 | 14 | 2 | 6 | 2 | 4 | 13 | 4 | 1 | 3 | 2 |
| 2002 | 20 | 10 | 10 | 10 | 7 | 3 | 2 | 1 | 8 | 4 | 2 | 2 | 2 |
| 2003 | 18 | 14 | 4 | 14 | 2 | 1 | 0 | 1 | 5 | 1 | 0 | 1 | 7 |
| 2004 | 14 | 13 | 1 | 13 | 1 | 2 | 1 | 0 | 4 | 0 | 0 | 0 | 2 |
| *Total* | *441* | *314* | *127* | *317* | *109* | *133* | *49* | *63* | *173* | *120* | *49* | *55* | *58* |

Table 4-2. Pearson's correlations (*r*) among frequencies of occurrences and mortalities. Variables shaded in grey were not independent from each other. Values between 1 and 0.5 were considered to have a strong positive correlation, while coefficients between 0.5 and 0 were considered to represent a weak correlation. Negative coefficients were conversely interpreted. A value of 0 indicated no relationship.

| | Occurrences – inside PAC | Occurrences – outside PAC | Total occurrences | Management kills | Public kills | Non-hunt kills | Hunt Kills |
|---|---|---|---|---|---|---|---|
| Occurrences – inside PAC | | | | | | | |
| Occurrences – outside PAC | 0.4827 | | | | | | |
| Total occurrences | 0.9105 | 0.8017 | | | | | |
| Management Kills | 0.5067 | 0.3494 | 0.5108 | | | | |
| Public Kills | 0.1191 | 0.1461 | 0.1503 | 0.3334 | | | |
| Non-hunt kills | 0.3301 | 0.2457 | 0.3413 | 0.7373 | 0.8012 | | |
| Hunt Kills | -0.1789 | -0.0621 | -0.1514 | -0.1824 | 0.3076 | 0.0483 | |

productivity variables were least influential (Table 4-5), but were present in models that were strongly supported by the data (Table 4-4).

Overnight visitation was positively associated with the frequency of occurrences outside the protected area complex (Table 4-4) and was the most important explanatory variable (Table 4-5). Growing season start and precipitation were also important variables (Table 4-5); years with higher precipitation and delayed growing season starts had fewer bear occurrences (Table 4-4). The number of open landfills was moderately important (Table 4-5), but was not present in the strongly supported models (Table 4-4). The frequency of occurrences outside of the protected area was negatively correlated with the number of open landfills (Table 4-4).

Backcountry visitation was the most influential variable (Table 4-5) and was positively associated with the total number of occurrences (Table 4-4). The number of open landfills was the next most influential variable (Table 4-5) and was negatively associated with the number of occurrences (Table 4-4). Precipitation was positively associated with the frequency of occurrences for the region (Table 4-4).

Table 4-3. Linear, quadratic, cubic, bent-cable, and piecewise regression models for trend analyses in occurrences within the protected area complex, outside of the protected area complex, and total occurrences. Models with a $\Delta AIC_c$ less than 2 are strongly supported by the data. Coefficients for the trend function (time, time$^2$, time$^3$, and time after the break point), standard errors (SE), and significance (*P*) values are shown. The break point is shown as the number of years after the initial year. k is the number of parameters estimated in the model and $\sigma$ is the error parameter used to estimate $AIC_c$. $\sigma^2$ is equal to the residual sum of squares divided by the sample size ($n$ = 22 for all models).

| Model | k | $\sigma$ | $AIC_c$ | $\Delta AIC_c$ | intercept | SE | *P* | time | SE | *P* | time$^2$ | SE | *P* | time$^3$ | SE | *P* | break point | SE | *P* | time after break | SE | *P* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Occurrences inside of protected area complex* | | | | | | | | | | | | | | | | | | | | | | |
| Time | 3 | 27.31 | 38.93 | 2.62 | 8.57 | 2.42 | <0.01 | 0.50 | 0.18 | 0.01 | | | | | | | | | | | | |
| Time + Time$^2$ | 4 | 18.82 | 38.39 | 2.08 | 1.20 | 3.28 | 0.74 | 2.36 | 0.66 | <0.01 | -0.08 | 0.03 | 0.01 | | | | | | | | | |
| Time+Time$^2$+Time$^3$ | 5 | 16.51 | 40.54 | 4.23 | 6.40 | 4.59 | 0.18 | -0.13 | 1.69 | 0.94 | 0.18 | 0.17 | 0.29 | -0.01 | 0.01 | 0.13 | | | | | | |
| Bent-cable | 5 | 15.14 | 39.71 | 3.4 | 4.85 | 2.23 | 0.04 | 1.02 | 0.23 | <0.001 | | | | | | | 17.05 | 1.44 | <0.001 | -2.41 | 1.30 | <0.001 |
| Piecewise | 4 | 15.13 | 36.31 | 0 | 4.85 | 2.08 | 0.03 | 1.02 | 0.19 | <0.001 | | | | | | | 17.05 | 1.44 | <0.001 | -3.42 | 0.87 | <0.001 |
| *Occurrences outside of protected area complex* | | | | | | | | | | | | | | | | | | | | | | |
| Time | 3 | 16.17 | 33.93 | 1.04 | 3.45 | 1.86 | 0.80 | 0.20 | 0.14 | 0.17 | | | | | | | | | | | | |
| Time + Time$^2$ | 4 | 13.53 | 35.24 | 2.35 | -0.71 | 2.78 | 0.80 | 1.24 | 0.56 | 0.04 | -0.05 | 0.02 | 0.07 | | | | | | | | | |
| Time+Time$^2$+Time$^3$ | 5 | 10.42 | 36.14 | 3.25 | 5.43 | 1.34 | 0.15 | -1.65 | 1.34 | 0.24 | 0.26 | 0.13 | 0.07 | -0.01 | 0.00 | 0.03 | | | | | | |
| Bent-cable | 5 | 10.57 | 36.28 | 3.39 | 0.30 | 1.99 | 0.88 | 0.67 | 2.96 | 0.01 | | | | | | | 15.09 | 2.05 | <0.001 | -1.10 | 0.67 | <0.001 |
| Piecewise | 4 | 10.57 | 32.89 | 0 | 0.30 | 1.84 | 0.87 | 0.67 | 0.19 | <0.01 | | | | | | | 15.09 | 2.05 | <0.001 | -1.77 | 0.56 | 0.01 |
| *Total occurrences* | | | | | | | | | | | | | | | | | | | | | | |
| Time | 3 | 60.30 | 46.50 | 4.48 | 12.03 | 3.59 | <0.01 | 0.70 | 0.27 | 0.02 | | | | | | | | | | | | |
| Time + Time$^2$ | 4 | 39.69 | 45.52 | 3.5 | 0.39 | 4.76 | 0.94 | 3.61 | 0.95 | <0.01 | -0.13 | 0.04 | 0.01 | | | | | | | | | |
| Time+Time$^2$+Time$^3$ | 5 | 28.88 | 45.88 | 3.86 | 11.83 | 6.07 | 0.07 | -1.77 | 2.23 | 0.44 | 0.45 | 0.22 | 0.06 | -0.02 | 0.01 | 0.02 | | | | | | |
| Bent-cable | 5 | 27.50 | 45.41 | 3.39 | 4.64 | 3.15 | 0.16 | 1.78 | 0.35 | <0.001 | | | | | | | 15.44 | 1.21 | <0.001 | -2.68 | 1.10 | <0.001 |
| Piecewise | 4 | 27.49 | 42.02 | 0 | 4.64 | 2.93 | 0.13 | 1.78 | 0.30 | <0.001 | | | | | | | 15.44 | 1.21 | <0.001 | -4.46 | 0.94 | <0.001 |

Table 4-4. The top 10 explanatory models for frequency of occurrences inside the protected area complex, outside the protected area complex, and total occurrences. Frequency of occurrences for 1983 through to 2004 were regressed against the number of open landfills, the amount of vehicle traffic, the amount of visitation to Kluane National Park and Reserve, the number of growing season days, the Julian start date for the growing season, mean temperature for May, and total amount of precipitation for May. Models are ranked by $\Delta AIC_c$. $\Delta AIC_c$ values have been converted to Akaike weights ($w$). Coefficients are shown if the variable was present in that model. k is the number of parameters estimated in the model and RMSE is the root mean square error parameter used to estimate $AIC_c$.

| Model Rank | Intercept | Landfills | Vehicle | Visitation | Season length | Season start | Mean May temp. | Total May precip. | k | RMSE | $AIC_c$ | $\Delta AIC_c$ | w |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Occurrences inside of protected area complex* | | | | | | | | | | | | | |
| 1 | 2.0935 | -- | -- | 0.0021 | -- | -- | -- | -- | 3 | 5.250 | 76.195 | 0.000 | 0.2455 |
| 2 | 7.0538 | -0.3519 | -- | 0.0019 | -- | -- | -- | -- | 4 | 5.085 | 76.688 | 0.493 | 0.1919 |
| 3 | -3.2573 | -- | 0.0173 | 0.0017 | -- | -- | -- | -- | 4 | 5.225 | 77.880 | 1.685 | 0.1057 |
| 4 | 19.6090 | -- | -- | 0.0019 | -- | -0.1284 | -- | -- | 4 | 5.239 | 78.000 | 1.805 | 0.0996 |
| 5 | 0.6056 | -- | -- | 0.0022 | -- | -- | -- | 0.0639 | 4 | 5.294 | 78.455 | 2.260 | 0.0793 |
| 6 | -2.5877 | -- | -- | 0.0019 | 0.0487 | -- | -- | -- | 4 | 5.339 | 78.832 | 2.637 | 0.0657 |
| 7 | 5.6051 | -0.3729 | -- | 0.0020 | -- | -- | -- | 0.0749 | 5 | 5.087 | 78.913 | 2.718 | 0.0631 |
| 8 | 2.2785 | -- | -- | 0.0019 | -- | -- | 0.1362 | -- | 4 | 5.350 | 78.917 | 2.722 | 0.0630 |
| 9 | -1.4350 | -- | 0.0346 | -- | -- | -- | -- | -- | 3 | 5.672 | 79.602 | 3.407 | 0.0447 |
| 10 | 2.8373 | -0.3461 | -- | 0.0018 | 0.0430 | -- | -- | -- | 5 | 5.185 | 79.751 | 3.556 | 0.0415 |
| *Occurrences outside of protected area complex* | | | | | | | | | | | | | |
| 1 | -0.1684 | -- | -- | 0.0010 | -- | -- | -- | -- | 3 | 4.051 | 64.796 | 0.000 | 0.2926 |
| 2 | -1.6997 | -- | -- | 0.0011 | -- | -- | -- | 0.0658 | 4 | 4.029 | 66.445 | 1.649 | 0.1282 |
| 3 | 20.4599 | -- | -- | -- | -- | -0.1172 | -- | -- | 3 | 4.267 | 67.075 | 2.279 | 0.0936 |
| 4 | 8.7635 | -- | -- | 0.0009 | -- | -0.0655 | -- | -- | 4 | 4.108 | 67.293 | 2.498 | 0.0839 |
| 5 | 1.4564 | -0.1153 | -- | 0.0010 | -- | -- | -- | -- | 4 | 4.116 | 67.381 | 2.585 | 0.0803 |
| 6 | 0.1664 | -- | -0.0011 | 0.0011 | -- | -- | -- | -- | 4 | 4.156 | 67.807 | 3.011 | 0.0649 |
| 7 | -0.5024 | -- | -- | 0.0010 | 0.0035 | -- | -- | -- | 4 | 4.156 | 67.812 | 3.016 | 0.0647 |
| 8 | 7.7230 | -0.1751 | -- | -- | -- | -- | -- | -- | 3 | 4.339 | 67.815 | 3.019 | 0.0647 |
| 9 | -0.1728 | -- | -- | 0.0010 | -- | -- | -0.0033 | -- | 4 | 4.157 | 67.815 | 3.019 | 0.0647 |
| 10 | 1.3157 | -- | 0.0098 | -- | -- | -- | -- | -- | 3 | 4.346 | 67.885 | 3.090 | 0.0624 |
| *Total occurrences* | | | | | | | | | | | | | |
| 1 | 1.9251 | -- | -- | 0.0031 | -- | -- | -- | -- | 3 | 7.634 | 92.670 | 0.000 | 0.1594 |
| 2 | 8.5102 | -0.4672 | -- | 0.0029 | -- | -- | -- | -- | 4 | 7.470 | 93.604 | 0.934 | 0.0999 |
| 3 | -1.0941 | -- | -- | 0.0033 | -- | -- | -- | 0.1297 | 4 | 7.569 | 94.185 | 1.515 | 0.0747 |
| 4 | 28.3725 | -- | -- | 0.0028 | -- | -0.1939 | -- | -- | 4 | 7.602 | 94.377 | 1.707 | 0.0679 |
| 5 | 5.7125 | -0.5076 | -- | 0.0030 | -- | -- | -- | 0.1447 | 5 | 7.322 | 94.935 | 2.265 | 0.0514 |
| 6 | -3.0909 | -- | 0.0162 | 0.0027 | -- | -- | -- | -- | 4 | 7.736 | 95.145 | 2.475 | 0.0462 |
| 7 | -3.0901 | -- | -- | 0.0029 | 0.0522 | -- | -- | -- | 4 | 7.795 | 95.483 | 2.813 | 0.0390 |
| 8 | 2.1056 | -- | -- | 0.0030 | -- | -- | 0.1329 | -- | 4 | 7.808 | 95.556 | 2.886 | 0.0376 |
| 9 | -7.9812 | -- | 0.0210 | 0.0028 | -- | -- | -- | 0.1461 | 5 | 7.607 | 96.616 | 3.946 | 0.0222 |
| 10 | 20.8641 | -0.3738 | -- | 0.0027 | -- | -0.1002 | -- | -- | 5 | 7.624 | 96.713 | 4.043 | 0.0211 |

Table 4-5. Importance values for variables used to explain annual frequencies of occurrences within the protected area complex, outside the protected area complex, and total occurrences. Variable importance is calculated by summing the Akaike weights for all model in which the variable is present. Variables are ranked by importance.

| | *Occurrences inside of protected area complex* | | *Occurrences outside of protected area complex* | | *Total occurrences* | |
|---|---|---|---|---|---|---|
| **Variable** | I | **Rank** | I | **Rank** | I | **Rank** |
| Landfills | 0.3332 | 2 | 0.2238 | 4 | 0.3220 | 2 |
| Vehicle | 0.2947 | 3 | 0.2060 | 5 | 0.2157 | 5 |
| Visitation | 0.8118 | 1 | 0.5904 | 1 | 0.8817 | 1 |
| Season length | 0.2017 | 6 | 0.2005 | 6 | 0.1776 | 6 |
| Season start | 0.2113 | 5 | 0.2464 | 3 | 0.2269 | 4 |
| Mean May temp. | 0.1811 | 7 | 0.1949 | 7 | 0.1698 | 7 |
| Total May precip. | 0.2178 | 4 | 0.2792 | 2 | 0.2877 | 3 |

## Trends in Mortalities

The best trend model for management-related mortalities was linear and increasing (Table 4-6). Quadratic and piecewise models were also strongly supported by the data, showing a decrease in the frequency of mortalities after 1993 (Table 4-6). The trend in public defence kills was best fit by a piecewise functional form. The frequency of public defence kills trended up until 1998 then declined (Table 4-6). However, the slopes for both halves of the regression were not significantly different from zero (Table 4-6). Total non-hunt mortality included accidental kills and poaching, in addition to management and public kills. The trend for total non-hunt mortality was best fit by the piecewise functional form (Table 4-6). Frequency of mortalities increased slowly prior to 1998 then decreased rapidly. The trend in hunting related mortalities was also best fit by piecewise regression, but hunt-related mortalities decreased up to 1993, then increased.

Backcountry visitation was the only explanatory variable in the top trend model for management-related mortalities (Table 4-7). Backcountry visitation was also the most influential variable, though vehicle traffic and the number of open landfills were also influential (Table 4-8). All three variables were positively correlated with the frequency of management mortalities (Table 4-8). Variables relating to berry productivity were the least influential variables (Table 4-8) and occurred only in models with moderate or weak support (Table 4-7).

Frequency of public defence kills was most strongly influenced by the number of open landfills (Table 4-8). More open landfills corresponded to more public defence kills (Table 4-7). Total precipitation and mean temperature were the next most influential explanatory variable. More public defence kills occurred in years with high precipitation and low average temperatures.

Frequency of non-hunt mortalities was most strongly influenced by the number of open landfills, the amount of vehicle traffic and growing season length (Table 4-8); all correlations were positive (Table 4-7). Models with strong support also included precipitation and growing season start date (Table 4-7). The number of mortalities in a year were positively associated with the amount of precipitation and negatively correlated with the start of the growing season (Table 4-7), indicating that the earlier the start of the growing season, the higher the number of non-hunt mortalities.

Frequency of hunting-related mortality was most strongly influenced by the amount of backcountry visitation (Table 4-8); however, unlike with other types of mortality, the correlation was negative (Table 4-7). Precipitation and growing season start date were also influential (Table 4-8). Number of open landfills and amount of vehicle traffic were present in models with moderate support (Table 4-7), but were the least influential variables on frequency of hunting-related mortality (Table 4-8).

Table 4-6. Linear, quadratic, cubic, bent-cable, and piecewise regression models for trend analyses in management kills, public kills, total non-hunt kills, and hunt kills. Models with a $\Delta AIC_c$ less than 2 are strongly supported by the data. Coefficients for the trend function (time, time$^2$, time$^3$, and time after the break point), standard errors (SE), and significance (*P*) values are shown. The break point is shown as the number of years after the initial year. k is the number of parameters estimated in the model and $\sigma$ is the error parameter used to estimate $AIC_c$. $\sigma^2$ is equal to the residual sum of squares divided by the sample size ($n$ = 22 for all models).

| **Model** | k | σ | $AIC_c$ | $\Delta AIC_c$ | **intercept** | SE | *P* | **time** | SE | *P* | **time$^2$** | SE | *P* | **time$^3$** | SE | *P* | **break point** | SE | *P* | **time after break** | SE | *P* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Management kills* | | | | | | | | | | | | | | | | | | | | | | |
| Time | 3 | 2.97 | 17.73 | 0 | 1.94 | 0.80 | 0.02 | 0.03 | 0.06 | 0.68 | | | | | | | | | | | | |
| Time + Time$^2$ | 4 | 2.27 | 18.18 | 0.45 | -0.21 | 1.14 | 0.86 | 0.56 | 0.23 | 0.02 | -0.02 | 0.01 | 0.03 | | | | | | | | | |
| Time+Time$^2$+Time$^3$ | 5 | 2.27 | 21.57 | 3.84 | -0.23 | 1.70 | 0.90 | 0.57 | 0.63 | 0.37 | -0.02 | 0.06 | 0.70 | 0 | 0.002 | 0.99 | | | | | | |
| Bent-cable | 5 | 2.28 | 21.63 | 3.9 | 0.30 | 1.11 | 0.79 | 0.30 | 0.17 | 0.09 | | | | | | | 11.08 | 2.95 | < 0.01 | -0.22 | -0.22 | < 0.01 |
| Piecewise | 4 | 2.28 | 18.22 | 0.49 | 0.30 | 0.99 | 0.76 | 0.30 | 0.13 | 0.03 | | | | | | | 11.08 | 2.95 | < 0.01 | -0.52 | 0.22 | 0.03 |
| *Public kills* | | | | | | | | | | | | | | | | | | | | | | |
| Time | 3 | 20.96 | 36.41 | 16.31 | 10.47 | 2.12 | < 0.001 | -0.23 | 0.16 | 0.18 | | | | | | | | | | | | |
| Time + Time$^2$ | 4 | 2.94 | 20.66 | 0.56 | 2.26 | 1.30 | 0.10 | 0.29 | 0.26 | 0.28 | -0.02 | 0.01 | 0.17 | | | | | | | | | |
| Time+Time$^2$+Time$^3$ | 5 | 15.04 | 39.65 | 19.55 | 19.98 | 4.38 | < 0.001 | -3.49 | 1.61 | 0.04 | 0.26 | 0.16 | 0.12 | -0.01 | 0.005 | 0.22 | | | | | | |
| Bent-cable | 5 | 2.77 | 23.50 | 3.4 | 2.93 | 0.97 | 0.01 | 0.04 | 0.10 | 0.71 | | | | | | | 16.62 | 2.73 | < 0.001 | -0.60 | 0.44 | < 0.01 |
| Piecewise | 4 | 2.77 | 20.10 | 0 | 2.92 | 0.90 | < 0.01 | 0.04 | 0.09 | 0.66 | | | | | | | 16.62 | 2.73 | < 0.001 | -0.64 | 0.35 | 0.08 |
| *Total non-hunt* | | | | | | | | | | | | | | | | | | | | | | |
| Time | 3 | 7.43 | 26.50 | 1.29 | 6.95 | 1.26 | < 0.001 | -0.08 | 0.10 | 0.42 | | | | | | | | | | | | |
| Time + Time$^2$ | 4 | 5.13 | 25.97 | 0.76 | 3.06 | 1.71 | 0.09 | 0.89 | 0.34 | 0.02 | -0.04 | 0.01 | 0.01 | | | | | | | | | |
| Time+Time$^2$+Time$^3$ | 5 | 4.98 | 29.09 | 3.88 | 4.41 | 2.52 | 0.10 | 0.26 | 0.93 | 0.78 | 0.03 | 0.09 | 0.79 | 0 | 0.003 | 0.79 | | | | | | |
| Bent-cable | 5 | 4.74 | 28.61 | 3.4 | 5.32 | 1.22 | < 0.001 | 0.15 | 0.12 | 0.23 | | | | | | | 17.69 | 1.29 | < 0.001 | -1.70 | 0.76 | < 0.001 |
| Piecewise | 4 | 4.73 | 25.21 | 0 | 5.32 | 1.15 | < 0.001 | 0.15 | 0.10 | 0.17 | | | | | | | 17.69 | 1.29 | < 0.001 | -1.85 | 0.56 | < 0.01 |
| *Total Hunt* | | | | | | | | | | | | | | | | | | | | | | |
| Time | 3 | 20.96 | 36.41 | 1.98 | 10.47 | 2.12 | < 0.001 | -0.23 | 0.16 | 0.18 | | | | | | | | | | | | |
| Time + Time$^2$ | 4 | 16.37 | 37.06 | 2.63 | 15.96 | 3.06 | < 0.001 | -1.60 | 0.61 | 0.02 | 0.06 | 0.03 | 0.03 | | | | | | | | | |
| Time+Time$^2$+Time$^3$ | 5 | 15.04 | 39.65 | 5.22 | 19.98 | 4.38 | < 0.001 | -3.49 | 1.61 | 0.04 | 0.26 | 0.16 | 0.12 | -0.01 | 0.005 | 0.22 | | | | | | |
| Bent-cable | 5 | 12.43 | 37.83 | 3.4 | 16.73 | 2.66 | < 0.001 | -1.33 | 0.43 | < 0.001 | | | | | | | 10.21 | 1.77 | < 0.001 | 0.55 | 0.33 | 0.11 |
| Piecewise | 4 | 12.43 | 34.43 | 0 | 16.73 | 2.41 | < 0.001 | -1.33 | 0.33 | < 0.001 | | | | | | | 10.21 | 1.77 | < 0.001 | 1.88 | 0.52 | < 0.01 |

Table 4-7. The top 10 explanatory models for frequency of management, public, total non-hunt, and hunt kills. Frequency of bear mortalities for 1983 through to 2004 were regressed against the number of open landfills, the amount of vehicle traffic, the amount of visitation to Kluane National Park and Reserve, the number of growing season days, the Julian start date for the growing season, mean temperature for May, and total amount of precipitation for May. Models are ranked by $\Delta AIC_c$. $\Delta AIC_c$ values have been converted to Akaike weights (w). Coefficients are shown if the variable was present in that model. k is the number of parameters estimated in the model and RMSE is the root mean square error parameter used to estimate $AIC_c$.

| Model Rank | Intercept | Landfills | Vehicle | Visitation | Season length | Season start | Mean May temp. | Total May precip. | k | RMSE | $AIC_c$ | $\Delta AIC_c$ | w |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Management kills* | | | | | | | | | | | | | |
| 1 | -0.6458 | -- | -- | 0.0005 | -- | -- | -- | -- | 3 | 1.597 | 23.828 | 0.000 | 0.3115 |
| 2 | -1.1162 | -- | -- | 0.0005 | -- | -- | -- | 0.0202 | 4 | 1.608 | 26.025 | 2.197 | 0.1038 |
| 3 | -1.4231 | 0.0552 | -- | 0.0005 | -- | -- | -- | -- | 4 | 1.615 | 26.205 | 2.377 | 0.0949 |
| 4 | -0.7197 | -- | -- | 0.0006 | -- | -- | -0.0544 | -- | 4 | 1.619 | 26.332 | 2.504 | 0.0891 |
| 5 | -6.6414 | 0.2004 | 0.0146 | -- | -- | -- | -- | -- | 4 | 1.624 | 26.465 | 2.637 | 0.0833 |
| 6 | -1.5915 | -- | -- | 0.0005 | 0.0098 | -- | -- | -- | 4 | 1.632 | 26.680 | 2.852 | 0.0749 |
| 7 | -1.1362 | -- | 0.0016 | 0.0005 | -- | -- | -- | -- | 4 | 1.634 | 26.730 | 2.902 | 0.0730 |
| 8 | -1.8777 | -- | -- | 0.0005 | -- | 0.0090 | -- | -- | 4 | 1.636 | 26.784 | 2.956 | 0.0710 |
| 9 | -0.6380 | -- | 0.0063 | -- | -- | -- | -- | -- | 3 | 1.733 | 27.422 | 3.594 | 0.0516 |
| 10 | -5.6851 | 0.1559 | 0.0092 | 0.0003 | -- | -- | -- | -- | 5 | 1.586 | 27.623 | 3.794 | 0.0467 |
| *Public kills* | | | | | | | | | | | | | |
| 1 | 1.5144 | 0.1212 | -- | -- | -- | -- | -- | -- | 3 | 1.861 | 30.567 | 0.000 | 0.1932 |
| 2 | 2.2636 | -- | -- | -- | -- | -- | -- | 0.0351 | 3 | 1.882 | 31.068 | 0.501 | 0.1503 |
| 3 | 3.4486 | -- | -- | -- | -- | -- | -0.1037 | -- | 3 | 1.889 | 31.216 | 0.649 | 0.1396 |
| 4 | 4.0168 | -- | -- | -0.0002 | -- | -- | -- | -- | 3 | 1.926 | 32.078 | 1.511 | 0.0908 |
| 5 | 1.0991 | 0.1107 | -- | -- | -- | -- | -- | 0.0311 | 4 | 1.847 | 32.130 | 1.562 | 0.0884 |
| 6 | -2.4826 | 0.2036 | 0.0068 | -- | -- | -- | -- | -- | 4 | 1.863 | 32.502 | 1.935 | 0.0734 |
| 7 | 3.6173 | -- | -0.0017 | -- | -- | -- | -- | -- | 3 | 1.952 | 32.661 | 2.094 | 0.0678 |
| 8 | 1.2612 | -- | -- | -- | -- | 0.0128 | -- | -- | 3 | 1.953 | 32.682 | 2.115 | 0.0671 |
| 9 | 2.1708 | 0.1007 | -- | -- | -- | -- | -0.0760 | -- | 4 | 1.873 | 32.742 | 2.175 | 0.0651 |
| 10 | 2.5898 | -- | -- | -- | 0.0023 | -- | -- | -- | 3 | 1.957 | 32.769 | 2.202 | 0.0642 |
| *Total non-hunt* | | | | | | | | | | | | | |
| 1 | -9.6995 | 0.4666 | 0.0232 | -- | -- | -- | -- | -- | 4 | 2.438 | 44.333 | 0.000 | 0.2054 |
| 2 | -15.9444 | 0.4749 | 0.0222 | -- | 0.0556 | -- | -- | -- | 5 | 2.331 | 44.579 | 0.245 | 0.1817 |
| 3 | -11.8944 | 0.4774 | 0.0257 | -- | -- | -- | -- | 0.0564 | 5 | 2.342 | 44.780 | 0.447 | 0.1643 |
| 4 | 1.8796 | 0.5438 | 0.0217 | -- | -- | -0.0938 | -- | -- | 5 | 2.356 | 45.038 | 0.704 | 0.1444 |
| 5 | -18.6585 | 0.4593 | 0.0236 | -- | 0.0820 | -- | -0.1592 | -- | 6 | 2.301 | 46.602 | 2.268 | 0.0661 |
| 6 | -15.9793 | 0.4806 | 0.0242 | -- | 0.0418 | -- | -- | 0.0409 | 6 | 2.318 | 46.911 | 2.577 | 0.0566 |
| 7 | -2.5300 | 0.5346 | 0.0240 | -- | -- | -0.0722 | -- | 0.0449 | 6 | 2.321 | 46.983 | 2.650 | 0.0546 |
| 8 | -19.1310 | 0.5321 | 0.0285 | -0.0004 | 0.0736 | -- | -- | -- | 6 | 2.328 | 47.104 | 2.771 | 0.0514 |
| 9 | -9.8368 | 0.4730 | 0.0240 | 0.0000 | -- | -- | -- | -- | 5 | 2.503 | 47.711 | 3.378 | 0.0379 |
| 10 | -9.6852 | 0.4654 | 0.0233 | -- | -- | -- | -0.0094 | -- | 5 | 2.504 | 47.723 | 3.389 | 0.0377 |
| *Total Hunt* | | | | | | | | | | | | | |
| 1 | 17.7343 | -- | -- | -0.0017 | -- | -- | -- | -- | 3 | 4.069 | 64.983 | 0.000 | 0.2345 |
| 2 | 8.4713 | -- | -- | -0.0021 | 0.0963 | -- | -- | -- | 4 | 3.933 | 65.377 | 0.394 | 0.1926 |
| 3 | 15.6703 | -- | -- | -0.0016 | -- | -- | -- | 0.0887 | 4 | 3.941 | 65.469 | 0.486 | 0.1839 |
| 4 | 26.4709 | -- | -- | -0.0018 | -- | -0.0641 | -- | -- | 4 | 4.128 | 67.507 | 2.525 | 0.0664 |
| 5 | 9.6750 | -- | -- | -0.0019 | 0.0688 | -- | -- | 0.0619 | 5 | 3.939 | 67.661 | 2.678 | 0.0615 |
| 6 | 17.8838 | -- | -- | -0.0018 | -- | -- | 0.1101 | -- | 4 | 4.144 | 67.678 | 2.696 | 0.0609 |
| 7 | 16.6305 | 0.0783 | -- | -0.0017 | -- | -- | -- | -- | 4 | 4.156 | 67.804 | 2.822 | 0.0572 |
| 8 | 17.7518 | -- | -0.0001 | -0.0017 | -- | -- | -- | -- | 4 | 4.174 | 68.002 | 3.020 | 0.0518 |
| 9 | 15.7064 | -- | -- | -0.0018 | -- | -- | 0.1643 | 0.0967 | 5 | 3.976 | 68.069 | 3.087 | 0.0501 |
| 10 | 7.0337 | 0.0917 | -- | -0.0020 | 0.0978 | -- | -- | -- | 5 | 4.012 | 68.468 | 3.486 | 0.0410 |

Table 4-8. Importance values for variables used to explain annual frequencies of management kills, public kills, total non-hunt kills, and hunt kills. Variable importance is calculated by summing the Akaike weights for all model in which the variable is present. Variables are ranked by importance.

| | *Management kills* | | *Public kills* | | *Total non-hunt* | | *Total Hunt* | |
|---|---|---|---|---|---|---|---|---|
| **Variable** | I | **Rank** | I | **Rank** | I | **Rank** | I | **Rank** |
| Landfills | 0.3100 | 3 | 0.4457 | 1 | 0.8623 | 1 | 0.1749 | 6 |
| Vehicle | 0.3419 | 2 | 0.2565 | 4 | 0.7638 | 2 | 0.1647 | 7 |
| Visitation | 0.6785 | 1 | 0.2454 | 5 | 0.1812 | 7 | 0.9626 | 1 |
| Season length | 0.2386 | 4 | 0.2099 | 6 | 0.3692 | 3 | 0.3376 | 3 |
| Season start | 0.1808 | 7 | 0.1995 | 7 | 0.2690 | 5 | 0.1750 | 5 |
| Mean May temp. | 0.1935 | 6 | 0.3058 | 3 | 0.1824 | 6 | 0.1760 | 4 |
| Total May precip. | 0.2173 | 5 | 0.3331 | 2 | 0.2936 | 4 | 0.3482 | 2 |

## Spatial Characteristics of Occurrences and Mortalities

*Explanatory models for occurrences and mortality distribution.*--I examined spatial factors that influenced occurrences inside and outside protected areas. All variables significantly explained the location of occurrences in the protected area complex (Table 4-9). Occurrences were often near secondary linear features, but distant from primary linear features (Table 4-9). Occurrences in protected areas took place further from landfills than expected, and close to water bodies (Table 4-9). Occurrences were more likely to take place at low elevations and in areas with high human infrastructure density (Table 4-9). The distance to secondary linear features was the strongest factor explaining the relative probability of an occurrence (Table 4-9). Although bear habitat was positively correlated with the distribution of occurrences, the magnitude of the standardized coefficient for habitat was small compared to other variables (Table 4-9). Therefore, while occurrences were most likely to happen in high-use bear habitats, variables other than habitat were the most influential in determining the spatial pattern of occurrences in protected areas (Table 4-9). In-sample validation indicated an excellent fit between data and the explanatory model (Table 4-10).

Outside the protected area complex, the distance from water and human infrastructure density were the only significant covariates for occurrences (Table 4-9). Probability of habitat use, distance to any type of linear feature, distance from landfills and elevation failed to significantly explain the location of bear occurrences (Table 4-9). Occurrences were associated with areas of high infrastructure density and close to water (Table 4-9). The magnitude of the standardized coefficient for infrastructure density was up to 65 times greater than other variables, indicating exceptional influence (Table 4-9). Model validation indicated good fit with the data (Table 4-10).

I examined the spatial factors that may influence non-hunting and hunting mortality. All variables except distance from landfills and distance from secondary linear features were significant for explaining the spatial distribution of non-hunting mortality (Table 4-11). Non-hunting mortality was positively correlated with habitat use and human infrastructure density (Table 4-11). This type of mortality was also most likely to happen close to water bodies and primary linear features, and at low elevation sites (Table 4-11). As with occurrences outside protected areas, the distribution of non-hunting mortality was most strongly influenced by human infrastructure density (Table 4-11). There was a good positive correlation between the binned frequency of mortalities and bin rank (Table 4-10).

Hunting mortalities were most likely to occur in areas with high density of human infrastructure and close to secondary linear features (Table 4-11). Both variables had similar degrees of influence on the distribution of successful hunt locations (Table 4-11). All other variables failed to explain the location of successful hunts (Table 4-11). Model validation indicated only moderate model fit with data (Table 4-10).

*Occurrence and mortality hot spots.*--Most occurrence hot spots did not change substantially in location or size between analysis time periods (Table 4-12). From 1980 to 1993, four of the six hot spots were concentrated in the Slims River Valley, one was centered on Destruction Bay and one centered on Haines Junction (Figure 4-4). After closure or electrification of the major landfills in the area (e.g., Congdon Creek in 1989 and Haines Junction in 1992), the occurrence hot spot near Destruction Bay disappeared, but a new hot spot appeared at

Table 4-9. Discrete choice models ($\alpha = 0.05$) for occurrences inside and outside of the protected area complex. Coefficients have been standardized as a means for comparing the effects of variables.

| variable | unstandardized coefficient† | std. error† | Wald Chi-square | *P* | df | standardized coefficient |
|---|---|---|---|---|---|---|
| *Occurrences inside of protected area complex* | | | | | | |
| Weighted habitat | 2.6371 | 0.8672 | 9.6721 | <.0019 | 1 | 0.1284 |
| Distance to water | -0.00152 | 0.000256 | 35.2160 | <.0001 | 1 | -0.5035 |
| Elevation | -0.00108 | 0.000219 | 24.4657 | <.0001 | 1 | -0.3175 |
| Human density | 0.00345 | 0.000426 | 65.4136 | <.0001 | 1 | 0.2311 |
| Distance to open landfill | 0.000056 | 9.70E-06 | 32.9904 | <.0001 | 1 | 0.7642 |
| Distance to primary roads | 0.000043 | 0.000012 | 12.7126 | 0.0004 | 1 | 0.2722 |
| Distance to secondary routes | -0.00051 | 0.000055 | 86.3016 | <.0001 | 1 | -1.5149 |
| *Occurrences outside of protected area complex* | | | | | | |
| Weighted habitat | -7.0569 | 4.9669 | 2.0186 | 0.1554 | 1 | -0.2784 |
| Distance to water | -0.00123 | 0.000540 | 5.2353 | 0.0221 | 1 | -0.2806 |
| Elevation | 0.000249 | 0.00144 | 0.0300 | 0.8625 | 1 | 0.0591 |
| Human density | 0.0256 | 0.00318 | 65.2221 | <.0001 | 1 | 2.0295 |
| Distance to open landfill | -2.82E-06 | 0.000025 | 0.0127 | 0.9104 | 1 | -0.0302 |
| Distance to primary roads | 0.00001 | 0.000071 | 0.0294 | 0.8638 | 1 | -0.0591 |
| Distance to secondary routes | 0.000194 | 0.000239 | 0.6543 | 0.4186 | 1 | 0.3848 |

†"E-x" indicates that the value before the E is multiplied by $10^{-x}$ where x is the value following the E.

Table 4-10. k-fold cross validation results for occurrence and mortality discrete choice models.

| **model** | **Spearman's rho (average)** | *n* |
|---|---|---|
| *Occurrences inside of protected area complex* | 0.9264 | 334 |
| *Occurrences outside of protected area complex* | 0.766 | 94 |
| *Total non-hunt mortalities* | 0.609 | 127 |
| *Total hunt mortalities* | 0.442 | 51 |

Table 4-11. Discrete choice models ($\alpha = 0.05$) for non-hunt and hunt mortalities. Coefficients have been standardized as a means for comparing the effects of variables.

| variable | unstandardized coefficient[†] | std. error[†] | Wald Chi-square | *P* | df | standardized coefficient |
|---|---|---|---|---|---|---|
| *Total non-hunt mortalities* | | | | | | |
| Weighted habitat | 7.3406 | 2.1082 | 12.1241 | 0.0005 | 1 | 0.2934 |
| Distance to water | -0.00134 | 0.0004 | 11.2048 | 0.0008 | 1 | -0.3092 |
| Elevation | -0.00296 | 0.00111 | 7.0254 | 0.008 | 1 | -0.6532 |
| Human density | 0.00638 | 0.000626 | 103.6923 | <.0001 | 1 | 0.5773 |
| Distance to landfills | 7.107E-06 | 0.000015 | 0.2256 | 0.6348 | 1 | 0.0728 |
| Distance to primary roads | -0.00007 | 0.000034 | 3.9518 | 0.0468 | 1 | -0.4527 |
| Distance to secondary routes | -0.00030 | 0.000163 | 3.4472 | 0.0634 | 1 | -0.5696 |
| *Total hunt mortalities* | | | | | | |
| Weighted habitat | 0.1766 | 3.2616 | 0.0029 | 0.9568 | 1 | 0.00589 |
| Distance to water | -0.00054 | 0.000452 | 1.4130 | 0.2346 | 1 | -0.1144 |
| Elevation | -0.00122 | 0.000881 | 1.9211 | 0.1657 | 1 | -0.2401 |
| Human density | 0.00437 | 0.00103 | 18.1347 | <.0001 | 1 | 0.3201 |
| Distance to landfills | -0.00003 | 0.00002 | 2.0646 | 0.1508 | 1 | -0.3377 |
| Distance to primary roads | -4.3E-06 | 0.000024 | 0.0332 | 0.8555 | 1 | -0.0448 |
| Distance to secondary routes | -0.00018 | 0.000089 | 4.092 | 0.0431 | 1 | -0.3864 |

[†] "E-x" indicates that the value before the E is multiplied by $10^{-x}$ where x is the value following the E.

Table 4-12. A two-sampled t-test was used to test for changes in size of occurrences and mortality hot spots over specified time periods ($\alpha = 0.05$). Unequal samples sizes among time periods may have biased hot spots sizes because time periods with fewer years of data, and hence fewer locations, were likely to have smaller hot spots than time periods with more locations. Time periods for mortalities were roughly equal and therefore less likely to be subject to this problem.

**Occurrence hot spots**

| 1980-1993 (time 1) | | | 1994-1997 (time 2) | | | 1998-2004 (time 3) | | |
|---|---|---|---|---|---|---|---|---|
| Cluster | Area | Points | Cluster | Area | Points | Cluster | Area | Points |
| 1 | 89.7394 | 24 | 1 | 5.80762 | 9 | 1 | 60.94886 | 23 |
| 2 | 36.06365 | 14 | 2 | 14.5843 | 7 | 2 | 102.90027 | 19 |
| 3 | 34.32651 | 12 | 3 | 14.93924 | 6 | 3 | 23.44713 | 8 |
| 4 | 54.53321 | 12 | 4 | 23.26221 | 5 | 4 | 13.30979 | 5 |
| 5 | 7.75052 | 11 | | | | 5 | 8.96946 | 5 |
| 6 | 4.88787 | 5 | | | | 6 | 2.26628 | 5 |
| mean | 37.883527 | | | 14.648343 | | | 35.306965 | |
| variance | 995.78386 | | | 50.81527 | | | 1527.2488 | |
| df | 6 | | | 5 | | | 10 | |
| t | 2.4469136 | | | 2.5705776 | | | 2.2281392 | |
| $P$ | 0.1328235 | | | 0.2620496 | | | 0.902501 | |
| *(comparison of time 1 to time 2)* | | | | *(comparison of time 2 to time 3)* | | | *(comparison of time 1 to time 3)* | |

**Mortality hot spots**

| 1980-1993 (time 1) | | | 1994-2004 (time 2) | | |
|---|---|---|---|---|---|
| Cluster | Area | Points | Cluster | Area | Points |
| 1 | 10.99547 | 12 | 1 | 0.38701 | 10 |
| 2 | 0.10571 | 10 | 2 | 0.32547 | 8 |
| 3 | 5.07494 | 5 | 3 | 5.10381 | 3 |
| 4 | 3.82866 | 4 | 4 | 0.45412 | 3 |
| 5 | 0.404 | 4 | 5 | 3.59324 | 3 |
| 6 | 3.2998 | 3 | | | |
| 7 | 0.32547 | 3 | | | |
| 8 | 0.32547 | 3 | | | |
| 9 | 11.55339 | 3 | | | |
| mean | 3.9903233 | | | 1.97273 | |
| variance | 20.345705 | | | 4.9909661 | |
| df | 12 | | | | |
| t | 2.1788128 | | | | |
| $P$ | 0.2855964 | | | | |
| *(comparison of time 1 to time 2)* | | | | | |

Congdon Creek Campground (Figure 4-4). There were four hot spots in the 1993 to 1997 analysis window, three in the Slims River Valley and one in the Haines Junction area. Similarly, in the 1997 to 2004 window, there were six major occurrence hot spots, four of which still persisted in the Slims River Valley, one in the Haines Junction area, and one in the Congdon Creek Campground area (Figure 4-4). Occurrence locations were strongly clumped in each analysis period and did not show substantial change in dispersion patterns (Figure 4-5).

Mortality location data were subdivided into dates prior to the Haines Junction landfill electrification in 1992 and dates after electrification. Mortalities that occurred in 1993 were pooled with data from 1992 and earlier because of a potential lag effect. Hot spot analysis identified nine areas from 1993 and earlier where bear mortality was concentrated. These areas were located in the vicinities of Burwash Landing, Destruction Bay, the Dutch Harbour and Congdon Creek Campgrounds, the Slims West trail in KNPR, Silver City, and Haines Junction (Figure 4-6). Analysis of locations from 1994 to 2004 showed four hot spots. Hot spots remained around Burwash Landing, Destruction Bay, and Congdon Creek Campground, but disappeared from the Dutch Harbour, Slims River Valley, Silver City, and Haines Junction areas (Figure 4-6). A new hot spot appeared in the Bear Creek area. The average size of mortality hot spots was not significantly different post-electrification (Table 4-12). Second order analysis of the spatial distribution of the locations showed significant clumping of mortalities prior to electrification of landfills. Mortalities were more clumped after than prior to electrification (Figure 4-7).

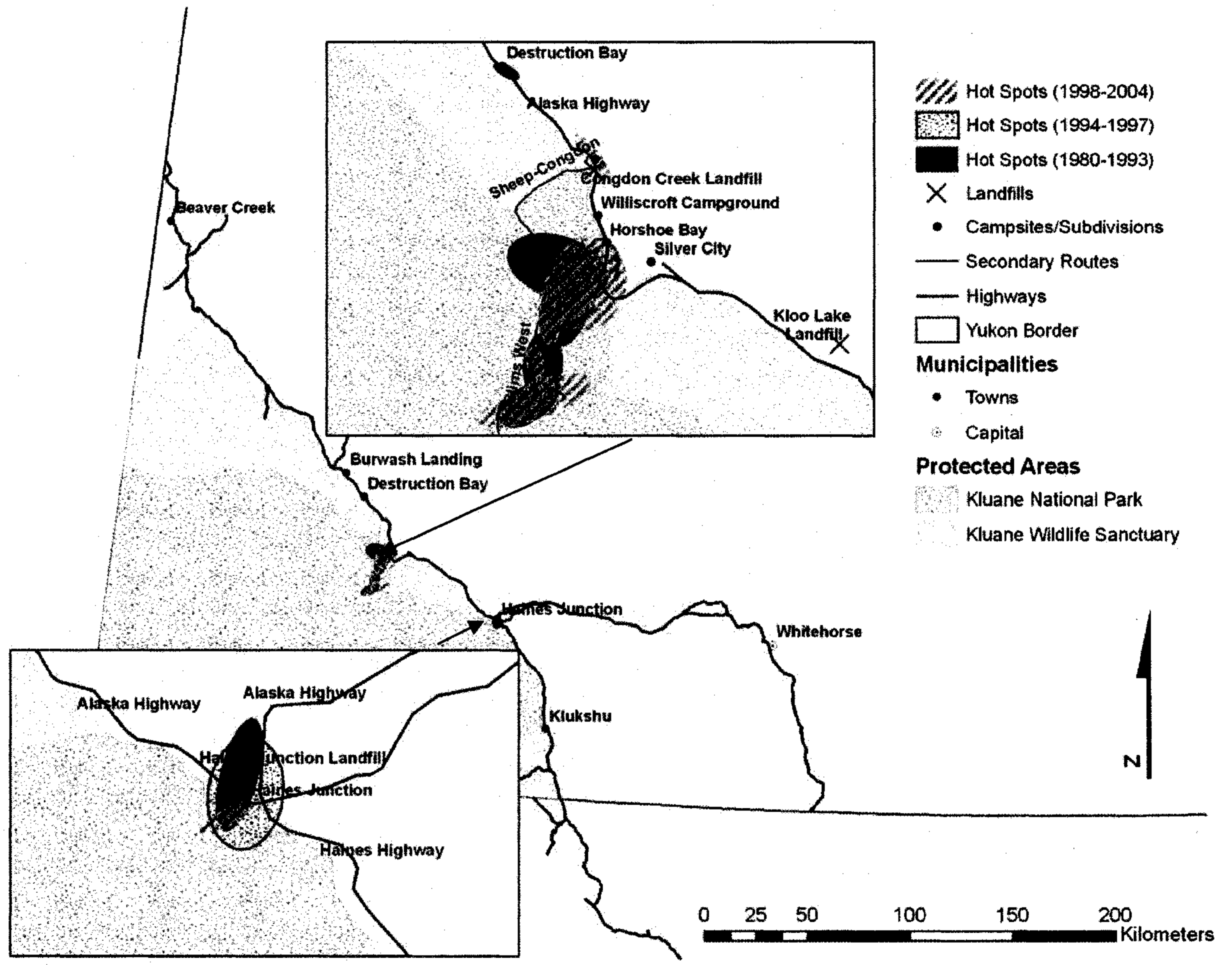


Figure 4-4. Occurrence hot spots in the Kluane Region. Six hot spots were detected for the time period 1980 – 1993. Four hot spots were detected for the time period 1994 – 1997, and six hot spots were detected for the time period 1998 – 2004.

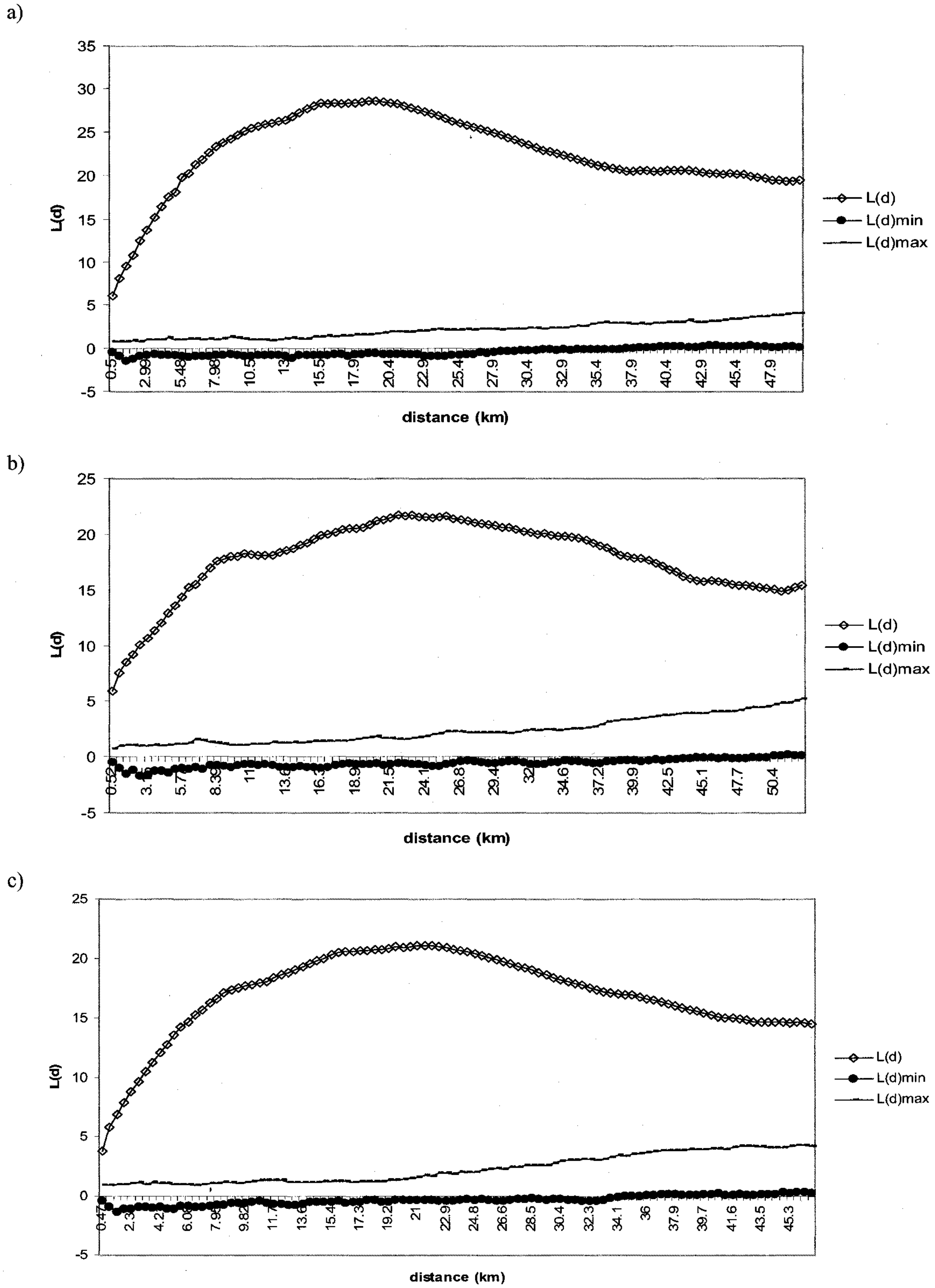


Figure 4-5. The observed L(d) and expected L(d)min and L(d)max envelope for occurrences for a) time period 1, 1980 – 1993, b) time period 2, 1994 – 1997, and c) time period 3, 1998 – 2004. Ripley's K was used to examine changes in the spatial dispersion of occurrences. In all time periods the observed L(d) is above the L(d)max, indicating significant clumping of occurrences.

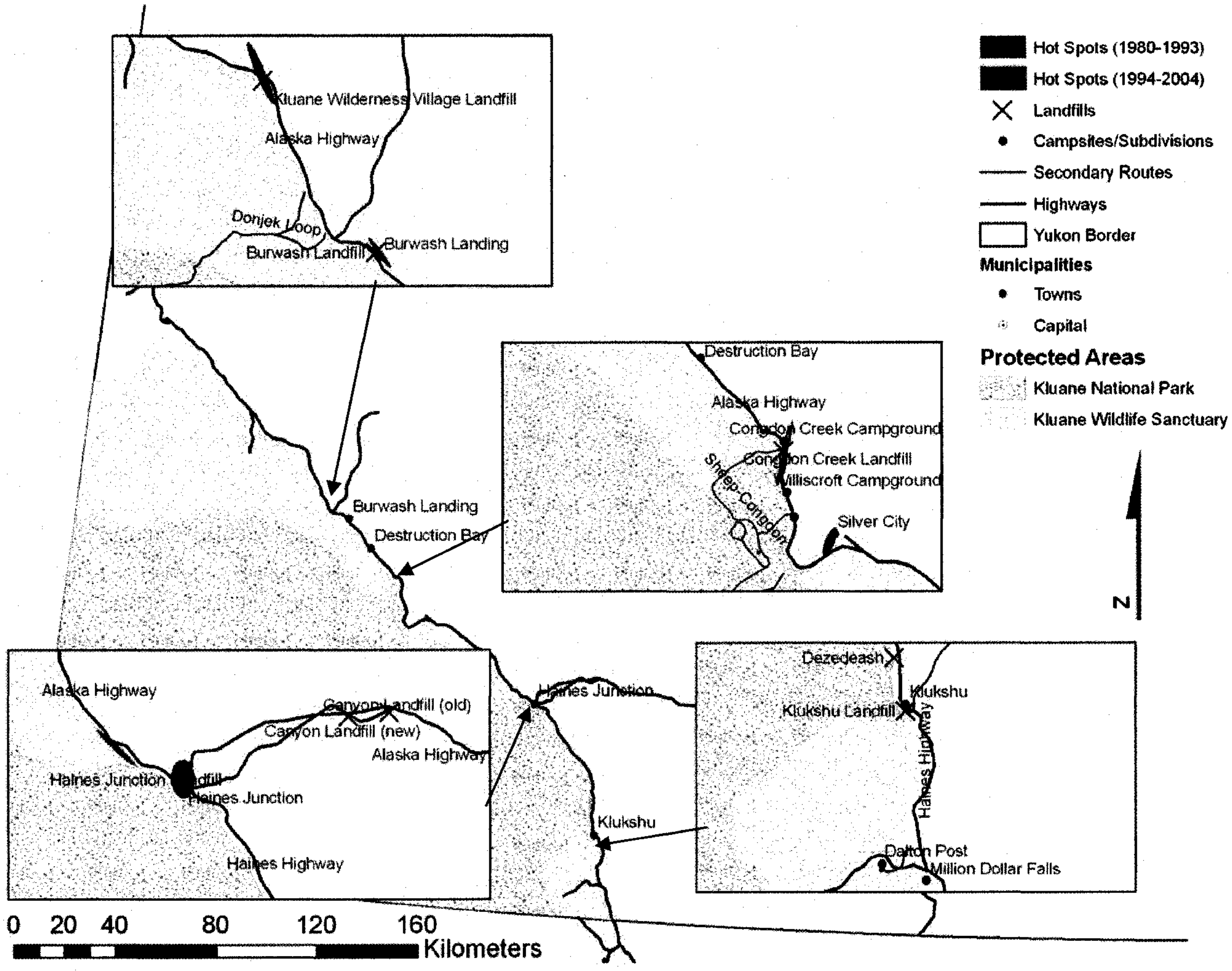


Figure 4-6. Non-hunt mortality hot spots in the Kluane Region. Nine hot spots were detected for the time period 1980 – 1993. Four hot spots were detected for the time period 1994 – 2004.

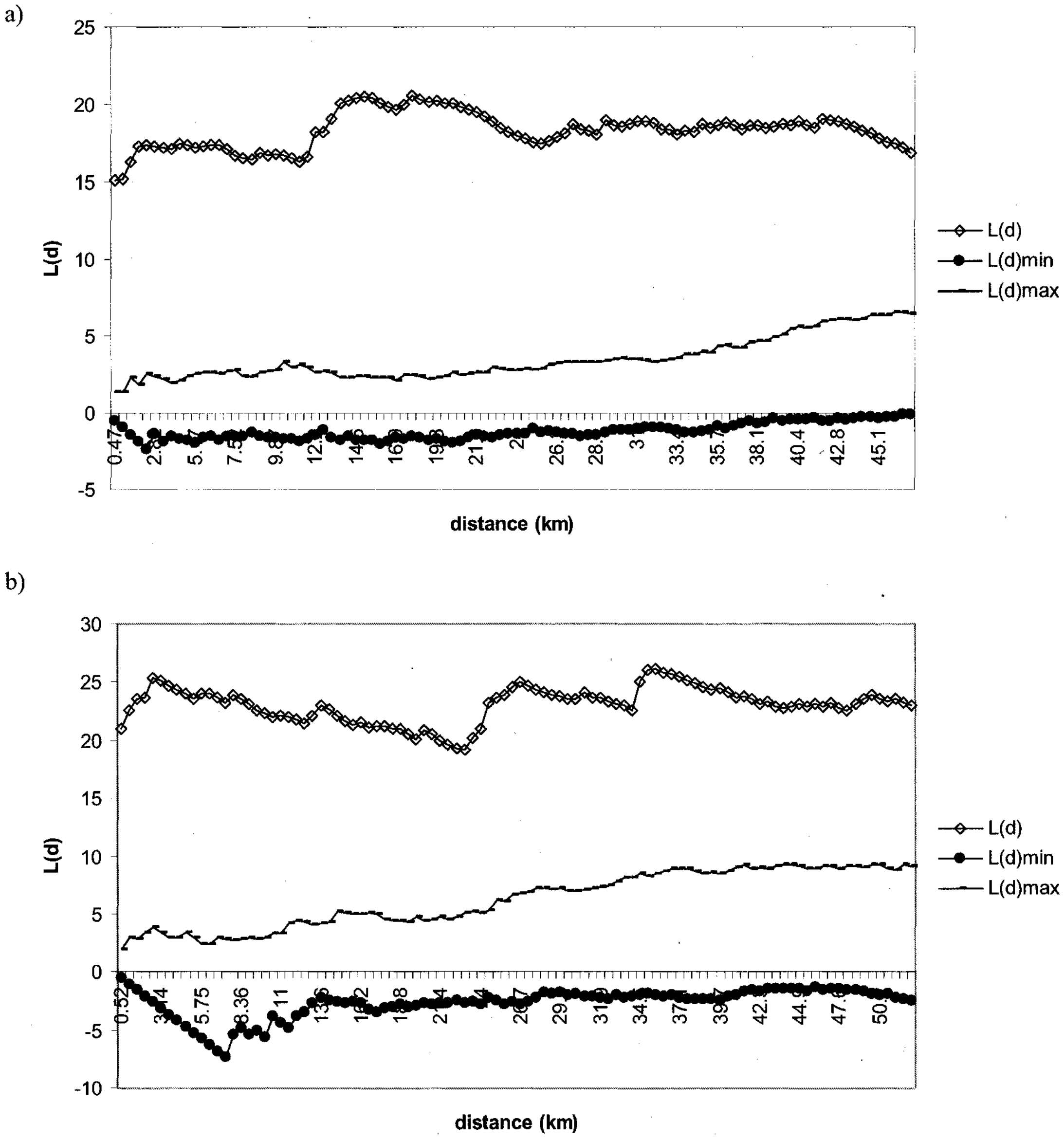


Figure 4-7. The observed L(d) and expected L(d)min and L(d)max envelope for grizzly bear mortalities for a) time period 1, 1980 – 1993, and b) time period 2, 1994 – 2004. Ripley's K was used to examine changes in the spatial dispersion of mortalities. In all time periods the observed L(d) is above the L(d)max, indicating significant clumping of mortalities.

## DISCUSSION

Management actions to reduce human-bear interactions were initiated in 1989; however, the frequency of occurrences did not decline until 1997 and the frequency of non-hunt mortalities did not decline until 1998. The eight-year delay between management actions and reduction in bear mortality was unexpected. A one- to two-year delay between closure or electrification of a landfill and decline in frequency of bear mortalities is common (Knight and Eberhardt 1984, Follman and Hechtel 1990). In the two years following a landfill closure the bears using that landfill as a major non-natural food source are displaced. To replace this food source, the human food-conditioned bears move into other areas occupied by people (Gunther et al. 1995, Davis et al. 2002), get into conflicts, and subsequently are killed (Craighead et al. 1995, Mattson et al. 1992). In Yellowstone National Park, closure of landfills was followed by an almost doubling of recorded mortalities as bears sought alternative food sources (Knight and Eberhardt 1984, Mattson et al. 1992, Craighead et al. 1995). In Kluane, once the number of open landfills started decreasing in 1989, the number of bear mortalities should have decrease by 1991. Instead, the number of mortalities continued to increase until 1998.

There are several possible reasons for the delayed response to management actions. For instance, the temporal spread of landfill closures and electrification over many years may have continually displaced bears. The displacement effect probably also caused the increased number of occurrences in the protected areas. Like in Yellowstone National Park, if the bear mortality rate in the Kluane Region increased in the two years following landfill closure or electrification, and given that closures or electrification took place every one to three years over a 13-year period, mortality rates were probably inflated throughout the entire time period by displacement of bears to other areas with human activity, and subsequent human-caused mortality. That is, each time a landfill was closed or electrified, the bear mortality rate increased. Just as this effect from closing or electrifying one landfill was dissipating, a new closure or electrification occurred and the mortality rate increased again.

Increased human activity may have also contributed to increased non-hunt mortality, negating the positive effects of landfill closures. More human activity directly increases the probability of a human-bear encounter, and, concordantly increases bear mortality (Gunther et al. 1995, Benn and Herrero 2002). While the number of open landfills decreased in the 1990s, the number of people recreating or living in the Haines Junction area increased (Yukon Territorial Government 2002). In some cases, when landfills closed, new problem areas developed. For instance, the mortality hot spot disappeared from the Haines Junction area, but a new hot spot appeared near the Bear Creek area, likely associated with the development of a new subdivision (MacIntosh Subdivision).

The trends of human-bear interactions may also have been affected by forage availability. Higher amounts of precipitation than average for the month of May can reduce berry crop abundance (Noble 1985). I found a positive correlation between the frequency of occurrences outside of the protected area complex or the frequency of mortalities and the total amount of precipitation for May. In years when berry crops fail, human-habituated grizzly bears, more often than otherwise, may use native and non-native foods near human developments, and are more prone to human-bear conflicts (Fuller and Sievert 2001). This is particularly true for adult females, who have high energetic demands associated with providing food for dependent young (Mattson et al. 1992). Management-related reductions in human-bear interactions in Kluane may have been masked by the effects of berry crop failure if the numbers of crop failures increased over the last two decades. No data were available for crop failure rates, but the total precipitation for May exhibited a slight increasing trend (Krebs and Boonstra 2001, Henry et al. 2005).

Indicators of berry productivity did not strongly correlate with the frequency of occurrences in the protected area complex. Rather, berry productivity-related variables appeared to explain human-use rather than berry crop abundance. For instance, years with later growing season starts and more precipitation had fewer occurrences in the protected area complex. These conditions are disadvantageous for berry crop abundance (Noble 1985) so should have resulted in more occurrences. More likely, backcountry visitation was lower in years that had a rainy or cold spring so there were fewer human-bear encounters.

Other factors may have accounted for changes in the frequency of mortality, but no data were available to model them. They include the time available to management staff for dealing with human-wildlife conflicts, the experience and personalities of individuals involved in managing human-bear conflicts, the personalities and tolerance of individuals living in high human-bear conflict zones, and public perception about the status of the bear population (Bath 1998). The time available to management staff for dealing with human-wildlife conflicts varies each year. If time is insufficient staff may elect to put animals down, rather than take time to assess alternate actions. Some staff may be more concerned about public injury and liability than others and are unwilling to 'wait and see' if a bear is a threat. Willingness of the public to report bear kills may depend on their fear of being prosecuted. Residents that are intolerant of bears in their backyard may feel more threatened than tolerant residents and, therefore, more apt to kill a bear on their property (Bath 1998, Sillero-Zubiri and Laurenson 2001, Naughton-Treves et al. 2003).

Like other studies (Benn 1998, Merrill and Mattson 2003, Wilson 2003, Nielsen et al. 2004a), I found that areas densely occupied by people had the highest frequency of occurrences and mortalities. However, mortalities had a stronger association than occurrences with high-use bear habitat. Bear mortalities were likely to happen when human activity juxtaposed high-use bear habitat. Occurrences were more strongly driven by prevalence of people on the landscape rather than the prevalence of bears. Hence, high prevalence of human activity does not necessarily result in high rates of bear mortality (Linnell et al. 2001). Rather, mortalities occur in areas where bears and people consistently encounter each other (Merrill and Mattson 2003, Wilson 2003).

Where humans and bears encounter each other, mortalities are then conditioned upon the probability that a human-bear interaction may turn problematic, and, subsequently, the probability that the resolution will be lethal for the bear. Whether or not a human-bear interaction will turn lethal is contingent on if the means to kill a bear (e.g., a firearm) is readily available (Mattson et al. 1996b, Merrill and Mattson 2003), public tolerance of bears (Røskaft et al. 2003), whether wildlife management policies permit killing of the bear, and if there is adequate enforcement of policies that discourage or prohibit killing of bears (Linnell et al. 2001). Human-bear interactions inside the protected area complex resulted in fewer bear mortalities per occurrence because management agencies did not initially respond with lethal control, the individuals involved in the occurrence were not armed, and human activity on the landscape was ephemeral (Mattson et al. 1996b, Merrill and Mattson 2003).

My findings were limited by several issues. First, certain kinds of human-caused mortalities have a much higher probability of being detected or reported than others (Mattson 1998, McLellan et al. 1999, Cherry et al. 2002). It is highly unlikely that the reported mortalities in the Kluane Region represent all human-caused grizzly bear mortality. Detection of additional deaths from poaching and accidental kills would require radio-monitoring of a large proportion of the population (Cherry et al. 2002). While I was able to obtain information on 12 poaching events, it is impossible to estimate the proportion of mortality that this represents. Results are thus biased toward reported mortalities.

Second, I was not able to obtain location information for all occurrences or mortalities. I was only able to obtain accurate information on locations for occurrences and mortalities in so far as spatial reference information was reported, or interviewees were able to recall or willing to disclose. Locations for hunting mortalities were particularly difficult to obtain because hunters felt that they be might jeopardizing future hunting opportunities. I cannot easily predict how this bias affects my findings, though, one could assume that access, necessary for people to move around on the landscape, would still have been a key variable in predicting unreported kill locations.

A third issue was that the frequency of hunt-related bear mortalities had a weak negative correlation with non-hunt mortalities (and occurrences). This indicated that there may be a mild compensatory effect of hunting on management kills or vice versa. That is, some harvested bears may be those otherwise predisposed to conflicts with humans. These bears occupy habitats close to human infrastructure and close to access points for hunters. Where bears are killed through management actions, fewer bears may be available to hunters. Conversely, where bears were killed through hunting, the number of bears that need to be killed through management actions may be reduced. Data were not available to evaluate the interaction between management and hunter kills.

Management agencies in the Kluane Region undertook major initiatives to manage grizzly bear attractants and educate the public about human-bear conflicts. These efforts were successful (also see McDougall and Young 2005). There was a rapid decline in the frequency of all occurrences after 1997 – the number of occurrences dropped from 39 in 1996 to 14 in 2004. Total non-hunt mortalities declined as well, though the response was not immediate and was less dramatic than for occurrences. However, management initiatives mitigated only a portion of management-related bear mortality. Mitigation efforts were primarily directed at recreation activities and landfills, but I found a close association between proximity to roads and frequency of bear mortalities. In conjunction with land-use planning processes, access management plans are integral for reducing human-caused bear mortality (Summerfield et al. 2004). These plans stipulate road density standards, the proportion of management units that should be roadless, the types of access (e.g., motorized versus non-motorized), the volume of traffic that may use a linear access feature, the seasons and timing of using access features, and include guidelines on road placement.

Some privately owned campgrounds and subdivisions also had high density of bear mortalities, but no mitigation efforts were specifically directed toward these developments. Mitigation of human-caused mortality in relation to roads, and placement of subdivisions, campgrounds or other infrastructure is most directly dealt with through land-use planning and regulatory processes (e.g., through land-use and development permitting, or regulations, policies and bylaws; Press et al. 1996). Developments should be placed to minimize the potential for human-bear conflict, and mitigations for conflicts need to be considered for each development. Mitigation measures, implemented through regulatory processes, should include use of electric fencing around attractants (Wilson et al. 2005), programs that promote reduction of attractants on private property, required use of bear proof containers on private property (Davis et al. 2002), and mandatory closures of private campgrounds at certain times of year, or after a certain number of human-bear conflicts (McDougall and Young 2005). Mitigation measures for private property have been suggested by national and provincial Bear Aware and Bear Smart Programs (Davis et al. 2002).

From 1980 to 1998, grizzly bear harvest and management mortality outside of the protected area complex exceeded prescribed rates (Table 4-1; McCann 1998), creating mortality sinks along the Haines and Alaska Highways. A resident hunter may harvest only one bear every three years with the Yukon Territory, but there currently is no annual limit to the number of bears that may be harvested from the Kluane Region (e.g., no regional harvest limit; Yukon Territorial Government 1997). Though management efforts have reduced the effects of landfills on the overall rate of mortality was not monitored. Given, the compensatory effect between management-related kills and grizzly bear harvest, management targets should be set to ensure that the combined mortality rate from hunt and non-hunt kills is accounted for. If one cause of mortality simply substitutes for the other, and overall rates still exceed sustainable limits for the population, management efforts will not be successful.

## CONCLUSIONS

Human-bear encounters may be impossible to eliminate in the Kluane Region, but management actions over the last two decades were effective in reducing the frequency of occurrences and bear mortalities. Management actions were directed toward reducing attractants available to bears, reducing human-bear encounter rates, and educating wilderness users on how to prevent conflicts with bears. However, as human activity increases in the region the efficacy of efforts to reduce human-bear conflicts may diminish. Limited increases in human activity could be accommodated if activities are managed properly. Analyses that explore the spatial and temporal characteristics of human-bear interactions can be used to help plan human land-use. In Kluane, like other areas of North America, occurrences and bear mortalities were close to linear access features and in areas with high human infrastructure density. Mortalities were likely to occur in areas with high human use and high bear use. If reduction of bear mortality is a goal, managers should restrict development of permanent dwellings or other infrastructure in high-use bear habitats. Management agencies may have to establish limits on recreational activities, particularly in high-use bear habitats. Management strategies will need to be multi-facetted. The locations of human-caused bear mortality is a function of how bears use their habitat, including how they responding to changes in food quality and biomass, human-related habitat changes, bear tolerance of humans and human tolerance of bears (Mattson 1990). Public education aimed at increasing tolerance for bears that occupy the human-bear habitat interface may also be an element in reducing bear mortalities (Bath 1998, Gunther et al. 2004). Without proper planning, occurrences and grizzly bear mortalities will increase as human activity increases. Managers must be vigilant to limit access into bear habitat, and prevent grizzly bear mortality sinks from developing or expanding.

# Chapter Five: Linking habitat to demography to assess effects of human land-use on grizzly bear populations in the southwest Yukon, Canada

## INTRODUCTION

Historically, humans have been the leading cause of the extirpation or reduction in abundance of grizzly bears (*Ursus arctos* L.) in many areas of North America. Human activities continue to be the leading threat to remaining populations (Keating 1986, Clark et al. 1996, Mattson et al. 1996a, Ross 2002). Management agencies have recognized the need to restore or protect grizzly bear populations, and are looking for cost-effective methods to determine acceptable thresholds for human impacts (Mattson et al. 1996b, Interagency Grizzly Bear Committee 1998, Mace et al. 1999, Nielsen 2005, Nielsen et al. 2006). The most direct way for managers to see if human activities impact population viability is to study changes in population size, and reproductive and mortality rates. However, bears are difficult to count because they are solitary, wide-ranging and typically occur at low densities. Individual bears must be tracked using telemetry systems to monitor reproduction and survival. To achieve desired statistical power for detecting changes in grizzly bear abundance and demographic rates, surveys may require repetition, large sample sizes, lengthy periods to collect data, and coverage of an extensive geographic area. Direct monitoring of population changes can be cost-prohibitive for management agencies.

A cost-effective alternative to directly monitoring populations is to measure the effects of human activity on grizzly bear habitat. For instance, habitat effectiveness and security area models can cost as little as a few thousand dollars to implement and can be applied to an extensive area. Habitat effectiveness is an estimate of the percentage of habitat available to bears after subtracting habitat alienated by human influences (Gibeau et al. 1996). Security areas are habitat patches large enough to allow grizzly bears to forage and meet their daily energetic requirements without encountering humans (Gibeau et al. 1996). For both models, the amount of alienated habitat is estimated by multiplying coefficients against a ranked habitat value. The coefficients, and often the habitat values, are estimated using expert-knowledge about a system. These models are referred to as expert-opinion models, which have been used to estimate the impacts of human land-use on grizzly bear habitat throughout North America (USDA Forest Service 1990, Purves and Doering 1998, Gibeau 2000).

Expert-opinion models, because of lack of statistical rigor, are often viewed as less reliable than empirical models (Nielsen et al. 2003, Stenhouse et al. 2003). Empirical models can be developed from grizzly bear location data to predict habitat occupancy using a set of explanatory variables (Mace et al. 1996, Manly et al. 2002). Location data may be acquired through sightings, telemetry, or indirectly through animal sign (e.g., scats, hair, dens; Apps et al. 2004, Ciarniello et al. 2005). An algorithm to describe the relative probability distribution of bears is developed given the current landscape window. The algorithm may be used to predict habitat occupancy, given future human land use scenarios.

Though habitat-based methods are relatively inexpensive, models that describe occupancy are limited if they do not link habitat to demographic processes (Van Horne 1983, O'Neil and Carey 1984; Hobbs and Haney 1990, Garshelis 2000, Tyre et al. 2001). If managers want to ensure conservation, they need to understand linkages between habitat characteristics they can change and demographic traits such as reproduction and mortality (Boyce and MacDonald 1999, Mitchell and Powell 2003, Naves et al. 2003). Location data can be differentiated into accounts pertaining to births versus deaths to develop separate explanatory habitat models that specify the effects of habitat features on grizzly bear reproduction and mortality. Theoretically, grizzly bear productivity is regulated by density-dependent mechanisms (McLellan 1994); therefore, a shortage of those resources necessary for reproduction, represented by spatially-explicit explanatory variables, would lead to decreased natality (Weins 1989). Similarly, grizzly bear mortality is primarily influenced by the degree of human occupancy or access, juxtaposed with high-use bear habitats (McLellan and

Shackelton 1988, McLellan 1990, Benn and Herrero 2002, Nielsen et al. 2004a). Human-related factors that influence bear mortality rates often can be represented by spatially-explicit variables such as roads density or distance from infrastructure. As the factors that increase bear mortality become prevalent, survival rates for bears should concurrently decrease (Merrill and Mattson 2003).

Naves et al. (2003) and Nielsen (2005) used habitat-based occupancy models for reproductive success (respectively, represented by the number of family groups or females) and mortality (represented by distance from human disturbance) to delineate source-like, refuge-like, attractive sink-like, and sink-like areas. 'Like' was used at the end of each habitat condition to represent the hypothetical state of the area without explicit consideration of demographic features. Habitats where local reproductive success is greater than local mortality support source-like populations, characterized by an excess of individuals, who must disperse outside their natal patch to find a place to settle and breed. Areas that have scarce food resources but low risk of human-caused mortality are refuge-like, allowing for population persistence. The finite growth rate in refuge-type habitat would be close to one. Habitats where reproductive success and human-caused mortality are high, and result in a finite growth rate of less than one, are attractive sink-like. Poor habitats, where local reproductive success is less than local mortality, are sink-like. Populations in sink habitats inevitably spiral to extinction without immigration from other areas.

While the framework proposed by Naves et al. (2003) and Nielsen (2005) is appealing, the assumption that the empirical habitat models developed using locations for births and deaths respectively correlate with rates for reproduction or mortality has not been validated. The assumption is non-trivial because habitat models often fail as predictors of abundance (Morrison 2001), and are therefore, likely poor predictors of other demographic features. The utility of habitat models for predicting fecundity or mortality is limited by the number of conditions used by the sampled individuals throughout an observation period. The number of conditions used, in turn, is dependent on how the sampled population is defined, how much individuals in the population move, how long the study occurs, and how frequently animals are sampled. The ability of a habitat model to predict phenomena beyond animal distributions is also contingent upon how resources are represented as variables in modeling equations.

Habitat selection models may be particularly biased when location information for bears is based on sightings or signs, rather than telemetry locations – although telemetry data may also be biased. In cases where telemetry data are unavailable, forage-productivity models have been used as surrogates for reproduction (Nielson et al. 2003, Merrill and Mattson 2003). Expert-opinion models (e.g., habitat effectiveness and security area) are often a fallback where there is limited information on bears or their forage. Expert-opinion models, although subjective, may correlate with demographic features better than empirical habitat models because they have the flexibility to directly incorporate knowledge specific to birth and death rates, and are not constrained to relaying information only on location or density of animals. However, like the empirical habitat models, neither forage productivity nor expert-opinion models have been tested for correlation with reproductive and mortality rates.

In this chapter, I appraised empirical habitat models, forage distribution models and expert-opinion models with respect to explaining reproductive and annual adult survival rates. Productivity was measured as survival of cubs-of-year to yearlings for each adult female. Empirical habitat models described the relative probability distributions for family groups, all adult females, adult males and mortality locations. Expert-opinion models included habitat effectiveness and security models. Using the framework developed by Naves et al. (2003) to classify the landscape into source-like, refuge-like, attractive sink-like and sink-like habitats, I used the best model, established by information-theoretic model selection criteria, for explaining reproductive and survival rates to predict population status for grizzly bears in the Greater Kluane area in the southwest Yukon, Canada. My objective was to test the performance of habitat-based methods for relaying information on demographic features and to promote informed application of habitat models for grizzly bear management.

## STUDY AREA

The study area (Figure 5-1) encompassed the full extent of all major third order watersheds in Kluane National Park and Reserve (KNPR) and the neighbouring area.

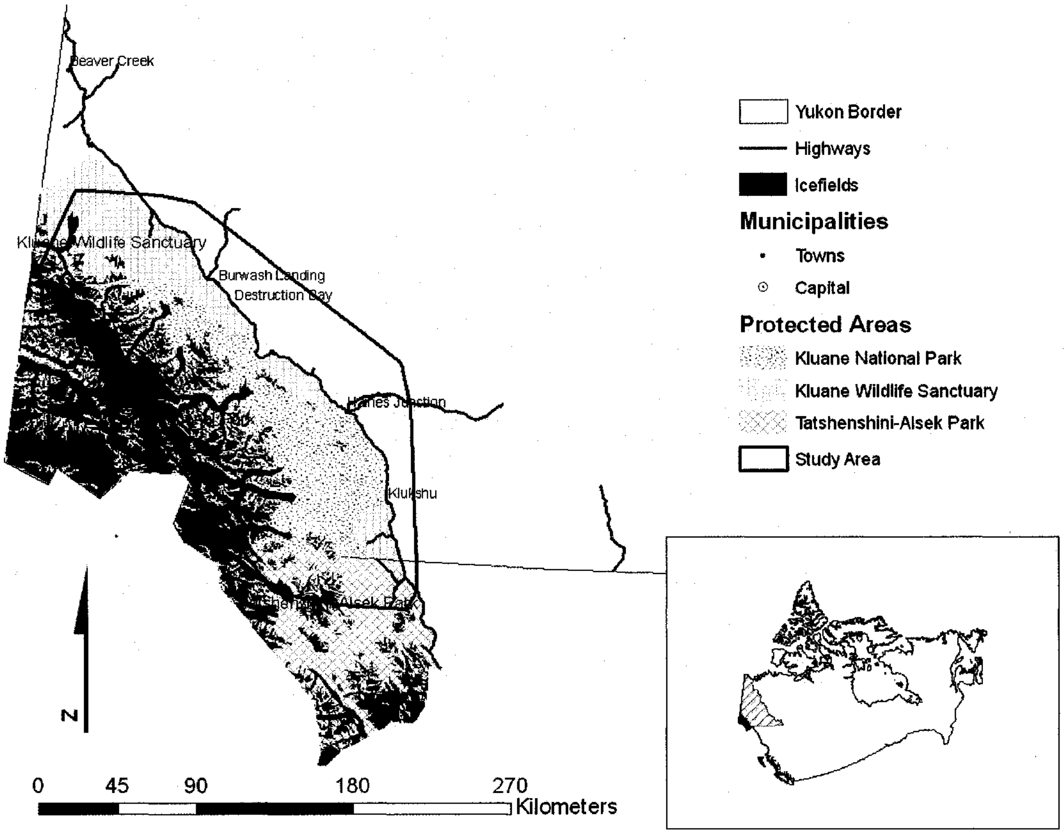


Figure 5-1. The study area in the Kluane Region, southwest Yukon, Canada for productivity and survival analyses. It encompassed portions of Kluane National Park Reserve, Kluane Wildlife Sanctuary, Tatshenshini-Alsek Park, and private and public lands outside the protected area complex.

## METHODS

### Grizzly Bear Monitoring

Between 1989 and 2004, 69 bears (31 males, 38 females; Table 5-1) were captured using either aerial darting or culvert traps, and were fitted with very high frequency (VHF) radio-collars. Females were captured only if they were unaccompanied by offspring, though they may have subsequently had offspring. Of the 69 individuals captured, 64 were initially captured within KNPR, three were initially captured in the Kluane Wildlife Sanctuary, and two were initially captured at the Haines Junction landfill.

Collared bears were monitored once per week or as often as weather permitted using fixed-wing aircraft (Table 5-2). Flights to monitor bear productivity started in early April of each year and continued through to denning. Aerial VHF relocations totalled 3941 and ranged between 26 and 593 relocations per year. The average distance between sequential locations ranged between 4.7 km and 11 km, depending on cohort and time of year (Table 5-2). During aerial relocations the bear identification number, date, time, and reproductive status were noted. The number of cubs accompanying an adult female was recorded. If the cubs-of-year or yearlings were not seen with the adult female on two subsequent and consecutive flights they were presumed dead. Yearlings were assumed dead if they did not emerge from the den with its mother. If the cubs were two years or older but were not accompanying the adult female they were presumed dead or dispersed.

### Home Range Calculations and Covariates for Survival and Productivity

I calculated the 95% fixed-kernel home range for each bear (Table 5-1) using Ranges 6 (Kenward et al. 2003). I used least-squares cross validation to assign a smoothing parameter (average h = 3981 for males and average

Table 5-1. Identification, gender (M = male, F = female), age, 95% fixed kernel home range size (km$^2$), year the bear entered the study, and year the bear exited the study.

| Bear ID | Gender | Age (when first entered study) | # of adult relocations | 95% Fixed-kernel Home Range Area (km$^2$) | Year entered study (as adult) | Exit year |
|---|---|---|---|---|---|---|
| KNP04 | F | 9 | 88 | 171.98 | 1989 | 1993 |
| KNP05 | F | 6 | 5 | 364.69 | 1991 | 1991 |
| KNP06 | F | 11 | 173 | 276.32 | 1991 | 1998 |
| KNP11 | F | 4 | 157 | 168.74 | 1991 | 1998 |
| KNP12 | F | 19 | 32 | 690.85 | 1989 | 1992 |
| KNP14 | F | 9 | 13 | 67.04 | 1991 | 1992 |
| KNP17 | F | 11 | 12 | 80.52 | 1992 | 1992 |
| KNP18 | F | 6 | 119 | 116.16 | 1992 | 2003 |
| KNP21 | F | 13 | 44 | 100.69 | 1992 | 1993 |
| KNP23 | F | 12 | 63 | 196.39 | 1992 | 1994 |
| KNP24 | F | 9 | 94 | 113.06 | 1992 | 1997 |
| KNP27 | F | 5 | 212 | 91.13 | 1992 | 2003 |
| KNP32 | F | 5 | 148 | 270.81 | 1992 | 1999 |
| KNP33 | F | 14 | 54 | 255.38 | 1992 | 1994 |
| KNP36 | F | 10 | 163 | 417.95 | 1992 | 2000 |
| KNP38 | F | 5 | 128 | 267.32 | 1995 | 2003 |
| KNP39 | F | 5 | 7 | 0.89 | 1995 | 1995 |
| KNP42 | F | 15 | 117 | 198.57 | 1993 | 1997 |
| KNP43 | F | 17 | 112 | 125.17 | 1993 | 1997 |
| KNP44 | F | 23 | 125 | 211.92 | 1993 | 1998 |
| KNP45 | F | 13 | 93 | 175.40 | 1993 | 1997 |
| KNP46 | F | 11 | 56 | 132.80 | 1993 | 1995 |
| KNP47 | F | 5 | 23 | 151.34 | 1994 | 1994 |
| KNP50 | F | 7 | 42 | 186.23 | 1994 | 1997 |
| KNP56 | F | 7 | 22 | 61.47 | 1995 | 1996 |
| KNP57 | F | 6 | 120 | 369.94 | 1995 | 2004 |
| KNP59 | F | 5 | 77 | 164.17 | 1995 | 1999 |
| KNP62 | F | 7 | 107 | 265.26 | 1996 | 2004 |
| KNP63 | F | 5 | 12 | 195.45 | 1998 | 2000 |
| KNP64 | F | 5 | 11 | 144.73 | 1999 | 2000 |
| KNP66 | F | 17 | 17 | 38.80 | 2000 | 2003 |
| KNP67 | F | 9 | 17 | 67.90 | 2002 | 2004 |
| KNP69 | F | 5 | 25 | 403.80 | 2002 | 2004 |
| KNP70 | F | 5 | 11 | 125.87 | 2002 | 2003 |
| KNP01 | M | unknown-adult | 26 | 1393.22 | 1989 | 1991 |
| KNP03 | M | unknown-adult | 18 | 646.61 | 1989 | 1990 |
| KNP07 | M | 5 | 18 | 543.50 | 1991 | 1992 |
| KNP09 | M | 22 | 79 | 2468.56 | 1991 | 1995 |
| KNP10 | M | 8 | 30 | 903.59 | 1991 | 1992 |
| KNP19 | M | 15 | 46 | 1089.48 | 1992 | 1995 |
| KNP20 | M | 14 | 32 | 976.36 | 1992 | 1993 |
| KNP26 | M | 15 | 27 | 707.40 | 1992 | 1993 |
| KNP29 | M | 10 | 51 | 487.77 | 1992 | 1994 |
| KNP31 | M | 8 | 52 | 324.42 | 1992 | 1995 |
| KNP34 | M | 10 | 43 | 619.32 | 1992 | 1997 |
| KNP35 | M | 6 | 31 | 300.16 | 1992 | 1993 |
| KNP40 | M | 6 | 76 | 1125.33 | 1993 | 1997 |
| KNP41 | M | 19 | 31 | 586.52 | 1993 | 1995 |
| KNP48 | M | 10 | 81 | 724.06 | 1993 | 1997 |
| KNP49 | M | 2 | 70 | 1892.03 | 1994 | 2002 |
| KNP51 | M | 5 | 39 | 1316.76 | 1995 | 1996 |
| KNP52 | M | 5 | 59 | 175.73 | 1995 | 1997 |
| KNP54 | M | 5 | 59 | 1757.40 | 1995 | 1997 |
| KNP55 | M | 9 | 39 | 620.63 | 1995 | 1996 |
| KNP60 | M | 17 | 13 | 28.60 | 1995 | 1996 |
| KNP61 | M | 6 | 33 | 179.27 | 1996 | 1997 |
| KNP68 | M | 7 | 7 | 97.90 | 2002 | 2003 |

Table 5-2. The average times and distances between relocations during the spring green-up (May 15 to July 21) and green-down (July 22 to September 30) by cohort. Standard errors (SE) are shown.

| | **Cohort** | *n* | **Average time between relocations (days)** | SE | **Average distance between relocations (km)** | SE |
|---|---|---|---|---|---|---|
| Green-up | Adult males | 281 | 7.98 | 0.35 | 10.63 | 0.60 |
| | Lone adult females | 476 | 9.17 | 0.33 | 5.55 | 0.23 |
| | Family groups | 201 | 9.9 | 0.56 | 4.67 | 0.62 |
| | Subadults | 102 | 8.49 | 0.67 | 5.61 | 0.63 |
| Green-down | Adult males | 315 | 9.13 | 0.41 | 11.04 | 0.64 |
| | Lone adult females | 632 | 10.25 | 0.37 | 6.12 | 0.29 |
| | Family groups | 193 | 10.44 | 0.59 | 5.65 | 0.32 |
| | Subadults | 182 | 8.71 | 0.49 | 6.45 | 0.56 |

h = 1942 for females). Only observations of adult bears were used in this and subsequent analyses. Data for subadults (four years or younger) were insufficient. Though Seaman et al. (1999) recommend using at least 30 observations to calculate kernel home ranges, exclusion of bears with few telemetry relocations would have disqualified individuals that died or left the study soon after collaring. This would have biased survival estimates high (see the following section on productivity and survival modeling). I assumed that the bias of overestimating survival rates was more problematic than the bias of underestimating home range size, particularly given that further analyses using home ranges were area-weighted (i.e., used the proportion of home range rather than absolute area). Further, I found a poor correlation between the number of relocations and estimated home range size ($r = 0.17$ for females, and $r = -0.13$ for males). Therefore, all bears with five or more relocations were included in analyses.

I created seasonal relative probability maps for adult male, family group and lone adult female grizzly bear occupancy using algorithms developed in Chapter 3. I averaged the seasonal maps to create an annual occupancy map for each cohort. I created a combined adult female map by summing the respective annual occupancy maps weighted by the proportion of the adult female subpopulation comprised of family groups and lone adult females (i.e., 19% for family groups and 81% for lone adult females; McCann 1998). The annual adult male, annual family group, and the annual combined adult female occupancy maps were used in subsequent analyses. For each of the three maps, I used a quantile classification function in the Spatial Analyst extension of ArcGIS 9.0 (ESRI 2004) to bin the averaged relative probability values into 10 ordinal occupancy classes. On the ordinal scale a value of one represented a relatively low probability of an occurrence, while a value of 10 represented a relatively high probability of an occurrence. I applied the quantile function only within the minimum convex polygon (MCP) for all telemetry locations (the original area in which the algorithms were developed). However, the study area for this paper extended outside of the MCP so I used the cut-point averaged relative probability values for each quantile to reclassify averaged relative probability values in the remainder of the study area. I sequentially reclassified the top one, two, three, four and five quantiles as high occupancy habitat. For each of the five different reclassifications, I calculated the proportion of combined adult female and family group high occupancy habitat for each female home range and the proportion of male high occupancy habitat for each male home range.

I created a relative probability distribution map for all human-caused (hunt and non-hunt) mortality using the data and procedures outlined in Chapter 4 for discrete choice analysis. Discrete choice analysis was performed using the logistic regression routine (PROC LOGISTIC) in SAS 9.0 (SAS Institute 2004) with the STRATA command to identify the choice set (Kuhfeld 2005). I used a full model design ($\alpha = 0.05$) with the following variables: the relative distribution of bears, elevation, distance to water, infrastructure density, distance to primary roads, distance to other linear features, and distance to open landfills.

To evaluate the discrete choice model, I used a quantile classification function to bin the relative probability values for the model into 10 ordinal classes. On the ordinal scale a value of one represented a relatively low probability of mortality, while a value of 10 represented a relatively high probability of mortality. I used a 5-fold partitioning design (Fielding and Bell 1997), training the model with an 80% random sub-sample of mortality point data and assessing model data with the remaining used points (Hosmer and Lemeshow 2001, Boyce et al. 2002). I matched the area-adjusted frequency of mortalities within a given bin for each fold against the corresponding rank of the bin and calculated Spearman's rank correlation ($r_s$; Boyce et al. 2002). I averaged the correlation coefficient across the five repetitions. If the averaged $r_s$ value was one, the frequency of mortalities and the rank had a perfect positive correlation. I considered values between 1 and 0.5 to have a strong positive correlation, while coefficients between 0.5 and 0 were considered to represent a weak correlation. Negative coefficients were conversely interpreted. A value of 0 indicated no relationship. I then sequentially reclassified the top one, two, three, four and five quantiles as 'high mortality risk' areas. For each of the five different reclassifications, I calculated the proportion of each bears' home range that was classified as high mortality risk.

I created a weighted probability map for major grizzly bear forage. Information on the presence and absence of four major grizzly bear forage species (*Shepherdia canadensis, Equisetum arvense, Oxytropis campestris,* and *Hedysarum alpinum*) was collected from 1551 plots throughout the Kluane Region (see Chapter 2). The dependent variable for plots with bear foods present were coded as "1," otherwise the dependent variable was coded as "0". I used logistic regression to model the probability of bear food occurrence using elevation and a quadratic term, distance to water, Tasselled Cap variables, direct annual solar radiation, slope, and presence of vegetation. I ran all possible models for each species using the APLR macro (Moore 2000) in SAS 9.0. Models were ranked using $\mathrm{AIC_c}$ (Burnham and Anderson 2002) and I used the top model for each species to create a probability distribution map. I applied the models outside of a mask for water bodies, ice and permanent snow, and elevations above 2000 m. Area under the receiver operating characteristic (ROC) curve was greater than 0.8 for all top models. I weighted the four resulting maps by the average proportion of the corresponding plant species contained within bi-weekly grizzly bear scat samples, adjusted to comprise 100% (i.e., *S. canadensis*

~ 33.1%, *E. arvense* ~ 23.4%, *O. campestris* ~ 16.5%, and *H. alpinum* ~ 27%; McCann 1998, McCormick 1999). Digestibility did not vary much among these plant species, so I based average proportions on fecal analysis uncorrected for detection or digestibility (Hewitt and Robbins 1996). I summed the four weighted maps. All cells equal to or greater than 0.25 were considered as 'high forage potential'. I calculated the proportion of each bears' home range with high forage potential.

I calculated the proportion of each home range that was scored as secure habitat, and that had 80% or greater realized habitat effectiveness using the methods of Gibeau (1998), Gibeau et al. (2001) and Purves and Doering (1998). For habitat effectiveness analysis I created a habitat potential map based on rankings of forage availability within land cover classes. Habitat potential theoretically reflects the inherent ability of the landscape to support bears without human activity. I based ranking of forage availability within each cover class on findings from McCormick (1999). I overlaid the habitat potential with a human disturbance layer. Habitat values up to given distances from a human disturbance feature were multiplied by coefficients (specified using expert opinion). I used the default distances and coefficients from Purves and Doering (2001). The output map theoretically reflected the realized ability of the landscape to support grizzly bears after taking into account human disturbance. For the security area analysis, I used the realized habitat map to identify suitable patches for foraging. All habitat patches that were large enough to meet the minimum average daily foraging radius for a female grizzly bear (Gibeau et al. 2001) were deemed secure. Most bear relocations in Kluane were found below 2000 m, so all habitat patches above 2000 m were not considered in the security area calculations.

## Productivity and Survival Models

I tested the explanatory variables for collinearity using Pearson's correlation coefficient (*r*), tolerance, and variance inflation function (VIF) diagnostics. All correlations with an absolute value greater than 0.7, or tolerance scores of 0.1 or less and individual VIF scores greater than 10 were assumed to be collinear. Security and habitat effectiveness were strongly correlated. For productivity models all occupancy variables were correlated and security was correlated with family group occupancy. I specified models so as to exclude pairings of collinear variables. All explanatory variables were normally distributed. I used the average annual recruitment of one-year olds for each collared female bears as an estimate of productivity (Table 5-3). Sample sizes were too small or were logistically unobtainable for all other measures of productivity (e.g., number of births per year, number of cubs surviving to disperse, number of subadults recruiting to age of first parturition). I treated each female as a sample unit ($n$ = 19). To reduce biases associated with capturing only lone adult females, an adult female had to be observed for a minimum of three years. This ensured that each female in the study had a chance to produce at least one litter.

Productivity data were normally distributed; therefore, I used linear regression to specify the effects of the covariates on grizzly bear productivity. I first considered each of the five reclassifications for high occupancy and high mortality risk habitat in a single-variable model and used the corrected Akaike's Information Criterion ($AIC_c$) to select the best re-categorization. I then considered all possible single-, two-, and three-variable models using proportion of the home range classified as the selected categorizations of high occupancy habitat for all adult females, family groups and high mortality risk habitat, and proportion having high forage potential habitat, proportion of effective habitat and proportion of secure habitat. Regression analyses were conducted in SAS 9.0. Notably, 19 is a small sample size for explanatory models with more than two parameters; therefore, I used $AIC_c$ to rank models. Like AIC, the $AIC_c$ metric favours models

Table 5-3. Number of years in study, number of litters, and number of cubs surviving to age one for the 19 adult females followed in the study. All females were followed for more than three years as adults.

| Bear ID | Age when first collared | Year bear entered study | Year bear exited study | Years in study | Number of litters produced | Number of litters surviving to age one | Number of yearlings produced | Number of yearlings per study year |
|---|---|---|---|---|---|---|---|---|
| KNP4 | 9 | 1989 | 1993 | 4 | 1 | 1 | 1 | 0.25 |
| KNP6 | 11 | 1991 | 1998 | 7 | 1 | 1 | 2 | 0.285714286 |
| KNP11 | 4 | 1993 | 1998 | 5 | 2 | 1 | 2 | 0.4 |
| KNP12 | 19 | 1989 | 1992 | 3 | 1 | 1 | 2 | 0.666666667 |
| KNP18 | 6 | 1996 | 2003 | 7 | 4 | 2 | 1 | 0.142857143 |
| KNP24 | 9 | 1992 | 1997 | 5 | 2 | 1 | 2 | 0.4 |
| KNP27 | 5 | 1993 | 2003 | 10 | 3 | 2 | 2 | 0.2 |
| KNP32 | 5 | 1993 | 1999 | 6 | 3 | 1 | 2 | 0.333333333 |
| KNP36 | 10 | 1992 | 2000 | 8 | 3 | 2 | 4 | 0.5 |
| KNP38 | 3 | 1996 | 2003 | 7 | 2 | 2 | 2 | 0.285714286 |
| KNP42 | 15 | 1993 | 1997 | 4 | 1 | 1 | 1 | 0.25 |
| KNP43 | 17 | 1993 | 1997 | 4 | 1 | 1 | 1 | 0.25 |
| KNP44 | 23 | 1993 | 1998 | 5 | 2 | 2 | 4 | 0.8 |
| KNP45 | 13 | 1993 | 1997 | 4 | 0 | 0 | 0 | 0 |
| KNP50 | 7 | 1994 | 1997 | 3 | 1 | 1 | 2 | 0.666666667 |
| KNP57 | 6 | 1995 | 2004 | 9 | 4 | 1 | 3 | 0.333333333 |
| KNP59 | 5 | 1996 | 1999 | 3 | 1 | 0 | 0 | 0 |
| KNP62 | 7 | 1996 | 2004 | 8 | 2 | 2 | 4 | 0.5 |
| KNP66 | 17 | 2000 | 2003 | 3 | 0 | 0 | 0 | 0 |

with few parameters; as the ratio of the number of parameters to sample size increases the value is further penalized. However, in small-sample applications, $\mathrm{AIC_c}$ estimates the expected discrepancy among models with less bias than AIC (Hurvich and Tsai 1989), and for models with a high number of parameters, the penalty term is for $\mathrm{AIC_c}$ can be much greater compared to AIC.

Mortality rate is derived by subtracting survival rate from 1. I estimated the survival rate as an annual probability for adult bears ($n$ = 60), where an adult was considered as any bear five years or older. I used the known-fate model available in Program MARK (White and Burnham 1999; White 2005) to estimate survival rates using a logit link function. The known-fate model is a linear binomial estimator that allows for staggered entry and the inclusion of covariates when modeling survival. All covariates were specified by bear, corresponding to individual home range. Covariates included the gender, proportion of home range classified as high occupancy habitat for adult males or adult females (corresponding to the bear's gender), proportion as high mortality risk habitat, proportion having high forage potential habitat, proportion of effective habitat and proportion of secure habitat as covariates in the model. I first used each of the five reclassifications for high occupancy and high mortality risk habitat in a single-variable model and used $\mathrm{AIC_c}$ to select the best categorization. Then using only the best categorization for high occupancy and high mortality risk habitat, in combinations with the other covariates I considered all possible single-, two- and three-variable models that met the criteria for collinearity.

Program MARK calculates a $\hat{c}$ parameter (Lebreton et al. 1992), which describes the degree of overdispersion in binomial models. I used $\hat{c}$ of the most highly parameterized model ($\hat{c}$ = 1.31) to assess goodness-of-fit (Cooch and White 2005). Values of three or less typically indicate a good model. Values greater than three indicate poor model fit.

I used a parsimonious modeling approach to select the best survival model. If $\hat{c}$ is greater than one, such as for my survival models, the data were considered overdispersed; Cooch and White (2005) recommend modifying model selection metrics for overdispersed models. In the case of $\mathrm{AIC_c}$, the log-likelihood is divided by $\hat{c}$ of the most highly parameterized model, producing a quasi-likelihood, or $QAIC_c$ (Burnham and Anderson 2002). If $\hat{c}$ is greater than one the contribution of the model likelihood to the $QAIC_c$ value will decline. The relative penalty for a given number of parameters will increase, and as $\hat{c}$ increases, the $QAIC_c$ tends to increasingly favour models with fewer parameters (Cooch and White 2005).

I calculated the $\Delta AIC_c$ and $\Delta QAIC_c$ score for each productivity and survival model, respectively. The change in score was calculated by subtracting the minimum score for the model set from the score for the model of interest. Typically, models with a $\Delta AIC_c$ or $\Delta QAICc$ between 0 and 2 have strong support. Models with a $\Delta AICc$ or $\Delta QAICc$ between 2 and 10 have less support and models with a $\Delta AICc$ or $\Delta QAIC_c$ greater than 10 have virtually no support (Anderson et al. 2001, Burnham and Anderson 2002).

## Bear Management Units

To facilitate development of a grizzly bear monitoring program, I partitioned the Kluane Region into bear management units (BMUs). BMUs serve as the basis for impact analyses, ensure that the analyses are spatially distributed over the entire management area, aid in identifying areas that may require specific management prescriptions, and coincide with the nature in which KNPR manages human-use activities (e.g., encapsulate whole trail systems). Typically BMUs are laid out with reference to major drainages, attempt to include subordinate drainages, and extend from the valley bottom to the hydrologic divide. BMUs must encompass enough bear habitat, and must remain in place for long enough to permit a resident adult female to replace herself with a recruit into the breeding population (IGBC 1998, McCann 2001). A minimum BMU size of 300 $km^2$ was chosen to represent the largest adult female annual home range recorded in the Kluane Region (298 $km^2$) and the weighted average multi-annual female home range size (305 $km^2$).

Bear management units were established using a watershed analysis in IDRISI 32 GIS software (Clark Labs 2003). Icefields were excluded from the analyses. I used a 30-m digital elevation model (DEM) to determine the enclosed watersheds according to the given aerial threshold. The selected threshold was the minimum number of pixels that must be included in the watershed. In this case, watersheds had to encompass at least 333 334 pixels. Watersheds were identified if they met or exceeded this threshold number of cells and if their outlets were within the image. To ensure there was enough bear habitat to sustain a female, the sum of occupancy values in each BMU had to be equal to or greater than the maximum sum of occupancy values within the observed multi-annual home ranges for females.

### Status of Bear Management Units

I calculated the proportion of each BMU that was comprised of high occupancy habitat, high mortality risk habitat, high forage probability habitat, effective habitat and secure habitat. I used the top models, as determined by model selection, to predict productivity and adult survival in each BMU. I subtracted the predicted adult survival rates from 1 to estimate the mortality rate. I assumed a 50:50 sex ratio (McCann 1998), and so divided the productivity by 2. I then multiplied this value by survival rates estimated by McCann (1998) for yearlings to subadults and subadults to adults (0.76, and 0.89, respectively) to estimate survival to a reproductively viable age (herein referred to as adjusted productivity). The resulting value indexed the potential of a female to annually replace herself with another female under the given habitat constraints. I used the population-level mortality rate (0.02; from the best adult survival model) as a benchmark for splitting BMU-specific adjusted productivity and mortality rates into 'high' and 'low' categories. BMU-specific mortality rates less than the population-level mortality rate were considered low, otherwise they were considered high. Adjusted productivity rates equal to or greater than the population-level mortality rate were considered high, otherwise they were considered low. Therefore, if the BMU-specific adjusted productivity and mortality rate both equalled 0.02, there was no net contribution by these two indices to the population growth rate. I assigned the population states described by Naves et al. (2003) to each BMU using the classification scheme in Table 5-4.

Table 5-4. Cut-off values for productivity and mortality rates used to classify bear management units into source-like, refuge-like, attractive sink-like, and sink-like population states.

| Population state | | Productivity | | Mortality |
|---|---|---|---|---|
| Source-like | *if* | > 0.02 | *and* | ≤ 0.02 |
| | *or* | = 0.02 | *and* | < 0.02 |
| Refuge-like | *if* | ≤ 0.02 | *and* | ≤ 0.02 |
| Attractive sink-like | *if* | > 0.02 | *and* | = 0.02 |
| Sink-like | *if* | < 0.02 | *and* | ≥ 0.02 |
| | *or* | = 0.02 | *and* | > 0.02 |

## RESULTS

### Productivity and Survival

Reclassifying the top quantile for all female occupancy and the top three quantiles for family group occupancy into 'high occupancy habitat', and the top five quantiles for the mortality model into 'high mortality risk habitat' was best for modeling productivity (Table 5-5). Productivity was most strongly predicted by and was positively related to the proportion of high occupancy family group habitat within the home range (Table 5-6). The model containing only mortality as an explanatory variable ranked second and was also strongly supported by the data (Table 5-6). Models containing forage availability were not strongly supported by the data. Notably, the percent variation in productivity explained by the top model was low ($R^2 = 0.12$) and model fit was not significant ($F_{1,17} = 2.40$, $P = 0.14$).

Reclassifying the top five quantiles for male and female bear occupancy into ‘high occupancy habitat’ and the top five quantiles for the mortality model into ‘high mortality risk habitat’ was best for modeling survival rates (Table 5-7). Twenty-five models were considered for estimating survival rates, including a model without covariates and models that considered males and females separately. Survival rates for males and females were high (98% ± 0.01) and did not differ between genders (Table 5-8). Survival rate was most strongly explained, irrespective of gender, by the proportion of the home range classified as high risk for mortality and high forage productivity (Table 5-8; $\chi^2 = 105.41$, $\mathrm{df} = 88$, $\hat{c} = 1.20$). Survival was negatively associated with mortality risk, indicating that increasing human activity within a home range correlated with decreasing survival probability. Survival was positively associated with the amount of forage availability. The next best model included the proportion of secure area as an explanatory variable and the third best model included the proportion of high occupancy habitat. The top three models were strongly supported by the data. All other models, including models without covariates, were only moderately supported by the data (Table 5-8).

Table 5-5. Single-variable productivity models (Productivity = $\beta_0 + \beta_1 x_{1i}$, where $x_1$ = proportion of high occupancy habitat for adult females and family groups or proportion of high risk mortality habitat for i, and i = the number of quantiles, 1 to 5, used to categorize high occupancy or high mortality risk habitat) using the proportion of within-home range high occupancy habitat for all adult females, family groups, and high mortality risk habitat. Single-variable models were used to select the number of quantiles grouped to form "high occupancy" or "high mortality risk" habitat. The number of parameters was consistent across all models. The root mean squared error (RMSE), $AIC_c$, $\Delta AIC_c$ and $R^2$ values are shown for each model. The top model for each variable is highlighted in grey.

*All adult females*

(Productivity = $\beta_0 + \beta_1 * \text{occupancy}_{ai}$, i = 1 to 5)

| **Number of quantiles (i)** | **RMSE** | **$AIC_c$** | **$\Delta AIC_c$** | **$R^2$** |
|---|---|---|---|---|
| 1 | 0.21968 | -51.0194 | 0 | 0.1053 |
| 2 | 0.22270 | -50.5006 | 0.518838 | 0.0805 |
| 3 | 0.22218 | -50.5894 | 0.430005 | 0.0848 |
| 4 | 0.22895 | -49.4488 | 1.570604 | 0.0282 |
| 5 | 0.23158 | -49.0148 | 2.004631 | 0.0057 |

*Family groups*

(Productivity = $\beta_0 + \beta_1 * \text{occupancy}_{fi}$, i = 1 to 5)

| **Number of quantiles (i)** | **RMSE** | **$AIC_c$** | **$\Delta AIC_c$** | **$R^2$** |
|---|---|---|---|---|
| 1 | 0.22544 | -50.0359 | 1.379973 | 0.0578 |
| 2 | 0.22171 | -50.6699 | 0.745987 | 0.0887 |
| 3 | 0.21740 | -51.4159 | 0 | 0.1238 |
| 4 | 0.21881 | -51.1702 | 0.245662 | 0.1124 |
| 5 | 0.22091 | -50.8073 | 0.608623 | 0.0953 |

*Mortality*

(Productivity = $\beta_0 + \beta_1 * \text{mortality}_i$, i = 1 to 5)

| **Number of quantiles (i)** | **RMSE** | **$AIC_c$** | **$\Delta AIC_c$** | **$R^2$** |
|---|---|---|---|---|
| 1 | 0.22771 | -49.6552 | 1.520237 | 0.0387 |
| 2 | 0.22534 | -50.0528 | 1.122661 | 0.0586 |
| 3 | 0.21892 | -51.1511 | 0.024309 | 0.1115 |
| 4 | 0.22028 | -50.9158 | 0.259647 | 0.1004 |
| 5 | 0.21878 | -51.1754 | 0 | 0.1126 |

Table 5-6. Linear regression models used to estimate productivity. The number of estimated parameters (k), root mean squared error (RMSE), AIC$_c$ and ΔAIC$_c$ scores and weights (w) are shown for each model. "Occupancy$_a$" signifies the occupancy model for all females and "Occupancy$_f$" the occupancy model for family groups.

| Model | k[†] | RMSE | AIC$_c$ | Δ AIC$_c$ | w |
|---|---|---|---|---|---|
| Occupancy$_f$ | 3 | 0.21740 | -51.4166043 | 0.00000 | 0.17072 |
| - Mortality | 3 | 0.21878 | -51.1757180 | 0.24089 | 0.15135 |
| Occupancy$_a$ | 3 | 0.21968 | -51.0199568 | 0.39665 | 0.14001 |
| Security | 3 | 0.22259 | -50.5198819 | 0.89672 | 0.10904 |
| - Mortality + Security | 4 | 0.21376 | -48.8001117 | 2.61649 | 0.04615 |
| - Mortality + Occupancy$_f$ | 4 | 0.21545 | -48.5018350 | 2.91477 | 0.03975 |
| Effectiveness | 3 | 0.22784 | -49.6339100 | 1.78269 | 0.07001 |
| - Mortality + Effectiveness | 4 | 0.21735 | -48.1679058 | 3.24870 | 0.03364 |
| - Mortality + Occupancy$_a$ | 4 | 0.21935 | -47.8195939 | 3.59701 | 0.02826 |
| - Forage | 3 | 0.23201 | -48.9445457 | 2.47206 | 0.04960 |
| - Effectiveness + Occupancy$_f$ | 4 | 0.22295 | -47.2007151 | 4.21589 | 0.02074 |
| - Forage + Occupancy$_f$ | 4 | 0.22358 | -47.0939882 | 4.32262 | 0.01966 |
| - Mortality - Forage | 4 | 0.22446 | -46.9448164 | 4.47179 | 0.01825 |
| Security + Occupancy$_a$ | 4 | 0.22491 | -46.8676623 | 4.54894 | 0.01756 |
| Occupancy$_a$ + Effectiveness | 4 | 0.22585 | -46.7101900 | 4.70641 | 0.01623 |
| - Forage + Occupancy$_a$ | 4 | 0.22623 | -46.6465994 | 4.77000 | 0.01572 |
| - Forage + Security | 4 | 0.22763 | -46.4112040 | 5.00540 | 0.01398 |
| - Mortality - Forage + Security | 5 | 0.21656 | -44.5473122 | 6.86929 | 0.00550 |
| - Forage + Effectiveness | 4 | 0.23356 | -45.4345964 | 5.98201 | 0.00858 |
| - Mortality - Forage + Effectiveness | 5 | 0.22026 | -43.9036553 | 7.51295 | 0.00399 |
| - Mortality + Security + Occupancy$_a$ | 5 | 0.2207 | -43.8274403 | 7.58916 | 0.00384 |
| - Mortality - Forage + Occupancy$_f$ | 5 | 0.22124 | -43.7348312 | 7.68177 | 0.00367 |
| - Mortality + Effectiveness + Occupancy$_f$ | 5 | 0.22223 | -43.5648008 | 7.85180 | 0.00337 |
| - Mortality + Effectiveness + Occupancy$_a$ | 5 | 0.22291 | -43.4489725 | 7.96763 | 0.00318 |
| - Mortality - Forage + Occupancy$_a$ | 5 | 0.22575 | -42.9679724 | 8.44863 | 0.00250 |
| - Forage - Effectiveness + Occupancy$_f$ | 5 | 0.23013 | -42.2387591 | 9.17785 | 0.00174 |
| - Forage + Security + Occupancy$_a$ | 5 | 0.23143 | -42.0247045 | 9.39190 | 0.00156 |
| - Forage + Effectiveness + Occupancy$_a$ | 5 | 0.2327 | -41.8161923 | 9.60041 | 0.00140 |

[†] RMSE and the intercept are included as parameter estimates

Table 5-7. Single-variable known-fate survival models (Survival = $\frac{\exp(\beta_0 - \beta_1 * x_{1i})}{1+\exp(\beta_0 - \beta_1 * x_{1i})}$, where $x_1$ = proportion of high occupancy habitat for adult females and family groups or proportion of high risk mortality habitat for i, and i = the number of quantiles, 1 to 5, used to categorize high occupancy or high mortality risk habitat) using the proportion of within-home range high occupancy habitat and high mortality risk habitat. Single-variable models were used to select the number of quantiles grouped to form "high occupancy" or "high mortality risk" habitat. The number of parameters was consistent across all models. The log-likelihood (LL), $AIC_c$ and $\Delta AIC_c$ values are shown for each model. The log-likelihoods are multiplied by -2. The top model for each variable is highlighted in grey.

*Occupancy* (Survival = $\frac{\exp(\beta_0 - \beta_1 * \text{occupancy}_{1i})}{1+\exp(\beta_0 - \beta_1 * \text{occupancy}_{1i})}$)

| **Number of quantiles** | **-2LL** | $AIC_c$ | $\Delta AIC_c$ |
|---|---|---|---|
| 1 | 121.130 | 125.16 | 1.08 |
| 2 | 121.187 | 125.217 | 1.137 |
| 3 | 121.350 | 125.38 | 1.3 |
| 4 | 120.870 | 124.9 | 0.82 |
| 5 | 120.050 | 124.08 | 0 |

*Mortality* (Survival = $\frac{\exp(\beta_0 - \beta_1 * \text{mortality}_{1i})}{1+\exp(\beta_0 - \beta_1 * \text{mortality}_{1i})}$)

| **Number of quantiles** | **-2LL** | $AIC_c$ | $\Delta AIC_c$ |
|---|---|---|---|
| 1 | 115.800 | 119.83 | 4.2 |
| 2 | 114.100 | 118.13 | 2.5 |
| 3 | 114.560 | 118.59 | 2.96 |
| 4 | 114.455 | 118.485 | 2.855 |
| 5 | 111.600 | 115.63 | 0 |

Table 5-8. Known-fate models used to estimate survival. The number of estimated parameters (k), log-likelihood values multiplied by -2 (-2LL), $QAIC_c$ and $\Delta QAIC_c$ scores and weights (w) are shown for each model. The $QAIC_c$ scores was adjusted for overdispersion using $\hat{c}$ = 1.31. The highest $\hat{c}$ was chosen from among the most highly parameterized models.

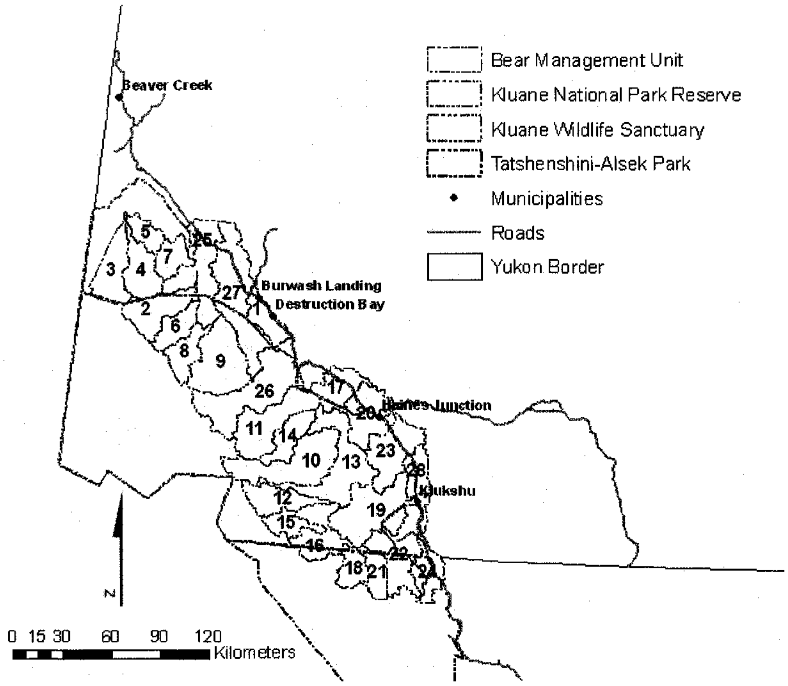
| **Model** | k[†] | **-2LL** | $QAIC_c$ | $\Delta QAIC_c$ | w |
|---|---|---|---|---|---|
| - Mortality + Forage | 3 | 105.4053 | 92.8263 | 0 | 0.32140 |
| - Mortality + Forage - Security | 4 | 105.1713 | 94.6770 | 1.8507 | 0.12642 |
| - Mortality + Forage - Occupancy | 4 | 105.3124 | 94.7928 | 1.9665 | 0.11978 |
| - Mortality + Forage + Effectiveness | 4 | 105.4053 | 94.8689 | 2.0426 | 0.11561 |
| - Mortality | 2 | 111.6040 | 95.8750 | 3.0487 | 0.08343 |
| - Mortality + Effectiveness | 3 | 110.1861 | 96.7450 | 3.9187 | 0.05183 |
| - Mortality + Security | 3 | 110.4706 | 96.9783 | 4.1520 | 0.04649 |
| - Mortality - Occupancy | 3 | 110.8943 | 97.3256 | 4.4993 | 0.03955 |
| - Mortality + Effectiveness - Occupancy | 4 | 108.1593 | 98.8074 | 5.9811 | 0.01847 |
| - Mortality + Security - Occupancy | 4 | 109.1249 | 99.5990 | 6.7727 | 0.01278 |
| Forage | 2 | 116.7111 | 100.0611 | 7.2348 | 0.01188 |
| Forage - Occupancy | 3 | 115.3622 | 100.9877 | 8.1614 | 0.00719 |
| Effectiveness - Occupancy | 3 | 113.7863 | 101.3687 | 8.5424 | 0.00602 |
| Forage + Effectiveness | 3 | 115.9850 | 101.4983 | 8.6720 | 0.00567 |
| Forage + Security | 3 | 116.3348 | 101.7851 | 8.9588 | 0.00552 |
| Constant survival | 1 | 121.3716 | 101.8592 | 9.0329 | 0.00496 |
| Effectiveness | 2 | 119.3450 | 102.2201 | 9.3938 | 0.00435 |
| Forage + Effectiveness - Occupancy | 4 | 112.3706 | 102.2593 | 9.4330 | 0.00381 |
| Security | 2 | 119.6926 | 102.5050 | 9.6787 | 0.00370 |
| Security - Occupancy | 3 | 115.2434 | 102.5630 | 9.7367 | 0.00345 |
| - Occupancy | 2 | 120.0539 | 102.8011 | 9.9748 | 0.00332 |
| Forage + Security - Occupancy | 4 | 113.5333 | 103.2124 | 10.3861 | 0.00238 |
| Gender-specific | 2 | 121.3510 | 103.8644 | 11.0381 | 0.00202 |

[†] $\hat{c}$ is included as a parameter estimate

## Bear Management Unit Status

Watershed analysis produced 28 BMUs (Figure 5-2). Predicted mortality rates within BMUs were 2% or less for most BMUs bordering the icefields (Figure 5-3). Mortality rates were above 2% in BMUs bordered by the Haines and Alaska Highways. The Jarvis, Haines, Kathleen, and Dezadeash Lake BMUs had the highest mortality rates. Dusty and Disappointment BMUs also had high mortality rates. The Teepee, Wolverine and Donjek River BMUs had the highest predicted productivity rates, while the Slims BMU had low productivity. Bear management units that bordered the icefields, including the Spring, Donjek, Lowell and Fisher BMUs, also had low predicted productivity (Figure 5-3).

The population status of each BMU was determined using the estimated adjusted productivity (AP) and mortality (M) rates (Table 5-9). No BMUs were classified as mortality sinks. Eight BMUs bordering the Haines and Alaska Highway and three BMUs in the interior of the Park were classified as attractive sink-like. The remaining twelve BMUs were categorized as source-like (Figure 5-3).



| BMU Number | BMU Name | Area (km$^2$) |
|---|---|---|
| 1 | Kluane Lake | 529 |
| 2 | Steele | 734 |
| 3 | Klutlan | 725 |
| 4 | St. Claire | 657 |
| 5 | Teepee | 314 |
| 6 | Spring | 442 |
| 7 | Wolverine | 391 |
| 8 | Donjek Glacier | 486 |
| 9 | Kluane Glacier | 1206 |
| 10 | Dusty | 1337 |
| 11 | Kaskawulsh River | 1085 |
| 12 | Lowell South | 595 |
| 13 | Alsek | 1291 |
| 14 | Disappointment | 499 |
| 15 | Fisher | 358 |
| 16 | Turnback | 750 |
| 17 | Jarvis | 566 |
| 18 | Range | 358 |
| 19 | Mush Bates | 1287 |
| 20 | Haines | 821 |
| 21 | Detour | 369 |
| 22 | Tatshenshini | 1150 |
| 23 | Kathleen | 909 |
| 24 | Blanchard | 503 |
| 25 | Donjek River | 1157 |
| 26 | Slims | 1494 |
| 27 | Duke | 1527 |
| 28 | Dezadeash Lake | 397 |

Figure 5-2. Twenty-eight bear management units delineated by watershed analysis. A minimum BMU size of 300 km$^2$ was chosen to match the largest adult female annual home range recorded in the Kluane Region and the weighted average multi-annual female home range size.

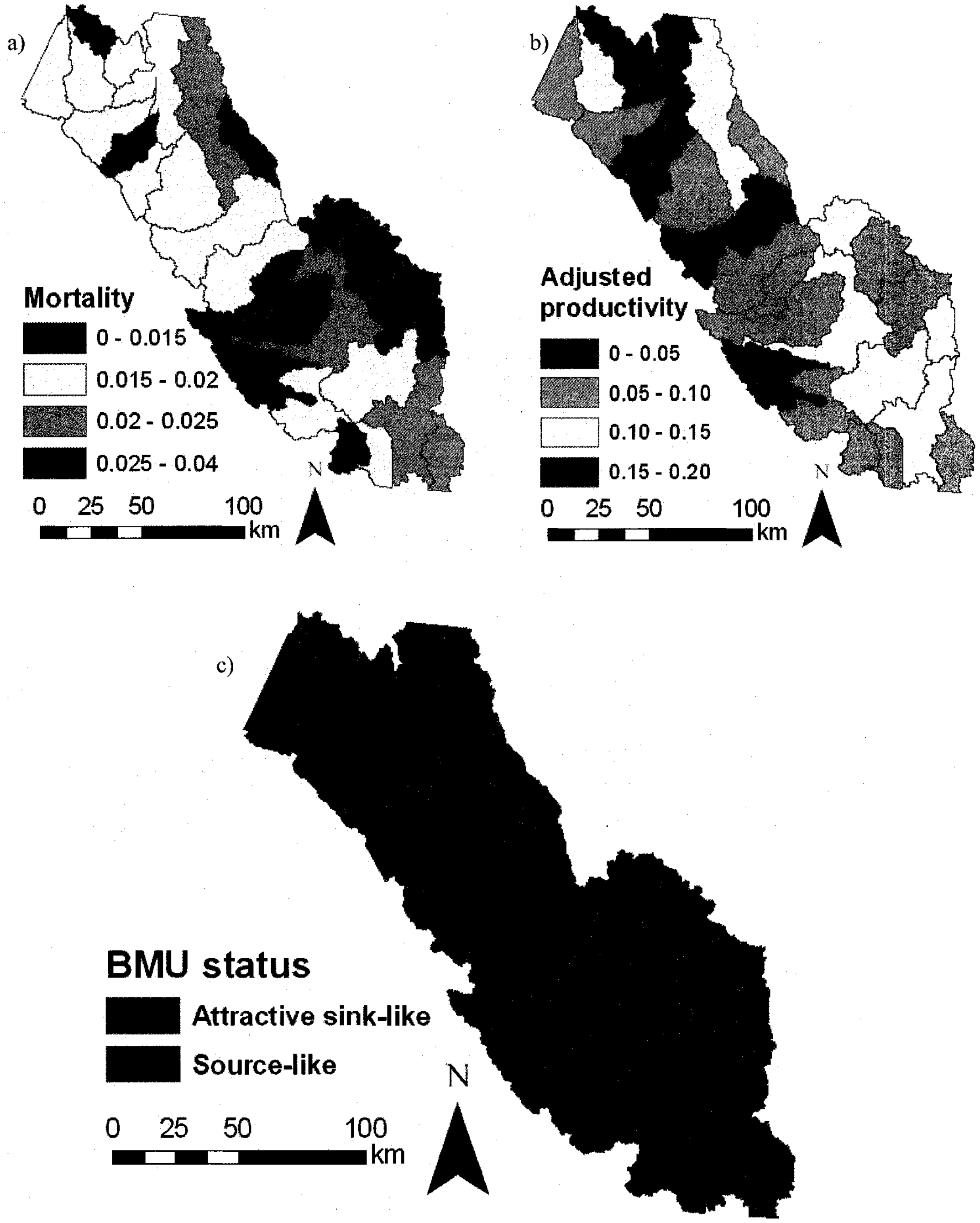


Figure 5-3. Predicted a) mortality and b) adjusted productivity for each bear management unit, and c) status. Bear management units with mortality rates higher than 0.02 and productivity higher than 0.02 were classified as attractive sink-line. Bear management units with mortality rates lower than 0.02 and productivity rates higher than 0.02 were classified as source-like.

Table 5-9. Model parameters, standard errors (SE) and significance values (*P*) for the models used to estimate productivity and survival for each bear management unit.

| **Model** | | **Coefficient** | **SE** | ***P*** |
|---|---|---|---|---|
| [†]Productivity | Intercept | 0.1123577 | 0.148824 | 0.461 |
| | Occupancy$_f$ | 0.6988916 | 0.450924 | 0.140 |
| *Survival | Intercept | 4.1977812 | 0.545369 | < 0.001 |
| | Mortality risk | -1.1999757 | 0.441076 | 0.008 |
| | Forage | 0.8957361 | 0.421697 | 0.036 |

[†] Adjusted productivity (AP) is calculated by dividing productivity by 2, multiplied this value by 0.76, and then 0.89 (or succinctly by 0.68).

*must logit transform the model to get survival estimates

## DISCUSSION

Researchers (Mace et al. 1996, Nielson 2005, Nielsen et al. 2006) often examine the impacts of human activity on grizzly bear populations using occupancy maps created from pooled habitat use data for lone adult females and family groups (all adult females). However, my results showed that considering the occupancy patterns of only family groups produced better explanatory models for the variation in cub productivity than the pooled occupancy map. The relative probability of a family group occupying a given habitat unit is strongly influenced by security related variables like terrain ruggedness; whereas habitat selection in lone adult females is strongly influenced by forage productivity (see Chapter 3). The occupancy layer for all adult females encompasses a broad representation of adult female habitat needs, including when they are not rearing young, and may theoretically provide information on fecundity, including a female's ability to find a mate, to increase body size (Hilderbrand et al. 1999) so as to confer competitive advantages, and develop adequate fat reserves so that they can conceive (Rogers 1976, Ramsay and Stirling 1988). Once a female has given birth, a cub's survival to yearling may be primarily influenced by its mother's ability to find security habitat (Elowe and Dodge 1989). Therefore, decisions to separate adult female data for development of occupancy models should be influenced by the desired measure of reproductive fitness being used to assess human land-use impacts.

The proportion of high occupancy habitat for family groups was a better explanatory variable for grizzly bear productivity than the within-home range proportion of high forage availability habitat, effective habitat, and secure habitat. Each variable represents a suite of factors that may affect cub survival. Though forage availability, habitat effectiveness and security areas may be important to reproduction and offspring survival, the factors represented by these variables do not include security due to terrain ruggedness or probability of encountering conspecifics. Like the forage availability variable, habitat effectiveness and security area variables provide information primarily about forage productivity because the habitat layers from which the variables were derived rank habitat quality based on vegetative food abundance. The habitat effectiveness and security area variables also represent the degree of human perturbation within a bear's home range, but given the subjectivity in developing these variables, the accuracy with which the variables represent this phenomenon is suspect. The family group occupancy variable, on the other hand, incorporates information on terrain ruggedness, forage availability, probability of encountering conspecifics, the degree of human perturbation and other factors that may be vital to reproduction.

The family group occupancy variable was also a better explanatory variable than the proportion of within-home range high mortality risk area. However, the model containing only the mortality risk variable was also strongly supported by the data, indicating that the degree of human perturbation in a home range influenced cub survival. Two mechanisms may be operating. First, family groups may have been displaced by humans and other bears from high quality forage habitats (Mattson et al. 1987), resulting in low quality forage availability, hence, reduced cub survival. Second, females with cubs may experience infanticide. Areas with high rates of bear mortality may have a high influx of non-resident bears, and these bears may be more likely to kill non-sire cubs (Wielgus and Bunnell 2000, Ben-David et al. 2004).

The majority of adult grizzly bear mortality in Kluane is human-caused (McCann 1998) so it follows that survival rates for all models strongly supported by the data were negatively correlated with the proportion of within-home range high mortality risk area. However, survival was also related to forage availability (positively correlated), indicating that food supply may be naturally regulating. This is not surprising given the greater role that natural mortality plays in bear population dynamics in Kluane relative to other protected area-complexes (e.g., 34% of known mortality in Kluane compared to 7.2% in Yellowstone; McCann 1998, Schwartz et al. 2006). In fact, for many terrestrial mammal species, the primary natural cause of population regulation is intraspecific competition for food (Sinclair 1989). Though starvation was not regularly observed, at least one collared bear in Kluane was suspected to have died while in poor body condition.

I categorized BMUs based on predicted productivity and survival rates. Using this classification, no mortality sinks were evident. However, the classification used to differentiate mortality sinks from attractive sinks merely considered the mortality rates, not the proportional effect that human activity and forage availability had on the mortality rate. Attractive sinks occur in habitats where human-caused mortality – not natural mortality – is high, whereas mortality sinks are generally associated with poor quality habitats. The low bear survival rates in the BMUs in the Alsek River Valley region (e.g., Dusty, Alsek, and Disappointment) are probably a result of low forage availability because human activity in these areas is limited. Therefore, these areas were classified as attractive sink-like but are probably effectively mortality sinks.

The entire front range of KNPR was also classified as attractive sink-like habitat. These findings are corroborated by information from management agencies on mortality rates (Yukon Territorial Government 2003). Most attractive sink-like BMUs bordered or partially contained Yukon Territorial Government game management subunits where the management threshold rate for bear mortality (2% for females and 6% for males) was exceeded (Yukon Territorial Government 2003). Human-caused mortality in these regions was split equally between hunting and management kills (McCann 1998). For these areas, conservation of a grizzly bear population may require management actions to reduce mortality rates, including a combination of reduced harvest, reduced access, and limiting or otherwise mitigating the effects of development in high occupancy bear habitats.

Source-like areas have high productivity and high survival. These areas exist primarily in the northern and southern interior of KNPR and abut the St. Elias icefields. Attractive sinks may rely on source-like BMUs to sustain bear populations (Doak 1995). The dual role of source-like BMUs in producing individuals for recruitment within and supplying emigrants to other BMUs substantiates a priority need for protecting these areas (Knight et al. 1988, Doak 1995). Further, with the high prevalence of attractive sink-like BMUs, management actions should be taken to reduce potential degradation of source-like BMUs. Management actions for preventing impacts on these BMUs would be similar to those for attractive sinks, though the current distance of these areas from human habitation offers *de facto* protection to bears.

The connectivity between source and attractive sink-like BMUs needs to be investigated (Noss 1991). Breakages in connectivity would impede re-population of sink-like BMUs. Kluane's terrain is rugged and valley bottoms, used by people for recreating, are also likely the primary travel routes for wildlife. For instance, the Alsek River, a major travel corridor, between the Range or Detour BMUs (source-like) and the Kathleen or Dezadeash BMUs (attractive sink-like), is one of the highest human use areas in KNPR. The effects of human activity on the permeability of this region to bear movement are largely unknown.

The objective of this study was to test the performance of habitat-based methods in relaying information on demographic features. The survival model fit indicated only slight overdispersion of data, and hence, high explanatory power (Lebreton et al. 1992) – understandable given the tight coupling between human land-use patterns and the distribution of bear mortality (Nielsen et al. 2004a, Chapter 4). Conversely, the proportion of high occupancy habitat available within a home range explained less than 12% of the variation in cub survival. In part, the model probably has poor explanatory power because of the low number of individuals represented in the study relative to the estimated number of parameters in the model. Additionally, the spatial explanatory variables used to develop the occupancy model may not have represented all the factors that affect reproduction (Johnson and Gillingham 2005). For instance, productivity may have been affected by annual and regional variation in weather; habitat descriptors are usually poor at describing the influence of weather on a population (O'Neil and Carey 1984). Productivity could also have been affected by competition for resources or conspecific interactions (Wielgus and Bunnell 1994, Wielgus and Bunnell 1995), and individual effects such as experience and age of the mother (Schwartz et al. 2003). Unfortunately, data were not available to investigate these potential influences. Where data are available, intraspecific competition can be modeled by considering the contemporaneous spatial distribution of conspecifics within each adult female's home range, and individual effects can be incorporated through use of mixed regression models.

Trajectories of BMUs were robust to how I reclassified the landscape into high occupancy habitat, but were sensitive to how I classified the landscape into and high mortality risk habitat (see Appendix 3 and Appendix 4). For instance, I binned the relative probability of occupancy or risk into quantile bins and then reclassified the top one, two, three, four, and five categories as 'high'. Regardless of how many classes I used to reclassify the occupancy maps into high occupancy habitat, population states remained the same. However, if I used fewer than the top three mortality ranks to represent high mortality risk, 28% of the population states changed from attractive sink-like to source-like. Consequently, population states should be treated only as relative values, and relativity can be evaluated across BMUs or across human land-use scenarios. Further, the correlation between habitat and fitness parameters should not be over-interpreted as habitat-based population regulation (Morris 1987, Morris 2003), and predicted recruitment and survival numbers should not be treated as literal. As such, I avoid explicitly predicting population trajectories in BMUs, and did not subtract productivity from mortality rates. If I were to do so, most BMUs would appear to be on a positive trajectory. Research in the Kluane Region produces contradictory results and shows that the population may be on a negative trajectory, decreasing at 3% per annum (McCann 1998). Predicting population demographics from habitat alone may produce overly-optimistic results.

There were three limitations for this study. First, I examined how variation in habitat affected yearling recruitment (e.g., survival of cubs), but did not examine the effect of habitat variation on other measures of reproductive success. In addition to survival of cubs, components of reproductive success include fertilization of ova and implantation of blastocysts, litter size, age of first parturition, and survival of cubs to subadults and subadults to adults. Sub-adult and adult recruitment may be a particularly important measure of reproductive success because, more so than other age groups, sub-adults may experience strong differences in mortality risk, variant on where they disperse (McLellan and Hovey 2001b). Recruitment of sub-adults to breeding status may be more sensitive than survival of cubs to changes to habitat. Unfortunately, sub-adult recruitment and adult recruitment were difficult to obtain because without collaring yearlings, it was difficult to track these individuals over time.

Age of first parturition and litter size are strongly influenced by the proximity of a population to carrying capacity, (Taylor et al. 1987, Miller et al. 2003, Schwartz et al. 2006), i.e., per capita forage availability (Schwartz et al. 2006). Litter size is also positively correlated with age of the reproducing female (Schwartz et al. 2003). Number of fertilized ova or probability of blastocyst implantation are strongly affected by quality of fat reserves (Rogers 1976, Ramsay and Stirling 1988, Tsubota et al. 1990, Samson and Huot 1995, Harlow et al. 2002), which are a product of per capita forage availability. Given that increased forage availability fosters larger litter sizes or greater probability of fertilization and implantation, the availability of high occupancy lone adult female habitat, which is more strongly associated with forage availability than high occupancy habitat for family groups (Chapter 3), might be a good predictor of these measures of reproductive success.

A second consideration was that survival or productivity rates were modeled as a linear function of the covariates; however, a linear change may not be appropriate if Allee effects or other density-dependent responses limit population size (McLellan 1994; Mattson and Merrill 2004). Third, this study did not consider issues surrounding landscape connectivity and gene flow (Lande 1988, Proctor et al. 2005). Given that the population in Kluane may be in decline, recolonization may be fundamental to understanding how human-use impacts affect the population dynamics (Doak 1995).

## CONCLUSIONS

In many grizzly bear studies, habitat is implicitly or explicitly defined as "a set of environmental features that is equated to a plant community, vegetative association, or cover type," or "the collection of resources and conditions necessary for occupancy" (Garshelis 2000). These definitions are consistent with the concept of "habitat use" (Garshelis 2000) and do not describe the relationship demographic processes may have to habitat. Although effective conservation requires specific, accurate, predictive models of wildlife-habitat relationships, models based solely on habitat elements cannot consistently and accurately estimate species' population responses. However, if habitat models are specific to demographic processes such as births or deaths, changes in the availability of resources that affect these processes, represented by spatial predictors of resource distribution, may correlate with population responses. That is, as the spatial factors that increase bear productivity or survival become prevalent, productivity and survival rates for bears should concurrently increase. I evaluated this hypothesis by assessing the effectiveness of occupancy for family groups and adult females and mortality risk models for explaining productivity and survival.

Among the habitat-based models for assessing impacts of human activity on grizzly bears, the proportion of high occupancy habitat within a bear's home range was positively correlated with and best described changes in productivity. However, occupancy models only explained a small portion of the variation in productivity. Mortality risk was a strong predictor of survival rates, but survival rates were sensitive to categorization of mortality probabilities into high or low mortality risk categories. Occupancy models and mortality risk, therefore, appear to be limited predictors of a population response to changes in habitat and utility for these tools is limited to relative comparisons about landscapes, rather than predicting numbers of individuals that may persist in a given landscape window.

In comparison to occupancy and mortality risk models, qualitative habitat effectiveness and security area models were inferior for predicting productivity and survival rates. However, model performance could be improved with better base habitat maps that incorporate information on more than just forage productivity and human disturbance. While use of the occupancy and mortality risk models are recommended, habitat effectiveness and security area models may be justified where telemetry or location information is unavailable to managers.

I evaluated habitat conditions in KNPR, recognizing the limitation of occupancy and mortality risk spatial layers to predict productivity and survival rates. Much of the periphery of Kluane and the surrounding area – areas close to human development – show high productivity and high mortality, indicating that these areas may act as attractive sinks. Conversely, bears in the northern and southern interior of Kluane appear to be secure, possibly acting as a source population. With the population potentially declining, managers should focus on efforts to abate mortality risk in the BMUs adjacent to the Haines and Alaska Highways, and proactively prevent human-caused mortality in the source-like BMUs in the interior of the Park.

While the framework developed here offers a way to evaluate relative outcomes of future land use scenarios, managers should not be complacent about the need for monitoring programs and should not rely solely on future scenario modeling to evaluate outcomes. Further, given the uncertainty in the relationship between habitat-related predictors and productivity or survival rates, it is imperative that managers monitor population demographics in relation to incremental changes in human activities.

# Chapter 6: Conclusions and recommendations

## SUMMARY OF FINDINGS

To prevent the decline of the Kluane grizzly bear population, Kluane National Park and Reserve initiated a research and monitoring program in 1989. My dissertation research is an outcome of that program and was identified as a key action in the Kluane National Park and Reserve Management Plan (Parks Canada 2002). Results and recommendations from this research project will be used to develop a long-term interagency management strategy for grizzly bear habitat and populations. The strategy is part of a nation-wide initiative to promote sustainable human-use within the national park system (Parks Canada 2001). This chapter summarizes the findings and offers recommendations relevant to my research.

I investigated four key topic areas. First, I examined the relationship between forage abundance and Tasselled Cap Transformation variables derived from satellite images. I then developed models for bear occupancy, incorporating distribution of higher status cohorts into the habitat models for lower status cohorts. I examined temporal and spatial patterns of mortality over a 22-year period in the Greater Kluane Region. Last, I examined the relationship between various habitat and mortality models and productivity and survival rates for bears in Kluane. The following is a summary of findings:

1. The Tasselled Cap Transformation of Landsat images produced variables superior to conventional land cover classifications for explaining variation in aggregate measures of forage abundance. Tasselled Cap Transformation provided continuous variables for linear occupancy estimation models while being more cost-effective to produce than land cover class variables. Forage productivity models that considered interactions terms between greenness and land cover classes were frequently no better for explaining forage abundance than models with

only Tasselled Cap variables. However, land cover classes were more useful for explaining the distribution of individual forage species. Land cover classes may also be useful for representing other aspects of life requirements of bears. For instance, moose, a food source for bears during the calving season, may be closely associated with wetlands, sub-alpine regions or closed canopy riparian areas (Geist and Francis 1999). Additionally, land cover classifications may be easier to use than Tasselled Cap variables for investigating the relationship between landscape pattern, such as inter-patch distance (Linke 2003), and bear habitat use. "Patches" may be easier to define using a conventional land cover classification rather than continuous variables like greenness. Furthermore, forage abundance might be better represented by maps of predicted probability distributions of the primary forage species (e.g., Nielsen et al. 2003), weighted by their seasonal importance in diet might. These maps could be generated using point location information on forage species and explanatory variables such as land cover classifications, slope, elevation, distances from hydrological features, and solar radiation. The latter four variables were consistently comparable or better than Tasselled Cap or land cover variables for explaining the distribution of forage on the landscape. Tasselled Cap layers may then be reserved for use in areas where there is little or no information that may lead to development of predictive models for primary forage species distribution.

2. When considering Tasselled Cap variables, regardless of the time of year that the corresponding satellite images represent, researchers typically only use greenness to model bear-habitat relationships. However, the seasonal timing of the images used to develop Tasselled Cap variables is important because the strength of the correlation between brightness, greenness, and wetness and forage availability changes depending on the phenological state of plants. For instance, I found that greenness was the most important variable for modeling forage distribution when using

satellite images from peak summertime, but when using fall images, brightness was a more important explanatory variable than greenness. During peak summer, greenness signatures vary widely across the landscape. When plants fully leaf-out, the reflectance from the soils below the leaf area is minimized. As plants senesce, the chlorophyll breaks down and the variation in greenness diminishes (Crist and Kauth 1986). Leaves also loose water, but as plants senesce, they shrivel and expose the soil below – which may or may not contain moisture (Jensen 1996). The signature for wetness becomes somewhat ambiguous. As signatures for greenness and wetness diminish and become homogenous, brightness becomes the predominant signature across the landscape and, hence, the most important variable for explaining variation in forage productivity.

3. This study reinforced that there is heterogeneity in habitat selection across demographic groups, and illustrated, in particular, the importance of modeling lone adult females and family groups separately. While the seasonal patterns of habitat use for all status groups followed patterns reported for other studies in northern and interior mountainous areas (Curatolo and Moore 1975, Pearson 1975, Reynold and Hechtel 1980, Murie 1981, Stemlock 1981, Hamer 1985), the influence of other cohorts on habitat use patterns of lower status groups had not been modeled before. Family groups appeared to segregate from other cohorts, in part, to avoid intra-specific aggression and to protect cubs. Segregation was also a product of differential response by each cohort to the distribution of human activity, and the distribution of forage. If segregation is a function of avoidance of conspecifics, habitat alterations could push adult males and lone adult females into regions where family groups take refuge, thereby increasing competition for resources or rates of infanticide. Cub survival may suffer as a consequence and the productivity of the population could decline.

4. From 1980 until recently, grizzly bear harvest and management mortality outside of the protected area complex exceeded prescribed rates (McCann 1998, Yukon Territorial Government 2003), creating attractive sinks along the Haines and Alaska Highways. Management agencies in the Kluane Region have made significant improvements in landfill and attractants management and public education initiatives. While these efforts reduced the frequency of occurrences and management-related mortalities, there was a substantial lag between the use of management tools to reduce human-bear conflicts and the decline of human-bear interactions and human-caused bear mortalities. Increased human activity in the region may have negated the positive effects of landfill closures. Intensity of human activity is positively correlated with the probability of human-bear encounters, and, concordantly positively correlated with rates of bear mortality (Gunther et al. 1995, Benn and Herrero 2002). While the number of open landfills decreased in the 1990s, the number of people recreating or living in the Haines Junction area increased (Yukon Territorial Government 2002). In some cases, when landfills closed, new problem areas developed. For instance, a mortality hot spot disappeared from the Haines Junction area, but a new hot spot appeared near the Bear Creek area, likely associated with the development of a new subdivision (MacIntosh Subdivision).

5. Though habitat-based methods for assessing impacts of human activities on grizzly bears are relatively inexpensive, their utility is limited if they do not express the relationship habitat has to demographic processes (Van Horne 1983, O'Neil and Carey 1984; Hobbs and Haney 1990, Garshelis 2000, Tyre et al. 2001). I appraised empirical habitat models, forage distribution models and expert-opinion models with respect to explaining reproductive and annual adult survival rates. Habitat occupancy variables were better for explaining variation in cub productivity than were mortality risk, forage distribution, habitat effectiveness and security area variables.

The habitat occupancy variable for all adult females was a better explanatory variable for fecundity than the occupancy variable that related only to family groups. However, the occupancy variables only explained a small portion of the variation in cub productivity. Mortality risk and forage distribution layers were the best explanatory variables for adult survival rates. The survival model generated using both variables fit the data well but was sensitive to the number of quantiles categorized as high mortality risk. Therefore, occupancy models and mortality risk are limited predictors of a population response to changes in habitat, and utility for these tools should be limited to relative comparisons, rather than predicting numbers of individuals that may persist in a given landscape window.

6. I used the best model, established by information-theoretic model selection criteria, for explaining reproductive and survival rates to predict population status for grizzly bears in the Greater Kluane Region. While productivity in the Bear Management Units (BMUs) adjacent to the highways was relatively high, mortality was also high. These areas, therefore, acted like attractive sinks and probably relied on the adjacent source areas to sustain a population. Source-like areas were in the northern and southern interior of Kluane National Park and Reserve and abutted the St. Elias Icefields.

## RECOMMENDATIONS

This project was undertaken to assist managers in conserving grizzly bear habitat and populations. Recommendations from my findings are as follows:

### *Recommendation 1: Reduce human-caused mortality*

High rates of human-caused mortality for grizzly bears have persisted in the Greater Kluane Region for over half a century (Pearson 1975). Mortality rates are unsustainable, particularly along the highway corridors (McCann 1998). The recovery of BMUs classified as attractive sink-like or the prevention of other BMUs from becoming attractive sinks will require management agencies to curtail human-caused mortality as human populations grow and developments increase. Five key actions can be taken to reduce human-caused mortality in the Kluane Region:

1. Continue efforts to reduce attractants, including efforts to fence landfills with electric fencing, promote use of bear-resistant containers and canisters and educate the public. These actions have been successful, but they must be continued in perpetuity to affect long-term grizzly bear population change.

    a. Currently, most waste management issues pertain to individual dwellings or businesses; therefore, efforts to promote electric fencing need to be directed toward private land owners.

    b. Parks Canada requires use of bear resistant canisters in high density bear areas throughout the Park. This likely has been a key management action in reducing human-bear conflicts. There are now few opportunities for bears to obtain food rewards within the Park boundary. Parks staff may consider requiring canister use throughout other regions of the Park. Yukon Territorial Government may also consider promoting use of canisters outside of the national park.

    c. Public educations programs have been instrumental in the success of many conservation initiatives. Public will to move land-use practices toward a conservation-based approach is fostered by public understanding of a conservation problem (Jacobson 1999). However, public education programs need to be persistently applied before the actions they are promoting become routine societal practice (Brewer 2001). Programs should be planned so that there is a pulse of education to target each new generation. Characteristics of successful education programs are discussed further in Britt and Hunter (1994), Jacobson and McDuff (1997), Jacobson (1999), Fien et al. (2001), and Robertson and Hull (2001).

2. Implement policies and by-laws that reduce availability of attractants around residences, camps and other human use facilities. Though the *Yukon Lands Act* requires that municipalities place electric fencing around public landfills, there are still private and/or illegal landfills operating without electrification. Outside of the Park, the Yukon Territory *Wildlife Act* prohibits any person from encouraging bears to become a public nuisance by feeding an animal, or leaving food or garbage in a place where wildlife can access it. *The Act* states that a person must take “reasonable precautions” to ensure that wildlife does not gain access to food or garbage. However, the concept of “reasonable precaution” is discretionary and usually assessed only after the human-wildlife conflict has occurred. Human-bear conflicts could be reduced by establishing by-laws or policies that explicitly state expectations for treatment of attractants. For instance, storing domestic garbage in regular bins outside of a residence is common practice in Haines Junction and other communities throughout the Yukon. Land-use permitting processes do not require users to store domestic garbage bins in a hard-sided building or wildlife resistant enclosure prior to disposal. There are also no policies or legislation to address use of grey water pits for domestic sewage, use of bird feeders, pet food, or outdoor grills, and maintaining livestock (such as chickens, turkeys, or pigs), storing petroleum products, curing meat, or maintaining vegetable gardens/farms, orchards or apiaries. Incineration, electric fencing and

bear-proof storage or containers should become common legislative or policy requirements for land-use practices.

3. Reduce or restrict access into high occupancy bear habitats. Occurrences and mortalities were strongly correlated with areas that had high human infrastructure density and areas proximal to linear access features. Across North America, access is a landscape feature consistently associated with high incidence of bear mortality. In addition to roads and trails, creek beds generally provide access to wilderness for all terrain vehicle users, mountain bikers, hikers and watercraft recreators. The need to control human access has been acknowledged in other national parks. Management strategies such as those employed in Banff National Park, Denali National Park and Yellowstone National Park have proven successful. Strict control of human access has been achieved through seasonal area closures, seasonal trail closures, day-use only restrictions, travel limited to mid-day only, designated camping and restrictions on minimum party size. Similar restrictions have been beneficial for reducing bear-human conflicts in Kluane. Implementation of further restrictions may be necessary, particularly as tourism grows, in places like the Slims River Valley and the Cottonwood Trail. Commensurate with this, and considering access management outside of the protected area, management agencies should prepare human access management plans for each BMU. The objective of the plans would be to retain effective habitat for grizzly bears. This can be done by: (1) restricting use of, or relocating some trails and roads, (2) regulating timing of use, and (3) limiting or disallowing overnight use of some areas. Priority should be given to areas having good quality grizzly bear habitat, and human use or developments whose impacts could be lessened through management actions. Planning, consideration should be given to ensure that some BMUs have no or limited access.

4. Implement land-use planning strategies that reduce development or inappropriate human uses of key habitats for bears. In the mid-1990s a collaborative land-use planning process was undertaken by management agencies in the Kluane Region (Yukon Territorial Government 1991). However, because of various socio-political reasons (e.g., Duerden et al. 1991), the land-use plan was never ratified or implemented. While bear mortality could proximally be reduced through attractant management, reducing the juxtaposition of human activities with high occupancy bear habitat addresses the ultimate causes of mortality. Bear mortalities are more likely to occur in areas where there is a high probability of a bear being present. Therefore, where possible, human activities need to be concentrated in areas where there is a low potential for bear occurrence. Commensurate with other land-use planning process that are now underway in the Yukon, a planning process for Kluane needs be re-initiated or the land-use plan from the 1990's needs to be revived, updated, and implemented.

5. Limit harvest mortality to a sustainable rate. Though the grizzly bear harvest declined through the 1990's morality rates still exceeded the prescribed 2% and 6% rates, for females and males, respectively. While, the Yukon Territorial Government prescribes a harvest rate, quotas only apply to non-resident hunters (Yukon Territorial Government 1997). Resident harvest is limited by a one grizzly bear in three years allowance for each person in the territory but there is no spatial control on the distribution of harvest. Hence, resident harvest for the entire Territory in any year can be concentrated in the Kluane Region. Harvest mortality is currently increasing. If this trend continues, harvest mortality will again, exceed the prescribed rate. Yukon Territorial Government should develop a limited-entry system that caps harvest and accounts for other sources of mortality. Similarly, the non-resident quota system currently does not

account for unreported human-caused mortality. Managers should account for unreported mortality when prescribing the total area quota.

*Recommendation 2: Plan human-use activities to reduce impacts to high occupancy habitat*

The availability of high occupancy habitat influences population productivity; therefore, habitat loss can have a significant influence on the population trajectory. Habitat loss occurs through: 1) direct loss through conversion of lands, and 2) indirect loss caused by displacement of bears by human activities. Results presented in Chapter 3 showed that bears avoided areas with relatively high human infrastructure density. Cohorts that used habitats closer to human infrastructure were more strongly affected by that variable. Human disturbance should be minimized in areas important for bears. Protection of habitat features such as high greenness, forest and shrub polygon edges, riparian zones, and areas with mid-range terrain ruggedness will be important for preventing or reducing disturbance.

*Recommendation 3: Do not rely solely on habitat-based models when making management decisions*

In the past, expert-opinion habitat effectiveness modeling was the primary tool used to measure the impact of human activities on bears. The model provided managers with a qualitative assessment of bear's foraging opportunities when human activities were taken into account. However, the model was highly subjective. Occupancy and mortality risk models built with resource selection functions offer a quantitative approach to measuring the potential impacts of human activity on grizzly bears. These models can then be combined to develop explanatory and predictive models that relate better than subjective models to demographic features. Where information on bear occurrence and mortality is available, these models should replace the more subjective models of the past.

Mortality models had excellent goodness-of-fit measures for explaining variation in survival rates across individuals. Conversely, habitat occupancy models developed in this research project were limited in explanatory power, accounting for less than 12% of the variation in productivity rates. Occupancy models, therefore, are limited as predictors of productivity rates. Given the uncertainty of habitats as predictors of individual productivity, a multi-faceted approach should be considered that: 1) where funding is available, monitors habitat and directly assesses productivity and survival parameters by monitoring individuals, and 2) incorporates risk of population decline given uncertainty (Murphy and Noon 1991) in productivity and survival rates (Walters 1986, Holt and Peterman 2006), and hence population growth rate. Risk-based approaches explicitly state the credibility of models and parameter estimates used in decision-making as a probability. The probabilities of potential outcomes are weighed against the cost or benefit to stakeholders or society (Maxwell et al. 2006).

*Recommendation 4: Landscape connectivity, secured through interagency co-operation, will be critical for persistence of bear populations in Kluane*

Immigration of grizzly bears through corridors from source-like BMUs to attractive sink-like BMUs may ameliorate the adverse local effects of human-caused mortality. These effects might otherwise result in population declines (Hegmann 1995; Carroll et al. 2004). Among wildlife species, grizzly bear population are particularly sensitive to the degradation of corridors because they occupy them for extensive periods of time as they disperse (Carroll et al. 2004). However, corridors are few owing to the mountainous nature of the entire region and are often areas where human activity is high. Most corridors in the Kluane Region span multiple jurisdictions, thus, effective protection requires trans-boundary management. Management models where inter-agency and multi-stakeholder groups with significant regional-scale responsibilities for management of grizzly bears are supported by a group of technical experts and local managers have been effective for sustaining grizzly bear and other species in other ecosystems. There is also a clear need for interagency management guidelines that provide security for grizzly bears as they cross jurisdictional boundaries.

*Recommendation 5: Land-use planning processes in the Kluane Region need to address: protected area size, the landscape context of the protected area complex (e.g., the surrounding matrix), and provision of buffer zones.*

A population viability analysis (PVA) may be conducted to identify a population size below which extinction is likely to happen (minimum viable population; MVP). Boyce et al. (2001) make recommendations on conducting a PVA for grizzly bears. Landscape planning can then consider matrix and buffer designs that would facilitate maintaining a population of grizzly bears well above this value. The edge of the surrounding matrix area will also be critical in determining the dynamics of immigration and emigration into and from the protected area complex. Newmark (1985) compared the identified legal boundaries with the biotic boundaries for the eight largest protected areas in western North America. Biotic boundaries were determined by watershed locations and the estimated areas needed to maintain the non-flying mammals with the largest home ranges. Seven of the eight reserves had biotic boundaries larger than their legal boundaries, by factors of 1.2 to 9.6 for MVPs of 50 and 6 to 96 for MVPs of 500. This work emphasized the conservation significance of the semi-wild public and private lands that may surround protected areas as buffers.

## INFORMATION GAPS

Several information gaps were identified. The following are recommendations for follow-up:

1) The habitat models developed in this project were strongly biased by time of day. Relocation information had to be obtained during daylight hours.

Management agencies should consider use of GPS collars to record information from a large number of individual bears. Habitat maps that consider all times of day could then be developed and used in the models. Likewise, more relocation information for the periods just prior to and just after denning would be beneficial for building habitat models for these times of year.

2) Recorded mortality rates do not necessarily reflect actual mortality rates. The degree of detection of grizzly bear deaths varies by cause, and the thoroughness of the reporting and recording of mortality data varies among jurisdictions and time periods. Thus, to identify a preliminary index of undetected mortality, data from the radio-collared population of grizzly bears in the Kluane Region and other regions need to be reviewed and compared with results from this project.
3) Hunters were not always willing to provide information on the spatial location of their kill site. Consequently, the sample size for hunt-related bear mortality was smaller than desired. Follow-up efforts should be directed toward obtaining more information on the spatial location of hunt-related kills. Management agencies should consider mandatory reporting of hunt locations.
4) The models developed in this paper did not explicitly investigate issues with landscape connectivity. Grizzly bears need to move across landscapes to forage in important seasonal habitats and find mates for breeding. There are many human-related impediments across a landscape that can be problematic to grizzly bear movements and habitat use. Landscape linkages may promote the persistence of grizzly bears by enabling movements at various spatial scales (Noss 1983, Noss 1987, Saunders and Hobbs 1991). Modeling is needed to assess landscape connectivity in the Kluane Region.
5) Continued collection of survival and productivity data would improve models and allow researchers to consider more complex models. In particular, data on subadult female survival were poor.

6) Agencies spend funds and resources to collect information on wildlife habitat uses, yet information on human use, which is critical for the management process, is often poor. Follow up should focus on ways to collect the appropriate human use information.

## CONCLUDING THOUGHTS

This study examined the cumulative impacts of human activity on grizzly bear habitat and populations in a northern ecosystem containing a protected area complex. Global conservation priorities primarily emphasize areas with the highest species richness or areas with species in imminent risk of extinction (Myers et al. 2000). Areas such a Kluane usually are of low concern to conservationists because public and agencies commonly associate northern terrestrial environments with pristine wilderness (e.g., Ricketts et al. 1999). Though the footprint for human land-use is smaller in the north than in southern environments, the latent global extinction risk for places like Kluane is high – some argue as high as severely disturbed wildlife habitats in Southeast Asia (Cardillo et al. 2006). With increasing prevalence of tourism quotas and outright moratoriums on human use in southern parks, increased demand for a remote wilderness experience, and increased economic development in the north, northern terrestrial ecosystems, including protected areas, are increasingly prone to human-wildlife land-use conflicts. Unfortunately, northern ecosystems have less capacity than southern ecosystems to withstand impacts from human land-use (Rohde 1992, Cardillo et al. 2006). The relative paucity of biodiversity and biomass compared to ecosystems at southern latitudes means that Yukon ecosystems have poor ecological resilience (Rapoport 1982, Stevens 1989, Peterson et al. 1998). Given the current and emerging human land-use pressures in the north, without proactive attention, wildlife populations for species such as grizzly bears will rapidly decline.

Conservation of large carnivores and conservation of other elements of biodiversity are linked (Linnell et al. 2000, Carroll et al. 2001). In many ecosystems, protecting large carnivores, *de facto*, facilitates preservation of other organisms (Noss et al. 1996, Linnell et al. 2000, Carroll et al. 2001). However, the causes of decline for each are not necessarily the same (Woodroffe 2000, Treves and Karanth 2003). Most terrestrial species have experienced population declines because of human-caused habitat change (Brooks et al. 2002). Large carnivores, however, are generally not specialized, and pristine conditions are not needed for their continued survival (Woodroffe 2001). While habitat loss has been cited as a fundamental concern for preserving some bear populations (Mattson and Merrill 2002, Ross 2002), the principal factor affecting their abundance is security from human conflict (Woodroffe 2001, Treves and Karanth 2003). Direct mortality appears to be the primary force driving grizzly bear populations to the brink of extirpation (Mattson et al. 1996b, Linnell et al. 2001, Woodroffe 2001, Benn and Herrero 2002). Roads and other linear access features are often a factor for high rates of human-caused bear mortality because they provide access for hunters, poachers, and others into regions where bears reside (McClellan 1989, Nielsen et al. 2004a). Societal tolerance for property damage is often low (Sillero-Zubiri and Laurenson 2001), and fear of human injury or mortality is often high (Kellert et al. 1996, Bath 1998, Røskaft et al. 2003). As such, coexistence may require that there are tracts of land with little to no human access and limited human activity.

The national park system is a primary means of protecting large carnivores in North America; however, most of the protected areas that comprise the system have not been designed to sustain populations of wide-ranging species (Newmark 1985, Mattson et al. 1996a). Many protected areas, particularly in mountainous regions, do not encompass enough area to provide for the lifetime home range requirements of a minimum viable population of grizzly bears (Weaver et al. 1996, Woodroffe and Ginsberg 1998). Most mountainous national parks are overwhelmingly comprised primarily of uninhabitable rock and ice (Banff Bow Valley Study 1996). Protected areas are often designed without linkages to other wildlife populations (Noss et al. 1996). Population status, particularly where bears experience high rates of human-caused mortality, becomes highly precarious with increasing geographical isolation from surrounding populations (Doak 1995). Kluane is unlike most mountain parks. Kluane is contiguous with three other parks, forming the world's largest protected area complex. The approximately 4000 km$^2$ of green belt in Kluane, which appears inadequate for maintaining a viable bear population, may rely heavily on influxes of bears from these adjacent areas. If high mortality rates continue unabated and there is no means to increase the land base for protection of bears, a key may be to focus on corridors and the surrounding source populations. Consequently, interagency dialogue will be a prominent part of grizzly bear conservation for Kluane.

Although the concepts of limiting or reducing human activity in important grizzly bear habitat or keeping corridors traversable for bears appears logical and relatively straight forward, perhaps the most challenging steps ahead will be implementation of new management prescriptions to achieve security for grizzly bears. Humans are not generally accepting of land-use policies that restrict individual liberties (Rutherford and Clark 2005), particularly when economic gains are being sacrificed. In the end, grizzly bears may prove to be the ultimate challenge in whether humans can coexist with nature (Kellert et al. 1996). The difficulty of coexisting with large carnivores is less about the carnivores than it is about societal values and perceptions (Primm and Clark 1996). Grizzly bears are relatively easy to manage;managing people  in cooperative ways that give grizzly bear populations reprieve is much more challenging.

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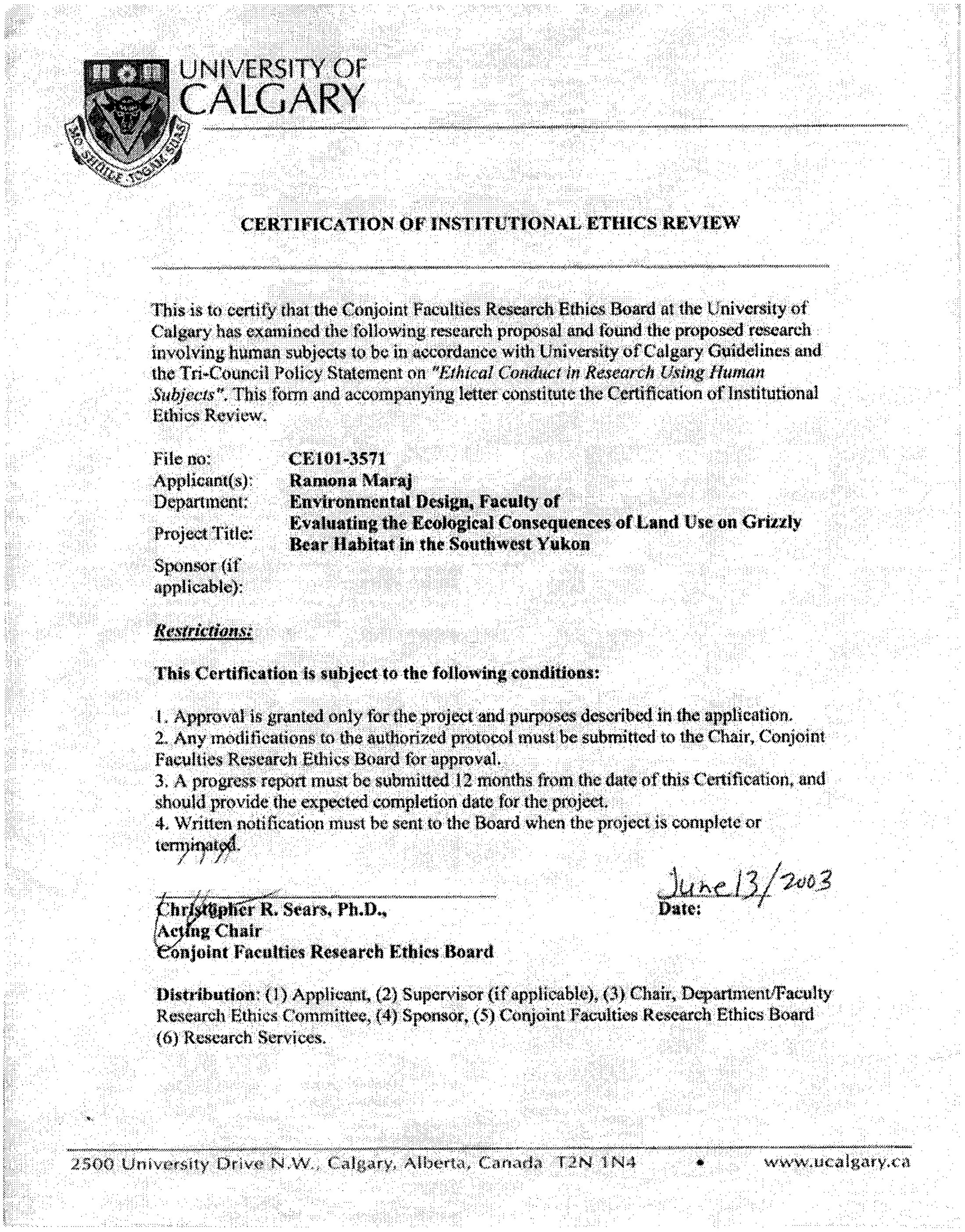
Appendix 1: Band colour and wavelengths for Landsat 5 TM imagery.

| **Band** | **Colour** | **Wavelength *(micrometers)*** |
|---|---|---|
| Band 1 | Blue | 0.45–0.52 |
| Band 2 | Green | 0.52–0.60 |
| Band 3 | Red | 0.63–0.69 |
| Band 4 | Near-infrared | 0.76–0.90 |
| Band 5 | Middle-infrared | 1.55–1.75 |
| Band 6 | Thermal infrared | 10.4–12.5 |
| Band 7 | Middle-infrared | 2.08–2.35 |

## Appendix 2: University of Calgary ethics approval for interviews.



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### CERTIFICATION OF INSTITUTIONAL ETHICS REVIEW

This is to certify that the Conjoint Faculties Research Ethics Board at the University of Calgary has examined the following research proposal and found the proposed research involving human subjects to be in accordance with University of Calgary Guidelines and the Tri-Council Policy Statement on *"Ethical Conduct in Research Using Human Subjects"*. This form and accompanying letter constitute the Certification of Institutional Ethics Review.

| | |
|---|---|
| File no: | **CE101-3571** |
| Applicant(s): | **Ramona Maraj** |
| Department: | **Environmental Design, Faculty of** |
| Project Title: | **Evaluating the Ecological Consequences of Land Use on Grizzly Bear Habitat in the Southwest Yukon** |
| Sponsor (if applicable): | |

***Restrictions:***

**This Certification is subject to the following conditions:**

1. Approval is granted only for the project and purposes described in the application.
2. Any modifications to the authorized protocol must be submitted to the Chair, Conjoint Faculties Research Ethics Board for approval.
3. A progress report must be submitted 12 months from the date of this Certification, and should provide the expected completion date for the project.
4. Written notification must be sent to the Board when the project is complete or terminated.

**Christopher R. Sears, Ph.D.,**
**Acting Chair**
**Conjoint Faculties Research Ethics Board**

June 13/2003
**Date:**

**Distribution:** (1) Applicant, (2) Supervisor (if applicable), (3) Chair, Department/Faculty Research Ethics Committee, (4) Sponsor, (5) Conjoint Faculties Research Ethics Board (6) Research Services.

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Appendix 3: Bent-cable and break point estimation macro for S-Plus:

```
hockey <- function(x,alpha1,beta1,beta2,brk,eps=diff(range(x))/100) {
    ## alpha1 is the intercept of the left line segment
    ## beta1 is the slope of the left line segment
    ## beta2 is the slope of the right line segment
    ## brk is location of the break point
    ## 2*eps is the length of the connecting quadratic piece

     x1 _ brk-eps
     x2 _ brk+eps
     b <- (x2*beta1-x1*beta2)/(x2-x1)
     cc <- (beta2-b)/(2*x2)
     a <- alpha1+beta1*x1-b*x1-cc*x1^2
     alpha2 _ - beta2*x2 +(a + b*x2 + cc*x2^2)

     lebrk <- (x <= brk-eps)
     gebrk <- (x >= brk+eps)
     eqbrk <- (x > brk-eps & x < brk+eps)

     result <- rep(0,length(x))
     result[lebrk] <- alpha1 + beta1*x[lebrk]
     result[eqbrk] <- a + b*x[eqbrk] + cc*x[eqbrk]^2
     result[gebrk] <- alpha2 + beta2*x[gebrk]
     result}

     ##start=list(alpha1=2, beta1=2, beta2=-4, brk=12))
```

Appendix 4: Sensitivity analysis changing the number of quantiles classified as high occupancy family group habitat for the top productivity model. No BMUs changed population state.

| BMU ID | BMU name | Five quantiles | Four quantiles | Three quantiles | Two quantiles | One quantile | Number of unique states |
|---|---|---|---|---|---|---|---|
| 1 | Kluane Lake | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | 1 |
| 2 | Steele | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 3 | Klutlan | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 4 | St. Claire | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 5 | Teepee | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 6 | Spring | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 7 | Wolverine | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 8 | Donjek Glacier | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 9 | Kluane Glacier | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 10 | Dusty | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | 1 |
| 11 | Kaskawulsh River | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 12 | Lowell South | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 13 | Alsek | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | 1 |
| 14 | Disappointment | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | 1 |
| 15 | Fisher | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 16 | Turnback | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 17 | Jarvis | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | 1 |
| 18 | Range | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 19 | Mush Bates | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 20 | Haines | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | 1 |
| 21 | Detour | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 22 | Tatshenshini | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | 1 |
| 23 | Kathleen | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | 1 |
| 24 | Blanchard | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | 1 |
| 25 | Donjek River | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 26 | Slims | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 27 | Duke | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | 1 |
| 28 | Dezadeash Lake | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | 1 |

**Proportion of BMUs that changed states = 0**

Appendix 5: Sensitivity analysis changing the number of quantiles classified as high mortality risk for the top survival model. Eight BMUs went from attractive sink-like to source like population states when fewer quantiles were classified as high mortality risk (highlighted in grey).

| BMU ID | BMU name | Five quantiles | Four quantiles | Three quantiles | Two quantiles | One quantile | Number of unique states |
|---|---|---|---|---|---|---|---|
| 1 | Kluane Lake | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | 1 |
| 2 | Steele | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 3 | Klutlan | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 4 | St. Claire | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 5 | Teepee | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 6 | Spring | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 7 | Wolverine | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 8 | Donjek Glacier | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 9 | Kluane Glacier | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 10 | Dusty | Attractive sink-like | Attractive sink-like | Attractive sink-like | Source-like | Source-like | 2 |
| 11 | Kaskawulsh River | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 12 | Lowell South | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 13 | Alsek | Attractive sink-like | Attractive sink-like | Source-like | Source-like | Source-like | 2 |
| 14 | Disappointment | Attractive sink-like | Attractive sink-like | Attractive sink-like | Source-like | Source-like | 2 |
| 15 | Fisher | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 16 | Turnback | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 17 | Jarvis | Attractive sink-like | Attractive sink-like | Attractive sink-like | Source-like | Source-like | 2 |
| 18 | Range | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 19 | Mush Bates | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 20 | Haines | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | 1 |
| 21 | Detour | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 22 | Tatshenshini | Attractive sink-like | Attractive sink-like | Source-like | Source-like | Source-like | 2 |
| 23 | Kathleen | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | Source-like | 2 |
| 24 | Blanchard | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | Source-like | 2 |
| 25 | Donjek River | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 26 | Slims | Source-like | Source-like | Source-like | Source-like | Source-like | 1 |
| 27 | Duke | Attractive sink-like | Attractive sink-like | Attractive sink-like | Source-like | Source-like | 2 |
| 28 | Dezadeash Lake | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | Attractive sink-like | 1 |

**Proportion of BMUs that changed states = 0.2857**