

GRIZZLY BEAR HABITAT SELECTION IS SCALE DEPENDENT

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Abstract. The purpose of our study is to show how ecologists' interpretation of habitat selection by grizzly bears (*Ursus arctos*) is altered by the scale of observation and also how management questions would be best addressed using predetermined scales of analysis. Using resource selection functions (RSF) we examined how variation in the spatial extent of availability affected our interpretation of habitat selection by grizzly bears inhabiting mountain and plateau landscapes. We estimated separate models for females and males using three spatial extents: within the study area, within the home range, and within predetermined movement buffers. We employed two methods for evaluating the effects of scale on our RSF designs. First, we chose a priori six candidate models, estimated at each scale, and ranked them using Akaike Information Criteria. Using this method, results changed among scales for males but not for females. For female bears, models that included the full suite of covariates predicted habitat use best at each scale. For male bears that resided in the mountains, models based on forest successional stages ranked highest at the study-wide and home range extents, whereas models containing covariates based on terrain features ranked highest at the buffer extent. For male bears on the plateau, each scale estimated a different highest-ranked model. Second, we examined differences among model coefficients across the three scales for one candidate model. We found that both the magnitude and direction of coefficients were dependent upon the scale examined; results varied between landscapes, scales, and sexes. Greenness, reflecting lush green vegetation, was a strong predictor of the presence of female bears in both landscapes and males that resided in the mountains. Male bears on the plateau were the only animals to select areas that exposed them to a high risk of mortality by humans. Our results show that grizzly bear habitat selection is scale dependent. Further, the selection of resources can be dependent upon the availability of a particular vegetation type on the landscape. From a management perspective, decisions should be based on a hierarchical process of habitat selection, recognizing that selection patterns vary across scales.

Key words: British Columbia, Canada; grizzly bear; habitat selection; resource selection function; spatial extent; telemetry; *Ursus arctos*.

INTRODUCTION

Research that focuses on the conservation of wildlife and their habitats requires knowledge of the manner in which scale affects our understanding of animal behavior and distribution (Addicott et al. 1987, Wiens 1989). Habitat managers must make decisions at a variety of scales: for example, when managing for forestry operations at the broadest scale, managers address issues of land use planning, such as designating parks and protected areas; at the intermediate scale, they manage for issues related to watershed or landscape planning, such as human access management and forest age class distribution; and at the finest scale, they address issues of stand-level management, such as clearcut size or tree species selection. Therefore, to

provide for the habitat requirements of wildlife species, managers must understand the pattern and consequences across different scales. Animals themselves are not responding to different scales but rather as managers and/or ecologists we may observe biological processes differently when we conduct analyses at multiple scales (Hobbs 2003). For example, a habitat attribute that is highly selected at a fine scale might be of little value if it is not located within a landscape containing other life requisites. Furthermore, a habitat attribute that is beneficial at one scale may be detrimental at another scale. Thus, the scale at which we observe animal responses to the landscape may influence our management decisions (Hobbs 2003). Accordingly, habitat selection studies should be scale dependent (Addicott et al. 1987, Boyce 2006). To provide information important to the management of grizzly bear (*Ursus arctos*) habitats, we examined how our understanding of habitat selection would vary across three different scales.

The importance of scale in our interpretation of biological processes, especially when drawing conservation and biological inferences from the results of

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habitat-selection studies, is coming to the forefront in ecological literature (Johnson 1980, Orians and Wittenberger 1991, Levin 1992, Anderson and Gutzwiller 1996, McLean et al. 1998). This is because we may observe different processes operating at multiple scales, and what may appear important at one scale may have little relevance at another, making results scale sensitive (Guisan and Thuiller 2005). Johnson (1980) suggested that habitat selection is a hierarchical process in which our observation of relationships can change along a continuum of spatial scale, an argument subsequently supported by a number of authors (Orians and Wittenberger 1991, Aebischer et al. 1993, Boyce et al. 2003). Because varying the extent of available habitats can provide diverse results (Johnson 1980, Garshelis 2000, Guisan and Thuiller 2005), some authors have claimed that conclusions from habitat selection studies are valid only within the spatial scale examined (Kotliar and Wiens 1990, Lord and Norton 1990). Thus, the applicability of management actions derived from examining only one scale might be limited to that scale.

Scale has two main components: grain and extent. Grain refers to the finest spatial resolution measured, whereas extent refers to the vastness of the landscape examined (Turner et al. 2001, Hobbs 2003). Varying either grain or extent can change the apparent magnitude of selection by the animal (Johnson 1980, O'Neill 1989, Boyce 2006), and responses by individuals of the same species may be influenced by our observations across scales (Mysterud and Ims 1998). It has been argued that a minimum of three scales should be examined in ecological studies because selection is constrained by the level above and clarified at the level below (O'Neill 1989). Thus, scales are nested within one another, and when availability changes so might the way in which we perceive the organism on the landscape (Johnson 1980).

The effects of scale on the manner in which we view habitat selection have been studied for other large mammals, including elk (*Cervus elaphus*; Boyce et al. 2003), muskoxen (*Ovibos moschatus*; Schaefer and Messier 1995), and caribou (*Rangifer tarandus*; Rettie and Messier 2000, Apps et al. 2001, Johnson et al. 2002, 2004a). However, for grizzly bears, most studies of habitat selection have employed only a single scale of analysis (Servheen 1983, Waller and Mace 1997, McLellan and Hovey 2001) or have focused on the possible segregation between males and females (Wielgus and Bunnell 1994, 1995, Waller and Mace 1997). Only three studies have addressed the effects of scale on selection patterns of grizzly bears (McLoughlin et al. 2002, Johnson et al. 2004b, Nielsen et al. 2004). Each of these studies concluded that scale-dependent habitat selection did indeed occur. Nielsen et al. (2004) examined three seasons of selection at two scales but focused solely on the selection of clearcuts with data pooled for males and females. Johnson et al. (2004b) studied the effects of scale on multispecies habitat

selection (i.e., grizzly bears, wolves, and caribou), concentrating on the spatial variation of resources. McLoughlin et al. (2002) examined the selection of the home range on the landscape (study area extent) and selection within the home range for males and females; results were limited to univariate analysis using selection ratios.

Johnson (1980) proposed four hierarchical orders of habitat selection: the geographic range of a species (first order), selection of a home range (second order), selection of patches of resources within the home range (third order), and selection of food items within the patch (fourth order). These scales of resource selection can be combined with Manly et al.'s (2002) sampling designs for resource selection studies. In design I (Manly et al. 2002) individual animals are not identified, measurements are made at the population level, and use and availability are sampled over the entire study area. In design II, individual animals are identified, use is quantified for each individual, and availability is measured at the population level. In design III, individual animals are identified and use and availability are sampled for each individual. Combining Johnson's (1980) second-order selection with Manly et al.'s (2002) design I, we are able to ask broad population-level questions, such as "where are the animals located on the landscape?" By constricting the scale of availability, we can ask more specific questions, such as "what are animals using within their home range?" (third-order selection, design III). Further, by employing different combinations of scale with design we are able to investigate whether the patterns of habitat use depend upon the availability of resources (Mysterud and Ims 1998).

We estimated separate resource selection functions (RSF) for female and male grizzly bears inhabiting mountain and plateau landscapes. By comparing model coefficients from various study designs and extents of available habitats we are able to evaluate whether our observations of habitat selection patterns by grizzly bears differed across three spatial scales. We assumed that the magnitude and/or direction of selection would vary according to scale. For example, we expected that the study-area-wide extent would yield models most explanatory of female grizzly bear habitat selection because the methods require blending second- and third-order scales; that is, availability must be drawn from an area much larger than the individual home ranges, thereby ensuring that the spectrum of variance across the landscape is represented (Boyce et al. 2003). Our objective was to document differences in our observation of grizzly bear habitat selection in central British Columbia (BC), Canada, across scales that are relevant to forestry management.

STUDY AREA

The 18 096-km² study area was located within the "working forest" in central-eastern British Columbia,

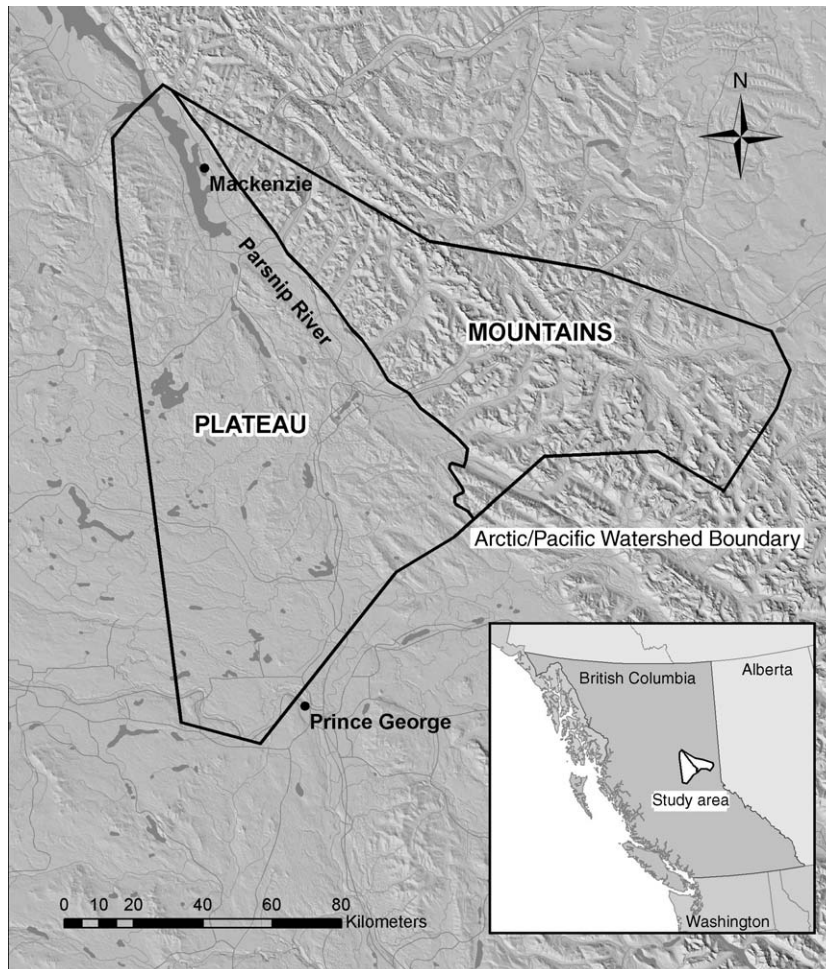


FIG. 1. Study area for grizzly bear habitat selection, including mountain and plateau boundary just east of the Parsnip River, British Columbia, Canada, 1998–2003.

Canada ($54^{\circ}39' N$, $122^{\circ}36' W$; Fig. 1). The study area boundary was defined based on the movements of radiocollared grizzly bears during the fall of 1997–2003, omitting eight outlier locations that fell west of the western boundary (Ciarniello 2006). Forestry was the predominant industry, and aside from small provincial parks, there were no protected areas. Each year during the study, timber harvesting expanded from the plateau up the main river valleys (Missinka, Hominka, Table, and Anzac Rivers) into relatively pristine mountainous landscapes.

The Parsnip Plateau comprised $10\,624\text{ km}^2$ of the study area, incorporating the northern limits of the city of Prince George and extending north past the town of Mackenzie. The rolling hills of the plateau were primarily in the sub-boreal spruce zone, with elevations ranging from 600 to 1650 m. Climax forests of lodgepole pine (*Pinus contorta*) dominated drier areas; white spruce (*Picea glauca*) was predominant on wetter sites, while black spruce (*Picea mariana*) bogs occurred in hydric sites. Mesic sites often consisted of spruce and

subalpine fir (*Abies lasiocarpa*) associations. Small patches of alpine, subalpine fir climax forests, as well as interior Douglas fir (*Pseudotsuga menziesii*) remained. The plateau was heavily modified by forestry activities, with the majority of logging occurring since the 1950s, resulting in a mosaic of successional stages (DeLong and Tanner 1996). The plateau had a mean annual temperature of 2.6°C , with 72 cm rainfall and 300 cm snowfall (DeLong et al. 1993, 1994).

We used the BC Ministry of Environment's ecosection line to divide the plateau from the Hart Ranges of the Canadian Rocky Mountains. Monitoring revealed limited movement, emigration, and immigration between the mountains and plateau (Ciarniello 2006). DNA population discreteness methods suggested mountain and plateau bears were subpopulations with movement and dispersal limited to males (Ciarniello 2006). At the home range and predetermined buffer scales, animals were typed in the landscape where they had $>50\%$ of their locations. Due to limited movement between landscapes, this only occurred for seven animals

(n [females] = 2, n [female locations] = 6, n [males] = 5, n [male locations] = 15).

The mountain area covered 7472 km², with elevations ranging from 720 to 2550 m. Lower-elevation valley bottoms leading from the mountains into the plateau were sub-boreal spruce, above which the predominant forest type was Engelmann spruce (*Picea engelmannii*)–subalpine fir associations, followed by the alpine-tundra zone (1400 m+). The alpine consisted of shrubs or krummholtz tree formations and lush heath communities. Subalpine grassland slopes were comprised of glacier lily (*Erythronium grandiflorum*), Indian heliopsis (*Veratrum viride*), and arrow-leaved groundsel (*Senecio triangularis*). Less than 1% of the study area was barren rock, alpine snow, or glacial ice. Mean annual temperature was 0.3°C, with 154 cm rainfall and 700 cm snowfall (DeLong et al. 1993, 1994).

METHODS

Bear capture and monitoring

Grizzly bears were captured between August 1997 and spring 2003, using aerial darting, leg snares, or culvert traps. The University of Alberta's Animal Care Committee, following the Canadian Council on Animal Care guidelines and principles, approved bear handling procedures (protocol number 307204). Bears were immobilized with Telazol (a 1:1 mixture of tiletamine hydrochloride and zolazepam hydrochloride; Fort Dodge Animal Health, Fort Dodge, Iowa, USA) at a dosage of 8 mg/kg. Ketaset (ketamine hydrochloride; Ayerst Veterinary Laboratories, Guelph, Ontario, Canada) was used as a top-up drug when necessary at a dosage of 2 mg/kg.

Bears were monitored using very high frequency (VHF) telemetry (Lotek, Aurora, Ontario, Canada; Televilt, Lindesberg, Sweden) twice per week from 1998 to 2000, once per week in 2001 and 2002, and a minimum of once every two weeks in 2003, using a fixed-wing aircraft (normally Cessna 185). All aerial telemetry locations were collected during daylight hours. Universal Transverse Mercator (UTM) coordinates were taken with a hand-held 12-channel Garmin GPS unit (Garmin, Romsey, Hampshire, UK). Locations were mapped and verified on 1:50 000 topographic maps. Multiyear (1998–2003) 100% minimum convex polygons (MCPs) were constructed using the program Animal Movement (Hooge and Eichenlaub 1997) for study animals with >10 locations that spanned the entire year. Comparisons of GPS and VHF telemetry obtained on the same animals have shown that VHF home ranges are normally underestimates of the actual home range size (Arthur and Schwartz 1999; L. M. Ciarniello, unpublished data). Home range size may be underestimated when <60 locations per animal are used to calculate the home range (Boulanger and White 1990, Arthur and Schwartz 1999). We used multiyear locations and 100% MCPs in an attempt to achieve the largest home range size for our home range scale; however, we caution the

reader that the home range of some animals may underrepresent the true size.

Scales of analysis

We examined three methods to assess how our observations of grizzly bear habitat use would vary according to scale. For all scales we removed locations when each bear moved to <1 km of its den site for fall and spring, because attributes for den site selection are different from those during foraging seasons (Ciarniello et al. 2005). We also removed all locations that fell within lakes and rivers. Habitat covariates were obtained from a GIS for the remaining used (i.e., bear location) and random locations. Separate models were calculated for males and females. For all designs, the following log-linear equation was assumed to characterize the influence of covariates on relative use, $w(x)$:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 \dots \beta_p x_p) \quad (1)$$

where β_i are selection coefficients estimated using logistic discriminant analysis for each of p covariates, x_i , for $i = 1, 2, \dots, p$ (Johnson et al. 2006). Bear telemetry locations were the used sites (1), and randomly generated locations were the available sites (0). Random locations were generated using the program HawthTools (Beyer 2004) for ArcGIS 8.3 (Environmental Systems Research Institute, Redlands, California, USA). Models were estimated using Stata 7.0 (Stata, College Station, Texas, USA).

Scale and design A: study-wide-scale design.—In this population-level design we examined covariates predicting the locations of bears on the landscape. To do this we drew availability from an area larger than the individual home range (Boyce 2006). We compared characteristics of areas used by bears vs. available areas drawn throughout the mountain or plateau study area (i.e., population level). Although individual animals were radiocollared, they were not identified in the model; therefore, we employed a design 1 (Manly et al. 2002), second- and third-order selection (Johnson 1980) at the landscape scale. Because some of the random locations fell within the home range of each animal we spanned both of Johnson's (1980) second- and third-order scales. To control for variation, bear locations were weighted for equal sample sizes among animals. Random locations were sampled at an intensity of 1 location/500 m² (i.e., 14 944 in mountains and 21 248 in plateau). Because we used animal locations to determine the boundary of the study area, we are confident that the study area extent was occupied by grizzly bears. We assumed that habitat availability was fairly static among years.

Scale and design B: home range scale design.—Given that bears selected their home ranges within the larger landscape, in this home range scale design we explored what bears were selecting within their home ranges and whether this differed from the selection of their home ranges on the landscape. Therefore, availability was

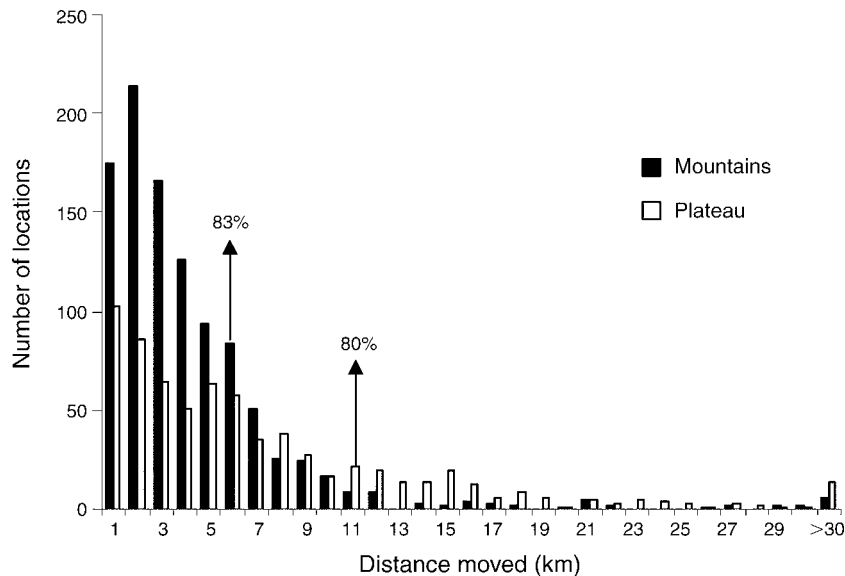


FIG. 2. Distance moved by grizzly bears between radiotelemetry locations ≤ 7 days apart in the mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada, 1998–2003. The distance that incorporated 80% of grizzly bear movements was used as the buffer size for the third-order resource selection functions (RSF) design.

limited and drawn only from within each bears' home range (design III, Manly et al. 2002). By limiting our available points to within the home range we employed a third-order study design (Johnson 1980). We used conditional logistic regression by pairing the random points to each bears' use points (Compton et al. 2002), thereby controlling for variation among individuals by treating each bear as a fixed effect. The random sample intensity was also 1 location/500 m² (n [females] = 4360 locations, n [males] = 7626 locations); however, the number of random locations varied according to the size of the individuals' home range.

Scale and design C: buffered home range scale design.—In this design we varied the extent of available habitats by drawing availability within a fixed buffer size surrounding each use location. Buffer sizes were determined by plotting the mean distance moved between telemetry locations as long as those locations were ≤ 7 days apart (Fig. 2). We believed that locations that were ≤ 7 days apart were more representative of animals' immediate decisions than those that were ≥ 7 days apart, as determined by plotting the distance moved between all consecutive locations. We chose a buffer size that incorporated a minimum of 80% of bear locations in each landscape because the majority of bears will have what is available for them within this distance (Boyce et al. 2003, Boyce 2006). This buffer size was 6 km for bears that lived in the mountains and 11 km for bears that lived on the plateau (Fig. 2). Because we buffered locations that fell on the boundary, a portion of the available habitats might be drawn from outside the home range. Therefore, while mostly third order, this design also incorporates some second-order properties (Johnson 1980). We again used conditional

logistic regression to control for variation among individuals (Compton et al. 2002). However, in this design, we paired 10 randomly generated points with each use point.

Geographic Information System data

We used Terrain Resources Inventory Maps (TRIM2; BC Ministry of Water, Land, and Air Protection, Victoria, British Columbia, Canada) to build digital elevation maps (DEM) to obtain elevation, slope, aspect, and hill shade data. Forest cover maps (FCM; BC Ministry of Forests, Prince George, British Columbia, Canada) were used to obtain the predominant forest stand and/or landcover type, as well as stand age. Road networks were built by amalgamating FCM with layers obtained from the major forestry operators within the study area: Canadian Forest Products (Canfor) East, Canfor West, the Pas Lumber, and Slocan Forest Product in Prince George, British Columbia, Canada. The GIS layers were visually crosschecked with Landsat imagery, and missing features were digitized. Raster layers (i.e., DEM, slope, aspect, hill shade, and distance to roads) had a resolution of 25 m. The forestry data (e.g., age, height, forest type) were based on vector GIS layers that were rasterized, also with a resolution of 25 m. For all categorical variables (e.g., land cover) selection for, or against, the remaining covariates is in relation to the withheld categories (see Table 1).

Model selection and validation

We used two methods for evaluating the effects of scale on our RSF designs: (1) comparisons between the rank of six candidate models and (2) comparisons within one candidate model. In method 1, based on the

TABLE 1. Description of variables from geographic information system layers used to select candidate models for male and female grizzly bears in mountain or plateau landscapes of the Parsnip River study area, British Columbia, Canada (1998–2003).

Variable	Type	Description
Primary landcover categories	categorical	Leading landcover type
Alpine		Dynamic, high-elevation, largely forb- and/or shrub-dominated parkland or krummholz subalpine fir (mountain, 23%; plateau, 0.1%)
Anthropogenic		Areas of human settlement or regular maintenance, such as along the railway line; excludes harvested areas (mountain, 0.2%, plateau, 1%)
Black spruce		Stands dominated by black spruce (mountain, 1%; plateau, 2%)
Douglas fir		Stands dominated by Douglas fir (mountain, 0.05%; plateau, 1%)
Meadow		Large, open, forb-dominated areas (mountain, 0.05%; plateau, 2%)
Mixed wood		Stands dominated by cottonwood, aspen, and/or common paper birch (mountain, 2%; plateau, 13%)
Pine		Stands dominated by lodgepole pine (mountain, 7%; plateau, 27%)
Rock/bare ground		Typically high-elevation mountaintops (mountain, 0.2%; plateau, 0.03%)
Shrub		None or few trees and large expanse of shrubs, most frequently occurred adjacent to swamps and rivers (mountain, 3%; plateau, 6%)
Spruce		Stands dominated by spruce species other than black spruce (mountain, 30%; plateau, 35%)
Swamp		Water table above ground surface (mountain, 0.5%; plateau, 3%)
True firs		Stands dominated by subalpine fir (mountain, 34%; plateau, 10%)
Topographic features		
Elevation	linear	Elevation above sea level
Forest height	linear	Height of the forest in meters (mountain, 0–43 m; plateau, 0–50 m)
Greenness	linear	Calibrated greenness values related to the amount of green biomass (lush green vegetation has high greenness values, sparse or senesced vegetation has lower values, and nonvegetated areas have very low greenness values; pixel resolution 30 m)
Hill shade	linear	Combination of slope and aspect to measure solar insolation as it varies with topography (azimuth, 225; sun angle, 45) (negative coefficients indicate selection for cooler, northeast aspects, while positive coefficients reflect selection for warmer southwest aspects)
Risk layer (human-influenced risk of mortality only)	linear	Evaluates the relative probability of grizzly bear mortality risk by landscape; built by assessing the relationship between grizzly bear mortality locations (1) and non-kill locations (0) using logistic regression (see Ciarniello 2006; the closer to 1, the greater the risk of mortality)
Distance to highway, primary logging road, or secondary/decommissioned logging road	linear	Straight-line distance to the nearest highway or primary or secondary logging road in meters (highway refers to the two-lane paved highway 97 North; primary logging roads were main arteries that serviced a number of blocks; secondary and decommissioned logging roads spurred off primary logging roads and were used to access clearcuts)
Stand age	categorical	Early seral, 0–45 years, including shrub, meadow, noncommercial brush, nonproductive brush, swamps, and alpine; young forest, 46–99 years; old forest, 100+ years

variables in Table 1, we chose a priori six candidate models that we deemed biologically relevant to grizzly bear habitat use (Anderson et al. 2000, Burnham and Anderson 2002) (Table 2). Inclusion of variables in the candidate set of models was based on field knowledge and published research on grizzly bear habitat selection

(Servheen 1983, Wielgus and Bunnell 1995, Waller and Mace 1997, McLellan and Hovey 2001, Nielsen et al. 2004). Grizzly bears have been shown to prefer habitats that contain a juxtaposition of forest structural stages (i.e., seral stages) (Herrero 1972, Waller and Mace 1997, McLellan and Hovey 2001, Nielsen et al. 2004). As such,

TABLE 2. Six a priori candidate models for grizzly bear habitat selection in the mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada.

Model	Model name	Landscape	Model structure
1	land cover model	mountains	alpine + true firs + spruce + shrub
		plateau	true firs + spruce + mixed wood + black spruce + shrub
2	mortality risk model	mountains	distance to primary logging road + distance to secondary logging road + risk layer + stand age
		plateau	distance to highway + distance to primary logging road + distance to secondary logging road + risk layer + stand age
3	seral model	both	stand age + greenness
4	terrain model	mountains	forest height + hill shade + elevation
		plateau	forest height + hill shade
5	all-inclusive land cover	mountains	land cover model + greenness + hill shade + risk layer + primary road + secondary road
		plateau	land cover model + greenness + hill shade + risk layer + distance to highway + distance to primary road + distance to secondary road
6	all-inclusive seral	mountains	stand age + greenness + hill shade + risk layer + distance to primary road + distance to secondary road
		plateau	stand age + greenness + hill shade + risk layer + distance to highway + distance to primary road + distance to secondary road

Note: Separate all-inclusive models were built for land cover classes and stand age due to collinearity.

we put forward a model (i.e., seral model) containing the set of covariates most strongly influenced by forest structural stage: stand age and greenness. Older age stands and nonvegetated areas have low greenness values, while early seral stands containing lush vegetation have high greenness values (Mace et al. 1999). Conversely, grizzly bears have been shown to avoid human use areas (Gibeau et al. 2002), and habitat selection patterns have been altered due to the presence of roads and trails (Mattson et al. 1987, McLellan and Shackleton 1989, Mace et al. 1996). Because high-quality habitats are generally roadless areas that also contain a juxtaposition of early-seral forests, then the opposite should be true for areas of high mortality risk. Thus, we also put forward a model that contained a set of covariates that we deemed as “risky” places to the survival of grizzly bears (i.e., mortality risk model, Table 2). We included stand age in the mortality risk model because it can affect the amount of security cover available to bears. We also considered a model based on a set of covariates that reflect the landscape’s terrain (i.e., terrain model). The mountains contained steep-sided slopes and rocky mountain peaks, and therefore, terrain may influence decisions by bears that lived in the mountains. Also, because there was a higher density of bears in our study area in the wetter predominant forest types (e.g., spruce) vs. the drier predominant forest types (e.g., pine) (Mowat et al. 2005), we examined the effects of predominant land cover type on grizzly bear habitat selection (i.e., land cover model). Lastly, we investigated whether a mix of the abovementioned covariates offered a more complete examination of habitat selection (i.e., the “all-inclusive” models). Due to collinearity between the predominant land cover type and stand age, we built separate “all-inclusive” models for these sets of covariates. Model variables were chosen based on their applicability to mountain or plateau landscapes. For example, we withheld the variable alpine from the

plateau vegetation model because there was no use by bears of alpine on the plateau and only small patches (0.1%) existed (Table 1).

Predictor variables were screened for collinearity. We assumed that collinearity was not a concern if correlations between predictor variables were <0.6 . If correlations between predictor variables were ≥ 0.6 they were not included in the same model. Within each scale of analysis we rank these six candidate models based on Akaike Information Criteria (AIC) to identify the most parsimonious model (Burnham and Anderson 2002). Because male bears had small sample sizes for candidate models with ≥ 7 variables (i.e., $n/K < 40$), final model selection for male bears was based on the difference in AIC corrected for small samples (AIC_c ; Burnham and Anderson 2002). The closer the normalized Akaike weights (AIC_w) to 1, the better the model (Anderson et al. 2000). Models were considered comparable if ΔAIC (or ΔAIC_c for male bears) values were < 2.0 (Burnham and Anderson 2002). Significant coefficients were those with confidence intervals that did not overlap 0 (Anderson et al. 2000).

In our second method, we examined the effects of scale by selecting one model and comparing the coefficients across the three scales. In this method, the number of random locations varied between designs; therefore, we could not use the AIC scores to rank models. Rather, to account for the difference in sampling intensity, we used fivefold cross-validation to compare the internal consistency of each model using a Spearman’s rank correlation (r_s) between predicted and observed frequencies (Boyce et al. 2002). Data were drawn at random and divided into five groups. A random draw of 20% of the data was used as a test sample, and an RSF model was estimated using the remaining 80% of the data. Then RSF predictions from this model were contrasted with the frequency of location in the withheld test data distributed across 10

TABLE 3. Resource selection function candidate model ranks for male and female grizzly bear habitat selection in the mountain (Mtns) and plateau landscapes of the Parsnip River study area, British Columbia, Canada.

Model	Study-wide				Home range				Buffer			
	Male		Female		Male		Female		Male		Female	
	Mtns	Plateau	Mtns	Plateau	Mtns	Plateau	Mtns	Plateau	Mtns	Plateau	Mtns	Plateau
Land cover	6	2	5	4	6	5	6	4	6	<i>1</i>	6	4
Mortality risk	4	4	4	3	3	<i>1</i>	5	3	5	<i>4</i>	5	3
Seral	2	5	3	5	2	6	3	5	3	5	3	6
Terrain model	5	6	6	6	4	4	4	6	1	<i>3</i>	4	5
All-inclusive land cover	3	1	1	1	5	3	1	1	4	<i>2</i>	1	1
All-inclusive seral	1	3	2	2	1	<i>2</i>	2	2	2	6	2	2

Note: Data in boldface italic type for male bears inhabiting the plateau landscape at the home range and buffer extents had ΔAIC_c values < 2.0.

RSF bins (Boyce et al. 2002). A higher number of locations in bins in which RSF scores approach 1 indicate an internally consistent model. Rank correlations across the five models were then averaged (\bar{r}_s). Estimates for the top-ranked mountain and plateau models were interfaced with GIS to create maps of relative probability of use by grizzly bears across each landscape.

RESULTS

We gathered 2005 non-denning-season locations on 33 female bears (mountains, $n = 1275$ locations on 17 bears; plateau, $n = 730$ locations on 16 bears) and 487 locations on 18 male bears (mountain, $n = 237$ locations on six bears; plateau, $n = 250$ locations on 12 bears). Twenty-three home ranges were constructed for bears in the mountains (female, $n = 17$; male, $n = 6$), while 28 were constructed for bears on the plateau (female, $n = 16$; male, $n = 12$).

In the mountains, three bears were monitored for one year (one female, two males), seven bears for two years (five females, two males), four bears for three years (females), three bears for four years (one female, two males), three bears for five years (females), and three bears for six years (females). In the spring, 710 locations were obtained on mountain bears (1998, $n = 159$; 1999, $n = 229$; 2000, $n = 136$; 2001, $n = 128$; 2002, $n = 44$; 2003, $n = 14$), 648 in summer (1998, $n = 178$; 1999, $n = 154$; 2000, $n = 149$; 2001, $n = 107$; 2002, $n = 48$; 2003, $n = 12$), and 154 in fall (1998, $n = 14$; 1999, $n = 31$; 2000, $n = 61$; 2001, $n = 29$; 2002, $n = 15$; 2003, $n = 4$). On the plateau, 11 bears were monitored for one year (two females, nine

males), 13 bears for two years (10 females, three males), two bears for three years (female), one bear for four years (female), and one bear for five years (female). In the spring, 410 locations were obtained on the plateau (1998, $n = 28$; 1999, $n = 55$; 2000, $n = 85$; 2001, $n = 170$; 2002, $n = 63$; 2003, $n = 9$), 369 in summer (1998, $n = 24$; 1999, $n = 42$; 2000, $n = 131$; 2001, $n = 131$; 2002, $n = 41$), and 201 in fall (1998, $n = 7$; 1999, $n = 26$; 2000, $n = 93$; 2001, $n = 58$; 2002, $n = 17$). Sample sizes for the fall season tended to be less than those obtained during summer and spring because we removed locations when bears were within 1 km of a known den site.

Rank of the six candidate models using resource selection functions

For male bears, patterns of habitat selection were dependent upon the scale of availability but for female bears the same top-ranked model was identified at each scale (Tables 3 and 4). At the study-wide and home range spatial extents, the distribution of male bears that resided in the mountains was best predicted by models that contained a set of covariates based on the structural stage of the forest, suggesting that prime foraging areas (i.e., early seral stages) were sought out by mountain males (Table 3). When the extent of availability was restricted to a buffer, the terrain model ranked first for mountain males. The terrain model did not include any human use variables, suggesting that small-scale habitat selection decisions by mountain males were based more on topography than was reflected by patterns of use seen at the larger scales.

TABLE 4. Top-ranked resource selection function model assessed using Akaike Information Criteria for male and female grizzly bear habitat selection in the mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada, 1998–2003.

Design	Extent	Mountains		Plateau	
		Male	Female	Female	Male
A	study-wide	AI seral	AI land cover	AI land cover	AI land cover
B	home range	AI seral	AI land cover	AI land cover	mortality risk model
C	buffer	terrain model	AI land cover	AI land cover	land cover

Note: AI indicates “all-inclusive.”

TABLE 5. Resource selection functions at three spatial scales for male grizzly bear habitat selection in the mountains landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003.

Covariate	Study-wide		Home range		Buffer	
	β	SE	β	SE	β	SE
Alpine	<i>1.745</i>	0.289	<i>0.720</i>	0.287	-0.042	0.304
Shrub	-0.041	0.514	0.113	0.477	-0.266	0.508
Spruce	<i>0.730</i>	0.321	0.107	0.280	<i>-0.823</i>	0.296
True firs	<i>0.711</i>	0.284	0.405	0.282	-0.352	0.301
Greenness	<i>0.049</i>	0.006	<i>0.027</i>	0.005	<i>0.029</i>	0.005
Hill shade	0.003	0.002	0.002	0.001	<i>0.004</i>	0.001
Risk layer	-7.210	4.193	-6.875	5.266	-0.734	5.707
Distance to primary road	<i>-6.34×10^{-5}</i>	1.90×10^{-5}	<i>-4.37×10^{-5}</i>	1.63×10^{-5}	1.90×10^{-5}	1.75×10^{-5}
Distance to secondary road	<i>-7.54×10^{-5}</i>	3.61×10^{-5}	<i>-9.02×10^{-5}</i>	4.04×10^{-5}	-6.02×10^{-5}	3.99×10^{-5}
k -fold (\bar{r}_s)	0.833		0.802		0.749	

Note: Regression coefficients (β) in boldface italic type had confidence intervals that did not include 0.

For male bears from the plateau, each scale resulted in a different top-ranked model, meaning that patterns of habitat selection varied according to the extent of availability (Table 3). At the study-wide extent, male bears from the plateau selected a number of the dominant land cover types, areas where the risk of mortality by humans was high, and against secondary logging roads. Interestingly, when availability was restricted to selection within the home range, there was no detectable selection for or against areas with a high risk of mortality, although they continued to avoid primary logging roads. The ΔAIC_c value for the mortality risk and all-inclusive seral models was <2.0 , suggesting support for these models was comparable (Burnham and Anderson 2002). In the all-inclusive seral model, male bears from the plateau selected for early seral age stands (i.e., 0–40 years) at the study-wide extent but there was no detectable selection for or against these stands at the home range and buffer extents. At the buffer scale, the land-cover-based models ranked highest, although the risk and terrain models also had $\Delta\text{AIC}_c < 2$. The commonality across these models was selection for land cover dominated by shrubs while avoiding primary logging roads.

Unlike males, female bears inhabiting mountain and plateau landscapes had the same first-ranked model at each scale (Table 3). Thus, we recorded differences in habitat selection between males and females. For females residing in both landscapes the all-inclusive land cover model ranked first at all scales, while the all-inclusive seral model ranked second. Across all scales, females on the plateau selected early seral stands, which reflects in part selection for early seral clearcuts. The ΔAIC values for these models were >2 , suggesting the all-inclusive land cover model was the most parsimonious for female habitat selection. For females that lived on the plateau, the mortality risk model ranked third for all scales of analysis, whereas the seral model ranked third across all scales for females from the mountains. Unlike the plateau, models including variables characterizing the risk of mortality from human causes were ranked low for the mountain bears. The terrain and

land-cover-based models consistently were the lowest-ranked models for female bears. At the study-wide scale, the distribution of female bears was least well explained by the more-simplified terrain-based model.

Resource selection function results for one candidate model at three scales

We chose the all-land-cover model to examine how scale affected the same RSF design because it ranked first most frequently based on AIC model selection (Table 4). For all bears, selection varied based on the extent of available habitat, although some variables were consistently selected (e.g., greenness) or avoided across scales. Based on fivefold cross validation, we could not discern that one extent was consistently a better predictor than another; rather, support for a model was dependent upon the bears' sex as well as landscape.

Mountain males.—For mountain males, selection for alpine habitats was strongest at the study-wide scale ($\beta = 1.75$), decreased as availability was restricted to the home range ($\beta = 0.72$), and had no detectable selection or avoidance at the smallest scale (Table 5, Fig. 3). Spruce-dominated forests were selected by bears throughout the study area and reflected the distribution of these forests on the landscape; alpine occurred at higher elevations, while spruce forests primarily occurred at lower elevations. Therefore, there was selection for these land cover types at the broadest scale but apparent avoidance of spruce when availability was restricted (Fig. 3). Consistent across scales was selection for green vegetation (i.e., higher greenness scores), the magnitude of which was slightly stronger at the population level but similar at the home range and buffer extents. At the population and home range scales, male bears in the mountains were found closer to primary and secondary/decommissioned logging roads than random. We suggest that this was due to males using these roads for travel as well as responding to foraging opportunities on early-seral vegetation associated with roadside clearing. We observed males along difficult-to-access secondary/decommissioned logging

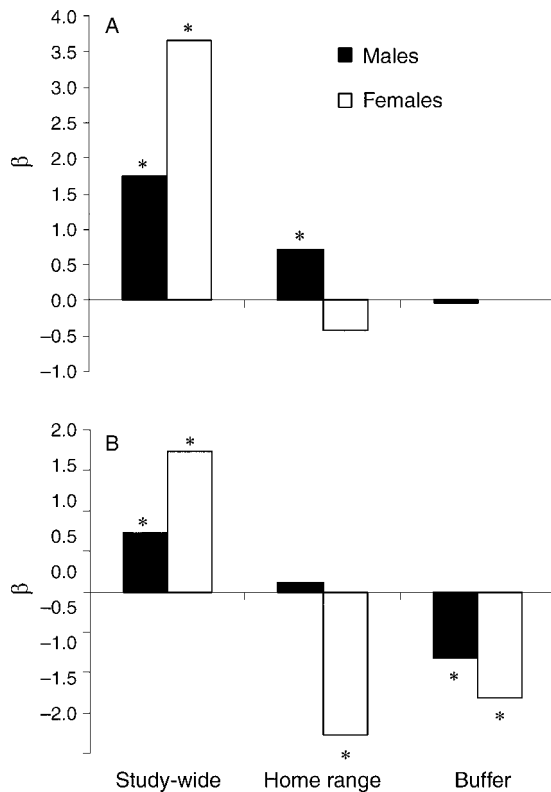


FIG. 3. Resource selection function coefficients (β) for male and female grizzly bears in the mountainous landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003, using (A) alpine landscapes and (B) spruce forests at three spatial scales. An asterisk indicates that the β value is significantly different from 0 based on a Wald statistic ($P < 0.05$).

roads on a number of occasions or foraging adjacent to roadways in early-seral-age clearcuts. When availability was restricted to a buffer, we could not detect selection for or against primary or secondary/decommissioned logging roads by male bears that lived in the mountains. Overall support was highest for the study-wide model with high internal consistency ($\bar{r}_s = 0.833$). Although the

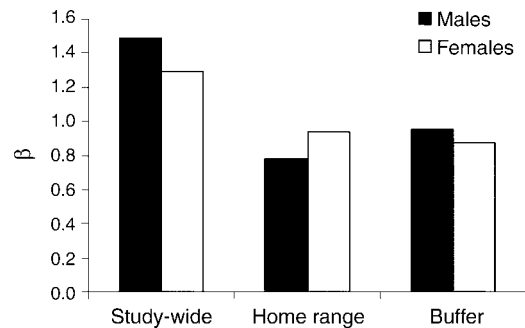


FIG. 4. Resource selection function coefficients (β) for male and female grizzly bears in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003, using shrub-dominated landscapes at three spatial scales. All values of β are significantly different from 0 based on a Wald statistic ($P < 0.05$).

internal consistency decreased with the extent, it remained moderately high (home range, $\bar{r}_s = 0.802$; buffer, $\bar{r}_s = 0.749$) across scales (Appendix A).

Plateau males.—At the study area extent the inclusion of shrubs, spruce, and true-fir land cover types were important predictors of the distribution of plateau male bears on the landscape (Table 6, Appendix B). The magnitude and significance of selection of land cover types decreased once the home range was established, and availability was restricted to what bears were selecting within their home ranges. Selection for shrub-dominated areas was the only consistent pattern across scales, although the magnitude decreased, being strongest for the study-wide extent, followed by the buffer and home range extents. Thus, plateau males selected resource units with shrubs when selecting their home range and included the presence of shrubs in their immediate decisions (buffer scale) (Table 6, Fig. 4). Early seral stages of shrub habitats provide foraging opportunities for plateau bears with increased early seral vegetation and also the opportunity of encountering moose (*Alces alces*; Ciarniello 2006). Furthermore,

TABLE 6. Resource selection functions at three spatial scales for male grizzly bear habitat selection in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003.

Covariate	Study-wide		Home range		Buffer	
	β	SE	β	SE	β	SE
Black spruce	0.385	0.621	0.462	0.603	0.431	0.632
Mixed wood	0.230	0.270	0.316	0.258	0.238	0.266
Shrub	<i>1.486</i>	0.258	<i>0.781</i>	0.260	<i>0.956</i>	0.272
Spruce	<i>0.815</i>	0.194	0.323	0.196	0.241	0.199
True firs	<i>0.723</i>	0.256	0.281	0.257	0.115	0.260
Greenness	<i>0.021</i>	0.007	0.005	0.007	0.011	0.007
Hill shade	0.006	0.004	0.005	0.003	0.003	0.003
Risk layer	<i>6.599</i>	2.587	2.956	4.095	3.301	4.046
Distance to highway	-3.17×10^{-5}	8.69×10^{-6}	-4.18×10^{-5}	1.25×10^{-5}	-2.42×10^{-5}	1.08×10^{-5}
Distance to primary road	7.26×10^{-5}	2.49×10^{-5}	8.15×10^{-5}	3.00×10^{-5}	7.20×10^{-5}	2.95×10^{-5}
Distance to secondary road	-1.86×10^{-5}	8.55×10^{-5}	-5.47×10^{-7}	1.06×10^{-4}	-4.16×10^{-5}	1.03×10^{-4}
k -fold (\bar{r}_s)	0.635		0.262		0.386	

Note: Regression coefficients (β) in boldface italic type had confidence intervals that did not include 0.

TABLE 7. Resource selection functions at three spatial scales for female grizzly bear habitat selection in the mountain landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003.

Covariate	Study-wide		Home range		Buffer	
	β	SE	β	SE	β	SE
Alpine	3.651	0.425	-0.430	0.471	0.018	0.407
Shrub	2.604	0.455	-0.070	0.501	0.301	0.441
Spruce	1.743	0.435	-1.765	0.475	-1.312	0.419
True firs	2.446	0.423	-1.050	0.470	-0.569	0.409
Greenness	0.043	0.002	0.027	0.002	0.031	0.002
Hill shade	0.004	0.001	0.004	0.001	0.003	0.001
Risk layer	-13.206	5.027	-3.547	6.131	1.39×10^{-38}	1.74×10^{-38}
Distance to primary road	-9.21×10^{-5}	8.19×10^{-6}	-1.11×10^{-5}	1.31×10^{-5}	1.71×10^{-6}	1.08×10^{-5}
Distance to secondary road	1.87×10^{-4}	1.41×10^{-5}	1.55×10^{-4}	2.18×10^{-5}	8.17×10^{-5}	1.73×10^{-5}
k -fold (\bar{r}_s)	0.963		0.934		0.970	

Note: Regression coefficients (β) in boldface italic type had confidence intervals that did not include 0.

shrub landscapes likely provide added security cover in a landscape with a high risk of human-influenced mortality (i.e., the plateau). Males that resided on the plateau were the only bears to use risky landscapes, although selection was significant only at the study-area-wide extent. Plateau males also suffered the highest mortality rates (Ciarniello 2006). Our earlier work found that male bears that did not avoid risky places were often removed through management actions or conflicts with humans (Ciarniello 2006).

Male bears that lived on the plateau used habitats closer to the highway than random, although this was likely an artifact of a power line that paralleled the highway corridor where the lack of canopy closure allowed for green vegetation to be available earlier to bears. In addition, a DNA population estimate conducted in 2000 revealed that the density of bears increased eastward across the plateau (Mowat et al. 2005). At all scales, plateau males avoided primary logging roads and the magnitude of the avoidance was similar across scales. Although we often located bears close to secondary and decommissioned logging roads, modeling revealed that use was not significantly different than random. Overall support was highest for the study-wide model with moderate internal consistency ($\bar{r}_s = 0.635$). Although the buffer model had the next highest internal consistency ($\bar{r}_s = 0.386$), followed by the home range extent ($\bar{r}_s = 0.262$), these models had low predictive capability. However, the low predictive success of the buffer and home range models was not surprising given that the all-inclusive land cover model was not the top-ranked model for plateau males at these scales (see Table 4).

Mountain females.—Study-wide patterns of selection for female bears that resided in the mountains showed strong selection for alpine landscapes ($\beta = 3.651$), followed by shrubs ($\beta = 2.604$), and high-elevation true firs ($\beta = 2.446$) (Table 7, Appendix C). However, selection of these forest cover types was largely scale dependent; covariates that were selected at the study-area-wide scale may be avoided at the home range and buffer extents (Fig. 3). While roughly 23% of the

mountainous landscape was alpine, home ranges of mountain females contained 43%. Thus, although mountain females highly selected alpine and shrub land cover types when establishing their home range, they showed random use when extent was restricted to the home range and buffer scales. Similarly, although they selected spruce and true firs while establishing their home range, they avoided them when selecting forest types within their home range. Consistent across scales was selection for higher greenness scores and warmer aspects. These two covariates are surrogates for bear foods by representing lush green vegetation, early seral stages, or early annual “green-up” of vegetation.

Mountain females selected against human risk areas when establishing their home range. However, this may reflect in part a bias in our radiocollared sample because some bears had low to no human-influenced mortality risk factors within their home ranges. Thus, when availability was restricted to the home range and buffer extents there was no detectable selection for or against risky areas. Unlike plateau bears, mountain females selected areas closer than random to primary logging roads at the study-wide extent and further distances from secondary logging roads across all scales. In the mountains, human use of primary logging roads was low due to their distance from settlements, making foraging adjacent to this road type much less risky than on the plateau. Further, primary roads tended to bisect low-elevation riparian areas from higher habitats. Thus, mountain bears with roads in their home ranges were required to cross these areas if selecting lower elevations in spring.

Across all scales, the all-inclusive land cover model had excellent predictive ability. Overall support was highest for the buffer scale ($\bar{r}_s = 0.970$, $P < 0.002$), suggesting that the immediate landscape most influenced habitat selection by mountain females, followed closely by the study-wide model ($\bar{r}_s = 0.963$) and the home range extent model ($\bar{r}_s = 0.934$).

Plateau females.—Black spruce ($\beta = 1.189$) and shrub ($\beta = 1.290$) landscapes were selected by female plateau bears at all spatial scales; however, the magnitude of

TABLE 8. Resource selection functions at three spatial scales for female grizzly bear habitat selection in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003.

Covariate	Study-wide		Home range		Buffer	
	β	SE	β	SE	β	SE
Black spruce	<i>1.189</i>	0.303	<i>0.978</i>	0.280	<i>1.034</i>	0.289
Mixed wood	0.230	0.163	0.115	0.150	0.112	0.148
Shrub	<i>1.290</i>	0.180	<i>0.938</i>	0.164	<i>0.878</i>	0.164
Spruce	<i>0.708</i>	0.128	<i>0.318</i>	0.121	<i>0.342</i>	0.120
True firs	-0.021	0.187	0.041	0.176	0.013	0.178
Greenness	<i>0.023</i>	0.004	<i>0.016</i>	0.004	<i>0.014</i>	0.004
Hill shade	<i>0.006</i>	0.002	0.004	0.002	<i>0.006</i>	0.002
Risk layer	-0.089	3.094	-2.708	3.426	-1.336	3.210
Distance to highway	-7.96×10^{-5}	6.32×10^{-6}	-4.66×10^{-5}	9.91×10^{-6}	-3.72×10^{-5}	8.50×10^{-6}
Distance to primary road	2.55×10^{-5}	2.22×10^{-5}	3.93×10^{-5}	2.50×10^{-5}	2.47×10^{-5}	2.34×10^{-5}
Distance to secondary road	-1.37×10^{-4}	8.96×10^{-5}	-1.47×10^{-4}	6.77×10^{-5}	-9.61×10^{-5}	6.68×10^{-5}
k -fold (\bar{r}_s)	0.944		0.802		0.656	

Note: Regression coefficients (β) in boldface italic type had confidence intervals that did not include 0.

selection was scale dependent (Table 8, Fig. 4, Appendix D). Approximately 6% of the plateau landscape contained shrubs, whereas shrubs comprised 12% of the home ranges of plateau females. We located females in the shrub areas of the plateau on 88 of 730 locations, ranking it as the fourth highest use of the 10 land cover types. Although plateau females were located in pine forests on 98 occasions, pine forests comprised 27% of the plateau landscapes. Female plateau bears avoided pine forests. Because pine was a withheld landcover type, selection for the remaining forest types increases.

Across scales, females on the plateau were distributed closer to highways; because we never located bears on the side of the highway and seldom located them adjacent to the highway, we believe this selection was an artifact attributed to three causes: (1) spring use of a power line corridor that paralleled the highway; (2) an increased number of bears in the eastern portions of the study area; and (3) because the highway bisected the plateau, there was low availability of close distances to the highway across the plateau. Within their home ranges female bears were located closer to secondary/decommissioned logging roads than random. However, when the extent of available habitat was restricted to an immediate buffer, confidence intervals overlapped 0, suggesting that selection for secondary/decommissioned roads may actually reflect the large number of those road types on the plateau landscape making those roads difficult for bears to avoid.

At the study-area-wide and home range extents, the all-inclusive land cover model had excellent predictive capability. Overall support was highest for the study-wide scale ($\bar{r}_s = 0.944$), followed by the home range extent ($\bar{r}_s = 0.802$). Interestingly, the buffer scale had only moderate predictive ability ($\bar{r}_s = 0.656$).

DISCUSSION

We examined the effects of altering spatial extent on our interpretation of habitat selection by grizzly bears. Our results show that our understanding of grizzly bear habitat selection is scale dependent; that is, our

interpretation of model results would vary between mountain and plateau landscapes, males and females, and across scales. Within sexes, however, there were patterns of selection for some variables that remained consistent across scales. Consequently, habitat managers should plan for different attributes, depending on the scale of land management decisions being addressed.

Our interpretation of results differed based on the scale examined, suggesting that scale indeed acts in a hierarchy distinguishing broad-level population questions from more fine-scale activity patterns for grizzly bears. Our results support the conclusion that decisions based only on one scale of analysis are limited in their scope (Kotliar and Wiens 1990, Lord and Norton 1990, Guisan and Thuiller 2005). For example, if a manager was provided with the results of the home range or buffer scales for mountain females (see Table 7) and subsequently used those results for land-use-level planning, such as the designation of parks or protected areas, they may erroneously conclude that the incorporation of alpine habitats into the proposed protected area was not necessary since the results of the RSF at these scales show no discernable selection for or against alpine habitats. However, by also examining the coefficients for land cover types at the study-wide scale, the manager is able to conclude that alpine habitats are indeed important to mountain females when establishing their home ranges on the landscape. In this example, because alpine habitat in the mountains was not limiting and a large amount was incorporated when females were establishing their home ranges on the landscape, when the extent of availability was restricted to that within the home range or a predetermined buffer scale, use of alpine habitat appeared to be random.

We also found the selection of habitats to be dependent upon availability on the landscape, making some patterns of selection vary across scales (Mysterud and Ims 1998, Guisan and Thuiller 2005). Thus, our ability to detect selection was influenced by the spatial heterogeneity within and between mountain and plateau landscapes. For example, similar to alpine areas, spruce

forests were highly sought after by mountain females at the study-wide extent, but were significantly avoided at the home range extent. Strong selection for spruce forests at the study-wide extent indicates that these landscapes were important to females that lived in the mountains. However, if we had examined only the home range scale, we may have erroneously concluded that female mountain bears avoided spruce. Thus, contrary to Van Horn (2002), we found that relevant ecological influences that occur at smaller scales may not be able to be discerned when RSF is built on too large a scale. Van Horn (2002) claimed that a problem exists if the extent is too small to capture a gradient. Rather, we found that large-scale patterns may overwhelm smaller-scale patterns. Specifically, selection of resources by individual bears might be obfuscated by large-scale variation in the availability of various foods, for example. As a result, we show support for examining three scales of analysis, as argued by O'Neill (1989): the patterns of selection for spruce forests were constrained at the study-wide extent and explained at the buffer extent. Similarly, on the plateau, alpine areas were limited to very small patches, and we did not record any female use of the alpine by plateau bears. Therefore, we could not model alpine landscapes for plateau bears, again making selection dependent upon availability, as suggested by Mysterud and Ims (1998).

Because we may observe and interpret biological processes differently at different scales, the "best" scale to address management decisions depends upon the management question (Boyce et al. 2003, Hobbs 2003, Boyce 2006); if the objective is to mitigate the effects of forestry through large-scale population-level land use planning, then the study-wide extent will reflect the broad distribution of grizzly bears throughout the area. Because random locations are drawn from the larger study area as well as within the home range, this larger scale allows one to answer more general questions relating to selection by grizzly bears for certain landscape features. However, when management questions become more specific, such as managing for human access, then it is best to limit availability to the home range, or even buffer, extents. Indeed, for species with limited daily movements it may be unrealistic for availability to be drawn from the entire study-wide extent. For example, an individual's decision to avoid predation or risky habitats may be based on their immediate surroundings rather than what is occurring at great distances from their current location. For a wide-ranging species such as a grizzly bear, more broad-level decisions appear to be made at the larger scales (i.e., incorporation of a habitat type into the home range, as discussed above) while short-term decisions, such as those related to access and predation, appear to be made at smaller scales occurring within the larger area. For example, male bears on the plateau selected for areas with a high risk of human-caused mortality at the study-

wide extent but use of those areas was random within the home range.

We found patterns of selection that were consistent across scales and sexes. Mountain and plateau females and mountain males selected for high greenness values. Further, mountain and plateau females also selected for warmer aspects at a similar magnitude. We suggest that consistent patterns across scales represent those attributes that are of fundamental importance to the life requisites of bears inhabiting northern environments. Warm aspects are the first to become snow-free and remain snow-free longer than cooler aspects. Similarly, areas with high greenness values tend to contain lush, rich vegetation and therefore have been used as a surrogate for high-quality bear forage (Mace et al. 1999). We suggest that consistent habitat use patterns across scales should be given priority when formulating land use plans.

One of the cautions with our results when applied to formulating management decisions is that we were limited to variables measured for commercial forestry operations and as such some attributes biologically relevant to grizzly bear habitat selection were not recorded (e.g., forb productivity). Furthermore, managers are often interested in making land management decisions, which require managing for landscape attributes, for example, connectivity. However, to be effective connectivity should be maintained between selected habitat patches, and the identification of those patches may not rely on the same covariates as in our larger-scale analysis.

In our analysis we altered the extent of availability but not the resolution (i.e., grain). Both grain and extent contribute to our understanding of wildlife populations (Hobbs 2003). Again we were somewhat limited by the attributes measured and resolution of our GIS layers; we believe that if we had been able to alter grain by including different attributes thought to be important to the distribution of wildlife, for example, measures of connectivity or forage items, we might anticipate even more dramatic variation across scales. Similarly, differences among scales are difficult to discern in areas where the vegetation is uniformly distributed across the landscape or where there is little topographic relief (Schaefer and Messier 1995). In homogeneous landscapes management decisions might be more discernable if one was to vary the grain as well as the extent. Currently, the management of some wildlife species in BC (e.g., caribou; Johnson et al. 2002, 2004b) is based on selection studies derived from attributes queried on GIS layers obtained from government agencies or forest companies. As such, these agencies and companies should consider the management of wildlife when establishing GIS layers.

Study design of RSF applied to management

By ranking models, we found that our understanding of patterns of selection changed depending on the scale

of availability for males but not for females. Between scales the greatest amount of variation occurred with male bears that lived on the plateau. We attribute this in part to the considerable home range sizes of plateau males, as large as 4361 km² (\bar{x} = 1759 km²; Ciarniello 2006), therefore the likelihood that all landscape types might be represented within the home range was greater (i.e., less variance among home ranges in relationship to the larger study area). The larger home range size of plateau males allowed them to encompass more attributes of the larger landscape; thus, when availability was restricted, selection was easier to discern between large and small scales. Alternatively, mountain females had the smallest range of variation between scales, likely because they have the smallest home range sizes (\bar{x} = 57 km²; Ciarniello 2006). However, all of the variation between scales by male bears cannot be explained by the differences in home range sizes because plateau females also showed consistent patterns of selection across scales and had similar home range sizes to mountain males (plateau females, \bar{x} = 446 km²; mountain males, \bar{x} = 443 km²; Ciarniello 2006). We believe the different patterns of selection by males and females has potential significance for management because not only should different management decisions be based on various scales of analysis but our results suggest that decisions might need to vary depending on the sex of the animal.

Our results appear to support segregation in habitat selection between sexes. Intraspecific predation on cubs and females has been suggested to limit grizzly bears (McLellan 1994, McLoughlin et al. 2002) and alter habitat selection (Wielgus and Bunnell 1994, 1995), thereby displacing females into other habitats (Weilgus and Bunnell 1995, Ben-David et al. 2004). Waller and Mace (1997) and McLoughlin et al. (2002) found that females did not avoid males when selecting home ranges, but rather avoidance was strongest at the smaller scales. We suggest that avoidance might be more difficult to detect at larger scales because larger scales reflect more broad-level selection patterns; for example, when selecting their home range on the landscape all bears may try to encompass some large patches of trees or shrubs for security. However, if we were able to differentiate the spatial location of the patch we might better detect avoidance at larger scales. Thus, at smaller scales it is easier to detect avoidance simply due to the finer selection patterns. For our results, the prominent selection for alpine, true-fir, and shrub landscapes at the study-wide extent by females that lived in the mountains might be interpreted as segregation from mountain males even though mountain males also were selecting alpine landscapes, but to a much lesser degree. If males push females into suboptimal and/or different habitats and management decisions tend to focus primarily on female habitat selection patterns (Nielsen et al. 2006), then those decisions might not identify the best habitats for bears.

For the plateau, we attribute the behavioral differences between sexes to habitat attributes rather than sexual segregation. Risk of mortality contributes to explaining the distribution and abundance of organisms (Lima and Dill 1990, Sutherland 1996, Fryxell and Lundberg 1998, Lima 2002, Hebblewhite et al. 2005). The main difference between males and females that lived on the plateau was that males entered human-risk areas. It is possible that for plateau males the pressure to attain large body sizes was greater than the chance of being killed; males were more willing to risk encounters with humans in an attempt to become dominant (Herrero 1985). Dominant individuals of many species tend to achieve a greater energy intake (Metcalf 1986) by having priority over food resources (Monaghan and Metcalf 1985, Stahl et al. 2001). In some cases a variable that is selected by an animal might not be necessarily beneficial to the animal. In cases where a variable is detrimental at one scale, managers should not manage on the habitat-selection patterns of that sex (e.g., male plateau bears at the study-wide scale). Resource selection functions are simply statistical descriptions of animal use of the landscape, and, as such, the proper interpretation of RSF results requires managers have a firm understanding of the ecology of the species in question.

We assumed that the study-wide extent design would be the most predictive scale, especially for females, because the large available area allows for the range of variation across the study area to be represented, even though use of distant areas may be unrealistic for the animal; the random landscape locations are drawn from the extent of the study area as well as within the home range (i.e., second and third order). Using fivefold cross-validation, the study area extent was the most predictive scale for female bears that lived on the plateau and for male bears in both landscapes. For mountain females, RSFs estimated using the buffer scale had only marginally better internal predictive capabilities than the study-area-wide scale. Therefore, in study areas where animal home ranges represent a portion of the overall variation in resources to be represented in the larger study area, management decisions may best be made at the study-area-wide scale.

In our second method we examined differences in RSF model coefficients within one model and found that by altering the extent of available habitat, both the direction and magnitude of some coefficients varied. Boyce et al. (2003) also found changes in the direction and magnitude of RSF coefficients when examining habitat use at four scales by elk. They stated that smaller extents can be expected to have smaller β values due to a restriction in the range of variance over smaller landscapes. For grizzly bear habitat selection, finer scales generally resulted in smaller β values, although for some variables selection was stronger at smaller scales. From a behavioral perspective, Rettie and Messier (2000) claim that for caribou, selection and

avoidance at larger scales indicate factors most responsible for limiting fitness, while smaller scales reflect less-important limiting factors. We found this to be consistent with our results for male bears that lived on the plateau; plateau males selected areas with a high risk of human-caused mortality at the study-wide extent, likely limiting the number of males on the plateau. As study design relates to management, we propose that if behavioral choice is the factor motivating a species' landscape selection, the matched-case control designs should best reflect this choice, regardless of model rank, because each animal is matched to the available points.

We recognize that both spatial and temporal scales are important considerations for habitat selection studies (Orians and Wittenberger 1991) and that our study assumed selection ignored variation over time (Boyce 2006). Grizzly bears have been shown to alter selection based on season (McLellan and Hovey 2001, Nielsen et al. 2004), and inclusion of season into our models likely would alter the results. For example, we were unable to investigate the effects that the spring breeding season had on male habitat selection. Males are known to travel widely while breeding, and it is possible that the differences between males and females may be partly explained by these extended movements. However, we were limited by the sample size afforded by VHF telemetry when applied to multivariable analysis. Similarly, we were limited to daytime aerial telemetry; it has been argued that grizzly bears display different diurnal and nocturnal patterns of selection (Schwartz and Arthur 1999, Gibeau et al. 2002, Nielsen et al. 2004). However, others studies have shown that grizzly and black bears were primarily diurnal or crepuscular (Garshelis and Pelton 1980, Bjarvall and Sandegren 1987, Rode et al. 2001). Regardless, our results show strong differences in how we would interpret and manage for habitat selection patterns based on the scale examined. Indeed, in cases in which sufficient sample sizes are available (e.g., GPS/telemetry studies), we believe it would be prudent to devise seasonal models for grizzly bears to reflect differences in RSF models.

Our results show that generally, when predicting patterns of habitat use, it is prudent to examine the manner in which our observations of biological processes may be altered by selection across multiple scales (O'Neill 1989, Hobbs 2003). Altering the scale of analysis illustrates the need for a priori focus of our management questions when designing research projects. The complex and varied pattern of selection we report between males, females, and mountain and plateau landscapes suggests that managers cannot make a perfect altered landscape for grizzly bears. The intricacy of the selection patterns and behavioral issues requires management decisions that traverse scales, suggesting that trade-offs between life requisites may need to be made. The advantage of examining three levels of scales is that it allows managers to identify,

focus, and therefore potentially monitor the impending costs and benefits of their management decisions.

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APPENDIX A

Maps depicting the relative probability of occurrence of male grizzly bears in the mountain landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003, based on study-wide extent, home range extent, and buffer extent (*Ecological Archives* A017-055-A1).

APPENDIX B

Maps depicting the relative probability of occurrence of male grizzly bears in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003, based on study-wide extent, home range extent, and buffer extent (*Ecological Archives* A017-055-A2).

APPENDIX C

Maps depicting the relative probability of occurrence of female grizzly bears in the mountain landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003, based on study-wide extent, home range extent, and buffer extent (*Ecological Archives* A017-055-A3).

APPENDIX D

Maps depicting the relative probability of occurrence of female grizzly bears in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003, based on study-wide extent, home range extent, and buffer extent (*Ecological Archives* A017-055-A4).