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Source: Journal of Wildlife Management, 71(5):1446-1457.

Published By: The Wildlife Society

DOI: <http://dx.doi.org/10.2193/2006-229>

URL: <http://www.bioone.org/doi/full/10.2193/2006-229>

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Components of Grizzly Bear Habitat Selection: Density, Habitats, Roads, and Mortality Risk

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ABSTRACT We used resource selection functions (RSF) to estimate the relative probability of use for grizzly bears (*Ursus arctos*) adjacent to the Parsnip River, British Columbia, Canada, 1998–2003. We collected data from 30 radiocollared bears on a rolling plateau where a large portion of the landscape had been modified by human activities, primarily forestry. We also monitored 24 radiocollared bears in mountain areas largely inaccessible to humans. Bears that lived on the plateau existed at less than one-quarter the density of bears in the mountains. Plateau bears ate more high-quality food items, such as meat and berries, leading us to conclude that food limitation was not responsible for the differences in densities. We hypothesized that plateau bears were limited by human-caused mortality associated with roads constructed for forestry activities. Independent estimates of bear population size from DNA-based mark–recapture techniques allowed us to link populations to habitats using RSF models to scale habitat use patterns to population density. To evaluate whether differences in land-cover type, roads, or mortality risk could account for the disparity in density we used the mountain RSF model to predict habitat use and number of bears on the plateau and vice versa. We predicted increases ranging from 34 bears to 96 bears on the plateau when switching model coefficients, excluding land-cover types; when exchanging land-cover coefficients, the model predicted that the plateau population would be 9 bears lower than was observed. Large reductions in the numbers of mountain bears were predicted by habitat-selection models of bears using the plateau landscape. Although RSF models estimated in mountain and plateau landscapes could not predict bear use and abundance in the other areas, contrasts in models between areas provided a useful tool for examining the effects of human activities on grizzly bears. (JOURNAL OF WILDLIFE MANAGEMENT 71(5):1446–1457; 2007)

DOI: 10.2193/2006-229

KEY WORDS British Columbia, density estimation, forestry, grizzly bear, habitat selection, mortality, risk, roads, resource selection function, *Ursus arctos*.

Landscapes contain temporal and spatial variation among and within habitat patches (Southwood 1977), and habitat selection has a direct impact on population density and behavior (Rosenzweig 1981). Frequently, the spatial distribution of foods has been used to explain the spatial distribution and dynamics of animals (MacArthur and Pianka 1966, Charnov 1976). In theory, animals should optimize their foraging strategy by choosing richer patches over poorer patches (Charnov 1976). Higher quality habitats are assumed to be linked to increased fitness at a given density, generally resulting in higher densities of animals in higher quality habitats (Fretwell and Lucas 1970, Garshelis 2000, Bock and Jones 2004). Also, experimental studies have shown that avoidance of predation risk can alter habitat selection (Gilliam and Fraser 1987, Abrahams and Dill 1989, Resetarits 2005).

In our study area, a relatively pristine mountainous landscape contained 4 times the density of grizzly bears (*Ursus arctos*) as an adjacent plateau landscape that had been heavily harvested for timber (Mowat et al. 2005). A similar pattern occurs in Alberta, Canada, where the highest density of bears exists in the mountains and bear densities decline further east in the foothills, where access to development has been greater (Boulanger et al. 2005). High-quality habitats close to areas of human use are often areas of high bear

mortality (Knight et al. 1988, McLellan 1989, Mattson and Merrill 2002, Nielsen et al. 2004), thereby negatively affecting populations (Mattson and Merrill 2002). Further, high-risk food-rich habitats that attract individuals can serve as local population sinks, or ecological traps (Delibes et al. 2001, Kristan 2003, Robertson and Hutto 2006). Consequently, individual occurrence and abundance are not necessarily related to habitat quality (Hobbs and Hanley 1990, Kristan 2003).

In areas with high food availability, particularly meat, bears tend to have increased reproductive success, larger body mass, and a higher population density (Hilderbrand et al. 1999). Elsewhere we reported significantly larger body masses, better condition, and higher cubs-of-the-year survival in our low-density area (i.e., the plateau); however, survival of subadult and adult bears was lower on the plateau than the mountains (Ciarniello 2006). Based on these observations we surmised that the density of bears on the plateau was limited by human-caused mortality linked to access afforded by forestry activities rather than habitat quality per se (Ciarniello 2006). In this paper, we evaluate this conclusion using 2 methods: 1) examining the foods consumed by bears that lived in the mountains compared with those that lived on the plateau to investigate whether bears on the plateau were limited by available forage; and 2) modeling the relationship between habitats and population structure using mechanistic and or statistical approaches to habitat selection.

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Recent habitat-modeling techniques suggest a way to link habitat selection and population structure (Rosenweig and Abramsky 1997, Boyce and McDonald 1999, Manly et al. 2002, Boyce and Waller 2003), but the efficacy of that approach has never been tested. Habitats for animals can be modeled using resource selection functions (RSF; Manly et al. 2002). Although these models are simply statistical descriptions of use of the landscape, RSF models can be linked to populations if reference areas exist where densities are known (Boyce and McDonald 1999). By combining the results of DNA mark-recapture population estimation with habitat-based density-modeling techniques it is possible to distribute density across the landscape. In particular, habitat-based density modeling can be used to evaluate whether differences in density is attributable to differences in habitat, roads, and or the risk of human-caused mortality. We think that such a link between land-cover features and population models may provide useful insights into the consequences of human activities on wildlife populations.

STUDY AREA

The 18,096-km² study area was centered along the Parsnip River in central-eastern British Columbia, Canada (54°39'N, 122°36'W; Fig. 1). The ecosection line, as delineated by the British Columbia Ministry of Water, Land and Air Protection (Victoria, BC, Canada), represents a topographic division between a plateau (10,624 km²) that contained rolling hills and flat valleys, and the west and east slopes of the Hart Ranges of the Rocky Mountains (7,472 km²). Elevations ranged from 600 m to 1,650 m in the plateau, and 720 m to 2,550 m in the mountains. The plateau was warmer and had less precipitation than the mountains (\bar{x} = 2.6° C, 72 cm rainfall, 300 cm snowfall vs. \bar{x} = 0.3° C, 154 cm rainfall, 700 cm snowfall; DeLong et al. 1993, 1994).

The subboreal spruce (SBS) biogeoclimatic zone dominated the plateau and some lower-elevation areas in the mountains (e.g., along major rivers). Most forests on the plateau were a mix of white spruce (*Picea glauca*), pine (*Pinus contorta*), and subalpine fir (*Abies lasiocarpa*). Black spruce (*Picea mariana*) bogs occurred in lower elevation wet areas. Interior Douglas-fir (*Pseudotsuga menziesii*) occurred in small portions on the plateau and lower elevation mountain valley bottoms. Aspen (*Populus tremuloides*), cottonwood (*P. balsamifera*), and paper birch (*Betula papyrifera*) were present within these forests, especially along riparian areas and in areas disturbed by logging or wildfires.

The Engelmann spruce-subalpine fir zone occurred above the SBS and dominated the mountainous portion of the study area. Higher elevation mountain habitats consisted of subalpine parkland predominantly comprised of subalpine fir and Engelmann spruce (*P. engelmannii*). Subalpine meadows supported forbs such as glacier lily (*Erythronium grandiflorum*), Indian hellebore (*Veratrum viride*), and arrow-leaved groundsel (*Senecio triangularis*). Large burns within the mountains had abundant huckleberries (*Vaccinium membranaceum*), blueberries (*Vaccinium myrtilloides*),

and Canadian buffalo-berry (*Shepherdia canadensis*). The alpine-tundra biogeoclimatic zone began at approximately 1,400 m and typically consisted of small shrubs or krummholz, heath communities. Barren rock or alpine snow and ice at elevations over 2,400 m were <1% of the study area.

The plateau landscape was harvested heavily for timber and logging was expanding in 4 main river valleys (Missinka, Hominka, Table, and Anzac rivers) leading from the plateau into mountainous areas. On the plateau, the majority of logging had occurred since the 1960s, resulting in a mosaic of forest habitats in various successional stages. There were 2 resource-based towns, 3 backcountry-logging camps, 2 sawmills, and an extensive network of forestry roads. A 2-lane paved highway bisected the plateau portion of the study area. In the mountains, the only permanent disturbances to bears were a railway line for coal extraction that extended onto the plateau and road networks expanding up the low-elevation valleys. Recreational activities occurred in both landscapes, including hunting, fishing, snowmobiling, and hiking. The majority of the study area was within the Arctic watershed where bears do not have access to salmon (*Oncorhynchus* spp.) runs. There were a few provincial parks within the study area, but they were small relative to the size of grizzly bear home ranges.

METHODS

Bear Capture

We captured grizzly bears using aerial darting, leg snares, or culvert traps and fitted them with very high frequency (VHF) collars (Lotek Inc., Aurora, ON, Canada), Global Positioning System (GPS) collars (Televilt Ltd., Lindesberg, Sweden), or ear-tag transmitters between August 1997 and spring 2003. We placed effort in trapping throughout the study area by varying both trapping methods (i.e., snares, culverts, and aerial darting) and distribution of trap sites. For example, we did not only rely on aerial darting in the mountains, but we also set snares in low-elevation forests and subalpine areas. Similarly, we aerial-darted in the subboreal forest of the plateau.

We immobilized bears with Telazol (tiletamine HCL and zolazepam HCL) and sometimes we added ketamine hydrochloride. We extracted a first premolar tooth for age determination (Matson's Laboratory, Milltown, MT). The University of Alberta's Animal Care Committee, following the Canadian Council on Animal Care guidelines and principles, approved bear handling procedures (protocol no. 307204).

Radiotelemetry

We monitored bears with VHF telemetry. We monitored bears during May–October at a frequency of twice per week in 1998–2002, once per week in 2001–2002, and a minimum of once every 2 weeks in 2003, using a single-engine fixed-wing aircraft. We obtained some aerial relocations from a helicopter. We used only low-level relocations in which we were confident of the position of the animal for analysis. Once we relocated the bear, we took

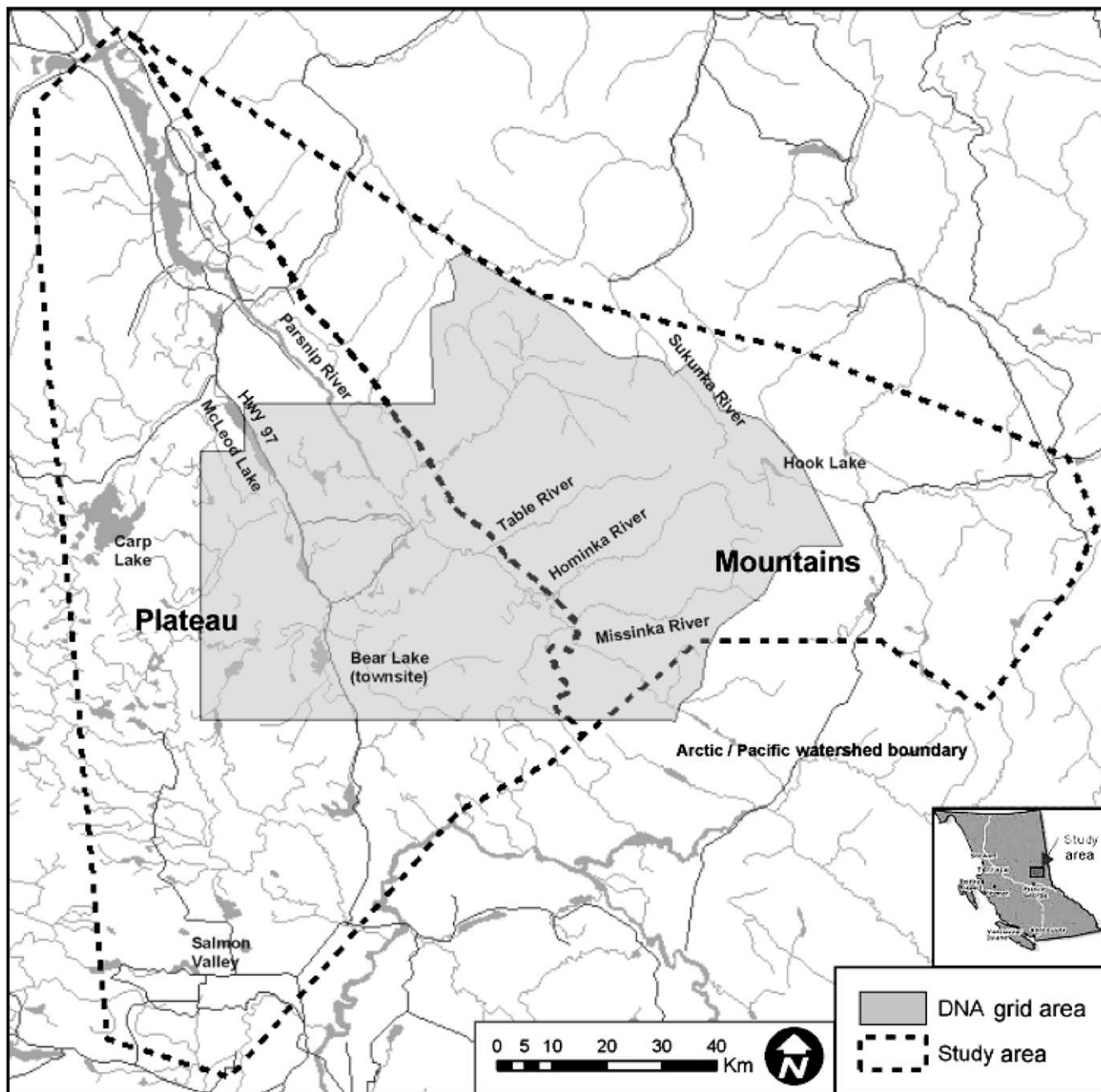


Figure 1. Study area for determining grizzly bear habitat use and density, including mountain and plateau boundary line just east of the Parsnip River, British Columbia, Canada, 1998–2003. The shaded box contained within the core of the larger study area represents the DNA-based population census boundary and encompassed mountain and plateau landscapes.

Universal Transverse Mercator (UTM) coordinates with a hand-held GPS unit. We further mapped relocations and verified them on 1:50,000 topographic maps. We classified relocations east of the ecosection line as mountain, whereas we referred to relocations on the west as plateau.

Although VHF relocations collected during daylight hours might not be representative during the entire diel period (Belant and Follmann 2002), we felt justified in assuming that our data were unbiased by time of day and year (season) because we monitored the bears extensively during all seasons. Also, because of the broad cross-section of radio-

collared bears by age, sex, and reproductive status, we assume that the locations were representative of the population as a whole.

We took a Polaroid photograph of each bear location. We placed a dot on the photograph marking the location of the bear and we provided a north arrow. We used the photo and UTM to identify the location for subsequent microsite habitat investigations.

Microsite Habitat Investigations

We visited a random sample of bear relocations to gain an understanding of the mechanisms of bear use. We

performed site investigations after the bear was known to have left the area and they usually occurred, with the exception of active carrion sites or den sites, within 7 days of the relocation. We centered a $10 \times 10\text{-m}$ (100-m^2) plot on what we determined to be the primary activity feature. We used criteria such as visual location, telemetry reliability, age of the sign, scat, hair, or tracks to identify such features. Because microsite investigations relied on radiotelemetry data (one point in time) we were limited in our ability to determine the primary activity (e.g., we were unable to watch bears and devise an activity budget). Therefore, rather than using time as a criteria for primary activity, we subjectively defined the primary activity by the predominant type of bear sign. We classified bear activities into foraging (i.e., ants, berries, carcass or meat, cambium, digging for roots, digging for rodents, grazing vegetation, nonnatural attractants, or bees or wasps), traveling, mortality of the bear, resting, rubbing on trees, denning, other, or unknown. We used chi-square tests to make comparisons between foods consumed by bears inhabiting the mountains and plateau (significance level was considered $\alpha < 0.05$).

Geographic Information System Data

We selected a set of predictor variables from Geographic Information System (GIS) data that characterized habitats that we thought were selected by grizzly bears (Table 1). If correlations between predictor variables were ≥ 0.7 we ran separate models for correlated variables to avoid collinearity (Sokal and Rohlf 2000).

We used terrain resources inventory maps (TRIM2; BC Ministry of Water, Land, and Air Protection, Victoria, BC, Canada) to build digital elevation maps (DEM) to obtain elevation, slope, aspect, and hillshade data. We used forest-cover maps (FCM; BC Ministry of Forests, Prince George, BC, Canada) to obtain the predominant forest stand or land-cover type, and stand age. We built road networks 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 Products Ltd., in Prince George, British Columbia, Canada. Raster layers (i.e., DEM, slope, aspect, hillshade, and distance to roads) had a resolution of 25 m (i.e., cell size 25×25 m). We based the forestry data (e.g., age, ht, forest type) on vector GIS layers that were rasterized, also with a resolution of 25 m.

Greenness is the second component of the standard tasseled cap transformation for Landsat 5 TM satellite data (White et al. 1997) and we calculated it for 4 satellite images using ERDAS®Imagine (Leica Geosystems, Atlanta, GA) at a 30-m pixel resolution. Greenness is an index of the amount of green herbaceous phytomass in a pixel (Mace et al. 1999). Pixels with lush green vegetation have high greenness values, sparse or senesced vegetation reflect lower greenness values, and nonvegetated areas have very low values (Mace et al. 1999).

We built the mortality risk layer by assessing the relationship between human-caused grizzly bear mortality locations (1) and nonmortality telemetry relocations (0)

using logistic regression (see Ciarniello 2006). We estimated separate mortality models for mountain and plateau landscapes (Ciarniello 2006). We scaled values 0–1; values closer to 1 represented higher security area (i.e., lower risk of human-caused bear mortality). We then used the fitted model in GIS to form a layer reflecting the relative probability of human-caused grizzly bear mortality across the study area.

Resource Selection Functions

We estimated resource-selection functions reflecting the relative probability of use for the foraging season using logistic regression. To capture the primary foraging season, we removed UTM radiotelemetry coordinates when each bear moved to < 1 km of its den site for autumn and spring. We employed a variation on Design 2 (Manly et al. 2002), third-order selection (Johnson 1980), at the landscape scale because the study area extent was occupied by grizzly bears. Following this design, we pooled data from individual animals and we calculated GIS attributes for each bear relocation (i.e., used resource units). By pooling data among years we assumed that habitat availability was fairly static, which we think is a fair assumption given the short duration of our study. We assumed the following logistic discriminant function to characterize the influence of covariates on relative use, $w(\mathbf{x})$:

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

where β_i are selection coefficients for each covariate, x_i , for $i = 1, 2, \dots, p$ (Johnson et al. 2006). Bear relocations represented used sites, and we assigned them a value of 1. To characterize availability, we assigned 36,192 randomly identified sites a value of zero ($1 \text{ location}/500 \text{ m}^2$, 14,944 in mountains and 21,248 in plateau). We generated random points using the program HawthTools (Beyer 2004) for ArcGIS® 8.3. We estimated models using Stata 7.0 (Stata Corporation, College Station, TX).

We considered a set of 5 candidate models that we deemed biologically relevant to grizzly bear habitat use (Anderson et al. 2000, Burnham and Anderson 2002). We chose candidate models that allowed us to examine whether the lower density of plateau bears was a function of the different landscape attributes between areas. Further, to apply the habitat-based density technique we needed the same coefficients in both plateau and mountain models. For example, because we did not record any bear use of the small area of alpine on the plateau we withheld alpine from analysis, even though alpine areas were common in the mountains and highly used by mountain bears. We based model selection on Akaike Information Criterion (AIC; Burnham and Anderson 2002); however, to make the models comparable we did not necessarily choose the individual model with the lowest AIC score (the most parsimonious model) but rather the best models in which each variable occurred within both landscapes. We used normalized Akaike weights (AIC_w) to evaluate whether a candidate model was the best model (Anderson et al. 2000).

Table 1. Description of variables from Geographic Information System layers used to select candidate models for grizzly bears in the mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada (1998–2003).

Variable	% landscape		Leading land-cover type
	Mountain	Plateau	
Primary land-cover categories used in modeling:			
True firs	34	10	Stands dominated by subalpine fir
Pine	7	27	Stands dominated by lodgepole pine
Spruce	30	35	Stands dominated by spruce species
Mixed-wood	2	13	Stands dominated by cottonwood, aspen, or common paper birch
Shrub	3	6	Areas with no or few trees and large expanse of shrubs, most frequently occurred adjacent to swamps and rivers or subalpine
Withheld land-cover categories:			
Alpine	23	0.1	Dynamic, high-elevation, largely forb- and or shrub-dominated parkland or krummholz subalpine fir
Black spruce	1	2	Stands dominated by black spruce
Douglas Fir	0.05	1	Stands dominated by Douglas fir
Meadow	0.05	2	Large, open forb-dominated areas
Rock and bare ground	0.2	0.03	Typically high-elevation mountain tops
Swamp	0.5	3	Water table above ground surface
Anthropogenic	0.2	1	Areas of human settlement or regular maintenance, such as along the railway line. Excludes harvested areas
Variable	Type		Description
Topographic features:			
Crown closure	Linear		Relative amt of gaps in a forest stand in 10% increments from closed or dense (100%) to open (0%)
Elevation	Linear		Elevation above sea level
Forest ht	Linear		Ht of the forest (m)
Greenness	Linear		Calibrated greenness values
Hillshade	Linear		Combination of slope and aspect to measure solar insolation as it varies with topography (azimuth: 225, sun-angle: 45). Negative coeff. indicate selection for cooler, northeast aspects, whereas positive coeff. reflect selection for warmer southwest aspects.
Risk layer (human-influenced risk of bear-mortality only)	Scaled 0–1		Evaluates the relative probability of grizzly bear mortality risk by landscape (see Ciarniello 2006)
Road	Linear		Straight-line distance to the nearest road in meters
Stand age	Categorical		Early seral 0–45 yr including shrub, meadow, noncommercial and nonproductive brush, swamps, and alpine. Young forest 46–99 yr. Old forest 100+ yr.

We considered coefficients with confidence intervals that did not overlap zero to be statistically significant.

We assessed the predictive capability of each model using a Spearman’s rank correlation based on 5-fold cross validation (Boyce et al. 2002). In this procedure, we estimated an RSF model using a random draw of 80% of the data and we used this model to predict the frequency of occurrence in the withheld 20% using 10 RSF bins; we repeated the process 5 times, replacing the withheld 20% and removing the next 20% (Boyce et al. 2002). A model that has strong predictive capabilities will have a higher number of locations in bins with the highest RSF scores. We used the highest ranked mountain and plateau models to create GIS maps of relative probability of grizzly bear use across each landscape.

Habitat-Based Density Modeling

Because the $w(\mathbf{x})$ values were skewed, we performed calculations using the square-root transformation of $w(\mathbf{x})$ to obtain RSF values that were proportional to probability of use (Keating and Cherry 2004, Johnson et al. 2006). First, we calculated an RSF score for each use and random landscape location. Using the random locations we then binned the landscape into 10% increments providing a

gradation from the poorest to the most-selected habitats. We scaled binned RSF scores (i.e., 0–1) for each landscape by dividing by the maximum RSF value. Then we calculated the relative use:

$$U(x_i) = \frac{w(x_i)A(x_i)}{\sum_j w(x_j)A(x_j)}$$

(2)

where $w(x_i)$ is the bin midpoint RSF value, and $A(x_i)$ is area for the i th habitat variable, x_i .

We obtained population densities for the mountains and the plateau from a DNA-based population estimate from spring 2000 at 49 bears/km² (95% CI = 43–59) in the mountains and 12 bears/km² (95% CI = 7–28) in the plateau (Mowat et al. 2005). We estimated the density of animals, $D(\mathbf{x})$, by the i th habitat type using:

$$D(x_i) = \frac{N \cdot U(x_i)}{A(x_i)}$$

(3)

Here the number of bears in the mountains or the plateau, N , is divided by the area of relative use, $A(x_i)$, characterized

Table 2. Resource-selection function model coefficients,^a standard errors, and 95% confidence limits^b for grizzly bear habitat selection in the mountain landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003.

Variables ^c	β	SE	L95%CL	U95%CL	AIC	AIC _w	Δ AIC
Crown closure	−0.018	0.003	−0.023	−0.012	7275.52	0.82	0.00
Greenness	0.035	0.002	0.032	0.039			
Hillshade	0.004	0.001	0.002	0.005			
True firs	−0.341	0.117	−0.570	−0.113			
Spruce	−0.960	0.137	−1.228	−0.691			
Pine	−0.347	0.287	−0.909	0.215			
Mixed-wood	−1.066	0.541	−2.125	−0.006			
Shrub	−0.079	0.176	−0.425	0.267			
Distance to highway	7.66E ^{−05}	3.75E ^{−06}	6.92E ^{−05}	8.39E ^{−05}			
Distance to primary logging road	−1.48E ^{−04}	7.20E ^{−06}	−1.62E ^{−04}	−1.34E ^{−04}			
Distance to secondary and decommissioned logging roads	1.56E ^{−04}	1.24E ^{−05}	1.32E ^{−04}	1.80E ^{−04}			
Risk of human-caused bear mortality	−21.108	3.507	−27.983	−14.234			

^a AIC = Akaike's Information Criterion; AIC_w = normalized Akaike wt; Δ AIC = AIC relative to the most parsimonious model.

^b L95%CL = lower 95% CL; U95%CL = upper 95% CL.

^c Bold variables had CIs that did not include zero.

by the respective habitat model (Boyce and McDonald 1999).

We then used the model coefficients for bear habitat selection in the mountains to see how well we could predict numbers and densities of bears on the plateau. Conversely, we predicted bear numbers and densities expected in the mountains based on the RSF model coefficients estimated for the plateau. We examined the effects of the following sets of variables: land-cover types (5 coeff./landscape), risk of human-caused bear mortality (1 coeff.), primary and secondary or decommissioned logging roads (2 coeff.), and the entire model (12 coeff.), on the predicted number of bears in the mountains versus the plateau. To do this we exchanged coefficients for only the variable(s) in question between landscape models while leaving the remaining variables and coefficients as they occurred in the original model. For example, when exchanging the predominant land-cover types, we exchanged only the model coefficients for true firs, spruce, pine, mixed woods, and shrubs (i.e., 5 coeff.), preserving all of the remaining 7 coefficients.

RESULTS

We monitored 24 bears that lived in the mountains (17 F: 7 M) and 30 bears that lived on the plateau (17 F:13 M), resulting in 1,527 locations in the mountains (1,281 F: 246 M) and 972 locations on the plateau (726 F:246 M).

Habitat Investigations

We visited 21% of randomly selected bear locations ($n = 534$) to conduct microsite habitat investigations (n [mountain] = 202, n [plateau] = 332). Bear foraging was the primary activity identified at 381 of the 534 (71%) sites visited. Grazing on grasses and forbs was common to both mountain and plateau bears ($\chi^2 = 0.069$, $P = 0.8$). However, bears that lived on the plateau foraged more on berries than bears that lived in the mountains ($\chi^2 = 7.31$, $P = 0.006$). Furthermore, bears that lived on the plateau scavenged or killed more large game ($\chi^2 = 11.72$, $P < 0.005$) and fed on more ants ($\chi^2 = 10.15$, $P < 0.005$) than bears that lived in the mountains. We investigated 27 carrion sites of apparent

prey on the plateau; the majority were moose (*Alces alces*), although we also recorded black bears (*U. americanus*), domestic cattle, and beavers (*Castor canadensis*). We recorded only one carcass in the mountains, which was a grizzly bear cub-of-the-year thought to have been killed by a radiocollared adult male. On one occasion a mountain bear was thought to be excavating a caribou (*Rangifer tarandus*) carcass from an avalanche path in spring. However, we were not able to access this site due to terrain limitations. Bears that lived in the mountains appeared to obtain the majority of their meat by digging for rodents, an activity we did not record for bears living on the plateau. We never detected bears eating fish, in part because they were primarily in the Arctic watershed and did not have access to spawning runs of salmon. Mountain bears dug for roots and bulbs of plants more than plateau bears ($\chi^2 = 43.28$, $P < 0.001$).

Resource-Selection Functions

Of the 5 candidate models examined, the model we used ranked first in the mountains and second on the plateau (Tables 2, 3). The Δ AIC value for first and second-ranked plateau models was 0.32, indicating that support for either model was comparable (Burnham and Anderson 2002). In the mountains the second-ranked model had a Δ AIC of 3.06; therefore, we chose the first-ranked mountain model.

In the mountains, 10 of the 12 variables measured had confidence intervals that did not include zero, suggesting that those parameters were predictors of mountain bear use of the landscape (Table 2, Fig. 2). The 5-fold cross-validation provided a mean Spearman's rank correlation between predicted and observed of 0.94 ($P < 0.002$), indicating that this model consistently predicted the distribution of bears. On the plateau, 7 of 12 variables measured had confidence intervals that did not include zero (Table 3, Fig. 3), yet the plateau model also had excellent predictive ability with $r_s = 0.93$ ($P < 0.002$).

Mountain bears used forested land-cover types of true firs, spruce, and mixed woods less than available (Table 2). Confidence intervals for pine and shrub land-cover included zero, suggesting no selection for these types. On the plateau,

Table 3. Resource selection function model coefficients,^a standard errors, and 95% confidence limits^b for grizzly bear habitat selection in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003.

Variables ^c	β	SE	L95%CL	U95%CL	AIC	AIC _w	Δ AIC
Crown closure	−0.008	0.002	−0.011	−0.004	7464.54	0.46	0.32
Greenness	0.015	0.004	0.008	0.022			
Hillshade	0.005	0.002	0.002	0.008			
True firs	0.074	0.175	−0.269	0.416			
Spruce	0.617	0.137	0.349	0.885			
Pine	−0.049	0.156	−0.356	0.257			
Mixed-wood	0.206	0.160	−0.107	0.519			
Shrub	1.071	0.160	0.758	1.384			
Distance to highway	−8.14E ^{−05}	5.23E ^{−06}	−9.16E ^{−05}	−7.11E ^{−05}			
Distance to primary logging road	2.08E ^{−05}	1.56E ^{−05}	9.85E ^{−06}	5.15E ^{−05}			
Distance to secondary and decommissioned log roads	−2.84E ^{−05}	5.59E ^{−05}	−1.38E ^{−04}	8.11E ^{−05}			
Risk of human-caused bear mortality	−3.875	2.663	−9.095	1.345			

^a AIC = Akaike’s Information Criterion; AIC_w = normalized Akaike wt; Δ AIC = AIC relative to the most parsimonious model.
^b L95%CL = lower 95% CL; U95%CL = upper 95% CL.
^c Bold variables had CIs that did not include zero.

we were able to detect selection by bears for spruce and shrub landscapes (Table 3). There was no detectable selection for or against true firs, mixed-wood, or pine-dominated forests by plateau bears.

Common to bears in both areas was selection for open canopies, higher greenness scores, and southwest-facing

aspects (i.e., hillshade). Bears in the mountains avoided landscapes where the risk of human-caused bear mortality was highest, whereas there was no detectable selection for or against these areas on the plateau.

Coefficients associated with road variables were opposite between mountain and plateau models. Bears in the

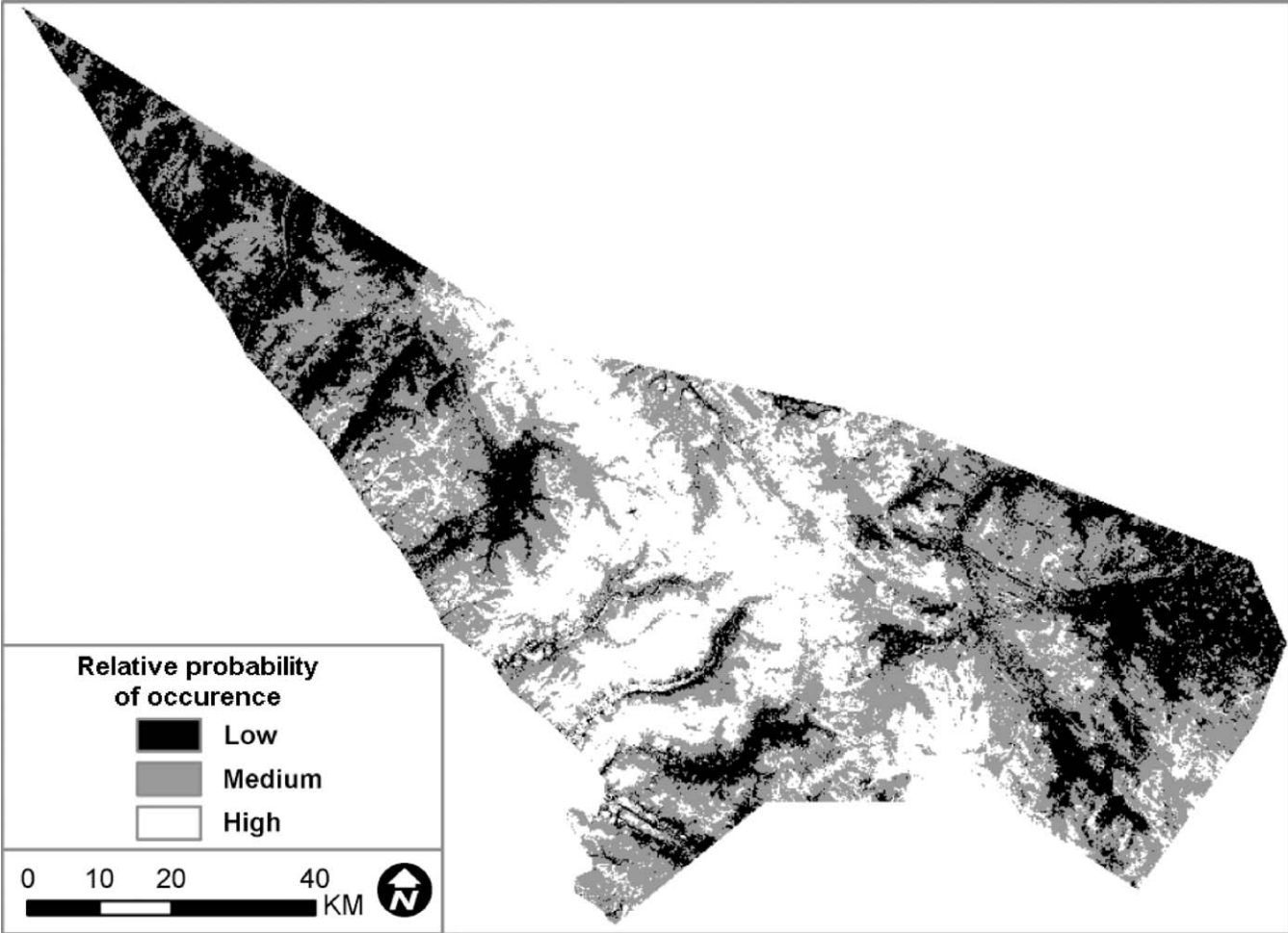


Figure 2. Relative probability of grizzly bear occurrence in the mountain landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003. Lighter areas represent an increased relative probability of use (greater resource selection function values).

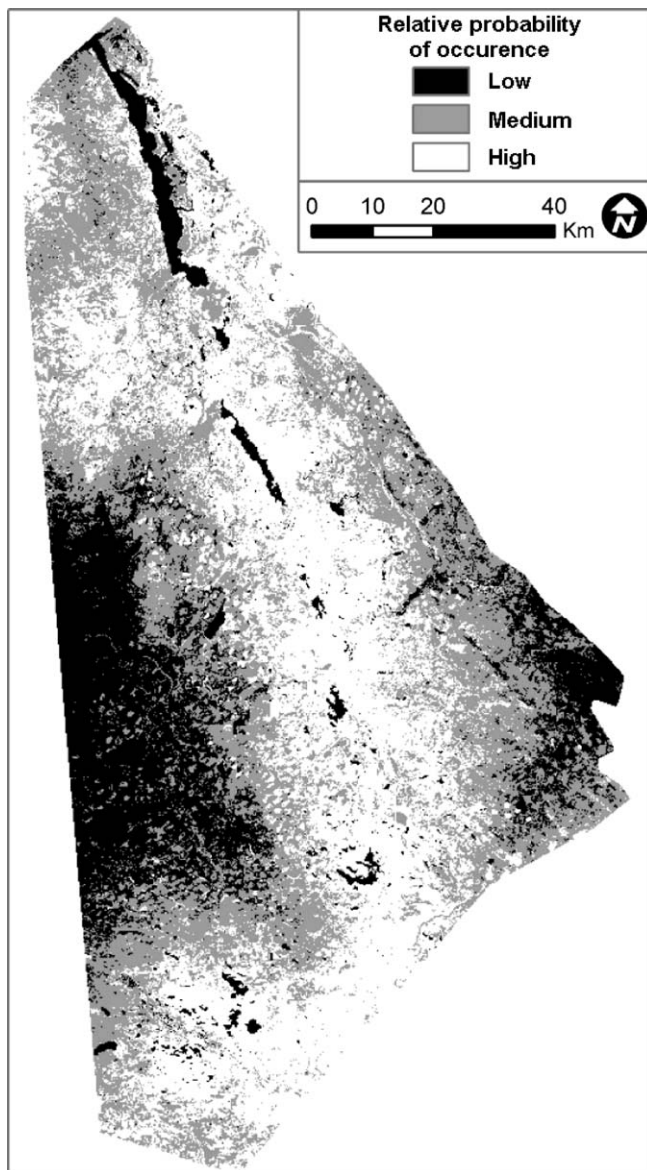


Figure 3. Relative probability of grizzly bear occurrence in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003. Lighter areas represent an increased relative probability of use (greater resource selection function values).

mountains were a greater distance than random from highways and secondary or decommissioned logging roads (Table 2). However, mountain bears used areas closer to primary logging roads. On the plateau, more bears were located closer to the highway than random (Table 3). There was no selection for or against secondary or decommissioned logging roads on the plateau. The lack of detectable selection may have been a product of the high density of these road types in the plateau; the average distance from a secondary road on the plateau was 558 m (\bar{x} [highway] = 13.46 km; \bar{x} [primary] = 3.17 km). Plateau bears avoided primary logging roads (Table 3).

Habitat-Based Density Modeling

In both landscapes there were proportionately more bears in bins with large RSF values (Figs. 4, 5). For an RSF to be

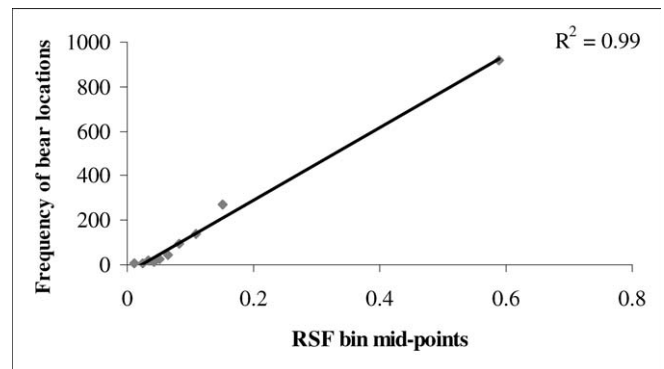


Figure 4. Frequency of the number of grizzly bears in each of the 10 resource selection functions (RSF) score landscape bins for the mountain landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003. We partitioned the mountain landscape into 10 bins of equal area. We applied the frequency of bear use to bins as defined from random locations and we calculated the number of bears in each habitat bin. Resource selection functions values are based on the bin mid-points.

truly proportional to the probability of use the frequency of use should be approximately linear relative to RSF (Johnson et al. 2006), so we used a square-root transformation of $w(\mathbf{x})$ values as the RSF. Even though the mountains and plateau were adjacent, when we recalculated $\sqrt{w(\mathbf{x})}$ values using the mountain model with the plateau data (and vice versa) and then compared those results with the observed $\sqrt{w(\mathbf{x})}$ values obtained using the mountain data and model (and vice versa), we found poor predictive capability between landscapes (Figs. 6, 7). We attribute these patterns to the fact that the available land-cover types, amount of primary and secondary or decommissioned roads, and risk of human-caused bear mortality were dissimilar between areas.

To clarify the role that differences in these covariates played between the mountains and plateau, we examined how grizzly bear density would be expected to change if we applied the observed RSF values in the mountains to the plateau RSF model (Table 4). For the plateau, all predicted densities fell within the confidence interval outlined in

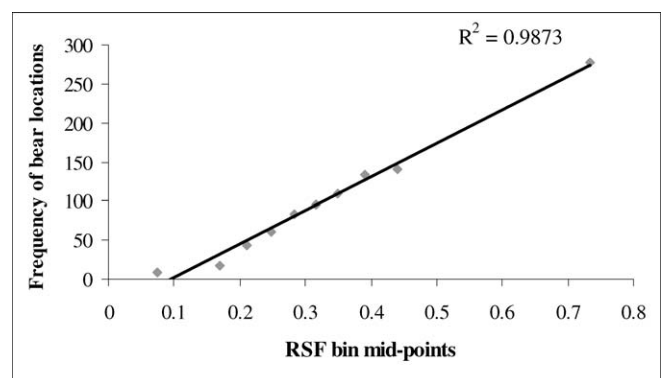


Figure 5. Frequency of the number of grizzly bears in each of the 10 resource selection functions (RSF) score landscape bins for the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003. We partitioned the plateau landscape into 10 bins of equal area. We applied the frequency of bear use to bins as defined from random locations and we calculated the number of bears in each habitat bin. Resource selection functions values are based on the bin mid-points.

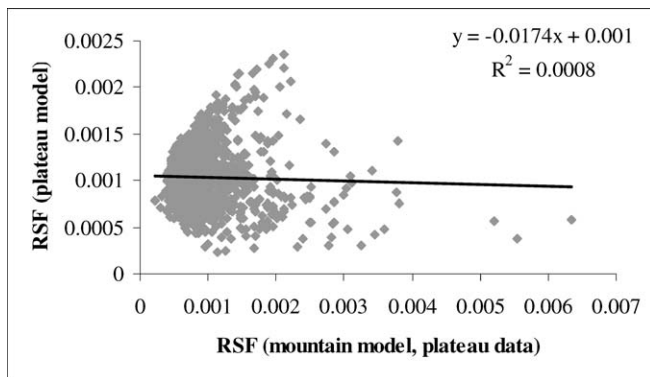


Figure 6. Plot of each resource selection function (RSF) point predicted in the plateau landscape versus the RSF scores predicted using the mountain model with the plateau data for the Parsnip River study area, British Columbia, Canada, 1998–2003. We define the RSF to be $\sqrt{[w(\mathbf{x})]}$ (see eq. 3).

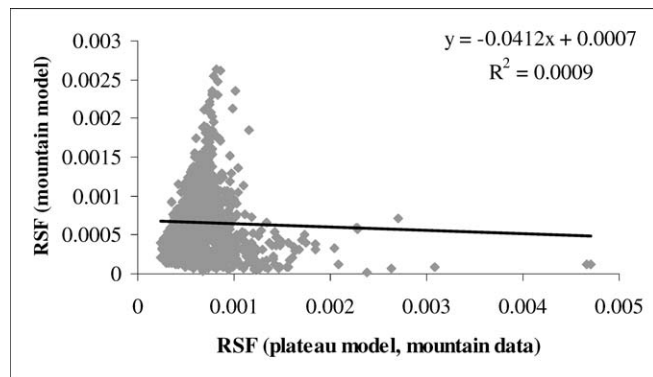


Figure 7. Plot of each resource selection function (RSF) point predicted in the mountain landscape versus the RSF scores predicted using the plateau model with the mountain data for the Parsnip River study area, British Columbia, Canada, 1998–2003. We define the RSF to be $\sqrt{[w(\mathbf{x})]}$ (see eq. 3).

Mowat et al. (2005; Table 4); however, the confidence interval represents a large range in density.

We estimated changes in population size obtained by switching models by comparing our estimated N with the observed N obtained from the DNA mark–recapture estimate adjusted for study area size ($N = 127$). The only predictor variables that predicted a reduced number of bears on the plateau were the available land-cover types. We predicted a decrease of 9 bears on the plateau (i.e., obs N of 127 bears in plateau study area minus predicted land-cover-swap N of 118 bears) when we applied the land-cover data from the mountains into the plateau RSF model. Conversely, the plateau population increased by 34 bears when we took the model coefficients associated with primary and secondary logging roads from the mountain model (i.e., if plateau bears avoided secondary logging roads similar to mountain bears, we would expect 34 more bears on the plateau landscape). If the risk of human-caused mortality was similar to what we observed in the mountains we estimate an increase of 49 bears on the plateau (Table 4). Lastly, we examined the effect of switching the model coefficients for all variables. If bears on the plateau had similar patterns of selection to mountain bears, we expect that the population of bears on the plateau would be 1.75 times higher than the observed population (predicted $N = 223$).

We also performed the analysis in reverse (i.e., using data from the plateau in the mountain RSF model). We predicted a lower density of grizzly bears when the plateau model was applied on the mountain landscape, which were well below the confidence intervals outlined in Mowat et al. (2005; Table 4). We obtained a slightly larger effect by switching the risk of human-caused mortality. We predicted a decrease to 31 bears (4 bears/1,000 km²) if the risk of human-caused mortality was similar to what we observed in the plateau. Similarly, swapping coefficients for primary and secondary or decommissioned logging roads, and available land-cover types provided a predicted N of 34–36 bears (5 bears/1,000 km²). Applying the plateau bear model to the mountain landscape reduced the model-predicted number of

bears in the mountains from the observed 363 bears to 42 bears (Table 4).

DISCUSSION

Our results suggest that the availability of foods does not appear to be limiting the density of bears on the plateau. Our habitat use data supported earlier work using stable isotopes, which revealed that plateau bears ate up to 10 times the amount of meat and or ants as mountain bears (Mowat and Heard 2006), whereas body condition indices showed they were considerably heavier and in better condition (Ciarniello 2006). Because body mass and access to meat has been correlated with increased density in grizzly bear populations (Hilderbrand et al. 1999), we expected the density of bears to be at least as high on the plateau as in the mountains. Instead, compared with other DNA-based population estimates in interior British Columbia, grizzly bear density in the mountains was high (McLellan 1989, Hovey and McLellan 1996), but density on the plateau was low (Mowat and Strobeck 2000) despite the high-calorie foods they consumed.

We suggest that the density of bears was affected by bear selection or avoidance of areas close to open roads and the risk of human-caused mortality rather than differences in habitat. We found no evidence that the 4-fold difference in bear density between the mountains and the plateau could be attributed to differences in the respective land-cover types. Indeed, based on differences in land-cover alone, swapping model coefficients predicted a reduction in the number of bears on the plateau. Because we exchanged coefficients for only the variables in question, this suggests the effect of habitat alone cannot account for the difference in the number of grizzly bears between the mountains and the plateau.

Our model-swapping results point to the importance of roads and associated risk of human-caused mortality on bear density between the mountains and the plateau, although the magnitude of response does not account for the entire 4-fold difference. We do not think that the selection by bears for areas closer to the highway on the plateau was a true road

Table 4. Expected grizzly bear numbers (*N*) and density in the mountain and plateau landscapes when we applied resource selection function model coefficients from the mountains to the plateau landscape and vice versa for the Parsnip River study area, British Columbia, Canada, 1998–2003.

Model covariates (coeff. exchanged)	Exp population density			
	Mountains		Plateau	
	<i>N</i>	Bears/1,000 km ²	<i>N</i>	Bears/1,000 km ²
Model-swapping results				
Land-cover types (true firs, spruce, pine, mixed-wood, and shrubs)	36	5	118	11
Roads (primary and secondary and decommissioned)	34	5	161	15
Risk of human-caused bear mortality (risk layer)	31	4	176	17
Entire model (all model coeff.)	42	6	223	21
DNA mark-recapture estimates ^a				
Obs population size (<i>N</i>)	363	49	127	12
CLs		43–59		7–28

^a From Mowat et al. (2005).

effect but rather a product of heavy bear use of a pipeline and power-line corridor that paralleled the highway. Those corridors were among the first areas to contain new growth in spring, providing good foraging conditions for bears.

We noted that unlike plateau bears, mountain bears primarily foraged in high-elevation open alpine and subalpine bowls in a landscape far less affected by humans. The attraction by mountain bears to high-elevation sites provided a natural separation between bears and humans. Earlier work revealed higher survival and less human-caused mortality of mountain bears (Ciarniello 2006). Few secondary logging roads, decreased logging traffic, distance from centers of human population, and late melting of snow in spring limited human use of even primary logging roads in the mountains, providing a degree of isolation. In the mountains, timber was mostly transported from the block to primary logging roads using helicopters, resulting in less traffic and a less extensive road network than on the plateau. We suggest that the higher relative probability of use near primary logging roads was because mountain bears were at a lower risk of human-caused mortality than plateau bears when foraging adjacent to these roads (Ciarniello 2006). On the plateau, the avoidance of areas near primary logging roads was presumably due to the high volumes of logging truck traffic. Numerous studies have documented avoidance of roads by bears (Mattson et al. 1987, McLellan and Shackleton 1988, Kasworm and Manley 1990, Mace et al. 1996).

Mountain bears avoided secondary or decommissioned-logging roads, whereas plateau bears selected areas closer to those road types. Earlier work showed that human-caused bear mortality was highest closest to secondary or decommissioned logging roads (Ciarniello 2006). We think that the extensive secondary and decommissioned road network (i.e., low-human-use roads) on the plateau, combined with the high risk of human-caused bear mortality in these areas (Ciarniello 2006), made the backcountry of the plateau an attractive sink (Delibes et al. 2001) or ecological trap (Schlaepfer et al. 2002, Nielsen et al. 2006, Robertson and Hutto 2006). We found that bears that lived on the plateau relied on foods found in early seral stands, particularly forbs, moose, ants, and berries. During the last 50 years since fire

suppression was implemented, logging has created the majority of early seral stands on the plateau. In the RSF analysis, selection for early seral stands was reflected in part by the selection for higher greenness scores and open canopies. The regenerating vegetation in cutblocks had high greenness scores, and bears were attracted to those areas.

Predictable or low levels of human use in spite of adverse consequences may allow bears to habituate (Herrero 1985, Jope 1985, McLellan and Shackleton 1989, Mace et al. 1996). In our study area, human use of the secondary or decommissioned road network appeared to be low except during the autumn hunting season. During spring, those roads were difficult to travel due to snow and surface mud, and during summer most people remained close to primary logging roads for camping or berry picking. However, during the autumn hunters in search of ungulates often used difficult-to-access backcountry roads on the plateau. Therefore, although RSF models predicted a high relative probability of occurrence in early seral areas, and forestry operations provided attractive early seral stage habitats for bears, they also have been responsible for an increased number of open roads on the landscape, which, in turn, has led to increased human access, contact with bears, and human-caused bear mortality (Ciarniello 2006).

Due to hypothesized opposite effects of roads, applying model coefficients from the plateau RSF to the mountain landscape predicted a decline in mountain bears. As timber-harvesting activities move further into the mountains, mountain bears will be subjected to more of the risks operating on the plateau landscape. We predict a decline in the number of mountain bears if human access is not properly managed and if mountain bears continue to use the landscape as modelled (e.g., selecting for closer distances to primary logging roads). The predicted decline in the number of mountain bears might in part be attributed to their not having learned cues necessary to survive in a high human-caused mortality-risk landscape (Schlaepfer et al. 2002, Nielsen et al. 2006).

Our results suggest that areas that are attractive to bears as predicted by RSF models could act as attractive sinks. We agree with Johnson et al. (2004:249) that if such patterns in mortality are not recognized conservation initiatives may be

“harmful” to population persistence. For example, if we had not previously examined the type and location of mortalities (Ciarniello 2006), we might have improperly interpreted model results by suggesting that increasing the number of roads (e.g., highways on the plateau or primary logging roads in the mountains) on the landscape would result in an increase in grizzly bears. However, if caution is applied during extrapolations, proper application of the link between habitat and density provides a useful tool for examining and quantifying the effects of human activities on grizzly bears.

We suggest that the decrease in density of mountain grizzly bears predicted by the plateau RSF model was also likely due to extrapolation to a landscape with a different suite of available resources regardless of similar underlying selection patterns by bears (Figs. 4, 5). Our results suggest caution when applying RSF results to different areas even though bears in both landscapes had comparable selection for variables that influence food availability in northern environments (i.e., SW-aspect hillshade values, open canopies, and higher greenness scores). Unlike Manly et al. (2002:187) where the presence of galaxiid fish were predicted “very well” at sites where trout were present, we predicted markedly different RSF models in our adjacent areas (Figs. 6, 7), even though both of our models had excellent internal predictive capability and were proportional to the probability of use. Such extrapolations have been completed for grizzly bears in the Bitterroot Mountains of Idaho and Montana, USA, where it was thought that bear densities could be predicted because the RSF models were from landscapes assumed to contain similar available resources (Boyce and Waller 2003). From our results, we suggest that extrapolation of RSF models into areas with a different suite of available resources may be misleading. For example, we had to omit a highly used land-cover type (i.e., alpine) by mountain bears when using the plateau model to predict the number of grizzly bears in the mountains, which likely underestimated mountain-bear density. We likely would have predicted a higher number of bears for the mountain landscape had grizzly bears on the plateau used alpine areas and had we been able to estimate the alpine beta coefficient.

The results of the habitat-based density modeling suggest that simply providing habitat is not enough to sustain grizzly bear populations at their current numbers. We predict that if our current system of forestry management continues, and logging roads remain accessible to the public after the timber has been extracted, the number of bears will decline. We suggest that for grizzly bears to remain viable outside of protected areas, we must maintain places secure from the risk of human-caused bear mortality across each landscape.

MANAGEMENT IMPLICATIONS

The opposite road coefficients and their effect on grizzly bear density suggest that emphasis should be placed on both the level and type of human use on roads rather than road networks. Access management plans should focus on reducing active road density. We suggest using indirect

techniques such as removal of a bridge prohibiting human access past the obstruction to influence the extent and location of human impacts. We also suggest placing core secure areas throughout working forests where regeneration of blocks is encouraged to promote early seral bear foods and human access is restricted. For example, we suggest leaving debris in blocks and on roadways to increase opportunities for bears to forage on ants while restricting human access. Similarly, allowing natural regeneration promotes berry-producing shrubs, whereas planting alder (*Alnus* spp.) on roadways restricts motorized access.

ACKNOWLEDGMENTS

Forest Renewal British Columbia, and the Forest Investment Accounts, through Canadian Forest Products Ltd., and the Pas Lumber, provided funding for the Parsnip Grizzly Bear Project. Slocan Forest Product Ltd., British Columbia Ministry of Water Land and Air Protection, British Columbia Ministry of Forests, and the McGregor Model Forest Association provided additional project support. L. Ciarniello received graduate support from the Natural Science and Engineering Research Council of Canada, the Province of Alberta Fellowship, and the University of Alberta. We thank J. Swenson, A. Derocher, C. Cassady St. Clair, and F. Schmiegelow for comments on the manuscript. The success of this project was possible due to field assistance provided by J. Paczkowski, E. Jones, G. Watts, I. Ross, C. Mamo, D. A. Bears, and numerous volunteers. H. Beyer provided GIS expertise. M. Woods and P. Hengeveld of the Peace-Williston Compensation Program allowed us to monitor some of their study animals. Comments provided by the Associate Editor and 2 anonymous reviewers improved this manuscript.

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Associate Editor: McCorquodale.