Quantifying grizzly bear habitat selection in a human disturbed landscape

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Abstract

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Understanding the use of habitat by large carnivores in the presence of ever increasing anthropogenic disturbance is crucial to managing threatened species. In the foothills of the Rocky Mountains in west-central Alberta, Canada the grizzly bear (*Ursus arctos*) faces such disturbance, and is especially susceptible due to their low fecundity and large home ranges. Grizzly bear mortality increases with proximity to human disturbance, leading to the conclusion that anthropogenic forest disturbance is incompatible with successful grizzly bear habitat

The purpose of this research is to evaluate grizzly bear habitat use as it relates to forest disturbance. The general approach was to quantify grizzly bear habitat use and compare to an expectation of use calculated through conditional randomization. The research involved two distinct analyses. First, grizzly bear use of natural edges (transitions between land cover classes) and anthropogenic landscape edges (roads, pipelines, and forest harvests) was quantified and compared between seasons and sex. Females were found to use anthropogenic edges more than natural edges, whereas males used natural edges more. Despite the increased mortality threat arising from increased human access around anthropogenic disturbances, female grizzly bears are using anthropogenic edges more than natural edges, meaning anthropogenic edges may not be incompatible with successful grizzly bear populations. Knowing that female grizzly bears use anthropogenic edges more allows managers to limit access to areas with specific edges desirable to female bears. While creating more disturbances is not the solution to managing for better grizzly bear habitat, limiting human access to areas of beneficial edge could decrease mortality risk.

Knowing that grizzly bears use edges, the second analysis quantified use of forest disturbances of varying ages, and determined what disturbance characteristics drive grizzly bear selection of forest disturbances. A 40-year forest disturbance dataset was generated through image differencing of the tasselled cap angle transformation of Landsat imagery (MSS, TM, ETM+). Disturbances were grouped into decades, and compared. Disturbances were labelled as selected or not selected through a randomization process, and selected disturbances were compared to not-selected disturbances using four landscape metrics: disturbance size, disturbance elevation, average tasselled cap transformation greenness, and distance from disturbance to nearest human settlement along a road network. Results indicate that bears select for larger disturbances in all seasons. Females select for disturbances with low remotely-sensed greenness in all seasons, where males select for disturbances with low remotely-sensed greenness in the spring and fall, but high remotely-sensed greenness in the summer. Females select for disturbances at a consistent elevation, whereas males show seasonal variation. Both sexes avoid the most recent disturbances from the 2000s. Females show greater selection of disturbances in the summer and fall, whereas males select disturbances in the fall the least. Knowing that bears select for large disturbances, and females select disturbances at a consistent elevation, forest managers can limit human access to these areas in order to limit human and bear interactions and reduce mortality risk.

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Co-authorship Statement

This thesis is the combination of two scientific manuscripts (chapters two and three) for which I am the lead author. The initial project structure was designed by Trisalyn Nelson and Mike Wulder, with the spatial analysis of grizzly bear habitat selection and forest disturbance as the main research issue. For these two articles I performed all the research and analysis, as well as the initial interpretation of results, and final manuscript preparation. Dr Scott Nielsen provided assistance with results interpretation and methods refinement. Dr. Gordon Stenhouse provided the data. Dr. Nelson, Dr. Wulder, and Dr. Nielsen provided important comments and suggestions incorporated into the final manuscript.

Chapter 1: Introduction

The increasing influence of human disturbance on the natural world has caused mass extinctions orders of magnitude beyond the natural rate (Raven 2002, Balmford et al. 2003). In order to better understand the impacts of human expansion on habitat use, a better understanding of how species adapt to human disturbance is necessary, as there is great variation between species' reactions to anthropogenic disturbance. Disturbances can decrease species fitness through elimination of habitat (Turner et al. 1994, Brooks et al. 1999) and increased exposure to predation (Courtois et al. 2007). Some species have also shown behavioural plasticity through adaptations to feeding and behaviour (Nielsen et al. 2004a, Boydston et al. 2006). Few species suffer greater impacts from anthropogenic disturbances than large predators, as low fecundity and large home ranges makes them especially susceptible to extirpation and extinction (Noss et al. 1996, Purvis et al. 2000)

The status of large predators is a cause for concern globally. There are examples of numerous large predators from many families facing extirpation and extinction. From tigers in southeast Asia (Seidensticker 1980) to wolverines in the United States (Aubry et al. 2007) to wild dogs in Africa (Gusset et al. 2008) large predators face increasing pressure from anthropogenic sources throughout their range. While there is acknowledgement of the problem from both national and international governing bodies, the complexity of these species makes conservation difficult (Clark et al. 1996, Weber and Rabinowitz 1996). The combination of ecological complexity with shifting human values (McFarlane and Boxall 2000, Kaczensky et al. 2011) makes managing these ecologically important species complicated.

The grizzly bear (*Ursus arctos*) is a large predator facing such threats. With large home ranges, seasonal and daily variations in diet (Munro et al. 2006), and low fecundity (Naves et al. 2003), grizzly bears are vulnerable to increasing human expansion. The grizzly bear is an important top-level predator in North America. However, it has been extirpated from much of its range (Banci et al. 1994). Historically the bear ranged across western North America, as far east as the Great Lakes and south to Mexico. While the current population in North America is under pressure from human development (Kendall et al. 2009, Festa-Bianchet 2010), the bear is also in peril in Japan (Sato et al. 2008), Scandinavia (Nellemann et al. 2007), and Spain (Naves et al. 2003). If these populations are to be maintained, understanding their interaction with anthropogenic disturbance is crucial, as human society continues to expand into important grizzly bear habitat.

The Alberta grizzly bear population is the focus of this project. There was a recommendation in 2002 to list the grizzly bear as threatened under Alberta's Wildlife Act. This recommendation was not accepted at the time, and the grizzly bear remained off the list until it was finally listed as threatened in 2010 (Clark and Slocombe 2011). Meanwhile, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) listed the grizzly bear as a species of special concern in 2002. However, the Canadian government did not list it under the Species at Risk Act (SARA) affording it no legal protection. While there are areas of the Alberta grizzly bears' range that fall in protected areas (provincial and national parks), most of their range puts them in close contact with human development. Most notably, this interaction occurs through the resource extraction industries, as forestry and oil and gas exploration play an important economic role in areas that overlap grizzly bear home ranges.

The interaction between humans and grizzly bears in our study area is complicated by two juxtaposing concepts. First, humans are directly responsible for the majority of grizzly bear mortality in areas of high anthropogenic disturbances (McLellan et al. 1999, Nielsen et al. 2004b). Benn and Herrero (2002) determined that 80% of grizzly bear mortalities in Banff and Yoho national parks were cause by direct human influence; 95% of these human caused mortalities occurred within 500m of a road or 200m of a trail. In another study in Yellowstone National Park, Schwartz et al. (2004) found that human-induced grizzly bear mortality (85% of known mortality) was more likely as motorized access increased. As bears move into closer contact with human development grizzly bear mortality increases through vehicle collisions, poaching and illegal hunting, and the removal of nuisance bears.

Increased human-caused grizzly bear mortality associated with increased human bear interactions around anthropogenic disturbances is juxtaposed by the fact that anthropogenic disturbances have been observed to provide grizzly bears in Alberta with important food resources (Nielsen et al. 2004a). Due to the long history of resource extraction in Alberta (Rhemtulla et al. 2002), intense fire suppression has eliminated natural forest clearings that are used by grizzly bears in other areas (Ciarniello et al. 2007). The selection of anthropogenic forest disturbances by grizzly bears varies between study areas, with bears avoiding disturbances (Zager et al. 1983, McLellan and Hovey 2001), using them as available (Berland et al. 2008), or selecting for them (Elgmork and Kaasa 1992, Nielsen et al. 2004a). In our study area, due to the lack of natural forest clearings, bears resort to anthropogenic forest disturbances for important food resources (Nielsen et al. 2004c). Understanding the conflict between increased human-caused mortality and grizzly bear selection of human disturbed areas is the purpose of this project, as developing a better understanding of grizzly bear habitat selection in areas of intense anthropogenic disturbance is integral to managing habitats for grizzly bear survival.

Performing this kind of wide-area habitat analysis is only possible using modern animal tracking systems and remote sensing technologies. Wildlife tracking has been buoyed by advances in GPS technology, and has been used in studies of a number of wide ranging species, e.g. whales (Watkins et al. 2002), caribou (Vors et al. 2007), wolves (Hayes and Russell 2011), and grizzly bears (Mace et al. 2008, Nielsen et al. 2010). Dense temporal data afforded by modern GPS tracking systems allows researchers to delve into fine scale habitat selection in ways not previously possible. The comparison of animal location to habitat is facilitated through satellite acquired habitat models, including habitat utilization metrics, such as resource selection functions (Manly 2002, Nielsen et al. 2009), and forest disturbance inventories (White et al. In Press). Remotely derived forest products provide a temporal and spatial consistency not otherwise possible. Our remotely derived data comes from the Landsat series of satellites (MSS, TM ETM+). The Landsat series of satellites provide a long temporal history, and as the Landsat database is now freely available (Woodcock et al. 2008) and there are plans to extend the Landsat mission (Wulder et al. 2008, Wulder et al. 2011) the work presented herein can be applied in many other study areas. The integration of novel datasets derived from remotely sensed imagery within a geographic information system enables researchers to perform complex analyses not previously possible; however, as data volumes grow, novel statistical analyses are necessary to maintain statistical rigour.

This project focuses on a comparison between observed grizzly bear habitat use and expected habitat use. Expectations are generated through randomization processes, which incorporate important assumptions not prevalent in aspatial, classical statistics. While randomization is a useful method for generation of expected distributions and has a tradition in aspatial statistics, it is important to extend methods to enable more ecologically meaningful comparisons than standard null hypotheses like complete spatial randomness (CSR). Under CSR the null hypothesis is always that observed spatial patterns are similar to patterns generated by random processes. In most cases, CSR is not a valid expectation in ecology (Fortin and Jacquez 2000, Martin et al. 2008). For instance, we have a plethora of research which indicates that certain habitat and food sources create favourable habitat for bears and we would not expect bears to use habitat randomly. By combining rich datasets with advanced approaches to conditional randomization we are able to quantify grizzly bear habitat use, and quantify grizzly bear selection of disturbances.

Research Focus

The current best estimate for the grizzly bear population in Alberta is 691 in lands under provincial jurisdiction (Festa-Bianchet 2010). This is a small population that, coupled with expanding human transportation networks and resource extraction activities, is vulnerable. Understanding grizzly bear’s interaction with forest disturbances is integral to providing forest managers with necessary information for managing areas of intense resource extraction.

Thesis Objective

This research is concerned with quantifying the varying nature of grizzly bear habitat selection as it relates to disturbances. By understanding how bears interact with forest disturbances human mitigation efforts can be made to optimize resource extraction activities to maintain grizzly bear habitat. This will be accomplished through two specific analyses.

1) Determine differences in grizzly bear use of anthropogenic and natural edges. This will be accomplished by determining the density of edge types in grizzly bear home ranges, and quantifying the rates of use of varying natural and anthropogenic edges.

2) Determine grizzly bear selection of forest harvests of varying age, and evaluate the characteristics of forest disturbances selected by grizzly bears. By determining the selection of different ages of regenerating forests, it may be possible to alter harvest regimes or manage access on the landscape to optimize grizzly bear habitat.

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Chapter 2: Quantifying grizzly bear use of natural and anthropogenic edges

Abstract

The effect of edges on habitat use by threatened species is an important management consideration. The study of edges has focused mostly on anthropogenic disturbances and the ways in which newly introduced edges affect animal behaviour. While anthropogenic edges are important in managing threatened species, natural edges have been mostly ignored. Our goal is to quantify grizzly bear (*Ursus arctos*) habitat use of landscape-level measures of habitat edge; both natural edges and edges created by anthropogenic disturbance will be considered. We define edges as transitions between land cover types (natural edges) or interruptions in natural land cover (anthropogenic edges). GPS telemetry data from 26 grizzly bears were collected from 2005 to 2009 in the foothills of the Rocky Mountains in west-central Alberta, Canada. Observed grizzly bear locations were compared to natural edges extracted from satellite derived land cover data and anthropogenic edges from existing vector datasets (roads, pipelines, and forest harvests). The Euclidean distance from each grizzly bear location to the nearest edge was calculated and labelled as used. Observed edge use statistics were compared to an expectation of edge use created through a conditional randomization of grizzly bear points. Results show variation between seasons and sexes in edge use and home range edge density. Natural shrub-conifer and shrub-mixed forest edges show little seasonal variation, with shrub-broadleaf transitions having increased use in the spring and summer. Wetland edges occur at higher density in female home ranges, but are used less than expected. Roads are used more than expected by females but used less than expected by males. Females use pipelines more than expected and more often than males; but males also show higher than expected use of pipelines in the spring. Seasonal differences indicate that females and males both occupy areas with higher edge density in the fall, possibly due to changes in feeding requirements. Overall, female bears use anthropogenic edges more frequently than natural edges, whereas male bears use natural edges more frequently than anthropogenic edges. Given that female bears preferentially select for anthropogenic edges, if managed carefully, anthropogenic disturbances are not always incompatible with successful grizzly bear populations.

Introduction

Understanding species' interactions with landscape edges is a primary goal of ecology. Edges are defined as the boundaries separating distinct habitat patches (Ries et al. 2004) and play an important role in ecosystem dynamics (Fortin et al. 2000). Edges alter the flow of energy, materials, and organisms, which, in turn, alters the composition of species (Ries et al. 2004). Creation of edge habitat can increase mortality as species are exposed to increased predation (Gardner 1998) or parasitism (Murcis 1995), or improve conditions as edges provide access to complimentary habitat patches in close proximity (Lay 1938, Ries and Sisk 2004). The introduction of edges into species' habitat is often linked to an increase in anthropogenic disturbances, which is a cause of species extinction worldwide (Raven 2002, Balmford et al. 2003). Understanding how species use both natural and anthropogenic edges is vital to wildlife management.

The grizzly bear (*Ursus arctos*) is an ideal case study for analyzing the use of natural and anthropogenic edges, as grizzly bears exist in diverse, multi-use environments, where increasing levels of anthropogenic disturbance are impacting traditional habitat (Berland et al. 2008, Mace et al. 1999, Festa-Bianchet 2010). Seasonal shifts in grizzly bear diet (Servheen 1983, Elgmork and Kaasa 1992, Klinka and Reimchen 2002, Munro et al. 2006) require an array of habitats that shift throughout the year. As edges can provide increased food resources at transitions between homogenous land cover types (Ries et al. 2004), they are often attractants to grizzly bears. While edges may provide benefits, the use of anthropogenic edges has been linked to increased grizzly bear mortality (Benn and Herrero 2002, Nielsen et al. 2002). With the increasing density of anthropogenic disturbances from road development and resource extraction (Nielsen et al. 2008), grizzly bears are exposed to more anthropogenic edges and fewer natural edges. Understanding the use of natural and anthropogenic edges by grizzly bears will assist in designing effective management plans.

Much research has been done on the use of anthropogenic disturbances in grizzly bear habitat with a focus on forest harvests and roads (Elgmork 1978, McLellan and Shackleton 1988, Kaczensky et al. 2003, Nielsen et al. 2004a, Roever et al. 2008b). It is important to understand grizzly bear use of anthropogenic edges as 90% of human-caused grizzly bear mortalities occur within 500 m of a road or 200 m of a trail (Benn and Herrero 2002). There is also evidence that grizzly bears avoid being within 500 m of roads (Waller and Servheen 2005) due to the associated mortality risk from vehicle collisions and hunters. However, grizzly bears have also been found to preferentially use areas within 1000 m of roads in other study areas (Kaczensky et al. 2003). In our same study area, grizzly bears have been shown to increase use of low traffic roads (Graham et al. 2010); however this varies by age, sex, and female reproductive status. Females and sub-adults cross roads more frequently than males (Chruszcz et al. 2003, Graham et al.

2010) possibly to avoid adult males (McLellan and Shackleton 1988), or due to variations in male diet or male survival around roads (Graham et al. 2010).

Grizzly bears' interactions with forest harvests are equally complex. Studies have shown a range of grizzly bear interaction with forest harvests including avoidance (Zager et al. 1983, McLellan and Hovey 2001), use as available (Wielgus et al. 2003, Berland et al. 2008), and selection (Nielsen et al. 2004a, Martin et al. 2010). Selection for clearcuts tends to occur in areas lacking natural forest clearings, often due to fire suppression associated with resource extraction industries (Schneider 2002). When natural disturbances are limited, bears use forest harvests due to increased food availability along edges and within young regenerating clearcuts (Elgmork 1978, Nielsen et al. 2004c). Studies of other populations have shown similar trends of grizzly bears selecting for anthropogenic disturbances. Sato et al. (2004) showed that an increase in grizzly bear encounters with humans was not a result of increased grizzly bear density, but rather a change in grizzly bear diet which relies more on sika deer (*Cervus nippon*) and human agriculture. As bears feed on the carcasses of control killed sika deer found in agricultural fields, and on the agricultural products themselves bears are found in increasingly closer contact with people.

While the relationship between grizzly bears and anthropogenic edges has been investigated in detail, the relationship with natural edges is less well researched. Natural land cover edges have been included in habitat models of grizzly bear resource use and show increasing distance to forest edge negatively affects the presence of important grizzly bear foods (Nielsen et al. 2010), and negatively affects habitat selection by adult female grizzly bears (Nielsen et al. 2006). These results indicate the importance of natural edges in grizzly bear habitat use, and also indicate a need for investigation of detailed use of differing edge types, especially including discrimination between natural edge types. As edges provide increased food resources (Ries et al. 2004) and grizzly bears have shown selection for anthropogenic edges, bears should show equal use of both natural and anthropogenic edges.

The goal of this research is to examine grizzly bear use of natural and anthropogenic landscape edges. There are two main objectives towards accomplishing this goal: 1) quantify edge density by edge type in available grizzly bear habitat (available being defined as area inside a bear's home range); 2) quantify and evaluate frequency of edge use. The hypotheses concerning these goals are 1) grizzly bears will use natural edges and anthropogenic edges equally; 2) edge use will vary seasonally and by sex.

Remotely sensed data provide a mechanism for analyzing the influence of edges on grizzly bear habitat across a large geographic area. Satellite imagery allows us to extract and analyze edges at a scale not possible with *in situ* measurements. Both edge location and the nature or type of edge can be quantified over large areas using remotely sensed data. Our general approach is to integrate remotely sensed and grizzly bear presence data through the following steps. First, we quantify natural edges on the landscape using earth observation data, and combine with existing vector datasets describing anthropogenic edge features. Second, we integrate edge data with grizzly bear telemetry data within a geographic information system to measure frequency of edge use and density of edges in bear home ranges. Finally, observed spatial patterns in edge use are compared to a null hypothesis of random habitat use conditioned on a resource selection function that accounts for many factors known to influence grizzly bear habitat selection. Given known variations in seasonal use of habitats and food resources (Munro et al. 2006), as well as sexual segregation of resources, analyses will be based on three seasonal periods and grizzly bear sex.

Methods

Study Area

The study area for this project is the Kakwa forest region in west-central Alberta, Canada (Figure 1). Land cover is characterized by montane forests, conifer forests, sub-alpine forests, alpine meadows, and high elevation snow, rock, and ice (Achuff 1994, Franklin et al. 2001). The elevation ranges from almost 2500 m in the west down to 600 m in the east. The land cover is dominated by forest; primarily conifer, with smaller patches of broadleaf and mixed forest. As elevation decreases from west to east, wetlands become increasingly common due to increased drainage (Franklin et al., 2001). Resource extraction industries have been active in the area for over 50 years with most forest disturbances in the area arising from the forest industry and oil and gas exploration (Schneider 2002).

Data

Telemetry Data

Telemetry data were recorded from 2005 – 2009 for 26 grizzly bears. Bears were captured using aerial darting, leg-hold snaring, and culvert traps (Stenhouse and Munro 2000). Capture efforts followed protocols accepted by the Canadian Council of Animal

Care for the safe handling of bears (Animal Use Protocol number 20010016). Each bear was fitted with a Tellus (Calgary, Alberta) GPS radio collar.

Grizzly bears have distinct feeding and behavioural patterns that vary throughout the year (Servheen 1983, Munro et al. 2006), necessitating variation in habitat use. Following previous research (Mace et al. 1999) telemetry data were partitioned seasonally based on shifts in diet and habitat. Spring is defined as den emergence to June 15th. Summer is defined as June 16th to August 15th, with fall defined as August 16th until October 15th (mean denning date). Bear telemetry points were also partitioned annually, creating sets of telemetry data for each season, year, and bear.

Telemetry points were cleaned based on positional dilution of precision (PDOP) which evaluates the three dimensional accuracy of GPS locations. Points with a PDOP greater than 10 were removed (D'Eon and Delparte 2005), and bears with seasonal telemetry data counting less than 50 points were removed from further processing due to the effect of small sample sizes on home range calculations (Seaman and Powell 1996). Data-processing resulted in 61 sets of yearly, seasonal telemetry points representing all 26 bears; see Table 1 for a summary.

Land cover

A satellite derived land cover dataset was obtained for extraction of natural edges (Franklin et al. 2001). The land cover dataset was created from a tasselled cap transformation (Huang et al. 2002) of Landsat TM data, a 100 m digital elevation model, and polygonal vegetation data from the Alberta vegetation inventory. The resulting 30 m resolution land cover dataset was compared to field data and had an accuracy of 80.16%. The original dataset contained 15 classes ranging from dense conifer to cloud and shadow, but was re-classified into 6 classes to facilitate the extraction of land cover transitions as described below in Table 2. Mean patch sizes are presented along with the land cover breakdown, indicating that the resolution of our land cover dataset (30 x 30 m or 900 m^2 pixels) is smaller than our minimum patch size.

Roads, Pipelines, and Forest Harvests

A series of vector layers were acquired as our anthropogenic edges and combined with natural edges extracted from the land cover dataset to create our edge inventory. A road network was obtained for the study area containing both major and minor roads (secondary and logging roads). A vector dataset for pipelines in the area was obtained, as these disturbances provide low-impact access to grizzly bear habitat (Nielsen et al. 2002). Both of these vector disturbance layers were based on the Alberta Sustainable Resource Development base feature dataset and were both updated through heads-up digitizing using medium to high resolution imagery (SPOT imagery and air photos).

Stand replacing forest disturbances were detected through image pair differencing of a series of satellite images from the Landsat series of satellites (see White et al. (In Press) for a detailed description of the image selection, image processing, and change detection process). All disturbances were converted from raster to vector polylines in order to integrate with the vector-based natural edge inventory. These edges were classified as forest harvests, and interpreted as anthropogenic disturbances.

Resource Selection Function

A resource selection function (RSF) was generated to provide a layer with which to condition our randomization process described later. While complete spatial randomness is a typical null hypothesis in spatial pattern analysis, it is a poor expectation for ecological processes which are known to vary based on environmental conditions (Cressie 1993). A RSF is a model that estimates the probability of use of a resource unit (Manly 2002). RSF models are usually estimated from observations of use versus available resource units (Boyce et al. 2002), and provide a statistically rigorous estimate of a habitat suitability index (Roloff and Kernohan 1999). RSFs have been used to estimate the effects of human disturbance on Elk (Edge et al. 1987), cattle grazing on southern mule deer (Bowyer and Bleich 1984), and grizzly bear habitat selection (Ciarniello et al. 2007, Nielsen et al. 2009). See Manly et al. (2002) for further discussion and explanation of RSF modeling design, and best practices.

We implemented a RSF model (Nielsen et al. 2009) to account for biological phenomena known to impact resources available to grizzly bears; however, edge related variables were removed from the model. The RSF model predicts resource selection based on land cover (wetland-tree, regenerating forest, shrub, wetland-herb, upland-herb, non-vegetated land), crown closure, species composition (conifer canopy), compound topographic index, as well as streams (Nielsen et al. 2009). Due to the seasonal flux of grizzly bear food availability, three models were designed, one for each grizzly bear season: spring (May 1st to June 15th), summer (June 16th to July 31), and fall (August 1 to October 15th). All three seasons used the same variables for estimation, with variation in coefficients. The models were created from a random sample of 90% of the data (training data), with the remaining kept aside for model evaluation (test data). Using spearman rank coefficients on the test data, the RSF model had p-values of 0.005, 0.0013, and 0.0010 for the spring, summer, and fall. The model explicitly excludes edge variables, in order to control for non-edge biological factors in known habitat selection. The assumption is that habitat selection processes that do not relate to use of edges are accounted for by the RSF, allowing statistical assessment of edge influences.

Analysis

The following steps, described in greater detail below, were taken to determine grizzly bear edge use. First, our vector-based anthropogenic edges (forest harvest edges, roads, and pipelines) were combined with natural edges extracted as vector data from a land cover dataset to create the edge inventory. Second, density of natural edges, anthropogenic edges, and grizzly bear telemetry points was calculated across the study area. Third, the edge inventory was intersected with grizzly bear home ranges to calculate home range edge density. Fourth, each set of grizzly bear telemetry points were randomly relocated 99 times. Randomization was restricted to the grizzly bear home ranges and conditioned on a seasonal RSF. Finally, observed grizzly bear locations and randomized grizzly bear locations were both compared to the edge inventory to evaluate edge use.

Edge Inventory: Natural and Anthropogenic Edges

Anthropogenic and natural edges were combined to create our GIS edge inventory (Table 3). First, anthropogenic edges were incorporated through the road, pipeline, and forest harvest datasets described above. Second, natural transitions between varying types of land cover were extracted from a land cover dataset (Wulder et al. 2009). A three pixel by three pixel (3x3) moving window was passed over the land cover dataset; homogenous windows were considered non-edges. If there was heterogeneity within the window, transitions were quantified. Less than 3% of the landscape had transitions with more than two land cover classes and were excluded due to their ecological complexity and small sample size. Edges were extracted from the 30 m resolution land cover dataset and converted to polylines for inclusion in our edge inventory.

Four land cover transitions were extracted for analyzing grizzly bear habitat use: shrub-conifer forest, shrub-mixed forest, shrub-broadleaf forest, and wetland-forest (all forest types). Transitions from forest (conifer, mixed, and broadleaf) to shrub were analyzed as many of the shrub areas represent forest clearings. Due to the overlap of shrub-forest edges (principally shrub-conifer edges) and forest harvests, natural edges that intersected forest harvests were removed from the natural edge inventory. The three classes of wetland to forest edges (wetland-conifer, wetland-broadleaf, and wetland-mixed) were combined into one wetland-forest edge class.

Calculate Density of Edges and Grizzly Bear Locations

Density of grizzly bear telemetry locations was calculated across the study area using kernel density estimation (KDE). The KDE bandwidth was estimated using least squares cross validation with a Gaussian kernel, with an output bandwidth of 1020 m. Final density of grizzly bear locations was classified as high, medium and low based on a three quantile break, meaning each of the three categories has an equal number of pixels.

Edge density was calculated across the study area for both natural and anthropogenic edges using kernel density estimation with a bandwidth of 1020 m in order to match the bear location density calculated above. Final densities were classified into high medium and low based on quantile classification, but the final quantiles were adjusted so that the class breaks match between the two edge metrics.

Calculate Home Range Edge Density

Edge density was calculated within the seasonal home range for each grizzly bear. A 95% by volume isopleth of a kernel density estimation (KDE) was used for home range delineation (Seaman and Powell 1996, Borger et al. 2006). The kernel approach to home range estimation was used as it accounts for multiple centres of activity (Powell 2000, Kenward 2001), is commonly used in wildlife management (Laver and Kelly 2008), and does not tend to overestimate home range area (Powell 2000). The bandwidth, which the kernel requires to define the region of data to include in each density estimate, was calculated for individual sets of bear telemetry locations using direct least-squares cross validation with a Gaussian kernel (Ruppert et al. 1995). Bandwidth values varied from 503 m to 988 m.

Once home ranges were created, the total length of each edge type in each home range was compared to the home range area to create an edge density in m/km^2. These densities were averaged for each season and sex class and compared using boxplots. The nature of home ranges by sex and season are also reported.

Randomizing Grizzly Bear Telemetry Data

Grizzly bear locations were randomized to generate expected distributions of edge use, see Figure 2. Randomization was limited spatially to the individual's home range, and conditioned on known habitat selection using a seasonal RSF (Fortin and Jacquez 2000, Smulders et al. 2010). By constraining the randomization we reduce type 1 errors, which are otherwise likely as complete spatial randomness is an unrealistic null hypothesis for ecological processes (Cressie 1993, Legendre 1993, Martin et al. 2008). As grizzly bears do not use landscapes randomly our methods account for biological processes that are already established (Nielsen et al. 2009), and accounted for by the seasonal RSF. The randomization was conditioned on the RSF by ensuring the distribution of RSF values in the randomized points matched the distribution of RSF values for the observed points. For each set of grizzly bear telemetry points, 99 sets of randomized points were generated and used to calculate expected edge use.

Comparison of Grizzly Bear Locations and Landscape Edges

Grizzly bear telemetry locations and randomized locations were integrated with the edge inventory to determine edge use. For grizzly bear locations (both observed and random) nearest edge was determined based on Euclidean distance, and edge type was recorded. Edge use was tabulated for each set of points as percentage of points using each edge type. Expected edge use was calculated by averaging edge use over all 99 randomizations. This expectation was compared to observed edge use through selection ratios (observed usage/expected usage). A selection ratio of one indicates edge is used as available, a value above one indicates greater than expected use, and values below one indicate less than expected use.

Results

Study Area Edge Density and Bear Location Density

Density of grizzly bear telemetry locations, anthropogenic edges, and natural edges was calculated across the study area using kernel density estimation. Results are presented in Figures 3, 4, and 5 respectively. Grizzly bear telemetry locations shows two distinct patches of grizzly bear data to the north and east of Grand Cache, Alberta as seen in Figure 3. The areas appear split by the only major road running through the centre of our study area. Anthropogenic edges show lower density in the south-west (Figure 4), in areas of higher elevation. Natural edges (Figure 5) show a fairly homogenous distribution except for a gap in the east of the study area,

Home Ranges and Edge Density

Home ranges were calculated for each set of grizzly bear telemetry points, and tabulated by sex and season (Table 4). Within sex comparisons show males have substantially larger home ranges in the spring and summer than in the fall, while females have slightly smaller home ranges in the fall. Between sexes, males show greater change in home range size across seasons than females, and more variation between minimum and maximum size. Females have smaller home ranges in the spring and summer than males, but males show smaller home ranges in the fall.

Comparison of home range edge density between seasons and sexes are presented in Figures 6 and 7. The seasonal trend for females indicates that edge density is the highest in the fall for all edge types. Males have fewer anthropogenic edges (roads, pipelines, and forest harvest edges) in their home ranges than females, especially forest harvest edges. While the trend is not as strong, males also have a higher density of edges in the fall for the three most common edges in their home ranges: forest harvest edges, shrub-conifer edges, and roads. Shrub-conifer and forest harvest edges are the most common edge type for both males and females. Roads and pipelines are the next most common edge for females, with males having a high density of roads and shrub-broadleaf edges.

Grizzly Bear Edge Use

The frequency of grizzly bear edge use is summarized in Table 5, with selection ratios presented in Table 6 comparing observed use to expected use. Females use wetland transitions more than males (4.74%, 5.77%, and 3.54% in spring, summer, and fall, compared to 0.71%, 1.75%, and 0.31% for males). However, female selection ratios for wetland edges are much lower than males, with selection ratios of 0.51, 0.55, and 0.48 for spring, summer, and fall respectively. For both sexes, the highest wetland edge selection ratio is in the summer, with higher than expected use by males (1.16). Both males and females use shrub-conifer and shrub-mixed forest edges as available throughout the year, with males increasing use of shrub-mixed forests in the fall. Shrub-broadleaf edges show increased use in the spring and summer for both sexes (1.32, 1.23 for females in the spring and summer, 1.21, 1.24 for males). A comparison of total use of anthropogenic and natural edges shows females using anthropogenic edges more than natural edges in all seasons, whereas males use natural edges more than anthropogenic edges in all seasons.

Use of anthropogenic edges shows more variation between sexes than natural edge use. Females use forest harvest edges as available in the spring and summer, but show increased use in the fall (selection ratio of 1.11), whereas males show less than expected use of forest harvests in the Spring (0.85) with expected use in the summer and fall. Males and females both use pipelines more than expected in the spring (selection ratio of 1.21 and 1.16 respectively), while females are observed to increase use in the summer (1.56). Females show increased use of roads in the spring and summer (1.44, 1.65) but use as available (1.05) in the fall. Males show avoidance of roads in all seasons, most substantially in the fall (0.69). The summary edge use ratios indicate that females are using anthropogenic edges more than natural, particularly in the summer and fall. Males show less of a difference between use of natural and anthropogenic edges, but appear to use natural edges more.

Discussion

The results presented above indicate that we can reject the null hypothesis that grizzly bears use natural and anthropogenic equally for both male and female grizzly bears. Female grizzly bears shower higher density of anthropogenic disturbance in their home range, show higher use of anthropogenic edges, and have higher selection ratios for anthropogenic edges. On the other hand, male grizzly bears show slightly higher density of natural edges in their home range, while using natural edges more than anthropogenic edges. Selection ratios indicate slightly higher use of natural edges by male grizzly bears (except for the use of pipelines in the spring, Table 6). While the null hypothesis can be rejected for both sexes, it is rejected differently, as females use anthropogenic edges more and males use natural edges more, indicating the importance of both edge types in grizzly bear management plans.

Grizzly bears show seasonal and sexual variation in their use of natural and anthropogenic edges. Analysis of home ranges reveals grizzly bears have higher density of edges in their home ranges in the fall. For females all edge types occur at a higher density. For males, roads, forest harvest edges, and shrub-conifer edges are found at a higher density in the fall, and are the three most prevalent edge types. In the fall, male home ranges are smaller (Table 4), perhaps due to focused feeding (hypophagia) and abundant food sources. Females appear to use edges as available in the fall (except for wetland edges, Table 5), while having higher overall density of edges; female grizzly bears are selecting for areas with high edge density, while using edges as available within that area. The seasonal variation in edge is highlighted by the higher edge density in the fall

Anthropogenic edges show more variation in use between sexes, with females using anthropogenic edges more than males, specifically roads and pipelines. Roads are important in grizzly bear habitat selection, as bears travel widely, and are sensitive to anthropogenic disturbance (Nielsen et al. 2004b, Waller and Servheen 2005, Roever et al. 2008b). With 90% of grizzly bear deaths occurring within 500 m of a road or 200 m of a trail (Benn and Herrero 2002) increased use of roads by grizzly bears likely causes increased mortality risk. Previous studies have shown that grizzly bear and road interactions vary according to study area and traffic volume (Chruszcz et al. 2003, Kaczensky et al. 2003, Graham et al. 2010). Our results follow recent work in this study area that shows the importance of roads in grizzly bear habitat use (Roever et al. 2008a). However, our results show a difference between road use by males and females, as females have home ranges with higher road density (compare Figures 4 and 5), and females show increased use of roads in all seasons (Tables 5 and 6). Increased use of roads by females is a problem for conservation as female survival is the driving force in maintaining a viable grizzly bear population (Bunnell and Tait 1981, Eberhardt et al. 1994). As increased road use is likely to increase grizzly bear mortality (Lyon and Zuuring 1996, Gibeau et al. 2002, Graham et al. 2010), increased female use of active roads is a management concern.

A corollary to the use of roads by female grizzly bears is the use of pipelines. Our results indicate that the use of pipelines follows similar patterns to the use of roads, with females using them more than males, although males show increased use in the spring when male home ranges are larger (see Table 4), and males are searching for mates (Hamer and Herrero 1990). Increased pipeline use by males could be an indication that while male grizzly bears generally avoid linear anthropogenic disturbances, pipelines are used in the spring when bears are emerging from hibernation, and food resources are scarce. The concern with increased use of roads and pipelines by female bears is the associated increase in mortality risk due to increased human access (McLellan 1998, Benn and Herrero 2002, Nielsen et al. 2004b). While pipelines allow for increased human access and interaction, it is lower intensity access than roads (Nielsen et al. 2002) perhaps mitigating much of the risk associated with roads.

Our work illuminates the behaviour of bears as it relates to individual natural edges and edge types. Certain natural transitions show variation in use by season (shrub-broadleaf, wetland), while other edges are used as available throughout the year (shrub-conifer, shrub-mixed). The shrub-broadleaf edges show increased use by both males and females in the spring and summer. The increased use could be a function of feeding patterns in the area, as bears feed more on forbs and ungulate calves in the spring and early summer before switching to berries and other fruit in the fall (Munro et al. 2006). Other grizzly bear habitat studies have shown broadleaf forests are generally avoided (Sato et al. 2008), which is different from the edge use results presented here. This is also an indication of feeding preferences, as bears in our study area are drawn towards broadleaf forest edges when foraging for forbs and ungulate calves.

Wetland edges are used more often by females than males (Table 5), and females occupy areas that have a higher density of wetland edges in their home ranges; however, edge selection ratios indicate females use wetland edges in their home ranges less than expected (Table 6). Grizzly bears have a negative association with wetland habitats (McLoughlin et al. 2002), as they contain few high quality foods. While this may be true, Roever et al. (2008b) suggest that these areas are also lower in road density, indicating they may have lower overall anthropogenic disturbance. While the amount of wetlands in our study area is very small (3.73% of study area), and the use by grizzly bears is low compared to other edges (highest edge use is by females in the summer at 5.77%), the low selection ratio in all seasons by females indicates that these edges are associated with processes affecting grizzly bear habitat selection and merit further research, as it appears female grizzly bears have home ranges with increased presence of wetlands while avoiding wetland edges inside their habitat.

Management Implications

The results presented here indicate that anthropogenic disturbance is not incompatible with grizzly bear habitat management. Grizzly bears are not avoiding anthropogenic edges; in fact, females appear to be selecting for them. Anthropogenic disturbances appear to be providing beneficial grizzly bear habitat, as the bears in our study appear to have adapted to this heavily managed landscape. Management may beneficially focus on reducing bear mortality and conflicts with humans by limiting human access to areas where disturbances are offering beneficial grizzly bear habitat. Maintaining natural edges in the landscape is also important, especially for male bears, and necessary to provide grizzly bears with beneficial natural habitat further from mortality threats associated with anthropogenic disturbances. Limiting access to the most desirable forest disturbances and maintaining natural edges should assist in creating sustainable grizzly bear habitat in this heavily managed landscape.

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Figures and Tables

Table 1 - Number of individual grizzly bears analyzed for each season with total number of telemetry points in brackets.

	Spring	Summer	Fall
Female	9 (9937)	14 (15009)	15 (20682)
Male	8 (5708)	11 (13629)	4 (5227)

Table 2 - Reclassification of land cover from 15 class original to resultant 6 classes used in analysis. Percent of total area and mean patch size are calculated based on available habitat (area inside grizzly bear home ranges).

Original Landcover	**Reclassified Landcover** (Percent of Total Area)	**Mean patch size**
Dense Conifer Forest	Conifer Forest (43.10%)	71433 m^2
Moderate Conifer Forest		
Open Conifer Forest		
Mixed Forest	Mixed Forest (19.80%)	11681 m^2
Broadleaf Forest	Broadleaf Forest (11.75%)	12965 m^2
Treed Wetland	Wetland (3.73%)	109553 m^2
Open Wetland		
Shrubs	Shrubs (17.78%)	116195 m^2
Herbaceous		
Agriculture		
Barren	Other (3.84%)	NA
Water		
Snow/Ice		
Cloud		
Shadow		

Table 3 - Summary of edge inventory, with natural and anthropogenic classification. Edge length is calculated based on available habitat (area inside grizzly bear home range)

Edge Class	Edge Type	Total Length (km)
Natural	Wetland	7371
	Shrub-Broad	4456
	Shrub-Mixed	8790
	Shrub-Conifer	21391
Anthropogenic	Road	8509
	Pipeline	4874
	Forest harvest	59667

Table 4 – Home range statistics for female and male grizzly bears in each season. Sizes are in km^2.

	Spring			Summer			Fall		
	Mean (km^2)	Min (km^2)	Max (km^2)	Mean (km^2)	Min (km^2)	Max (km^2)	Mean (km^2)	Min (km^2)	Max (km^2)
Male	240.93	25.14	441.11	214.32	25.57	596.29	71.75	38.96	115.62
Female	102.51	38.27	218.34	108.12	52.25	262.51	96.11	31.88	448.30

Table 5 – Percentage of observed telemetry locations found nearest each type of landscape edge for males and females in each season.

		Forest Harvest (%)	Pipeline (%)	Road (%)	Anthro total (%)	Shrub-Broad (%)	Shrub-Conifer (%)	Shrub-Mixed (%)	Wetland (%)	Natural total (%)
Female	Spring	46.42	3.55	9.23	**59.20**	4.82	26.95	4.28	4.74	**40.79**
	Summer	49.54	3.70	9.85	**63.09**	7.07	19.37	4.70	5.77	**36.91**
	Fall	51.94	3.54	6.08	**61.56**	4.82	24.40	5.67	3.54	**38.43**
Male	Spring	15.01	1.42	4.80	**21.23**	20.37	45.89	11.80	0.71	**78.77**
	Summer	24.34	0.67	2.55	**27.56**	13.49	46.43	10.77	1.75	**72.44**
	Fall	15.78	0.37	5.12	**21.27**	10.25	54.52	13.64	0.31	**78.72**

Table 6 - Selection ratios comparing percentage of observed telemetry locations found nearest each type of landscape edge to expected percentages generated through randomization (observed/expected).

		Forest Harvest	Pipeline	Road	**Anthro**	Shrub-Broad	Shrub-Conifer	Shrub-Mixed	Wetland	**Natural**
Female	Spring	0.98	1.16	1.44	**1.06**	1.32	1.06	0.85	0.51	**1.00**
	Summer	1.05	1.56	1.65	**1.17**	1.23	0.83	0.97	0.55	**0.88**
	Fall	1.11	1.07	1.05	**1.10**	0.88	0.95	1.05	0.48	**0.91**
Male	Spring	0.83	1.21	0.94	**0.88**	1.21	1.00	0.95	1.00	**1.04**
	Summer	1.08	0.59	0.71	**1.03**	1.24	0.93	1.05	1.16	**1.01**
	Fall	0.99	0.57	0.69	**0.91**	1.04	0.97	1.45	0.40	**1.06**

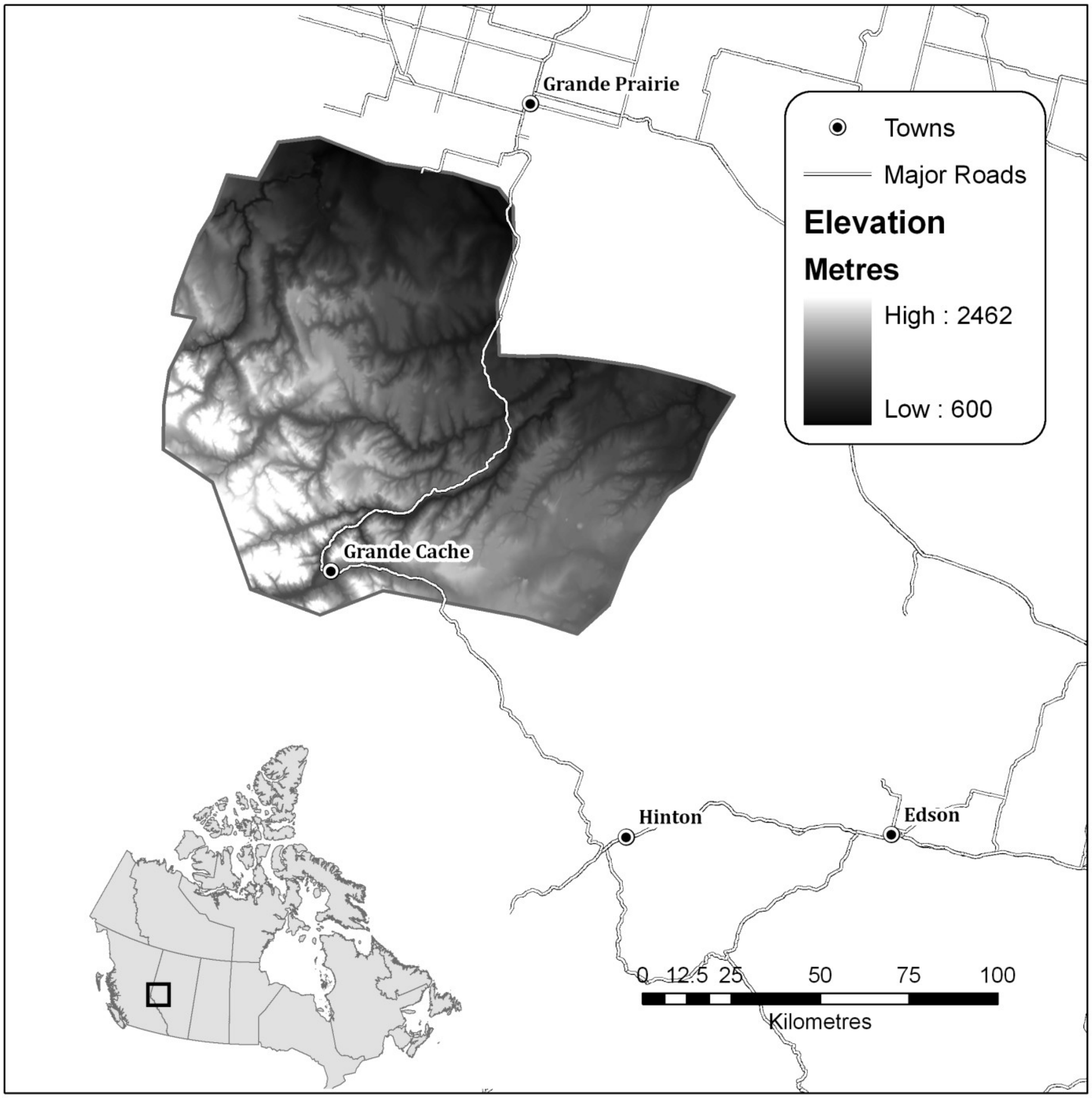

Figure 1 - The study area is located in the eastern foothills of the Rocky Mountains, west of Edmonton, Alberta, Canada. Centred at 118° W and 54° N.

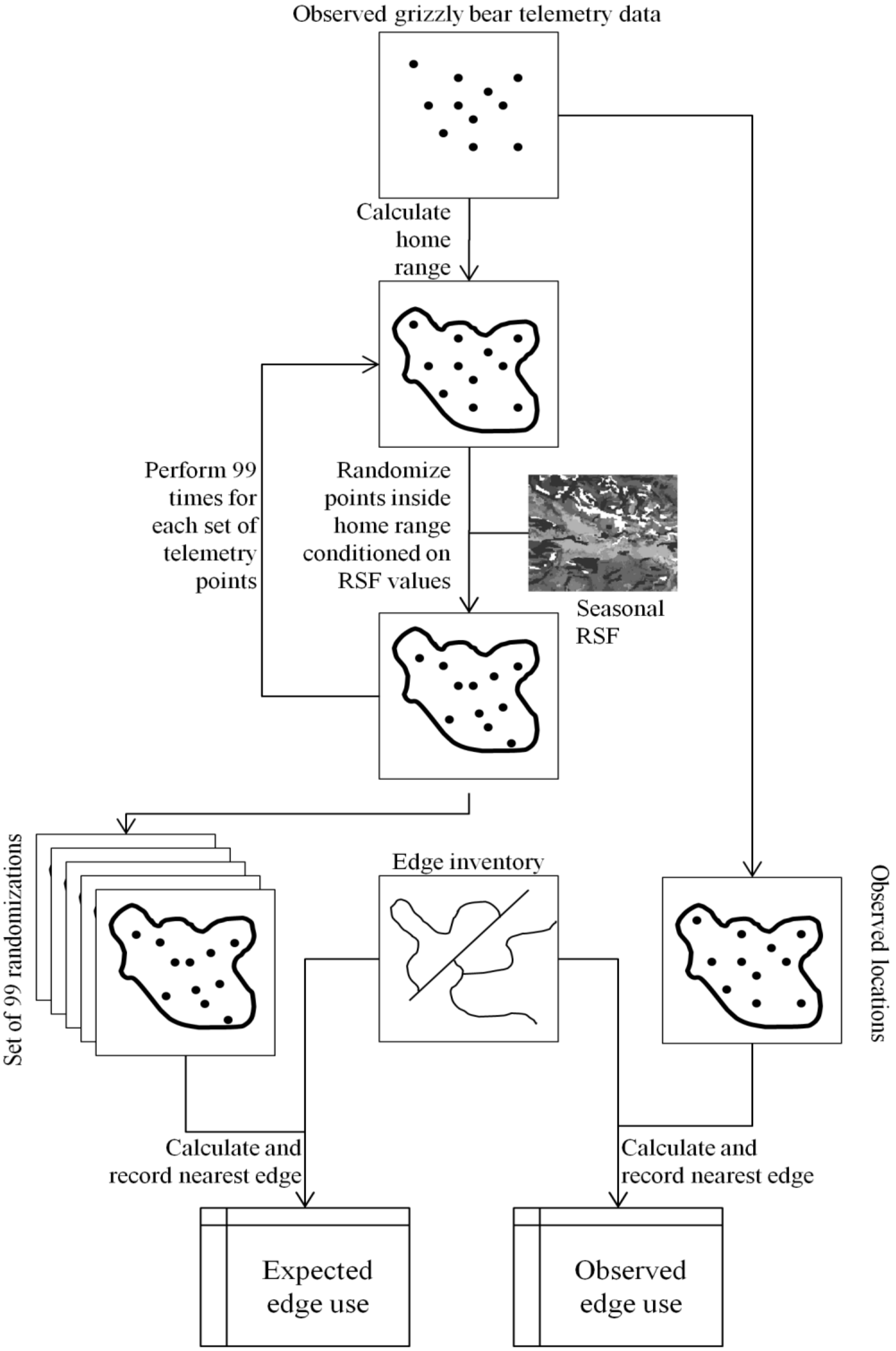

Figure 2 - Randomization process for calculating selection ratios of observed to expected habitat use.

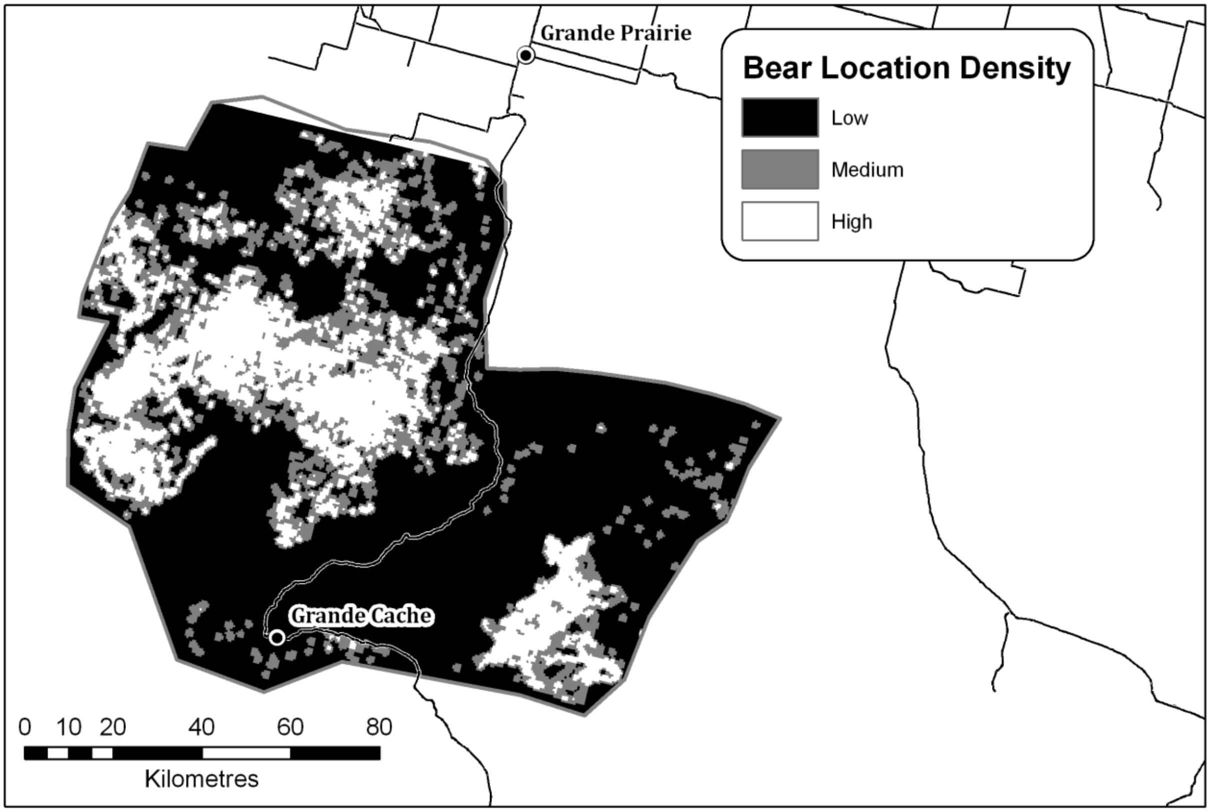

Figure 3 – Density of grizzly bear telemetry locations in study area.

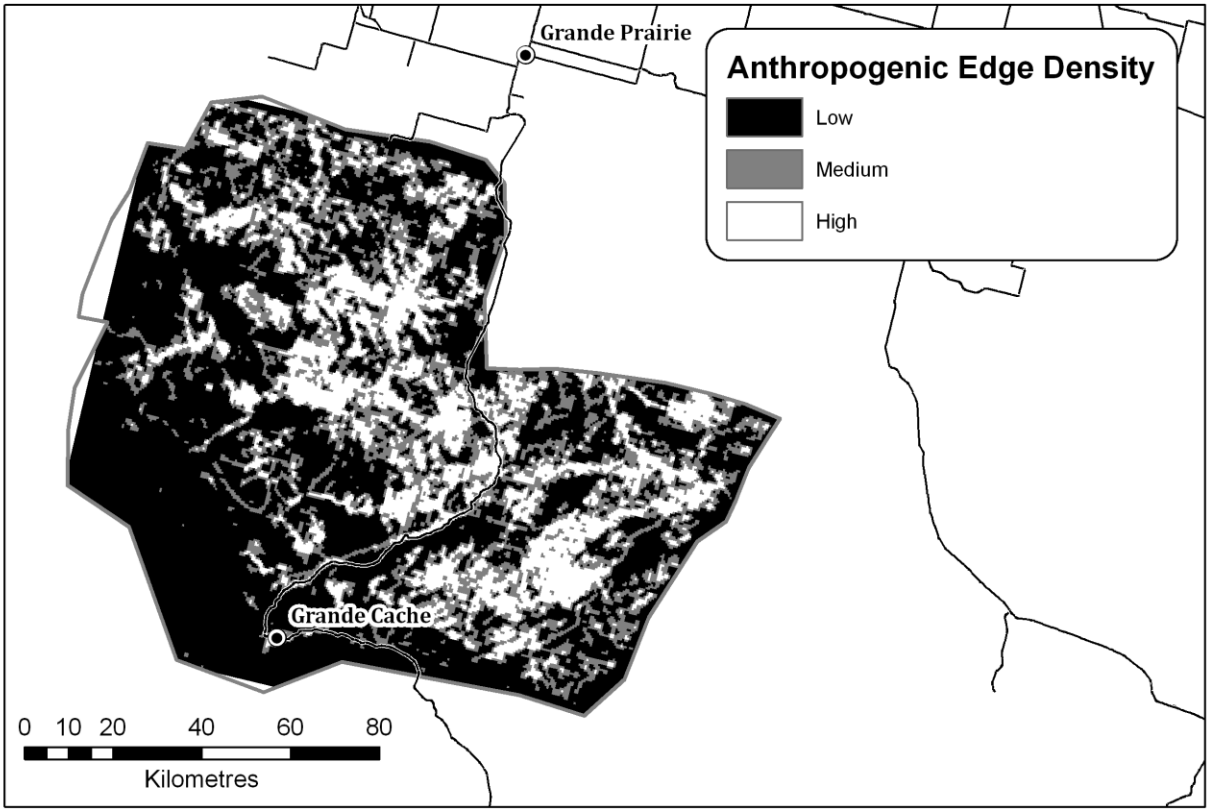

Figure 4 - Density of anthropogenic edges across the study area.

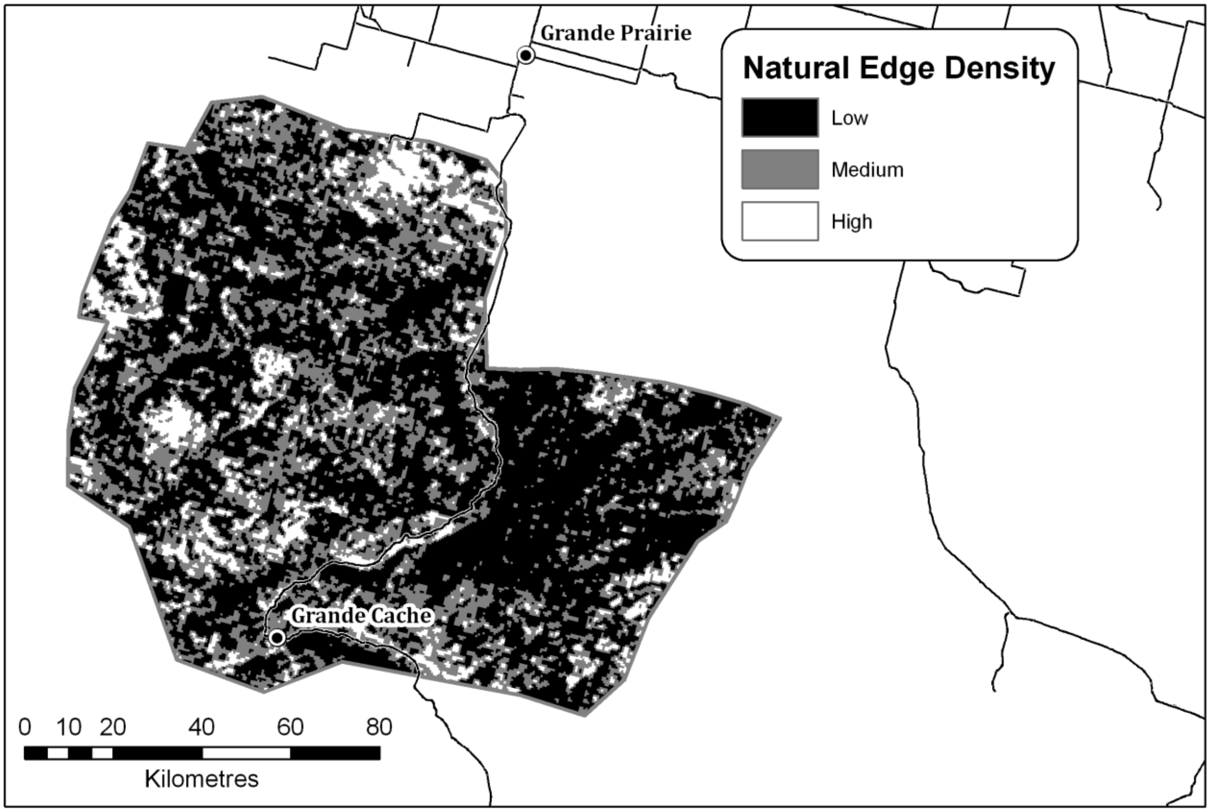

Figure 5 - Density of natural edges in the study area

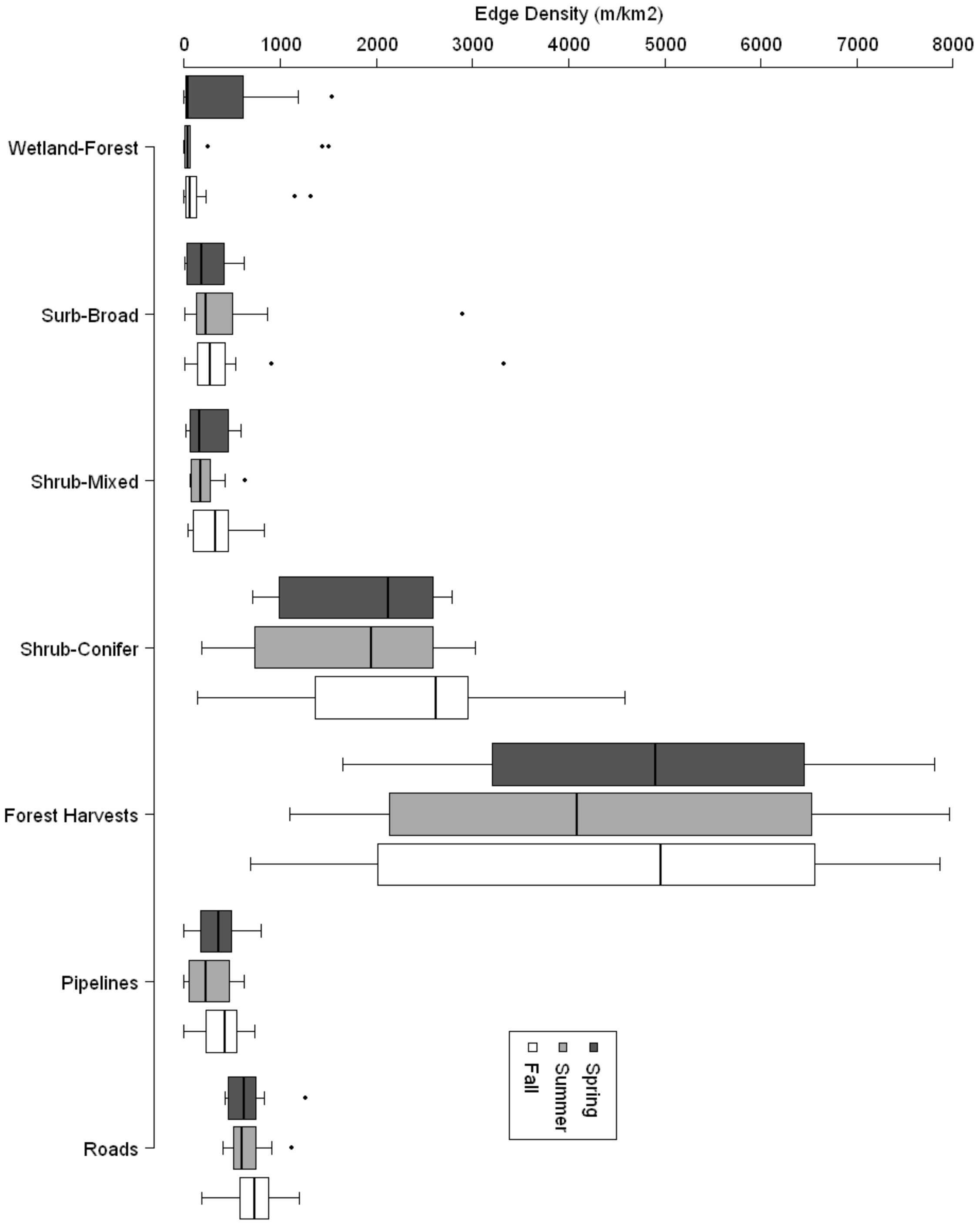

Figure 6 - Boxplots representing edge density (m/km^2) in individual home ranges for female grizzly bears for each edge type across each of the three seasons.

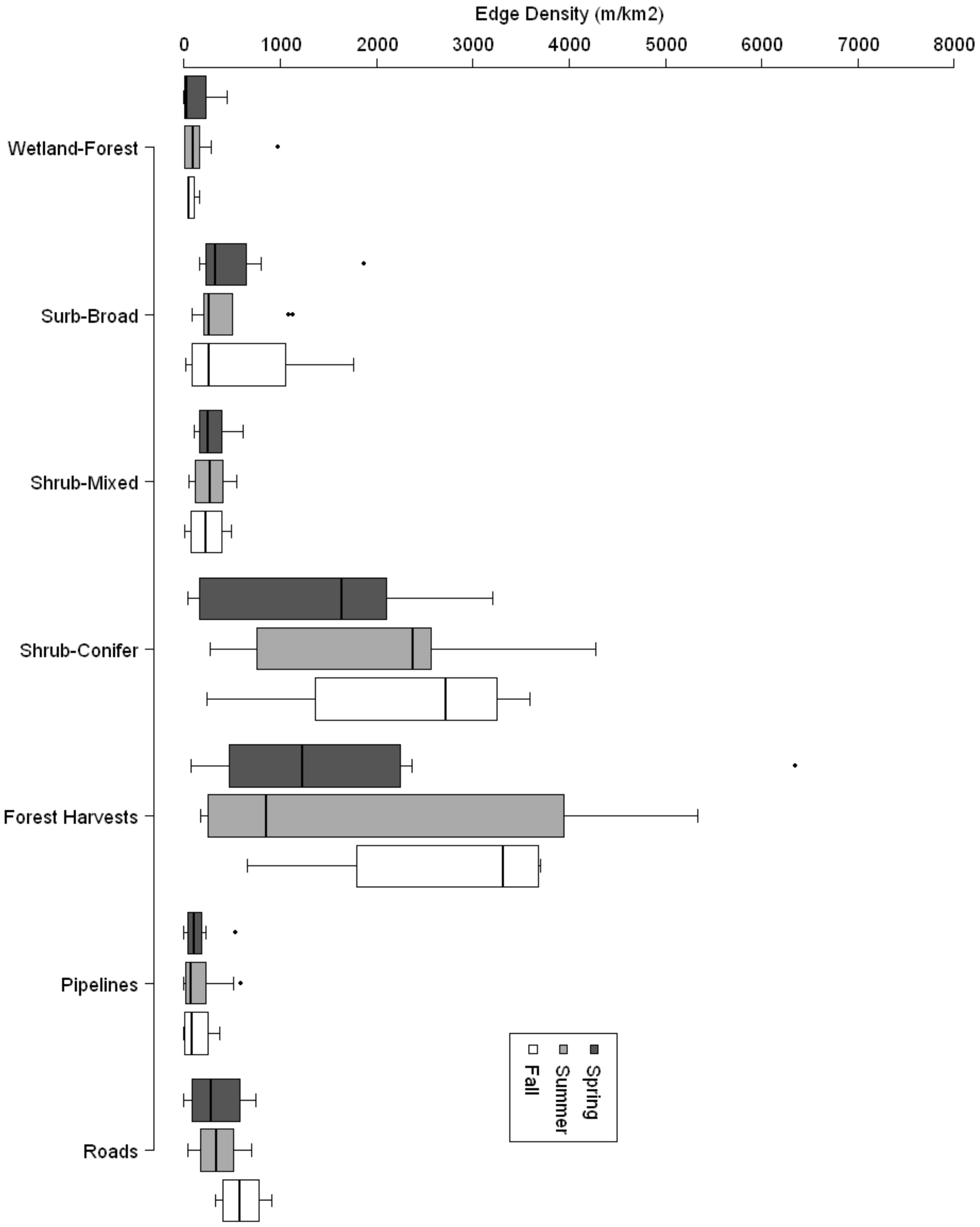

Figure 7 - Boxplots representing edge density (m/km2) in individual home ranges for male grizzly bears for each edge type across each of the three seasons.

Chapter 3: Impact of disturbance characteristics and age on grizzly bear habitat selection

Abstract

Grizzly bears have complex reactions to forest disturbances due to their use of forest clearings for foraging, large home ranges, and the continued expansion of human settlements into undisturbed grizzly bear habitat. Determining the spatial and temporal variation in grizzly bear (*Ursus arctos*) use of disturbed forest areas is required to improve our understating of habitat use by threatened populations in areas of on-going forest management activities. The goal of this paper is to quantify how grizzly bears interact with forest disturbances over time, through the integration of a four decade long remotely sensed disturbance data set and a detailed telemetry database. Historical forest disturbance data were obtained though image differencing of the tasselled cap angle of 14 Landsat images covering the period of 1973-2008. Collars fitted with global positioning systems (GPS) were used to collect telemetry data for 22 adult grizzly bears (8 females, 14 males) from 2005-2009 in the eastern slopes of the Canadian Rockies. The resultant telemetry data were partitioned based on known biological variation in habitat selection into sex and seasonal groups. Density of grizzly bear telemetry locations was calculated for each forest disturbance and compared to expected density via a randomization conditioned on observed trends in overall habitat use. The comparison of observed and expected density of grizzly bear telemetry locations allowed disturbances to be labelled as selected or non-selected. Each disturbance was attributed with characteristics (area, elevation, average tasselled cap transformation (TCT) greenness, and distance to nearest populated place) which were compared between selected and non-selected disturbances using a Mann-Whitney U-test. Results indicated that males select for disturbances that occurred in the 1970s the most frequently; females demonstrated equal selection of disturbances occurring over all tested epochs outside of the 2000s (including 1990s, 1980s, and 1970s). Females were found to select for disturbances more in the summer and fall than the spring. The characteristics of disturbances selected by females indicates females select for larger disturbances with lower TCT greenness and a consistent elevation. Males show lower selection of disturbances in the fall than in other seasons, and lower selection than females in the summer and fall. Compared to females, disturbances selected by males are larger, and show seasonal variation in TCT greenness and elevation. While disturbances have become smaller through time, both sexes selected for larger disturbances from all decades. For our study area in west central Alberta, Canada (119° W, 54° N) females appear to select for disturbances over a consistent range of elevations. Limiting access to disturbances at 1250 – 1300 m could reduce human and bear interaction and decrease grizzly bear mortality risk.

Introduction

On-going management of forests for resource extraction (largely for timber harvest and oil and gas exploration / development) has altered the natural disturbance regime, with forest fires declining substantially through fire suppression and forest harvest replacing fire as the primary agent of disturbance (Tande 1979, Andison 1998, Johnson et al. 2001). Anthropogenic disturbances can have substantive effects on flora and fauna (Swanson and Franklin 1992, Wilcove et al. 1998, Nielsen et al. 2008), and can alter the life histories of wildlife (Bengtsson et al. 2000). Black bears have been found to select for regenerating forest stands over mature conifer forests (Brodeur et al. 2008). Elk avoid areas following a disturbance despite an increase in herbaceous biomass, with avoidance being driven by the threat of wolf predation (Hebblewhite et al. 2009). Other predators avoid areas subject to forest harvests on a seasonal basis, such as the Canadian Lynx where, in winter, there is a lack of cover to support prey, and deep snow which impedes movement (Squires et al. 2010). The cross species effects of forest harvests on habitat selection indicate the opportunity for managing forest disturbances for species conservation.

Grizzly bear habitat use is affected by anthropogenic forest disturbance (Nielsen et al. 2004a, Schwartz et al. 2006), due to bears' large home ranges and slow reproductive rates, which makes them especially susceptible to extirpation (Purvis et al. 2000). The change from a fire-driven disturbance regime to a forest harvest driven regime is a worldwide phenomena in productive forests (Smith 2000, Drever et al. 2006) and changes the nature of forest disturbances in grizzly bear habitat. The seasonal shifts in grizzly bear diet (Mowat and Heard 2006) and habitat selection means that variations in the disturbance regime can drastically affect the feeding and behavioural patterns of resident bears (Nielsen et al. 2004a). This is especially true in west-central Alberta, Canada, where human population growth and resource extraction activities have drastically altered the landscape (Smith 2000).

Grizzly bear reaction to forest harvests has been documented in a number of areas, with bears avoiding forest harvests (Zager et al. 1983, McLellan and Hovey 2001), using them as available (Berland et al. 2008), or selecting for them (Elgmork and Kaasa 1992, Nielsen et al. 2004a). The selection of forest harvests occurs in areas where anthropogenic suppression of forest fires eliminates natural forest clearings, forcing bears to look elsewhere for important resources (Nielsen et al. 2004c). The use of regenerating forest harvests through time is an important aspect of grizzly bear habitat selection, as it has implications for forest management. Nielsen et al. (2004a) showed seasonal variation in selection of forest harvests, with female bears selecting for young (0-5 years post disturbance) and old (>40 years) forest harvests in the fall, while selecting for intermediate aged disturbances in the spring. While grizzly bear use of forest harvests is complex, it is important to consider that use of any age of forest harvest brings with it increased mortality risk due to the capacity for an increase in human and bear interactions (McLellan and Shackleton 1988, Benn and Herrero 2002, Nielsen et al. 2004b, Schwartz et al. 2010).

A review of the use of regenerating forest disturbances by mammals indicates that knowledge of disturbance use by large predators is inadequate (Fisher and Wilkinson 2005). Progress in developing an understanding of large predators' use of regenerating forests has been limited by availability of disturbance data, particularly long-term, large area data. Improved disturbance data are possible via remote sensing where change detection and mapping procedures may be applied. Based upon differing sensor specifications there is a diverse range of spatial and temporal resolutions of satellite imagery, which allows for varying scales of research questions. For example, Moderate Resolution Imaging Spectroradiometer (MODIS) imagery has been used for continental and global disturbance detection (Mildrexler et al. 2009) and has the advantage of a high temporal resolution (daily revisit rate). The Landsat satellites have been acquired and archived for approaching 40 years (1972 – present) with images that cover a large area (~185 km x 185 km) allowing for long-term analysis of forest disturbance at a spatial resolution that informs on both natural and anthropogenic activities (Wulder et al. 2008). A recent (2008) change in data policy by the United State Geological Survey has resulted in free and open access to the Landsat archive (Woodcock et al. 2008), which when combined with the a commitment to continuity of measures through future missions (Wulder et al. 2008, Wulder et al. 2011) makes Landsat especially desirable for long-term forest monitoring. New data fusion techniques also allow for the combination of MODIS and Landsat data into products that benefit from the strengths of both satellites (Hilker et al. 2009, Gaulton et al. 2011).

The goal of this paper is to quantify grizzly bear use of regenerating forest harvests from 1973-2008 in west central Alberta, Canada. This will be accomplished through two analyses: 1) quantifying density of grizzly bear telemetry locations within remotely sensed forest disturbances of different ages to determine which disturbances grizzly bears select for; 2) comparing forest disturbance characteristics (i.e., disturbance area, elevation, remotely-sensed greenness, and distance to populated place) between selected and non-selected disturbances. All comparisons are stratified by sex and season, as variation in sex and seasonal feeding affects habitat selection (Munro et al. 2006).

The four metrics used to characterize forest disturbances enable assessment of hypotheses of grizzly bear disturbance use. First, disturbance size is assessed to address the hypothesis that grizzly bears select for larger disturbances. Second, the elevation of disturbances enables testing of the hypothesis that grizzly bears will select for higher elevation disturbances (Nellemann et al. 2007), but also that females will select for higher elevation disturbances than males, due to avoidance of males (Wielgus and Bunnell 1995, McLellan 1998, Roever et al. 2008). Third, remotely sensed greenness (Tasselled Cap

Transformation (Huang et al. 2002)), is an estimate of forest regeneration. We hypothesize that as forests regenerate grizzly bears will select for disturbances with higher remotely sensed greenness values (Mace et al. 1999, Nielsen et al. 2002), but greenness will have less of an impact on disturbance selection in older disturbances as vegetation stabilizes. Finally, distance to populated place along a road network is a measure of human access to grizzly bear habitat. We hypothesize that grizzly bears will select for disturbances further from human settlements due to associated mortality risk (Nielsen et al. 2004b).

Our approach to integrating remotely sensed forest disturbance and grizzly bear telemetry data sets is to use a Geographic Information System (GIS) and spatial analysis to assess which disturbances have higher densities of telemetry data (or use) than would be expected based on processes of random habitat use. The null hypothesis that habitat is used randomly is referred to as complete spatial randomness (CSR) (Cressie 1993). As is often the case in ecology, CSR is an unrealistic null model (Legendre 1993) as grizzly bears are known to prefer some habitats to others (Mace et al. 1999, Nielsen et al. 2002), and grizzly bear movement is known to be non-random (Martin et al. 2008, Smulders et al. 2010). To meet our goals, we implement a novel methodology for spatial randomization that is statistically rigorous and determine if disturbances are used more or less than expected conditional to observed patterns of habitat use. While other studies have relied on underlying habitat selection information (Smulders et al. 2010) or *a priori* distributions of observed use patterns (Edwards et al. 2007), our methodology is transferable without assumptions concerning the species' use of the landscape or the nature of the species' movement.

Methods

Study Area

We studied a population of grizzly bears in an 11,000 km^2 landscape in west-central Alberta, Canada (Figure 1). The area comprises a diverse, multi-use landscape with high elevation snow, rock, and ice in the west, down to low elevation rolling foothills, characterized by anthropogenic disturbances in the east. The elevation ranges from 2446 m down to 549 m. The forested area has been managed for resource extraction for over 50 years (Andison 1998), with a substantial increase since the 1980s (Ripley et al. 2005, White et al. In Press). The resultant fire suppression has resulted in resource extraction industries becoming the dominant disturbance regime. The short growing season and the lack of high protein food sources (such as salmon), causes lower bear densities (Festa-Bianchet 2010) when compared to other populations in North America (Mowat and Heard 2006), Japan (Sato et al. 2004), and Scandinavia (Bellemain et al. 2005).

Data

Grizzly bear telemetry data

From 2005-2009, GPS location data (telemetry data) were collected on 22 grizzly bears. Aerial darting and leg-hold snaring were used to capture bears and attach GPS devices (Stenhouse and Munro, 2000). Capture efforts followed protocols accepted by the Canadian Council of Animal Care for the safe handling of bears (Animal Use Protocol number 20010016). Two types of GPS collars were fit onto bears: Tellus (Calgary, Alberta) GPS radio collars or Advanced Telemetry System (ATS, Minnesota, USA) GPS radio collars. Both collars collected locations at one hour intervals, only non-denning data were analyzed.

Grizzly bear telemetry data were processed post collection to remove locations with low spatial accuracy. Accuracy was evaluated using positional dilution of precision (PDOP) which measures the three dimensional accuracy of GPS readings. PDOP values greater than 10 were removed (D'Eon and Delparte 2005). Following research, telemetry data were partitioned based on seasonal behaviour: spring (den emergence to June 15th), summer (June 16th until August 15th), and fall (August 16th until October 15th), see Table 1 for a summary of our grizzly bear demographics.

Disturbance data

Stand replacing disturbances were detected by through image pair differencing following White et al. (In Press). Disturbances were detected through differential comparisons of 14 growing season images spanning 1973-2008 from the Landsat Multi-Spectral Scanner (MSS), Thematic Mapper (TM), and Enhanced Thematic Mapper Plus (ETM+) satellites (see Table 2). Each image was orthorectified to a single image in 1995 with a root mean square error of less than 30 m. Clouds and shadows were masked out using a combination of manual and automated approaches (White et al. In Press). Images were converted to top of atmosphere following Han et al. (2007), using coefficients from Chander et al. (2009).

A Tasselled Cap Transformation (TCT) was computed for each image, with the arctangent of the brightness to greenness ratio calculated and differenced between image pairs (the Tasselled Cap Angle, or TCA (Powell et al. 2010)). A threshold was applied to each image difference pair and used to establish stand replacing disturbances (White et al.

In Press). Disturbances were grouped into four decades for use in later comparisons, and a summary of average decadal characteristics are presented. Due to cloud cover and a general lack of images for the 1980s in the Landsat archive over our study area there is only one image that was useful for assessing change. The paucity of images in the 1980s may be problematic as TCA values can return to pre-disturbance levels within 5-10 years (White et al. In Press), indicating a need for circumspect interpretations of trends representative of this epoch.

Disturbance characterization data

The following data were used to characterize forest disturbances and assess hypotheses of disturbance use. First, a digital elevation model (DEM) with a 100 m resolution was obtained from GeoBase, a Canadian Government geographic data warehouse (http://www.geobase.ca). The elevation data were obtained in the form of two 1:250,000 map sheets according to the National Topographic Data Base (NTDB). Vertical accuracy information was calculated for each map sheet using the linear map accuracy standard (LMAS) and averaged 75 m. Second, a tasselled cap transformation was performed on a single Landsat ETM+ scene from October 9th, 2009 and the greenness values were extracted. Analogous to the outcomes of a principle components analysis, the TCT greenness index compresses the multi-band Landsat data into a single value understood to combine the spectral characteristics of green vegetation (Crist and Cicone 1984), focusing on the difference between the visible and near-infrared bands, see equation 1 (Huang et al. 2002).

$$\begin{aligned} TCT_{greenness} = &- 0.3344 * B_{blue\text{-}green} - 0.3544 * B_{green} - 0.5466 * B_{red} \\ &+ 0.6966 * B_{near\ IR} - 0.0242 * B_{mid\ IR} - 0.2630 * B_{short\ wave\ IR} \end{aligned} \qquad \text{eqn. (1)}$$

The coefficients above may be interpreted to show the importance of photosynthetically active wavelengths to the calculation of the TCT greenness component. Finally, a vector road dataset and a populated places dataset were obtained for estimating network distance from forest disturbances to human population. The vector road dataset is based on the Alberta Sustainable Resource Development base feature dataset. The road data were updated through heads-up digitizing using medium and high resolution imagery (SPOT imagery and air photos). Populated places were obtained from the Canadian Geographical Names Data Base (CGNDB) through GeoBase. The CGNDB contains the approved names of all places in Canada as point locations. For our purposes, places were limited to locations defined as city, town, village, or hamlet as these represent the locations of human population. While there are other locations of human presence (temporary resource-extraction camps, public and private campsites and parks as examples) the lack of data preclude integration of these variables.

Analysis

The following steps, detailed below and summarized in Figure 2, were implemented to determine the selection and characteristics of forest disturbances used by grizzly bears. First, grizzly bear telemetry data were used to generate home ranges at two scales: for individual bears (individual home ranges) and for all telemetry locations stratified by sex and season (population home ranges). Individual home ranges were used to calculate summary statistics describing the presence of disturbance in individual bear home ranges. Population home ranges were used to constrain the randomization procedure, as will be described. Second, grizzly bear telemetry data (stratified by sex and season) were randomized within population home ranges and used to assess the null hypothesis that grizzly bear use of forest disturbance was random conditional to observed trends in habitat use. Third, both selected and non-selected disturbances were attributed with landscape characteristics (i.e., area, elevation, TCT greenness, and network distance to nearest populated place). Finally, the characteristics of selected disturbances were compared to non-selected disturbances, and disturbance characteristics were compared between sexes and seasons.

Creation of grizzly bear home ranges

Home ranges were generated using kernel density estimation (KDE) (Seaman and Powell 1996, Borger et al. 2006). KDE was chosen as it is a common home range method in wildlife management (Powell 2000), does not over-estimate area (Powell et al. 2010), and can account for multiple centres of activity (Laver and Kelly 2008). Bandwidth was estimated using least-squares cross validation using a Gaussian kernel (Ruppert et al. 1995).

Two sets of home ranges were generated, one for individual bears, per season, per year (labelled individual home ranges), and the second for all telemetry locations partitioned by sex and season (labelled population home ranges). Individual grizzly bear home ranges were generated at the 95th percentile by volume contour and used to evaluate the number of telemetry locations within disturbances and to estimate the area of each bear's home range that was disturbed. Population home ranges were generated at four levels: the 50th, 75th, 95th, and 100th percentile by volume contours (note the 100% contour is technically a 99.99th percentile by volume home range). These population home ranges were used to constrain the conditional randomization.

Randomization of grizzly bear telemetry data

Randomization is a flexible approach for evaluating habitat selection. However, typically randomization is used to test the null hypothesis of CSR, which is unacceptable for most ecological questions (Tobler 1970, Cressie 1993, Fortin and Jacquez 2000). When conducting randomization in ecology, it is important to control for factors known to influence the spatial properties of the data as very few ecological processes are expected to occur randomly. Spatial dependence is another way to conceptualize the inappropriateness of CSR. If there is spatial dependence in the observed data, the randomization should mimic the level of spatial dependence if the processes are being captured realistically (Fortin and Jacquez 2000). Our methodology accounts for inherent spatial autocorrelation by maintaining observed density of grizzly bear points within varying levels of grizzly bear home ranges. Grizzly bear telemetry data were randomized within the multi-level population home ranges to account for varying density of use. For each set of grizzly bear points (single sex for a single season), randomization was performed by randomizing the location of the grizzly bear telemetry data and ensuring the density of the randomized points matched the level of the KDE home range. This means the 50th percentile home range has 50% of the random points, the 75th percentile has 75% of the points (with 25% of those falling outside of the 50th percentile home range), while the 95th percentile home range contains 95% of the points. The remaining 5% of the points were allocated within the 100th percentile home range. This randomization method essentially performs a spatial weighting and ensures the random points are distributed throughout the home range following the observed patterns of use in the original telemetry data.

Determining disturbance selection

The four decadal disturbance inventories were intersected with both the observed grizzly bear telemetry data and the randomized grizzly bear data to determine grizzly bear density in each disturbance. The grizzly bear density metrics provide an observed grizzly bear density and an expected grizzly bear density (from the randomization process) for each forest disturbance. For each of the forest disturbances, therefore, it is possible to determine if the disturbance has significantly higher bear density than expected at random. Disturbances with significantly higher grizzly bear density were labelled selected and compared to non-selected disturbances through four forest characterization metrics (area, elevation, TCT greenness, and distance to populated place).

Characterizing forest disturbances with landscape characteristics

Each forest disturbance was characterized with four variables based on the nature of the disturbance and its distance to human access. First, disturbance area was calculated in hectares. Second, average disturbance elevation was calculated from the digital elevation raster. Third, average TCT greenness was calculated for each disturbance. Finally, distance to nearest populated place was calculated along a road network. Distance was calculated from the boundary of the forest disturbance to the nearest road (or at the intersection of the disturbance boundary and the road network), and along the road network to the nearest populated place (stored as a point location). For our network calculations, all roads were treated as two-way roads, and no limitations on travel were incorporated. Many GIS applications utilize Euclidean distance, and this is applicable when evaluating processes that operate in a linear fashion (e.g.-noise). However, when attempting to investigate processes that do not follow straight lines, such as human access, Euclidean distance is often a poor surrogate of actual distance travelled. When studying grizzly bears, distance to roads is often calculated as Euclidean distance (McLellan and Shackleton 1988, Roever et al. 2008, Graham et al. 2010) which is appropriate when investigating grizzly bears, as they can travel the landscape in generally straight lines. When attempting to measure human access to the landscape, network distance is more realistic as it addresses accessibility by human population, rather than Euclidean distance from human population to disturbance.

Disturbance comparison

Selected and non-selected disturbances were compared using the forest characterization metrics described above. Based on the randomization process each disturbance was labelled as selected or non-selected. Partitioned by sex and season, a statistical comparison between selected and non-selected disturbances was made using a Mann-Whitney U-test. The disturbance characteristics were also compared visually. A boxplot of disturbance greenness through time was generated to assist in explanation of the selection of disturbances as it relates to TCT greenness.

Results

The population home ranges (generated through kernel density estimation) are visualized in Figure 3. Individual home ranges were used to summarize disturbances in grizzly bear habitat, and were averaged across sex and season, see Table 3. Females show higher use of disturbance than males, having 14.78% to 22.33% of their telemetry locations found in forest disturbances, whereas 11.08% - 11.85% of male telemetry locations were located within disturbances. The percent of home range disturbed shows females with more area of disturbance in their home range than males. Both sexes show more telemetry locations in forest disturbances than area of home range disturbed in all seasons except females in the spring.

In order to interpret disturbance use by grizzly bears through time, our forest disturbance inventory was summarized for each decade, Table 4. Disturbance size has changed since the 1970s with the most current disturbances (2000s) being less than 1/6th the size of disturbances from the 1970s. The elevation associated with disturbances remains constant for the 1970s, 1990s, and 2000s, with disturbances from the 1980s showing a higher elevation, although this jump in elevation may be an artefact of the bias in our change detection methodology arising from the long temporal gap in our image inventory. We see an expected trend in the TCT greenness values, as older disturbances have higher values than younger disturbances. Distance to nearest populated place shows little trend through time.

Grizzly bear disturbance selection is presented as percentage of disturbances selected (Table 5). Females show greater selection of disturbances in the summer and fall for disturbances from the 1970s, 1980s, and 1990s, but not for the newest disturbances from the 2000s. Females select the most recent disturbances from the 2000s the least, except in the spring. Males select fewer disturbances in the fall for all decades. Males show a preference for older disturbances in the spring and summer, but lower selection of disturbances in all other situations.

Area of disturbance appears to affect selection of disturbances, with significant differences ($\alpha = 0.05$) between selected and non-selected disturbances, Figure 4. Both sexes show selection for larger disturbances, significantly larger for disturbances in the 2000s, 1990s, and 1970s for all three seasons, but not for disturbances from the 1980s.

The nature of disturbances in our study area shows increased elevation of disturbances in the 1980s in both selected and non-selected disturbances (Figure 5). Females select for disturbances at a consistent elevation throughout the year. Males change selection seasonally with summer showing selection of lower elevation disturbances than in the spring or fall; significantly lower for disturbances from the 2000s, 1990s, and 1970s.

Females show selection for disturbances with greenness lower than the non-selected disturbances for all decades except for the 1970s, see Figure 6. Disturbances selected by females have significantly lower than expected greenness in the 2000s and 1990s for all three seasons. Disturbances selected by males show more seasonal variation, with a preference for disturbances with significantly higher greenness in the summer for all decades, but selection of disturbances with lower greenness in the fall. Change in TCT greenness through time is presented in Figure 7, chief to the trends evident are the greater variance in values for the more recent disturbances, with a stabilization of mean values and a lessening of variance over time. Shortly after a disturbance, herbaceous growth will drive the greenness signal; a stabilization of greenness will occur as succession processes unfold. The similar means and decreased variance of the TCT greenness values for the oldest captured disturbances relate the maturing stand conditions. Mean values change little after year 10, but greenness measures become less variable.

Both sexes of grizzly bears select for disturbances further from populated places in the spring, see Figure 8. There is variation between seasons, as females select for disturbances closer to populated places for intermediate aged disturbances in the summer and fall.

Discussion

Our results confirm that grizzly bears use disturbances at a higher frequency than available within their home range, though there are variations between sexes and seasons. Females use disturbances more than expected, having 14.68% - 22.33% of their locations found in disturbances (relative to 13.73% - 15.88% of their habitat being disturbed). If bears used disturbances as available, we would expect to find their use of disturbances equivalent with the area of disturbance in their home range. The use of disturbances by males is more similar to the amount available (11.08% - 11.85% used vs. 9.74% - 10.33% available). As shown in other studies (Nielsen et al. 2004a), selection of disturbances varies by season.

In addition to season, our results indicate that age of disturbance is an important factor in grizzly bear selection of forest disturbances. Both male and female grizzly bears use the most recent disturbances from the 2000s less than disturbances from other decades, indicating that fresh disturbances are not as appealing to grizzly bears as intermediate or older disturbances, either because of a lack of food resources (Nielsen et al. 2004c) or the presence of humans (Benn and Herrero 2002, Nielsen et al. 2004b). For females, disturbances outside of the 2000s showed increased selection in the summer and fall. Males show increased selection of older disturbances as well, selecting for 1970s disturbances the most, but show the lowest levels of disturbance selection in the fall for all decades.

Beyond age of disturbance, other characteristics also affect grizzly bear habitat selection. Our hypothesis that grizzly bears will select for larger disturbances could not be rejected for some decades (2000s, 1990s, and 1970s). Current management regimes create small clearcuts (<40 ha) in a checkerboard of forest and forest harvest (Smith et al. 2003). As disturbances have become smaller through time (White et al. In Press) disturbance area could be affecting how grizzly bears use the landscape.

Disturbances selected for by grizzly bears are significantly larger than the non-selected disturbances in the 2000s, 1990s, and 1970s but not significant at all for the disturbances of the 1980s (although this could be an effect of bias in our change detection methods). While the disturbances in the 1970s are generally much larger, selected disturbances are still significantly larger than non-selected disturbances. Current forest management practices are being re-thought in a natural disturbance framework, where harvests are designed to emulate natural disturbance regimes (Swanson and Franklin 1992, Nielsen et al. 2008) leading to larger, more secluded forest harvests. In this re-modelling, knowing grizzly bears select for larger disturbances is important. When considering the selection of these disturbances, it is important to remember that disturbances from the 1970s are 40 years old during this study, and should not be considered open forest disturbances. While the presence of 40-year-old vegetation is possible, these disturbances still see increased selection by grizzly bears, and 1970s disturbances selected by grizzly bears are still significantly larger than non-selected disturbances.

Although grizzly bears appear to derive some benefit from use of larger disturbances, road density tends to increase with management regimes designed to have larger, more isolated disturbances (Nielsen et al. 2008). Given that 95% of human caused bear mortality occurs within 500m of roads or 250 m of trails increasing disturbance size could limit the number of disturbances and the number of associated forestry roads. While recent research suggests that natural disturbance based forestry, with larger, more isolated cuts is not beneficial to grizzly bears (Nielsen et al. 2008) due to the associated increased road density, increasing forest harvest size in the current management paradigm may create more appealing grizzly bear habitat, while limiting road development. Management can also limit human access to larger disturbances to limit associated mortality risk.

Our hypothesis that grizzly bears will select for higher elevation disturbances is also not rejected, with both sexes selecting for higher elevation disturbances in all seasons except for males in the summer. Females select for higher elevation disturbances than males from all decades in the summer only. Grizzly bears have shown increased use of higher elevation areas to avoid human contact (Ciarniello et al. 2007, Nellemann et al. 2007), indicating the importance of elevation in habitat selection. Our results show females select for disturbances at a consistent elevation throughout the year while male selection varies between seasons. Grizzly bear feeding patterns should lead bears to lower, wetter habitat in the summer where food resources are greater (Servheen 1983, Mowat and Heard 2006). The difference in elevation of selected disturbances between male and female grizzly bears could be an indication of sexual segregation of habitat (Rode et al. 2006) where males are utilizing preferred habitat and forcing females into less suitable habitat (Wielgus and Bunnell 1995).

Our hypothesis that grizzly bears will select for disturbances with higher TCT greenness values was partially rejected. Grizzly bears select for less green disturbances (except for males in the summer) which contradicts our hypothesis, but this trend is not present in the oldest disturbances, confirming our hypothesis that selection of older disturbances will be less affected by TCT greenness. Our results also confirm the results of White et al. (In Press) that TCT greenness levels can recover to pre-disturbance levels within 10 years, as we see our disturbances reaching a plateau of TCT greenness around year 12 (Figure 7). Previous research has shown increased TCT greenness is an indicator of positive grizzly bear habitat (Mace et al. 1999, Nielsen et al. 2002). At a landscape scale, greenness is an indicator of vegetation presence and vigour, certainly capable of differentiating regenerating forest from barren alpine areas, which explains positive grizzly bear selection associated with greenness. When comparing re-generating forest disturbances, greenness does not appear to be an indicator of beneficial grizzly bear habitat as bears select for less green forest disturbances. Remotely sensed greenness may be related to positive grizzly bear habitat as an indicator of the presence of green vegetation. As such, we should not be expect the absolute level of remotely sensed greenness to be related to positive grizzly bear habitat selection. Females select for disturbances with lower than expected TCT greenness values in all seasons. This could be due to increased greenness being an indication of increased growth, making travel difficult or making rooting more difficult. However, female selection of disturbances with low TCT greenness could be another indication of females selecting for lower quality habitat due to pressure from male habitat selection (Wielgus and Bunnell 1995, Rode et al. 2006), especially in the summer where males show selection of disturbances with significantly higher TCT greenness values.

Our hypothesis that grizzly bears will stay further from human settlements is not rejected for females, but is rejected for males in the summer and fall. Spring is a time when grizzly bears are emerging from hibernation, and are generally far from populated places (Goldstein et al. 2010). Our results show female grizzly bears are more consistent in the distances to populated places associated with selected disturbances, whereas males are more willing to travel closer to human settlements, especially in the summer. This is in contrast to other studies which show males staying further from populated locations, with females occupying areas closer to humans (Nellemann et al. 2007). While much analysis has been done on the interaction of grizzly bears and roads (McLellan and Shackleton 1988, Kaczensky et al. 2003, Roever et al. 2008) our analysis considers network distance to human settlements as a measure of anthropogenic access to grizzly bear habitat. As increased human access to grizzly bear habitat increases mortality risk (Noss et al. 1996, Benn and Herrero 2002), developing a more thorough understanding of access may assist in planning for enhancing grizzly bear habitat.

Conclusion

There is evidence that age of disturbance is an important factor in grizzly bear selection of forest disturbances, however, disturbance characteristics are also important. Disturbances that are larger, at higher elevations, further from people, and with lower remotely sensed greenness values show some seasonal selection by grizzly bears. Understanding selection preference provides new management avenues. Increasing size of forest harvests will create more disturbances of the size selected by grizzly bears, as the current small (<40ha) cuts are smaller than generally selected. The consistent elevation of disturbances selected by females should direct conservation efforts to those elevations, and direct future research to determine the nature of grizzly bear disturbance selection and elevation.

Developing an approach for the integration of remotely sensed forest disturbances with spatially and temporally dense telemetry data is an important step in evaluating habitat use in studies of movement data. With the opening of the Landsat archive for free public access (Woodcock et al. 2008) and the expectation of Landsat continuity (Wulder et al. 2008, Wulder et al. 2011) the methodology presented here is applicable to many other telemetry studies and other habitat related questions. As our randomization methods are data-driven and do not rely on supplementary data concerning habitat use, the methods can be applied in other studies of animal movement without *a priori* knowledge of the species. Integration of remotely sensed disturbances with telemetry data and a randomization process in a geographic information system allows for in-depth analysis of habitat selection not otherwise possible.

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Figures and Tables

Table 1 - Demographics of grizzly bear telemetry points.

Sex	Number of bears	Number of points
Female	8	43058
Male	14	22369

Table 2 - Landsat images from which forest disturbances were derived. Number of disturbances indicates the number detected between the image and the next image in chronological order. Rate of change is calculated using Puyravaud's formula (Puyravaud, 2003) taken from White et al. (In Press). Rate of change describes the rate at which areas without change become areas with change.

Sensor	Path/Row	Date	Number of disturbances	Decade	Rate of change (%)
MSS	50/22	1973-09-16	792	1970s	-0.22
MSS	50/22	1976-09-27	168		
MSS	50/22	1978-07-25	358		
MSS	50/22	1981-08-14	437	1980s	-0.04
TM	46/22	1990-09-06	498	1990s	-0.27
TM	46/22	1991-07-23	1438		
TM	46/22	1995-09-04	1644		
TM	46/22	1997-09-25	1784		
ETM+	46/22	2000-09-25	1231	2000s	-0.48
ETM+	46/22	2001-09-28	1658		
ETM+	46/22	2002-09-15	3091		
TM	46/22	2004-08-11	7861		
TM	46/22	2006-06-30	5266		
TM	46/22	2008-08-06	--		

Table 3 - Summary of grizzly bears telemetry locations in disturbances, and area of grizzly bear home range that is disturbed.

		Points in disturbance (%)	Area of home range disturbed (%)
Female	Spring	14.78	15.88
	Summer	22.33	15.38
	Fall	19.37	13.73
Male	Spring	11.85	9.74
	Summer	11.79	10.33
	Fall	11.08	9.17

Table 4 – Average disturbance characteristics for all forest disturbances.

	Hectares	Elevation (m)	Greenness	Distance (m)
2000	4.10	1113	10.5	54594
1990	6.87	1121	17.5	60020
1980	12.51	1258	17.95	52101
1970	26.04	1072	18.68	60344

Table 5 – Percentage of disturbances selected, relative to all available disturbances, by each reproductive class for each decade of disturbances for each season.

	Number of disturbances	Adult female			Adult male		
		1	2	3	1	2	3
2000	19407	2.54%	3.56%	3.21%	1.5%	1.99%	1.25%
1990	5364	2.39%	7.14%	6.32%	3.08%	5.15%	1.99%
1980	437	1.35%	7.28%	5.12%	3.77%	3.5%	0.27%
1970	1318	3.94%	10.77%	7.64%	8.92%	8.28%	1.21%

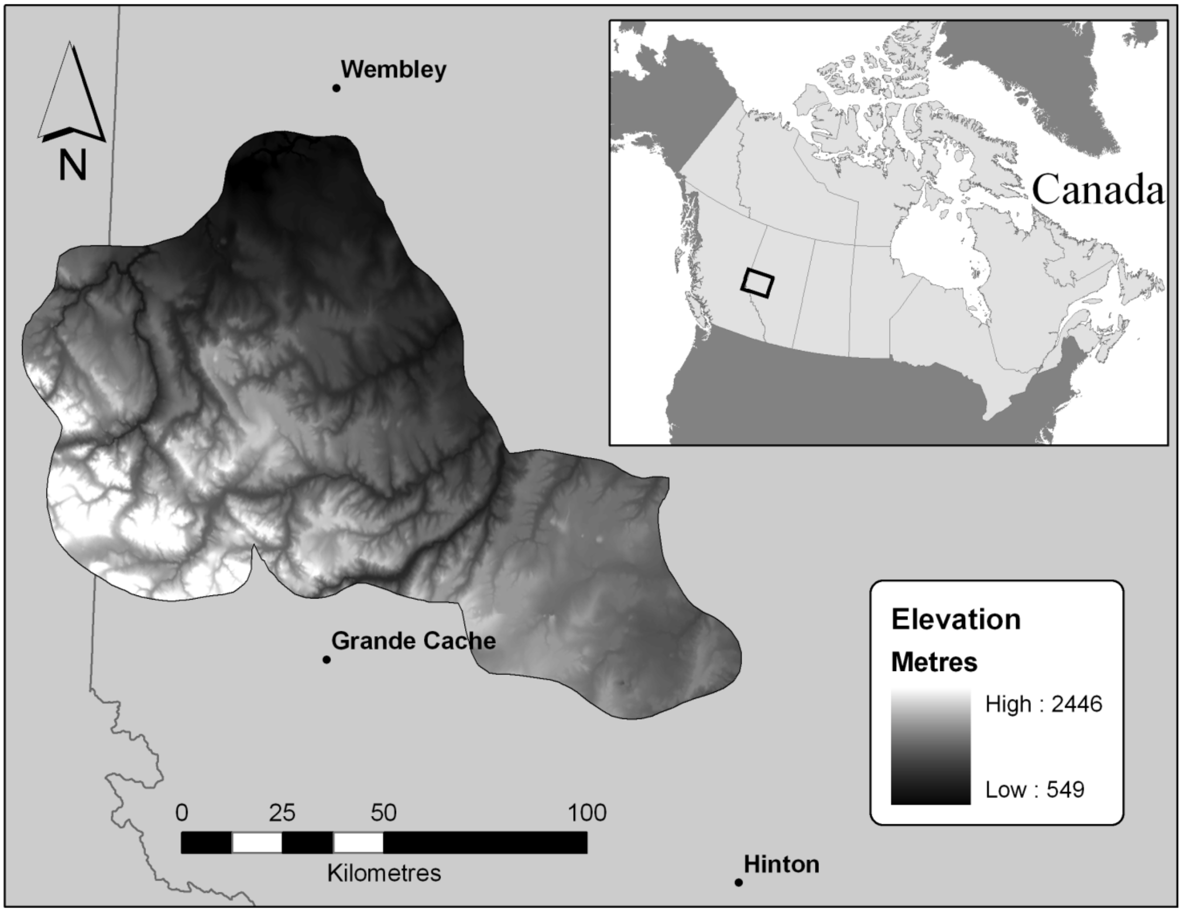

Figure 1 - Study area located in the eastern slopes of the Canadian Rocky Mountains west of Edmonton, Alberta, Canada. Study area is centred at 118° W and 54° N.

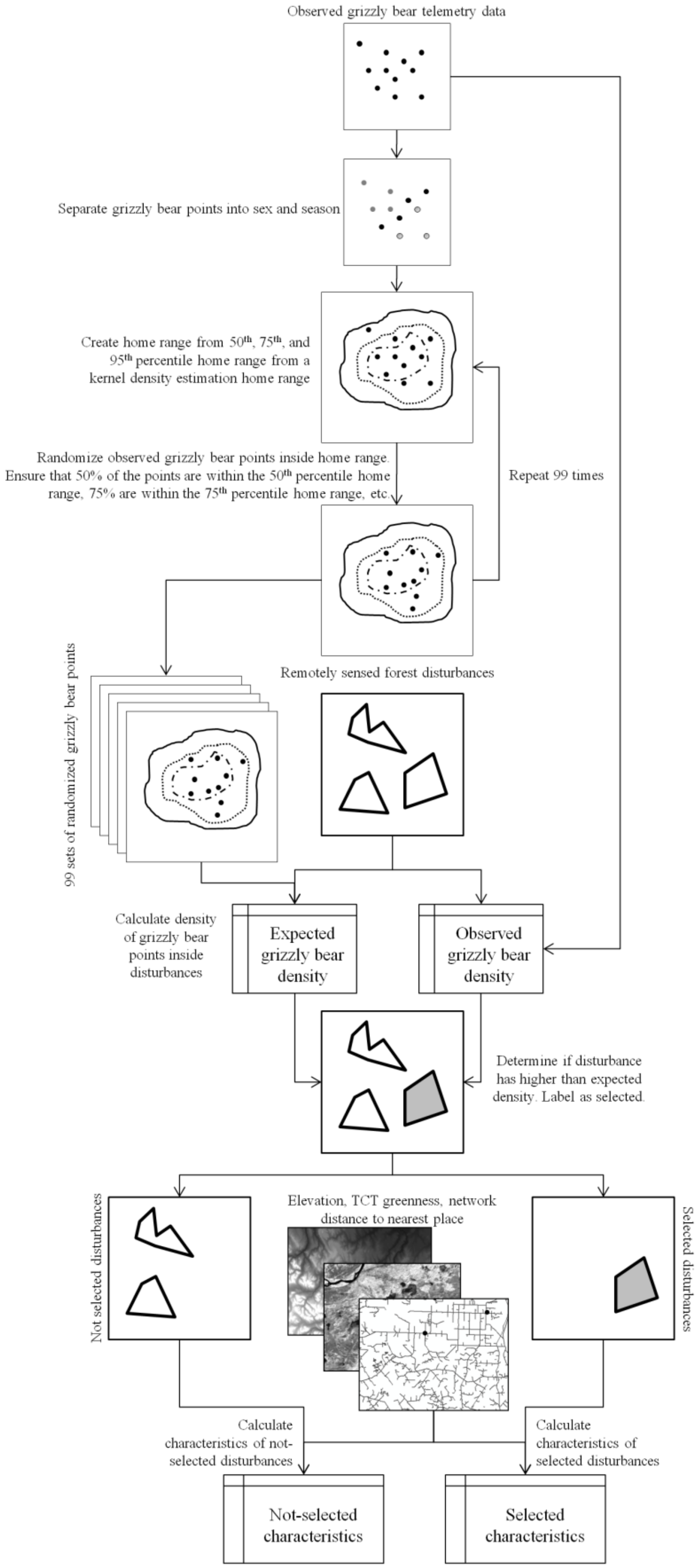

Figure 2 - Flowchart describing randomization process to determine selected disturbances and consequent comparison of disturbance characteristics between selected and not selected disturbances

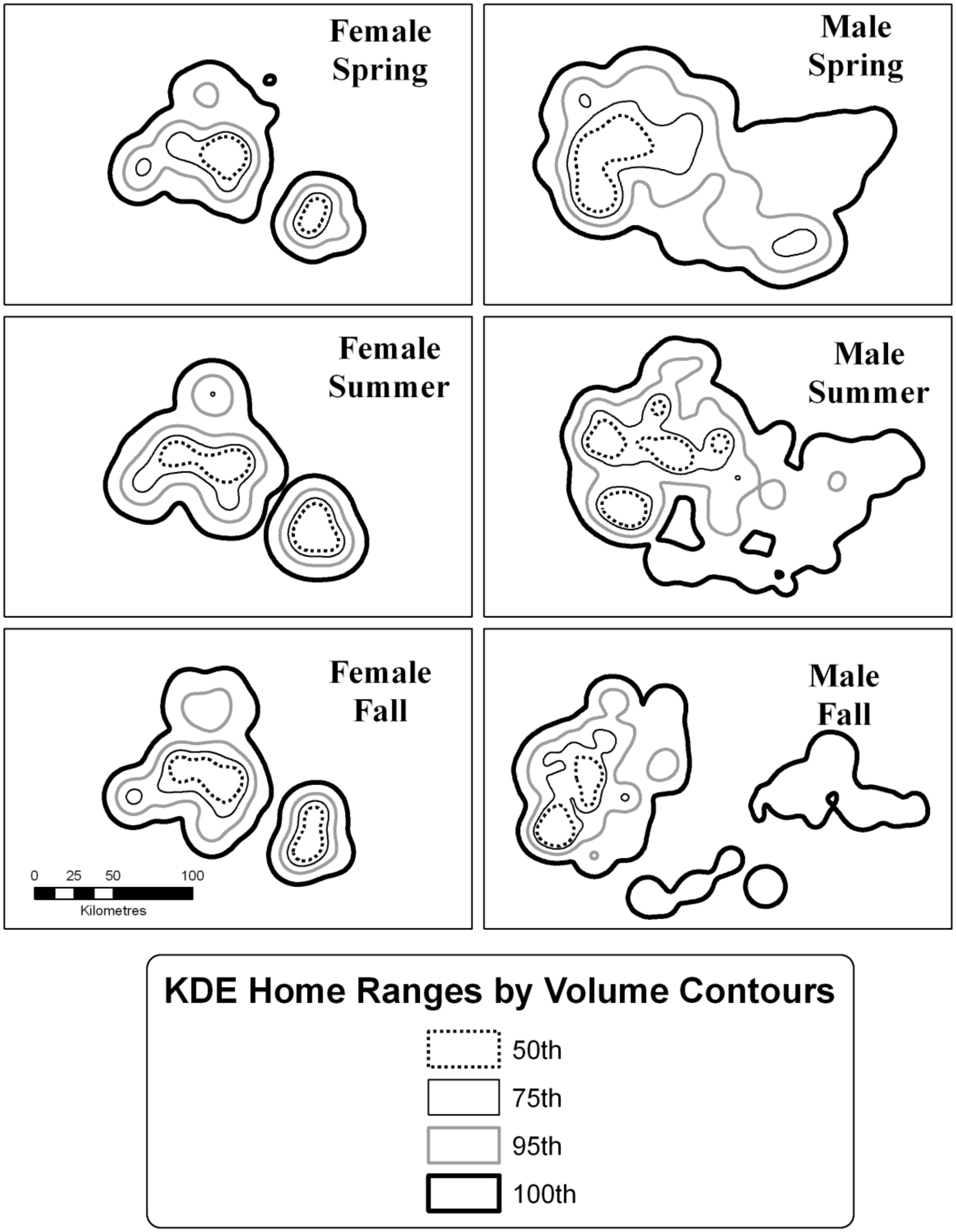

Figure 3 - Comparison of home ranges for each sex in each season. Four home ranges were generated at 50th, 75th, 95th, and 100th by volume contours of a kernel density estimation.

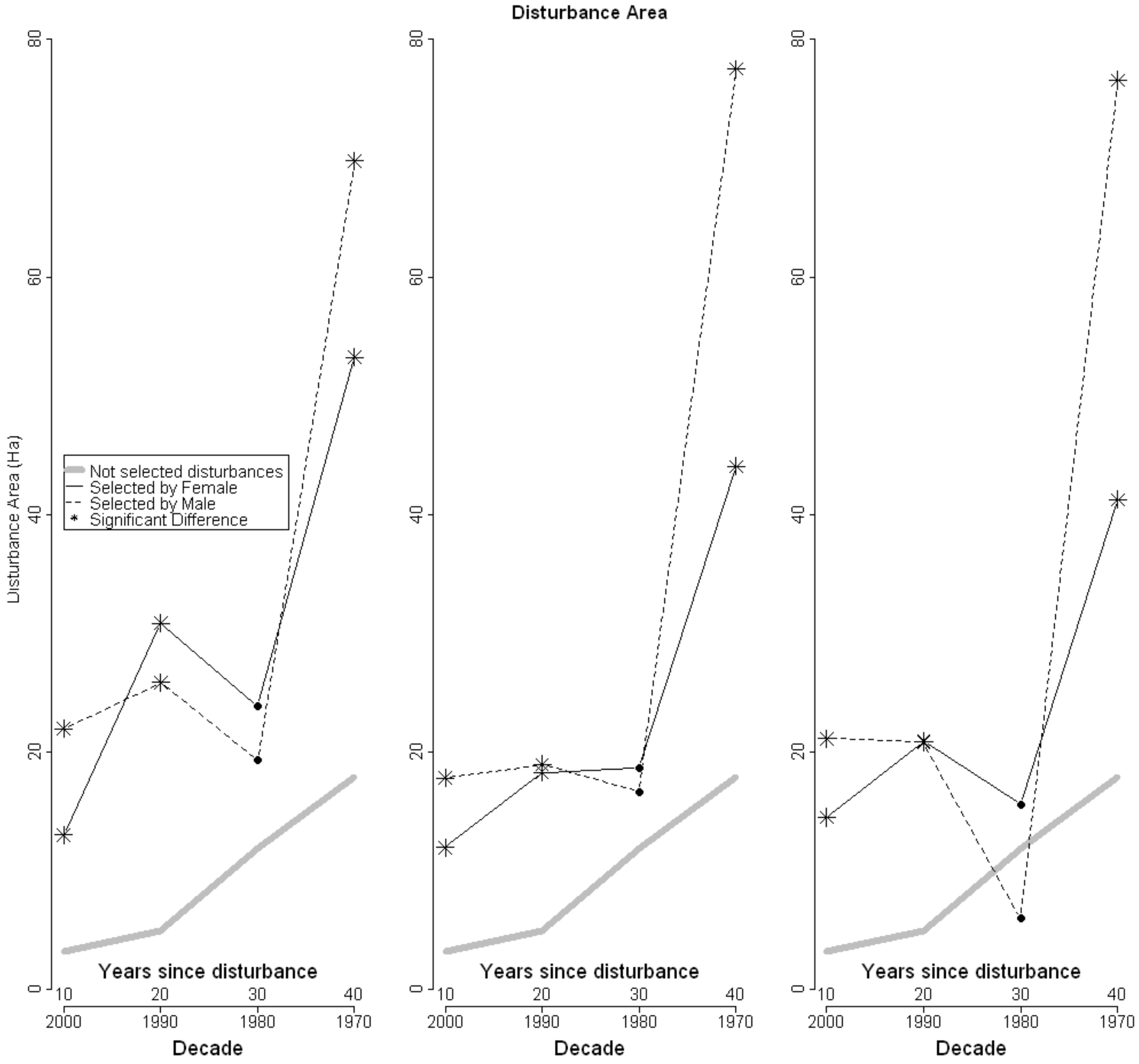

Figure 4 - Comparison of disturbance area between selected and non-selected disturbances for adult male and adult female grizzly bears for spring (left), summer (centre), and fall (right). Stars indicate a significant difference between the characteristics of the selected disturbances and the not select disturbances.

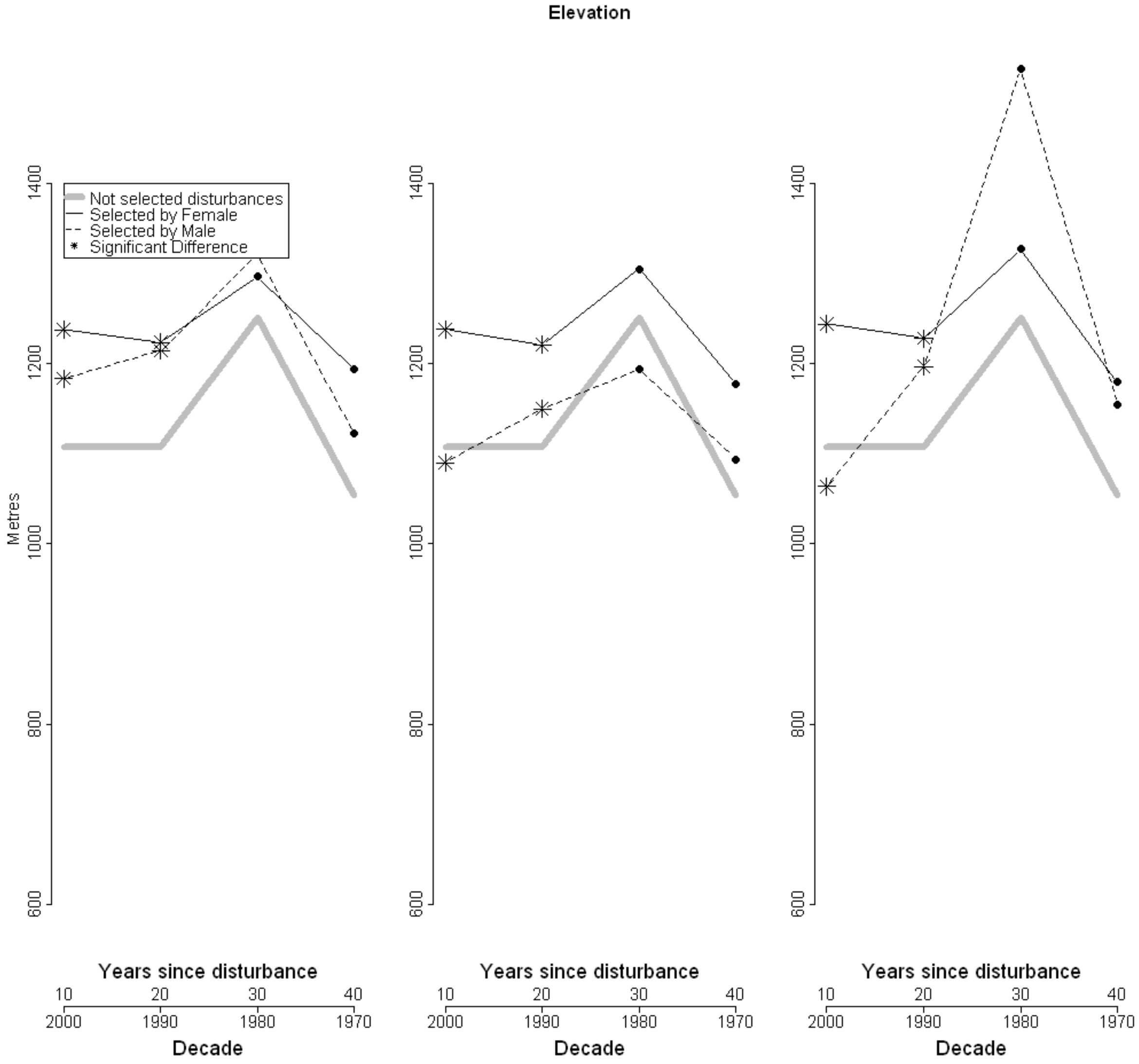

Figure 5 - Comparison of average elevation between selected and non-selected disturbances for adult male and adult female grizzly bears for spring (left), summer (centre), and fall (right). Stars indicate a significant difference between the characteristics of the selected disturbances and the not select disturbances.

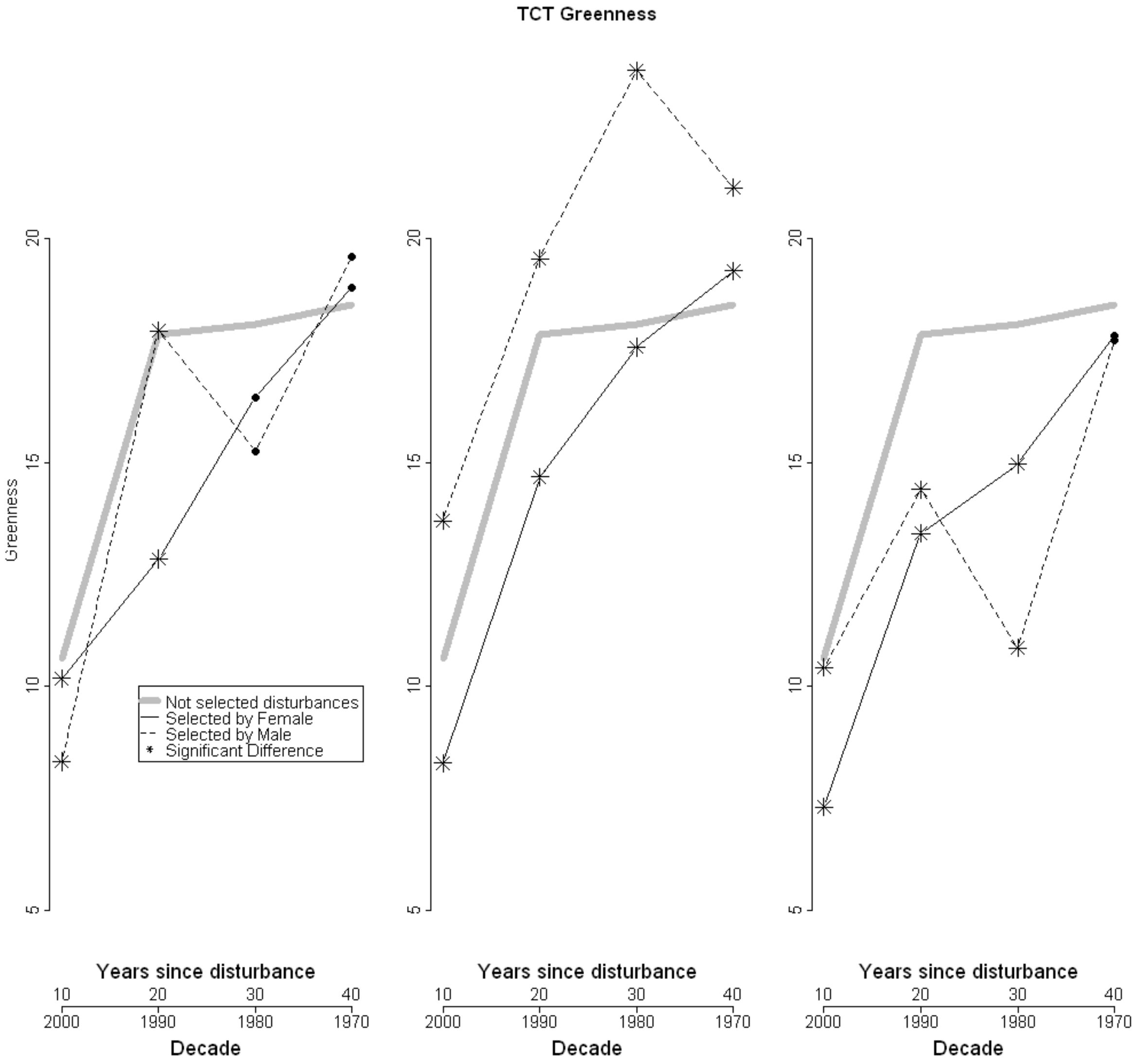

Figure 6 - Comparison of average TCT greenness between selected and non-selected disturbances for adult male and adult female grizzly bears for spring (left), summer (centre), and fall (right). Stars indicate a significant difference between the characteristics of the selected disturbances and the not select disturbances.

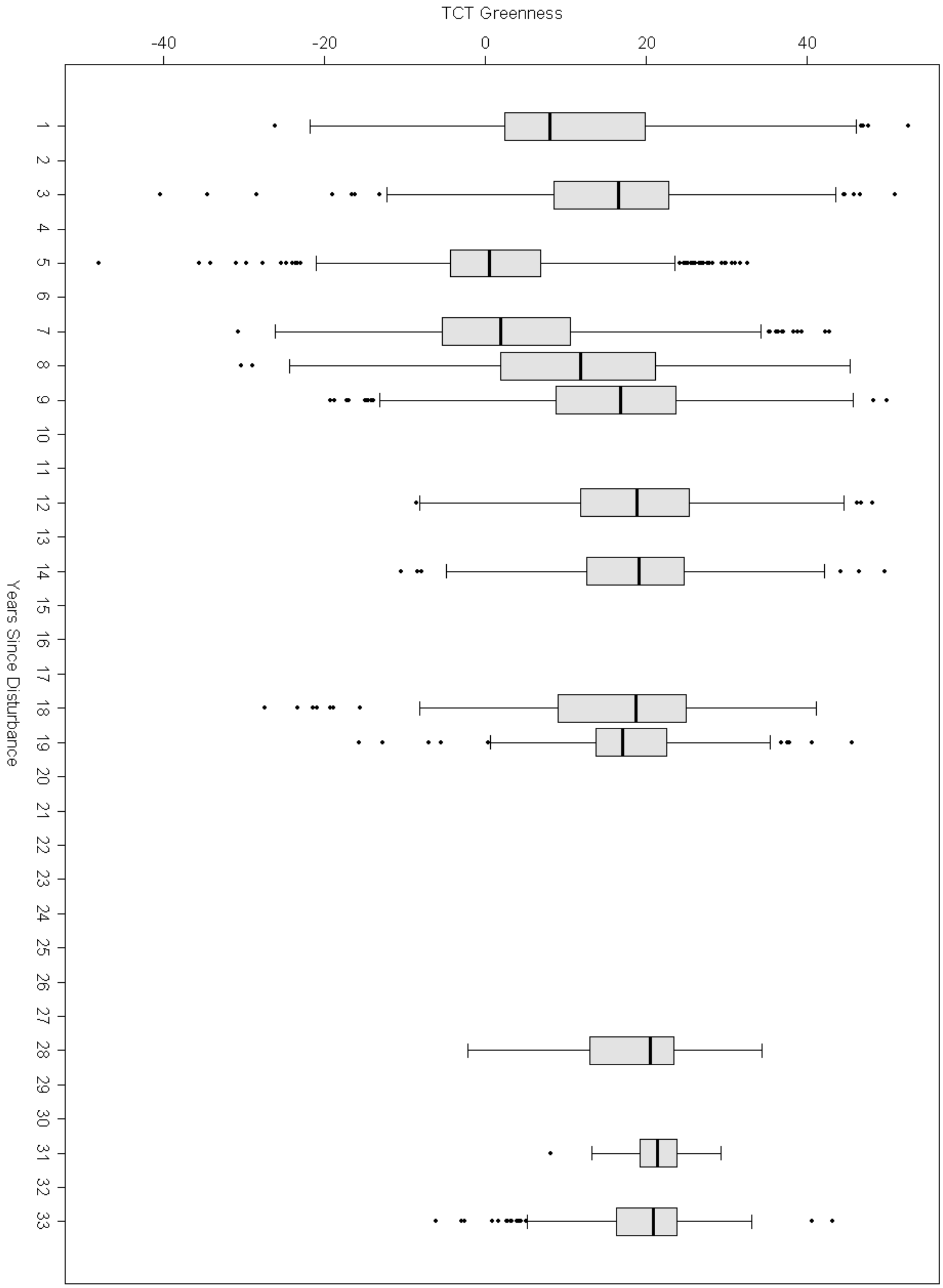

Figure 7 - Boxplot of disturbance TCT greenness through time.

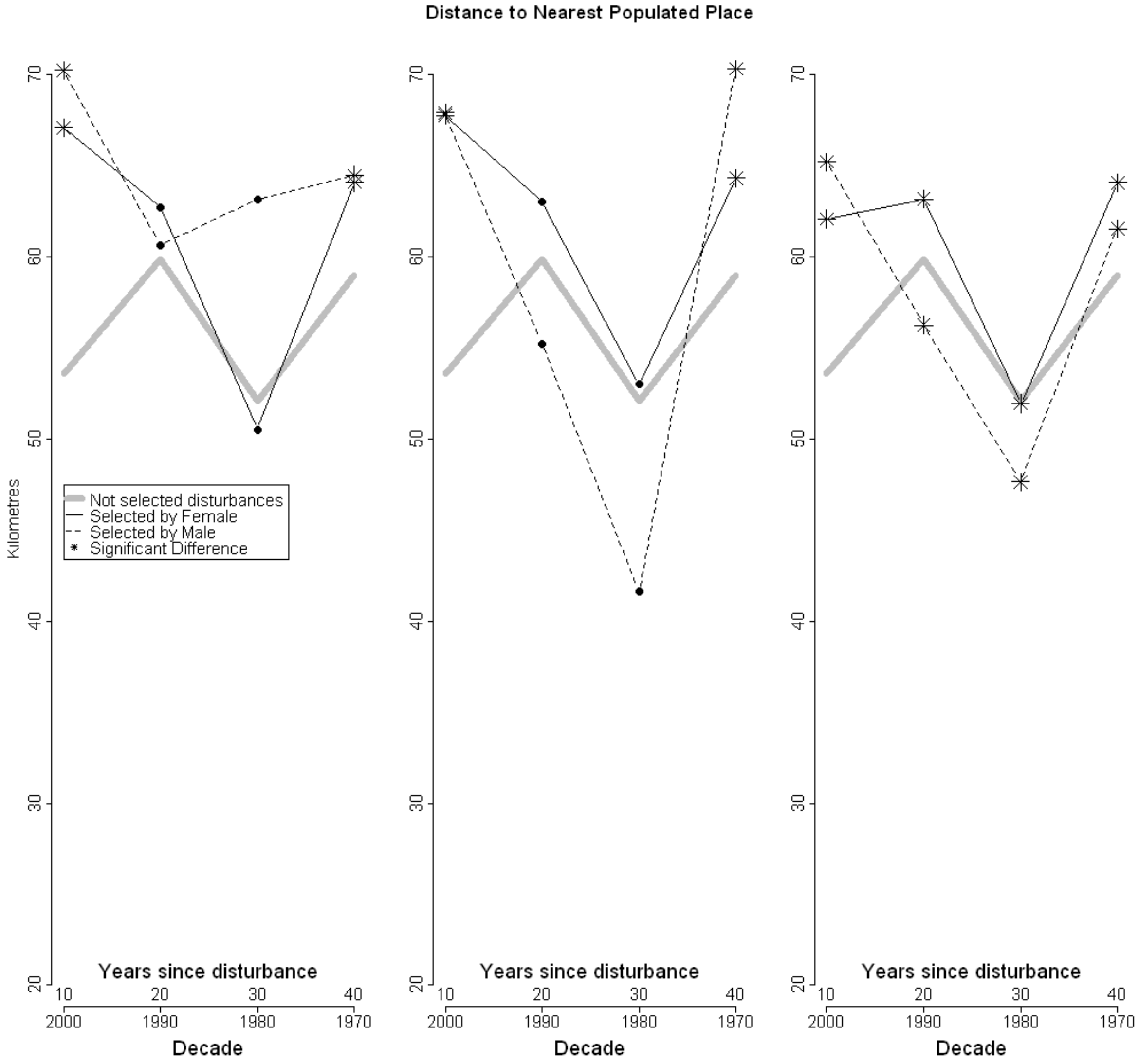

Figure 8 - Comparison of distance to nearest populated place between selected and non-selected disturbances for adult male and adult female grizzly bears for spring (left), summer (centre), and fall (right). Stars indicate a significant difference between the characteristics of the selected disturbances and the not select disturbances.

Chapter 4: Conclusion

The deleterious effects of human expansion on large predators are a problem world-wide (Noss et al. 1996, Purvis et al. 2000). Large predators are often considered keystone, or umbrella species (Noss et al. 1996) as they are important ecosystem moderators, and direct conservation of their habitat leads to indirect conservation of many other species. Large predators face multiple pressures with habitat degradation being an important factor in most cases (Weber and Rabinowitz 1996). While large predators play an important social and cultural role in our society (Kellert et al. 1996, McFarlane and Boxall 2000) protection of their habitat faces increasing pressure from an expanding human population, and increasing desire for natural resources. In order to develop better management plans concerning large predators in areas of human settlements, understanding how these animals interact with both natural and anthropogenic forest disturbances is essential.

The focus of this research was to develop an understanding of the interaction between grizzly bears and forest disturbance. The study area is the foothills of the Rocky Mountains in west-central Alberta, Canada. The foothills have a long history of resource extraction (Smith 2000) which has created a landscape dominated by anthropogenic disturbance. The dominance of the resource extraction industries has lead to intense fire-suppression, creating a disturbance regime that is driven by anthropogenic disturbance instead of fire. In other areas, grizzly bears avoid anthropogenic disturbance in favour of higher-elevation, natural forest clearings (Ciarniello et al. 2007). In our study area, grizzly bears have adapted to utilize anthropogenic disturbances in place of naturally occurring fire disturbances (Nielsen et al. 2004a). As grizzly bear use of anthropogenic forest disturbance is a known factor of grizzly bear habitat selection, and given that the majority of known grizzly bear mortalities are found near these disturbances (Benn and Herrero 2002, Nielsen et al. 2004b), understanding how grizzly bear use of anthropogenic disturbance differs from grizzly bear use of natural forest disturbance will support management of grizzly bear habitat.

To meet the goals of this research, two analyses were undertaken. First, in chapter two, I investigated grizzly bear use of both natural and anthropogenic edges. Second, in chapter three, I investigated grizzly bear use of forest disturbances through time and the characteristics of disturbances selected by grizzly bears.

Edges represent important features in habitat selection, as they provide the benefits of varying landcover types in close proximity and can provide habitat not available in either adjacent landcover type (Ries et al. 2004). I investigated grizzly bear use of both natural and anthropogenic edges as both are indicators of variations in landcover, however anthropogenic edges are of special importance due to associated mortality risk (Nielsen et al. 2004b, Graham et al. 2010). Analysis focused on comparing observed grizzly bear use of landscape edges to an expectation of use based on a conditional randomization process. Conditional randomization controlled for known grizzly bear habitat selection not related to the use of edges, which allowed our analysis to avoid comparisons to complete spatial randomness (CSR) (Cressie 1993, Fortin and Jacquez 2000).

Results indicate grizzly bears show variation in edge selection by season and sex: females used anthropogenic edges more than natural edges, whereas male bears used natural edges more than anthropogenic edges. Investigations into grizzly bear home ranges found females to have more anthropogenic edges in their home range than males. Both sexes showed higher home range edge density in the fall than in other seasons. Females used anthropogenic edges more than males, specifically roads, while males showed more variation in their edge use between seasons. Both sexes showed increased use of shrub-broadleaf edges in the spring and summer, indicating the importance of considering seasonal affects when managing grizzly bear habitat. The increased use of roads by female bears is a management concern, as they are the drivers of population stability (Bunnell and Tait 1981). While the results indicate that anthropogenic disturbance is not necessarily incompatible with grizzly bear habitat use, the increased mortality risk associated with anthropogenic disturbance is still a concern (Benn and Herrero 2002, Nielsen et al. 2002). Knowledge of female use of anthropogenic disturbance should direct management efforts towards limiting human access to specific disturbances grizzly bears find attractive.

In chapter three, I investigated grizzly bear use of forest disturbances of varying ages. Disturbance data from 1973-2008 were derived from image differencing of the tasselled cap angle (Powell et al. 2010) of a series of satellite images (White et al. In Press). A conditional randomization process was developed to quantify disturbances with higher than expected grizzly bear use, and these selected disturbances were compared to non-selected disturbances through four disturbance characteristics (disturbance area, elevation, tasselled cap transformation greenness, and distance to nearest populated place). The randomization process differed from the methods in chapter two in that they do not rely on secondary data or a priori knowledge of grizzly bear habitat use. Instead, the randomization process used data-driven home range density metrics to guide the randomization of grizzly bear locations.

Results indicate that both sexes selected the most recent disturbances (from the 2000s) the least. Females showed increased use of disturbances in the summer and fall, whereas males showed a preference for the oldest disturbances (1970s) in the spring and summer, with very low selection in the fall for all ages of disturbance. The comparison of characteristics between selected disturbances and non-selected disturbances revealed a number of interesting trends. Both sexes selected for larger disturbances in almost all seasons and decades. Females showed selection of disturbances at a consistent elevation, where males showed more seasonal variation, including moving closer to human settlements in the summer, contradicting movement patterns of grizzly bears in Scandinavia (Nellemann et al. 2007). As well, female grizzly bears selected for disturbances that have lower remotely-sensed greenness in all seasons and decades. While remotely-sensed greenness has proven an indicator of positive grizzly bear habitat, this is generally through identification of regenerating disturbances in landscapes containing alpine meadows (Mace et al. 1999, Nielsen et al. 2002). When comparing forest disturbances, remotely-sensed greenness does not indicate positive grizzly bear habitat. These results indicate possibilities for limiting access to important grizzly bear habitat. Focusing access management efforts on large disturbances at higher elevations could alleviate pressure on female grizzly bears.

Research Contributions

The first contribution of this thesis to the geographical discipline is the randomization methodology implemented in chapters two and three. The methods presented have wide applications as increasing volumes and types of data make interpretation in a classical statistical paradigm difficult or impossible (Fortin and Jacquez 2000). Randomization methods are particularly useful when applied to telemetry data, which are becoming increasingly common in ecological studies. Spatial autocorrelation is inherent in telemetry data and is a concern when performing any statistical analysis. Traditional statistics often makes assumptions that observations are independent and from a known distribution. With the increasing temporal frequency of modern telemetry data, animal locations cannot be considered independent. Conditional randomization allows for statistical evaluation of complex geographical data without relying on a null hypothesis of complete spatial randomness (Cressie 1993) or assumptions about observation independence.

The first randomization method (chapter two) incorporates existing knowledge of grizzly bear habitat use in order to isolate the effects of landscape edges. By relying on secondary data to describe the landscape, we were able to isolate the effects of grizzly bear use of edges. While this method is advantageous when habitat use data are available, the reliance on other data makes wider implementation more difficult. Our data-driven randomization in chapter three avoids relying on habitat selection models, meaning the methods developed can be applied to telemetry data studies without detailed knowledge of the movement patterns and habitat use of the study species. While the advantage of this method is its independence from other data, randomization occurs without concern for the landscape factors driving habitat selection. Both methods are suitable depending on the research questions being addressed and the secondary data available.

The second contribution of this research concerns grizzly bear conservation and management of the landscape for grizzly bear habitat. By developing an understanding of how grizzly bears interact with their landscape (especially human disturbed landscapes) areas of increased grizzly bear habitat use can be protected. A key result from this research is that female grizzly bears use anthropogenic edges more than natural edges, indicating anthropogenic disturbance is not incompatible with grizzly bear habitat selection. While the use of anthropogenic disturbances in our study area has been established as it concerns forest harvests (Nielsen et al. 2004a) and roads (Roever et al. 2008), the comparison between the selection of natural and anthropogenic disturbances allows forest managers to find specific areas to target for grizzly bear habitat conservation.

While chapter two indicates the importance of anthropogenic disturbance in grizzly bear habitat selection, chapter three identifies specific characteristics of forest disturbances that are attractive to grizzly bears. Female grizzly bear show a preference for larger disturbances at a consistent elevation across seasons (1250 m - 1300 m). As well, disturbances with lower than average remotely-sensed greenness are selected for by female grizzly bears. Understanding the characteristics that make disturbances attractive to grizzly bears can direct conservation efforts. By limiting access to disturbances that are attractants to grizzly bears, human-bear encounters can be lowered, which lowers grizzly bear mortality risk.

Research Opportunities

The results of this thesis lead to research opportunities in both spatial analysis and grizzly bear conservation. The novel randomization methods in chapters two and three allow for more thorough analysis of grizzly bear habitat by allowing researchers to analyze telemetry data in a spatially explicit manner without relying on comparisons to complete spatial randomness. The methods in chapter two allow researchers to incorporate *a priori* knowledge of the study species into analyses of habitat use. The methods in chapter three take a different approach by requiring no previous knowledge of the species' habitat use. While our randomization methods are designed to avoid a comparison to complete spatial randomness, they could be integrated with other randomization methods in wildlife biology. Conditional random walks and levy walks are often used for comparison with wildlife data (Edwards et al. 2007). While these methods incorporate autocorrelation inherent in telemetry data, randomization performed without regard to the nature of the landscape limits its applicability. Combining the inherent spatial auto-correlation of random walks with landscape driven randomization, or data driven randomization, could provide better expectations of use for comparison with telemetry data. Increasing use of rigorous spatial analysis in studies of telemetry data and incorporating controls for known spatial autocorrelation in the data will improve analysis, and lead to more accurate and appropriate results and management strategies.

As it concerns grizzly bear habitat management, there are numerous research questions to be addressed arising from this thesis. First, while I have identified attributes of disturbances that increase selection by grizzly bears (larger area, consistent elevation, etc.) much of this was done without controlling for other known factors influencing grizzly bear habitat selection. While our randomization methods account for inherent spatial patterns in the observed telemetry data, additional control data, such as time of day (Munro et al. 2006) or the presence of male bears (Wielgus and Bunnell 1995, Rode et al. 2006), could be incorporated to better identify important aspects of grizzly bear use of forest disturbances. Through further investigation into variables affecting grizzly bear use of natural and anthropogenic forest disturbances, access management can be adjusted to limit human and bear interactions and lower mortality risk in areas of positive grizzly bear habitat.

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