Distribution of subadult grizzly bears in relation to human development in the Bow River Watershed, Alberta

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Abstract: We studied the relationship between human development and activity, and subadult grizzly bears (*Ursus arctos*) by comparing the distribution of radiotelemetry locations from 23 subadult versus 29 adult grizzly bears during 1994–2000 in the Bow River Watershed of Alberta, Canada. We used logistic regression to model significant differences in the spatial distribution of subadult and adult grizzly bears and analysis of variance (ANOVA) to test for significant differences in temporal distribution. Subadult bears were significantly closer to high-use roads and at lower elevations than adult bears. Both subadult and adult bears were significantly closer to high-use roads and at lower elevations during human inactive periods (1800–0700) than during human active periods (0700–1800). Subadult bears were closer to high-use roads regardless of the time of day, and therefore predisposed to greater encounter rates with humans. Consequently, subadult bears had a greater chance of becoming habituated to humans and of being killed or removed from the population by humans than adult bears. In areas with high levels of human use, we recommend that grizzly bear managers consider the population effects of these losses.

Key words: Alberta, Banff National Park, Bow River Watershed, development, grizzly bear, habituation, logistic regression, subadult, *Ursus arctos*

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Grizzly bear populations have only persisted where large areas of relatively secure habitat are retained and where human-induced mortality is low (Servheen 1990). Habitat loss, hunting pressure, self-defense kills, illegal kills, garbage, and increased access all place pressure on remaining grizzly bear populations both inside and outside national parks. In Southern Alberta, the grizzly population exists in a narrow strip of land 30–60 km wide between the Continental Divide and the prairies to the east. The Bow River Watershed in Alberta is one of the most developed landscapes in the world where grizzly bears persist (Gibeau and Herrero 1998).

The survival and reproductive success of adult female grizzly bears is fundamental to viable grizzly bear populations. For their reproductive potential to be realized, however, recruitment of their offspring into the population is required. One of the most vulnerable periods for grizzly bears is the subadult stage, when a bear becomes independent of its mother but is not yet of breeding age (Mattson et al. 1992).

Subadult grizzly bears have been found to avoid other bears, particularly adult male bears (Mattson et al. 1987), occupy areas where humans have already displaced other bears (Mattson 1990, Olson et al. 1997), and be disproportionately represented near human activity and developments (Mattson et al. 1987, McLellan and Shackleton 1988). Sub-adult bears may also use temporal spacing to increase security from more dominant bears (Gunther 1990, MacHutchon et al. 1998).

Our objective was to further understand the relationships between human development and activity, subadult grizzly bear landscape use, and potential recruitment. Specifically, we asked if the landscape use in areas of high human activity of subadult grizzly bears was temporally or spatially different than that of adult bears.

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We predicted that subadult grizzly bears would occupy habitats nearest high-use roads and trails and use lower quality habitat than adult grizzly bears, particularly adult male bears. We also predicted that subadult bears would be closer to high-use roads, trails, and high quality habitat during human active periods and would be more visible to humans than adult bears. We also discuss the implications of our findings for subadult survival.

Study area

Our study area was in the Continental Ranges of the Canadian Rocky Mountains; we focused on the Bow River Watershed from its headwaters to approximately where it meets the prairies (Fig. 1). The study area encompassed $>$11,000 km^2 and included portions of Banff National Park (BNP), Alberta Provincial Forest reserve, several provincial parks, private lands, and the towns of Canmore, Banff, and Lake Louise.

Human presence was widespread inside and outside of BNP. The city of Calgary (population 900,000), approximately 100 km from the eastern boundary of Banff, was the primary gateway for tourists visiting BNP and other parts of the study area (Statistics Canada 2000). Annual visitation to BNP reached over 5 million by 1995 (Pacas 1996). Two major transcontinental transportation routes, the Trans Canada Highway (TCH) and the Canadian Pacific Railway (CPR) mainline, and several high-speed, 2-lane highways intersected the study area. Other types of human development included hotels, ski hills, campgrounds, golf courses, backcountry lodges, and an extensive network of equestrian, hiking, biking, and ski trails.

Methods

Radiotelemetry

Grizzly bears were captured, radiomarked, and monitored between 1994 and 2000. Individuals were equipped with either a conventional VHF (very high frequency) radiocollar (Lotek Engineering, Newmarket, Ontario, Canada) or a VHF eartag transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA). Aerial locations were collected following techniques of Mech (1983) and were recorded with a GPS in the plane. Ground locations were collected using a portable receiver, roof-mounted omni-directional antenna, and 3-element, hand-held Yagi antenna. The loudest signal or null method was used to determine bearings from 2 or more locations (Nams and Boutin 1991). Bearings were plotted on 1:50,000 scale topographic maps or 1:20,000 universal transverse Mercator (UTM) grid coordinate system ortho-corrected aerial photographs with bear locations recorded to the nearest 100 m. Through testing with radiocollars placed in known locations, an average telemetry error of 150 m was recorded (Gibeau 1998).

Bears were located at least once per week from the air, weather permitting. Ground locations were collected opportunistically on a daily basis. Aerial locations were biased toward the early morning hours; ground locations were biased toward areas accessible by road and where observers could travel easily (Gibeau and Herrero 2000). We divided telemetry locations into 2 data sets to account for biases involved with collection. The data sets were:

1. Aerial: only aerial locations and the most unbiased sample. Comparisons of age–sex classes indicated how adults and subadults differed at a landscape scale.
2. Road: aerial and ground telemetry locations $<$3500 m from high-use roads. The 3500 m distance was approximately half the width of valleys within the study area that included high-use roads. This area was accessible by road, so we assumed sampling within this area was unbiased. For analysis, 1 location was randomly selected during periods of relatively high human activity (0700–1800 hr), and 1 during periods of low human activity (1800–0700 hr).

Bears were classified as adult female ($\geq$6 years old), adult male ($\geq$7 years old), subadult female (independent and $<$6 years old), or subadult male (independent and $<$7 years old). We assumed that bears within each age–sex class exhibited similar behavior to pool data across bears. We acknowledge that in pooling bears and using location as the experimental unit, we may overestimate statistical significance; thus we emphasize the magnitudes of differences.

Map layers and variables

We used a human-use layer developed for a habitat effectiveness model for Banff, Yoho, and Kootenay National Parks (Gibeau 2000). This layer identified human developments and activity including the TCH, high-use paved roads, railway, and high-use trails. High use was defined as $>$100 vehicles or people per month during May–October; low use was defined as $<$100 vehicles or people per month during May–October. Distance to each telemetry location from high-use roads (including the railway) and high-use trails were derived using Idrisi Geographic Information Systems (GIS) software (Eastman 1997).

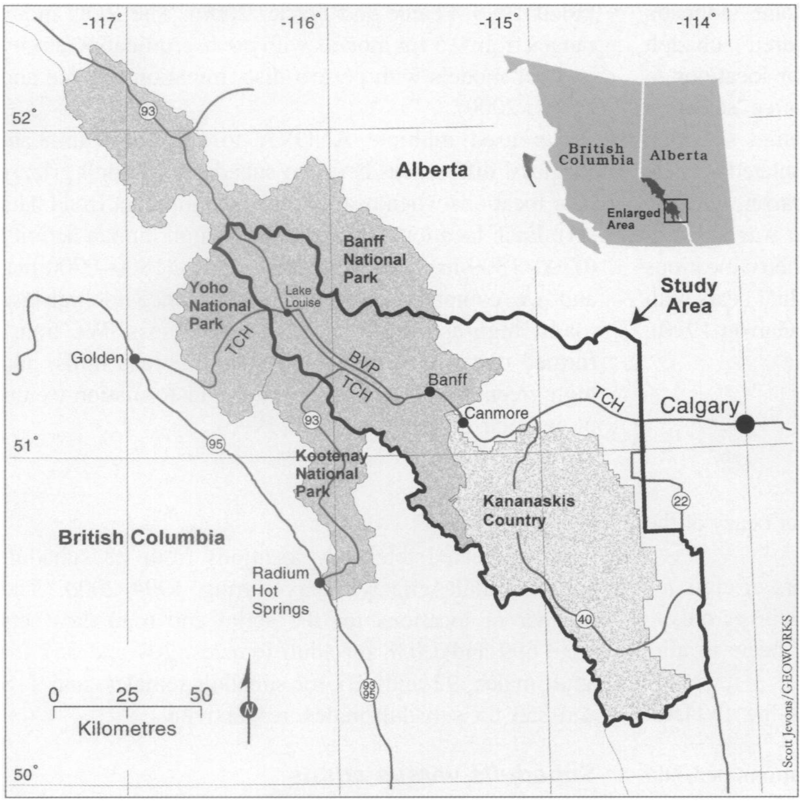

Fig. 1. The study area, highlighting the Bow River Watershed and the network of high-speed, high-volume highways within the Central Canadian Rocky Mountains.

Habitat type was determined using a land cover map with 30-m pixel resolution from Landsat Thematic Mapper (TM) imagery with 8 classes (J. Wierzchowski, 2000, Landsat TM-based vegetation/greenness mapping project, Geomar Consulting Ltd., Grand Forks, British Columbia, Canada). Habitat type included conifer, shrub, deciduous, graminoid, avalanche chutes, water, snow–ice, and rock–bare soil. Land cover was classified for each telemetry location using Idrisi GIS. Few locations were found in water or snow–ice, so these habitat classes were omitted from further analyses. We did not account for possible errors in classification.

Habitat quality contributes directly to nutritional condition of bears and may therefore be an important indicator of reproductive success (Bunnell and Tait 1981, Stringham 1990). A measure of habitat quality in the Bow River Watershed was modeled by Gibeau (2000) using Landsat TM satellite images transformed into a greenness band using the tasseled cap transformation (Mace et al. 1999). Increasing values of greenness were related to increased reflectance of deciduous, green vegetation (Mace et al. 1999). Use and expected values for each greenness class calculated from aerial telemetry locations indicated that the 4 highest classes were used more than expected by grizzly bears based on availability (Gibeau 2000). The 4 highest greenness classes were combined into a single GIS layer to represent high quality habitat (Gibeau 2000). We measured the distance of telemetry locations to high greenness with Idrisi.

Elevation, slope, and aspect for each location were extracted from a digital elevation model of the study area with 30-m resolution. To compare aspect as a continuous variable, we included it as 2 ratio-scale (0 to 1) variables, one depicting north to south and the other depicting east to west aspects (Apps et al. 2001).

Grizzly bears in the Central Rocky Mountains forage for key plant and animal foods seasonally and shift their seasonal land use to areas where these foods occur in abundance. Based on this seasonal shift in focus on important food species, we classified all locations as occurring in 1 of 2 seasons: pre-berry season (den emergence–15 July) and berry season (16 July–den entrance).

How visible an individual bear is while in the presence of humans may give a relative indication of how habituated that bear is to humans. If a bear was seen while being located by field technicians on the ground, the location was classified as "visual".

Analyses

We used stepwise multiple logistic regression to identify which combinations of variables best predicted subadult and adult grizzly bear locations for both aerial and road data sets (Hosmer and Lemeshow 1989). Logistic regression is often used in resource selection analyses involving radio telemetry data comparing used versus available (random) locations to determine probabilities of resource selection based on what is available (Manly et al. 1993, Trexler and Travis 1993). In this case,

we assumed that availability was constant (Johnson 1980, Garshelis 2000). We then compared subadult grizzly bear locations to adult grizzly bear locations to determine how subadult and adult resource selection differed, rather than how subadult resource selection differed from what was available. We calculated logistic regression models for each data set and season, with the dependent variable coded 0 if the location was an adult bear and 1 if it was a subadult bear. Telemetry locations were weighted to avoid bias toward individual bears with a greater number of locations (White and Garrott 1990). We used the following weighting formula:

$$w_{ij} = \overline{N}_i / N_{ij}((N/2)/N_i)$$

w_{ij} = weight assigned to each location for bear j of the ith class
$\overline{N}_i$ = mean number of locations for bears of class i
N_{ij} = number of locations for bear j of class i only
N = total number of locations for all j bears in all i classes
N_i = number of locations for all bears of the ith class.

Only locations from bears with $\geq$6 locations per data set and season were used in the analyses. We compared all age–sex classes and included 9 independent variables: distance to high-use roads, distance to high-use trails, elevation, slope, aspect (split into 2 continuous variables—south and west), habitat type, distance to high greenness, and bear sightability. Variables were screened for multicollinearity using Pearson's correlation coefficients (Tabachnick and Fidell 1996), and non-redundant ($r < 0.7$) variables were entered into a stepwise multiple logistic regression using SPSS (SPSS Inc. 1999). The significance of logistic models was determined by comparing the log-likelihood χ^2 for each model against the log-likelihood χ^2 for a model with the constant (intercept β_o) as its only parameter (Hosmer and Lemeshow 1989). Variables were considered significant ($P < 0.05$ to enter a variable) or not significant ($P > 0.10$ to remove a variable) to the final model. The significance of variable coefficients was evaluated using χ^2 tests of Wald statistics, and the contributions of each variable were assessed from the sign (negative or positive) and strength (P value) of their coefficients (Hosmer and Lemeshow 1989, Mace et al. 1999). We calculated the percent of correct predictions for each model and the relative operating characteristic curve (ROC) index to rate the probability that a model would correctly discriminate subadult and adult grizzly bear locations (Tabachnik and Fidell 1996, Pearce and Ferrier 2000). The ROC index ranges from 0.5 for models with no discrimination ability to 1 for models with perfect discrimination (Pearce and Ferrier 2000).

We used multiple ANOVA to test for significant temporal differences between subadult and adult grizzly bear locations when near human development (road data set). Each location occurred during high human activity (0700–1800 hr) or low human activity (1800–0700 hr), and we compared elevation and distance to high-use roads, high-use trails, and high greenness. We transformed distance to high-use roads, high-use trails, and high greenness with a square root transformation to improve their distributions (Zar 1996).

Results

We collected telemetry locations from 23 subadult and 29 adult grizzly bears during 1994–2000. The number of locations for the aerial and road data sets were 699 and 1,038 for adult females, 204 and 357 for adult males, 92 and 497 for subadult females, and 118 and 253 for subadult males, respectively.

Subadults versus adults

We used 20 adult female, 9 adult male, 11 subadult female, and 10 subadult male bears for logistic regression models with the aerial data set. We used data from 12 adult female, 7 adult male, 8 subadult female, and 9 subadult males for models with the road data set.

Pre-berry season. On average, subadult females were found 50% and 57% closer to high-use roads (aerial and road data set, respectively) than were adult females, as well as at lower elevations and at more southerly and westerly aspects than adult females. Subadult females were 36% and 52% closer to high-use roads (aerial and road data set, respectively) and 45% closer to high-use trails than were adult male bears, as well as on more southerly aspects than adult male bears (Table 1, 2).

Subadult males were at lower elevations and 38% closer to high-use roads at a landscape scale than adult females. Subadult males were sighted 61% more often than adult females when <3500 m from high-use roads. Use of the landscape by subadult males was similar to use by adult males; however, subadult males were sighted 107% more often when <3500 m from high-use roads and were 21% closer to high-use roads, on average in the aerial data set (Table 1, 2).

On average, subadult bears of both sexes were 43% and 30% closer to high-use roads than adults (aerial and road data set, respectively). Subadults were also at lower

Table 1. Variable mean and standard deviation for each age–sex group during pre-berry season, aerial and road data sets for model parameters to assess grizzly bear distribution in the Bow River Watershed, Canada, 1994–2000.

Age–sex group	Data set	Stat	Distance to road (m)	Distance to trails (m)	Distance to greenness (m)	Elevation (m)	Slope (degrees)	South	West	Visual (%)[a]
Subadults	aerial	mean	4102	1569	176	1829	17	0.58	0.53	n/a
		SD	5046	1856	206	279	12	0.26	0.30	
	road	mean	710	1270	144	1683	12	0.55	0.55	24
		SD	809	1329	175	226	10	0.28	0.29	
Adults	aerial	mean	7169	1879	173	1949	20	0.55	0.50	n/a
		SD	7076	2418	292	281	12	0.27	0.31	
	road	mean	1019	1260	184	1762	15	0.49	0.52	17
		SD	921	1578	198	259	11	0.30	0.29	
Subadult females	aerial	mean	3837	1430	179	1825	17	0.62	0.57	n/a
		SD	5105	1486	208	273	12	0.24	0.29	
	road	mean	453	1052	146	1709	12	0.58	0.62	16
		SD	529	1201	177	215	1	0.26	0.28	
Subadult males	aerial	mean	4754	1909	167	1839	17	0.49	0.41	n/a
		SD	4857	2514	200	292	11	0.27	0.29	
	road	mean	897	1428	143	1664	12	0.52	0.50	29
		SD	918	1395	173	231	9	0.30	0.28	
Adult females	aerial	mean	7648	1536	148	1991	21	0.57	0.50	n/a
		SD	7393	1501	187	269	12	0.26	0.31	
	road	mean	1062	915	166	1807	16	0.51	0.51	18
		SD	947	1073	179	263	11	0.30	0.29	
Adult males	aerial	mean	5992	2724	235	1847	16	0.52	0.51	n/a
		SD	6093	3707	452	285	11	0.29	0.29	
	road	mean	945	1851	216	1684	15	0.45	0.54	14
		SD	872	2060	223	233	12	0.30	0.29	

[a]Percent of locations within each age–sex group which were classified as a visual sighting.

elevations, on more southerly aspects, and seen 41% more often than adult bears when <3500 m from high-use roads (Table 1, 2).

Berry season. Subadult females were 45% and 36% closer to high-use roads than were adult females (aerial and road data set, respectively), and 35% further from high greenness. Subadult females were at lower elevations than adult females and sighted 10% more often <3500 m from high-use roads. On average, subadult females were 35% and 25% closer to high-use roads and 38% and 57% closer to high-use trails than were adult males (aerial and road data set, respectively). Subadult females were at higher elevations than adult males and 25% further from high greenness at a landscape scale (Table 3, 4).

Subadult males were found 105% further from high-use trails and at 11% lower elevations than adult females. Subadult males were 27% closer to high-use roads and 77% further from high greenness than were adult females at a landscape scale. Subadult males were sighted 70% more often than adult females and differed from them in their use of shrub and deciduous habitats, although not in a consistent direction. None of the variables were consistent significant predictors in models comparing subadult to adult males (Table 3).

Subadult bears of both sexes were 32% closer to high-use roads, 27% further from high-use trails, and 53% further from high greenness than were adult bears at a landscape scale.

Human active versus inactive periods

Data from 7 adult female, 3 adult male, 7 subadult female, and 3 subadult male bears were available for temporal analysis of locations using the road data set. The number of locations per bear varied from 5–13 during the human inactive period for the subadult classes, 8–21 for adult males, and 13–61 for adult females. The number of locations during the human active period varied from 28 and 247 locations per bear. Locations were weighted by bear and time of day to avoid bias toward individual bears.

Differences were evident for distance to high-use roads during the human active and inactive periods for

Table 2. Multiple logistic regression results comparing subadult to adult grizzly bears during the pre-berry season in the Bow River Watershed, Canada, 1994–2000. Beta values and standard errors for significant ($P < 0.05$) variables, aerial, and road datasets.

Model	Data set	Distance to road (m)	Distance to trails (m)	Distance to greenness (m)	Elevation (m)	Slope (degrees)	Visual	South	West	Habitat type[a] 1	2	3	4	5	6	Constant	R^2	% correct	ROC curve area
Subadults	aerial	−0.0001	—	—	−0.001	—	n/a	—	—	—	—	—	—	—	—	2.12	0.09	59.9	0.69
vs. adults	SE	0.00001			0.0003														
	road	−0.0002	0.0001	−0.002	−0.001	−0.02	0.33	1.08	—	−0.21	—	—	—	—	0.72	3.02	0.12	63.3	0.64
	SE	0.00006	0.00003	0.0003	0.0003	0.01	0.12	0.18		0.08					0.28				
Subadult	aerial	−0.0001	—	—	−0.001	—	n/a	0.93	0.73	0.02	—	—	—	−0.53	—	1.75	0.20	66.9	0.76
female	SE	0.00001			0.0004			0.33	0.26	0.01				0.23					
vs. adult	road	−0.001	0.0003	−0.001	−0.002	—	−0.42	0.91	0.68	—	—	−0.54	—	0.79	—	2.62	0.26	71.9	0.70
female	SE	0.0001	0.00006	0.0004	0.0004		0.17	0.23	0.22			0.25		0.25					
Subadult	aerial	−0.0001	−0.0003	—	—	0.03	n/a	1.06	—	—	—	—	—	—	—	−0.18	0.17	62.4	0.69
female	SE	0.00003	0.00008			0.01		0.49											
vs. adult	road	−0.001	−0.0004	—	0.003	−0.05	−0.74	1.80	—	—	—	—	—	1.39	−1.54	−5.67	0.37	74.9	0.82
male	SE	0.0002	0.00006		0.0006	0.01	0.23	0.32						0.40	0.69				
Subadult	aerial	−0.0001	0.0001	—	−0.001	—	n/a	—	−1.14	0.57	—	—	−0.42	—	—	2.38	0.19	66.3	0.74
male	SE	0.00001	0.00004		0.0004				0.26	0.25			0.17						
vs. adult	road	0.0002	0.0005	−0.002	−0.003	−0.02	0.74	0.80	—	—	0.57	—	—	−2.54	1.37	5.33	0.26	66.6	0.74
female	SE	0.00009	0.00007	0.0004	0.0004	0.01	0.17	0.24			0.22			0.68	0.37				
Subadult	aerial	−0.0001	−0.0001	—	—	—	n/a	—	−1.29	—	—	—	—	—	—	1.06	0.08	61	0.63
male	SE	0.00003	0.00004						0.42										
vs. adult	road	0.0003	—	−0.001	—	−0.05	0.57	1.18	—	—	0.69	—	—	−2.61	1.50	−0.04	0.20	66.6	0.66
male	SE	0.00012		0.0005		0.01	0.23	0.34			0.33			0.94	0.52				

[a]1 = conifer, 2 = shrub, 3 = deciduous, 4 = gramminoid, 5 = avalanche, 6 = rock, bare soil.

Table 3. Variable mean and standard deviation for each age–sex group during berry season, aerial and road data sets for model parameters to assess grizzly bear distribution in the Bow River Watershed, Canada, 1994–2000.

Age–sex group	Data set	Stat	Distance to road (m)	Distance to trails (m)	Distance to greenness (m)	Elevation (m)	Slope (degrees)	South	West	Visual (percent)[a]
Subadults	aerial	mean	5322	1989	208	1889	17	0.51	0.51	n/a
		SD	4677	2454	274	308	11	0.26	0.31	
	road	mean	817	1602	184	1700	12	0.53	0.57	14
		SD	872	3058	209	258	10	0.28	0.28	
Adults	aerial	mean	7868	1570	136	1968	18	0.52	0.49	n/a
		SD	7258	2200	172	263	11	0.28	0.30	
	road	mean	1035	1403	162	1806	14	0.53	0.52	9
		SD	923	2133	194	272	10	0.28	0.29	
Subadult females	aerial	mean	4515	1420	174	1949	18	0.53	0.50	n/a
		SD	4371	1712	215	282	11	0.26	0.32	
	road	mean	690	1057	188	1743	12	0.58	0.63	11
		SD	790	1207	221	231	9	0.23	0.29	
Subadult males	aerial	mean	6063	2510	239	1835	16	0.50	0.51	n/a
		SD	4830	2880	316	321	11	0.27	0.31	
	road	mean	930	2087	181	1662	12	0.49	0.52	17
		SD	924	3986	197	274	10	0.32	0.27	
Adult females	aerial	mean	8262	1244	135	2002	19	0.55	0.49	n/a
		SD	7337	1372	174	251	11	0.28	0.29	
	road	mean	1082	997	135	1861	15	0.52	0.51	10
		SD	959	1116	166	263	10	0.29	0.29	
Adult males	aerial	mean	6993	2293	139	1891	15	0.44	0.49	n/a
		SD	7017	3270	169	275	11	0.27	0.30	
	road	mean	922	2451	228	1674	13	0.45	0.53	8
		SD	821	3310	235	247	9	0.28	0.29	

[a]Percent of locations within each age–sex group which were classified as a visual.

all age–sex classes during both the pre-berry season ($F = 18.7$; 1, 1681 df; $P < 0.001$) and berry season ($F = 12.2$; 1, 1326 df; $P < 0.001$). All age–sex classes were closer to high-use roads during the human inactive period than during the human active period (Fig. 2). Subadult bears did not differ significantly from adults in their temporal movements around high-use roads, with all age–sex classes showing significantly greater avoidance of high-use roads during the human active period. Although marginally significant, pre-berry season differences in temporal movement were also found for each age–sex class for distance to high-use trails ($F = 3.3$; 1, 1681 df; $P = 0.071$), distance to high greenness ($F = 3.2$; 1, 1681 df; $P = 0.076$), and elevation ($F = 3.4$; 1, 1681 df; $P = 0.066$). Berry season differences in the temporal movements of each age–sex class were not significant for distance to high-use trails, distance to high greenness, or elevation. During both seasons all but subadult males were found closer to high-use trails during the human inactive period. All classes were found at lower elevations during the human inactive period (Fig. 3). Again, subadult classes did not differ significantly from adults in their temporal movements.

Discussion

Our results indicated that subadult and adult bears differed in their spatial distribution on the landscape. These differences in spatial distribution may result from intraspecific avoidance. Studies suggest that a consequence of intraspecific avoidance is differential distribution of bears by age and sex class (Hornocker 1962, Egbert and Stokes 1976, Tate and Pelton 1983, Mattson 1990). Both Egbert (1978) and Wielgus (1993) suggested that adult males were dominant, followed by females with young, single adult females, and subadults. Subadult females were the least dominant of all. According to this hypothesis, subdominant animals should avoid dominant animals (adult males and male-occupied habitats) according to their size and vulnerability to predation, or dominance and aggressiveness (Hornocker 1962, McCullough 1981, Stringham 1983, Wielgus 1993). In areas where humans and grizzly bears coexist, such as the Bow River Watershed, adult grizzly bears avoid areas close to people, probably because such avoidance gives greater security (Gibeau 2000). Subadult bears may use habitat with less security (closer to humans) to avoid adult bears. The closeness of humans may provide refuge and an

Table 4. Multiple logistic regression results comparing distribution of subadult to adult grizzly bears during berry season in the Bow River Watershed, Canada, 1994–2000. Beta values and standard errors for significant ($P < 0.05$) variables, both aerial and road datasets.

Model	Data set	Distance to road (m)	Distance to trails (m)	Distance to greenness (m)	Elevation (m)	Slope (degrees)	Visual	South	West	Habitat type[a] 1	2	3	4	5	6	Constant	R^2	% correct	ROC curve area
Subadults	aerial	−0.0001	0.0001	0.001	−0.001	0.014	n/a	—	—	—	—	—	—	—	—	1.22	0.11	60.1	0.66
vs. adults	SE	0.00001	0.00003	0.0003	0.0003	0.007													
	road	—	—	—	−0.002	—	0.65	0.67	0.72	−0.21	−0.36	—	—	0.30	—	2.84	0.10	58.5	0.62
	SE				0.0002		0.15	0.17	0.17	0.11	0.18			0.14					
Subadult	aerial	−0.0001	0.00001	0.001	—	—	n/a	—	—	—	—	—	—	—	—	0.37	0.14	60.4	0.68
female	SE	0.00001	0.00005	0.0004															
vs. adult	road	−0.0003	0.0002	0.001	−0.002	—	0.46	1.17	1.19	—	—	—	—	—	—	1.65	0.18	65.9	0.68
female	SE	0.00007	0.00005	0.0003	0.0003		0.19	0.22	0.19										
Subadult	aerial	−0.0001	−0.0002	0.002	0.002	—	n/a	1.01	—	—	—	—	—	—	—	−4.09	0.21	66.7	0.71
female	SE	0.00002	0.00006	0.0007	0.0005			0.44											
vs. adult	road	−0.001	−0.0005	—	0.004	−0.03	—	1.12	1.11	—	—	—	—	—	—	−6.55	0.32	71.5	0.76
male	SE	0.0001	0.00006		0.0005	0.01		0.33	0.29										
Subadult	aerial	0.00004	0.0003	0.002	−0.001	—	n/a	—	—	—	−0.58	0.83	—	—	—	2.20	0.25	66.8	0.71
male	SE	0.00001	0.00004	0.0003	0.0003						0.23	0.43							
vs. adult	road	—	0.0003	—	−0.004	0.032	1.13	—	0.46	−0.31	0.60	−0.75	−0.38	—	0.77	6.08	0.27	66.1	0.72
female	SE		0.00005		0.0004	0.009	0.20		0.23	0.12	0.18	0.25	0.17		0.33				
Subadult	aerial	—	—	0.002	−0.001	0.027	n/a	0.78	—	—	—	—	—	—	—	1.29	0.10	57	0.61
male	SE			0.0005	0.0005	0.01		0.42											
vs. adult	road	—	—	—	—	—	0.70	—	—	−0.65	—	—	—	0.94	—	0.22	0.09	62.2	0.58
male	SE						0.30			0.15				0.34					

[a]1 = conifer, 2 = shrub, 3 = deciduous, 4 = gramminoid, 5 = avalanche, 6 = rock, bare soil.

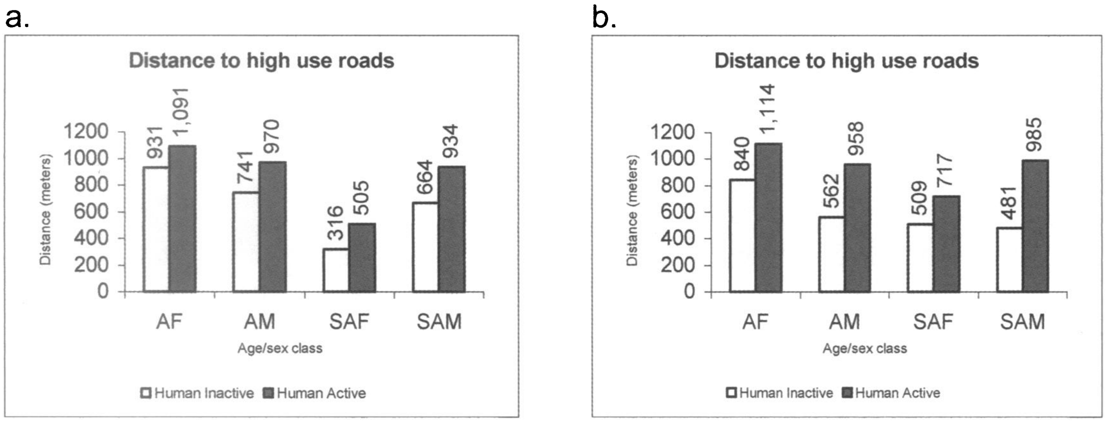

Fig. 2. Average distance to high-use roads for each age–sex class for grizzly bears during the human active period (0700–1800 hr) and the human inactive period (1800–0700 hr) during (a) pre-berry season, and (b) berry season, using the road data set only, for the Bow River Watershed, Canada, 1994–2000.

opportunity for subadult bears to use higher quality foods otherwise pre-empted by dominant adults (Mattson et al. 1987, McLellan and Shackleton 1988, Gibeau 2000). During the pre-berry season, subadult bears, particularly subadult female bears, were found significantly closer to high-use roads and high greenness than were adult bears.

Similar relationships have been found in Yellowstone National Park where adult male grizzlies were less likely to be near humans and more likely to use backcountry areas, while subadults were more likely to use areas nearest humans (Mattson et al. 1987, 1992). Adult females and subadults also tended to occupy areas near humans more than adult males along spawning streams on Admiralty Island (Warner 1987), along roads in the Flathead River Valley in British Columbia (McLellan and Shackleton 1988), and along roads in Denali National Park, Alaska (Tracy 1977).

At least one other hypothesis may explain the differences we found in spatial distribution between adults and subadults. Perhaps a significant proportion of subadults that live near people are killed before they become adults, and thus most surviving adults are more distant from development. Current data does not allow us to choose between competing hypotheses.

Habitat type was often a significant variable in our logistic regression models comparing subadult to adult grizzly bears. However, habitat type and the sign of beta values were inconsistent, making interpretation and any attempt at conclusions regarding differences in habitat use by subadult and adult bears difficult. In the Flathead River Valley in British Columbia and Montana, McLellan and Hovey (2001*a*) found bears used elevation and habitats differentially by season, but not by age and sex class.

Both subadult and adult grizzly bears responded to different levels of human activity in the Bow River Watershed. Olson et al. (1998) suggested that where population density is high relative to the food base, competition and avoidance should drive some bears to feed during less preferred hours. According to this hypothesis, we expected subadult bears to be located closer to human development than adult bears during periods of high human activity. Contrary to our prediction, subadult and adult grizzly bears were equally inclined to move away from development during periods of high human activity and move closer during periods of low human activity. Despite similar temporal movements, subadult bears were found closer to high-use roads than adult bears regardless of time of day. This pattern might indicate continued spacing between dominant and subdominant classes, as well as response to human activity.

Other studies have shown that human activities may cause bears to make temporal and spatial adjustments in their activity patterns (Roth 1983, Roth and Huber 1986, Ayres et al. 1986, Warner 1987). Human traffic along open roads displaces most grizzly bears from 100 to 900 m, and this displacement is greatest during periods of high human activity (Mattson et al. 1987, McLellan and Shackleton 1988, Kasworm and Manley 1990). McLellan and Shackleton (1988) found that grizzly bears near industrial activity in the Flathead used roads and nearby areas at night but avoided them in the day. Schoen and Beier (1988) reported that bears remained in the vicinity of intensive road building adjacent to a salmon spawning

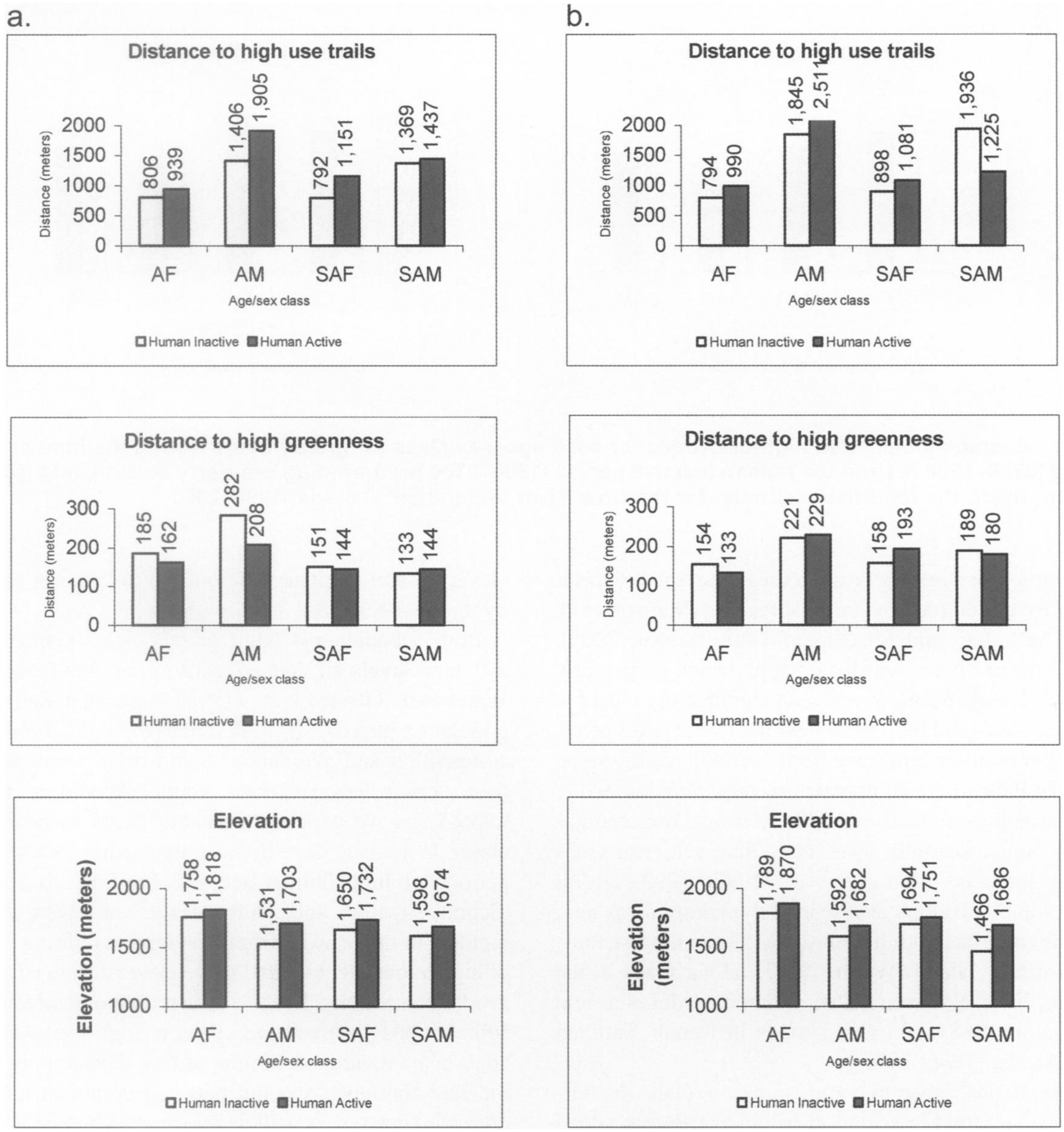

Fig. 3. Elevation and average distance to high-use trails and high greenness for each grizzly bear age–sex class during the human active period (0700–1800 hr) and human inactive period (1800–0700 hr), (a) pre-berry and (b) berry season, using the road data set only, for the Bow River Watershed, Canada, 1994–2000.

stream, moving away from the construction when people were active but returned during the evening. Clevenger et al. (1990) found that activity patterns of an adult male brown bear in Spain were largely nocturnal when human activity in the bear's range was high or when using open habitats.

Although spending time near humans in the Bow River Watershed may give subadult bears access to better habitats, it also puts them at significantly greater risk of mortality, both from management removals due to habituation problems and mortality on major transportation corridors such as highways and railroads. Benn and Herrero (2002) reported that all of 95 human-caused mortalities recorded in Banff and Yoho National Parks during 1971–98 occurred <500 m from a road or <200 m from a trail. Seventy-one percent of these deaths were due

to problem wildlife control, followed by highway and railway mortalities (19%; Benn and Herrero 2002). Forty-nine percent of the research bears captured by the Eastern Slopes Grizzly Bear Project between 1993 and 1999 were subadult bears, yet subadults comprised 66.7% of known mortality of research bears and 65% of all known grizzly bear mortality during these years (Gibeau and Herrero 2000). McLellan et al. (1999) reported that annual survival rates of radiocollared subadult male grizzly bears in the Rocky Mountains between 1975 and 1997 were less than other age–sex classes and that subadult male mortality rates due to management and citizen control killing were higher than other age–sex classes. Subadult males tend to disperse to areas outside their natal ranges (Blanchard and Knight 1991, McLellan and Hovey 2001*b*). Young males may therefore be predisposed to conflict with humans because they are more mobile, tend to use unfamiliar areas, and are often found close to humans (Clevenger and Pelton 1990, Swenson et al. 1998, Pease and Mattson 1999). As a consequence, mortality rates of subadult male bears tend to be higher than for subadult female bears (McLellan et al. 1999).

Their association with human activity makes subdominant bears significantly more vulnerable to habituation to people than other bears (Gunther 1990). Habituation is defined as a decline in an animal's response following repeated exposure to an inconsequential stimulus (Petrinovich 1973). The inconsequential stimulus becomes incorporated into what the animal perceives as its general environment (Jope 1985). Studies have suggested that there are differences among age, sex, and reproductive classes in the likelihood and level of habituation to humans (Egbert and Stokes 1976, Bunnell and Tait 1981, Mattson 1990). Five of 6 (83%) grizzly bear translocations due to dangerous levels of habituation to humans in the Bow River Watershed between 1993 and 1999 were subadult males (Gibeau and Herrero 2000). Of known habituated female grizzly bears requiring aversive conditioning in Banff National Park and Kananaskis Country between 1993 and 2000, 3 of 5 were subadults. The other 2 were young adults (6 and 7 years old), both of whom began habituating to humans before reaching adulthood. Habituation of subadults is prevalent in other bear studies. McLellan and Shackleton (1988) found that independent yearlings and some subadult grizzlies reacted less to people and vehicles than other age classes. Adult females with cubs and subadult bears were more easily habituated to humans than other bears in Yellowstone National Park (Mattson et al. 1987, 1992). In a study comparing wild black bears (*U. americanus*) to habituated black bears in Great Smoky Mountains National Park in Tennessee and North Carolina, McLean and Pelton (1990) reported that 47% of problem male bears were subadults while only 29% of wild male bears were subadults. Similarly, 34% of problem females were subadults whereas only 19% of wild females were subadults.

Habituation has major implications to bear populations confronted by even a moderate density of humans (Mattson 1990). Although habituation may increase the efficiency of bear habitat use in some instances by reducing displacement and minimizing the frequency of energy-demanding responses, habituated grizzly bears in certain areas are subject to higher mortality rates (Meagher and Fowler 1989, Mattson et al. 1992, Pease and Mattson 1999). Studies in Yellowstone National Park have shown that bears habituated to human activity but still eating natural foods were killed 3 times as often by humans as bears that were not habituated (Mattson et al. 1992). Habituation may lead to greater risk of injury to humans (Herrero 1985, 1989). Herrero (1989) found that for all 12 grizzly bear-inflicted deaths that occurred in Glacier National Park, Montana, Yellowstone National Park, and Banff National Park between 1967 and 1986, the bear involved was either food-conditioned, habituated, or both.

The future of any population is found in the subadult (especially female) classes. Results from this work indicate that in the Bow River Watershed subadult male and female grizzly bears are more prone to interaction with humans than adults. This interaction translates directly to increased risk of human-caused mortality. For viable grizzly bear populations to persist in the Bow River Watershed, grizzly bear and habitat management must ensure that subadult bears are not removed in excess of their replacement.

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Literature cited

APPS, C.D., B.N. MCLELLAN, T.A. KINLEY, AND J.P. FLAA. 2001. Scale-dependent habitat selection by mountain caribou, Columbia Mountains, British Columbia. Journal of Wildlife Management 65:65–76.

Ayers, L.A., L.S. Chow and D.M. Graber. 1986. Black bear activity patterns and human induced modifications in Sequoia National Park. International Conference on Bear Research and Management 6:151–154.

Benn, B., and S. Herrero. 2002. Grizzly bear mortality and human access in Banff and Yoho National Parks, 1971–98. Ursus 13:213–221.

Blanchard, B., and R. Knight. 1991. Movements of Yellowstone grizzly bears. Biological Conservation 58:41–67.

Bunnell, F., and D. Tait. 1981. Population dynamics of bears—implications. Pages 75–98 *in* T.D. Smith and C. Fowler, editors. Dynamics of large mammal populations. John Wiley and Sons, New York, New York, USA.

Clevenger, A.P., and M.R. Pelton. 1990. Pre and post breakup movements and space use of black bear family groups in Cherokee National Forest, Tennessee. International Conference on Bear Research and Management 8:289–295.

———, F.J. Purroy, and M.R. Pelton. 1990. Movement and activity patterns of a European brown bear in the Cantabrian Mountains, Spain. International Conference on Bear Research and Management 8:205–211.

Eastman, J.R. 1997. Idrisi for Windows, User's Manual. Clark University, Worcester, Massachusetts, USA.

Egbert, A. 1978. The social behavior of brown bears at McNeil River, Alaska. Dissertation, Utah State University, Logan, Utah, USA.

———, and A. Stokes. 1976. The social behavior of brown bears on an Alaskan salmon stream. International Conference on Bear Research and Management 3:41–56.

Garshelis, D. 2000. Delusions in habitat evaluation: Measuring use, selection, and importance. Pages 111–164 *in* L. Boitani and T. Fuller, editors. Research techniques in animal ecology: Controversies and consequences. Columbia University Press, New York, New York, USA.

Gibeau, M.L. 1998. Use of urban habitats by coyotes in the vicinity of Banff, Alberta. Urban Ecosystems 2:129–139.

———. 2000. A conservation biology approach to management of grizzly bears in Banff National Park, Alberta. Dissertation, Resources and Environment Program, University of Calgary, Alberta, Canada.

———, and S. Herrero. 1998. Roads, rails and grizzly bears in the Bow River Valley, Alberta. Pages 104–108 *in* G.L. Evink, editor. Proceedings of the International Conference on Ecology and Transportation, Florida Department of Transportation, Tallahassee, Florida, USA.

———, and ———. 2000. Eastern Slopes Grizzly Bear Project: A progress report for 1999. University of Calgary, Alberta, Canada.

———, ———, J. Kansas, and B. Benn. 1996. Grizzly bear population and habitat status in Banff National Park. Chapter 6 *in* J. Green, C. Pacas, L. Cornwell, and S. Bayley, editors. Ecological outlooks project: A cumulative effects assessment and futures outlook of the Banff Bow Valley. Prepared for the Banff Bow Valley Study, Department of Canadian Heritage, Ottawa, Ontario, Canada.

Gunther, K.A. 1990. Visitor impact on grizzly bear activity in Pelican Valley, Yellowstone National Park. International Conference on Bear Research and Management 8:73–78.

Herrero, S. 1985. Bear attacks: Their causes and avoidance. Nick Lyons Books/Winchester Press, Piscataway, New Jersey, USA.

———. 1989. The role of learning in some fatal grizzly bear attacks on people. Pages 9–14 *in* Bear–people conflicts: Proceedings of a symposium on management strategies. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.

Hornocker, M.G. 1962. Population characteristics and social and reproductive behavior of the grizzly bear in Yellowstone National Park. Thesis, Montana State University, Bozeman, Montana, USA.

Hosmer, D.W., and S. Lemeshow. 1989. Applied logistic regression. John Wiley and Sons, New York, New York, USA.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Jope, K.L. 1985. Implications of grizzly bear habituation to hikers. Wildlife Society Bulletin 13:32–37.

Kasworm, W., and T. Manley. 1990. Road and trail influences on grizzly bears and black bears in Northwest Montana. International Conference on Bear Research and Management 8:79–84.

Mace, R.D., J.S. Waller, T.L. Manley, K. Ake, and W.T. Wittinger. 1999. Landscape evaluation of grizzly bear habitat effectiveness in Western Montana. Conservation Biology 13:367–377.

MacHutchon, A.G., S. Himmer, H. Davis, and M. Gallagher. 1998. Temporal and spatial activity patterns among coastal bear populations. Ursus 10:539–546.

Manly, B., L. McDonald, and D. Thomas. 1993. Resource selection by animals: Statistical design and analysis. Chapman and Hall, New York, New York, USA.

Mattson, D.J. 1990. Human impacts on bear habitat use. International Conference on Bear Research and Management 8:33–56.

———, R.R. Knight, and B.M. Blanchard. 1987. The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. International Conference on Bear Research and Management 7:259–273.

———, B.M. Blanchard, and R.R. Knight. 1992. Yellowstone grizzly bear mortality, human-habituation, and whitebark pine seed crops. Journal of Wildlife Management 56: 432–442.

McCullough, D.R. 1981. Population dynamics of the Yellowstone grizzly bear. Pages 173–196 *in* T.D. Smith and C. Fowler, editors. Dynamics of large mammal populations. John Wiley and Sons, New York, New York, USA.

McLean, P., and M. Pelton. 1990. Some demographic comparisons of wild and panhandler bears in the Smoky

Mountains. International Conference on Bear Research and Management 8:105–112.

MCLELLAN, B.N. 1990. Relationships between human industrial activity and grizzly bears. International Conference on Bear Research and Management 8:57–64.

———, AND D.M. SHACKLETON. 1988. Grizzly bears and resource extraction industries: Effects of roads on behaviour, habitat use and demography. Journal of Applied Ecology 25:451–460.

———, AND F. HOVEY. 2001*a*. Habitats selected by grizzly bears in a multiple use landscape. Journal of Wildlife Management 65:92–99.

———, AND ———. 2001*b*. Natal dispersal of grizzly bears. Canadian Journal of Zoology 79:838–44.

———, ———, R. MACE, J. WOODS, D. CARNEY, M. GIBEAU, W. WAKKINEN, AND W. KASWORM. 1999. Rates and causes of grizzly bear mortality in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. Journal of Wildlife Management 63:911–920.

MEAGHER, M., AND S. FOWLER. 1989. The consequences of protecting problem grizzly bears. Pages 141–144 *in* Bear–people conflicts: Proceedings of a symposium on management strategies. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.

MECH, L.D. 1983. Handbook of animal radio-tracking. University of Minnesota Press, Minneapolis, Minnesota, USA.

NAMS, V.O., AND S. BOUTIN. 1991. What is wrong with error polygons? Journal of Wildlife Management 55:172–176.

OLSON, T.L., B.K. GILBERT, AND R.C. SQUIBB. 1997. The effects of increasing human activity on brown bear use of an Alaskan river. Biological Conservation 82:95–99.

———, R.C. SQUIBB, AND B.K. GILBERT. 1998. Brown bear diurnal activity and human use: A comparison of two salmon streams. Ursus 10:547–555.

PACAS, C. 1996. Human use in the Banff Bow Valley: Past, present and future. Chapter 3 *in* J. Green, C. Pacas, L. Cornwell, and S. Bayley, editors. Ecological outlooks project: A cumulative effects assessment and futures outlook of the Banff Bow Valley. Prepared for the Banff Bow Valley Study. Department of Canadian Heritage, Ottawa, Ontario, Canada.

PEARCE, J., AND S. FERRIER. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling 133:225–245.

PEASE, C.M., AND D.J. MATTSON. 1999. Demography of the Yellowstone grizzly bears. Ecology 80:957–975.

PETRINOVICH, L. 1973. A species-meaningful analysis of habituation. Pages 141–162 *in* H. Peeke and M. Herz, editors. Habituation. Academic Press, New York, New York, USA.

ROTH, H.U. 1983. Diel activity of a remnant population of European brown bears. International Conference of Bear Research and Management 5:223–229.

———, AND D. HUBER. 1986. Diel activity of brown bears in Plitvice Lakes National Park, Yugoslavia. International Conference of Bear Research and Management 6:177–181.

SCHOEN, J.W., AND L.R. BEIER. 1988. Brown bear habitat preferences and brown bear logging and mining relationships in Southeastern Alaska. Alaska Department of Fish and Game Project W-22-6, Job 4.17, Juneau, Alaska, USA.

SERVHEEN, C. 1990. The status and conservation of bears of the world. International Conference of Bear Research and Management Monograph Series Number 2.

SPSS INC. 1999. SPSS for Windows: Base 10.0 Applications Guide. Chicago, Illinois, USA.

STATISTICS CANADA. 2000. Community profiles. Statistics Canada, Ottawa, Ontario, Canada. www.statcan.ca, accessed 20 March 2001.

STRINGHAM, S.F. 1983. Roles of adult males in grizzly bear population biology. International Conference of Bear Research and Management 5:140–151.

———. 1990. Grizzly bear reproductive rate relative to body size. International Conference on Bear Research and Management 8:433–443.

SWENSON, J.E., F. SANDEGREN, AND A. SODERBERG. 1998. Geographic expansion of an increasing brown bear population: Evidence for presaturation dispersal. Journal of Animal Ecology 67:819–826.

TABACHNICK, B.G., AND L.S. FIDELL. 1996. Using multivariate statistics. Third edition. Harper Collins, Northridge, California, USA.

TATE, J., AND M.R. PELTON. 1983. Human–bear interactions in Great Smokey Mountains National Park. International Conference on Bear Research and Management 5:312–321.

TRACY, D. 1977. Reactions of wildlife to human activity along Mount McKinley National Park Road. Thesis, University of Alaska, Fairbanks, Alaska, USA.

TREXLER, J., AND J. TRAVIS. 1993. Nontraditional regression analyses. Ecology 74:1629–1637.

WARNER, S.H. 1987. Visitor impact on brown bears, Admiralty Island, Alaska. International Conference on Bear Research and Management 7:377–382.

WHITE, G.C., AND R.A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

WIELGUS, R. 1993. Causes and consequences of sexual habitat segregation in grizzly bears. Dissertation, University of British Columbia, Vancouver, British Columbia, Canada.

ZAR, J.H. 1996. Biostatistical analysis. Third edition. Prentice-Hall, Inc., Upper Saddle River, New Jersey, USA.

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