

## **Quantifying Grizzly Bear Selection of Natural and Anthropogenic Edges**

BENJAMIN P. STEWART, *University of Victoria, Department of Geography, PO Box 3050 STN CSC, Victoria, BC, V8W 3P5, Canada*

TRISALYN NELSON, *University of Victoria, Department of Geography, PO Box 3050 STN CSC, Victoria, BC, V8W 3P5, Canada*

KAREN LABEREE, *University of Victoria, Department of Geography, PO Box 3050 STN CSC, Victoria, BC, V8W 3P5, Canada*

SCOTT E. NIELSEN, *Department of Renewable Resources, University of Alberta, Edmonton, Alberta, T6G 2H1, Canada*

MICHAEL A. WULDER, *Canadian Forest Service (Pacific Forestry Centre), Natural Resources Canada, Victoria, BC, V8Z 1M5, Canada*

GORDON STENHOUSE, *Foothills Research Institute, Hinton, Alberta, T7V 1X6, Canada*

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Trisalyn A. Nelson

Spatial Pattern Analysis and Research Laboratory,  
Department of Geography, University of Victoria,  
PO Box 3060, Victoria, BC,  
V8W 3R4, Canada

Phone: 250/472-5620; Fax: 250/721-6216

Email: trisalyn@uvic.ca

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## 2 ABSTRACT

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

24  
25 **KEY WORDS:** Alberta, anthropogenic disturbance, conditional randomization, edge, grizzly  
26 bear, habitat selection, resource selection function, *Ursus arctos*.

## 27 28 INTRODUCTION

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

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

48 2004), increased mortality risks to grizzly bears derive from anthropogenic edges (Benn and  
49 Herrero 2002, Nielsen et al. 2004b).

50 Our research objectives were to 1) quantify density of edge types in available grizzly bear  
51 habitat and 2) quantify and evaluate the frequency of edge selection. Grizzly bears use an array  
52 of habitats throughout the year because of seasonally dynamic food values (Nielsen et al. 2003,  
53 Munro et al. 2006). In addition, grizzly bears are sexually dimorphic (Rode et al. 2006), and  
54 males often select different habitat from females (McLellan and Shackleton 1988, Rode et al.  
55 2006, Graham et al. 2010). Thus, we examined edge selection by sex and by foraging season. We  
56 hypothesized that 1) grizzly bears will show similar selection of natural and anthropogenic edges  
57 and 2) edge selection will vary seasonally and by sex.

58

### 59 **STUDY AREA**

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

69

### 70 **METHODS**

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

81 Following previous research (Nielsen et al. 2009), we partitioned data seasonally, based  
82 on shifts in diet and habitat. We defined spring as 1 May to 15 June, summer as 16 June to 31  
83 July, and fall as 1 August until 15 October (the mean denning date). We also partitioned grizzly  
84 bear telemetry points annually, creating sets of telemetry data for each season, year, and bear.  
85 We obtained 9,937 telemetry locations from 9 individual female bears and 5,708 locations from  
86 8 males in spring, 15,009 locations from 14 females and 13,629 locations from 11 males in  
87 summer, and 20,682 telemetry locations from 15 female bears and 5,227 locations from 4 males  
88 in fall. We performed analysis for each sex, in each season, grouping data across years. We  
89 eliminated erroneous telemetry data based on positional dilution of precision (PDOP; >10, D'Eon  
90 and Delparte 2005) and we eliminated data for seasons with less than 50 points per bear to avoid  
91 the effect of small sample sizes on home range calculations (Seaman and Powell 1996).

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

94 tasselled cap transformation (Huang et al. 2002) of Landsat-5 Thematic Mapper (TM) data, a  
95 100-m digital elevation model, and polygonal vegetation data from the Alberta vegetation  
96 inventory (Alberta Sustainable Resource Development [ASRD] 2005). The resulting 30-m  
97 spatial resolution land cover dataset had an overall accuracy of 80.16% when compared to field  
98 data (see Franklin et al. 2001 for details). The original land cover dataset contained 15 classes,  
99 ranging from dense conifer to cloud and shadow, but we simplified the classification into 6  
100 classes (conifer forest, mixed forest, broadleaf forest, wetland, shrubs, and other) to facilitate the  
101 extraction of land cover transitions.

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

108 We identified stand replacing forest disturbances from logging through image pair  
109 differencing of a series of satellite images from the Landsat series of satellites (see White et al.  
110 2011 for a detailed description of the image selection, image processing, and change detection  
111 process). We converted disturbances from raster to vector polylines to integrate with the vector-  
112 based linear features described above.

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

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

130 To create a geographic information system (GIS) edge inventory (Table 2), we used  
131 existing data on anthropogenic edges (roads, pipelines, and forest harvests) and generated our  
132 own data for natural edges based on transitions in land cover (Wulder et al. 2009). We passed a  
133 3-pixel by 3-pixel moving window over the land cover dataset with edges defined based on  
134 differences in land cover from adjacent pixels. We classified the central pixel of the moving  
135 window as an edge if the window was heterogeneous, indicated by the presence of  $\geq 2$  land cover  
136 classes. We excluded transitions with  $> 2$  land cover classes because of ecological complexity  
137 and small sample size ( $< 3\%$ ).

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

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

143 We estimated home ranges for each season using 95% volume isopleth kernel density  
144 estimates (KDE) using the SD extension of R (Seaman and Powell 1996, Bowman and Azzalini  
145 1997:112–117, Borger et al. 2006). We defined bandwidth for KDE estimates using direct least-  
146 squares cross validation (LSCV) with a Gaussian kernel (Ruppert et al. 1995). Bandwidth values  
147 varied from 503 m to 988 m. To delineate the home range of the population, we conducted  
148 LSCV using all points, with an indicated bandwidth of 1,020 m. Once we defined home ranges,  
149 we calculated the total length of each edge type by individual home range, as well as at the  
150 population level. We estimated edge selection ratios by dividing the edge density in an individual  
151 home range by the edge density in the population-level home range.

152 To evaluate if grizzly bears used edges more than expected, we classified each telemetry  
153 location based on the nearest edge type. For each bear, in each season, we calculated the  
154 percentage of telemetry points closest to each edge. We compared the observed percentage of  
155 each type of edge to a statistical distribution of edges generated via randomization or Monte  
156 Carlo procedures. We spatially limited the randomization to the individual's home range and  
157 conditioned locations on known habitat selection using a seasonal RSF (Fortin and Jacquez 2000,  
158 Smulders et al. 2010). By conditioning the randomization on the RSF, we reduced type 1 errors  
159 associated with unrealistic comparisons to complete spatial randomness (Cressie 1993, Legendre  
160 1993, Martin et al. 2008). The conditional randomization ensured that the randomized points  
161 showed the same frequency distribution of RSF values as the observed telemetry locations.

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

## 168 **RESULTS**

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

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

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

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

193

## 194 **DISCUSSION**

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

199 Our results support previous studies that reported male and female grizzly bears select for  
200 different habitats (McLellan and Shackleton 1988, Gibeau et al. 2002, Graham et al. 2010).  
201 Researchers have suggested explanations such as females trying to avoid infanticide by males  
202 (McLellan and Shackleton 1988), competitive exclusion by the more dominant males (Mattson et  
203 al. 1987), or selection for different food types (e.g., males feeding on ungulates; Munro et al.  
204 2006, Graham et al. 2010). Although understanding the reasons for differences in habitat  
205 selection between the sexes was beyond the scope of this study, observing that males select  
206 natural edges, whereas females select anthropogenic edges, allows researchers to develop more  
207 refined hypotheses.

208 Selection for anthropogenic edges by female grizzly bears was consistent with other  
209 studies that reported female grizzly bears being closer to anthropogenic features than their male  
210 counterparts (Mattson 1990, Rode et al. 2006, Graham et al. 2010). In particular, female grizzly  
211 bears have been found to select roads to a greater extent than males (Roever et al. 2008, Graham  
212 et al. 2010). With 90% of grizzly bear deaths occurring within 500 m of a road or 200 m of a trail  
213 (Benn and Herrero 2002), increased use of habitat near roads by female grizzly bears has  
214 implications for mortality risk and potentially for grizzly bear conservation, as female survival is  
215 the dominant vital rate affecting population viability (Bunnell and Tait 1981; Eberhardt et al.  
216 1994; Nielsen et al. 2006, 2008). The increasing number of roads, due to continued resource  
217 extraction (Graham et al. 2010), represents a growing risk to females and therefore to the grizzly  
218 bear population. Although pipelines do allow for increased human access, pipelines affect human  
219 access much less than roads (Nielsen et al. 2002); thus, pipelines likely carry less risk of  
220 mortality.

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

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

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

246 With the impetus to acquire adequate fat reserves for hibernation, fall is considered to be  
247 the most critical foraging period for grizzly bears (Nielsen et al. 2006). During fall, bears feed  
248 primarily on berries (*Vaccinium* spp) in areas typically with canopy cover  $\leq 50\%$  (Nielsen et al.  
249 2004c). In addition to berries, the consumption of roots, such as sweet vetch, resumes during fall  
250 and these foods are a primary source of protein for grizzly bears (Coogan et al. 2012). Chruszcz  
251 et al. (2003) found males in proximity to low volume roads during fall, and both of our results  
252 (edge selection ratio  $>1$  and statistically unexpected habitat selection) highlight the use of roads  
253 by males during fall. The female grizzly bears in our study not only selected all anthropogenic  
254 edges during fall, but all of the shrub edges as well. We suggest that the selection of edges during  
255 fall by grizzly bears would indicate the role of edge habitat in providing critical foods prior to  
256 denning.

257 Forest harvest edge was the most abundant edge in our study area (51.9% of all edges),  
258 and females still had proportionally more forest harvest edge in their home ranges than in the  
259 study area. In addition, both males and females were found to be closer than expected to forest  
260 harvest edge during summer and fall, which is consistent with earlier studies that found grizzly  
261 bears selected forest harvests during summer (Nielsen et al. 2004a) and fall (Nielsen et al. 2006).  
262 Nielsen et al. (2004a) hypothesized that grizzly bears used the logged areas as a resource  
263 surrogate for natural openings, which may be scarce because of fire suppression (Schneider  
264 2002). In addition, Nielsen et al. (2004a) determined that grizzly bears were most often closest to  
265 the edge of the forest harvest.

266 Forest harvest edges can be considered to be functionally analogous to the natural edge,  
267 shrub-to-conifer. The increased food resources at transitions between homogenous land cover  
268 types (Nielsen et al. 2004c, Ries et al. 2004) often attract grizzly bears (Nielsen et al. 2004a,  
269 2009, 2010). Shrub-dominated areas contain many bear foods such as roots, insects, and fruit  
270 (Nielsen et al. 2004c, Munro et al. 2006), and conifer stands provide cover (Nielsen et al. 2004a).  
271 Given the extent of forest harvest edges in our study area, it is striking that in any season  $>45\%$   
272 of all male bear locations were closest to the shrub-to-conifer edge. Furthermore, the shrub-to-  
273 conifer edge was the only edge type that occurred to a greater extent in male home ranges than in  
274 the study area in all seasons. With abundant forest harvest edges, the preference of the natural  
275 edge by male grizzly bears is an important observation. If the heavier use of anthropogenic edges  
276 by females is caused by competitive exclusion from the natural edges by males, then further

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

### 279 **MANAGEMENT IMPLICATIONS**

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

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

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312

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314 **LITERATURE CITED**

- 315 Achuff, P. L. 1994. Natural regions, subregions and natural history themes of Alberta: a  
316 classification for protected areas management. Alberta Environmental Protection,  
317 Edmonton, Canada.
- 318 Alberta Sustainable Resource Development [ASRD]. 2005. Alberta vegetation inventory  
319 interpretation standards. Version 2.1.1. Chapter 3 - vegetation inventory standards and  
320 data model documents. Resource Information Management Branch, Edmonton, Alberta,  
321 Canada.
- 322 Alberta Sustainable Resource Development [ASRD]. 2008. Alberta grizzly bear recovery plan.  
323 Alberta species at risk recovery plan No.15. Fish and Wildlife Division, Edmonton,  
324 Alberta, Canada.
- 325 Balmford, A., R. E. Green, and M. Jenkins. 2003. Measuring the changing state of nature. *Trends*  
326 *in Ecology and Evolution* 18:326–330.
- 327 Benn, B., and S. Herrero. 2002. Grizzly bear mortality and human access in Banff and Yoho  
328 National Parks, 1971–98. *Ursus* 13:213–221.
- 329 Berland, A., T. Nelson, G. Stenhouse, K. Graham, and J. Cranston. 2008. The impacts of  
330 landscape disturbance on grizzly bear habitat use in the Foothills Model Forest, Alberta,  
331 Canada. *Forest Ecology and Management* 256:1875–1883.
- 332 Borger, L., N. Franconi, G. Midhele, A. Gantz, F. Meschi, A. Manica, S. Lovari, and T. Coulson.  
333 2006. Effects of sampling regime on the mean and variance of home range size estimates.  
334 *Journal of Animal Ecology* 75:1393–1405.
- 335 Bowman, A., and A. Azzalini. 1997 Applied smoothing techniques for data analysis: the kernel  
336 approach with S-Plus illustrations. Oxford University Press, Oxford, United Kingdom.
- 337 Bowyer, R. T., and V. C. Bleich. 1984. Effects of cattle grazing on selected habitats of southern  
338 mule deer. *California Fish and Game* 70:240–247.
- 339 Bunnell, F. L., and D. E. N. Tait. 1981. Population dynamics of bears - implications. Pages 75–  
340 98 *in* C. W. Fowler, and D. W. Smith, editors. *Dynamics of large mammal populations*.  
341 John Wiley and Sons, New York, New York, USA.
- 342 Cattet, M. R. L., K. Christison, N. A. Caulkett, and G. B. Stenhouse. 2003. Physiologic  
343 responses of grizzly bears to different methods of capture. *Journal of Wildlife Diseases*  
344 39:649–654.
- 345 Chruszcz, B., A. P. Clevenger, K. E. Gunson, and M. L. Gibeau. 2003. Relationships among  
346 grizzly bears, highways, and habitat in the Banff-Bow Valley, Alberta, Canada. *Canadian*  
347 *Journal of Zoology* 81:1378–1391.
- 348 Ciarniello, L. M., M. S. Boyce, D. C. Heard, and D. R. Seip. 2007. Components of grizzly bear  
349 habitat selection: density, habitats, roads, and mortality risk. *Journal of Wildlife*  
350 *Management* 71:1446–1457.
- 351 Clark, D. A., and D. S. Slocombe 2011. Grizzly bear conservation effort in the Foothills Model  
352 Forest: appraisal of a collaborative ecosystem management effort. *Policy Science* 4:1–11.
- 353 Coogan, S. C. P., S. E. Nielsen, and G. B. Stenhouse. 2012. Spatial and temporal heterogeneity  
354 creates a “brown tide” in root phenology and nutrition. *ISRN Ecology*, Article ID  
355 618257.
- 356 Cressie, N. A. C. 1993. *Statistics for spatial data*. Wiley, Toronto, Canada.
- 357 D'Eon, R., and D. Delparte. 2005. Effects of radio-collar position and orientation on GPS radio-  
358 collar performance, and the implications of PDOP in data screening. *Journal of Applied*  
359 *Ecology* 42:383–388.

- 360 Eberhardt, L. L., B. M. Blanchard, and R. R. Knight. 1994. Population trend of the Yellowstone  
361 grizzly bear as estimated from reproductive and survival rates. *Canadian Journal of*  
362 *Zoology* 72:360–363.
- 363 Edge, W. D., C. L. Marcum, and S. L. Olson-Edge. 1987. Summer habitat selection by elk in  
364 western Montana: a multivariate approach. *Journal of Wildlife Management* 51:844–851.
- 365 Edwards, M. A., A. E. Derocher, K. A. Hobson, M. Branigan, and J. A. Nagy. 2011. Fast  
366 carnivores and slow herbivores: differential foraging strategies among grizzly bears in the  
367 Canadian Arctic. *Oecologia* 165:877–889.
- 368 Festa-Bianchet, M. 2010. Status of the grizzly bear (*Ursus arctos*) in Alberta: update 2010.  
369 Alberta Sustainable Resource Development, Edmonton, Canada.
- 370 Forman, R. T. T. 1995. Land mosaics. The ecology of landscapes and regions. Cambridge  
371 University Press, Cambridge, United Kingdom.
- 372 Fortin, M.-J., and G. M. Jacquez. 2000. Randomization tests and spatially auto-correlated data.  
373 *Bulletin of the Ecological Society of America* 81:201–205.
- 374 Fortin, M.-J., R. J. Olson, S. Ferson, L. Iverson, C. Hunsaker, G. Edwards, D. Levine, K. Butera,  
375 and V. Klemas. 2000. Issues related to the detection of boundaries. *Landscape Ecology*  
376 15:453–466.
- 377 Franklin, S. E., G. B. Stenhouse, M. J. Hansen, C. C. Popplewell, J. A. Dechka, and D. R.  
378 Peddle. 2001. An Integrated Decision Tree Approach (IDTA) to mapping land cover  
379 using satellite remote sensing in support of grizzly bear habitat analysis in the Alberta  
380 Yellowhead ecosystem. *Canadian Journal of Remote Sensing* 27:579–592.
- 381 Gardner, J. L. 1998. Experimental evidence for edge-related predation in a fragmented  
382 agricultural landscape. *Australian Journal of Ecology* 23:311–321.
- 383 Gibeau, M. L., A. P. Clevenger, S. Herrero, and J. Wierzchowski. 2002. Grizzly bear response to  
384 human development and activities in the Bow River Watershed, Alberta, Canada.  
385 *Biological Conservation* 103:227–236.
- 386 Graham, K., J. Boulanger, J. Duval, and G. B. Stenhouse. 2010. Spatial and temporal use of  
387 roads by grizzly bears in west-central Alberta. *Ursus* 21:43–56.
- 388 Huang, C., B. Wylie, L. Yang, C. Homer, and G. Zylstra. 2002. Derivation of a tasselled cap  
389 transformation based on Landsat 7 at-satellite reflectance. *International Journal of*  
390 *Remote Sensing* 23:1741–1748.
- 391 Lay, D. W. 1938. How valuable are woodland clearings to birdlife? *Wilson Bulletin* 50:254–256.
- 392 Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74:1659–1673.
- 393 Mace, R. D., J. S. Waller, T. L. Manley, K. Ake, and W. T. Wittinger. 1999. Landscape  
394 evaluation of grizzly bear habitat in Western Montana. *Conservation Biology* 13:367–  
395 377.
- 396 Manly, B. F. J. 2002. Resource selection by animals: statistical design and analysis for field  
397 studies. Springer, London, United Kingdom.
- 398 Martin, J., C. Calenge, P. Y. Quenette, and D. Allainé. 2008. Importance of movement  
399 constraints in habitat selection studies. *Ecological Modelling* 213:257–262.
- 400 Mattson, D. J. 1990. Human impacts on bear habitat use. *International Conference on Bear*  
401 *Research and Management* 8:33–56.
- 402 Mattson, D. J., R. R. Knight, and B. M. Blanchard. 1987. The effects of developments and  
403 primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming.  
404 *Bears: Their Biology and Management* 7:259–253.

- 405 McLellan, B. N., and D. M. Shackleton. 1988. Grizzly bears and resource-extraction industries:  
406 effects of roads on behaviour, habitat use and demography. *Journal of Applied Ecology*  
407 25:451–460.
- 408 McLoughlin, P. D., R. L. Case, R. J. Gau, H. D. Cluff, R. Mulders, and F. Messier. 2002.  
409 Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian  
410 Arctic. *Oecologia* 132:102–108.
- 411 Munro, R. H. M., S. E. Nielsen, G. B. Stenhouse, and M. S. Boyce. 2006. Seasonal and diel  
412 patterns of grizzly bear diet and activity in west-central Alberta. *Journal of Mammalogy*  
413 87:1112–1121.
- 414 Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in*  
415 *Ecology & Evolution* 10:58–62.
- 416 Nielsen, S. E., M. S. Boyce, and G. B. Stenhouse. 2004a. Grizzly bears and forestry I. Selection  
417 of clearcuts by grizzly bears in west-central Alberta, Canada. *Forest Ecology and*  
418 *Management* 199:51–65.
- 419 Nielsen, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. M. Munro. 2002. Modeling grizzly bear  
420 habitats in the Yellowhead ecosystem of Alberta: taking autocorrelation seriously. *Ursus*  
421 13:45–56.
- 422 Nielsen, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. M. Munro. 2003. Development and  
423 testing of phonologically driven grizzly bear habitat models. *Ecoscience* 1:1–10.
- 424 Nielsen, S. E., J. Cranston, and G. B. Stenhouse. 2009. Identification of priority areas for grizzly  
425 bear conservation and recovery in Alberta, Canada. *Journal of Conservation Planning*  
426 5:38–60.
- 427 Nielsen, S. E., S. Herrero, M. S. Boyce, R. D. Mace, B. Benn, M. L. Gibeau, and S. Jevons.  
428 2004b. Modelling the spatial distribution of human-caused grizzly bear mortalities in the  
429 Central Rockies ecosystem of Canada. *Biological Conservation* 120:101–113.
- 430 Nielsen, S. E., G. McDermid, G. B. Stenhouse, and M. S. Boyce. 2010. Dynamic wildlife habitat  
431 models: seasonal foods and mortality risk predict occupancy-abundance and habitat  
432 selection in grizzly bears. *Biological Conservation* 143:1623–1634.
- 433 Nielsen, S. E., R. H. M. Munro, E. L. Bainbridge, G. B. Stenhouse, and M. S. Boyce. 2004c.  
434 Grizzly bears and forestry II. Distribution of grizzly bear foods in clearcuts of west-  
435 central Alberta, Canada. *Forest Ecology and Management* 199:67–82.
- 436 Nielsen, S. E., G. B. Stenhouse, H. L. Beyer, F. Huettmann, and M. S. Boyce. 2008. Can natural  
437 disturbance-based forestry rescue a declining population of grizzly bears? *Biological*  
438 *Conservation* 141:1193–2207.
- 439 Nielsen, S. E., G. B. Stenhouse, and M. S. Boyce. 2006. A habitat-based framework for grizzly  
440 bear conservation in Alberta. *Biological Conservation* 130:217–229.
- 441 Raven, P. H. 2002. Science, sustainability, and the human prospect. *Science* 297:954–958.
- 442 Ries, L., R. J. Fletcher, J. Battin, and T. D. Sisk. 2004. Ecological responses to habitat edges:  
443 mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution*  
444 *and Systematics* 35:491–522.
- 445 Ries, L., and T. D. Sisk. 2004. A predictive model of edge effects. *Ecology* 85:2917–2926.
- 446 Rode, K. D., S. D. Farley, and C. T. Robbins. 2006. Sexual dimorphism, reproductive strategy,  
447 and human activities determine resource use by brown bears. *Ecology* 87:2636–2646.
- 448 Roever, C. L., M. S. Boyce, and G. B. Stenhouse. 2008. Grizzly bears and forestry I: road  
449 vegetation and placement as an attractant to grizzly bears. *Forest Ecology and*  
450 *Management* 256:1253–1261.

- 451 Ruppert, D., S. J. Sheather, and M. P. Wand. 1995. An effective bandwidth selector for local  
452 least squares regression. *Journal of the American Statistical Association* 90:1257–1270.
- 453 Schneider, R. R. 2002. *Alternative futures: Alberta's boreal forest at the crossroads*. Federation  
454 of Alberta Naturalists, Edmonton, Alberta, Canada.
- 455 Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density  
456 estimators for home range analysis. *Ecology* 77:2075–2085.
- 457 Smulders, M., T. A. Nelson, D. E. Jelinski, S. E. Nielsen, and G. B. Stenhouse. 2010. A spatially  
458 explicit method for evaluating accuracy of species distribution models. *Diversity and*  
459 *Distribution* 16:996–1008.
- 460 Stenhouse, G. B., and R. H. M. Munro. 2000. *Foothills Model Forest Grizzly Bear Research*  
461 *Program: 1999 Annual Report*. Foothills Model Forest, Hinton, Alberta, Canada.
- 462 White, J. C., M. A. Wulder, C. Gomez, and G. B. Stenhouse. 2011. A history of habitat  
463 dynamics: characterizing 35 years of stand replacing disturbance. *Canadian Journal of*  
464 *Remote Sensing* 37:234–251.
- 465 Wulder, M. A., B. P. Stewart, M. E. Andrew, M. Smulders, T. Nelson, N. C. Coops, and G. B.  
466 Stenhouse. 2009. Remote sensing derived edge location, magnitude, and class transitions  
467 for ecological studies. *Canadian Journal of Remote Sensing* 35:509–522.
- 468

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470

471 **FIGURE CAPTIONS**

472 Figure 1. The location of the grizzly bear study area located in the Kakwa forest region, of the  
473 eastern foothills of the Rocky Mountains, Alberta, Canada, 2005–2009. Centered at 118° W and  
474 54° N, the study area was west of Edmonton, Alberta, Canada.

475 Figure 2. The ratio of edge length in individual female grizzly bear home ranges relative to the  
476 edge length for the entire study area in the Kakwa forest region, Alberta, Canada, from 2005–  
477 2009. Horizontal bars inside each box indicate median values. Upper and lower ends of the  
478 boxes represent 75th and 25th percentile values, respectively, and vertical lines represent highest  
479 and lowest values that are not outliers.

480 Figure 3. The ratio of edge length in individual male grizzly bear home ranges relative to the  
481 edge length for the entire study area in the Kakwa forest region, Alberta, Canada, from 2005–  
482 2009. Horizontal bars inside each box indicate median values. Upper and lower ends of the  
483 boxes represent 75th and 25th percentile values, respectively, and vertical lines represent highest  
484 and lowest values that are not outliers.

485

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	
	$\beta$	SE	$\beta$	SE	$\beta$	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

492

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 ( $P \leq 0.05$ ).



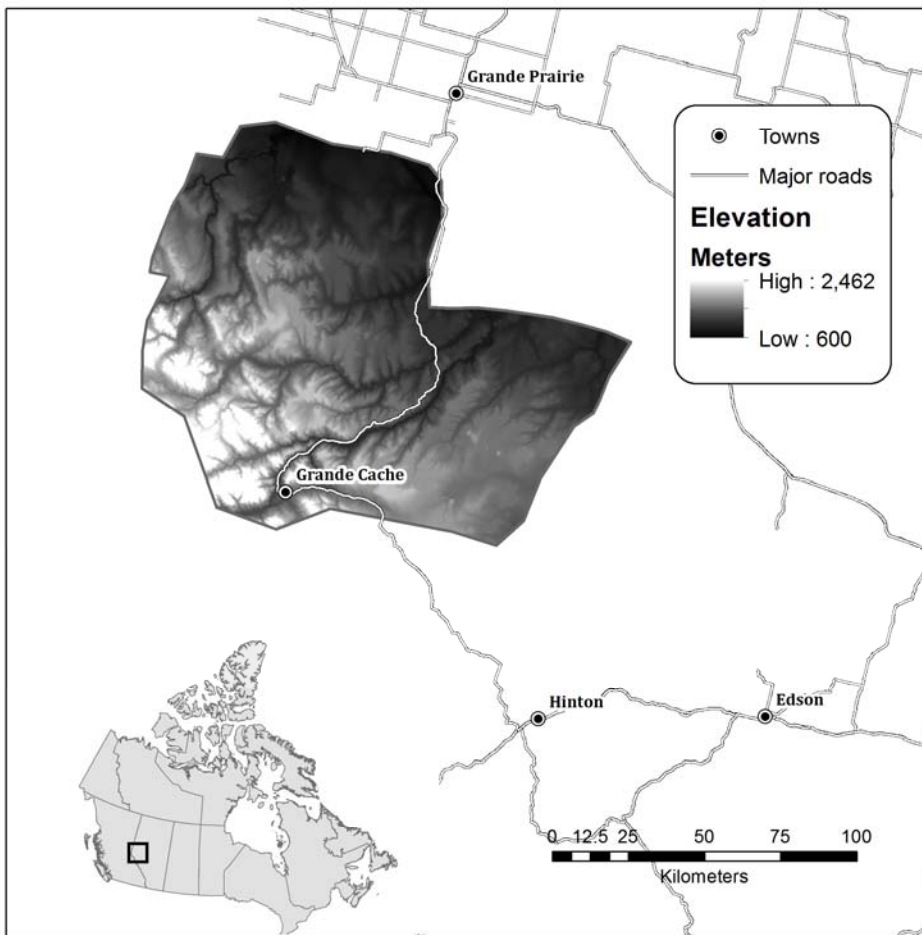


Figure 1. The location of the grizzly bear study area located in the Kakwa forest region, of the eastern foothills of the Rocky Mountains, Alberta, Canada, 2005–2009. Centered at 118° W and 54° N, the study area was west of Edmonton, Alberta, Canada.

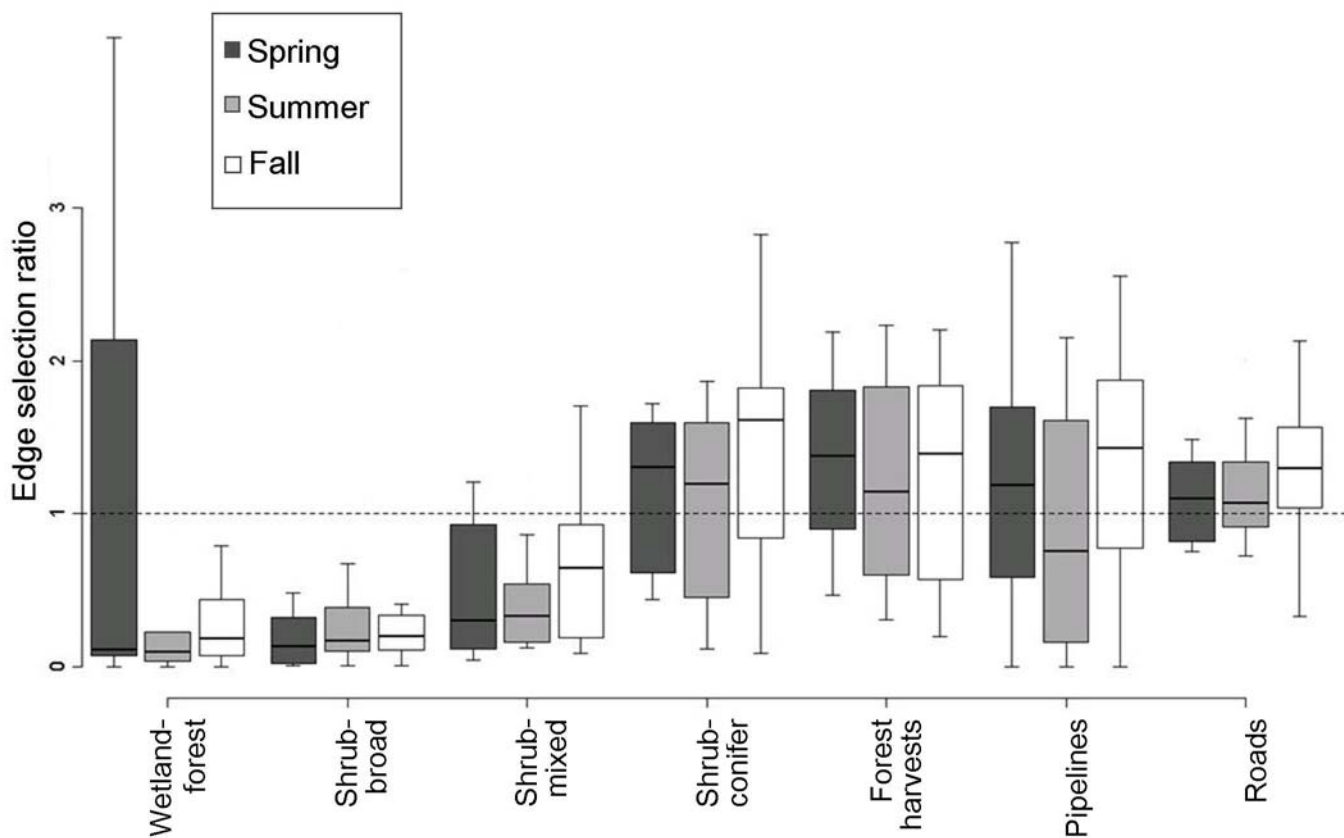


Figure 2. The ratio of edge length in individual female grizzly bear home ranges relative to the edge length for the entire study area in the Kakwa forest region, Alberta, Canada, from 2005–2009. Horizontal bars inside each box indicate median values. Upper and lower ends of the boxes represent 75th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

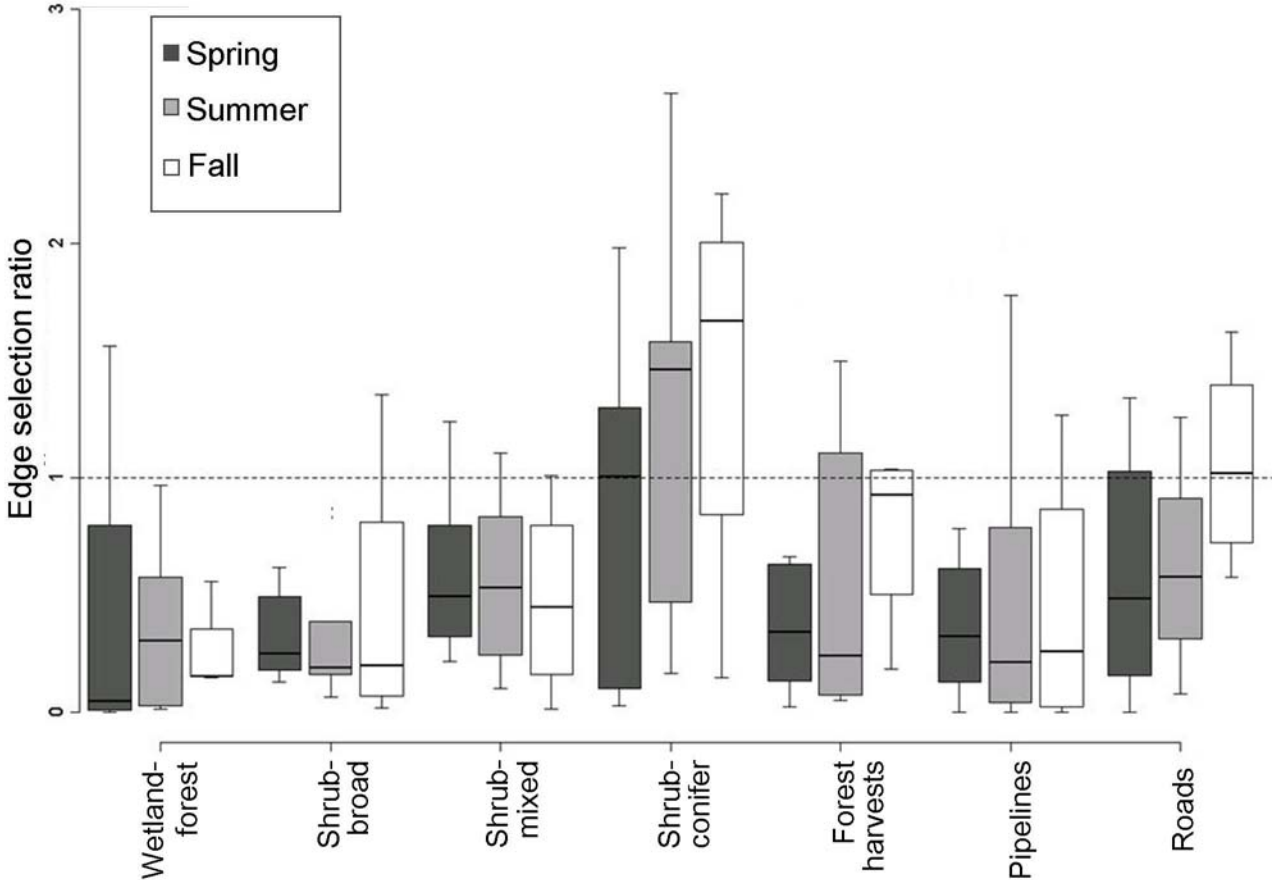


Figure 3. The ratio of edge length in individual male grizzly bear home ranges relative to the edge length for the entire study area in the Kakwa forest region, Alberta, Canada, from 2005–2009. Horizontal bars inside each box indicate median values. Upper and lower ends of the boxes represent 75th and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