

Quantifying Grizzly Bear Selection of Natural and Anthropogenic Edges

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ABSTRACT

Understanding the use of edges by threatened species is important for conservation and management. Whereas the effects of anthropogenic edges on threatened species have been studied, the effects of natural edges are unknown. We studied grizzly bear (*Ursus arctos*) habitat selection in relation to different landscape-level measures of edge, both natural and anthropogenic. We used a database of global positioning system telemetry data collected from 26 grizzly bears from 2005 to 2009 in the foothills of the Rocky Mountains in west-central Alberta, Canada. We quantified grizzly bear locations relative to natural edges extracted from satellite-derived land cover data and anthropogenic edges from existing vector datasets (roads, pipelines, and forest harvests). To compare edge distance from observed telemetry points statistically, we generated a distribution of expected points through a conditional randomization of an existing resource selection function describing grizzly bear habitat use without respect to edges. We also measured the density of edges within home ranges and compared this to the overall population to create an edge selection ratio. In general, females selected anthropogenic edges, whereas males selected natural edges. Both sexes selected the natural transition (edge) of shrub to conifer. Females had a greater selection ratio for road edges than males in all seasons, and males had a greater selection ratio for roads in the fall than in other seasons. Only females selected for pipeline edges. Our results indicated that edge habitat was selected by both males and females, mostly in the fall. Given human access to bear habitat is often facilitated by anthropogenic edges (e.g., roads), improved management of these features may minimize human conflicts. In particular, we highlight the importance of the natural transition of shrub to conifer to grizzly bears.

KEY WORDS: Alberta, anthropogenic disturbance, conditional randomization, edge, grizzly bear, habitat selection, resource selection function, *Ursus arctos*.

INTRODUCTION

As edges represent the interface between distinct habitat patches, unique ecosystem characteristics may occur near edges (Forman 1995, Fortin et al. 2000, Ries et al. 2004). Creation of edge habitat can increase mortality as species may be exposed to greater rates of predation (Gardner 1998, Nielsen et al. 2004b) and brood parasitism (Murcia 1995). However, edges may also improve habitat conditions by providing access to resources in distinct habitat patches in close proximity (Lay 1938, Forman 1995, Ries and Sisk 2004). Mature forest cover in proximity to disturbed areas also provides for herbaceous food sources near the relative security and shelter of forest cover (Nielsen et al. 2004a, 2004c). Anthropogenic disturbances (e.g., logging, road-building) commonly create edge habitats (Raven 2002, Balmford et al. 2003). However, understanding how a species uses all the edges in their habitat, both natural and anthropogenic, is important for wildlife management.

Grizzly bears (*Ursus arctos*) of west-central Alberta provide an ideal case study for analyzing the use of natural and anthropogenic edges. Designated as threatened in 2010 by the Alberta government (Clark and Slocombe 2011), grizzly bears exist in diverse, multi-use environments, where increasing anthropogenic disturbances are affecting traditional habitat (Mace et al. 1999, Berland et al. 2008, Festa-Bianchet 2010). Human developments related to resource extraction have led to an increased density of roads and support infrastructure (Nielsen et al. 2008) that has resulted in more anthropogenic edges and fewer natural edges. Although additional food resources are generally characteristic of any edge (Forman 1995, Ries et al.

2004), increased mortality risks to grizzly bears derive from anthropogenic edges (Benn and Herrero 2002, Nielsen et al. 2004b).

Our research objectives were to 1) quantify density of edge types in available grizzly bear habitat and 2) quantify and evaluate the frequency of edge selection. Grizzly bears use an array of habitats throughout the year because of seasonally dynamic food values (Nielsen et al. 2003, Munro et al. 2006). In addition, grizzly bears are sexually dimorphic (Rode et al. 2006), and males often select different habitat from females (McLellan and Shackleton 1988, Rode et al. 2006, Graham et al. 2010). Thus, we examined edge selection by sex and by foraging season. We hypothesized that 1) grizzly bears will show similar selection of natural and anthropogenic edges and 2) edge selection will vary seasonally and by sex.

STUDY AREA

The study area was the Kakwa forest region in west-central Alberta, Canada (Fig. 1). Land cover was characterized by montane forests, conifer forests, sub-alpine forests, alpine meadows, and high elevation snow, rock, and ice (Achuff 1994, Franklin et al. 2001). Located on the eastern slopes of the Rocky Mountains, elevation ranged from almost 2,500 m down to 600 m. As elevation decreased from west to east, wetlands became increasingly common due to moderate slopes and the collection of water from the alpine areas (Franklin et al. 2001). Resource extraction industries have been active in the area for a number of decades with most forest disturbances in the area arising from forest management, and more recently, oil and gas exploration (Schneider 2002, White et al. 2011).

METHODS

We obtained telemetry data from 2005–2009 for 26 grizzly bears as part of the Foothills Research Institute Grizzly Bear Program (FRI). Program researchers captured bears using aerial darting from helicopters, leg-hold (cable) snares, and culvert traps (Stenhouse and Munro 2000, Cattet et al. 2003) following protocols accepted by the Canadian Council of Animal Care for the safe handling of bears (Animal Use Protocol number 20010016). Researchers fitted captured bears with a Televilt brand global positioning system (GPS) collar (Tellus 1 or Tellus 2; Followit, Lindesberg, Sweden), which collected grizzly bear locations once per hour. Researchers collected data from collars monthly on data-upload flights using fixed-winged aircraft. Researchers used very high frequency (VHF) to upload the data as the ultra-high frequency (UHF) was not functioning.

Following previous research (Nielsen et al. 2009), we partitioned data seasonally, based on shifts in diet and habitat. We defined spring as 1 May to 15 June, summer as 16 June to 31 July, and fall as 1 August until 15 October (the mean denning date). We also partitioned grizzly bear telemetry points annually, creating sets of telemetry data for each season, year, and bear. We obtained 9,937 telemetry locations from 9 individual female bears and 5,708 locations from 8 males in spring, 15,009 locations from 14 females and 13,629 locations from 11 males in summer, and 20,682 telemetry locations from 15 female bears and 5,227 locations from 4 males in fall. We performed analysis for each sex, in each season, grouping data across years. We eliminated erroneous telemetry data based on positional dilution of precision (PDOP; >10, D'Eon and Delparte 2005) and we eliminated data for seasons with less than 50 points per bear to avoid the effect of small sample sizes on home range calculations (Seaman and Powell 1996).

We obtained and used a satellite-derived land cover dataset to define natural edges (Franklin et al. 2001). The land cover dataset was the outcome of integrating data from a

tasselled cap transformation (Huang et al. 2002) of Landsat-5 Thematic Mapper (TM) data, a 100-m digital elevation model, and polygonal vegetation data from the Alberta vegetation inventory (Alberta Sustainable Resource Development [ASRD] 2005). The resulting 30-m spatial resolution land cover dataset had an overall accuracy of 80.16% when compared to field data (see Franklin et al. 2001 for details). The original land cover dataset contained 15 classes, ranging from dense conifer to cloud and shadow, but we simplified the classification into 6 classes (conifer forest, mixed forest, broadleaf forest, wetland, shrubs, and other) to facilitate the extraction of land cover transitions.

We used a series of vector layers to define anthropogenic edges and combined these with natural edges extracted from the land cover dataset to create our edge inventory. Our vector layers included road network data containing both major and minor roads (secondary and logging roads) and pipeline data. We based our linear vector disturbance data on the Alberta Sustainable Resource Development base feature dataset, which we updated through heads-up digitizing using medium- to high-resolution imagery (SPOT imagery and air photos).

We identified stand replacing forest disturbances from logging through image pair differencing of a series of satellite images from the Landsat series of satellites (see White et al. 2011 for a detailed description of the image selection, image processing, and change detection process). We converted disturbances from raster to vector polylines to integrate with the vector-based linear features described above.

To assess selection for edges, we needed a control for comparison. Although random sampling is often used in spatial pattern analyses, complete spatial randomness is a poor expectation for ecological processes (Cressie 1993, Fortin and Jacquez 2000). We used an existing ecological model describing general bear habitat, a resource selection function (RSF), to condition the randomization process described below. Resource selection functions estimate the relative probability of use of a resource unit (Manly 2002) and have been widely used in wildlife habitat selection studies (Bowyer and Bleich 1984, Edge et al. 1987, Ciarniello et al. 2007, Nielsen et al. 2009).

We modified an existing RSF model created by Nielsen et al. (2009). We removed edge-related variables from the model and recalculated variable coefficients and RSF values (see Nielsen et al. 2009 for further details on model development and testing). Because of the seasonal flux of grizzly bear food availability, we derived a separate model for each season (spring, summer, and fall). We used the same variables for all 3 seasons, but coefficients varied (Table 1). Our adaptation of the RSF explicitly excluded edge variables to control for non-edge factors associated with grizzly bear habitat selection. In doing so, we accounted for the selection processes that do not relate to use of edges with the RSF and focused our statistical assessment on edge influences.

To create a geographic information system (GIS) edge inventory (Table 2), we used existing data on anthropogenic edges (roads, pipelines, and forest harvests) and generated our own data for natural edges based on transitions in land cover (Wulder et al. 2009). We passed a 3-pixel by 3-pixel moving window over the land cover dataset with edges defined based on differences in land cover from adjacent pixels. We classified the central pixel of the moving window as an edge if the window was heterogeneous, indicated by the presence of ≥ 2 land cover classes. We excluded transitions with > 2 land cover classes because of ecological complexity and small sample size ($< 3\%$).

We identified 4 land cover transitions: shrub-to-conifer forest, shrub-to-mixed forest, shrub-to-broadleaf forest, and wetland-to-forest (all forest types). We focused on shrub-to-forest

(conifer, mixed, and broadleaf) transitions as many of the shrub habitats represented forest clearings. Because of the sparseness of wetland transitions, the wetland-to-forest transition included wetland-to-conifer, wetland-to-broadleaf, and wetland-to-mixed.

We estimated home ranges for each season using 95% volume isopleth kernel density estimates (KDE) using the SD extension of R (Seaman and Powell 1996, Bowman and Azzalini 1997:112–117, Borger et al. 2006). We defined bandwidth for KDE estimates using direct least-squares cross validation (LSCV) with a Gaussian kernel (Ruppert et al. 1995). Bandwidth values varied from 503 m to 988 m. To delineate the home range of the population, we conducted LSCV using all points, with an indicated bandwidth of 1,020 m. Once we defined home ranges, we calculated the total length of each edge type by individual home range, as well as at the population level. We estimated edge selection ratios by dividing the edge density in an individual home range by the edge density in the population-level home range.

To evaluate if grizzly bears used edges more than expected, we classified each telemetry location based on the nearest edge type. For each bear, in each season, we calculated the percentage of telemetry points closest to each edge. We compared the observed percentage of each type of edge to a statistical distribution of edges generated via randomization or Monte Carlo procedures. We spatially limited the randomization to the individual's home range and conditioned locations on known habitat selection using a seasonal RSF (Fortin and Jacquez 2000, Smulders et al. 2010). By conditioning the randomization on the RSF, we reduced type 1 errors associated with unrealistic comparisons to complete spatial randomness (Cressie 1993, Legendre 1993, Martin et al. 2008). The conditional randomization ensured that the randomized points showed the same frequency distribution of RSF values as the observed telemetry locations.

We performed 99 randomizations for each set of grizzly bear points. We calculated edge use for the random datasets the same as for the observed telemetry data, which provided an observed edge use and an expectation of edge use from the 99 randomizations. We selected a statistical significance level of $P \leq 0.05$ for our tests. For each sex and season class, we reported the closest edge type by average percent of observations and indicated when more than 50% of bears had observed telemetry locations closer than expected to a specific disturbance.

RESULTS

Female bears were more likely to be in habitats with a greater amount of anthropogenic edge and shrub conifer edge (ratio >1) regardless of season (Fig. 2). In general, edge selection ratios were highest in fall and lowest in summer for female grizzly bears in our study. Female selection for wetland-to-forest edges was highly variable in spring.

Males generally had smaller edge selection ratios than females (Fig. 3). Shrub-to-conifer edges were the only edges that consistently occurred in greater densities in male home ranges than in the study area. Road densities in male bear home ranges were greater than in surrounding areas only in fall. In addition to roads, male edge selection ratios were greatest in fall for shrub-to-conifer and forest harvests.

In all seasons, males had a greater percentage of telemetry locations closest to natural edges compared to anthropogenic edges (Table 3). During fall, greater than 50% of female telemetry locations were closer to natural edges than statistically expected based on the RSF model. Males had greater than 50% of their locations closer to natural edges in both summer and fall. We observed females to be closest to wetland edges more than males (4.7%, 5.8%, and 3.5% of telemetry locations in spring, summer, and fall, compared to 0.7%, 1.8%, and 0.3% for males). Neither sex selected wetlands more than expected based solely on availability. Both sexes selected shrub-to-conifer edges more than other natural edges.

Both males and females selected for anthropogenic edges more than statistically expected based on the RSF model in summer and fall (Table 3). In any season, females were more often near anthropogenic edges than were males (59.2–63.1% relative to 21.2–27.6% of telemetry points, respectively). Relative to anthropogenic edges, both male and female bears were more frequently closest to forest harvests, followed by roads and pipelines. Only females selected pipelines (in summer and fall). For both sexes, >50% of bears showed no selection for anthropogenic edges in spring.

DISCUSSION

In contrast to selection of anthropogenic edges by bears, relatively little research has addressed the selection of natural edges. We found that the female grizzly bears in this study selected anthropogenic edges over natural edges. In contrast, male grizzly bears generally selected natural edges over anthropogenic edges.

Our results support previous studies that reported male and female grizzly bears select for different habitats (McLellan and Shackleton 1988, Gibeau et al. 2002, Graham et al. 2010). Researchers have suggested explanations such as females trying to avoid infanticide by males (McLellan and Shackleton 1988), competitive exclusion by the more dominant males (Mattson et al. 1987), or selection for different food types (e.g., males feeding on ungulates; Munro et al. 2006, Graham et al. 2010). Although understanding the reasons for differences in habitat selection between the sexes was beyond the scope of this study, observing that males select natural edges, whereas females select anthropogenic edges, allows researchers to develop more refined hypotheses.

Selection for anthropogenic edges by female grizzly bears was consistent with other studies that reported female grizzly bears being closer to anthropogenic features than their male counterparts (Mattson 1990, Rode et al. 2006, Graham et al. 2010). In particular, female grizzly bears have been found to select roads to a greater extent than males (Roever et al. 2008, Graham et al. 2010). 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 habitat near roads by female grizzly bears has implications for mortality risk and potentially for grizzly bear conservation, as female survival is the dominant vital rate affecting population viability (Bunnell and Tait 1981; Eberhardt et al. 1994; Nielsen et al. 2006, 2008). The increasing number of roads, due to continued resource extraction (Graham et al. 2010), represents a growing risk to females and therefore to the grizzly bear population. Although pipelines do allow for increased human access, pipelines affect human access much less than roads (Nielsen et al. 2002); thus, pipelines likely carry less risk of mortality.

We found the selection of edges by grizzly bears to vary with season. Females were only significantly closer than expected to shrub-to-mixed edge during spring. Digging of sweet vetch, a common feeding activity in early spring, is known to occur frequently in shrub areas (Munro et al. 2006), and females were possibly selecting this edge for feeding opportunities adjacent to cover. Although the females in our study had a greater proportion of anthropogenic edges in their home ranges than available in the study area during spring, they were not statistically closer than expected to these edges as determined by the RSF. Thus, we cannot say that females were selecting anthropogenic edges in spring. This is consistent with other studies that did not detect selection of forests harvests (Nielsen et al. 2004a) or roadside habitat during spring (Graham et al. 2010).

Previous studies have documented a negative association between grizzly bears and wetlands (McLoughlin et al. 2002), as they contain few high quality foods. We were unable to find evidence for the selection of wetland edges by females or males. However, the selection ratios for wetland edges in spring for females were highly variable and likely reflected individual variation in the use of this edge habitat. Munro et al. (2006) associated ungulate kills with wetland forests during late spring. The degree of carnivory by female grizzly bears was reported to vary substantially among individuals (Edwards et al. 2011). We postulate that the variability in spring wetland edge selection exhibited by female grizzly bears in our study could be related to the use of these edges by particular females that prey on ungulates.

Both male and female bears in our study were found to be closer than expected to anthropogenic edges and shrub-to-conifer edges during summer. Grizzly bears are known to forage on forbs, grasses, insects, and other foods associated with disturbed or herbaceous sites during summer (Munro et al. 2006). However, the unexpected selection of these edges indicated that the RSF was under-predicting use of shrub-to-conifer and anthropogenic edges by grizzly bears in summer.

With the impetus to acquire adequate fat reserves for hibernation, fall is considered to be the most critical foraging period for grizzly bears (Nielsen et al. 2006). During fall, bears feed primarily on berries (*Vaccinium* spp) in areas typically with canopy cover $\leq 50\%$ (Nielsen et al. 2004c). In addition to berries, the consumption of roots, such as sweet vetch, resumes during fall and these foods are a primary source of protein for grizzly bears (Coogan et al. 2012). Chruszcz et al. (2003) found males in proximity to low volume roads during fall, and both of our results (edge selection ratio >1 and statistically unexpected habitat selection) highlight the use of roads by males during fall. The female grizzly bears in our study not only selected all anthropogenic edges during fall, but all of the shrub edges as well. We suggest that the selection of edges during fall by grizzly bears would indicate the role of edge habitat in providing critical foods prior to denning.

Forest harvest edge was the most abundant edge in our study area (51.9% of all edges), and females still had proportionally more forest harvest edge in their home ranges than in the study area. In addition, both males and females were found to be closer than expected to forest harvest edge during summer and fall, which is consistent with earlier studies that found grizzly bears selected forest harvests during summer (Nielsen et al. 2004a) and fall (Nielsen et al. 2006). Nielsen et al. (2004a) hypothesized that grizzly bears used the logged areas as a resource surrogate for natural openings, which may be scarce because of fire suppression (Schneider 2002). In addition, Nielsen et al. (2004a) determined that grizzly bears were most often closest to the edge of the forest harvest.

Forest harvest edges can be considered to be functionally analogous to the natural edge, shrub-to-conifer. The increased food resources at transitions between homogenous land cover types (Nielsen et al. 2004c, Ries et al. 2004) often attract grizzly bears (Nielsen et al. 2004a, 2009, 2010). Shrub-dominated areas contain many bear foods such as roots, insects, and fruit (Nielsen et al. 2004c, Munro et al. 2006), and conifer stands provide cover (Nielsen et al. 2004a). Given the extent of forest harvest edges in our study area, it is striking that in any season $>45\%$ of all male bear locations were closest to the shrub-to-conifer edge. Furthermore, the shrub-to-conifer edge was the only edge type that occurred to a greater extent in male home ranges than in the study area in all seasons. With abundant forest harvest edges, the preference of the natural edge by male grizzly bears is an important observation. If the heavier use of anthropogenic edges by females is caused by competitive exclusion from the natural edges by males, then further

decreases to the amount of the shrub-to-conifer edge could indirectly increase the mortality risk for female grizzly bears by leaving them with fewer habitat options.

MANAGEMENT IMPLICATIONS

The Alberta Grizzly Bear Recovery Plan (ASRD 2008) identified the management of human access to grizzly bear habitat as a key strategy to maintain and recover viable populations in the province. Decisions regarding the timing and location of human access controls need to be based on sound scientific information to be not only effective at reducing human-caused grizzly bear mortality, but to be transparent and credible to ensure maximum human compliance. Our data indicated that female grizzly bears selected anthropogenic edges over natural edges within our study area. Ongoing forest and energy sector development in Alberta's grizzly bear habitat continues to increase the number of anthropogenic edges and consequently increases mortality risks for grizzly bears, creating new concerns related to land management decisions and grizzly bear recovery efforts. Human access in core grizzly bear habitat in Alberta should be limited and controlled to increase survival rates of female bears using these areas.

We believe considering both edge types in grizzly bear research, conservation, and land use planning is important. When studying habitat requirements and generating RSFs, we expect models that include edge variables to perform better. However, this research indicates that natural and anthropogenic edges should be included with separate coefficients because of different impacts on habitat selection. For management, maintaining natural edges in the landscape is necessary to provide bears with critical habitat farther from mortality threats associated with human access. Limiting access to habitat that is heavily selected by bears during the fall ungulate hunting season, when human use is extensive and grizzly bear mortality from humans due to self-defense and illegal kills is at the highest rate (ASRD 2008), is a serious but important management challenge.

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FIGURE CAPTIONS

Figure 1. The location of the grizzly bear study area located in the Kakwa forest region, of the eastern foothills of the Rocky Mountains, Alberta, Canada, 2005–2009. Centered at 118° W and 54° N, the study area was west of Edmonton, Alberta, Canada.

Figure 2. The ratio of edge length in individual female grizzly bear home ranges relative to the edge length for the entire study area in the Kakwa forest region, Alberta, Canada, from 2005–2009. Horizontal bars inside each box indicate median values. Upper and lower ends of the boxes represent 75th and 25th percentile values, respectively, and vertical lines represent highest and lowest values that are not outliers.

Figure 3. The ratio of edge length in individual male grizzly bear home ranges relative to the edge length for the entire study area in the Kakwa forest region, Alberta, Canada, from 2005–2009. Horizontal bars inside each box indicate median values. Upper and lower ends of the boxes represent 75th and 25th percentile values, respectively, and vertical lines represent highest and lowest values that are not outliers.

486 **TABLES**

487 Table 1. Variables used in the resource selection function (RSF) model created to condition the
 488 randomization for a statistical distribution of edges available to grizzly bears in the Kakwa forest
 489 region, Alberta, Canada from 2005–2009. Note that LC indicates that the variable is from a land
 490 cover classification of Landsat satellite imagery; DEM denotes Digital Elevation Model.
 491 Regenerating sites are those that were subject to harvest and are not yet treed.

Variable	Spring		Summer		Fall	
	β	SE	β	SE	β	SE
wetland-treed (LC)	−0.995	0.109	−1.193	0.087	−0.691	0.078
regenerating forest (LC)	−1.953	0.197	−1.894	0.169	−2.400	0.173
shrub (LC)	−1.561	0.167	−2.543	0.137	−3.247	0.150
wetland-herb (LC)	−5.008	0.197	−4.910	0.187	−4.877	0.179
upland-herb (LC)	−0.957	0.177	−2.077	0.149	−3.088	0.162
non-vegetated (LC)	−3.608	0.165	−3.040	0.163	−4.335	0.172
crown closure-treed sites (LC)	−0.021	0.002	−0.025	0.002	−0.031	0.001
crown closure-regenerating forest sites (LC)	−0.001	0.002	−0.003	0.002	−0.019	0.002
species composition in upland treed sites (LC, DEM)	−0.006	0.001	−0.016	0.001	−0.011	0.001
compound topographic index (150-m average) (DEM)	0.003	0.011	0.090	0.009	0.209	0.009
distance to nearest stream	−0.550	0.068	−1.366	0.060	−1.050	0.059

493 Table 2. Calculated total lengths of natural and anthropogenic edge inventory in available grizzly
 494 bear habitat from the Kakwa forest region, Alberta, Canada, 2005–2009.

Edge class	Edge type	Total (km)
Natural	Wetland	7,371
	Shrub-broadleaf	4,456
	Shrub-mixed	8,790
	Shrub-conifer	21,391
Anthropogenic	Road	8,509
	Pipeline	4,874
	Forest harvest	59,667

495 Table 3. Percentage of observed telemetry locations found nearest each type of landscape edge for male and female grizzly bears in
 496 each season for the Kakwa forest region, Alberta, Canada from 2005–2009.

497

		Wetland	Shrub-	Shrub-	Shrub-	Natural	Forest			Anthropogenic
		-forest	broadleaf	mixed	conifer	total	harvest	Pipeline	Road	total
	Spring	4.7	4.8	4.3*	27.0	40.8	46.4	3.6	9.2	59.2
F	Summer	5.8	7.1	4.7	19.4*	36.9	49.5*	3.7*	9.9*	63.1*
	Fall	3.5	4.8*	5.7*	24.4*	38.4*	51.9*	3.5*	6.1*	61.6*
	Spring	0.7	20.4	11.8	45.9	78.8	15.0	1.4	4.8	21.2
M	Summer	1.8	13.5*	10.8*	46.4*	72.4*	24.3*	0.7	2.6*	27.6*
	Fall	0.3	10.3*	13.6	54.5*	78.8*	15.8*	0.4	5.1*	21.3*

498 *Indicates when >50% of bears were significantly closer than expected (based on conditional randomization) to an edge ($P \leq 0.05$).

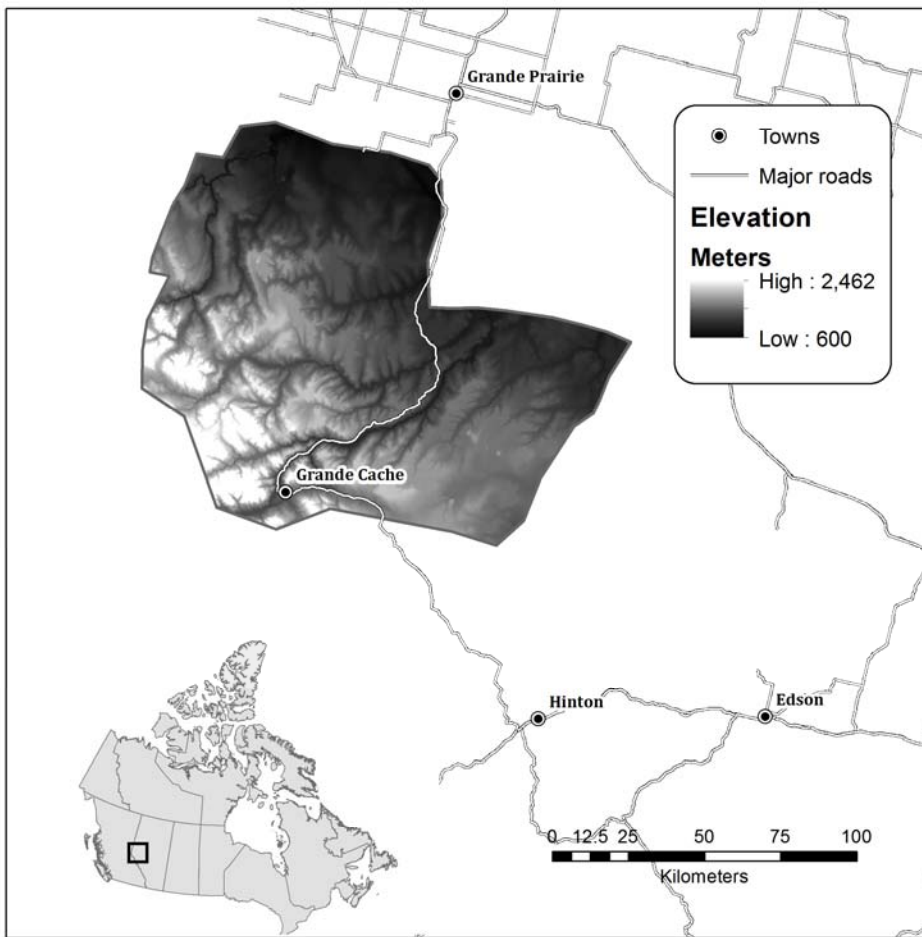


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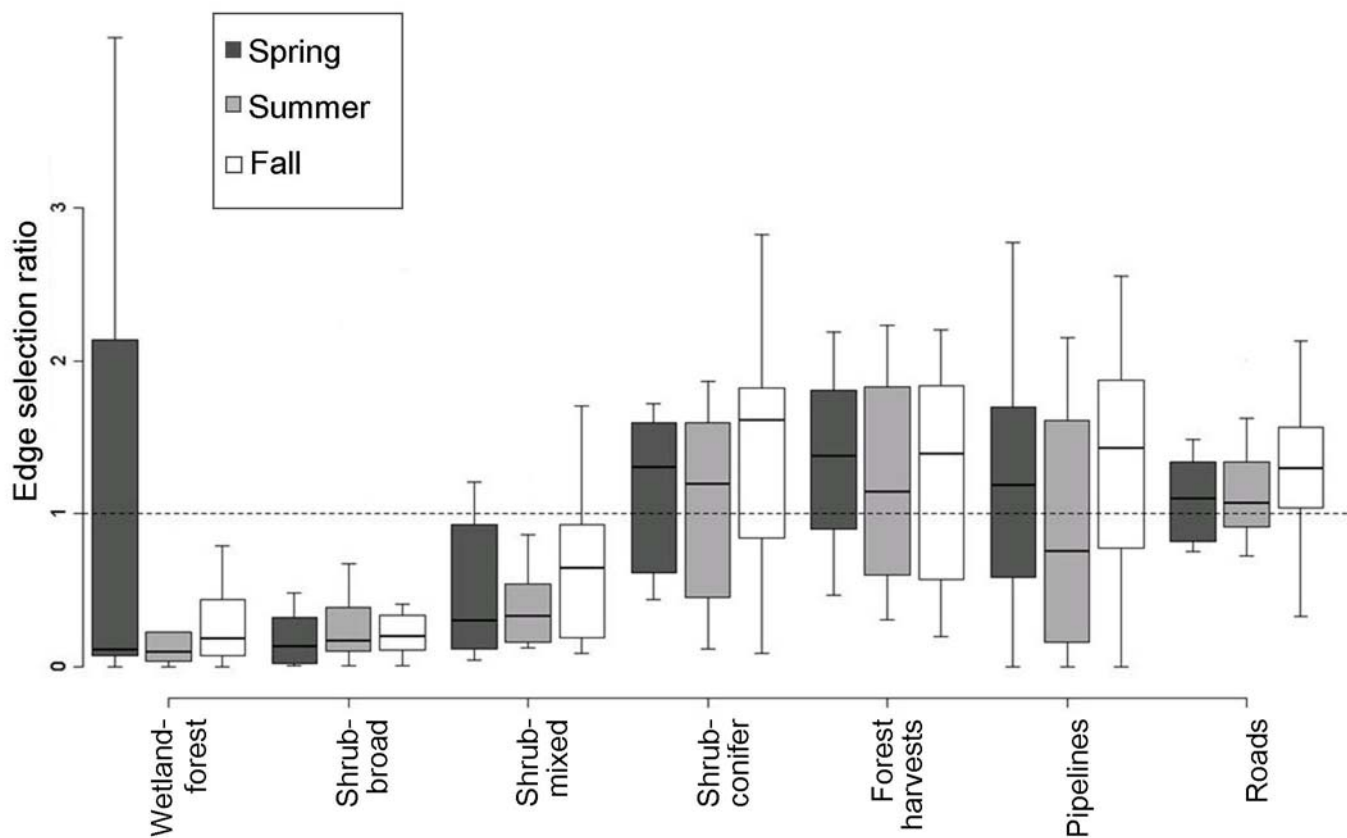


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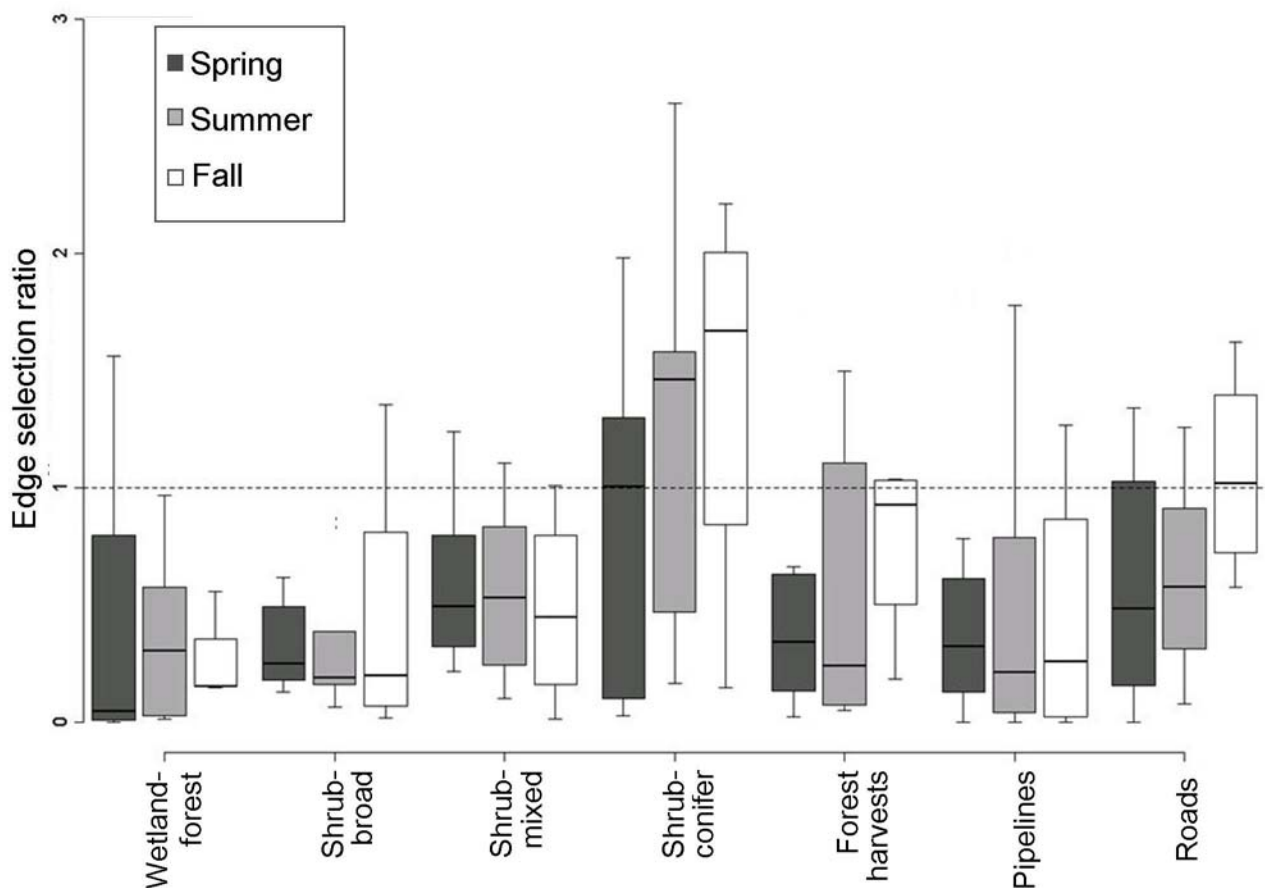


Figure 3. The ratio of edge length in individual male grizzly bear home ranges relative to the edge length for the entire study area in the Kakwa forest region, Alberta, Canada, from 2005–2009. Horizontal bars inside each box indicate median values. Upper and lower ends of the boxes represent 75th and 25th percentile values, respectively, and vertical lines represent highest and lowest values that are not outliers.