Spatial analysis of factors influencing long-term stress and health of grizzly bears (*Ursus arctos*) in Alberta, Canada

by

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B.Sc., University of Victoria, 2011
B.A., University of Alberta, 2005

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ABSTRACT

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A primary focus of wildlife research is to understand how habitat conditions and human activities impact the health of wild animals. External factors, both natural and anthropogenic that impact the ability of an animal to acquire food and build energy reserves have important implications for reproductive success, avoidance of predators, and the ability to withstand disease, and periods of food scarcity. In the analyses presented here, I quantify the impacts of habitat quality and anthropogenic disturbance on indicators of health for individuals in a threatened grizzly bear population in Alberta, Canada.

The first analysis relates spatial patterns of hair cortisol concentrations, a promising indicator of long-term stress in mammals, measured from 304 grizzly bears to a variety of continuous environmental variables representative of habitat quality (e.g., crown closure, landcover, and vegetation productivity), topographic conditions (e.g., elevation and terrain ruggedness), and anthropogenic disturbances (e.g., roads, forest harvest blocks, and oil and gas well-sites). Hair cortisol concentration point data were integrated with continuous variables by creating a stress surface for male and female bears using kernel density estimation validated through bootstrapping. The relationships between hair cortisol concentrations for males and females and environmental variables were quantified using random forests, and landscape scale stress levels for both genders was predicted based on observed relationships. Low female stress levels were found to correspond with regions with high levels of anthropogenic disturbance and activity. High female stress levels were associated primarily with high-elevation parks and protected areas. Conversely, low male stress levels were found to correspond with parks and protected areas and spatially limited moderate to high stress levels were found in regions with greater anthropogenic disturbance. Of particular concern for conservation is the observed relationship between low female stress and sink habitats which have high mortality rates and high energetic costs.

Extending the first analysis, the second portion of this research examined the impacts of scale-specific habitat selection and relationships between biology, habitat quality, and anthropogenic disturbance on body condition in 85 grizzly bears represented using a body condition index. Habitat quality and anthropogenic variables were represented at multiple scales using isopleths of a utilization distribution calculated using kernel density estimation for each bear. Several hypotheses regarding the influence of biology, habitat quality, and anthropogenic disturbance on body condition quantified using linear mixed-effects models were evaluated at each habitat selection scale using the small sample Aikake Information Criterion. Biological factors were influential at all scales as males had higher body condition than females, and body condition increased with age for both genders. At the scale of most concentrated habitat selection, the biology and habitat quality hypothesis had the greatest support and had a positive effect on body condition. A component of biology, the influence of long-term stress, which had a negative impact on body condition, was most pronounced within the biology and habitat quality hypothesis at this scale. As the scale of habitat selection was represented more broadly, support for the biology and anthropogenic disturbance hypothesis increased. Anthropogenic variables of particular importance were distance decay to roads, density of secondary linear features, and density of forest harvest areas which had a negative relationship with body condition. Management efforts aimed to promote landscape conditions beneficial to grizzly bear health should focus on promoting habitat quality in core habitat and limiting anthropogenic disturbance within larger grizzly bear home ranges.

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CO-AUTHORSHIP STATEMENT

This thesis is the combination of two scientific manuscripts for which I am the lead author. The initial project structure was provided by Dr. Trisalyn Nelson and Dr. Marc Cattet, for which the spatial analysis of factors influencing long-term stress and health in grizzly bears was identified as a key research opportunity. For these two scientific journal articles, I performed all research, data analysis, initial interpretation of results, and final manuscript preparation. Dr. Chris Darimont provided assistance with defining research questions and interpretation of results. Dr. Gordon Stenhouse provided the data and assistance with interpretation of results. Dr. Nelson, Dr. Cattet, Dr. Darimont, and Dr. Stenhouse supplied editorial comments and suggestions incorporated into the final manuscript.

1.0 INTRODUCTION

1.1 Research context

The health and survival of wildlife is predicated upon the ability of individuals to occupy habitat with resources adequate for meeting nutritional needs (Morrison 2001). Animals require access to consistent and predictable food sources in order to maintain and develop body tissue and mass (Barboza et al. 2009). Factors, both natural and anthropogenic, which disrupt the ability of an animal to feed and optimize energetic reserves have health related consequences that impact reproductive ability (Trites & Donnelly 2003; Parker et al. 2009), the capacity to mount an immune system response (Møller et al. 1998), and to survive periods of food scarcity (Poulle et al. 1995; Verrier et al. 2011). Currently, numerous wildlife populations are threatened as a result of increasing anthropogenic pressures, including habitat loss and fragmentation (Wilcox & Murphy 1985; Brooks et al. 2002), and climate change (Travis 2003; Thomas et al. 2004), which alter the distribution and availability of habitat. At greatest risk of population decline due to anthropogenic disturbances are large-bodied species with diminished geographic range, low population densities, low fecundity, and which occupy high trophic levels (Purvis et al. 2000; Cardillo et al. 2005). A number of large predators of the Rocky Mountains of North America, such as wolves, cougars, and grizzly bears, satisfy most, if not all, of these conditions (Noss et al. 1996; Weaver et al. 1996; Kellert et al. 2002).

Efforts to detect declines in wildlife populations and assess population trends have typically focused on relating spatial patterns of species distributions or population density estimates based on mark-recapture programs, or field surveys, with change in landscape patterns and habitat characteristics (e.g., Nichols 1992; Davies et al. 2000; Wabakken et al. 2001; Fahrig 2003). However, as Ellis et al. (2012) note, assessment of change in species' distributions are retrospective and do not provide estimates regarding population declines until after they have occurred, often rendering conservation efforts ineffective. Further, population density estimates are resource- and time-intensive, and may suffer from problems in terms of accuracy and precision as it often proves difficult to effectively sample the entire population and estimates are susceptible to population closure violations (Boulanger et al. 2004a; Boulanger et al. 2004b). As a result, population demographics may be underestimated, or worse, overestimated which may have implications regarding the efficacy of management decisions.

The potential of health measures in conservation for providing real-time, rather than retrospective, information regarding the response of individuals and populations to changing environmental conditions is growing (Wikelski & Cooke 2006). In particular, the role of long-term stress and its impacts on health and disease is increasingly recognized as an important consideration in evaluations of the long-term viability of wild vertebrate populations (Reeder & Kramer 2005; Wikelski & Cooke 2006). Health of animals is frequently estimated using a body condition index (BCI). The BCI provides a scaled representation of the health of an animal based on mass while controlling for body length (Jakob et al. 1996). While a number of methods exist which are used to estimate body condition from empirical mass/length measurements (Stevenson & Woods 2006), the most frequently employed are residuals (both unstandardized and standardized) from an ordinary least squares linear regression of body mass over body length which correlate with structural size (Schulte-Hostedde et al. 2005). Resulting index values, which capture structural size of the animal while remaining independent of body size, provide an effective means for measuring and comparing the health of individuals within a population (Schulte-Hostedde et al. 2001; Cattet et al. 2002).

External stressors are described as either acute (i.e., short term) or chronic (i.e., long-term), depending on the duration of the health consequences in the animal (Boonstra 2013). While an acute stressor of short duration may impact the behaviour of an animal over the long-term (Wiedenmayer 2004), exposure to prolonged or frequent stressors over a long-period of time (e.g., weeks, months, or years) resulting in a chronic stress response has been linked to more serious health impairments (McEwen & Wingfield 2003). Vertebrates respond to noxious external stimuli through the activation of the hypothalamic-pituitary-adrenal axis with the resultant release of glucocorticoids, such as cortisol, into the blood circulation (Sheriff et al. 2011), with the goal of maintaining or re-establishing homeostasis (McEwen & Wingfield 2003). However, if the energetic demands required responding to the stressor exceed the energetic reserves of an animal over the long-term, and secretion of glucocorticoids reaches elevated levels without abating, resulting allostatic overloading may result in pathology or even death (McEwen & Wingfield 2003). The continued circulation of glucocorticoids has also been linked to decreased growth and reproductive capacity in some species (Wingfield & Sapolsky 2003; Reeder & Kramer 2005).

Given the detrimental health effects of long-term stress, cortisol concentrations measured from saliva, blood, feces, and hair (von der Ohe & Servheen 2002; Palme et al. 2005; Sheriff et al. 2011) have been used to quantify the long-term stress response in animals such as the northern spotted owl (Wasser et al. 1997), squirrel gliders (Brearley et al. 2012), ungulates (Millspaugh et al. 2001; Ashley et al. 2011; Wasser et al. 2011), wolves (Creel et al. 2002), and grizzly bears (von der Ohe et al. 2004; Macbeth et al. 2010). In a number of recent studies compromised health in individuals associated with a long-term stress response have been linked to observed population declines (Trites & Donnelly 2003; Bejder et al. 2006; Charbonnel et al.

2008). In some cases, evidence has suggested a relationship between the observed long-term stress response and anthropogenic disturbance and activities (Walker et al. 2005; Arlettaz et al. 2007; Charbonnel et al. 2008; Brearley et al. 2012). However, while the utility and importance of health metrics such as hair cortisol concentrations has been recognized, their use and integration with datasets representing both habitat quality and anthropogenic disturbance is still lacking thereby limiting the scope of possible inference (Ellis et al. 2012). Cooke & O'Connor (2010) suggest conservation research integrating health metrics should focus on threatened and at-risk populations in order to maximize the applicability of potential cause-and-effect conclusions.

1.2 Research focus

The grizzly bear population of Alberta, Canada represents a unique opportunity to study the impacts of environmental conditions on long-term stress and health, as well as the resulting implications in regard to the long-term viability of a population. The grizzly bear (*Ursus arctos*) is a flagship species in conservation efforts (Noss et al. 1996; Carroll et al. 2001), and with less than 700 individuals remaining, was listed as *Threatened* in 2007 (Alberta Sustainable Resource Development & Alberta Conservation Association 2010). Numbers of grizzly bears in Alberta have been reduced as a result of habitat fragmentation and loss, primarily due to the development of roads, settlements, resource extraction activities, agriculture, and recreation (Ross 2002; Laliberte & Ripple 2004), and direct mortality through overhunting, poaching, management removal, and defense of life and property (Weaver et al. 1996; Garshelis et al. 2005). Patterns of land-use have also resulted in genetically fragmented sub-populations which may not be viable in the long-term (Proctor et al. 2012).

As omnivores, grizzly bears consume a wide variety of food sources resulting in complex spatial and temporal patterns of habitat selection over large areas (Munro et al. 2006). Recent advances in radio-telemetry tracking of wildlife as a result of increased precision of global positioning systems (GPS) have created new opportunities to understand animal behaviour and habitat selection (Hulbert & French 2001). Modelling habitat quality and disturbance over large areas has also been greatly enhanced by remote sensing technologies which offer extensive spatial cover and consistent temporal return intervals (McDermid et al. 2005). Using geographic information systems (GIS) and novel spatial modelling techniques, it is now possible to combine and analyze disparate environmental data and convert them into products beneficial for conservation and wildlife conservation management (Goodchild et al. 1996; Gotway & Young 2002; Manly et al. 2002; Fortin et al. 2006; Steiniger & Hay 2009; Walter et al. 2011).

In the absence of natural disturbance, a number of studies have shown grizzly bears select anthropogenic-disturbed habitats with high human activity due to the availability of critical foods (Nielsen et al. 2004; Roever et al. 2008; Stewart et al. 2012). While anthropogenic-disturbed habitats may offer the opportunity for bears to enhance their body condition, the benefit may be negated by the energetic requirements, and long-term stress response, potentially associated with sink habitats.

1.3 Thesis objective

This research is concerned with understanding how changing environmental conditions impact long-term stress and body condition in grizzly bears of Alberta. The aim of the research is to employ novel spatial methods to integrate a variety of spatial data in order to quantify the influence of habitat quality and anthropogenic disturbance on long-term stress, represented using hair cortisol concentrations (Macbeth et al., 2010) and body condition, represented using a body condition index developed for *ursids* (Cattet et al. 2002), in grizzly bears. This aim will be addressed by accomplishing the following:

1) Develop a spatially explicit model which quantifies gender-specific differences in the long-term stress response associated with habitat quality and anthropogenic disturbance.
2) Quantify how habitat selection, expressed across a continuum of geographic scales, influences body condition of individual bears in relation to biology (including long-term stress), habitat quality, and anthropogenic disturbance.

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2.0 Factors influencing long-term stress in the grizzly bear (*Ursus arctos*) population of Alberta, Canada

2.1 Abstract

Non-invasive measures of long-term stress in free ranging mammals are an increasingly important approach for understanding physiological responses to landscape conditions. Using a spatially and temporally expansive dataset of hair cortisol concentrations generated from a threatened grizzly bear (*Ursus arctos*) population in Alberta, Canada, we quantified how patterns of anthropogenic disturbance and habitat quality impact long-term stress in grizzly bears. We used random forest models to quantify the influence of variables representing habitat quality and anthropogenic disturbance within grizzly bear habitat on observed spatial patterns of hair cortisol concentrations for male and female grizzly bears. Separate models were developed for regions inside and outside of parks and protected areas to account for substantial differences in anthropogenic disturbance within the study area. Variance explained in the random forest models ranged from 55.34% to 74.96% for males and 58.15% to 68.46% for females. Our results revealed geographic and gender differences in the spatial distribution of the modelled hair cortisol concentration values. The predicted long-term stress response was higher for females compared to males and high hair cortisol values were more spatially continuous for females. High female hair cortisol concentration values were generally associated with moderate to high elevation areas inside and adjacent to parks and protected areas, while low values were found to coincide with areas of substantial anthropogenic disturbance. In contrast, low male hair cortisol concentrations values were associated with parks and protected areas and moderate to high values were found in regions with more industrial activity. Observed patterns in females are particularly concerning as low-stress coincides with areas where bears have increased risk of human-caused mortality. Future grizzly bear conservation efforts should attempt to better understand the observed spatial and gender based stress response to landscape conditions.

2.2 Introduction

Spatial patterns of species decline and extinction have been linked to complex interactions among anthropogenic factors, such as habitat loss and fragmentation (Wilcox & Murphy 1985; Bender et al. 1998; Brooks et al. 2002), over-exploitation (Purvis et al. 2000), climate change (Travis 2003; Thomas et al. 2004), and competition with invasive species (Gurevitch & Padilla 2004; Didham et al. 2007). Whereas many large predators lack the behavioural plasticity necessary to adapt to rapid change (Weaver et al. 1996), at greatest risk are large-bodied predators with diminished geographical range, small population size, low fecundity, and which occupy higher trophic levels (Russell et al. 1998; Purvis et al. 2000; Cardillo et al. 2005). To date, efforts to examine spatial patterns of species decline have focused primarily on changing patterns of species distributions, abundance, and mortality in response to anthropogenic activities and habitat fragmentation (Guisan & Thuiller 2005; Ewers & Didham 2006; Elith & Leathwick 2009). Although such studies provide essential understanding about how wild populations have responded to changing environments, they are generally retrospective due to a temporal disconnect between the disturbance event and associated population decline (Ellis et al. 2012). What effective policy intervention requires are real-time measures of potential stressors with associated spatial methods to reliably understand where individuals within populations might be at most risk of declines.

Recently, measures of the physiological response of individual animals to habitat conditions and stressors are emerging as a viable approach for analyzing contemporary impacts of habitat quality and disturbance on the health and fitness of individual animals and population performance (Romero 2004; Ellis et al. 2012). Cortisol concentrations measured from saliva, blood, feces, and hair (von der Ohe & Servheen 2002; Palme et al. 2005; Sheriff et al. 2011) have been used to quantify long-term stress responses in animals such as the northern spotted owl (Wasser et al. 1997), squirrel gliders (Brearley et al. 2012), ungulates (Millspaugh et al. 2001; Ashley et al., 2011; Wasser et al. 2011), wolves (Creel et al. 2002), and grizzly bears (von der Ohe et al. 2004; Macbeth et al. 2010). Vertebrates respond to noxious external stimuli by activation of the hypothalamic-pituitary-adrenal axis with the resultant release of glucocorticoids, such as cortisol, into the blood circulation (Reeder & Kramer 2005), which allows the organism to respond to the stressor with the goal of maintaining or re-establishing homeostasis (McEwen & Wingfield 2003). However, persistent or repeated exposure to stressful stimuli, and resultant continued circulation of glucocorticoids, have been found to impair immune system performance, increase susceptibility to disease, and decrease growth and reproductive capacity in some species (Wingfield & Sapolsky 2003, Reeder & Kramer 2005; Ellis et al., 2012).

An emblematic species of western North America, the grizzly bear (*Ursus arctos*) has experienced substantial reduction in its historic range due to human settlement and development (Laliberte & Ripple 2004). Conservation of remaining localized populations is difficult due to conflicting public opinion and land-use (Kellert et al. 2002). The grizzly bears in Alberta, Canada, have recently been estimated to include fewer than 700 individuals (Alberta Sustainable Resource Development & Alberta Conservation Association 2010) , and as a result the provincial population was listed as *Threatened* in 2010 (Clark & Slocombe 2011). Grizzly bears in Alberta occupy a landscape heavily impacted by human activities and resource extraction. Industrial activities (e.g., forestry, oil and gas exploration, mining, and agriculture) and extensive road networks are prevalent throughout grizzly bear habitat within the province resulting in a highly fragmented multi-use landscape (Berland et al. 2008; Proctor et al. 2012). Although a number of parks and protected areas exist, many are subject to a wide variety of recreational pursuits and high human visitation rates. Anthropogenic land-use and open road access features represent primary causes of grizzly bear mortality, as bears have been found to select anthropogenic-disturbed habitats to exploit seasonal food availability, which has increased contact with humans (McLellan & Hovey 2001; Nielsen et al. 2004a; Berland et al. 2008). Further, patterns of land-use have resulted in genetically fragmented small sub-populations which might not be viable in the long-term (Proctor et al. 2005; Proctor et al. 2012). Less clear is how these activities, which vary spatially and in their character, affect real-time physiology of individuals.

Spatial patterns of anthropogenic land-use, forest conditions, and topography also influence the distribution of available resources (e.g., Nielsen et al. 2004b). Conceptually, habitat quality accounts for the range of conditions which have an impact on the health of an animal occupying the habitat (Morrison 2001). True to their description as opportunistic omnivores, the diet of grizzly bears in Alberta is generally low in protein consisting mostly of green vegetation, fruits, and insects (Nielsen et al. 2004b; Mowat & Heard 2006), although ungulate consumption varies seasonally (Munro et al. 2006). Accounting for spatial variability in environmental factors, such as crown closure, landcover, vegetation productivity, and elevation, which influence the availability of food resources and have an impact on the health of individuals, is an important consideration when assessing the relationship between landscape conditions and physiology (Hellgren et al. 1993; Kitaysky et al. 2007).

We know that human impacts to the landscape, including habitat loss and alteration (Alberta Sustainable Resource Development & Alberta Conservation Association 2010), contribute to grizzly bear mortality (McLellan et al. 1999; Benn & Herrero 2002; Nielsen et al. 2004c). Yet, little is understood regarding how human activities and habitat quality affect bears physiologically. Given small grizzly bear population sizes (Proctor et al. 2012), densities, and reproductive rates (Knight & Eberhardt 1985), research on the interaction between physiological status and landscape conditions is essential. Although physiological status can be represented by a wide range of metrics, we specifically focus on long-term stress in this study because of growing recognition that long-term stress is an important factor linking ecological change with impaired health and population performance in wildlife (Wikelski & Cooke 2006; Sheriff et al. 2010). Accordingly, our goal is to quantify spatial relationships between landscape conditions and the long-term stress response in grizzly bears by statistically integrating a spatially and temporally broad dataset of hair cortisol concentrations (HCC) with data representing environmental conditions. To meet this goal we address the following objectives:

1. Quantify impacts of habitat quality and anthropogenic landscape disturbance on observed spatial patterns of HCC in Alberta grizzly bears.

2. Develop a spatially explicit model to predict HCC across grizzly bear habitat based on current landscape conditions.

3. Interpret the spatial distribution of predicted HCC values using data describing the relative importance and security of grizzly bear habitat.

To address these objectives, novel spatial methods are required to integrate HCC data with spatially continuous data representing environmental conditions and to quantify observed relationships. Methods presented here, including marked point pattern analysis using kernel density estimation and non-parametric regression using random forests, provide an effective means for analyzing ecological data and are appropriate for future research on wildlife and HCC.

2.3 Study area

The study was carried out for five grizzly bear management units (BMUs) in Alberta, Canada (Figure 2.1). Representing an area of nearly 111,000 km^2, the Grande Cache, Yellowhead, Clearwater, Livingstone, and Castle BMUs are divided by major east-west transportation corridors. As such, the BMUs largely represent genetically isolated populations, although some inter-population movement does occur (Proctor et al. 2012). Due to the geographic extent of the study area, vegetation, topography, and local weather conditions are highly variable. Elevation ranges from 450 m to 3500 m and increases from east to west. In the western mountainous region, habitat types include alpine and sub-alpine ecosystems comprised of fir (*Abies* spp.), pine (*Pinus* spp.), and spruce (*Picea* spp.), and wet-meadow complexes (Ecological Stratification Working Group 1995; Stenhouse et al. 2005). To the east, lower elevation foothills comprised of mixed-wood forests of pine, aspen and poplar (*Populus* spp.), spruce, and balsam fir (*Abies balsamea*) represent a transitional zone between the Rocky Mountains and the prairies (Ecological Stratification Working Group, 1995). Mean temperatures range from 12°C in the summer to -7.5°C in the winter, and mean annual precipitation is 450-800 mm. Major grizzly bear foods found in the region include herbaceous plant growth such as *Hedysarum* spp, *Shepherdia canadensis*, *Arctostaphylos uva-ursi*, *Equisetum* spp, *Taraxacum officinale*, and *Trifolium* spp, insects, and ungulates (Nielsen et al. 2004b; Nielsen et al. 2010).

Resource extraction activities within the BMUs also vary spatially. They include forestry, oil and gas exploration, mining, and agriculture. To service resource extraction activities, an extensive network of roads exists which has provided access to grizzly bear habitat resulting in increased human-bear conflict and mortality (Benn & Herrero 2002; Nielsen et al. 2004c; Graham et al. 2010). These roads and areas are also widely used for recreation, including hunting, fishing, hiking, and trail-riding with all-terrain vehicles and snowmobiles. A network of parks and protected areas, including Jasper, Banff, and Waterton National Parks, as well as a number of provincial parks and wilderness reserves, which generally exclude resource extraction activities, are also found throughout the BMUs.

2.4 Materials and Methods

2.4.1 Ethics statement

Grizzly bear hair collection was undertaken as part of an initiative to conduct a population inventory program for this species. The population inventory work was carried out at the request of the Government of Alberta (Environment and Sustainable Resource Development) by the Foothills Research Institute's Grizzly Bear Program (FRIGBP) and followed the techniques described by Woods et al. (1999) and Proctor et al. (2004). This inventory program was approved by the Alberta Department of Sustainable Resource Development animal care committee, and by Parks Canada when sampling occurred in their jurisdiction, in each year of data collection. Annual research permits and animal care approvals were obtained from both provincial and federal agencies responsible for permits and licensing of these activities.

2.4.2 Hair cortisol concentrations

Cortisol concentrations (picograms per milligram of hair - pg/mg) were measured from grizzly bear hair samples obtained annually from 2004 to 2008. Hair is a stable medium that can be collected non-invasively from free-ranging animals (Macbeth et al. 2010). It can be transported and stored with relative ease (e.g., paper envelope at room temperature) and substances incorporated into growing hair, including cortisol, can remain detectable for years to centuries (Webb et al. 2010). These attributes make the hair cortisol concentration particularly effective for quantifying long-term stress in far-ranging species such as grizzly bears (Macbeth et al. 2010; Meyer & Novak 2012). Samples were collected using non-invasive barbwire hair snags randomly placed within 7 km x 7 km grid cells and repositioned at 14 day intervals throughout known grizzly bear habitat in each BMU during the spring and early summer (Boulanger et al. 2005). Grizzly bears are not provincially endangered and were not considered a threatened species during the time when this sampling occurred. All samples were collected on provincial and federal lands under the authority of the Government of Alberta (Environment and Sustainable Resource Development and Alberta Parks) and the Government of Canada (Parks Canada). Because cortisol accumulates in hair for the duration of its growth, the HCC values used in this analysis represent a stress signal from the period of hair growth during the year preceding hair sample collection (see Macbeth et al. (2010) for details regarding procedures to extract cortisol concentrations from grizzly bear hair). In total, 304 HCC values (*n* = 168 females, *n* = 136 males) from genetically distinct individual grizzly bears were obtained from the five BMUs. HCC point data values ranged from the lowest level of detection at 0.16 pg/mg in both males and females to a high of 14.94 pg/mg in males and 23.66 pg/mg in females. However, the HCC data included a number of outliers as the interquartile range extended from only 0.34 pg/mg to 1.36 pg/mg for males and 0.49 pg/mg to 1.74 pg/mg for females.

2.4.3 Habitat quality

We represented grizzly bear habitat for the study period by integrating a variety of spatial data (Table 2.1). Percent crown closure and percent conifer were modelled and scaled from 0 % to 100 % through classification of Landsat Thematic Mapper (TM) 5 and Landsat 7 Enhanced Thematic Mapper Plus (ETM+) imagery informed by topographic derivatives from a digital elevation model (DEM) (McDermid 2005a). Land cover was classified into eight classes: upland trees, wetland trees, upland herbs, wetland herbs, shrubs, water, barren land, and snow/ice, using Landsat TM 5 and ETM+ 7 imagery, and topographic derivatives (Franklin et al. 2002; McDermid et al. 2005b). We assessed terrain conditions using a DEM detailing elevation for the study area obtained from the Government of Canada spatial data portal Geobase and resampled to 1 km grid cells. A terrain ruggedness index, providing a measure of terrain complexity and variability (Wilson & Gallant 2000), and a compound topographic index, which represents potential soil moisture based on slope, catchment area, and upstream water sources (Gessler et al. 1995), were derived from the DEM.

We used indices from the Dynamic Habitat Index (DHI) (Berry et al. 2007; Coops et al. 2008), which has been linked to observed spatial patterns of avian species (Coops et al. 2009), biodiversity gradients (Andrew et al. 2012), and home range size of carnivores (Nilsen et al. 2005), to characterize vegetation productivity in the study area. The DHI indices are calculated from remotely sensed imagery and summarize annual trends in monthly images of the fraction of photosynthetically active radiation (fPAR). In this study, fPAR is derived from Advanced Very High Resolution Radiometer (AVHRR) reflectance values with a spatial resolution of 1 km from 2003 to 2007 (Coops et al. 2008; Fontana et al. 2012). The DHI is comprised of three indices representing vegetation productivity: cumulative greenness, variation in greenness, and minimum cover (Duro et al. 2007; Coops et al. 2008). Cumulative greenness, which represents total vegetation productivity, is estimated annually by summing monthly fPAR observations. Variation in greenness, representative of seasonal changes in productivity, and consequently the availability of food resources, is calculated using the coefficient of variation in values over a year. Highly seasonal landscapes, such as alpine environments, where greenness values vary substantially due to snowpack, receive higher values than regions which are productive year round, such as evergreen forests (Coops et al. 2008). The minimum cover is an estimate of the lowest level of vegetative productivity available year round and may influence the persistent usage of habitat by herbivorous species. As production of leafy biomass and fruits consumed by grizzly bears is seasonally dependent (Hamer & Herrero 1987; Munro et al. 2006), regions with high seasonality and cumulative greenness, as well as high minimum cover, are likely representative of high quality grizzly bear habitat.

We characterized the incidence of habitat usage by grizzly bears throughout the study area using resource selection functions (RSFs) where the probability of habitat usage is ranked from 0 (low) to 10 (high) (Nielsen et al. 2002; Nielsen et al. 2009). An RSF models the probability of use of a resource, relative to its availability, based on occurrence patterns of an animal on the landscape (Manly et al. 2002). The RSFs developed for this study area are based on a third order selection (Johnson 1980), and as such the modelled probability of habitat usage by grizzly bears is representative of selection at the patch level (see Nielsen et al. (2002) for RSF model details and accuracy). Separate RSF models were developed for male and female bears in three seasons, hypophagia (1 May to 15 June), early hyperphagia (16 June to 31 July), and late hyperphagia (1 August to 15 October), as well as the maximum observed RSF value for all three seasons.

2.4.4 Anthropogenic influence

Anthropogenic features we considered for the study periodSpa included roads, railways, oil and gas well-sites, cut-lines, power-lines, pipelines, and forest harvest blocks (Table 2.1). Anthropogenic data were provided by Alberta Sustainable Resource Development and are mapped and updated by the FRIGBP based on appearance of disturbance features in Landsat imagery. We represented roads, railways, and oil and gas well-sites using an exponential distance decay function, e^{-ad} where d is the distance in metres to feature and a was fixed at 0.002 (Nielsen et al. 2009). The distance decay surfaces decrease linearly from a value of 1 at the location of the anthropogenic feature to a value of 0 at a distance of approximately 2000 m. We represented secondary anthropogenic linear features, such as cut-lines, power-lines, and pipelines, as a cumulative linear density per 1 km^2 grid cell (km/km^2).

We divided forest harvest blocks into two classes (≤ 15years old; > 15 years old) to account for regeneration and resultant differences in grizzly bear food availability present within the harvested areas (Nielsen et al. 2004b; Stewart et al. 2012). We assessed the influence of forest harvest blocks by calculating the proportion area cut in 1 km^2 grid cells. Resultant grid cells ranged from a value of 1 representing an area which has been completely harvested, to 0 representing no harvesting had occurred in the area. Finally, we modelled the influence of the parks and protected areas in the region, which represent a noted contrast in terms of land-use compared to the surrounding landscape, based on proportion parks and protected area within a 10 km radius from 1 km^2 grid cells. Values ranged from 1 for cells completely within parks and protected areas to 0 when no parks and protected areas were in the immediate vicinity.

2.4.5 Conservation areas and habitat security

Core and secondary grizzly bear conservation areas, based on observed patterns of grizzly bear occurrence, resource availability, and road density, have been mapped within the five BMUs (Nielsen et al. 2009). Core conservation areas, which are meant to act as a population source, are defined as regions with high quality habitat (using RSF scores as surrogates) and road densities below 0.6 km/km^2. Secondary conservation areas also contain high quality habitat, however road densities are higher at 1.2 km/km^2 which increases the risk of mortality and decreases the population source capacity of the area. Within these regions, habitat states have been assessed by characterizing the landscape based on habitat quality and mortality risk (Nielsen et al. 2006). In this analysis we incorporate three defined habitat states in 1 km^2 grid cells: secure habitat (low mortality risk), sink habitat (high mortality risk), and non-critical habitat. Combined with the present network of parks and protected areas, the core and secondary conservation units as well as the observed habitat states were used to help interpret geographic relationships in the modelled distribution of HCC values within the five BMUs.

2.4.6 Kernel density estimation of hair cortisol concentration

To integrate the HCC point data with spatially continuous habitat and anthropogenic variables, we converted HCC data from points to a continuous raster using kernel density estimation. Kernel density estimation of a marked point pattern was defined by

$$g(u) = \frac{\sum_i k\left(e(u) - x_i\right) v_i}{\sum_i k\left(e(u) - x_i\right)}$$

, where k is a Gaussian kernel, the HCC point data values are given by $v_1, ..., v_n$ at locations $x_1, ..., x_n$, u are the smoothed HCC values, and $e(u)$ is an edge correction factor based on the reciprocal of the kernel mass

$$\frac{1}{e(u)} = \int_W k(v - u)\, dv$$

inside the observation window or spatial extent W (Nadaraya 1964; Diggle 1985). The spatial extent was defined separately for males and females in each BMU as the minimum convex polygon (MCP) of HCC sample locations (Worton 1987). Kernel values were stored in a 1 km cell matching the spatial resolution of landscape variables. A 9 km kernel bandwidth was defined; 9 km corresponds to the average daily area used by an adult female grizzly bear (Nielsen et al. 2002) and was supported by least-squares cross-validation, which identifies the bandwidth that minimizes the summed squared error between observed values and smoothed values.

We assessed the influence of individual HCC points on the stability of the smoothed male and female surfaces by generating 99 leave-one-out bootstrap HCC kernel density surfaces for validation (Bowman & Azzalini 1997). We quantified uncertainty in the HCC surfaces for each BMU by determining the proportion of pixels which fell within a 95% confidence interval ($p < 0.01$) of similar observed values in the bootstrap surfaces (Nelson et al. 2006). We compared the distribution and central tendency of the values in the smoothed HCC surfaces to the original HCC values using Kolmogorov-Smirnov and Mann-Whitney U tests.

2.4.7 Random forest models

We used random forests to quantify the influence of habitat and anthropogenic variables on the spatial distribution of male and female grizzly bear HCC values. A non-parametric recursive regression method, random forests combine multiple regression trees built using bootstrap samples of data (Breiman 2001). Each individual regression tree is grown to its maximum size using random subsets of predictor variables (Cutler et al. 2007). Trees are combined by averaging and estimation of response values is performed using the withheld out-of-bag observations (Prasad et al. 2006; Cutler et al. 2007). The model variance explained is assessed based on the accuracy of the prediction of out-of-bag data. Random forests have been found to be ideally suited to ecological data as they do not require linear relationships, effectively model variable interactions, can handle missing data and correlated variables, are more stable than traditional regression trees to minor changes in input data, and have high predictive power (Breiman 2001; Prasad et al. 2006; Cutler et al. 2007). Variable importance in random forest models is characterized using two complementary output metrics. The first is a normalized comparison of the mean square error of model predictions with predictions generated using randomly permuted predictor values from the out-of-bag data (Cutler et al. 2007). Essentially, this compares the model predictions to predictions from randomly generated variable values. The second is the averaged total decrease in node impurity attributed to splitting on each variable measured using the residual sum of squares, and provides an indication of node prediction accuracy attributed to each variable.

We ran random forest models for both male and female grizzly bears using a random subset of 50% of the available data. The remaining 50% of the data were withheld for model validation. Each model included 1000 trees in order to allow stabilization of out-of-bag error and 18 variables were randomly selected for consideration at each split. Due to varying landscape conditions and anthropogenic influence inside and outside of parks and protected areas, we produced secondary random forest models with an in-parks and protected areas/outside-parks and protected areas distinction in order to explore potentially differing variable importance.

We used validated random forest models to predict male and female HCC values in 1 km^2 grid cells for the area of the five BMUs outside the confines of the MCP's used in the development of the KDE surfaces. We explored relationships between the 10 most influential variables and the predicted HCC values by summarizing the mean predictor values which corresponded with the lower (0.16 – 0.45 pg/mg: low HCC response), inner (0.46 – 1.62 pg/mg: moderate HCC response), and upper (> 1.62 pg/mg: high HCC response) quantiles of the original HCC data. These same HCC value breaks were used to summarize the percentage of pixels within the area of each BMU which could be classified as a high, moderate, or low HCC.

To aid interpretation of predicted HCC values, we assessed the associations between HCC values and parks and protected areas, core conservation areas, and secondary conservation areas based on the frequency distribution of male and female HCC values occurring within each of these management units. We also assessed relationships between the predicted male and female HCC values and classified secure, sink, and non-critical habitat types using frequency distributions based on 1 km^2 pixel associations.

2.5 Results

2.5.1 Validation of HCC kernel density layers

Comparison of input HCC values and generated KDE HCC surfaces indicated that the KDE represented the range and spatial distribution of HCC values. Greater than 80% of pixels in the HCC KDE surfaces for all five BMUs fell within the 95% confidence interval ($p < 0.01$) when compared to values in the 99 leave-one-out bootstrap surfaces. Kolmogorov-Smirnov and Mann-Whitney U tests showed the attributes of HCC KDE surfaces were not significantly different than measured HCC values in each of the BMUs (Table 2.2).

2.5.2 Male HCC models

Using random forest metrics, habitat quality and anthropogenic influence variables considered explained 74.28% of the variance in the male HCC data (MSE = 0.17). Validation of the male model using the withheld data returned an R^2 of 0.71. Proportion parks and protected areas was the most influential variable in the male model (Figure 2.2A). Habitat quality variables with the greatest influence included the three topographic metrics (elevation, terrain ruggedness index, and compound topographic index), the DHI metrics (cumulative greenness, variation in greenness, and minimum cover), as well as canopy cover and the late hyperphagia RSF. Influential anthropogenic variables included distance decay to roads, and to a lesser extent distance decay to railways and the density of secondary linear features (Figure 2.2A). Mean variable values associated with low, moderate, and high predicted HCC values revealed generalized trends in the relationships between variables and HCC values. Examining the 10 most influential variables, high predicted HCC values (>1.62 pg/mg) in males were generally associated with lower proportion protected area, elevation, terrain ruggedness, and DHI coefficient of variation, as well as high distance decay to roads, DHI minimum cover and cumulative greenness, compound topographic index, crown closure, and late hyperphagia RSF (Table 2.3).

Evaluation of the influence of differing landscape conditions inside and outside parks and protected areas on the modelled HCC response altered the importance of predictor variables. The male grizzly bear outside-parks and protected areas model explained 55.34% of the variance in the HCC data (MSE = 014; R^2 = 0.72). Excluding the influence of parks and protected areas increased the importance of density of secondary linear features and proportion of forest harvest blocks greater than 15 years old (Figure 2.2B). The male in-parks and protected areas model explained 74.96% of the variance (MSE = 0.07, R^2 = 0.84), similar to the total model. While the influence of variables related to habitat quality, such as elevation, terrain ruggedness, crown closure, and DHI metrics, was similar to the total model, the importance of distance decay to roads increased substantially for males when the spatial extent of the model was restricted to parks and protected areas (Figure 2.2C).

HCC values predicted using the total male random forest model showed the geographic pattern of long-term stress in males was generally low in national parks, in the west of the study area, and increased in non-protected and low elevation regions to the east and south (Figure 2.3A). The highest HCC values for males were restricted to zones in and around smaller protected areas, while low and moderate HCC values were more frequent and continuously distributed on the landscape (Table 2.4). Frequency distributions of predicted HCC values associated with parks and protected areas, core conservation areas, and secondary conservation areas revealed similar trends. Low male HCC values had more frequent spatial associations with parks and protected areas (Figure 2.4A). Regions designated as core conservation areas had a higher frequency of moderate male HCC values, while secondary conservation areas were associated with moderate to high male HCC values (Figure 2.4A). In terms of secure, sink, and non-critical habitat designations, moderate to high male values were more frequently associated with non-critical and sink habitats (Figure 2.4B).

2.5.3 Female HCC models

Total female random forest models explained 68.46% (MSE = 0.21; R^2 = 0.70) of the variance in female HCC values. Variable importance was similar to the total male model, as proportion parks and protected areas was again the most influential variable (Figure 2.2D). Important habitat variables in the total female model included the three topographic metrics, the three DHI metrics, crown closure, the hypophagia RSF, and percent conifer. Important anthropogenic variables included distance decay to roads and railways, as well as the proportion of forest harvest blocks less than 15 years old. Generalized trends in the relationships between the mean values of the 10 most influential variables associated with low, moderate, and high predicted female HCC values opposed those in the male model. High predicted female HCC values (> 1.62 pg/mg) were associated with high proportion parks and protected areas, elevation, terrain ruggedness, DHI variation in greenness and minimum cover, and hypophagia RSF values (Table 2.3). High female HCC values were also associated with low values of distance decay to roads, DHI cumulative greenness, proportion of forest harvest blocks less than 15 years old, and crown closure.

The female outside-parks and protected areas model had a higher variance explained (67.61%; MSE = 0.20; R^2 = 0.71), compared to the female inside-parks and protected areas model (58.15%; MSE = 0.15; R^2 = 0.58). The change in variable importance was more pronounced in the female outside-parks and protected areas model, compared to the similar male model, as the influence of proportion of forest harvest blocks less than 15 years old, distance decay to railways, and distance decay to oil and gas well-sites all increased (Figure 2.2E). However, unlike the male inside-parks and protected areas model, restricting the female model to landscape conditions within parks and protected areas decreased the influence of all anthropogenic variables while increasing the influence of the DHI and topographic metrics (Figure 2.2F).

Geographic patterns in the predicted long-term stress response of female grizzly bears contrasted predicted male HCC patterns. Predicted female HCC values were generally low in the eastern portions of the study area where anthropogenic disturbance is concentrated and increased substantially in the foothills and high elevation parks and protected areas in the west (Figure 2.3B). As a result, low female HCC values were more frequently associated with secondary conservation areas and sink habitats (Figure 2.4C; Figure 2.4D). High, moderate, and low predicted female HCC values were more evenly distributed on the landscape, and high female values had a far greater geographic representation compared to similar male HCC values (Table 2.4). Similar to males, the Livingstone BMU had the greatest percent area with high female HCC values, while the Grande Cache BMU had the greatest concentration of low male and female HCC values (Table 2.4).

2.6 Discussion

Grizzly bears in Alberta, Canada face a myriad of challenges as a result of increasing anthropogenic pressure and habitat fragmentation throughout their current range. While knowledge regarding causes of mortality, habitat usage, and spatial patterns of habitat fragmentation and loss is considerable, less is known regarding the physiological response of grizzly bears to observed landscape conditions (Macbeth et al. 2010). Considering the potentially detrimental impacts of long-term stress on immune system performance, reproductive capacity, and growth (Reeder & Kramer 2005), combined with low reproductive rates and population densities observed in grizzly bears (Knight & Eberhardt 1985; Proctor et al. 2012), the results of our study provide timely information regarding impacts of current landscape conditions on the physiological status of grizzly bears in the province.

Through the integration of HCC point data with continuous landscape variables using spatial methods, we have shown that despite the absence of gender based differences in the range of input HCC values, the physiological stress response in regards to landscape conditions amongst male and female grizzly bears is dissimilar and is manifest in geographically distinct patterns. Generally, we found higher elevation protected areas and foothills with rugged terrain, which exhibit high seasonality, moderate total productivity, and low minimum cover, as well as minimal anthropogenic influence, were associated with moderate to high female HCC values. Essentially, an elevated female stress response was linked to areas previously modelled as relatively high quality habitat, with minimal anthropogenic disturbance and low mortality risk compared to surrounding areas. In marked contrast, low to moderate female stress shows a geographic relationship with regions that have a higher concentration of anthropogenic disturbance such as roads and forest harvest blocks.

The observed spatial association between low to moderate female stress and anthropogenic disturbance poses a potentially potent conservation concern to grizzly bear populations. The absence of high stress levels likely means females will continue to show extensive use of dangerous landscapes, thereby jeopardizing the reproductive demographic of the population. Female grizzly bears have been found to select anthropogenic-disturbed habitats, both inside and outside of parks and protected areas, due to increased availability of herbaceous foods (Benn & Herrero 2002; Nielsen et al. 2004a; Munro et al. 2006; Roever et al. 2008; Graham et al. 2010; Stewart et al. 2013). As fire suppression outside of parks and protected areas is extensive throughout the study area, anthropogenic disturbance features provide breaks in continuous forest promoting growth of essential grizzly bear foods along forest edges (Nielsen et al. 2004b; Stewart et al. 2013). However, caloric and physiological gains associated with selecting anthropogenic-disturbed habitats may be offset by an elevated risk of mortality associated with these habitats (Nielsen et al. 2008). Association of low female HCC values and such high-risk (e.g., high chance of mortality) high-reward (e.g., food availability) habitat suggests both a willingness to risk human contact in order to maximize food intake as well as a degree of habituation to such contact (Elfström et al. 2012).

Within major protected areas in the west of the study area, anthropogenic disturbance is largely restricted to roads, railways, trails, and town infrastructure in comparison to the industry focused landscape surrounding them. Natural disturbances, such as wildfires and avalanches, feature more prominently on the landscape and create forest canopy openings conducive to the growth of herbaceous grizzly bear foods also present in alpine areas (Hamer & Herrero 1987; Hamer 1996; Pengelly & Hamer 2006). Our results indicate that while landscape conditions in the regions parks and protected areas appear to benefit male grizzly bears, as shown by the low modelled stress levels, the same conditions resulted in high stress levels in females.

We suggest that sexual segregation amongst male and female grizzly bears may partly explain the opposing stress levels found in parks and protected areas. Females with cubs in other study areas, including Sweden and Alaska, generally avoid areas occupied by males in order to reduce the risk of infanticide (Libal et al. 2011; Elfström et al. 2012; Steyaert et al. 2013). In order to avoid males, females have been found to make greater use of sub-optimal habitats and areas in close proximity to humans (Rode et al. 2006; Elfström et al. 2012; Steyaert et al. 2013). While it was not possible to specifically consider females with cubs in our analysis, female offspring tend to occupy home-ranges that take in part of, or are in close proximity, to the home-range of their mother (Blanchard & Knight 1991; Proctor et al. 2004; Støen et al. 2005; Dahle et al. 2006), and as such habitat selection patterns for female adults may reflect natal selection patterns learned from their mothers (Nielsen et al. 2013). Consequently, as adults females may still occupy a landscape distinct from males in the region. Male HCC values in parks and protected areas were generally low, and associated with moderate to high elevation seasonal habitats, which have minimal canopy cover and are far from roads (moderate HCC values were associated with regions closer to roads in parks). Male grizzly bears in the region have been found to make greater use of naturally occurring edge habitats caused by disturbance (Stewart et al. 2013), and a willingness to occupy high quality habitat in parks and protected areas adjacent to roads and trails with good cover (Gibeau et al. 2002). If males are in fact dominating, or excluding female usage of, quality habitat in parks and protected areas resulting in sexual segregation of habitat usage, and give the paucity of high quality grizzly bear habitat in these geographically restricted areas (Gibeau et al. 2001), the resulting disparity in resources available to each gender could help explain observed geographic differences in the stress response. In contrast, outside of parks and protected areas where resources available to grizzly bears are in higher abundance as a result of the greater frequency and distribution of disturbance features, sexual segregation of high quality habitat is unlikely to be as prevalent. This may in fact be reflected in the similar low to moderate stress response seen in both genders outside of parks and protected areas.

We have shown that the geographic dissimilarity in the physiological stress response of grizzly bears appears to be both context-dependent (Brearley et al. 2012), and similar to northern spotted owls (Wasser et al. 1997), gender-specific. Similar to black bears (Hellgren et al. 1993), and grizzly bears in other regions (von der Ohe et al. 2004), the availability of, and ability to procure, resources appears to impact spatial patterns of the modelled stress response in Alberta grizzly bears. Our results also reflect findings in species such as squirrel gliders (Brearley et al. 2012), ungulates (Millspaugh et al. 2001; Wasser et al. 2011), and wolves (Creel et al. 2002), where the measured stress response varies according to the density, distribution, and perhaps most importantly, the nature of anthropogenic disturbance and activities throughout their habitat. However, our findings extend the benefits of understanding the relationship between landscape conditions and stress to include a spatial component useful for real-time policy intervention.

Numerous studies examining spatial distributions and causes of grizzly bear mortality have suggested restricting human access in recently disturbed areas by closing roads will decrease the incidence of mortality (McLellan et al. 1999; Nielsen et al. 2004c; Berland et al. 2008; Nielsen et al. 2008; Stewart et al. 2012). We suggest that closing roads and restricting human access, while increasing the distribution of early seral stage forest habitats, would not only reduce mortality rates, it would also afford female grizzly bears the opportunity to occupy a low-stress landscape with environmental conditions conducive to maximizing body condition. Securing high-risk, low-stress multi-use habitats may also benefit population dynamics by increasing female reproductive rates and carrying capacity. It should be noted that reducing human access would also benefit male grizzly bears, as the male stress response in regions with high levels of anthropogenic disturbance and activity was generally low to moderate. As males tend to make less use of anthropogenic-disturbed habitats with high rates of human activity (Graham et al. 2010; Stewart et al. 2013), reducing human access may allow males to increase their usage of resources in these regions while incurring less risk. Similarly, increasing the frequency and distribution of disturbance features resulting in a greater abundance of edge habitats and young forests in parks and protected areas, while restricting human access to these areas, would increase the amount of habitat available to grizzly bears.

2.7 Conclusions

Managing for the physiological well-being of wild animals requires an understanding of how behaviour and landscape conditions impact animal health. Using emerging non-invasive metrics of long-term stress in animals, such as cortisol concentration in hair, it is now possible to expand conservation efforts beyond simply managing for known causes of mortality which impact population dynamics. Current extensions of our research include modelling the impacts of individual behaviour and the effects of interaction on stress, predicting changes in long-term stress based on future disturbance patterns and climate change, and exploring spatial relationships between stress and body condition. Our methods may also be applicable in spatial analyses of point sampled stress metrics taken from other far ranging wild animals (e.g., polar bears (Bechshøft et al. 2011)). Finally, while models presented here are specific to the grizzly bear population of Alberta, many populations in western North America occupy landscapes with similar environmental stressors. Consequently our findings may offer an indication of similar interactions in other regions. Future species conservation efforts should therefore attempt to better understand gender and spatial based differences in the physiological response of grizzly bears to landscape conditions.

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Table 2.1 Habitat quality and anthropogenic disturbance variables used to predict HCC response in grizzly bears.

Abbreviation	Variable	Range
Habitat quality		
cc	Percent crown closure (%)	0 – 100
pctcon	Percent conifer (%)	0 – 100
lcover	Landcover (categorical)	1 – 8
dhi_cum	Dynamic Habitat Index – cumulative greenness (unitless)	0.33 – 18.50
dhi_cv	Dynamic Habitat Index – coefficient of variation (unitless)	0.19 – 1.35
dhi_min	Dynamic Habitat Index – minimum cover (unitless)	0 – 0.40
rsf_s1	Resource Selection Function – hypophagia (categorical)	0 – 10
rsf_s2	Resource Selection Function – early hyperphagia (categorical)	0 – 10
rsf_s3	Resource Selection Function – late hyperphagia (categorical)	0 – 10
rsf_max	Resource Selection Function – maximum value (categorical)	0 – 10
elev	Elevation (m)	450 – 3500
tri	Terrain ruggedness index (unitless)	0 – 189.33
cti	Compound topographic index (unitless)	3.86 – 18.03
Anthropogenic disturbance		
rd_dd	Roads – distance decay (unitless)	0 – 1
rail_dd	Railways – distance decay (unitless)	0 – 1
wl_dd	Oil and gas well-sites – distance decay (unitless)	0 – 1
ln_den	Secondary linear features – density (km/km^2)	0 – 7.28
cblk_l	Forest harvest blocks – ≤ than 15 years old (% cut/km^2)	0 – 100
cblk_g	Forest harvest blocks – > than 15 years old (% cut/km^2)	0 – 100
pa	Proportion parks and protected area (unitless)	0 – 1

Table 2.2 HCC kernel density estimation validation results by bear management unit (BMU)

BMU	Proportion data within 95% CI ($p < 0.01$)	Kolmogorov-Smirnov	Mann-Whitney U
Castle	0.89	$p = 0.07$	$p = 0.09$
Livingstone	0.86	$p = 0.12$	$p = 0.17$
Clearwater	0.88	$p = 0.09$	$p = 0.08$
Yellowhead	0.88	$p = 0.16$	$p = 0.14$
Grande Cache	0.87	$p = 0.21$	$p = 0.27$

Table 2.3 Mean values of the 10 most influential variables in the total random forest models associated with lower, mid, and upper quantiles of the predicted HCC response in male and female grizzly bears.

Variable	**HCC range (pg/mg)**		
	0.16 - 0.45	0.46 - 1.62	> 1.62
Males			
pa	0.85	0.13	0.17
elev	2164.92	1277.83	1690.15
rd_dd	0.01	0.56	0.36
tri	33.87	10.67	21.32
dhi_cv	0.71	0.43	0.41
dhi_min	0.04	0.11	0.14
dhi_cum	6.02	11.11	10.13
cti	6.62	14.12	10.80
cc	17.22	43.66	48.76
rsf_s3	3	4	6
Females			
pa	0.01	0.12	0.68
elev	940.91	1427.64	1980.69
rd_dd	0.69	0.55	0.12
tri	3.88	12.15	29.49
dhi_cv	0.43	0.53	0.65
dhi_min	0.11	0.11	0.06
dhi_cum	11.47	8.42	6.54
cblk_l	0.03	0.02	0.01
cc	47.10	39.54	30.76
rsf_s1	2	5	6

Table 2.4 Percent area of the bear management units (BMU) and study area classified as low, moderate, and high HCC based on the geographic distribution of predicted male and female HCC values.

BMU	**Low HCC (0.16 – 0.45 pg/mg)**		**Moderate HCC (0.46 – 1.62 pg/mg)**		**High HCC (> 1.62 pg/mg)**	
	Male (%)	Female (%)	Male (%)	Female (%)	Male (%)	Female (%)
Castle	2.93	6.83	95.67	58.90	0.73	33.58
Clearwater	22.17	10.22	75.92	49.34	1.76	40.61
Grande Cache	13.04	51.86	83.47	26.96	0.91	18.60
Livingstone	11.54	0.54	78.53	42.61	8.37	55.29
Yellowhead	13.04	34.37	74.60	27.95	1.30	34.77
Total study area	16.11	33.89	79.90	33.53	1.88	30.47

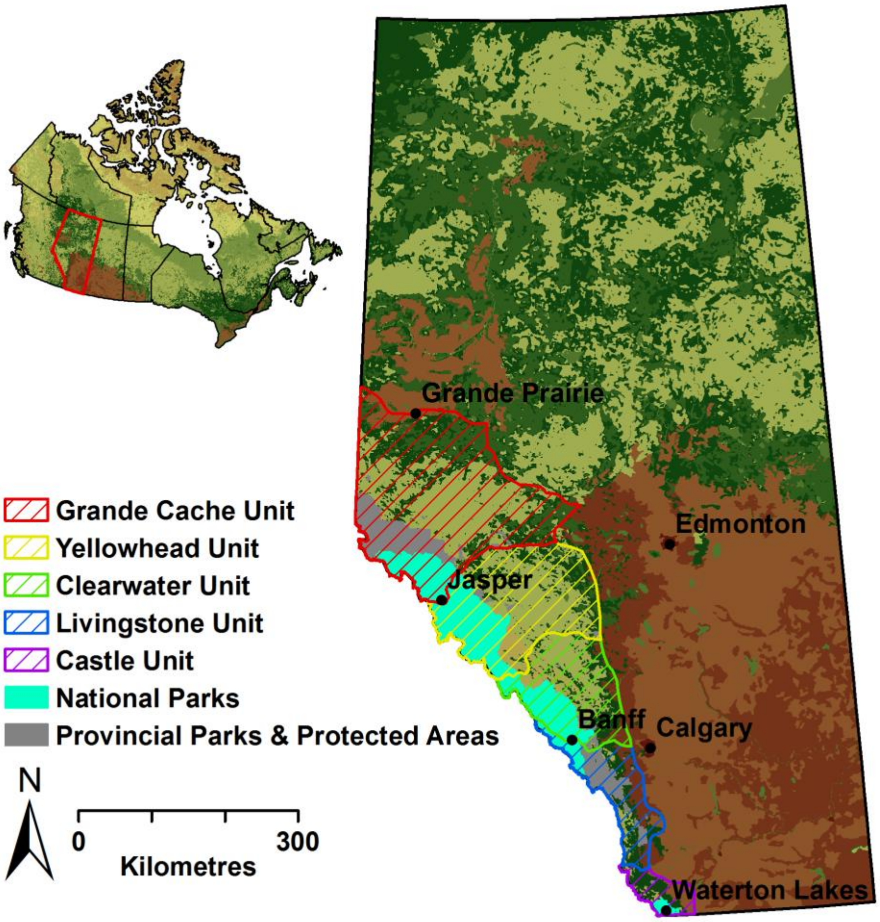

Figure 2.1 Study area location in Alberta, Canada.

Grizzly bear hair samples were collected in each bear management unit during a single summer (Yellowhead – 2004; Clearwater – 2005; Livingstone – 2006; Castle – 2007; Grande Cache – 2008).

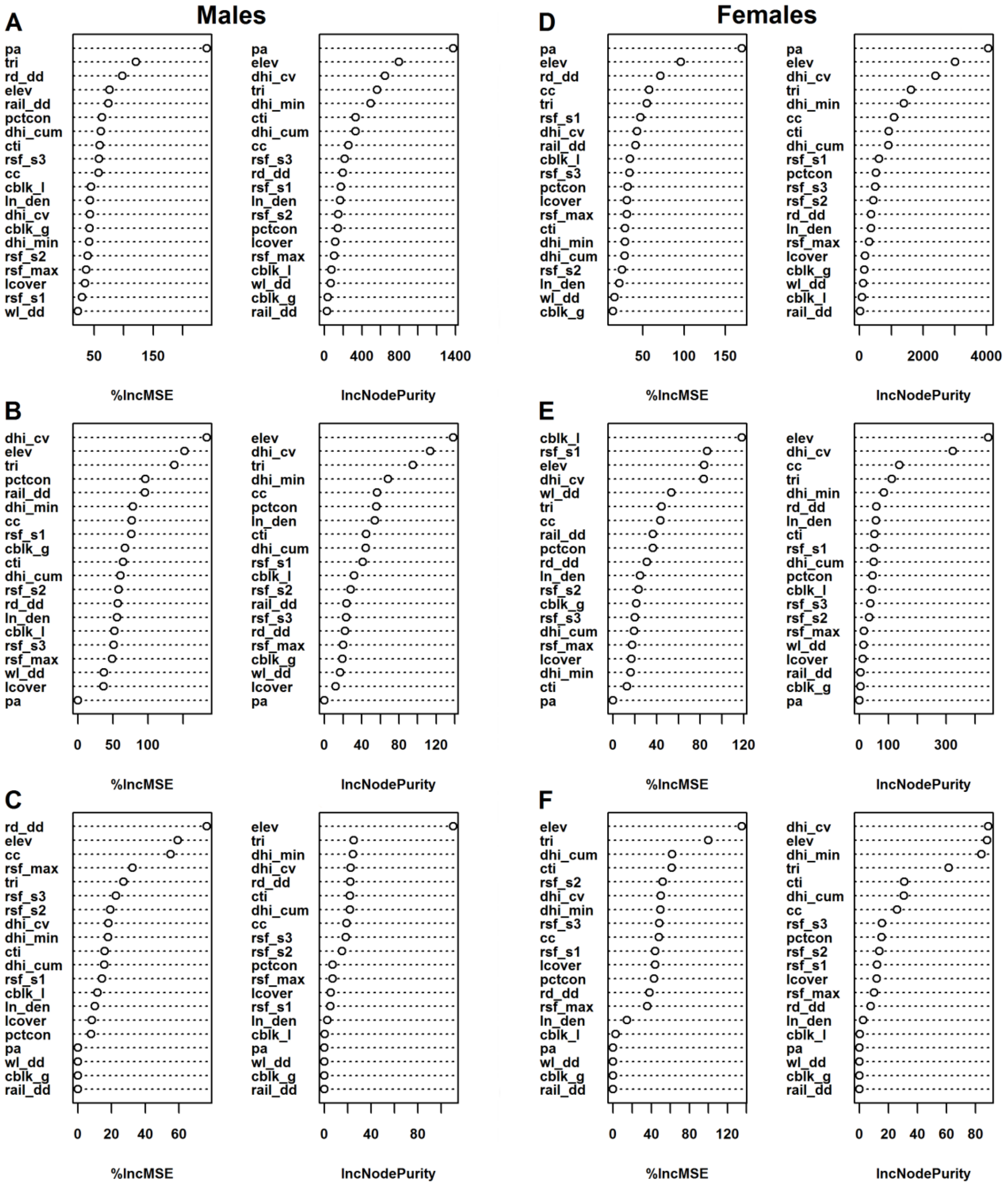

Figure 2.2 Variable importance metrics from male and female HCC random forest models.

Variable importance for the male (A) total model, (B) outside-parks and protected areas model, and (C) inside-parks and protected areas model, as well as the female (D) total model, (E) outside-parks and protected areas model, and (F) inside-parks and protected areas model. Variable importance plots on the left of each panel (%IncMSE) represent the normalized comparison of the mean square error of model predictions and predictions generated using random permutations of the out-of-bag data. Variable importance plots on the right of each panel (IncNodePurity) represent the averaged total decrease in node impurity, measured using the residual sum of squares, attributed to splitting on each variable.

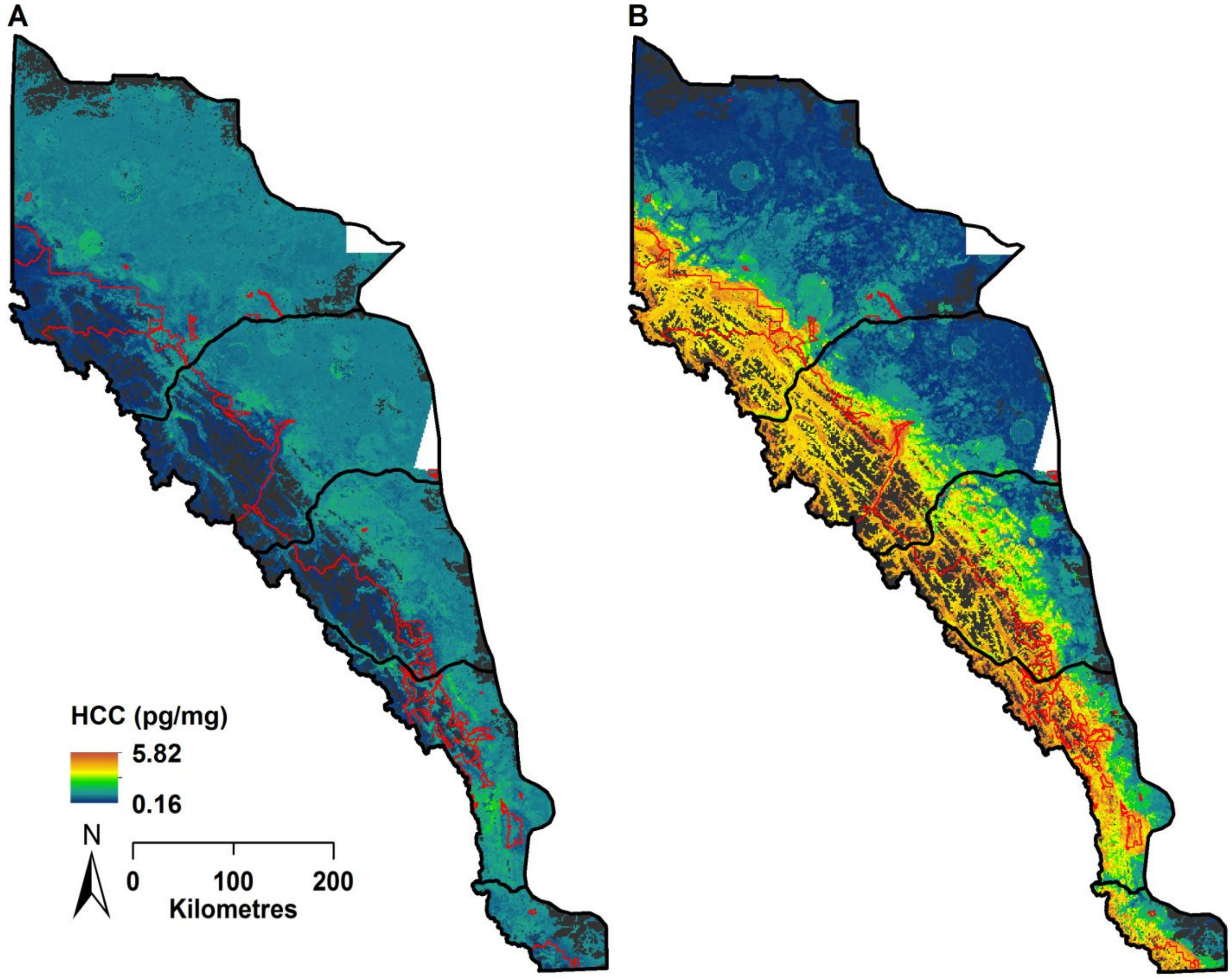

Figure 2.3 Geographic distribution of the predicted HCC response from gender-specific total random forest models.

Predicted HCC values for (A) male and (B) female grizzly bears. Parks and protected areas are shown in red. Regions of non-habitat (e.g., rock and ice) are shown in grey.

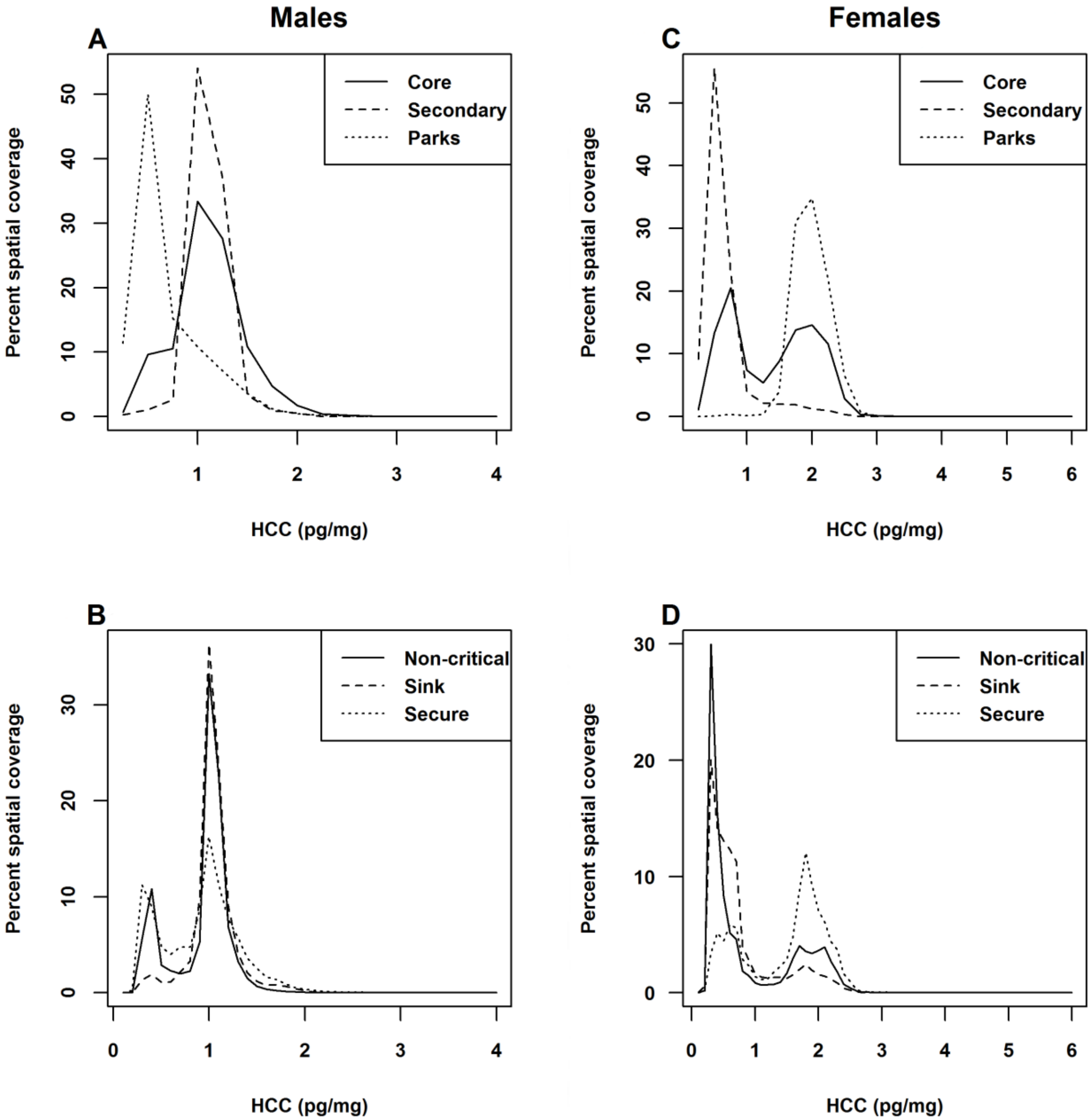

Figure 2.4 Frequency distributions of predicted HCC values associated with conservation management units and habitat states.

Percent spatial coverage of predicted HCC values associated with (A – males; C – females) parks and protected areas, core conservation areas, and secondary conservation areas, as well as (B – males, D – females) secure, sink, and non-critical habitat states.

3.0 Scale-specific factors impacting body condition of grizzly bears (*Ursus arctos*) in Alberta, Canada

3.1 Abstract

Understanding how ecological factors, including anthropogenic disturbance, impact the health of wildlife provide important guidance for conservation efforts. Here, we test competing hypotheses about predictors of grizzly bear (*Ursus arctos*) health, expressed as body condition, in a threatened population in Alberta, Canada. To characterize factors that might influence health at various spatial scales, habitat selection was represented using the 25th, 50th, 75th, and 95th percentile isopleths of utilization distributions defined with kernel density estimation. At each habitat selection scale we used AIC_c ranking of linear mixed-effects models to test hypotheses about how biology (e.g., age, gender, and reproductive status), habitat quality (e.g, forest conditions, landcover, vegetative productivity, and topography), anthropogenic disturbance (e.g, roads and resource extraction activities), and a previously modelled measure of long-term stress, the hair cortisol concentration, might influence body condition of grizzly bears. At all scales, biological variables were the strongest predictors of body condition. Males had higher body condition than females, and in both sexes body condition increased with age. Body condition in the 25th percentile habitat selection model was best explained by biological and habitat quality variables ($R^2 = 0.40$). At broader habitat selection spatial scales, the influence of anthropogenic variables increased. Influential anthropogenic variables in the 50th ($R^2 = 0.42$), 75th ($R^2 = 0.45$), and 95th ($R^2 = 0.52$) percentile models included roads, density of secondary linear features, proportion parks and protected areas, and density of forest harvest areas. We observed limited evidence of a relationship between compromised body condition and long-term stress or habitat quality. Though our results suggest grizzly bear body condition is influenced primarily by biological factors, at broader spatial scales energetic demands associated with selection of human disturbed habitats may negatively impact body condition. Accordingly, management activities aimed at promoting grizzly bear health should emphasize habitat quality within core habitat areas and limit anthropogenic disturbance within larger grizzly bear home ranges.

3.2 Introduction

An increasing focus of wildlife research is to understand how ecological factors, including human activities, impact the health of wild animals. Access to high quality food resources is required to accumulate and retain fat deposits, which has a direct impact on the body condition, and hence the energetic reserves, of an animal (Jakob et al. 1996). In turn, body condition affects reproductive performance (Cameron et al. 1993; Woodroffe & MacDonald, 1995; Guinet et al. 1998), vulnerability to predation (Murray 2002), the ability to withstand disease and pathogens (Møller et al. 1998), and the ability to survive periods of food scarcity (Millar & Hickling 1990; Verrier et al. 2011). For species such as bears (*Ursidae*), which endure annual prolonged periods of fasting, maximizing body condition over a short summer season is essential to ensure energy demands are met over the winter. The occurrence of natural or anthropogenic disturbances that disrupt or limit the availability of food, and thereby compromise the body condition of individuals, may have profound impacts on the health and fitness of individuals and, consequently, the long-term persistence of threatened or endangered populations.

With fewer than 700 individuals remaining, the grizzly bear (*Ursus arctos*) was listed as *Threatened* in Alberta, Canada in 2010 (Alberta Sustainable Resource Development & Alberta Conservation Association 2010; Clark & Slocombe 2011). Grizzly bears in Alberta occupy a landscape heavily impacted by anthropogenic disturbance, including large-scale and accelerating resource extraction (Garshelis et al. 2005). Industrial activities, including forestry, oil and gas explorations, and mining, which all require an extensive road network, are prevalent throughout grizzly bear habitat. These roads provide access to grizzly bear habitat for both industry and recreational pursuits, contributing to human-bear conflict and high rates of bear mortality (McLellan et al. 1999; Benn & Herrero 2002; Nielsen et al. 2004a).

Habitat selection, and associated impacts on health and mortality, by grizzly bears within a multi-use heterogeneous landscape is complex (Nielsen et al. 2002). Due to extensive fire suppression throughout potential grizzly bear habitat within the region, resource extraction activities have replaced fires to become the dominant forest disturbance (Andison 1998; Rhemtulla et al. 2002; White et al. 2011). In some regions, anthropogenic disturbance features result in avoidance of adjacent suitable habitat areas (Gibeau et al. 2002). However, a number of studies have also shown that grizzly bears in Alberta select areas associated with anthropogenic disturbances (Nielsen et al. 2004b; Berland et al. 2008; Graham et al. 2010) and edge habitats (Stewart et al. 2013), such as roads, forest harvest blocks, and well-sites. Such selection is thought to be driven by the presence and abundance of foods not found in the surrounding forests (Nielsen et al. 2004c; Roever et al. 2008). As the diet of grizzly bears in the region has been found to be comprised primarily of herbaceous foods and fruits that are generally low in nutritional quality (Mowat & Heard 2006; Munro et al. 2006; Nielsen et al. 2010), the distribution and access to high quality foraging sites in the context of human activities has important implications for the health of individuals.

While anthropogenic disturbances may offer an opportunity for bears to optimize body condition, the benefits may be outweighed by the mortality risk and energetic demands associated with these habitats (Frid & Dill 2002; Nielsen et al. 2006; Nielsen et al. 2008). Further, there is growing recognition that long-term stress in wild vertebrates in response to continued exposure to noxious external stimuli may have important ramifications for the health of individuals (Romero 2004; Reeder & Kramer 2005; Ellis et al. 2012). Environmental stressors, resulting from both natural and anthropogenic sources, have been associated with physiological impairment and population declines in a number of species (Trites & Donnelly, 2003; Kitaysky et al. 2007; Wasser et al. 2011; Brearley et al. 2012)

Given escalating human activities within grizzly bear habitat across their range, research can reveal how impacts of changing patterns of habitat quality and anthropogenic disturbance might influence the health of individual grizzly bears within the province. Health of animals can be estimated indirectly using a body condition index (BCI), which quantifies the energy stores of an animal based on mass while controlling for body length (Jakob et al. 1996). While several methods can estimate body condition from field measurements (see Jakob et al. 1996; Green 2001; Stevenson & Woods 2006 for a detailed discussion of strengths and weaknesses of body condtion metrics), the most frequently employed is comprised of residuals (both unstandardized and standardized) from an ordinary least squares linear regression of body mass over body length, the latter which correlates with structural size (Schulte-Hostedde et al. 2005). For species such as grizzly bears, where functional energetic reserves may vary substantially among individuals depending on age, gender, and diet (Hilderbrand et al. 1999; Rode et al. 2001;

McLellan 2011), the use of a BCI represents a useful metric for quantifying the health of individuals within a population.

Here we present the results of an analysis quantifying the impacts of biology, habitat quality, and anthropogenic disturbance on the health of male and female grizzly bears represented using a BCI developed for *Ursids* (Cattet et al. 2002; Cattet et al. 2008). We relate locations of observed seasonal bear habitat selection, based on Global Positioning System (GPS) radio-telemetry, represented at multiple scales to a spatially expansive and temporally explicit dataset representing forest conditions, land-cover, anthropogenic disturbance, and a large-scale gender-specific stress response. By applying linear mixed-effects models (Pinheiro & Bates 2000), we test several competing hypotheses within an information-theoretic framework (Burnham & Anderson 2002) regarding the influence of biology and landscape condition (habitat and anthropogenic disturbance) on the health of individual grizzly bears.

3.3 Study area

The study was conducted in the Grande Cache, Yellowhead, Clearwater, Livingstone, and Castle bear management units (BMUs) in Alberta, Canada (Figure 3.1). Representing an area of nearly 111,000 km^2, vegetation, topography, local weather conditions, and human activities are highly variable. Elevation ranges from 450 m to 3500 m, increasing from east to west. Habitat types include alpine and sub-alpine ecosystems, mixed-wood forests, and wet-meadow complexes (Stenhouse et al. 2005). Mean temperatures range from 12°C in the summer to -7.5°C in the winter, and mean annual precipitation is 450-800 mm (Ecological Stratification Working Group 1995). Resource extraction activities include forestry, oil and gas exploration, and mining, which are serviced by an extensive network of primary and secondary roads. These roads also provide recreational access within grizzly bear habitat for a variety of activities including hunting, fishing, hiking, and trail-riding with all-terrain vehicles and snowmobiles. A network of federal and provincial parks and protected areas, which generally exclude resource extraction activities, are also found throughout the BMUs.

3.4 Materials and Methods

3.4.1 Body condition index and Biological variables

We assessed the health of 85 individuals (*n* =39 males; *n* = 46 females) captured between 1999 and 2010 using a body condition index (BCI). The BCI values represent the standardized residuals from a linear regression of total body mass against straight-line body length (Cattet et al. 2002). BCI values ranged from -2.38 (low body condition) to 2.8 (high body condition) for both males and females. Bears were captured during the spring and summer by the Foothills Research Institute Grizzly Bear Project (FRIGBP) using a combination of leg-hold snares, culvert traps and aerial darting. A VHF ear-tag transmitter and a GPS radiocollar were attached to each bear. Prior to 2004, animal locations were transmitted every four hours but increased to between one and two hour intervals from 2004 on. The age, determined by microscopic analysis of a premolar section (Stoneberg & Jonkel 1966), gender, reproductive status (i.e., with or without cubs), and number of times the bear had been previously captured (Cattet et al. 2008), were recorded for each individual (Table 3.1). Captures followed protocols accepted by the Canadian Council of Animal Care for the safe handling of bears (University of Saskatchewan's Committee on Animal Care and Supply Protocol number 20010016).

To explore the potential effects of long-term stress on body condition (Ellis et al. 2012), we quantified the mean value of a previously modelled landscape scale measure of long-term stress based on hair cortisol concentrations (Macbeth et al. 2010) for each bear in the study area. This measure is gender-specific and characterizes spatial variations in stress resulting from observed habitat conditions and anthropogenic disturbance throughout the study area (see Chapter 2). Specifically, female grizzly bears were found to have a lower stress levels in areas with higher anthropogenic disturbance and higher stress levels in parks and protected areas. In contrast, stress in males was lowest in parks and protected areas, and moderate to high in areas with substantial anthropogenic disturbance. Based on the physiological impacts of long-term stress (Reeder & Kramer 2005), we predicted an inverse association between stress levels and BCI values.

3.4.2 Multi-scale habitat selection

We characterized grizzly bear habitat selection at four spatial scales using telemetry data from the year and season during which each bear was captured and its BCI recorded. Seasons were defined as spring (April 1 – May 30), mating (June 1 – June 30), and summer (July 1 – October 30). We computed a seasonal fixed-kernel density utilization distribution surface for each bear which we contoured at the 25th, 50th, 75th, and 95th percentiles (Worton 1989; Seaman & Powell 1996). The bandwidth was defined by least-squares cross validation (Worton 1989). The 95th percentile represents the standard wildlife home range. It is typically defined as the maximal area travelled by an animal to obtain food, mate, and care for young (Burt 1943), and is the most common spatial unit used when examining habitat selection (e.g., McLoughlin et al. 2002; Berland et al. 2008; Laver & Kelly 2008). The 25th percentile isopleth of the utilization distribution was selected to represent the area of most concentrated habitat selection based on the telemetry data. Additional spatial scales, the 50th and 75th percentiles, represented a continuum of habitat selection scales from the area of most concentrated selection to home range. Incorporating intermediate scales of the utilization distribution has been suggested because finer scale representations of the home range may provide less biased estimates of habitat selection (Anderson 1982; Seaman et al. 1999; Börger et al. 2006). Further, factors influencing grizzly bear habitat selection have been found to be scale-dependent (Ciarniello et al. 2007), and as such we theorized that relationships between BCI and heterogeneous landscape conditions may also depend on the observed scale of habitat selection. We predicted habitat quality will be a stronger predictor of health at finer scales, as bears strive to maximize their nutritional uptake in productive habitat patches (McLoughlin et al. 2000). Conversely, when habitat selection is represented more coarsely we predicted the density of anthropogenic disturbance will gain importance (Berland et al. 2008; Stewart et al. 2012).

3.4.3 Habitat quality metrics

Habitat variables, which were temporally matched with the year and season each bear was captured, are listed in Table 3.1. Forest conditions within the habitat selection areas were quantified based on the variance in crown closure, variance in percent conifer, and proportion upland tree cover classified using Landsat Thematic Mapper (TM) 5 and Landsat 7 Enhanced Thematic Mapper Plus (ETM+) imagery and topographic derivatives from a digital elevation model (DEM) (Franklin et al. 2003; McDermid 2005a). We represented the percentage of regenerating forest within each area based on recent forest disturbances (e.g., forest harvest blocks and fires) identified using Landsat 5 TM and 7 ETM+ imagery. Using a land cover map of the study area derived from Landsat 5 TM and 7 ETM+ imagery, as well as a DEM, we determined the percent of each habitat selection area classified as shrubs and herbs, as well as barren land (Franklin et al. 2002; McDermid 2005b). We assessed terrain conditions within habitat selection areas using a DEM detailing elevation obtained from the Government of Canada spatial data portal Geobase. A terrain ruggedness index, providing a measure of terrain complexity and variability (Wilson & Gallant 2000), and a compound topographic index, which indicated potential soil moisture modelled from slope, catchment area, and upstream water sources (Gessler et al. 1995), were derived from the DEM and represented using the mean values found in each habitat selection area .

We used indices from the Dynamic Habitat Index (DHI) to characterize vegetation productivity within the habitat selection area of each bear (Berry et al. 2007; Coops et al. 2008). The DHI is comprised of three indices which are calculated by summarizing annual trends in monthly images of the fraction of photosynthetically active radiation (fPAR) derived from Advanced Very High Resolution Radiometer (AVHRR) reflectance values (Fontana et al. 2012). The first of the indices, cumulative greenness, represents total vegetation productivity which is estimated annually by summing monthly fPAR observations. The second is the variation in greenness; this is calculated using the coefficient of variation in fPAR values over a year and is representative of annual changes in productivity, and consequently, the availability of food resources. Finally, minimum cover is an estimate of the lowest level of vegetative productivity available year round based on monthly fPAR values. We extracted the mean values of the three indices associated with each individual habitat selection area.

3.4.4 Anthropogenic disturbance metrics

We considered anthropogenic features such as roads, oil and gas well-sites, cut-lines, power-lines, pipelines, forest harvest blocks, and proximity to human settlements in the analysis (Table 3.1). All data were provided by Alberta Environment and Sustainable Resource Development and are mapped and updated by the FRIGBP based on appearance of disturbance features in Landsat 5 TM and 7 ETM+ imagery. We represented the localized influence of roads and oil and gas well-sites within habitat selection areas by using an exponential distance decay function, e^{-ad} where d is the distance in metres to the feature and a was fixed at 0.002 (Nielsen et al. 2009). We represented secondary linear anthropogenic features, such as cut-lines, power-lines, and pipelines, as a cumulative linear density within the zones (km/km^2).

We divided forest harvest blocks into two classes (≤ 15years old; > 15 years old) to account for regeneration and resultant differences in grizzly bear food availability present within the harvested areas (Nielsen et al. 2004c; Stewart et al. 2012). We assessed the influence of forest harvest blocks by calculating the proportion area cut within each habitat selection area based on the two age classes. We represented the proximity of each habitat selection area to the nearest populated place by calculating the mean Euclidean distance of the zone to human settlements which were defined based on persistent night time light derived from the Defence Meteorological Survey Program Operational Linescan System (Wulder et al. 2011). Finally, we represented the influence of parks and protected areas in the region, which represent a noted contrast in terms of land-use compared to the surrounding industrialized landscape, based on the proportion parks and protected area contained within the individual habitat selection area.

3.4.5 Statistical analysis

We quantified scale-dependent effects of biology, habitat quality, and anthropogenic disturbance on BCI using hierarchical linear mixed-effects models (Pinheiro & Bates 2000; Zuur et al. 2009) combined with model selection based on the small sample Aikake Information Criterion (AIC_c) (Hurvich & Tsai 1989; Burnham & Anderson 2002). We tested several competing models at each habitat selection scale based on *a priori* hypotheses (Table 3.1). Specifically, we examined the influence of biological, habitat, and anthropogenic variables in isolation to determine if any specific variable grouping alone was more influential in explaining BCI. Other models took the form of combining biological variables exclusively with habitat and anthropogenic variables as grizzly bear habitat selection is known to be influenced by age and gender (Nielsen et al. 2004b; Berland et al. 2008; Nielsen et al. 2013; Stewart et al. 2013). We also considered the combined influence of habitat and anthropogenic variables in a single model to determine whether landscape conditions in the absence of biological effects were sufficient to explain observed patterns in BCI. Finally, we considered a global model at each scale to account for all potential variables (and their interactions) impacting BCI.

We used linear mixed-effects models to eliminate potential pseudoreplication resulting from both the sampling design of the BCI data and overlap among calculated seasonal habitat selection zones (Bolker et al. 2009). Annual efforts to capture bears and collect BCI measurements were generally restricted to a single BMU and were primarily concentrated in the defined spring season and mating season resulting in limited geographic distance among BCI sample locations. By incorporating a hierarchy of random effects based on season and year we were able to stratify the model in order to avoid groupings of repeated measures. This also allowed us to explore the influence of potential seasonal changes in body condition related to differential habitat selection according to season and gender (Munro et al. 2006; Nielsen et al. 2010). In order to account for potential spatial autocorrelation among landscape values resulting from habitat selection zone overlap among individuals, we incorporated a Gaussian spatial correlation structure into each model based on positional vectors of centroids derived from the habitat selection zone contours (Pinheiro & Bates 2000). At each spatial scale, we calculated the mean Euclidean distance among the centroids of the habitat selection zone contours. The mean distance was incorporated as the range in the Gaussian spatial correlation structure (Pinheiro & Bates 2000). As a result, pairwise habitat selection zone contours that fell within the mean range at each scale were considered to be spatially autocorrelated. In order to assess the influence of the spatial correlation structure in the global models, we compared them with and without the spatial structure using AIC_c values (Zuur et al. 2009). As the AIC_c values in the global models fit using the spatial correlation structure were significantly lower, we fit all subsequent models using the defined spatial structure (see Table 3.2).

Before fitting models, all variables were centered and scaled to aid interpretability of regression coefficients (see Figure 3.2) (Schielzeth 2010). Based on our hypotheses regarding changing influence of habitat and anthropogenic disturbance metrics on BCI across scales, we derived best-fit habitat and anthropogenic models at each scale. In order to limit redundancy and collinearity among habitat and anthropogenic variables, we first excluded those with a Pearson correlation coefficient exceeding 0.6 and a variance inflation factor exceeding 5. We used backwards stepwise regression with a $p < 0.1$ significance level to select influential habitat and anthropogenic variables (Venables & Ripley 1999). Aikake weights (w_i) based on the AIC_c values were used to select the candidate model with most support in the data at each scale (Burnham & Anderson 2004). The w_i are the normalized (sum to 1) model likelihoods of all the candidate models and represent the probability that a given model is the "best" based on the input data and hypotheses considered (Burnham & Anderson 2002; Burnham & Anderson 2004). As suggested by Zuur et al. (2009), we refit the models with the highest w_i using restricted maximum likelihood estimation (REML) to limit bias in the final regression coefficients. Finally, we assessed the variance explained by fixed effects in the top model based on a marginal R^2, and the cumulative variance explained by both fixed and random effects using a conditional R^2 (Nakagawa & Schielzeth 2013).

The best-fit models, as well as the global models, were used to assess assumptions in both fixed and random effects, including normal distribution of residuals and random effects, and constant variance, at each habitat selection scale (Pinheiro & Bates 2000; Zuur et al., 2009). We found no evidence of correlation of predictor variables in any of the models considered and within-group residuals of the four best-fit models appeared to be normally distributed (Figure 3.3). We assessed the normality of random effects by plotting the best linear unbiased estimators for each model (Pinheiro & Bates 2000). These were acceptable for all global and best-fit models considered.

3.5 Results

Linear mixed-effects models revealed that correlates with BCI varied among the four habitat selection scales (Table 3.2). Conditional R^2 values, summarizing the variance explained by the fixed and random effects, were higher in the 25th percentile model (0.79) compared to the 50th (0.66), 75th (0.66), and 95th percentile models (0.69). In all four models considered, predicted BCI values were similar during the spring ($\mu\beta = -0.89$) and mating ($\mu\beta = -0.93$) seasons, and higher during the summer season ($\mu\beta = 0.88$). At the 25th percentile habitat selection zone scale, a model including biology and habitat variables showed the highest support among candidate models ($w_i = 0.84$) with fixed effects explaining 40% of the variation in the BCI data (R^2; LME: $\beta = -1.25 \pm 0.34$, $df = 46$, $t = -3.64$, $p < 0.001$) (Figure 3.3). In contrast, a model with biology and anthropogenic effects strongly outperformed other models at the 50th ($w_i = 0.67$), 75th ($w_i = 0.75$), and 95th ($w_i = 0.42$) percentile habitat selection scales (Table 3.2). Specifically, these models explained 42% of the variation in BCI in the 50th percentile model (R^2; LME: $\beta = -0.69 \pm 0.30$, $df = 47$, $t = -2.28$, $p = 0.026$), 45% of the variation in the 75th percentile model (R^2;

LME: $\beta = -0.73 \pm 0.29$, $df = 47$, $t = 0.29$, $p = 0.012$), and 52% of the variation in BCI in the 95th percentile model (R^2; LME: $\beta = -0.89 \pm 0.29$, $df = 43$, $t = -3.07$, $p = 0.003$) (Figure 3.3).

As values for the majority of the biological variables were fixed across all four models, their influence across the scales of the analysis did not vary substantially. At all four scales, the interaction between age and gender variables had a strong positive relationship with BCI (Tables 3.3, 3.4, 3.5, & 3.6). BCI generally increased with age, and was higher in males compared to females (Figure 3.4). The number of previous captures did not exhibit a clear influence on BCI, as estimated values were highly variable. Females with dependent offspring exhibited a wide range of BCI values, and the variable had a weak influence in all four models (Figure 3.4). While the relationship between BCI and long-term stress varied slightly across all four scales, higher modelled stress values were generally associated with lower BCI (Figure 3.4). Of the four habitat selection scales, the relationship between BCI and long-term stress was most pronounced at the 25th percentile scale ($t = -1.73$, $p = 0.088$) (Table 3.3).

Amongst habitat variables considered in the 25th percentile habitat selection scale, variation in elevation had the strongest positive relationship with BCI ($t = 4.20$, $p < 0.001$). Individuals with greater variation in elevation within the habitat selection zones had higher BCI values (Table 3.3). Similar positive relationships with BCI were found with the proportion regenerating forest ($t = 3.53$, $p < 0.001$), and minimum cover ($t = 3.27$, $p = 0.002$). While variation in elevation and minimum cover variables exhibited a positive relationship with BCI, the interaction term between the two variables had a negative relationship with BCI ($t = -3.56$, $p = 0.001$). The interaction suggests BCI was lower when variation in elevation increased but only when minimum cover also increased.

Anthropogenic variables became stronger predictors of BCI as the spatial scale of habitat selection increased (Tables 3.4, 3.5, & 3.6). Among the anthropogenic variables considered, only distance decay to roads and density of secondary linear features were included in all the final models at the 50th, 75th, and 95th percentile scales (Figure 3.4; Tables 3.4, 3.5, & 3.6). Modelled relationships showed habitat selection zones further from roads were strongly associated with higher BCI values at the 75th ($t = 2.90$, $p = 0.005$) percentile scale (Table 3.5). Individuals with higher densities of secondary linear features within habitat selection zones had lower BCI values at the 50th ($t = -0.76$, $p = 0.003$) and 75th ($t = -1.99$, $p = 0.050$) percentile scales (Figure 3.4;

Tables 3.4 & 3.5). The distance to people, which was included in the selected 75th (*t* = -2.01, *p* = 0.049) and 95th (*t* = -2.14, *p* = 0.035) percentile models, exhibited a negative relationship with BCI (Figure 3.4; Tables 3.5 & 3.6). The 95th percentile model, representing the coarsest representation of grizzly bear habitat selection, included the largest number of anthropogenic variables (Table 3.6). Density of forest harvest blocks aged 15 years or older had the strongest negative effect on BCI (*t* = -3.16, *p* = 0.002), while the density of those aged less than 15 years (*t* = -0.58, *p* = 0.564) predicted slightly higher, but also negative, BCI values. In contrast, the inclusion of a quadratic term for density of forest harvest blocks aged 15 years or older had a positive relationship with BCI (*t* = 3.085, *p* = 0.003) (Figure 3.4).

3.6 Discussion

We used the body condition index as a metric to quantify the health of individual grizzly bears within Alberta, Canada. When this information is coupled with spatial data on animal movement, a more complete understanding of what factors – and at what spatial scale – might drive variation in these important fitness measures over space and time is developed. At all habitat selection scales, body condition of bears was lower during the spring and mating seasons compared to the summer, consistent with other studies showing body condition is lowest following den emergence, and highest immediately prior to den entry as bears accumulate fat reserves before winter (Barboza et al. 1997; Hilderbrand et al. 1999; McLellan 2011). We did observe a slight decrease in body condition during the mating season compared to the spring which can be attributed to shifting priorities within the population away from feeding to mating and the associated energetic demands (Steyaert et al. 2012).

In addition to temporal trends, biology played an important role in BCI. As a result of gender-specific patterns of habitat selection, potential nutritional benefits afforded to males are reflected in higher observed BCI values compared to females. Generally, adult males have larger home ranges than females and juveniles (Nagy & Haroldson 1990; Dahle & Swenson 2003; Dahle et al. 2006), allowing them to occupy a wider diversity of habitats. In grizzly bears, sexual size dimorphism is hypothesized to contribute to sexual segregation in habitat selection as large adult males select for high quality habitat (Rode et al. 2006). In our study area, where herbaceous foods, roots, and fruits comprise the majority of the diet of grizzly bears (Mowat & Heard 2006; Munro et al. 2006), seasonal selection of productive vegetative habitats may be prioritized by males as herbaceous diets may not meet the energetic requirements dictated by their size (Rode et al. 2001). Predation on ungulates, which is generally limited to the late spring and represents the main source of dietary protein in the region (Munro et al. 2006), is likely also dominated by males (Hobson et al. 2000), though predation patterns are dependent on ungulate density (Mowat & Heard 2006). Previous studies have noted that females with offspring occupy sub-optimal or sink habitats in closer proximity to humans usually avoided by males (McLellan 2005; Libal et al. 2011; Elfström et al. 2012). Although these patterns likely decrease risk of infanticide, these habitats may not fully meet nutritional needs as they have higher energetic demands and represent a significant mortality risk (Nielsen et al. 2006). Further, female grizzly bears are philopatric and as such female offspring tend to occupy home ranges which are similar in nature and in close proximity to those of their mothers (Proctor et al. 2004; Støen et al. 2005) as a result of natal learning (Smulders et al. 2012; Nielsen et al. 2013).

Across genders, our hypothesis that habitat quality within the core area of selection impacted BCI was confirmed. Specifically, models that included biology and habitat variables had the greatest support at the finest scale of the analysis (i.e., 25th percentile habitat selection). This is consistent with suggestions of the importance of bottom-up drivers; that is, individuals preferentially occupy habitat areas where available resources provide them the opportunity to maximize body condition (Nielsen et al. 2002; Nielsen et al. 2010). Variables that are a proxy representation of habitat quality (i.e., proportion regenerating forest and minimum cover), represent sources of herbaceous foods (Munro et al. 2006) and have a positive correlation with the presence of ungulates (Michaud 2012), both of which are significant food resources for grizzly bears (Mowat & Heard 2006; McLellan 2011). Bears whose habitat selection included greater variation in elevation and terrain ruggedness were also found to have higher body condition. We suggest that such complex topography offers not only a greater diversity of habitat and resources associated with elevation gradients, but also *de facto* protection from human activity (Benn & Herrero 2002; Nielsen et al. 2004). However, our model does suggest a limit to the benefit of variability in elevation; habitat that are selected in higher elevations have lower baseline levels (i.e., minimum cover) of vegetation productivity (Coops et al. 2008), and food resources (Munro et al. 2006).

While biology was important in all models, the support for a joint biology and anthropogenic hypothesis increased as grizzly bear habitat selection patterns were more coarsely delineated. This supported our second prediction that the influence of anthropogenic disturbance features on body condition would increase as the scale of habitat selection increased. Wildlife home ranges are typically defined at the 95th percentile scale (Laver & Kelly 2008). However, the percentile scale of the home range is inversely related to the probability of habitat selection as the coarsest representation of the home range will include areas used infrequently (Powell 2000). Our results suggest potential energetic gains or costs associated with habitat receiving limited usage, particularly those with greater incidence of anthropogenic disturbance, may have a disproportionate impact on body condition.

Generally, bears whose habitat selection was influenced more by anthropogenic features had lower body condition. Observed relationships between the remaining anthropogenic variables and BCI values can be interpreted in terms of trade-offs between availability of food resources in many anthropogenic disturbances and the energetic demands and risks associated with occupying these habitats. Anthropogenic variables of particular importance were roads and secondary linear disturbance features, both of which have been linked to grizzly bear habitat selection (Linke et al. 2005; Graham et al. 2010; Stewart et al. 2013). Bears whose habitat selection patterns were further from roads had higher BCI values. While edge habitats associated with roads represent potential sources of food (Roever et al. 2008), bears that use habitats near roads are at greater risk of mortality (Benn & Herrero 2002; Nielsen et al. 2004), may be more vigilant (Frid & Dill 2002), and are more likely to engage in a costly flight response (McLellan & Shackleton 1988; Gibeau et al. 2002). Our findings suggest energetic losses associated with these behaviours may result in compromised body condition. While areas adjacent to roads represent potential sources of foods, roads are a significant source of mortality and the lower body condition of bears using areas near roads may have long term implications in terms of the health of individuals and reproductive success. Near road mortality is particularly concerning as female bears in the region have been found to utilize areas adjacent to roads more frequently than males (Graham et al. 2010).

The energetic costs associated with roads may also extend to surrounding habitats and disturbance features. For example, grizzly bears have been found to select forest harvest areas due to the increased availability of foods not found in surrounding even aged forests (Nielsen et al. 2004b; Nielsen et al. 2004c). However, roads adjacent to forest harvest blocks have been found to negate potential health gains associated with forest harvests due to increased mortality resulting from human access to these areas (Nielsen et al. 2008). Further, studies have found roads adjacent to forest harvest blocks may limit usage of these productive habitats (McLellan & Shackleton 1988). Here, we observed a negative relationship between forest harvest blocks of both age classes and BCI values despite the apparent energetic benefits of food availability in these disturbances. We suggest that bears whose habitat selection patterns are strongly influenced by forest harvests may actually expend energy when foraging in these habitats as a result of the vigilance required due to continued human access provided by roads which warrants further study. Interestingly, when habitat selection patterns included only moderate proportions of older forest harvests, BCI values responded favourably, which suggests bears may actually benefit from heterogeneous forest conditions resulting from harvesting. We propose that closing roads in areas with recent forest harvests will not only reduce bear mortality (Nielsen et al. 2008), but also may also provide a health benefit to bears utilizing these habitats.

Secondary linear disturbance features, such as cut-lines, pipelines, and power-lines, provide off-road access in grizzly bear habitat and represent a substantial source of landscape fragmentation resulting in increased edge density and altered forest patch configuration (Linke et al. 2008). Estimates of cut-line densities specifically in regions with extensive oil and gas exploration are approximately 15m/ha (Lee & Boutin 2006). Despite recent studies showing grizzly bears, particularly females, select edge habitats associated with anthropogenic disturbances (Stewart et al. 2013), Linke et al. (2005) suggest the changing configuration of forest patches (e.g., increasing mean patch distance) resulting from these disturbance features may force bears to expend more energy moving between habitat areas. As the relationship between the density of secondary linear features and BCI values was non-linear, it appears that edge habitats resulting from these features, and associated food resources, have a positive relationship with body condition at low densities. Conversely, in areas with high densities of secondary linear features, energetic demands resulting from increasing landscape fragmentation had a negative impact on BCI values, as suggested by Linke et al. (2005).

We anticipated strong and negative associations between BCI and long-term stress. Stress was indexed as a spatially explicit modelling product and a component of habitat quality. Consistent with this prediction, the relationship between body condition and long-term stress was apparent, but most pronounced in the 25th percentile model. The relationship was non-linear, suggesting that while high long-term stress decreases body condition in bears, low and moderate stress exposure does not seem to impose a strong influence on body condition. While we modelled the impacts of long-term stress on body condition, it is important to note that compromised body condition may in fact result in long-term stress, as depleted energetic reserves may not allow an animal to effectively respond to external stimuli resulting in increased circulation of glucocorticoids (McEwen & Wingfield 2003; Johnstone et al. 2012). However, a number of studies have found baseline cortisol levels in vertebrates increase in response to persistent external environmental stressors resulting in compromised body condition (e.g., Kitaysky et al. 1999; Suorsa et al. 2003; Bonier et al. 2009). In contrast, low and moderate cortisol levels may provide vertebrates with the means to cope with environmental change and human activity (Reeder & Kramer 2005; Blas et al. 2007). The association between long-term stress and habitat quality observed here provides preliminary evidence that stress-related deficiencies in body condition in grizzly bears may be related to habitat quality and warrant further study.

3.7 Conclusions

The health of grizzly bears in response to landscape conditions is complex as bears are highly individualistic. Habitat selection, and resultant health benefits or costs, depends on the gender, age, and reproductive status of individuals. Typically, management decisions regarding the impacts of landscape conditions on wildlife habitat selection patterns are informed on broad scale patterns of selection (i.e., the 95th percentile isopleth of the utilization distribution). While informative, finer scale representations of habitat selection can provide important insights into the conditions associated with areas more intensively utilized. Here we have demonstrated that biology (including our proxy for long-term stress), habitat quality, and anthropogenic disturbance differentially impact the health of male and female grizzly bears. Further, the influence of landscape condition metrics is scale-specific as grizzly bear habitat selection varies spatially and by scale. At the finest scale of habitat selection considered, metrics representing potential resource availability, topographic conditions, and long-term stress most influenced grizzly bear body condition. As habitat selection was characterized more broadly, the influence of anthropogenic disturbance features, in particular roads, secondary linear disturbance features, and forest harvest blocks, gained importance over variables representing habitat quality. Management efforts that aim to promote landscape conditions that are beneficial to the health of grizzly bears should emphasize habitat quality within core habitat areas and limit the impacts of anthropogenic disturbance within larger grizzly bear home ranges.

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Table 3.1 Variables and hypotheses considered to predict grizzly bear body condition index values at four spatial scales.

Hypotheses	**Variables**	**Rational**
Biology only	Gender (Female/Male)	Gender based differences in habitat selection
	Age[1]	Older bears may exhibit a competitive advantage in habitat selection
	Offpring	Females with cubs may alter habitat selection in order to avoid adult males
	Long-term stress[1]	High observed levels of long-term stress may be detrimental to body condition
	Number of previous captures	Multiple handlings impose a negative effect on body condition
Habitat only	Variation in crown closure[1]	Affects vegetation abundance by influencing light reaching the forest floor
	Variation in percent conifer[1]	Influences herbaceous species distribution
	Variation in proportion upland tree cover	Influences herbaceous species distribution and availability of ungulates
	Percent regenerating forest	Recent forest disturbances have greater abundance of herbaceous foods
	Percent shrub cover	Availability of herbaceous foods and berries may impose an effect on body condition
	Percent barren land cover[1]	Availability of foods in alpine environments may impose an effect on body condition.
	Soil wetness[1]	Influences availability of herbaceous foods and ungulates
	Terrain ruggedness	Influences human access to grizzly bear habitat
	Variation in elevation	Climate gradients associated with changing elevation influence landcover and impacts human access
	Cumulative greenness(DHI)	Total vegetation productivity influences availability of foods
	Seasonality (DHI)	Seasonal changes in productivity influence availability of foods
	Minimum cover (DHI)	Lowest estimated annual productivity determines minimal availability of foods
Anthropogenic only	Proportion forest harvest blocks aged > 15 years[1]	Availability of foods and human activity vary with time since forest disturbance
	Proportion forest harvest blocks aged ≤ 15 years	Availability of foods and human activity vary with time since forest disturbance
	Proportion parks and protected area[1]	Safe haven and contrast to surrounding industrialized landscape
	Distance decay to roads	Provide human access to grizzly bear habitat, significant source of mortality
	Distance decay to well-site	Create forest edges and contribute to landscape fragmentation
	Density secondary linear features[1]	Cut-lines, pipelines, and power-lines create forest edges and contribute to landscape fragmentation
	Distance to people	Relative proximity of grizzly bear habitat to human settlements
Biology + Anthropogenic	Biology + Best-fit anthropogenic	Gender and age based differences in selection of anthropogenic-disturbed habitats
Biology + Habitat	Biology + Best-fit habitat	Gender and age based differences in habitat usage and resource selection
Anthropogenic + Habitat	Best-fit anthropogenic + Best-fit habitat	Influence of landscape conditions exclusively
Biology + Anthropogenic + Habitat	Biology + Best-fit anthropogenic + Best-fit habitat	Cumulative impacts of biology, anthropogenic influence, and habitat conditions

[1] Indicates variables that were also considered using a quadratic term in order to represent potential non-linear relationships with BCI

Table 3.2 Top models by habitat selection scale, *k* = number of parameters, AIC_c, ΔAIC_c = difference in AIC_c from top model, and w_i = weight of evidence supporting the model

Scale	**Candidate models**	**k**	**AIC_c**	**ΔAIC_c**	**w_i**
25th percentile	**Biology + Habitat**	14	200.83	0.00	0.84
	Biology + Habitat + Anthropogenic	16	204.88	4.05	0.11
	Biology + Anthropogenic	11	207.54	6.71	0.03
	Biology	9	208.62	7.78	0.02
	Habitat	10	238.36	37.52	0.00
	Habitat + Anthropogenic	12	240.20	39.37	0.00
	Anthropogenic	7	246.51	45.68	0.00
	Global model[1]	-	247.82	-	-
50th percentile	**Biology + Anthropogenic**	12	207.53	0.00	0.67
	Biology	9	208.97	1.44	0.33
	Biology + Habitat	18	217.78	10.25	0.00
	Biology + Habitat + Anthropogenic	15	219.95	12.42	0.00
	Anthropogenic	13	242.43	34.90	0.00
	Habitat	7	246.15	38.62	0.00
	Habitat + Anthropogenic	10	248.26	40.73	0.00
	Global model[1]	-	267.61	-	-
75th percentile	**Biology + Anthropogenic**	12	204.25	0.00	0.75
	Biology + Habitat	13	207.94	3.69	0.12
	Biology	9	208.97	4.73	0.07
	Biology + Habitat + Anthropogenic	16	209.31	5.06	0.06
	Habitat	8	239.34	35.09	0.00
	Anthropogenic	11	242.24	38.00	0.00
	Habitat + Anthropogenic	7	244.36	40.11	0.00
	Global model[1]	-	254.73	-	-
95th percentile	**Biology + Anthropogenic**	16	207.24	0.00	0.42
	Biology + Habitat	14	208.10	0.85	0.27
	Biology	9	208.10	0.86	0.27
	Biology + Habitat + Anthropogenic	21	211.99	4.75	0.04
	Habitat	9	240.08	32.84	0.00
	Anthropogenic	16	244.80	37.56	0.00
	Habitat + Anthropogenic	11	245.13	37.90	0.00
	Global model[1]	-	261.14	-	-

[1] AIC_c of global model fit without the spatial correlation structure.

Table 3.3 Parameter estimates (± SE) for the top model predicting body condition index at the 25th percentile habitat selection utilization scale. R^2 marginal = 0.40, R^2 conditional = 0.79. Model was refit using Restricted Maximum Likelihood Estimation (REML). Significant effects are indicated in bold.

Parameter	**Estimate**	**± SE**	**df**	**t-value**	**p-value**
Intercept	-1.25	0.34	46	-3.64	**< 0.001**
Offspring	-0.13	0.25	46	-0.53	0.597
Age x Gender (Female)	0.04	0.02	46	2.18	**0.032**
Age x Gender (Male)	0.13	0.02	46	7.41	**< 0.001**
Long-term stress (quadratic)	-0.09	0.05	46	-1.73	**0.088**
Number of previous captures	0.17	0.13	46	1.29	0.200
Proportion regenerating forest	0.26	0.07	46	3.53	**<0.001**
Minimum cover	0.19	0.06	46	3.27	**0.002**
Soil wetness (quadratic)	0.03	0.05	46	0.64	0.525
Variation in elevation	0.36	0.09	46	4.20	**< 0.001**
Minimum cover x Variation in elevation	-0.23	0.06	46	-3.56	**0.001**

Table 3.4 Parameter estimates (± SE) for the top model predicting body condition index at the 50th percentile habitat selection scale. R^2 marginal = 0.42, R^2 conditional = 0.66. Model was refit using Restricted Maximum Likelihood Estimation (REML). Significant effects are indicated in bold.

Parameter	**Estimate**	**± SE**	**df**	**t-value**	**p-value**
Intercept	-0.69	0.30	47	-2.28	**0.026**
Offspring	0.07	0.31	47	0.23	0.822
Age x Gender (Female)	0.03	0.02	47	1.49	0.140
Age x Gender (Male)	0.14	0.02	47	7.65	**<0.001**
Long-term stress (quadratic)	-0.03	0.08	47	-0.44	0.664
Number of previous captures	-0.03	0.14	47	-0.20	0.844
Distance decay to roads	0.31	0.10	47	3.05	0.450
Density secondary linear features (quadratic)	-0.04	0.05	47	-0.76	**0.003**
Proportion parks and protected area (quadratic)	0.07	0.05	47	1.59	0.117

Table 3.5 Parameter estimates (± SE) for the top model predicting body condition index at the 75th percentile habitat selection scale. R^2 marginal = 0.45, R^2 conditional = 0.66. Model was refit using Restricted Maximum Likelihood Estimation (REML). Significant effects are indicated in bold.

Parameter	**Estimate**	**± SE**	**df**	**t-value**	**p-value**
Intercept	-0.73	0.29	47	0.29	**0.012**
Offspring	0.05	0.30	47	0.30	0.856
Age x Gender (Female)	0.02	0.02	47	1.29	0.203
Age x Gender (Male)	0.15	0.02	47	8.16	**<0.001**
Long-term stress (quadratic)	0.05	0.08	47	0.60	0.551
Number of previous captures	-0.03	0.14	47	-0.21	0.831
Distance decay to roads	0.40	0.14	47	2.90	**0.005**
Density secondary linear features (quadratic)	-0.26	0.13	47	-1.99	**0.050**
Distance to people	-0.17	0.09	47	-2.01	**0.049**

Table 3.6 Parameter estimates (± SE) for the top model predicting body condition index at the 95th percentile habitat selection scale. *R^2* marginal = 0.52, *R^2* conditional = 0.69. Model was refit using Restricted Maximum Likelihood Estimation (REML). Significant effects are indicated in bold.

Parameter	**Estimate**	**± SE**	**df**	**t-value**	**p-value**
Intercept	-0.89	0.29	43	-3.07	**0.003**
Offspring	0.11	0.29	43	0.37	0.714
Age : Gender (female)	0.02	0.02	43	1.31	0.193
Age : Gender (male)	0.14	0.02	43	7.49	**<0.001**
Long-term stress (quadratic)	-0.08	0.09	43	-0.98	0.328
Number of previous captures	0.03	0.14	43	0.20	0.843
Forest harvest block (> 15 years)	-0.53	0.17	43	-3.16	**0.002**
Forest harvest block (≤ 15 years)	-0.06	0.11	43	-0.58	0.564
Forest harvest block (> 15 years) (quadratic)	0.25	0.08	43	3.09	**0.003**
Distance decay to roads	0.30	0.13	43	2.37	0.204
Distance to people	-0.18	0.08	43	-2.14	**0.035**
Proportion protected area (quadratic)	0.07	0.05	43	1.42	0.159
Density secondary linear features (quadratic)	-0.05	0.05	43	-0.96	0.339

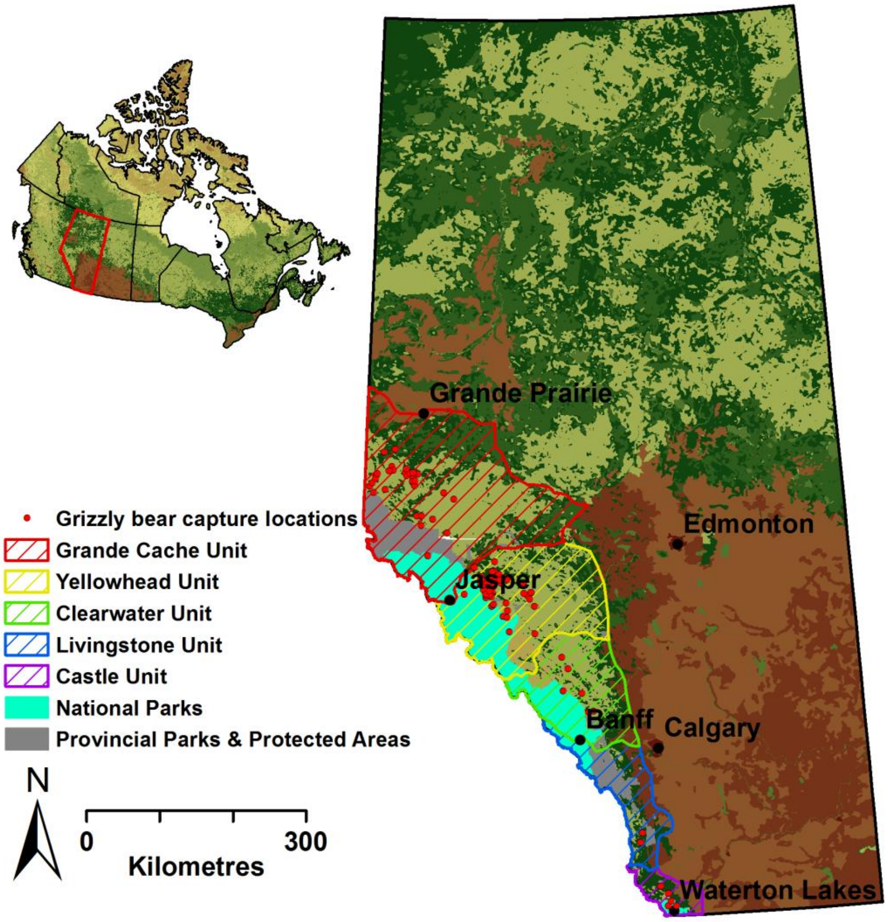

Figure 3.1 Study area in Alberta, Canada including the five bear management units.

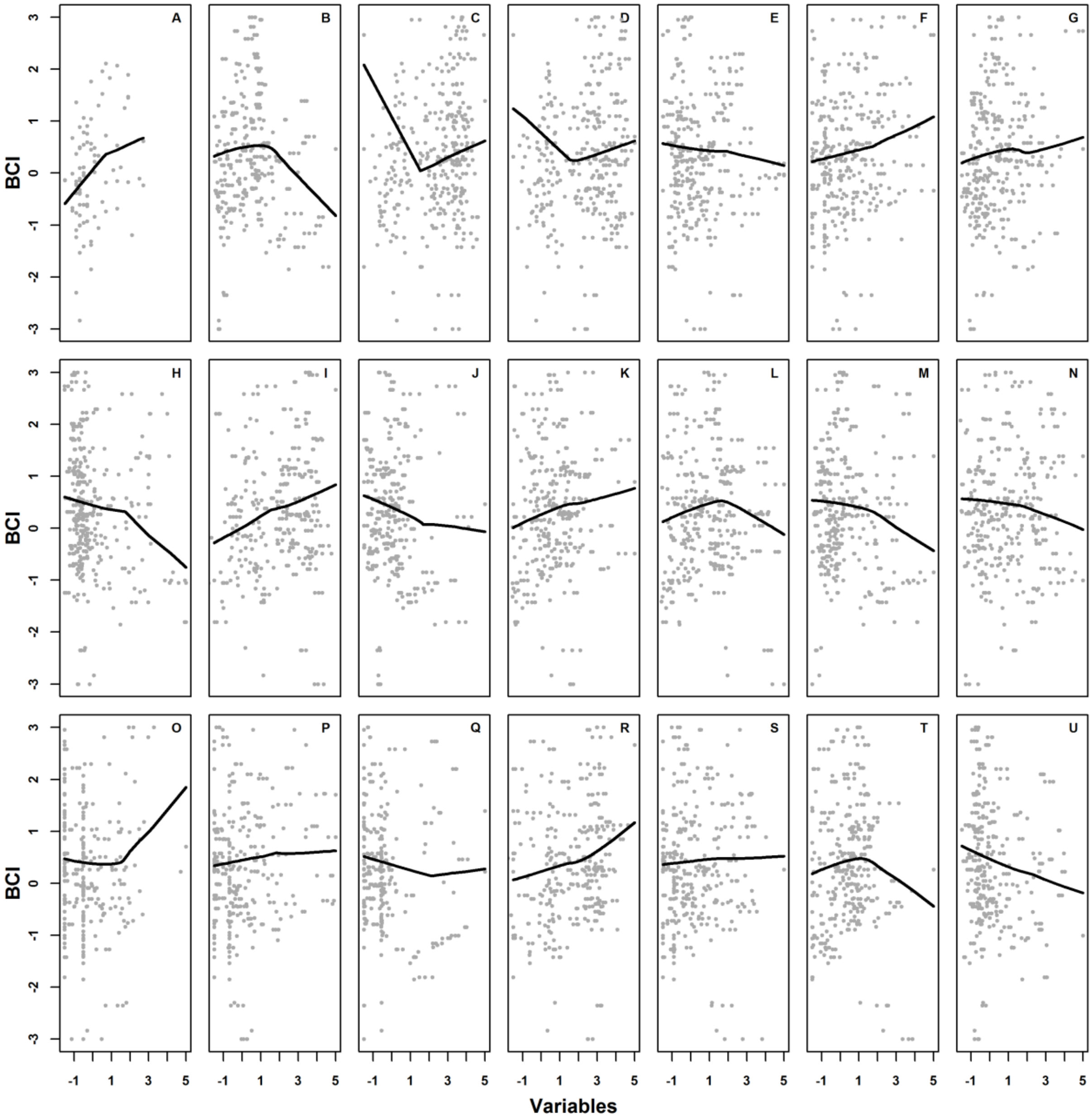

Figure 3.2 Observed relationships between BCI and biological, habitat, and anthropogenic variables.

All variables are centered and scaled to a mean of zero. Relationships are fitted using LOESS smoothing (span = 1). Variables: A) Age B) Long-term stress C) Crown closure - variation D) Percent conifer - variation E) Proportion upland tree cover - variation F) Proportion regenerating forest G) Proportion shrub cover H) Proportion barren land cover I) Cumulative greenness J) Seasonality K) Minimum cover L) Soil wetness M) Terrain ruggedness N) Elevation - variation O) Proportion forest harvest area (aged > 15 years) P) Proportion forest harvest area (aged ≤ 15 years) Q) Proportion protected area R) Roads - distance decay S) Well sites - distance decay T) Density of secondary linear features U) Distance to people

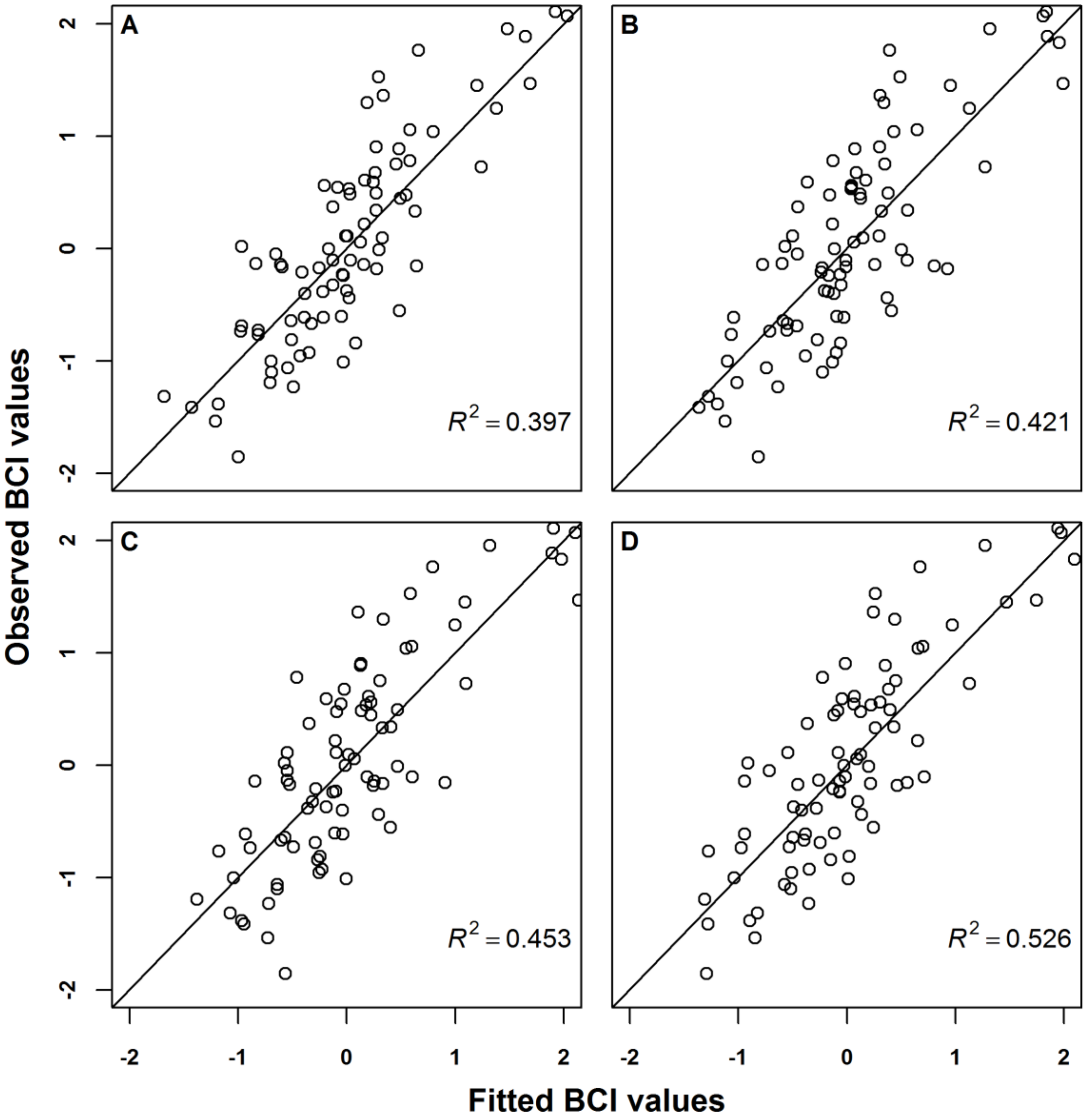

Figure 3.3 Observed vs. fitted mixed-effects model BCI values.

A) 25th percentile habitat selection model B) 50th percentile habitat selection model C) 75th percentile habitat selection model D) 95th percentile habitat selection model

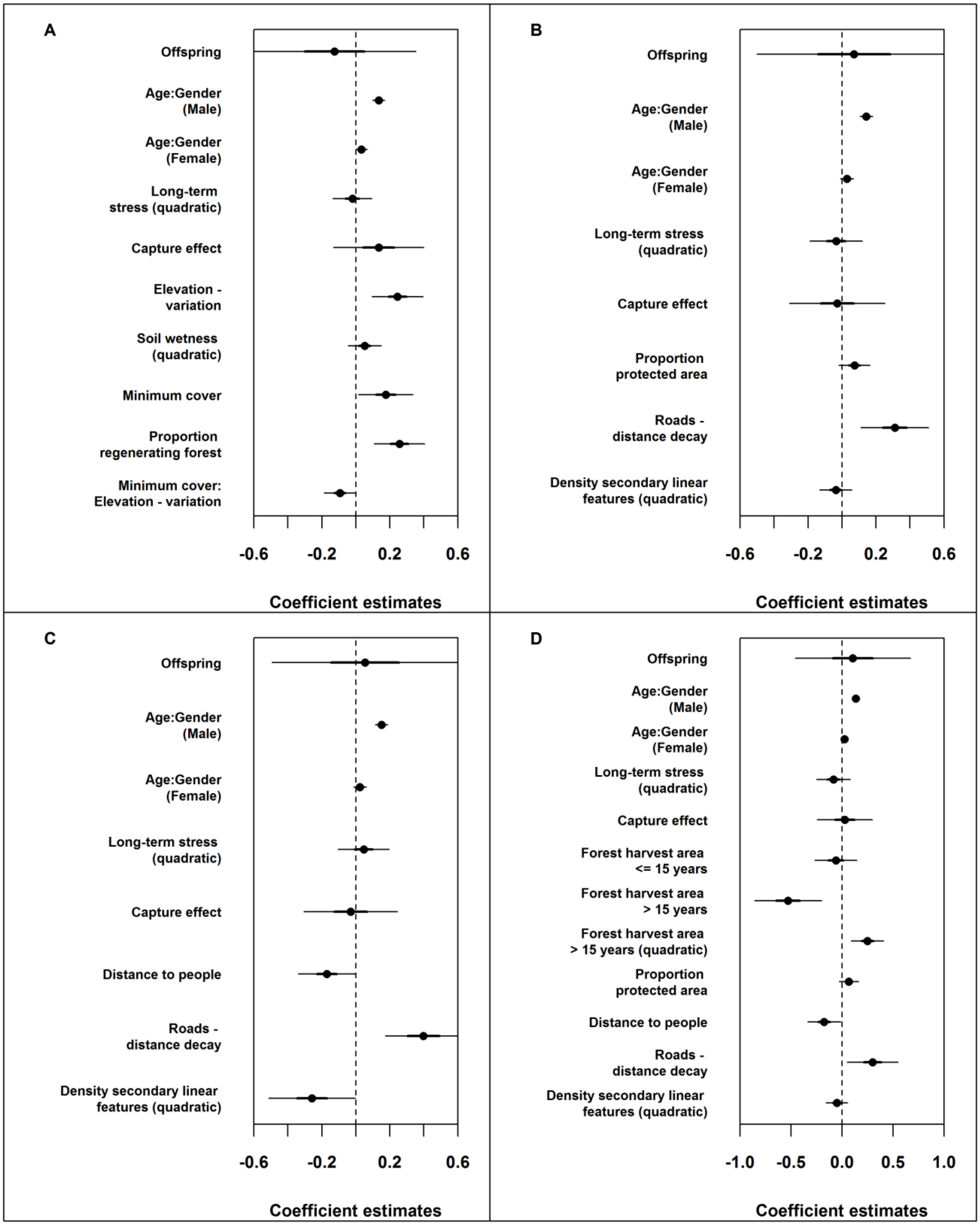

Figure 3.4 Estimated parameter coefficients to predict grizzly bear body condition index at four spatial scales.

Bold lines represent the 50% confidence intervals, whereas narrow lines represent the 95% confidence intervals for each parameter. A) 25th percentile habitat selection model B) 50th percentile habitat selection model C)75th percentile habitat selection model D) 95th percentile habitat selection models

4.0 CONCLUSION

4.1 Discussion and Conclusions

Grizzly bears are a primary conservation concern in North America (Carroll et al. 2001; Noss et al. 2002). As one of the largest predators on the continent which occupy large areas, protection of grizzly bears and their habitat is considered to be of benefit to ecosystems and other species (Carroll et al. 2003; Carroll et al. 2004). However, conservation of remaining populations has proven difficult due to conflicting public opinion and land-use policies (Mattson et al.1996; Kellert et al. 2002). Grizzly bear habitat selection is also highly variable, both spatially and temporally (Munro et al. 2006; Ciarniello et al. 2007a), and has been found to incorporate areas near human activity (Blanchard & Knight 1991; Nielsen et al. 2004a; Roever et al. 2008a), further compounding difficulties in management planning.

Considerable research has examined how anthropogenic activities and land use contribute to observed patterns of grizzly bear habitat selection and mortality (e.g., McLellan et al. 1999; Benn & Herrero 2002; Nielsen et al. 2004b; Garshelis et al. 2005; Ciarniello et al. 2007b). A central theme in these studies is the influence of features which provide human access to grizzly bear habitat, such as roads, trails, and railways, and are a primary factor in grizzly bear mortality. There is also evidence which suggests landscape fragmentation due to anthropogenic features has resulted in altered habitat selection patterns (Linke et al. 2005), and reduced landscape permeability (Chruszcz et al. 2003; Singleton et al. 2004; Proctor et al. 2012), creating a number of genetically isolated sub-populations which may not be viable over the long-term (Proctor et al. 2012). Further, while a number of studies have demonstrated bears select habitat associated with anthropogenic disturbance due to increased availability of foods (Nielsen et al. 2004c; Roever et al. 2008b; Stewart et al. 2012) which allow bears to maximize body condition, the mortality risk presented by these habitats outweighs potential gains (Nielsen et al. 2006; Nielsen et al. 2008).

While research has illustrated how anthropogenic disturbance and habitat quality impact mortality and grizzly population dynamics, little is understood regarding how these same factors impact the health of individuals. Access to habitat which meets nutritional needs is a primary factor in determining the health of individuals, their reproductive capacity, and the long-term viability of populations (Morrison 2001). Factors which disrupt the availability of quality habitat, or which result in an energetic imbalance, have negative health consequences for animals (McEwen & Wingfield 2003). However, as noted by Ellis et al. (2012), research examining the relationship between landscape conditions and animal physiology has been lacking. The goal of this research was to quantify the spatial relationships between habitat quality, anthropogenic disturbance, and grizzly bear health using two novel datasets detailing long-term stress and body condition of individuals. To meet the research goal, two objectives were addressed: 1) a spatially explicit model was developed to predict spatial patterns of long-term stress in male and female grizzly bears in relation to habitat quality and anthropogenic disturbance; and 2) examine how scale-specific patterns of habitat selection, and associated landscape conditions, biology, and long-term stress influence body condition of individuals.

In Chapter 2, I developed a model to quantify and predict impacts of habitat quality and anthropogenic disturbance on spatial patterns of long-term stress in male and female grizzly bears. The stress response was represented using hair cortisol concentrations (HCC) taken from 304 individuals (Macbeth et al. 2010). The predicted long-term stress response in regards to landscape conditions differed substantially for male and female grizzly bears, as shown by the geographically distinct patterns. High female HCC values were generally associated with high elevation parks and protected areas and foothills with rugged terrain, which have high seasonality, low minimum cover, and minimal anthropogenic activity. Low to moderate female stress shows a spatial relationship with regions that have a higher concentration of anthropogenic disturbance features, such as roads and forest harvest blocks. In contrast, male HCC values were generally low in parks and protected areas, and associated with moderate to high elevation seasonal habitats, minimal crown closure, and occur far from roads. Gender-specific differences in selection of habitats associated with anthropogenic disturbance may partly explain observed geographic dissimilarity in the stress response as female grizzly bears have been found to use these habitats more frequently than males, both inside and outside of parks and protected areas, due the availability of herbaceous foods (Nielsen et al. 2004c; Roever et al. 2008b; Graham et al. 2010; Stewart et al. 2013). Sexual segregation, resulting from female avoidance of males due to the risk of infanticide (McLellan 2005; Rode et al. 2006; Libal et al. 2011; Smulders et al. 2012; Steyaert et al. 2013), and philopatric habitat selection patterns in the female demographic (McLellan & Hovey 2001; Proctor et al. 2004; Støen et al. 2005; Nielsen et al. 2013), may also explain the observed spatial trends in the stress response if females are in fact occupying sub-optimal habitat due to avoidance of males.

Potential conservation implications associated with the observed spatial patterns in male and female long-term stress were illustrated by examining the distribution of stress values in association with parks and protected areas, core and secondary habitat areas, and sink and secure habitat (Nielsen et al. 2006; Nielsen et al. 2009). Of particular concern are the strong associations of low female stress values with sink habitats, and higher stress values associated with parks and protected areas, core habitat areas, and secure habitat. These patterns suggest females are willing to occupy high-risk high-reward habitats in order to maximize food intake thereby putting the reproductive demographic of the population at higher risk of mortality. In parks and protected areas, where available high quality habitat is in deficit (Gibeau et al. 2001), areas occupied by females may not be meeting caloric requirements resulting in an elevated stress response. Closing roads and restricting human access, while increasing the distribution of early seral stage forest habitats, may not only reduce mortality rates (Nielsen et al. 2004a), it may also provide both male and female grizzly bears with health benefits associated with these habitats.

In Chapter 3, I modelled the influence of habitat quality and anthropogenic disturbance on body condition, represented using a body condition index (Cattet et al. 2002), of grizzly bears based on seasonal and scale-specific patterns of habitat selection. Habitat selection by grizzly bears in a heterogeneous landscape is complex (Ciarniello et al. 2007a), as grizzly bears will occupy large home ranges depending on energetic requirements (McLoughlin et al. 2000; Dahle et al. 2006; Rode et al. 2006), and seasonal behaviours (Dahle & Swenson 2003; Munro et al. 2006; Smulders et al. 2012). Evaluation of several a priori hypotheses regarding the influence of biology, habitat quality, and anthropogenic disturbance on body condition index values across a continuum of habitat selection scales revealed interesting trends in hypothesis support. Across all scales, biological factors were important, as males were found to have higher body condition which increased with age in both genders. A possible explanation for this pattern is sexual segregation resulting from sexual size dimorphism, and the associated nutritional requirements, as well as female avoidance of male bears due to infanticide and philopatric habitat selection (Proctor et al. 2004; McLellan, 2005; Rode et al. 2006; Smulders et al. 2012; Nielsen et al.

2013). At the scale of most concentrated habitat selection, the biology and habitat selection hypothesis had the greatest support, as habitat quality variables representing elevation, soil wetness, minimum vegetation cover, and proportion regenerating forest were associated with increased body condition. As habitat variables considered represent proxies for food availability, their influence on body condition in the area most used by a bear is supported by the fact that animals require and will occupy habitat which allows them to meet nutritional requirements (Morrison 2001). Interestingly, the relationship between environmental conditions and long-term stress was most pronounced at the scale of most concentrated habitat selection, suggesting a link between stress related to energetic reserves associated with habitat quality and food availability in grizzly bears (McEwen & Wingfield 2003).

As the scale of habitat selection was represented more broadly, the importance of anthropogenic variables increased. Generally, anthropogenic disturbance features were associated with lower body condition index values. Anthropogenic variables of particular importance were roads and secondary linear disturbance features including cut-lines, pipelines, and power-lines. While both roads and linear features provide access to grizzly bear habitat, the density of roads has been identified as a factor of particular concern due to high rates of mortality associated with roads (Benn & Herrero 2002; Nielsen et al. 2004a; Ciarniello et al. 2007b), and potential energetic costs associated with habitat selection near roads (McLellan & Shackleton 1988; Frid & Dill 2002; Gibeau et al. 2002). The influence of roads and human activity associated with them may extend to habitat and disturbance features in the surrounding area as forest harvest blocks, which contain abundant important grizzly bear foods (Nielsen et al. 2004c), were also found to have a negative impact on grizzly bear body condition. Secondary linear features represent a significant forest disturbance feature in Alberta which have altered the configuration of forest patches (Lee & Boutin 2006; Linke et al. 2008). While grizzly bears, in particular females, will select habitat associated with anthropogenic edges due to the presence of foods (Stewart et al. 2013), results presented here support Linke et al. (2005) who hypothesized energetic costs associated with increased fragmentation resulting from edge density would negate potential gains from food availability. Based on observed scale-specific relationships between habitat quality, anthropogenic disturbance, and grizzly bear body condition, management efforts should be focused to enhance habitat quality within core habitat areas and limit anthropogenic disturbance within larger grizzly bear home ranges.

4.2 Research Contributions

The first major contribution of this research was the development of a model to predict long-term stress in male and female grizzly bears based on the relationship between hair cortisol concentrations, habitat quality, and anthropogenic disturbance. To my knowledge, the results presented here represent the first attempt to link patterns of long-term stress with environmental conditions in grizzly bears. Linking stress and environmental conditions is a significant contribution to the fields of conservation physiology, ecology, and biology, and highlights the utility of a spatial approach when dealing with wildlife health metrics. Despite the well-established nature of stress and health metrics in wildlife research (Romero 2004; Reeder & Kramer 2005; Macbeth et al. 2010; Sheriff et al. 2011), to date studies linking these metrics with environmental conditions, including both habitat quality and anthropogenic influence, have been lacking (Wikelski & Cooke 2006; Ellis et al. 2012). The threatened nature of grizzly bear populations across much of their range, combined with their status as an apex predator and umbrella species for conservation, makes them an ideal subject species for examining relationships between long-term stress and environmental conditions (Cooke & O'Connor 2010). Grizzly bears are large, wide ranging animals which occupy a wide variety of habitats due to their omnivorous diet. Further, despite high mortality and increasing anthropogenic pressures on their habitat, grizzly bears have proven remarkably adept at adapting their behaviours to anthropogenic-disturbed habitats. Prior to this research little was known regarding how environmental conditions across their range impacted long-term stress in grizzly bears.

The second major contribution of this research extends the knowledge gained in the first analysis to include impacts of biology and environmental conditions on body condition of grizzly bears providing a more complete understanding of how habitat selection patterns within a highly disturbed heterogeneous landscape influence health. Building upon the results of Ciarniello et al. (2007a), who suggested grizzly bear habitat selection is scale dependent, I show that these scale dependent patterns of habitat selection have an impact on grizzly bear body condition. Parallels can also be drawn between the results of the two analyses, particularly in terms of the impacts of anthropogenic disturbance. For example, roads were an important variable in both analyses, and their proximity elicited a stronger stress response in males compared to females. However, bears whose patterns of habitat selection were further from roads had higher body condition. These results suggest the presence of an energetic mismatch stemming from selection of habitats adjacent to anthropogenic disturbances. Numerous studies which have quantified impacts of anthropogenic disturbance and activities on grizzly bear behaviour and mortality have recommended restricting access to grizzly bear habitat in an effort to reduce exposure to humans and mortality rates (Benn & Herrero 2002; Gibeau et al. 2002; Nielsen et al. 2004a). Given food availability present within disturbed habitats, the results of the two analyses presented here provide further support for restricting human access in grizzly bear habitat and extend the potential impacts to include a tangible health benefit for grizzly bears.

The third major contribution of this research highlights the utility of spatial analysis when working with a wide variety of disparate data in a multi-disciplinary context. As Nelson (2012) notes, demonstrating the benefits of spatial explanatory modelling is an important precursor to wide-spread adoption of spatial methods and data. This research effectively integrates data from a variety of scientific fields, including remote sensing, wildlife biology, conservation physiology, and landscape ecology, within a geographic framework. Spatial methods, such as kernel density estimation (KDE), KDE surface validation, and scale-specific habitat selection based on utilization distributions, provide robust methods for researchers to incorporate point based health metrics with continuous landscape variables. Further, synthesizing complex spatial results in cartographic form, as shown here, provides novel products which are of great use to management and scientists from other fields (Armstrong & Densham 2008; Nelson 2012). As such, methods developed and presented here have clearly demonstrated the utility of a spatial approach and can be applied in other wildlife research.

4.3 Research Opportunities

The methods and findings in this thesis present many new and exciting research opportunities. In recognition of the importance of understanding the health of wildlife in relation to environmental conditions, stress based metrics are being collected from an increasingly diverse array of free-ranging species including polar bears (Bechshøft et al. 2011), ungulates (Millspaugh et al. 2001; Ashley et al. 2011; Wasser et al. 2011), wolves (Creel et al. 2002), birds (Blas et al. 2007), and even marine mammals such as killer whales (Ayres et al. 2012). When using point based non-invasive stress metrics, such as hair cortisol concentrations (Macbeth et al. 2010), methods presented in this thesis provide an effective means of representing spatial variability in the stress response across the landscape. Applied to similar stress metrics, the methods presented here provide an effective and easily interpretable comparison from a conservation management perspective of spatial patterns of stress across taxa which occupy the same functional range.

It would also be interesting to extend this research to quantify impacts of conspecific interaction and competition on stress and body condition in grizzly bears. While many of the patterns and results presented here suggest the potential influence of sexual segregation in habitat selection, it was not possible to these quantify these behaviours. As we know habitat selection patterns, and resultant access to foods, are highly subject to gender and reproductive status (Nielsen et al. 2002; Dahle & Swenson 2003; Dahle et al. 2006; Berland et al. 2008; Stewart et al. 2013), conspecific factors which limit access to necessary habitat likely play an important role in long-term stress and health of grizzly bears, and potentially other *ursids*. Finally, a great deal of attention, with good reason, has been given to understanding the impacts of anthropogenic disturbance on grizzly bear habitat. However, as the diet of grizzly bears in areas such as Alberta is comprised primarily of herbaceous foods, roots, and berries (Mowat & Heard 2006), it would be interesting to explore the impact of climate change on the availability of these foods and potential impacts on grizzly bear body condition, particularly as this analysis provided preliminary evidence of a relationship between stress and resource availability. By combining available telemetry data, food models (Nielsen et al. 2010), and high temporal and spatial resolution climate data (Wang et al. 2012; Holmes et al. 2013), such an analysis would be possible.

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