

Impact of disturbance characteristics and age on grizzly bear habitat selection

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A B S T R A C T

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Grizzly bears (*Ursus arctos*) have complex reactions to forest disturbances due to their use of forest clearings for foraging, their large home ranges, and the continued human expansion into undisturbed grizzly bear habitat. The goal of this paper is to quantify how grizzly bears interact with forest disturbances over time in west-central Alberta in order to inform habitat management decisions. This is accomplished using a four-decade remotely sensed disturbance history and detailed grizzly bear movement and habitat use information. Global positioning systems (GPS) collars were used to collect telemetry data for 22 adult grizzly bears (8 females, 14 males) from 2005 to 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 avoided. 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 avoided disturbances using a Mann–Whitney *U*-test. Male bears selected for 30–40-year-old disturbances more frequently than younger disturbances; females demonstrated equal selection of all ages of disturbances except those less than 10 years old. Females selected for disturbances more in the summer and fall than the spring. Disturbances selected by female bears were larger, with lower TCT greenness, and a consistent elevation (1250–1300 m) across seasons and disturbance age. Male bears showed 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 were larger, and more likely to show seasonal variation in greenness and elevation. Both sexes selected for larger disturbances of all ages, although disturbance size has generally decreased through time. Limiting human access to disturbances with characteristics attractive to grizzly bears will reduce grizzly bear and human interactions, and reduce mortality.

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Introduction

Anthropogenic disturbances can have substantive effects on flora and fauna (Nielsen, Stenhouse, Beyer, Huettmann, & Boyce, 2008; Swanson & Franklin, 1992; Wilcove, Rothstein, Dubow, Philips, & Losos, 1998), and can alter the life histories of wildlife (Bengtsson, Nilsson, Franc, & Menozzi, 2000). On-going management of forests for resource extraction, largely for timber harvest

and oil and gas exploration and development, has altered the natural disturbance regime. Forest fires have declined substantially through fire suppression and forest harvests have replaced fire as the primary agent of disturbance (Andison, 1998; Johnson, Miyaniishi, & Bridge, 2001; Tande, 1979). Changes in disturbances impact wildlife: black bears select for regenerating forest stands over mature conifer forests (Brodeur, Ouellet, Courtois, & Fortin, 2008). However, elk avoid areas following disturbance, despite an increase in herbaceous biomass, due to the threat of wolf predation (Hebblewhite, Munro, & Merrill, 2009). Other predators may avoid disturbed areas seasonally. For example, in winter, areas of forest harvest are avoided by the Canadian lynx due to the lack of cover to

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support predation while the deep snow impedes movement (Squires, Decesare, Kolbe, & Ruggiero, 2010). The variation in disturbance use between species presents an opportunity for managing forest disturbances for conservation.

Grizzly bear habitat use is strongly affected by anthropogenic forest disturbance (Nielsen, Herrero, et al., 2004; Schwartz et al., 2006). The change from a fire-driven disturbance regime to one driven by forest harvests is a worldwide phenomenon in productive forests (Drever, Peterson, Messier, Bergeron, & Flannigan, 2006; Smith, 2000) and has changed the nature of forest disturbances in grizzly bear habitat. Seasonal shifts in grizzly bear diet (Mowat & Heard, 2006; Munro, Nielsen, Stenhouse, & Boyce, 2006) require grizzly bears to vary habitat use (Nielsen, Herrero, et al., 2004). Many important food resources are found in anthropogenic forest disturbances, meaning the disturbance regime can dramatically affect grizzly bear habitat selection. 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 and is variable across studies. Research has shown bears avoiding forest harvests (McLellan & Hovey, 2001; Zager, Jonkel, & Habeck, 1983), using them as available (Berland, Nelson, Stenhouse, Graham, & Cranston, 2008), or selecting for them (Elgmork & Kaasa, 1992; Nielsen, Herrero, et al., 2004). The selection of forest harvests appears to occur in areas where anthropogenic suppression of forest fires eliminates natural forest clearings, forcing bears to look elsewhere for important resources (Nielsen, Herrero, et al., 2004). The use of regenerating forest harvests through time is an important aspect of grizzly bear habitat selection due to its implications for forest management. Nielsen, Boyce, and Stenhouse (2004) showed seasonal variation in selection of forest harvests, with female bears selecting for young (0–5 years post-disturbance) and old (>40 years post-disturbance) forest harvests in the fall,

while selecting for intermediate-aged (>5 and \leq 40 years) 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–bear interactions (Benn & Herrero, 2002; McLellan & Shackleton, 1988; Nielsen, Herrero, et al., 2004; Schwartz, Haroldson, & White, 2010).

A review of the use of regenerating forest disturbances by mammals suggests that our knowledge of disturbance use by large predators is inadequate (Fisher & 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. Solving this knowledge gap has been made possible through remote sensing. The diverse range of spatial and temporal resolutions of satellite imagery creates numerous mapping options. For example, Moderate Resolution Imaging Spectroradiometer (MODIS) imagery has been used for continental and global disturbance detection (Mildrexler, Zhao, & Running, 2009) and has the advantage of a high temporal resolution (daily revisit rate), but only moderate spatial resolution. With the opening of the Landsat archive (Woodcock et al., 2008), imagery is available, free of charge, from 1972 to the present. Large footprints ($\sim 185 \text{ km} \times 185 \text{ km}$) and a high resolution relative to forest disturbance monitoring allows for long-term analysis of forest disturbances at a spatial resolution that informs on both natural and anthropogenic activities (Stewart, Wulder, McDermid & Nelson, 2009; Wulder et al., 2008).

The goal of this paper is to quantify grizzly bear selection of regenerating forest harvests from 1973 to 2008 in west-central Alberta, Canada. In doing so we will demonstrate how geographical data and methods may be used to better understand the impacts of disturbance on wildlife, and how this can inform on habitat management plans. Our goal will be accomplished through two analyses: 1) quantify density of grizzly bear telemetry locations

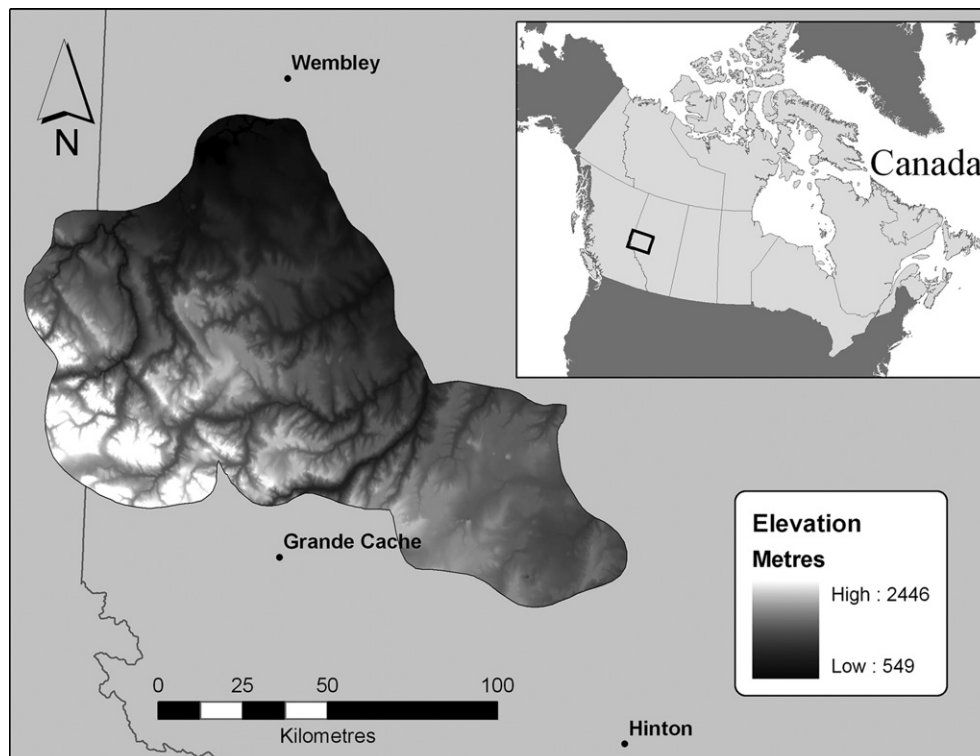


Fig. 1. Study area located in the eastern slopes of the Canadian Rocky Mountains west of Edmonton, Alberta, Canada. Study area is centred at 118° W and 54° N .

within forest disturbances of different ages, identified via remote sensing, to determine which disturbances are selected by grizzly bears; 2) compare forest disturbance characteristics between selected and avoided disturbances.

Though our methods our detailed below our general approach involves integrating remotely sensed forest disturbance and grizzly bear telemetry datasets 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, CSR is an unrealistic null model (Legendre, 1993) as grizzly bears are known to prefer some habitats to others (Mace, Waller, Manley, Ake, & Wittinger, 1999; Nielsen, Boyce, Stenhouse, & Munro, 2002), and grizzly bear movement is known to be non-random (Martin, Calenge, Quenette, & Allain, 2008; Smulders, Nelson, Jelinski, Nielsen, & Stenhouse, 2010). To address this, we use a novel spatial randomization approach that is statistically rigorous to 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.

To meet our second objective, we will use four metrics, disturbance size, elevation, remotely sensed greenness, and distance to populated place, to characterize forest disturbances and validate our hypotheses of grizzly bear disturbance selection. Our first hypothesis is that grizzly bears select for larger disturbances. Second, the elevation of disturbances enables testing of our 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 (McLellan, 1998; Roever, Boyce, & Stenhouse, 2008; Wielgus & Bunnell, 1995). Our third hypothesis relates to remotely sensed greenness (Tasselled Cap Transformation (Huang, Wylie, Yang, Homer, & Zylstra, 2002)), which 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, Herrero, et al., 2004).

Methods

Study area

We studied a population of grizzly bears in an 11,000 km² landscape in west-central Alberta, Canada (Fig. 1). The study area comprises a diverse, multi-use landscape with high elevation snow, rock, and ice in the west and low elevation rolling foothills, characterized by anthropogenic disturbances in the east. The elevation ranges from 2446 m 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, Scrimgeour, & Boyce, 2005; White, Wulder, Gomez, & Stenhouse, 2011). The fire suppression in this area 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 & Heard, 2006), Japan (Sato, Aoi, Kaji, & Takatsuki, 2004), and Scandinavia (Bellemain, Swenson, Tallmon, Brunberg, & Taberlet, 2005).

Data

Grizzly bear telemetry data

From 2005 to 2009, Global Positioning System (GPS) location data (telemetry data) were collected on 22 grizzly bears (Table 1). Aerial darting, leg-hold snaring and culvert traps were used to capture bears and attach GPS radio collars (Stenhouse & 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). We used GPS collars (Tellus – Lindesberg, Sweden) programmed to collect locations at hourly intervals during the non-denning period.

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 & Delparte, 2005). Following previous grizzly bear 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 the grizzly bear demographics.

Disturbance data

We utilized a 14-year change database described by White et al. (2011) and readers are referred there for further details. Briefly, stand replacing disturbances were detected through paired 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. Images were converted to top of atmosphere following Han et al. (2007), using coefficients from Chander, Markham, and Helder (2009) (see details on pre-processing in White et al., 2011). 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 change detected by each two time periods and used to establish stand replacing disturbances.

Disturbances were grouped into four decades for use in later comparisons and a summary of average decadal characteristics were calculated. Due to cloud cover and a general lack of images for the 1980s (an era of commercialization of the Landsat program, see Wulder et al. (2008)) in the Landsat archive over our study area, there is only one image that was useful for assessing change during the 1980s. The paucity of images in the 1980s may be problematic as TCA values can return to pre-disturbance levels within 5–10

Table 1
Demographics of grizzly bear telemetry points.

Sex	Number bears	Number of telemetry points		
		Spring	Summer	Fall
Female	8	13,249	11,706	16,524
Male	14	103,90	17,563	17,044

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. (2011). 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	—		

years (White et al., 2011), indicating a need for circumspect interpretations of trends representative of this decade.

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 to 75 m.

Second, a TCT was performed on a single Landsat ETM + scene from October 9th, 2009 and the greenness values were extracted. Analogous to the outcomes of a principal 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 & Cicone, 1984), focussing on the difference between the visible and near-infrared bands (Eq. (1)) (Huang et al., 2002).

$$\begin{aligned}
 TCT_{greenness} = & -0.3344 * B_{blue-green} - 0.3544 * B_{green} \\
 & - 0.5446 * B_{red} + 0.6966 * B_{near\ IR} \\
 & - 0.0242 * B_{mid\ IR} - 0.2630 * B_{short\ wave\ IR} \quad (1)
 \end{aligned}$$

Infrared radiation is scattered by the cellular structure of green vegetation while the visible bands are absorbed by chlorophyll (Crist & Cicone, 1984). Thus, higher density of green vegetation will correspond to higher TCT greenness values.

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.

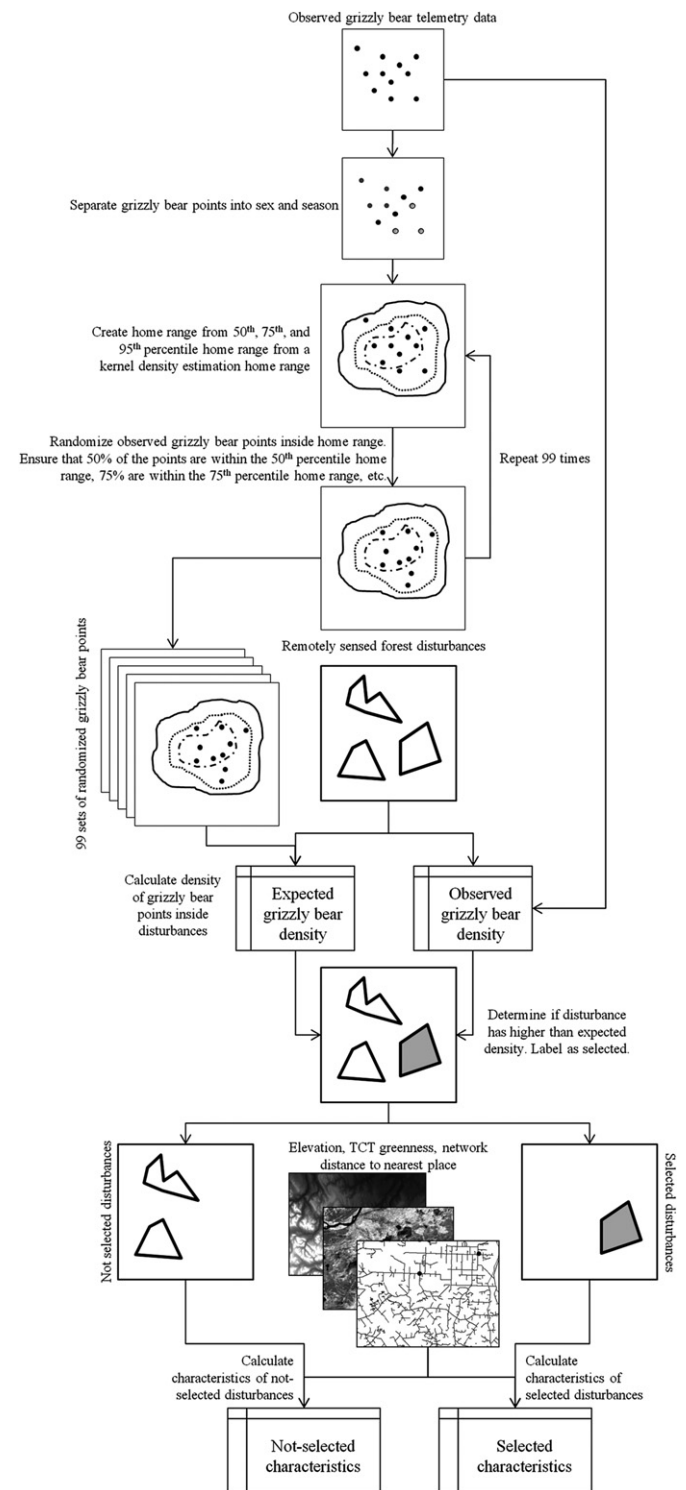


Fig. 2. Flowchart describing randomization process to determine selected disturbances and consequent comparison of disturbance characteristics between selected and not selected disturbances.

Analysis

To determine the selection and characteristics of forest disturbances by grizzly bears, a Monte Carlo machine learning approach was employed (i.e., [Andresen, 2009](#)) and a number of steps were taken ([Fig. 2](#)). First, grizzly bear telemetry data were used to generate home ranges at two scales: for individual bears (individual-level home ranges) and for all telemetry locations stratified by sex and season (population-level home ranges). Individual home ranges were used to calculate summary statistics describing the presence of disturbances in individual bear home ranges. Population home ranges were used to constrain the randomization procedure, as described next. 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. The randomization process allowed us to label each disturbance as either selected or avoided. Third, both selected and avoided 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 avoided 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) ([Borger et al., 2006](#); [Seaman & Powell, 1996](#)). KDE was chosen as it is a common home range method in wildlife management ([Powell, 2000](#)) that does not over-estimate area ([Powell et al., 2010](#)) and can account for multiple centres of activity ([Laver & Kelly, 2008](#)). The KDE smoothing parameter was estimated using least-squares cross validation and implemented on a Gaussian kernel ([Ruppert, Sheather, & Wand, 1995](#)).

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 ([Cressie, 1993](#); [Fortin & Jacquez, 2000](#); [Tobler, 1970](#)). 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 ensuring the density of the randomized points matched the level observed within the KDE home range. Specifically, 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.

Determining disturbance selection

The four decadal disturbance inventories (1970s, 1980s, 1990s, 2000s) were intersected with both the observed grizzly bear telemetry data and the randomized grizzly bear data to determine bear density in each 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 those with significantly lower bear density than expected at random were labelled avoided.

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

Characterizing forest disturbances with landscape characteristics

Each forest disturbance was characterized with the four forest metrics to determine the nature of the disturbance and its distance to human access. First, disturbance size 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. Network distance from populated places to forest disturbances is a better measure of human access to grizzly bear habitat than Euclidean distance, as human movement is limited by available access routes.

Disturbance comparison

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

Results

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, with 14.78–22.33% of their telemetry locations found in forest disturbances compared to 11.08–11.85% of male telemetry locations located within disturbances. Females show a greater percentage of disturbances in their home range than males. Both sexes show more telemetry locations in forest disturbances than expected based on the area of disturbance in their home range 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](#)). Forest disturbance size has changed since the

Table 4

Average disturbance characteristics for all forest disturbances.

	Area (m ²)	Elevation (m)	Greenness	Distance (m)
2000	41,037	1113	10.50	54,594
1990	68,750	1121	17.51	60,020
1980	125,155	1258	17.95	52,101
1970	260,460	1072	18.68	60,344

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		
		Spring	Summer	Fall	Spring	Summer	Fall
2000	19,407	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%	3.50%	0.27%
1970	1318	3.94%	10.77%	7.64%	8.92%	8.28%	1.21%

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 all disturbances except those 20–30 years old 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. Results show disturbances in the 2000 decade have higher TCT greenness values than disturbances in the 1970s, indicating expected forest regeneration. 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 all disturbances over 10 years old. Females select disturbances less than 10 years old the least, except in the spring. Males select fewer disturbances of all ages in the fall. 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 avoided disturbances (Fig. 3 – significance is indicated by stars on the figure). Both sexes show selection for larger disturbances, significantly larger for all ages of disturbances except those 30–40 years old.

The nature of disturbances in our study area shows increased elevation of disturbances in the 1990s and 2000s, relative to the 1970s, in both selected and avoided disturbances (Fig. 4 – significance is indicated by stars on the figure). 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 all ages of disturbance except those 30–40 years old.

Females show selection for disturbances with greenness lower than the avoided disturbances for except for the 30–40-year-old disturbances (see Fig. 5 – significance is indicated by stars on the

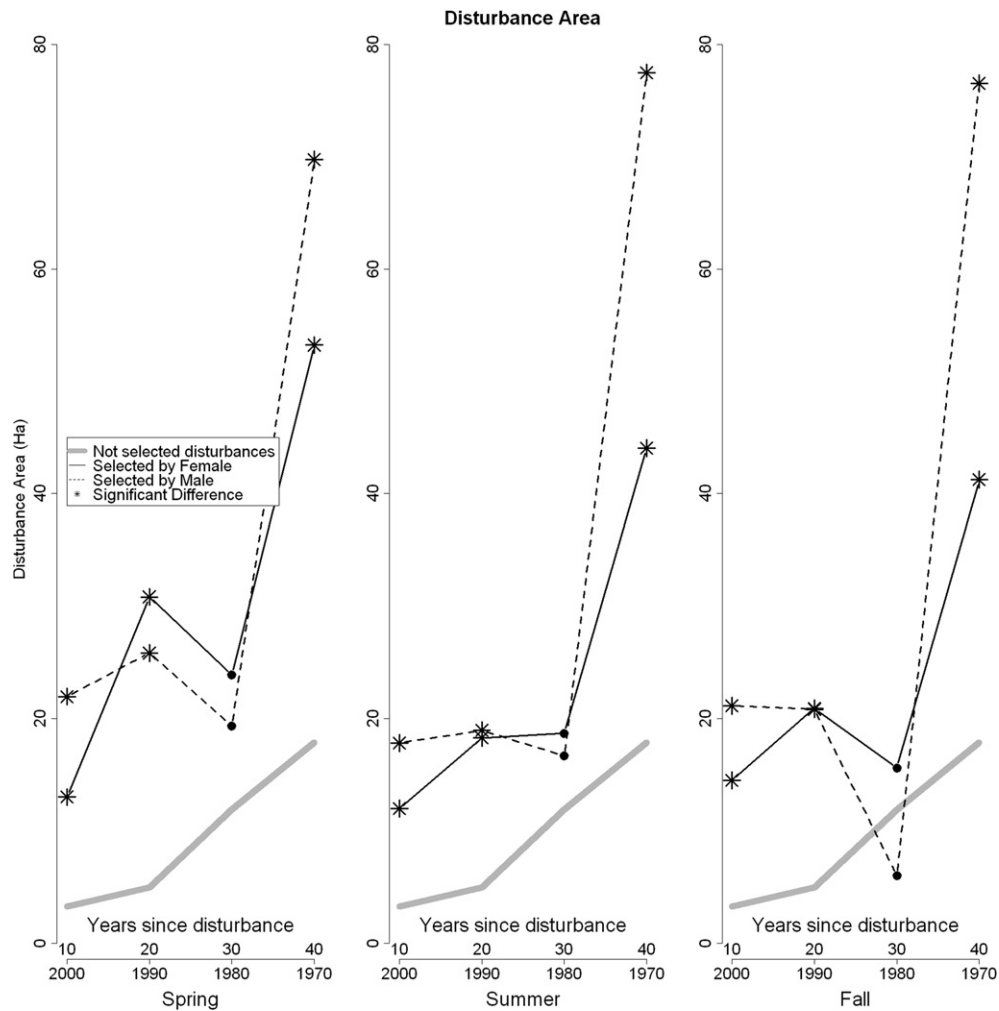


Fig. 3. Comparison of disturbance area between selected and non-selected disturbances for adult male and adult female grizzly bears for spring, summer, and fall. Stars indicate a significant difference ($\alpha = 0.05$) between the characteristics of the selected disturbances and the not select disturbances. Note that the data for the 1980s are limited and, therefore, results are preliminary.

figure). Disturbances selected by females have significantly lower than expected TCT 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 TCT greenness in the summer for all decades, but selection of disturbances with lower TCT greenness in the fall. There is greater variance in the selection of TCT greenness for more recent disturbances, with a stabilization of mean values and a lessening of variance over time (Fig. 6). Mean values change little after year 10, but measures become less variable.

Both sexes of grizzly bears select for disturbances further from populated places in the spring (see Fig. 7 – significance is indicated by stars on the figure). There is variation between seasons, as females select for disturbances closer to populated places for intermediate-aged disturbances in the summer and fall.

Discussion

GIS and remote sensing are useful technologies for supporting wildlife research (e.g., Aguilar & Farnworth, 2012). We have undertaken a spatial pattern and data-driven approach to quantify the use and nature of disturbances of various ages. Our results agree with previous studies (Elgmork & Kaasa, 1992; Nielsen, Herrero, et al., 2004) that have shown grizzly bears use disturbances at

a higher frequency than available within their home range. However, not surprisingly, there are variations between sexes. Females show a greater use of available disturbances than males; indicating the importance of maintaining forest disturbances for optimal grizzly bear habitat selection. Since it has been established that anthropogenic forest disturbances are important sources of grizzly bear food (Nielsen, Herrero, et al., 2004) and females show increased selection of these disturbances, focussing on limiting human access to the most beneficial disturbances is an important goal for habitat conservation. Determining which disturbances are most beneficial is critical in designing management regimes, and our results indicate selected disturbances show substantial differences from avoided disturbances.

The results of our study indicate that age of disturbance is an important factor in grizzly bear selection of forest disturbances. Both male and female grizzly bears selected disturbances less than 10 years old at the lowest rate, 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, Munro, et al., 2004) or the presence of humans (Benn & Herrero, 2002; Nielsen, Herrero, et al., 2004). For females, disturbances older than 10 years showed increased selection in the summer and fall. Males show increased selection of older disturbances as well, selecting for 30–40-year-old disturbances the most, but showing the lowest levels of disturbance selection in the fall for all decades.

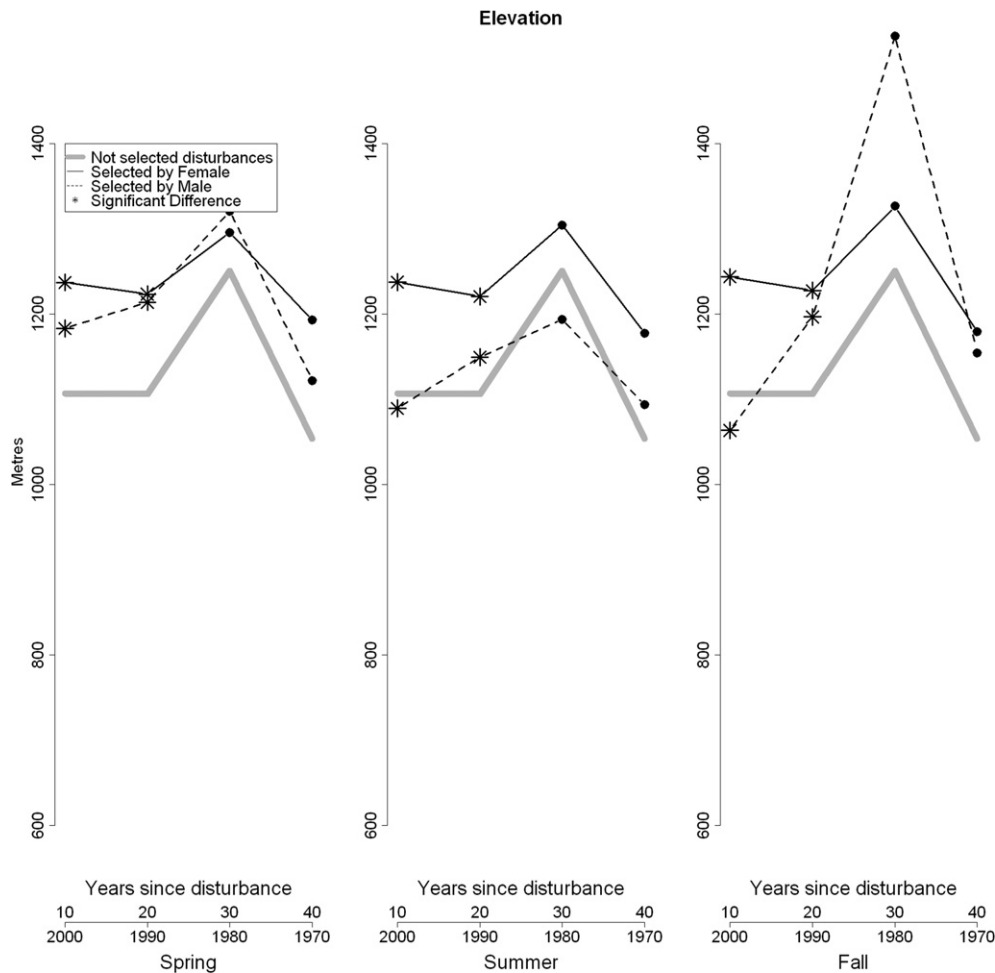


Fig. 4. Comparison of average elevation between selected and non-selected disturbances for adult male and adult female grizzly bears for spring, summer, and fall. Stars indicate a significant difference ($\alpha = 0.05$) between the characteristics of the selected disturbances and the not select disturbances. Note that the data for the 1980s are limited and, therefore, results are preliminary.

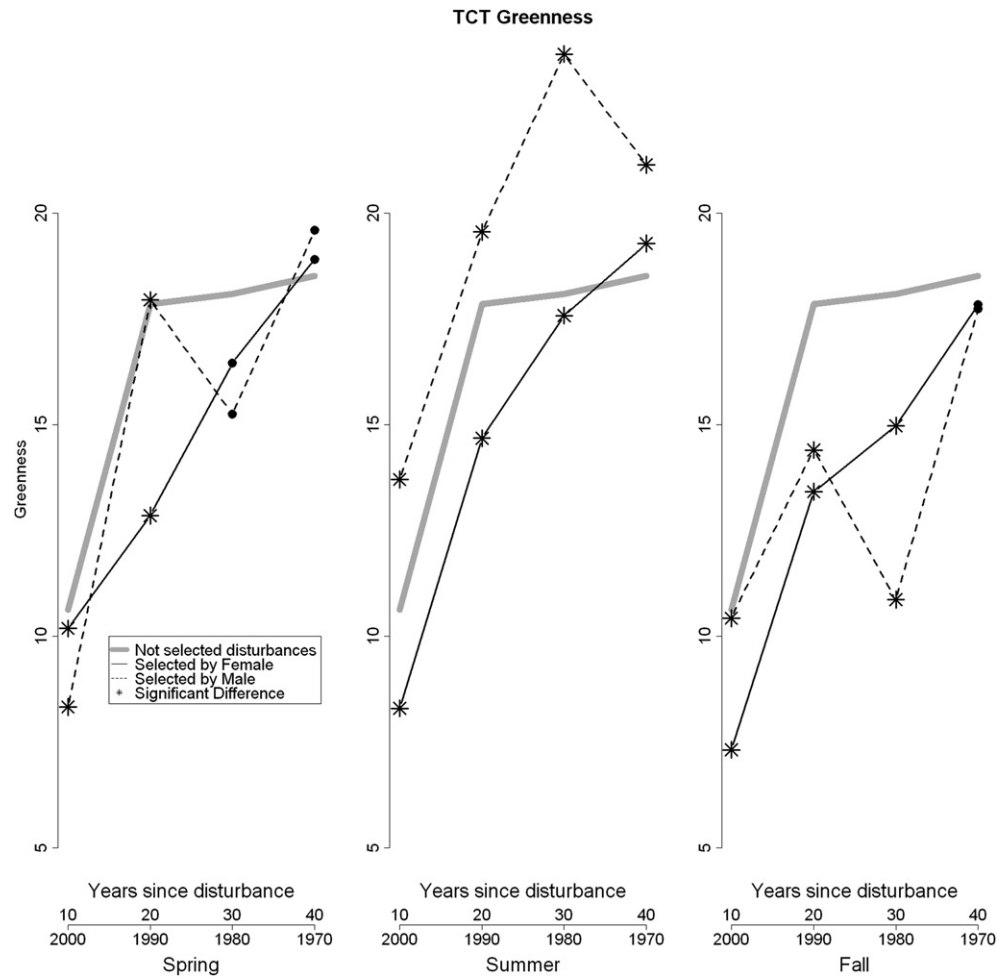


Fig. 5. Comparison of average TCT greenness between selected and non-selected disturbances for adult male and adult female grizzly bears for spring, summer, and fall. Stars indicate a significant difference ($\alpha = 0.05$) between the characteristics of the selected disturbances and the not select disturbances. Note that the data for the 1980s are limited and, therefore, results are preliminary.

Beyond age of disturbance, other characteristics also affect grizzly bear habitat selection. Our hypothesis that grizzly bears will select for larger disturbances was supported for all disturbances except those from the 1980s. Current management regimes create small clearcuts (<40 ha) in a checkerboard of forest and forest harvest (Smith, Russell, Burke, & Prepas, 2003). As disturbances have become smaller through time (White et al., 2011), disturbance size could be affecting how grizzly bears use the landscape. This is an especially important consideration as new forest management paradigms related to mitigating the effects of mountain pine beetle are increasing forest harvest size in Alberta (Mathey & Nelson, 2010; Schneider, Cecilia Arienti, Stelfox, Farr, & Boutin, 2009).

Selected disturbances are significantly larger than avoided disturbances of all ages except for disturbances of the 1980s (20–30 years old) (although this could be an effect of bias in our change detection methods). While the oldest disturbances are generally much larger, selected disturbances are still significantly larger than avoided disturbances. Current forest management practices are being re-thought in a natural disturbance framework, where harvests are designed to emulate natural disturbance regimes (Nielsen et al., 2008; Swanson & Franklin, 1992) leading to larger, more secluded forest harvests. In this re-modelling, knowing that grizzly bears select for larger disturbances is important for management considerations. When considering the selection of these disturbances, it is also 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.

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 500 m of roads or 250 m of trails (Benn & Herrero, 2002), increasing disturbance size could limit the number of disturbances and the number of associated forestry roads. Recent research suggests that natural disturbance-based forestry, with larger, more isolated cuts is not beneficial to grizzly bears due to the associated increased road density (Nielsen et al., 2008). However, increasing forest harvest size in the current management paradigm may create more appealing grizzly bear habitat and could be considered with limited road development. Given the draw of larger disturbances as habitat for grizzly bears, management actions should be considered to limit human access in order to limit associated mortality risk. The shape and configuration of larger harvesting areas may also be important to consider when reducing visibility of bears using these areas.

Our hypothesis that grizzly bears will select for higher elevation disturbances was supported, with both sexes selecting for higher elevation disturbances in all seasons except for males in the

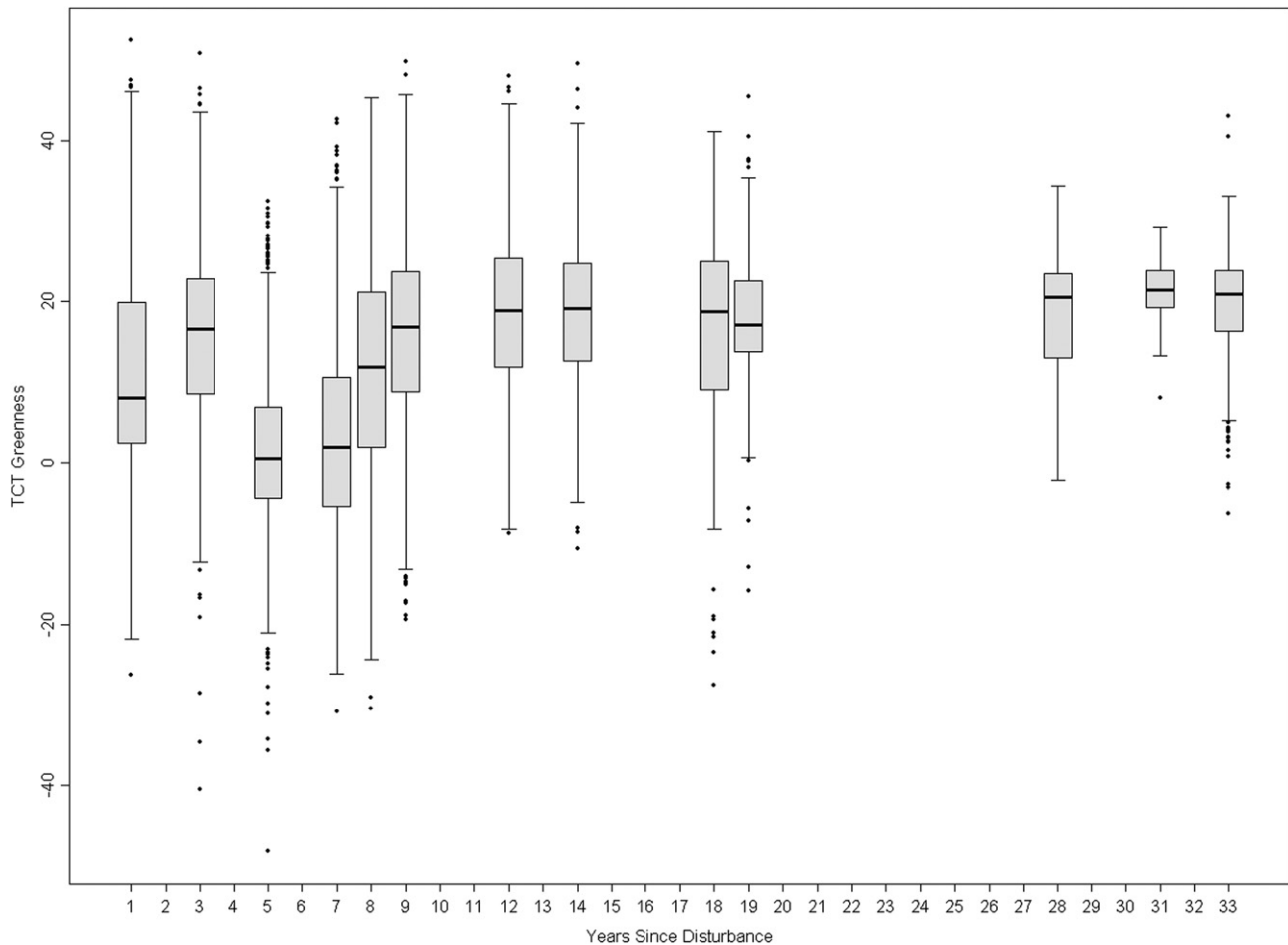


Fig. 6. Boxplot of disturbance TCT greenness through time. The boxplots of are based on median values. Note that the data for the 1980s are limited and, therefore, results are preliminary.

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, Boyce, Heard, & Seip, 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 (Mowat & Heard, 2006; Servheen, 1983). The difference in elevation of selected disturbances between male and female grizzly bears could be an indication of sexual segregation of habitat (Rode, Farley, & Robbins, 2006).

Our hypothesis that grizzly bears will select for disturbances with higher TCT greenness values was rejected for almost all ages of disturbance. Except for males in summer, grizzly bears selected for disturbances with lower TCT greenness values. However, this trend was not as dramatic in the oldest disturbances, confirming our hypothesis that selection of older disturbances will be less affected by TCT greenness. Shortly after a disturbance, herbaceous growth will drive the TCT greenness signal; a stabilization of TCT greenness will occur as succession processes unfold (Han et al., 2007; Kauth & Thomas, 1976). Similar means and decreased variances of TCT greenness values for the oldest disturbances relate to maturing stand conditions. White et al. (2011) found TCT greenness levels recovering to pre-disturbance levels within 10 years. Our results

roughly support this finding as we see our disturbances reaching a plateau of TCT greenness values around year 12 (Fig. 6). At the landscape-scale, TCT greenness is an indicator of vegetation presence and vigour and is certainly capable of differentiating regenerating forest from barren alpine areas, which explains positive grizzly bear selection associated with remotely sensed greenness (Mace et al., 1999; Nielsen et al., 2002). When comparing regenerating forest disturbances, TCT greenness does not appear to be an indicator of beneficial grizzly bear habitat as bears select for less green forest disturbances. Thus, while remotely sensed greenness may be positively related to grizzly bear habitat as an indicator of the presence of green vegetation, we should not expect the absolute level of TCT greenness values to correspond with grizzly bear habitat selection. 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 (Rode et al., 2006; Wielgus & Bunnell, 1995), 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 was supported for females, but was 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, Poe, Suring, Nielsen, & McDonald, 2010). In that context our results are not surprising as both sexes selected disturbances further from populated places in the spring. While

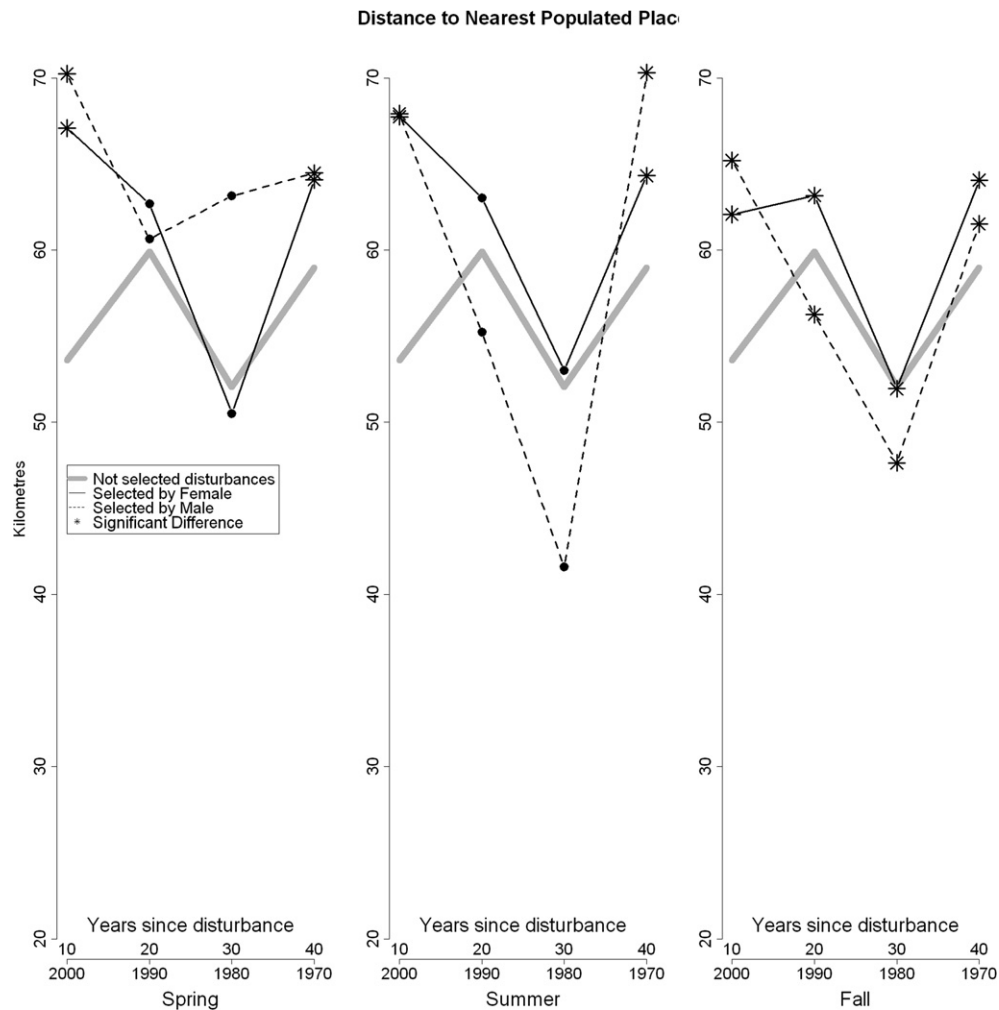


Fig. 7. Comparison of distance to nearest populated place between selected and non-selected disturbances for adult male and adult female grizzly bears for spring, summer, and fall. Stars indicate a significant difference ($\alpha = 0.05$) between the characteristics of the selected disturbances and the not select disturbances. Note that the data for the 1980s are limited and, therefore, results are preliminary.

female grizzly bears were more consistent in their selection of disturbances with respect to distance to populated place, the males in this study were found to be more willing to travel closer to human settlements, especially in the summer. Our results are different from previous studies that have shown males staying further from populated locations, while females occupying areas closer to humans (Nellemann et al., 2007). While much analysis has been done on the interaction of grizzly bears and roads (Kaczensky et al., 2003; McLellan & Shackleton, 1988; Roever et al., 2008), our analysis considers network distance to human settlements as a measure of anthropogenic access to grizzly bear habitat. The interaction between grizzly bear habitat use and disturbance is complex. While some disturbance provide resources for bears, increased human access to grizzly bear habitat increases mortality risk (Benn & Herrero, 2002; Noss, Quigley, Hornocker, Merrill, & Paquet, 1996). When disturbances are providing resources, access to these areas should be limited to reduce the likelihood of human-caused mortality.

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 increased seasonal selection by grizzly bears. Understanding selection preference provides new management avenues and criteria. For instance, it may be best to limit access in the locations with habitat characteristics similar to those most utilized by bears. Increasing size of forest harvests will create more disturbances of the size selected by grizzly bears, as the current small (<40 ha) cuts are smaller than generally selected. The consistent elevation of disturbances selected by females is an important finding and could direct conservation efforts. Conservation of the female grizzly bear population is integral to maintaining a healthy grizzly bear population. Further research into this trend would be of value to determine the nature of the relationship between grizzly bear disturbance selection and elevation.

Development of methods for combining and analyzing large datasets is important in advancing geographic research. 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, White, Masek, Dwyer, & Roy, 2011) the methodology presented here is applicable to many other geographical studies that utilize remotely sensed data products. 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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