Denning behavior and den site selection of grizzly bears along the Parsnip River, British Columbia, Canada

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Abstract: The Parsnip River area in British Columbia (BC), Canada, provides important habitat for grizzly bears (*Ursus arctos*). This area contains 2 adjacent topographic regions: (1) a relatively pristine portion of the Hart Ranges of the Canadian Rocky Mountains, and (2) a plateau on which timber harvests have occurred. Increasing human modification of both landscapes may affect the quality of grizzly bear habitat. Therefore, we examined denning behavior and den-site selection of grizzly bears in this area based on data from 61 grizzly bears radiocollared between 1997 and 2002 (34 plateau, 27 mountain bears). Adult females residing in the mountainous landscape arrived earlier to their denning areas (14 Oct versus 26 Oct), entered dens earlier (23 Oct versus 9 Nov), and emerged later (11 May versus 24 Apr) than plateau females, spending on average 36 days longer in their dens (200 days versus 164 days). Dens used in consecutive years by mountain females tended to be closer to one another ($\bar{x}$ = 2.4 km) than those of plateau females ($\bar{x}$ = 5.1 km). Dens in the mountains were excavations into sloping ground (74%), or natural caves (26%), using rocks as the primary stabilizing structure (47%). Resource selection functions (RSF) revealed that mountain grizzly bears selected dens in alpine habitats at mid-to-upper elevations. Plateau bears mainly excavated dens under the base of trees (90%), where roots stabilized material (80%). These dens primarily were located in older-aged forest stands ranging from 45–99 years (40%) or >100 years (50%); RSFs further revealed that grizzly bears on the plateau selected stands with tall trees. Plateau dens also were located away from roads, possibly because of less disturbance and because older trees were farther from roads.

Key words: British Columbia, den site, fidelity, grizzly bear, modeling, radiotelemetry, resource selection functions, selection, timber harvest, *Ursus arctos*

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Grizzly bears (*Ursus arctos*) inhabiting northern latitudes may spend 5 to 6.5 months each year in a den (Vroom et al. 1980, Judd et al. 1986, Van Daele et al. 1990, Friebe et al. 2001, Seryodkin et al. 2003). During denning, bears do not eat, urinate, or defecate and must rely on fat reserves attained during the non-denning period (Hellgren 1998). Dens are constructed or selected to provide thermal insulation (Vroom et al. 1980) and security cover (Seryodkin et al. 2003) for denning bears and birthing sites for pregnant females (Swenson et al. 1997). Understanding the den site requirements of grizzly bears is fundamental in a landscape that is subject to increasing modification. Resource extraction activities may remove denning habitats and facilitate human access and disturbance through road construction. Disturbance of hibernating grizzly bears has been documented to reduce reproductive success of pregnant females (Swenson et al. 1997), and den abandonment has been linked to a greater probability of death for dependent offspring (cubs and yearlings; Linnell et al. 2000). If we understand what den structures bears select, resource managers can better manage for those features when developing sustainable forest harvest plans.

Grizzly bear den site selection varies by region (Vroom et al. 1980). The denning ecology of grizzly bears in the arctic watershed of central British Columbia (BC) has not

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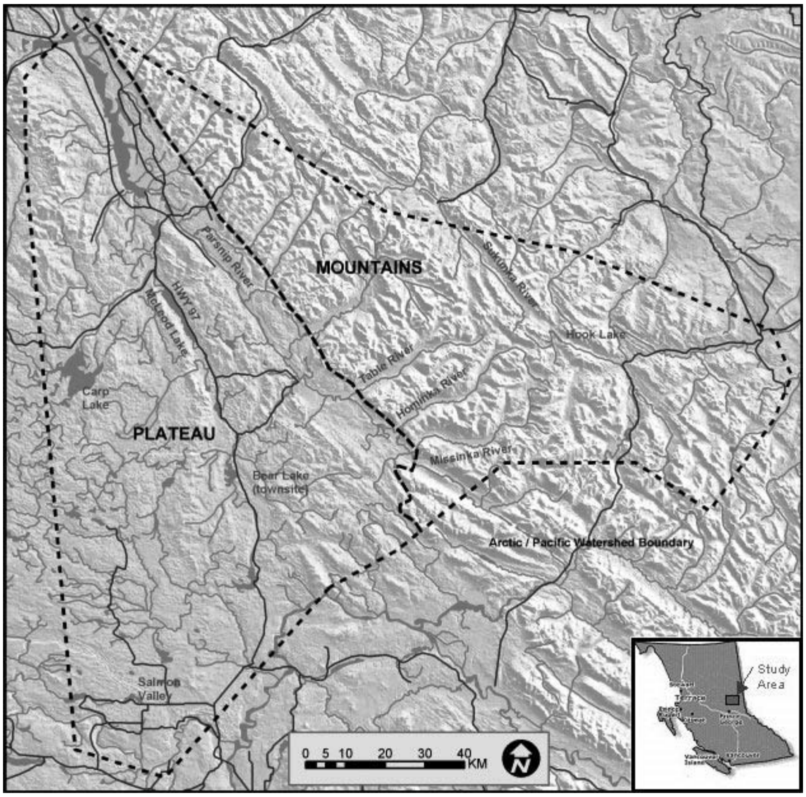

Fig. 1. Study area to determine denning habitat of grizzly bears in mountain and plateau areas, British Columbia, Canada, 1998–2003.

been studied previously. This area contains mountain and plateau landscapes, and it is believed that grizzly bears in the area may behave similarly to other interior BC bears by denning within mountain habitat, traveling to plateau or flatland areas upon den emergence, and moving back to the mountains during berry season, where they remain to den (McLellan and Hovey 2001). We investigated whether grizzly bears inhabiting the plateau landscape in central BC exhibited a different pattern of den site selection, timing of den entry and exit, and denning structures compared with those inhabiting the mountainous landscape.

Study area

The study site, approximately 18,100 km^2, was contained within a 'working forest' in central-eastern British Columbia (54°39′N, 122°36′W) and was delineated by using a composite minimum convex polygon (MCP) of bear locations collected during the study, omitting 8 outlier locations on the western boundary (Fig. 1). The Hart Range of the Central Canadian Rocky Mountains comprised 7,472 km^2 of the study area. The mountainous landscape was relatively pristine, although most low-elevation valleys contained logged areas of varying sizes. Unlike other areas of the Rocky Mountains, most of the landscape in the Hart Range was largely open alpine–parkland habitat. The highest peak was 2,500 m, and $<1\%$ of the area contained glacial rock and ice. Mountain valleys consisted of subalpine fir (*Abies lasiocarpa*) and spruce (*Picea glauca* × *P. engelmannii*) with less lodgepole pine (*Pinus contorta*) than the plateau. The proportion of subalpine fir became progressively greater with increasing elevation. The area above treeline was primarily alpine parkland and typically consisted of small shrubs or krummholz form trees, shrub–forb–sedge (*Carex* spp.) meadows, and wide avalanche chutes.

The rolling hills and flat valleys of the plateau comprised 10,624 km^2 and have been used for timber harvest since about 1960. In the wetter portion east of Highway 97, the old growth forests of the plateau were comprised of white spruce (*P. glauca*) and spruce–fir (*A. lasiocarpa*) associations. There also were small remnants of Douglas-fir (*Pseudotsuga menziesii*) on southern aspects with coarse soils. In the drier area west of Highway 97, climax forests were largely lodgepole pine. Only small patches of high-elevation, subalpine fir occurred on the plateau. The plateau was warmer and drier than the mountains with a mean annual temperature of 2.6°C and 72 cm of rainfall compared with the mountains (0.3°C and 154 cm of rainfall; DeLong et al. 1993, 1994). The mountains also received over twice the mean annual snowfall (700 cm) than the plateau (300 cm; DeLong et al. 1993, 1994).

Methods

Radiotelemetry

From August 1997 to fall 2002, 61 bears were captured (27 mountains, 34 plateau; 22 males, 39 females) using aerial darting, leg snares, or culvert traps. Twenty-five bears were fitted with collars equipped with a global positioning system (GPS; Televilt, Lindesberg, Sweden), whereas 36 received VHF (very high frequency) collars (Lotek, Newmarket, Ontario, Canada). Bear ages were estimated using cementum annuli of an upper premolar (Matson's Laboratory, Milltown, Montana, USA). Female bears were classified into 4 categories based on age and reproductive status: (1) females that entered the den pregnant and emerged from denning with cubs of the year (cubs, hereafter), (2) females with young that entered the den with offspring passing their first through fourth birth date while denned, (3) lone females $\geq$4 years of age and not in the company of offspring (presumably not pregnant on den entry), and (4) subadult females $\leq$3 years of age and not in the company of their mother. Female categorization followed Friebe et al. (2001); however, we used $\geq$4 years as our age of transition from subadult to adult rather than 3 years. We classified age based on site-specific knowledge of reproduction (e.g., 2 4-year-old females produced cubs whereas 2 other 4-year-olds denned with their mother) and independence of young from their mothers. Males were classified as subadult ($\leq$3) or adult ($\geq$4 years).

Bears were monitored from April to December using aerial VHF and GPS telemetry to determine timing of den entry and exit and the habitat characteristics of den sites. Dens were relocated and verified by helicopter in late February. Universal Transverse Mercator (UTM) coordinates were obtained using a hand-held 12-channel GPS unit (average horizontal displacement error = 5 m). We sampled the habitat characteristics for the exact den location (single pixel).

Duration of denning

Arrival at the denning area in fall was defined as when bears moved to $\leq$1 km of that winters' den site. The arrival date was calculated as the mid-point between the date bears were first located at the den site and the date of the prior location (Van Daele et al. 1990, Davis 1996, Friebe et al. 2001). If the prior location was $>$14 days earlier, we did not calculate a den area arrival date (Haroldson et al. 2002). We used 14 days between flights because it allowed for a break during volatile weather conditions, which occurred frequently during late fall and early spring.

Den entry dates were calculated as the mid-point between the date when no fresh sign of bear activity was visible at the den site (Judd et al. 1986) and the date of the previous location. Den emergence date was calculated as the mid-point between the date of first evidence of bear activity and the date of the previous location with no bear sign if that location was $\leq$14 days (Haroldson et al. 2002). The number of days between the den entry and emergence dates was the denning duration.

Where applicable, dates recorded by the GPS-collars were used. GPS locations were taken sufficiently frequently (4–6 per day or 4 every other day) that the specific dates of bear arrival in the den area, denning, and emergence could be determined. Statistical comparisons between denning duration and distance between consecutive den sites for the mountains and plateau were calculated using the Mann-Whitney *U*-test. Analysis of variance (ANOVA) was used to determine whether bear denning differed by reproductive status, age, or location.

Den investigations

After bears exited dens we visited den sites to record den type (excavated, cave, nest) and stabilizing material (root mass, rock, soil). Sites were accessed using a helicopter as well as ground transportation to reduce bias associated with sampling bears that denned close to roads. We used the ground investigations to gain an understanding of fine-scale attributes associated with den sites that cannot be obtained from the geographic information system (GIS) database. The GIS databases were designed to depict attributes important to commercial logging operations, which were not necessarily attributes most biologically relevant to bears.

GIS data

Digital elevation maps (DEM) were built from terrain resources inventory maps (TRIM2; BC Ministry of Water, Land, and Air Protection, Victoria, Canada) and were used to obtain elevation, slope, and aspect for bear den sites and random locations. Forest cover maps (FCM) and road networks were obtained from the BC Ministry of Forests, Canadian Forest Products (Canfor) East, Canfor West, the Pas Lumber, and Slocan Forest Products Limited in Prince George, British Columbia, Canada. These map layers were used to obtain land-cover type, stand age, and distance to roads. All raster layers (DEM, slope, aspect, hillshade, distance to roads, forest age) had a resolution (pixel size) of 25 m.

Land-cover types. Locations that occurred within forested polygons were categorically classified using the leading tree species (mixed wood, true firs, Douglas-fir, spruce, or pine). Locations that occurred in non-forested polygons were classified into alpine, shrub, swamp, meadow, rock–bare ground, or anthropogenic categories based on the vegetation described in the forest cover database.

Stand age and related classifications. Forest cover maps provided ages for all commercial forest types, which we classified into 3 categories: early seral (<45 years), young forest (46–99 years), and old forest (≥100 years). Early seral comprised herb and shrub–herb stages with an open coniferous canopy that facilitated vigorous growth in the understory. Young forests generally were dense, closed canopy coniferous forests with reduced understory, whereas old forests were self-thinning with canopy gaps that facilitated vigorous understory growth (BC Ministry of Forests 1998).

We were limited by the GIS database because habitats of non-commercial value (i.e., alpine, meadows, swamps, and urban) did not contain age information. Therefore, if an age class was not assigned we examined the non-productive and non-commercial descriptors to gain information regarding those land-cover types. From those descriptors, we classified shrub, meadow, non-commercial brush, non-productive brush, and swamps into the early seral age class. We considered alpine as a unique age class due to its unique dynamic features. In the plateau, settlements and some agricultural areas were classified in the GIS database as urban. However, in the mountains some forests and right-of-ways surrounding the railway and mines also were classified as urban because they were not available to be harvested, distinguishing those areas from the urban areas on the plateau. Therefore, we added an anthropogenic (human influence) category to distinguish these areas from the urban land-cover classes.

Forest height. Forest height in meters was highly correlated with stand age, so these variables could not be used in the same model.

Hillshade. Hillshade measured solar insulation as it varied with topography. Hillshade was estimated by a combination of slope and aspect data from the DEM, which was used to estimate the average amount of shade during the course of the year at any pixel. Warm southwest facing (225°) slopes of 45° received the greatest hillshade values, whereas cooler northeastern slopes corresponded to the lowest hillshade values.

Distance to the nearest road. Road network data from FCM, TRIM, Canfor East, Canfor West, the Pas Lumber, and Slocan Forests Products Limited were combined and used to determine the Euclidean distance to the nearest road. The majority of roads within the study area were logging roads, but a 2-lane paved highway bisected the plateau.

Resource selection functions

Because den sites have little or no variation (that is, there are single or few observations for each animal) we used a special case of Design I studies (Manly et al. 1993:7, Manly et al. 2002). In our design, individual animals were identified and attributes of resource units such as den sites were quantified. Because the entire study area contained grizzly bears and a few radiocollared animals traveled between the 2 landscapes, we assumed that bears were free to explore either mountain or plateau landscapes. Thus, availability was measured for each landscape at the population level (Manly et al. 1993, 2002) by generating random locations using Hawth's Tools (Beyer 2004) for ArcGIS® 8.3 (Environmental Systems Research Institute, Redlands, California, USA) at 1 location/km^2 (7,472 in mountains and 10,624 in plateau). Characteristics of the den site and random locations were compared assuming the following log-linear model:

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

where the $\beta_i s$ are selection coefficients for a vector $\mathbf{x}$ of covariates (habitat and terrain variables), x_i, for $i = 1, 2, \ldots p$, estimated using logistic regression. We assumed that habitat availability was fairly static among years, so we pooled the data. Models were estimated using Stata 7.0 (Stata Corporation, College Station, Texas, USA).

By definition, RSF is proportional to the probability of use of a resource unit and, as such, the intercept, β_0, is not used (Manly et al. 1993, 2002). To construct the likelihood, we conditioned on the realized samples and computed the relative probability of being used and a value proportional to the probability that the unit is in the available sample, given a unit is in the tested or available sample, respectively. Therefore, from the way the likelihood is constructed, a small number of used samples compared with a large number of random samples does not present a problem. Non-intercept coefficients and standard errors are not affected because

Table 1. Median fall arrival date to <1 km of a known den site location, median den entry date, and median emergence date for grizzly bears in the mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada (1998–2003). Den emergence dates were not calculated for bears that emerged before the first survey flight in any given year.

		Den arrival		Den entry		Den emergence			
Landscape	Group	Median	*n*	Median	*n*	Median	Range	*n*	Number of bears emerged prior to 1st spring flight
Mountain	females	14 Oct	25	23 Oct	28	11 May	27 Apr–27 May	32	6 (5 >27 Apr and 1 >30 Apr)
	males	8 Nov	2	23 Nov	2	5 May	24 Apr–18 May	3	2 (1 >13 Apr and 1 >27 Apr)
	migrators[a]	10 Nov	2	23 Nov	2	8 Apr		1	1 (>13 Apr)
	subadults	21 Oct	1		0	28 May		1	0
Plateau	females	26 Oct	16	9 Nov	17	24 Apr	4 Apr–1 May	10	7 (5 >27 Apr and 2 >30 Apr)
	males		0		0	27 Apr		1	0
	subadults	14 Nov	8	20 Nov	7	15 Apr	8–24 Apr	3	0

[a]Migrators were bears that lived primarily on the plateau but denned in the mountains.

they stabilize after a sufficient number of available locations are included (T. McDonald, Western EcoSystems Technology, Cheyenne, Wyoming, USA, personal communication, 2004). In this design we could not estimate the sampling fractions.

We followed the information theoretic approach of Burnham and Anderson (1998) and Anderson et al. (2000) and determined a set of candidate models that we deemed biologically relevant. Final model selection was based on Akaike information criteria difference for small samples (AIC_c; Burnham and Anderson 1998); the model with the lowest AIC_c score represents the most parsimonious model. The probability that candidate models are the best models is provided by the normalized Akaike weights (AIC_{cw}) (Anderson et al. 2000). Significant coefficients were those whose 95% confidence intervals did not include 0. The parameter estimates of the highest-ranked model were used to calculate and map the relative probability of occurrence of grizzly bear dens across the study area. We used 5-fold cross validation to assess the predictive capability of the top-ranked model (Boyce et al. 2002). For each of the 5 iterations, 20% of the data were retained and the frequency of these test data were compared against predictions from models constructed using the remaining 80% within 10 RSF bins (Boyce et al. 2002). We used Spearman's rank correlation to test whether the number of locations increased in bins with greater RSF scores as a measure of the predictive capability of the model.

Results

We located 86 den sites (68 female, 9 male, 9 unidentified). Seventy-seven dens were used by 41 radiocollared bears (34 females, 7 males). The 9 animals of unidentified gender were associated with den sites we encountered incidentally. Den sites of 19 radiocollared bears (18 females, 1 male, 55 den sites) were used for >1 year.

Twenty-nine (33.7%) and 57 (72.3%) of the den sites occurred in the plateau and mountain portions of the study area, respectively. On the plateau, female bears ($n = 16$) occupied 24 dens; males ($n = 2$) used 2 dens. Sibling pairs (male–male, male–unknown, and female–female) occupied the remaining 3 plateau den sites. In the mountainous landscape, female bears ($n = 17$) occupied 42 dens; males ($n = 4$) used 6 dens. The 9 dens encountered incidentally were all in the mountains. Average age of bears denning on the plateau was 7.5 years ($n = 28$, range 1–22) compared with 12.0 years ($n = 48$, range 3–20) for bears denning in the mountains.

Timing of denning events

Den area arrival and entry. Female bears in the mountains arrived at their den areas on 14 October, 12 days earlier than plateau bears (26 Oct); subadults arrived 24 days earlier (14 Nov; Table 1). The 2 bears that moved from the plateau to the mountains had similar arrival dates to plateau bears (10 Nov).

Female bears in the mountains spent an average of 10 days in the vicinity of their den sites prior to denning ($n = 20$), with a mean entry date of 23 October ($n = 28$). Female bears that lived on the plateau spent 11 days ($n = 15$) at their den sites prior to denning and entered their dens 17 days later than mountain females (9 Nov, $n = 17$). Subadult bears on the plateau averaged 10 days ($n = 7$) at their den sites prior to denning. The 2 male bears in the mountains used the den area an average of 14 days prior to denning.

Den emergence. We determined only a mean den emergence date for female plateau bears for 2 of the 5 years. Conservatively, the mean date of emergence for

Table 2. Mean denning duration for grizzly bears in the mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada, 1998–2003. Differences were calculated in days between the same groups in each landscape. Approximate number of months spent in the den sites was calculated using an average 30 days per month.

	Mountain				Plateau				
Group	Denning duration	Range	*n*	Months	Denning duration	Range	*n*	Months	Difference (days)
All adult females	200	136–221	22	6.7	164	141–186	10	5.5	36
Pregnant females	206	191–221	6	6.8	177	169–186	3	5.9	29
Females with young	193	136–207	7	6.4	165	141–184	3	5.5	28
Females with young (minus plateau migrators[a])	202	194–207	6	6.7	165	141–184	3	5.5	37[b]
Lone females	202	193–220	9	6.7	154	146–159	4	5.1	48
Male	152	n/a	1	5.1	n/a	n/a	0	n/a	n/a
Subadults	n/a	n/a	0	n/a	153	139–166	3	5.1	n/a

[a]Migrators were bears that lived primarily on the plateau but traveled to the mountains to den.
[b]Thirty-seven days represents the difference between resident mountain bears with young versus resident plateau bears with young.

bears that lived on the plateau was 24 April (range 4 Apr to 1 May), whereas bears that lived in the mountains emerged 11 May (range 27 Apr to 27 May; Table 1). The bears that moved from the plateau to the mountains to den had emergence dates more similar to plateau bears (8 Apr).

Mountain females averaged 8.5 days $\leq$1 km from their den sites after emergence ($n = 33$, range 0–29 days), whereas plateau females averaged 6 days ($n=11$ females, range 0–11 days). By group, mountain females with cubs averaged 11 days ($n=9$) within 1 km of their den site, whereas plateau females with cubs averaged 8 days ($n=3$). Mountain females with young averaged 10.5 days ($n=9$) within 1 km of the den compared with 6 days for plateau females with young ($n = 3$); lone mountain females averaged 6 days ($n=15$) and lone plateau females averaged 5 days ($n=5$). We only had data on 1 plateau male that remained within 1 km of his den site for 3 days after emergence, whereas males that lived in the mountains averaged 6 days ($n=4$, range $=$ 3–10 days).

Duration of denning. Adult female bears that lived in the mountains spent >1 month longer in their dens than those that lived on the plateau (Table 2). Denning duration varied by landscape (n [plateau] $=10$, n [mountain] $=22$; $P < 0.001$) but not by year (n [plateau] $= 10$ $P = 0.068$, n [mountain] $= 22$; n [year] $= 5$; $P = 0.321$). Pregnant females on the plateau had a longer denning duration than lone females (n [plateau pregnant] $= 3$; n [plateau lone] $=4$; $P=0.025$; n [mountain pregnant] $=6$; n [mountain lone] $= 9$; $P = 0.443$). In both landscapes, there was no statistical difference in denning duration between pregnant females and females with young, although pregnant females spent 12 (plateau) and 13 (mountains) days longer in their den sites. Male bears and subadults had the shortest duration of denning (Table 2). ANOVA revealed that neither age ($F = 1.245$, 10,11 df, $P=0.279$) nor reproductive status ($F=1.304$, 2,19 df, $P=0.296$) was associated with denning duration for mountain females. However, when considered together, both age ($F=4.984$; 9,1 df, $P=0.045$) and reproductive status ($F=6.823$, 2,8 df, $P=0.035$) influenced denning duration for plateau bears. On 22 occasions bears emerged before the first spring flight (13 plateau and 9 mountain bears).

Table 3. Type of den and den re-use for 39 den sites used by grizzly bears in the mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada, 1998–2003.

	Mountains				Plateau			
Den type	Dens	%	Dens re-used	%	Dens	%	Dens re-used	%
Excavated	14	74	3	27	17	85	1	6
Excavated rock	0				1	5	1	100
Natural cave	5	26	5	100	0			
Tree cavity	0				1	5	1	100
Ground nest	0				1	5	0	
Unknown	0		3		0			
Total	19	100	8	42	20	100	3	15

Den area fidelity

Only 2 bears (1 female with young, 1 male) moved outside their core home range to den. Both bears lived primarily on the plateau, denned in the mountains, and returned to the plateau the subsequent spring.

For 19 bears (12 mountain, 7 plateau), we had den locations for >1 consecutive year. The mean distance

Table 4. Forest age at 39 den sites used by grizzly bears in the mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada, 1998–2003.

	Mountains				Plateau			
Den type	Alpine	>100	45–99 yr	≤45 yr	Alpine	>100	45–99 yr	≤45 yr
Excavated	10	4				8	8	1
Excavated rock						1		
Natural cave	4	1						
Tree cavity						1		
Ground nest								1
Mean (%)	74	26	0	0	0	50	40	10

between subsequently used den sites was 2.4 km for mountain females ($n = 11$ bears, $n = 36$ dens, SE $= 0.45$ km, range $= 0$–9 km) and 5.1 km for plateau females ($n = 7$ bears, $n = 16$ dens, SE $= 1.4$ km, range $= 1.2$–11.7 km; $n = 32$; $P = 0.068$). One 3-year-old male in the mountain area had den locations 12 and 44 km apart, respectively.

Types of den structures

We visited 39 of the 86 den sites (45%): 19 mountain den sites (33%) and 20 plateau sites (69%). Most dens were excavated into the sides of slopes (74% mountains, 90% plateau; Table 3). In the mountains, bears also used natural caves for den sites (5%). Natural cave sites likely were underrepresented in the mountains because many were on slopes too steep to safely access. We did not find any natural caves on the plateau, although 1 excavated den site had rocks as the stabilizing material, forming a durable, cave-like structure.

Rocks (47%, $n = 9$) were the primary stabilizing structure for dens in the mountains, followed by roots (37%, $n = 7$), a combination of roots and rocks (11%, $n = 2$), and roots, rocks, and clay soil (5%, $n = 1$). Roots (80%, $n = 16$) were the primary stabilizing material for dens on the plateau, followed by no stabilizing material (10%, $n = 2$), rock (5%, $n = 1$), and root and soil combination (5%, $n = 1$).

Forest stand structure at investigated den sites

Investigated dens in the mountains were primarily located in the alpine ($n = 14$, 74%), followed by the upper reaches of the Engelmann spruce–subalpine fir habitat ($n = 5$, 26%) (Table 4). Only small patches of alpine habitat existed on the plateau. Ninety percent of den sites investigated on the plateau were in forest stands ≥45 years, with 50% occurring in stands >100 years of age (Table 4). All forest stands contained tall trees. We also noted that the 2 dens in early seral stands were located under the roots of large stumps or deciduous trees that remained in the stand.

Den re-use

Eleven of the 36 (30.5%) dens for which a determination could be made showed signs of previous use, whereas 25 (69%) dens were made during the year of investigation (Table 3). Re-use for 3 sites was undetermined because the chamber or tunnel had largely

Table 5. Resource selection function (RSF) candidate models indicating the relative probability of grizzly bear den site ($n = 57$) occurrence in the mountain landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003. Model 1, with the lowest AIC$_c$ score, represents the best model based on the combination of precision and parsimony.

Rank	Variables	Coefficient	SE	95%CI	AIC$_c$	ΔAIC$_c$	AIC$_c$*w*
Model 1	alpine	5.216	1.472	2.330–8.101	588.12	0.00	0.38
	true firs	1.513	0.770	0.004–3.021			
	hillshade	0.006	0.007	−0.007–0.020			
	alpine × hillshade	−0.012	0.007	−0.026–0.003			
Model 2	alpine	3.248	0.727	1.824–4.672	588.52	0.40	0.31
	true firs	1.509	0.769	0.002–3.017			
	hillshade	−0.004	0.002	−0.008–$-6.6E^{-05}$			
Model 3	forest height	−0.135	0.024	−0.183–−0.087	589.63	1.52	0.18
	elevation	0.036	0.010	0.016–0.056			
	elevation squared	$-1.2E^{-05}$	$3.45E^{-06}$	$-1.9E^{-05}$–$-5.65E^{-06}$			
Model 4	alpine	3.350	0.724	1.932–4.769	590.07	1.95	0.14
	true firs	1.520	0.769	0.012–3.028			
Model 5	alpine	3.245	0.732	1.811–4.679	591.44	3.32	0.07
	true firs	1.482	0.770	−0.027–2.992			
	distance to nearest road	$3.85E^{-05}$	$3.86E^{-05}$	$-3.7E^{-05}$–$1.14E^{-04}$			

Table 6. Resource selection function (RSF) candidate models indicating the relative probability of grizzly bear den site (n = 29) occurrence in the plateau landscape of the Parsnip River study area, British Columbia, Canada, 1998–2003. Model 1, with the lowest AIC_c score, represents the best model based on the combination of precision and parsimony.

Rank	Variables	Coefficient	SE	95%CI	AIC_c	ΔAIC_c	$AIC_c w$
Model 1	forest height	0.051	0.020	0.012–0.090	396.33	0.00	0.35
	hillshade	−0.015	0.008	−0.031–3.77E^{-04}			
Model 2	forest height	0.053	0.020	0.013–0.093	396.73	0.40	0.29
	elevation	0.002	0.001	−1.89E^{-04}–0.004			
Model 3	forest height	0.051	0.020	0.012–0.089	397.04	0.71	0.25
Model 4	forest height × distance to nearest road	1.86E^{-05}	6.18E^{-06}	6.51E^{-06}–3.07E^{-05}	398.66	2.33	0.11
Model 5	mixed wood	0.460	0.764	−1.038–1.958	407.46	11.13	0.00
	true firs	1.050	0.708	−0.337–2.438			
	spruce	1.206	0.556	0.115–2.296			
	douglas-fir	1.852	1.122	−0.348–4.051			

collapsed. Den re-use in the mountains was 50% ($n = 8/16$), compared with 15% ($n = 3/20$) on the plateau. All dens with durable or permanent structures ($n = 7$; caves, tree cavity, excavated rock) were used by grizzly bears during >1 winter. Re-use of excavated dens was much less likely. Only 2 bears re-used a den they were known to have used before.

Resource selection analysis

We present 5 of 10 ecologically plausible RSF models examining the relative probability of grizzly bear den site occurrence by landscape (Tables 5, 6). Alpine and true firs (Engelmann spruce and sub-alpine fir) were the best predictors of grizzly bear den site occurrence for the mountain landscape (Table 5, model 1, Fig. 2). The 5-fold cross validation provided a mean Spearman's Rank correlation of 0.792 (P = 0.01), indicating that this model had excellent predictive capability and predictions were statistically significant. The ΔAIC_c values for the top 4 models in the mountain landscape were <2.0, indicating that the support for models 1–4 was similar (Burnham and Anderson 1998). The commonality between those models was selection for alpine or true fir habitat types that had lower forest heights and occurred at mid-high elevations. The parameter estimate for elevation-squared revealed there was an optimum mid-elevation range for den site placement (Table 5, model 3). We documented no dens in the low elevation sub-boreal spruce forests, early seral habitats, or anthropogenic areas, preventing us from modeling these features. An interaction between alpine and hillshade was used to test whether alpine den sites tended to be on mesic northeast (i.e., negative coefficient)

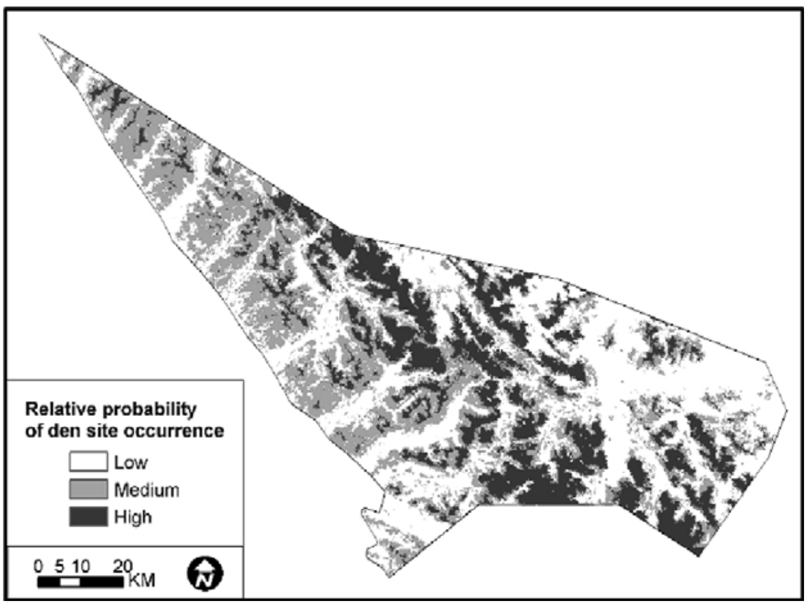

Fig. 2. Relative probability of grizzly bear den site occurrence in the mountain landscape, British Columbia, Canada, 1998–2003. Darker areas represent an increased probability of den site occurrence (greater RSF values).

Fig. 3. Relative probability of grizzly bear den site occurrence in the plateau landscape, British Columbia, Canada, 1998–2003. Darker areas represent an increased probability of den site occurrence (greater RSF values).

slopes. However, confidence intervals for hillshade and the alpine–hillshade interaction included 0, suggesting poor inference for those parameter estimates. Model 5 was the model with the least parsimony, as shown by its high AIC_c score, low AIC_c weight, and $\Delta AIC_c > 2$.

In the plateau, models 1–3 were similar (i.e., $\Delta AIC_c <$ 2, Table 6, Fig. 3). The commonality between those models was the selection for higher forest heights for den site placement. The 5-fold cross validation provided a mean Spearman's Rank correlation of 0.527 ($P = 0.1$), indicating that the top-ranked model had low predictive capability. The negative hillshade value indicated selection for cooler northeast aspects; however, the confidence intervals included 0, suggesting poor inference. Selection for higher elevations was minor for bears that lived on the plateau likely because the relief was not as great as within the mountains (model 2). The fourth ranked model revealed that grizzly bears selected den sites in stands with taller trees that were away from roads; although the ΔAIC_c places less importance on this model, it is important from a management perspective. Forest stand type ranked as the least parsimonious model (model 5). Grizzly bears selected spruce forests over pine; however, for the remaining stand types confidence intervals overlapped 0. We documented no dens in black spruce, shrubs, meadows, swamps, rock–bare ground, or anthropogenic landscapes.

Discussion

There were notable differences in the timing of denning and the land-cover type of den sites selected by bears that lived in the mountains and those that lived on the plateau. Bears that lived in the mountains arrived earlier at denning areas and had a longer denning duration. We found that average denning dates varied between the 2 landscapes but not among years. Pregnant females had the longest denning duration, whereas subadult plateau bears and adult males had the shortest denning duration. These findings are consistent with brown bears in central Sweden (Friebe et al. 2001), Admiralty and Chichagof Islands, Alaska (Schoen et al. 1987), and the Greater Yellowstone Ecosystem (Haroldson et al. 2002), but dissimilar to Russia, where no intraspecific differences were detected (Seryodkin et al. 2003). Similar to our findings, pregnant females were found to den first on Kodiak Island (Van Daele et al. 1990), in the Mission Mountains of Montana (Servheen and Klaver 1983), and in Yellowstone (Judd et al. 1986, Haroldson et al. 2002). However, in the Swan Mountains of Montana, females with young were found to den first (Mace and Waller 1997).

Van Daele et al. (1990) reported similar patterns of den entry and emergence dates between bear populations that lived within 70 km of each other on Kodiak Island, Alaska; entry and emergence also were separated by 2 to 3 weeks for females that lived in the southwestern portion. The authors hypothesized that the difference in denning behavior was attributed to varying food availability across the study area. Similarly, American black bears (*U. americanus*) in the warmer Kenai Peninsula of Alaska denned 2 weeks earlier and emerged later than those in the colder climate of the Susitna River (Schwartz et al. 1987), although these authors attributed the difference to weather and physical condition. There is general agreement that denning behavior may be triggered by a reduction in availability of forage items (Servheen and Klaver 1983, Schoen et al. 1987, Haroldson et al. 2002) and the reproductive status of individuals (Van Daele et al. 1990, Mace and Waller 1997). We believe those triggers also existed in our study area: the mountains were subjected to harsher weather conditions than the plateau, resulting in a shorter growing season. The longer duration of denning, earlier arrival at den site areas, and greater den-area fidelity resulted in a shorter non-denning period for mountain bears. A shorter non-denning period implies an overall reduction in the time available for foraging in the mountains compared with the plateau.

Most grizzly bears denned in their respective mountain or plateau areas. Only 2 bears denned outside their core home range, moving from the plateau to the mountains to select a den site. The first was a family unit (GF35 and her two 4-year-old offspring) that moved 40.5 km from the plateau to the mountains to den. This observation also was the only evidence of a female moving between landscapes in any season. The other observation was a large adult male that primarily resided on the plateau. Some large adult males have been known to travel between the 2 landscapes (Ciarniello et al. 2003). Grizzly bears, however, readily adapt physiologically to their environment; for example, in areas with late salmon (*Oncorhynchus* spp.) runs in Alaska, some male grizzly bears did not enter a den (Van Daele et al. 1990). Unlike resident mountain bears, these 2 migrating plateau bears had entrance and emergence dates more similar to plateau bears and immediately traveled to the plateau for early foraging opportunities. All other bears were located in the vicinity of their den sites at some point during the non-denning period. Friebe et al. (2001) also found that most bears denned within their core home range and visited their denning areas during the non-denning season. They suggested that bears may select their denning area during the non-denning season (Friebe et al. 2001).

Bears primarily excavated dens into the sides of slopes, and dens excavated by grizzly bears have been reported often (Vroom et al. 1980, Van Daele et al. 1990, Seryodkin et al. 2003). However, bears that lived in the mountains also used natural cave dens. We believe caves are important den sites for mountain grizzly bears, and especially important as natal den sites. We also noted bears using caves during the non-denning period. Natural caves likely provide cool places to bed during the non-denning season, while offering added security in alpine landscapes. Mountain cave dens were associated with (1) extensive clumps of bear hair deposited at various times, (2) >1 bear (as evidenced by mixed DNA samples), and (3) some worn rock structures, suggesting long-term use by a number of different bears. The use of cave dens also was reported for brown bears in Trentino, Italy and, similar to our findings, dens often were located on steep slopes difficult for people to access (Groff et al. 1998). The authors suggested that selection for steep slopes likely reflects selection for increased security (Groff et al. 1998). A study in Banff National Park also reported the use of cave dens, although the authors focused on excavated dens (Vroom et al. 1980). Bears on Admiralty Island, Alaska, denned in cave dens but those dens were considered "atypical" (Schoen et al. 1987:299).

All of the natural cave dens showed signs of re-use, as did the tree cavity and the excavated cave den. The only unstable den with evidence of previous use was an excavated den site associated with 1 other successful den and 1 attempt. Because the 3 dens were 1–2 m apart, we believe the bear had fidelity toward the denning area rather than the den site. In a synthesis paper on bear denning, Linnell et al. (2000) cited similar results with low re-use of excavated or ground dens and a greater frequency of re-use of natural caves and tree cavities. Some authors have suggested that high den re-use is positively correlated with low den availability (Lindzey and Meslow 1976, Schwartz et al. 1987, Linnell et al. 2000). Mace and Waller (1997) suggested that denning habitat is limited when bears travel extensively outside their normal home ranges to den. In our study the commonality between dens that were re-used was related to the stability of the den structure. We believe that den sites likely were not limited in either landscape. Bears often used pre-existing stable dens when available or otherwise excavated dens that usually were used only once.

Bears selected different land-cover features for denning depending on the landscape they occupied. We suggest that plateau bears selected older forests to avoid human disturbances prevalent in the early seral forests and open areas (e.g., disturbance by hunters and forestry workers in the fall). Moose (*Alces alces*) hunting season ended 5 November, but most hunting occurred in the plateau portion of the study area between 10 and 25 October (about 10,000 hunter days), corresponding with bears arriving at their denning areas (Table 1). The only measure of disturbance in the model was distance to the nearest road. Plateau bears selected for areas away from roads, which likely was correlated with selection for older forests where road densities were lower. On the plateau, all hunters accessed the area by truck or all-terrain vehicle, so there was extensive use of the entire road network. Linnell et al. (2000) indicated that grizzly bears avoided human activity areas, including roads and industrial activity, for den-site selection; bears selected distances of 1–2 km from those areas. Those authors also suggested that grizzly bears may tolerate human activity and noise during denning if the disturbance is >1 km from the den site; however, if regular visits by humans occurred early in the denning season, bears often abandoned their den sites (Linnell et al. 2000). Swenson et al. (1996 in Linnell et al. 2000) found that brown bears selected den sites >3 km from villages and >1 km from roads. Disruption during the denning period has been documented to decrease reproductive success of brown bears (Swenson et al. 1997, Linnell et al. 2000) and increase winter weight loss of black bears (Goodrich and Berger 1994). Thus, frequent disruptions in early seral areas may cause some bears to avoid those areas when selecting a den site. Due to the lack of site-specific human use data, we were unable to include a disturbance variable into our plateau model, which could have improved the predictive capacity. In the alpine portion of the mountains, there were no roads and few hunters. Hunters accessed those areas on foot after flying in or by hiking or horseback from the roads in commercial forests at lower elevations. Disturbance of mountain bears by humans was limited due to the inaccessibility of the terrain, especially during winter. Also, selection by bears for higher elevation alpine habitat provided a natural separation between low elevation valley bottom forestry operations and den site placement. Therefore, environmental variables provided excellent predictive capability in the mountain portion of the study area.

Management implications

The Parsnip River area is subject to modifications due to resource extraction and recreational use. Roads are required for timber harvest and, once established, often provide recreational access into backcountry areas. Resource managers need information on the requirements of grizzly bears to preserve denning habitat and to minimize disruption to hibernating bears during winter logging operations.

The habitat map for plateau den sites (Fig. 3) shows a low relative probability of use of clear-cut areas and early seral stands. For den sites on the plateau, management should focus on maintaining some large tracts of forest in old-growth and reducing the density of open roads within and adjacent to those stands to limit disturbance. Swenson et al. (1997) suggested that human activity should be avoided within 100–1,000 m of active den sites. Disturbance of hibernating bears due to winter logging operations has been shown to result in a greater probability of mortality of grizzly bear offspring (Swenson et al. 1997). Thus, several large patches of mature forest should be maintained within every 300–400 km^2 area, an area equivalent to the mean annual home range of plateau females (Ciarniello et al. 2003). Five plateau den sites were located on the west side of McLeod Lake. We identified this area as an important denning habitat for plateau bears; as such, this area would be a good candidate area for an old-growth reserve.

We also observed plateau grizzly bears denning in young forest stands if large trees were present within the stand. Also, many plateau dens were excavated into slopes adjacent to riparian areas. Consequently, within forest harvest areas, retention of large trees within riparian areas and retention of wildlife tree patches within cut areas should promote stand-level diversity, thereby enhancing the future value of those stands for grizzly denning habitat in regenerating forests.

In the mountain area, impacts on denning habitat areas were relatively low. However, recent mining and oil and gas developments may affect alpine denning habitat, and mountainous alpine areas are experiencing increasing levels of winter disturbance from motorized backcountry recreation, including snowmobiles, snowcat skiing, and helicopter skiing. The expansion of forest road networks contributes to increased winter access to alpine areas. Managing the level of winter access and disturbance in alpine areas may not only be important for grizzly denning habitat, but also for other wildlife such as caribou (*Rangifer tarandus*), mountain goats (*Oreamnos americanus*), and wolverine (*Gulo gulo*).

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