BioOne COMPLETE

Comparison of Grizzly Bear Ursus arctos Demographics in Wilderness Mountains Versus a Plateau with Resource Development

Authors: Ciarniello, Lana M., Boyce, Mark S., Seip, Dale R., and Heard, Douglas C.

Source: Wildlife Biology, 15(3) : 247-265

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/08-080

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Wildl. Biol. 15: 247-265 (2009)
DOI: 10.2981/08-080
© Wildlife Biology, NKV
www.wildlifebiology.com

Original article

Comparison of grizzly bear *Ursus arctos* demographics in wilderness mountains versus a plateau with resource development

Lana M. Ciarniello, Mark S. Boyce, Dale R. Seip & Douglas C. Heard

We studied migration, birth rate and death rate of 59 grizzly bears *Ursus arctos* on a plateau (N = 29) with extensive forestry activities, and adjacent relatively undeveloped mountains (N = 30) during 1998-2003, to examine population parameters and/or limiting factors that might have contributed to a large difference in grizzly bear density between landscapes. Female bears in our low-density area (i.e. plateau) were heavier, in better condition, and more often accompanied by cubs than their mountain counterparts. Survival rates were comparable for adult bears but were significantly lower for subadult bears on the plateau. All deaths of bears which lived on the plateau for which cause of death was identified were human-caused as compared with one of three in the mountains. Plateau bear deaths were highest in fall coinciding with people hunting other species. Density-dependent factors appeared to be more important to mountain bear demographics, whereas bears on the plateau appeared to be limited by human-caused bear mortality. Forest harvest did not appear to have negative effects on reproductive parameters of female bears, but associated towns and roads allowed for high human-caused bear mortality. We did not record female dispersal between landscapes leading us to conclude that dispersal from the mountains is unlikely to offset human-caused mortality on the plateau.

Key words: British Columbia, demography, grizzly bear, mortality, resource selection function, roads, survival, Ursus arctos

Lana M. Ciarniello & Mark S. Boyce, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T6G 2E9, Canada - e-mail addresses: aklak@telus.net (Lana M. Ciarniello); boyce@ualberta.ca (Mark S. Boyce)
Dale R. Seip, British Columbia Ministry of Forests and Range, 1011 4th Ave, Prince George, British Columbia, V2L 3H9, Canada - e-mail: dale.seip@gov.bc.ca
Douglas C. Heard, British Columbia Ministry of Environment, 4051 18th Ave, Prince George, British Columbia, V2N 1B3, Canada - e-mail: doug.heard@gov.bc.ca

Corresponding author: Lana M. Ciarniello

Received 19 November 2008, accepted 4 May 2009

Associate Editor: Shyamala Ratnayeke

Grizzly bears *Ursus arctos* have high mortality rates in areas near human activity (Mattson & Merrill 2004, Nielsen et al. 2004), and grizzly bear conservation may be compromised by the rapidly expanding development of human access into their range. Wildlife managers require information that identifies the drivers which regulate or limit population change. We studied grizzly bears in central British Columbia (BC), Canada, during 1998-2003, on a plateau with relatively high levels of human activity and in a relatively pristine adjacent mountainous area. At the outset of our study, we assumed that we were monitoring a population of bears that travelled between landscapes. In 2000, a DNA based mark-recapture study concluded that grizzly bear density in the mountainous area was higher than in the adjacent plateau (12 bears/1,000 km^2 plateau, CI: 7-28 and 49 bears/1,000 km^2 mountains, CI: 43-59;

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Mowat et al. 2005). DNA finger printing using 15 polymorphic genetic markers revealed that bears captured in either landscape were genetically distinguishable, suggesting limited migration between the landscapes (Ciarniello 2006). We were interested in identifying the causes for the difference in densities and the apparent lack of movement between landscapes.

Mowat et al.'s (2004) model of factors affecting grizzly bear densities in North America suggests that higher density of bears in the mountains was primarily a result of higher precipitation leading to greater primary productivity, but also might be related to higher reported human-caused mortality and higher human and livestock presence, an index of unreported human-caused mortality, on the plateau. Ciarniello et al. (2007a) used a statistical approach to model the relationship between selected variables and population structure and concluded that the risk of human-caused bear mortality had a greater effect on differences in bear density than differences in land-cover type or roads. Here we use aerial telemetry monitoring to assess the amount of movement by male and female bears between the landscapes. We also monitored reproductive parameters of female bears to determine if differences existed by landscape. We examine age-specific mortality and primary risk factors related to mortality, because this information is useful when considering questions of sustained yield management.

Survival of adult males was lower in two hunted areas (75-80%) compared with two non-hunted (96-98%) areas in Alaska; however, survival of young (all ages) was significantly higher in hunted areas (57-67%) than in non-hunted areas (34%; Miller et al. 2003). For adult female grizzly bears, annual survival was comparable between two hunted areas (89-96%; McLellan et al. 1999, Miller et al. 2003) and four non-hunted areas (91-97%; McLellan et al. 1999, Miller et al. 2003, Schwartz et al. 2006). During our study, mountain and plateau landscapes were managed using the same allowable hunting kill rate so we hypothesized that there should not be differences in survival rates between landscapes attributable to the permitted hunt.

Human activities have been reported as the primary factor influencing grizzly bear density, because they can result in loss of suitable habitats and increased human-caused mortality of bears (Servheen 1984, Mattson & Merrill 2002). In naturally regulated populations, the survival of adult grizzly bears is high (McLellan 1990). Intra-specific killing, especially of cubs, may be important in naturally regulated populations (McLellan 1994), but in most grizzly bear populations, human-caused mortality is the primary cause of death for adult bears (McLellan 1990, Mattson & Merrill 2004, Nielsen et al. 2004, Schwartz et al. 2006). Human-induced mortality was cited as the primary factor influencing grizzly bear population viability (Eberhardt et al. 1994) and includes the legal 'permitted' kill by hunters and 'non-permitted' deaths such as: illegal kills, livestock depredation, problem wildlife and collisions with vehicles. The magnitude of human-caused mortality for grizzly bears has been related to the density of human settlements and roads (Mattson et al. 1987, Nagy et al. 1989, Mace et al. 1996, Nielsen et al. 2004). We hypothesized that the extensive road networks on the plateau provided increased human access resulting in higher non-permitted sources of human-caused bear mortality in this landscape.

Reproductive parameters, body size and animal condition also might help to interpret the differences in the number of bears inhabiting different areas. Bears that have access to predictable meat supplies are larger (Hilderbrand et al. 1999, Miller et al. 2003, Ben-David et al. 2004), and large body size has been linked to increased reproductive success (Stringham 1990, Welch et al. 1997) with the variance in reproductive parameters appearing to be related to nutritional condition (Hilderbrand et al. 1999, Ben-David et al. 2004). We could not identify any human-made structures (e.g. highways, towns) near the topographic divide separating mountains from plateau. Therefore, we assumed bears would freely travel between areas, and there would be no difference in reproductive parameters, body size and condition.

We identified primary risk factors and reproductive parameters associated with the difference in bear density between the relatively pristine mountain landscape and the adjacent plateau which was harvested heavily for timber. Our objectives were to evaluate: 1) movement of grizzly bears between mountainous and plateau landscapes, 2) reproductive parameters in the two areas, 3) age-specific mortality, and 4) primary risk factors related to mortality. Understanding the primary limiting factors (see Sinclair 1989) for grizzly bears inhabiting publicly owned Crown forested land (hereafter working forests) will be crucial to the development of sound management practices for bears, especially those residing outside of protected areas.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Material and methods

Study area

Our study area of 18,096 km^2 was located in central-eastern British Columbia (BC), Canada (54° 39'N, 122° 36'W), including the northern limits of the city of Prince George extending north past the town of Mackenzie. The ecosection line, as delineated by the BC Ministry of Environment, was used to divide the study area into two major landscapes (Fig. 1):

- The Parsnip Plateau (hereafter plateau), which covered 10,624 km^2 of rolling hills and flat valleys in the sub-boreal spruce (SBS) biogeoclimatic zone. Extrapolating DNA-based mark-recapture estimates (12 bears/1,000 km^2, CI: 7-28; Mowat et al. 2005) for the study area size results in 127.5 grizzly bears on the plateau. Climax forests in the wetter portion of the plateau were dominated by white spruce *Picea glauca*, and lodgepole pine *Pinus contorta* occurred mainly in dryer portions. Most plateau landcover types were a mix of white spruce and pine or spruce and subalpine fir *Abies lasiocarpa* associations. The plateau was modified by forestry activities, with approximately 12% of the area clearcut in a 20-year period (1970-1990; DeLong & Tanner 1996). The majority of logging had taken place since 1950, and resulted in a mosaic of cutblocks and successional stages. The plateau had mean annual temperature of 2.6°C, with 72 cm rainfall, and 300 cm snowfall (DeLong et al. 1993, 1994). Elevations ranged from 600 m to 1,650 m a.s.l.
- The Hart Ranges of the Canadian Rocky Mountains (hereafter mountains). The mountain population was distributed over 7,472 km^2 and contained both east and west slopes of the Rockies. Adjusting estimated population density (49 bears/1,000 km^2, CI: 43-59; Mowat et al. 2005) for the study area size results in 366 grizzly bears in the mountains. The primary forest type was SBS in the valley bottoms and Engelmann spruce *Picea engelmannii* - subalpine fir in the subalpine. Valley bottoms were predominantly a mix of white spruce and subalpine fir, and higher-elevation habitats consisted of subalpine parkland dominated by subalpine fir. Subalpine grassland slopes were comprised of lush forb communities. The alpine-tundra zone, beginning at approximately 1,400 m a.s.l, typically consisted of shrubs or krummholtz tree formations and heath communities. Of the study area, <1% was barren rock, alpine snow or glacial ice. Timber harvest was a relatively recent activity in the mountains beginning in approximately 1969. Each year harvesting expanded further up the four main river valleys

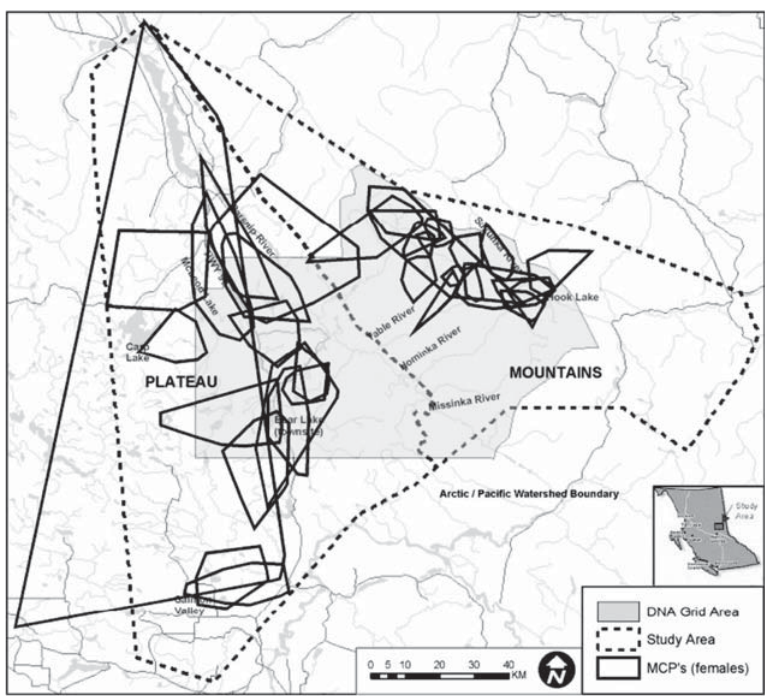


Figure 1. Study area for monitoring grizzly bear survival, including mountain and plateau boundary just east of the Parsnip River, British Columbia, Canada, during 1998-2003. The DNA-based population census boundary is represented by the shaded box contained within the core of the larger study area and encompassed both mountain and plateau landscapes. The polygons represent 100% MCPs for female bears for all sample years combined (1998-2003).

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

(Missinka, Hominka, Table and Anzac Rivers) leading deeper into mountainous areas. Approximately 2% of the mountain area had been clearcut between 1969 and 1990 (B.C. Integrated Land Management Bureau 2006 data). The mean annual temperature was 0.3°C, with 154 cm rainfall and 700 cm snowfall. Elevations ranged from 720 m to 2,550 m a.s.l.

Both mountain and plateau landscapes were within the working forest with only a few small provincial parks. Forestry was the predominant industry in the study area, and the plateau contained the majority of timber-extraction activities. Other potential disturbances to grizzly bears included the resource-based towns of Bear Lake and Mackenzie, Highway 97, a railway line through the mountains for coal extraction, three sawmills, two logging camps, and various consumptive and non-consumptive recreational activities, such as hunting, fishing, trapping and off-highway recreational vehicles (e.g. snowmobiles and ATV).

Bear capture

Bears were captured from August 1997 through fall 2002 using a combination of Aldrich foot snares placed at baited sites, aerial darting from helicopter, culvert traps and free-range darting. Each year, there were two main capture periods for both landscapes: late April through early June and September through October.

The University of Alberta's Animal Care Committee, following the Canadian Council on Animal Care guidelines and principles, approved bear handling procedures (protocol #307204). We immobilized bears with Telazol (tiletamine HCL/zolazepam HCL) at a dosage of 8 mg/kg administered using the Palmer Cap-Chur Inc. system (Powder Springs, GA, USA). Ketamine hydrochloride was used as a top-up drug when necessary at a dosage of 2 mg/kg. We measured chest girth and assessed reproductive status of immobilized bears following Jonkel (1993). Pinching the layer of fat surrounding the bears' ribs and flanks was used to assess body condition. Bears were assigned a condition based on the thickness of their fat layer with 'excellent' representing a very thick fat layer and 'poor' representing very thin or no fat layer. A primary capture crew member was present at each capture event, and we attempted to standardize this metric among the participating individuals. A first premolar tooth was extracted for age determination (Mattson's Laboratory, Milltown, Montana). We classified bears of <4 years of age as subadults (i.e. lone bear or with sibling) and juveniles (i.e. still in the company of their mother), whereas adults were ≥ 4 years of age as long as they were not accompanied by their mother. Despite considerable effort we did not catch any female bears <7 years old in the mountains. Therefore, we also have provided comparisons for adult females using ≥ 7 years of age. Body mass was measured where possible. If mass could not be measured (e.g. steep mountain slopes), we used the chest girth/weight relationship outlined in Jonkel (1993) to estimate bear mass. We found that Jonkel's method provided a good fit when compared with our known bear weights. Statistical comparisons of capture condition and litter size between groups of bears was calculated using a Mann-Whitney U-test with a significance level of $\alpha < 0.05$. We used analysis of covariance (ANCOVA) to determine whether our results for home-range size, capture weights and capture condition were affected by differences in age rather than landscape.

Monitoring and home range

Bears were outfitted with either a combination of 12 channel Televilt GPS-Simplex™ Global Positioning System (GPS) collars (Televilt/TVP Positioning AB, Lindesberg, Sweden) or VHF (very high frequency) collars (Lotek, Newmarket, Ontario, Canada) and/or ear-tag transmitters. Bears were monitored from capture until their death, lost/failed collar, or through denning using a single engine fixed-wing aircraft and occasionally a helicopter. Monitoring occurred twice a week from 1998 to 2000, weekly in 2001 and 2002, and every two weeks in 2003, dependent upon weather conditions and aircraft availability. Due to the low fix rate of GPS collars (Gau et al. 2004), and mixing of VHF and GPS data, we used only the VHF aerial locations to calculate home-range size. All aerial telemetry locations were collected during daylight hours. Substantial effort was directed at obtaining accurate low level aerial locations and/or visual observation. Universal Transverse Mercator (UTM) coordinates were taken with a hand-held 12 Channel Global Positioning System unit. Locations were mapped and verified on 1:50,000 topographic maps. For study animals with >10 locations throughout the year, multi-year (1998-2003) 100% Minimum Convex Polygons (MCP) were constructed using the program Animal Movement (Hooge & Eichenlaub 1997). For bears monitored over multiple years, we

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

used the MCP size from the year that contained the greatest number of locations.

We also used VHF monitoring to evaluate dispersal and migration between landscapes. We define dispersal as the separation of dependent offspring from their mother and subsequent establishment of their own home range. Migration was used to refer to movement back and forth between landscapes.

After two consecutive relocations where the bears' signal was on mortality (i.e. 30-40 beats per minute), we visited locations to determine cause of death. Natural deaths refer to any deaths where humans or their activities were not the direct cause. Non-permitted kills refer to bears shot by people who did not hold a legal license, including poaching and species misidentification.

Reproduction

Reproductive status of bears was assessed annually during capture events and at den emergence. If a visual observation of the bear was obtained during monitoring, the number of animals present, along with an estimate of their age class (cub of the year (COY), yearling, two-year old, subadult and adult) were recorded. We used only known-aged litters to estimate an average inter-birth interval. Because we did not capture any female bears in the mountains <7 years of age, reproductive status was only determined for bears ≥ 7 years of age.

Survival

Weekly survival rates, $\hat{S}_t$, for radio-collared grizzly bears were estimated using a staggered entry Kaplan-Meier design following Pollock et al. (1989):

$$\hat{S}_t = \prod_{i=1}^{n} \left[1\text{-}\left(\frac{d_i}{r_i}\right)\right] \qquad (1),$$

where n refers to the number of times bears were checked, d_i is the number of deaths, and r_i is the number of bears at risk recorded at time i. Annual survival was calculated by taking the product of weekly survival for all 52 weeks. The variance for survival rates was estimated using Greenwood (1926):

$$\mathrm{var}(\hat{S}_t) = \hat{S}_t^2 \left[\sum_{i=1}^{n} \left(\frac{d_i}{r_i(r_i\text{-}d_i)}\right)\right] \qquad (2).$$

We used the known date when radio-collars were removed during trapping, limited-entry hunts, or problem-wildlife kills. We lost contact with six bears due to what we believed to be failure of GPS transmitters; two of these bears were sighted wearing their failed collars. These records were censored at the last known location on the date when a missing bear went off-line. Our calculated mortality rates might be conservative, because it is possible that some of the missing bears were killed and the transmitter destroyed. For bears that died during the aerial tracking period, or dropped their collars between flights, the midpoint between the flight before and the mortality-emitted flight was used as the bear's off-line or death date as long as that time span was ≤ 14 days. We omitted (i.e. censored) the known deaths of four male bears (three subadults and one young adult: three legal hunts and one problem wildlife), because we lost contact with them for periods ranging from eight months to 1.5 years. For bears that dropped their collars in their den sites, the mean den emergence date was used as the off-line date (Ciarniello et al. 2005). All such dens were investigated to document that the bear lived through the denning period (Ciarniello et al. 2005).

We present results by males and females for all ages combined, bears <7 years, and bears ≥ 7 years. We used seven years because we did not capture any female mountain bears <7 years thereby having comparable categories between landscapes. We used a *z*-test for survival analysis to determine if the differences were statistically significant ($\alpha < 0.05$).

Risk of human-caused bear mortality

Risky areas for human-caused bear mortality were identified by combining known deaths recorded during our study (N = 11) with 150 permitted and non-permitted (i.e. poaching, collision with vehicles and problem wildlife) kill locations that occurred within the study area acquired from the BC Ministry of Environment Compulsory Inspections Databases during 1990-2003. Hunters were required to report their location data with precision of 1 km. For the plateau, we compared 972 use locations representing 32 bears (N = 18 females and 14 males) with 106 (N (provincial database) = 98 + N (study) = 8) mortality locations. For the mountains, we compared 1,527 use locations on 30 bears (N = 19 females and 11 males) with 55 mortality locations (N (provincial database) = 52 + N (study) = 3). By comparing bear use with bear mortality, we were able to examine the riskiest places for bears while taking into account that bears chose to be there (Nielsen et al. 2006).

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Table 1. Rank of seven candidate models indicating the relative risk of mortality for grizzly bears inhabiting the plateau landscape of the Parsnip River study area, British Columbia, Canada. Models were estimated by comparing mortality locations with study bear non-mortality telemetry locations (using equation 3).

Rank	Candidate model variables	AIC_c	ΔAIC_c	AIC_cw
1	I) Distance to highway, primary logging, secondary & decommissioned roads II) Predominate forest cover types (withheld spruce) III) Greenness	623.75	0	1.00
2	I) Distance to highway, primary logging, secondary & decommissioned roads II) Greenness III) Elevation	666.67	42.92	$4.78E^{-10}$
3	I) Distance to highway, primary logging, secondary & decommissioned roads II) Stand age (categorical)	669.01	45.26	$1.49E^{-10}$
4	I) Distance to highway, primary logging, secondary & decommissioned roads II) Greenness	669.98	46.24	$9.11E^{-11}$
5	I) Distance to highway, primary logging, secondary & decommissioned roads II) Stand age (continuous)	680.72	56.97	$4.26E^{-13}$
6	I) Distance to highway, primary logging, secondary & decommissioned roads	680.77	57.02	$4.15E^{-13}$
7	I) Distance to cutblock II) Greenness	683.08	59.34	$1.3E^{-13}$

A logistic discriminant function (Seber 1984: 308-317) was estimated to contrast the distribution of grizzly bear mortality locations with radio-telemetry locations representing the available locations where kills might have occurred (0), for mountain and plateau landscapes using the log-linear equation:

$$m(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 \ \ldots \ \beta_p x_p) \quad (3),$$

where the relative probability of mortality, m(x), was influenced by coefficients, β_i, for each covariate, x_i, for $i = 1, 2, \ldots p$, estimated using logistic regression (Johnson et al. 2006).

Secure habitats for grizzly bears are often roadless areas containing a juxtaposition of forest types and successional stages (Mattson et al. 1987, McLellan & Shackleton 1989, Mace et al. 1996). Conversely, areas with close contact between humans and bears sometimes result in high human-caused bear mortality (Mattson & Merrill 2002, Nielsen et al. 2004), and selection patterns by bears have been altered due to the presence of roads and trails (Mattson et al. 1987, McLellan & Shackleton 1989, Mace et al. 1996). Based on these studies, we chose sets of covariates which we thought would contribute to grizzly bear mortality (Tables 1 and 2).

Model covariates included the predominant forest cover types of alpine, black spruce *P. mariana*, spruce species (withheld reference category), true firs, Douglas fir *Pseudotsuga menziessi* var. *glauca*,

Table 2. Rank of seven candidate models indicating the relative risk of mortality for grizzly bears inhabiting the mountain landscape of the Parsnip River study area, British Columbia, Canada. Models were estimated by comparing mortality locations with study bear non-mortality telemetry locations (using equation 3).

Rank	Candidate model variables	AIC_c	ΔAIC_c	AIC_cw
1	I) Distance to primary logging, secondary & decommissioned roads II) Greenness III) Elevation	361.84	0	1.00
2	I) Distance to primary logging, secondary & decommissioned roads II) Predominant forest cover types (withheld spruce) III) Greenness	372.86	11.02	$4.02E^{-03}$
3	I) Distance to primary logging, secondary & decommissioned roads II) Elevation	383.05	21.21	$2.46E^{-05}$
4	I) Distance to primary logging, secondary & decommissioned roads II) Stand age (categorical)	395.97	34.13	$3.86E^{-08}$
5	I) Distance to primary logging, secondary & decommissioned roads II) Greenness	398.95	37.11	$8.69E^{-09}$
6	I) Elevation	399.72	37.88	$5.92E^{-09}$
7	I) Distance to primary logging, secondary & decommissioned roads	419.26	57.42	$3.39E^{-13}$

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

pine, mixed wood, shrubs, swamps, meadows and anthropogenic landscapes (i.e. urban) obtained from forest cover maps (FCM: BC Ministry of Forests, Prince George, BC). 'Urban' typing on the plateau included the outlying human settlements surrounding Mackenzie and McLeod Lake, the McLeod Lake First Nations reserve, the Bear Lake townsite, and some southern agricultural areas approaching the city of Prince George. However, in the mountains, areas that were not available for timber harvest, such as the right-of-way surrounding the railway, were classified as 'urban', thereby generally having low or no human use. Elevation above sea level, slope, and aspect data were obtained from digital elevation maps built from terrain resources inventory maps (TRIM2: BC Ministry of Water, Land, and Air Protection, Victoria, Canada). Greenness provides an index of the amount of lush green biomass and was calculated for four satellite images using ERDAS® Imagine (Atlanta, Georgia, USA) at a 30 m pixel resolution. High greenness values indicate lush green vegetation as compared with non-vegetated areas, which have very low greenness values (Mace et al. 1999).

For each landscape, we ranked seven *a priori* candidate models and used Akaike Information Criteria for small sample sizes (AIC_c) to determine the most parsimonious model (see Tables 1 and 2; Burnham & Anderson 1998, Anderson et al. 2000). We present the best model as determined by the normalized Akaike weights (AIC_w). We considered significant coefficients to be those with confidence intervals that did not overlap 0. A Spearman's rank correlation obtained using 5-fold cross validation was used to assess the internal consistency of the model (Boyce et al. 2002). Model estimates were then interfaced with GIS to create maps of relative probability of human-influenced mortality risk to grizzly bears across each landscape.

Road information

Locations gathered from the ground, air or the BC government's Compulsory Inspection (CI) database were used to query a straight-line distance to the nearest road using ArcGIS® 8.3 (Environmental Systems Research Institute, Redlands, California, USA). We amalgamated road network layers obtained from Forest Cover Maps (BC Ministry of Forests, Prince George, BC), with those provided by Canadian Forest Products (Canfor) East, Canfor West, The Pas Lumber, and Slocan Forest Products Ltd. (Prince George, BC, Canada). Road networks were visually verified by crosschecking Landsat 5 TM images obtained from Spatial Mapping (on behalf of Canadian Forest Products Ltd. and the BC Ministry of Forests). Roads were classified into three categories: highway, primary logging road, or secondary/decommissioned logging road. Highway refers to the 2-lane paved Highway 97 North. Primary logging roads were main arteries that serviced a number of cutblocks. Secondary logging roads spurred off primary logging roads and were used to access cutblocks. We noticed inconsistencies in the GIS databases with respect to the status of the road and our knowledge of the landscape. Specifically, we lumped decommissioned with secondary roads because true ground access could not be determined using available GIS data.

Results

We captured 18 mountain and 19 plateau females, and 11 mountain and 11 plateau males, for a total of 59 grizzly bears captured during 1998-2003. Adult females were slightly older in the mountains than on the plateau, but there was little or no difference for males (Table 3). No subadult females were captured in the mountains despite a large effort. Sample

Table 3. Mean age at first capture for grizzly bears in mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada, for all sample years (1997-2003).

	Mountains				Plateau			
Bear group	x̄ age 1st capture	Range	SE	N	x̄ age 1st capture	Range	SE	N
Females - adults ≥4 years[1]	Same as below				9.5	4-18	1.57	11[2]
Females - adults ≥7 years[3]	12	7-22	0.96	18	12	7-18	1.66	7[2]
Females - subadults	None captured			0	2	1-4	0.53	7
Males - adult	8	5-16	1.7	6	9	4-17	2.4	5
Males - subadult	2	1-3	0.32	5	2	1-4	0.45	6

[1] Adults were bears ≥4 years of age as long as they were not accompanied by their mother.

[2] One additional adult female's age could not be confirmed and was omitted from this analysis. At capture, she was estimated to be 10 years old.

[3] Comparison provided because no female bears captured in the mountains were <7 years old and therefore represents a subset of the bear group adults ≥4 years.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

sizes were similar for the remaining groups (see Table 3).

Movements of radio-collared bears

During 1998-2003, we gathered 2,475 locations for female grizzly bears ($\bar{x}$ = 75/bear, SE = 8.4, range: 14-175) and 549 locations for males ($\bar{x}$ = 31/bear, SE = 5.3, range: 13-109). We monitored one adult female which moved a straight-line distance of 40.5 km from the plateau to the mountains for denning (see Fig. 1). She was the only radio-collared female to move between these two landscapes, and the family group returned to the plateau upon den emergence (Ciarniello et al. 2005). Of the adult males, two traveled between the landscapes, and three subadult males dispersed from the mountains to the plateau (Fig. 2). On the plateau, both male and female bears crossed Highway 97 and the Parsnip River (see Figs. 1 and 2). There did not appear to be any barriers to movement within or between landscapes. Nevertheless, 53 of the 59 bears remained in their landscape of capture (see Figs. 1 and 2).

Home-range sizes

Adult females that resided in the mountains had significantly smaller home-range sizes than adult females that resided on the plateau when examined individually even after accounting for differences in age (ANCOVA: F = 9.36, df = 2, 23, P(age) = 0.29, P(landscape) = 0.004; $\bar{x}$ (mountain) = 58 km^2, SE = 8, N (home ranges) = 16; $\bar{x}$ (plateau) = 361 km^2, SE = 92, N (home ranges) = 10). Due to sample sizes, we did not further partition the data by the presence of cubs/offspring; since plateau bears were more often accompanied by young and had larger home-range sizes, the differences would have been even more pronounced. Only one lone subadult female plateau bear was monitored. She had a home-range size of 1,607 km^2 (N (locations) = 30).

After accounting for differences in age, there was no statistical difference in home-range size of adult males which resided in the mountains compared with adult males which resided on the plateau when examined individually (ANCOVA: F = 2.34, df = 2, 5, P = 0.19, P(age) = 0.23, P(landscape) = 0.11; $\bar{x}$ (mountain) = 627 km^2, SE = 153, N (home range) = 4, N (locations) = 98; $\bar{x}$ (plateau) = 1,056 km^2, SE = 226, N (home range) = 4, N (locations) = 114), but sample sizes were small. Male plateau bears' home ranges were larger when we included multiple years (ANCOVA: F = 3.23, df = 2, 9, P = 0.09; P (age) = 0.24, P (landscape) = 0.04; $\bar{x}$ (mountains) = 462 km^2, SE = 116, N (home range) = 7, N (locations) = 174; $\bar{x}$ (plateau) = 1,717 km^2, SE = 684, N (home range) = 5, N (locations) = 132). A lone subadult male monitored in the mountains had a home range size of

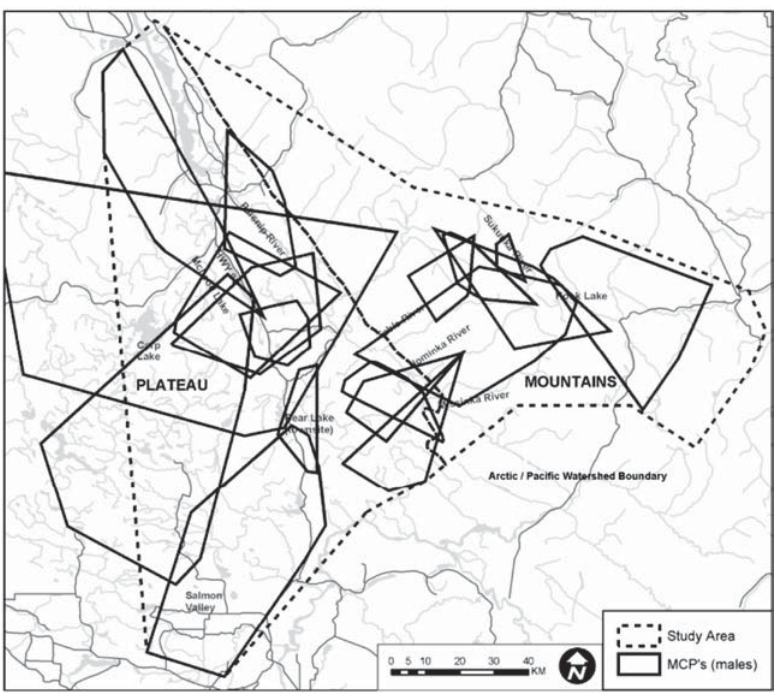


Figure 2. 100% minimum convex polygons for male grizzly bears in the Parsnip River study area, British Columbia, Canada, for all sample years combined (1998-2003). The dashed line indicates the boundary between the mountain and plateau landscapes.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Table 4. Reproductive status at den emergence for female grizzly bears in mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada, for all sample years (1997-2003). Unlike the plateau, all female bears captured in the mountains were ≥7 years of age. Bears monitored for multiple years were assessed each spring for their reproductive status and have been treated as independent. Numbers in brackets represent percent values.

	Mountains (%)	Plateau (%)	
	Number of mothers		
Bear group	≥7 year only	≥7 year only	All ages
Adult female producing COYs	13 (21)	4 (17)	14 (24)
Adult females with offspring older than COYs	18 (30)	13 (57)	14 (55)
Lone females	30 (49)	6 (26)	6 (21)
Mountains vs plateau		P = 0.058	P = 0.010

150 km^2 (N = 26). Three lone subadult males were monitored on the plateau ($\bar{x}$ = 1,830.22 km^2, SE = 836.27, N (locations) = 88).

Litter size

We examined the reproductive status of plateau females regardless of the age of the mother, and found that plateau female bears were more often accompanied by offspring than mountain females (P = 0.01; Table 4). When we omit mothers on the plateau that were <7 years of age, the difference in reproductive status between the landscapes was marginally significant (P = 0.058; see Table 4). Mountain bears averaged 1.93 cubs per litter (SE = 0.14, range: 1-3, N = 13), whereas bears that lived on the plateau averaged 2.0 cubs per litter (P = 0.81, SE = 0.31, range: 1-3, N = 7).

The age of 1st reproduction for three plateau females was one at four years and two at five years ($\bar{x}$ = 4.3 years, SE = 0.33). One radio-marked plateau female was never accompanied by cubs from the age of 5-8. At capture at age 5, this female had pink teats, suggesting she had not previously produced cubs (recapture age 7), indicating a minimum mean age of first reproduction at 5.5 years.

We were unable to estimate the age of primiparity for mountain bears, because all females captured in the mountains were adults. We monitored one mountain female for five consecutive years (age 8-12) which was not accompanied by cubs, and another mountain female (of age 9-15) for seven consecutive years prior to being accompanied by cubs. For both of these females, the mammae were not developed at the time of initial capture suggesting they had not previously nursed cubs. If correct, this indicates a minimum age of primiparity of 13.5 years; although the sample size is small, this is twice the age of bears on the plateau and might be indicative of a large difference between landscapes. In both landscapes, the oldest females to produce cubs were 21 years of age.

Inter-birth interval

We monitored one plateau female which had a 3-year inter-birth interval, and one mountain female which had a 4-year inter-birth interval, however, in the late fall, she lost her litter. We monitored two mountain females which were in the company of their young for four years. One of these females dropped her collar, and the remaining female did not have cubs the three subsequent years of monitoring after her separation, making her inter-birth interval a minimum of eight years.

Independence

We recorded the age at which offspring became independent from their mothers for three family groups (N (mountains) = 1, N (plateau) = 2). We monitored two family groups in the mountains, representing five offspring, from birth over the next four years. One litter became independent at the end of September at 3.75 years of age. The other female dropped her collar also during the last week of September while still in the company of her 3.75-year-old offspring.

On the plateau, one mother separated from her three cubs at 2.8 years old. We also aged at 3-4 years by cementuma, a subadult male captured in a plateau family group. This bear and his sibling became independent from their radio-collared mother the following year at the age of 4-5 years.

Capture condition and body mass

Female bears on the plateau were in better condition than female bears in the mountains even after accounting for differences in age (all captures ANCOVA: F = 6.17, df = 2, 32, P = 0.005; P (age) = 0.74, P (landscape) = 0.006). Regardless of the season, no adult female mountain bears (N = 18) were assessed as being in excellent condition, with the majority in poor condition (78%; age range: 7-22 years, $\bar{x}$ = 12 years, N = 14). Conversely, the majority of adult plateau females were in good (50%) condition, and only two (20%) were in poor condition (age range: 4-18 years, $\bar{x}$ = 10 years, N = 11). If age was a factor, we would have expected opposite results with older mountain females being in better condition than younger plateau females.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

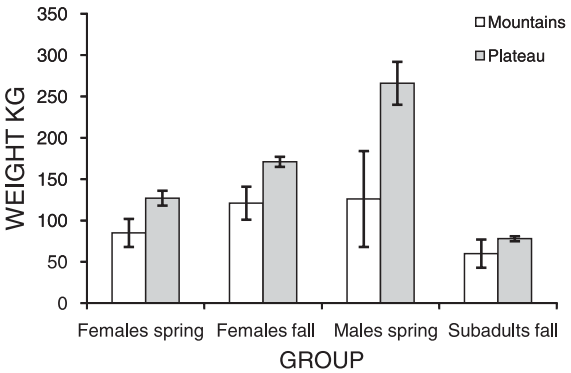


Figure 3. Comparisons of mean initial capture weights in kilograms by age classes for grizzly bears in mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada, for all sample years (1997-2002). Only the first capture event for each animal was used. Subadults and juveniles were bears <4 years of age. Adults were bears ≥4 years of age as long as they were not accompanied by their mother. Spring captures occurred from late April to the beginning of June. Fall captures occurred during September to mid-October. Differences were calculated in kilograms between the same groups in each landscape.

Differences in condition among male bears were less pronounced than among females and may be explained by differences in bear age rather than landscape (spring captures ANCOVA: $F = 7.60$, $df = 2, 15$, $P = 0.005$; P (age) = 0.002, P (landscape) = 0.24, N (mountain) = 10, N (plateau) = 8). In each landscape, we captured two adult male bears in excellent condition. We did not capture any adult males in fair or poor condition on the plateau (N = 5) as opposed to half of the adult males captured in the mountains (N = 3 of 6). All juvenile bears captured in the mountains were in poor condition.

Adult female plateau bears were heavier in spring ($P = 0.02$, $\bar{x} = 42$ kg heavier, spring N (mountain) = 16, spring N (plateau) = 5) and appeared to be heavier in fall ($\bar{x} = 50$ kg heavier) than adult female mountain bears although the sample size in the mountains was small (fall N (mountain) = 2, fall N (plateau) = 6; Fig. 3). The variation in capture age was not responsible for the differences in body mass since the mean capture age of adult females captured in spring was similar in the two landscapes, and all bears used in spring analyses were ≥7 years of age (adult female ANCOVA: $F = 8.44$, $df = 2, 18$, $P = 0.003$; P (age) = 0.81, P (landscape) = 0.0008; age range (mountain): 7-22 years, $\bar{x}$ years = 11.75; age range (plateau): 7-17 years, $\bar{x} = 10.4$ years).

Spring-captured adult male plateau bears were also heavier than adult male bears which inhabited the mountains; however, the difference was likely attributed to age rather than landscape (ANCOVA: $F = 18.56$, $df = 2, 6$, $P = 0.003$; P (age) = 0.006, P (landscape) = 0.16, $\bar{x} = 140$ kg difference, age range (mountain): 5-8 years, $\bar{x} = 6.2$ years, N (spring) = 5; age range (plateau): 4-17 years, $\bar{x} = 10.25$ years, N = 4). There was no significant difference between subadult/juvenile spring capture weights ($P = 0.62$, age range (mountain): 2-3 years, $\bar{x} = 2.25$, N = 4; age range (plateau): 1-4 years, $\bar{x} = 2.06$, N = 5).

Adult and subadult survival

Kaplan-Meier annual survival rates were similar for adult (≥7 years) female bears in the two landscapes (S (mountains) = 0.96, SE = 0.02; S (plateau) = 0.92, SE = 0.08, $P > 0.2$; Table 5). We were unable to estimate survival for subadult mountain females

Table 5. Staggered-entry Kaplan-Meier annual survival estimates by category of grizzly bears in mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada, for all sample years combined (1997-2003). Four male bears that died were not used in these estimates due to the length of time between last contact and their death, i.e. >14 days.

Bear Group	Annual survival rate	SE	CV	L95%CL	U95%CL	N	N dying	N censored
Mountain - females ≥7 years	0.96	0.02	0.03	0.92	1.00	18	2	0
Plateau - females ≥7 years	0.92	0.08	0.09	0.76	1.00	8	1	0
Plateau - females <7 years[1]	0.77	0.1	0.13	0.57	0.97	10	4	0
Plateau - females (all ages)	0.82	0.07	0.09	0.68	0.96	18	5	0
Mountain - males ≥7 years	1	0				4	0	0
Plateau - males ≥7 years	1	0.00				3	0	0
Plateau - males <7 years	0.62	0.16	0.25	0.31	0.92	11	4	3
Mountain - males <7 years	1	0.00				4	0	0
Mountain - males (all ages)	1					8	0	1
Plateau - males (all ages)	0.66	0.14	0.22	0.38	0.94	14	4	3
Mountains and plateau (all bears)	0.9	0.03	0.03	0.84	0.95	58	11	4 males
Plateau - all males & females	0.79	0.06	0.08	0.66	0.91	32	9	3 males
Mountain - all males & females	0.97	0.02	0.02	0.93	1.00	26	2	1 male

[1]This comparison could not be completed for mountain females because all mountain females captured were ≥7 years of age.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Table 6. Grizzly bear offspring survival in mountain and plateau landscapes of the Parsnip River study area, British Columbia, Canada, for all sample years (1997-2003). Offspring whose mothers lost radio-collars while in the company of young were omitted. Bears monitored for multiple years were treated as independent.

	Mountain					Plateau				
	Number of					Number of				
Age class	family groups	cubs	Survivers	Dead	% Dying	family groups	cubs	Survivers	Dead	% Dying
COYs	10	19	7	12	63	6	13	13	0	0
Yearlings - known	4	8	6	2	25	6	14	10	4	29
2 years old - known	3	7	6	1	14	1	3	3	1	33
3 years old - known	1	2	2	0	0	0				n/a
4-5 years old - known	0				n/a	1	2	2	0	0
1 or 2 years - estimate	0				n/a	1	2	2	0	0
>2 years - estimate	6	7	7	0	0	3	6	6	0	0
Total	24	43	28	15		18	40	36	5	

because all mountain females captured were ≥7 years. Subadult plateau females had a 0.77 (SE = 0.10) survival rate. The three adult males captured on the plateau survived until they dropped their collars (S = 1.00), whereas subadult plateau males had a 0.62 (SE = 0.16) survival rate and few survived to become adults. Survival rates were high for adult (N = 4) and subadult (N = 4) mountain males (S = 1.00). Overall, bears that lived in the mountains had a significantly greater chance of surviving than bears that lived on the plateau ($P < 0.01$).

Cub-of-the-year (COY) survival

No COYs were recorded to have died on the plateau (N = 13); however, 63% of COYs born in the mountains did not survive to be yearlings (N = 19; Table 6). We investigated a location of a radio-collared male which lived in the mountains and found a consumed COY. We do not know whether this male killed the COY.

Mortality descriptions

We recorded the death of three radio-collared adult mountain bears (Table 7). The two natural deaths were adult females (7 and 21 years of age), and the legal hunting death was a 7-year-old male.

On the plateau, 12 radio-collared bears died (five females and seven males; see Table 7). One was an adult female (seven years), four were subadult females ($\bar{x}$ (age) = 3, range: 1-4 years), and seven were subadult males ($\bar{x}$ (age) = 3). Four (three females and one male) of the five non-permitted bears killed were not reported to authorities and were located by their tracking device. On the plateau, all deaths for which we could accurately attribute the cause were human-caused (N = 10).

Mortality timing and location

Most bear deaths occurred in the fall (N = 8 of 15; 53%), followed by spring (N = 5; 33%) and summer (N = 2; 13%). No bears were documented to have died during the winter denning period. All fall deaths were on the plateau. Three of the five non-permitted fall kills were associated with hunter-killed moose *Alces alces* carcasses. A grouse *Dendragapus canadensis* hunter shot one bear as problem wildlife, and a rancher shot one bear in defense of life or property.

Omitting the two natural deaths, six of the nine bears shot within our study area were within 100 m of a secondary or decommissioned logging road, one carcass was reported along a decommissioned

Table 7. Causes of mortality for radio-collared grizzly bears compared with results in the British Columbia compulsory inspection database by mountain and plateau landscapes surrounding the Parsnip River study area, British Columbia, Canada during 1997-2003.

	Study sample		Provincial database	
Cause of bear deaths	Mountains	Plateau	Mountains	Plateau
Natural[1]	2 (67%)	0	0	0
Human caused - permitted	1 (33%)	3 (33%)	49 (94%)	34 (35%)
Human caused - not permitted	0	5 (42%)	0	5 (5%)
Human caused - problem wildlife	0	2 (17%)	3 (6%)	59 (60%)
Unknown	0	2 (17%)	0	0
Total	3	12	52	98

[1]A large adult radio-collared male killed one lone female and the other was either killed by the same adult male or scavenged by the male.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

road, but could not be located, one was shot on a primary logging road, and one was 340 m from the highway.

Four bears died outside the study area: three were shot by people positioned on a secondary or decommissioned logging road and one on a ranch. All 12 non-natural plateau bear deaths occurred within 400 m of a road; only the two natural deaths were >500 m from a road (622 m and 9.7 km, respectively).

Province of BC's Compulsory Inspection Database

Using the BC Province's database, we found a 1.46-fold difference (adjusted per ha basis) in the number of grizzly bears killed on the plateau (N = 98) vs the

Table 8. Comparison of grizzly bear population ecology findings between mountain and plateau landscapes surrounding the Parsnip River study area, British Columbia, Canada during 1997-2003.

Parameter	Mountain	Plateau
Density	4x higher (Mowat et al. 2005) DNA based mark-recapture census (49 bears/1,000 km^2).	25% of mountain density (12 bears/1,000 km^2; Mowat et al. 2005)
Discreteness based on telemetry:		
Males all ages	Dispersal & movement - three subadult males dispersed to plateau and two adult males used both areas.	Movement - two adult males used both areas.
Females all ages	Discrete.	Mostly discrete - one female moved to mountains to den.
Home range:		
Adult females	Smaller.	Larger.
Adult males	No difference?	No difference?
Subadult males	May be smaller (small sample)	May be larger (small sample)
Capture age:		
Adult females	Older average.	Younger average.
Adult males	Similar, slightly younger	Similar, slightly older
Subadult females	None captured despite effort	7 captured
Subadult males	No difference	No difference
Capture condition:		
Adult females	Lower	Higher
Adult males	Higher? (difference likely due to age)	Lower? (age effect)
Subadult males	Lower (small sample)	Higher
Capture weight:		
Adult females	Lighter	Heavier
Adult males	Higher difference likely due to age	Lower? (age effect)
Subadult males	No difference	No difference
Reproduction:		
1st reproduction	Older? (inferred from sample)	Younger (small sample)
Litter size	Similar	Similar
Birth interval	Longer? (small sample)	Shorter? (small sample)
Independence age	Older? (small sample)	Younger? (small sample)
Young all ages	Less often accompanied by young	More often accompanied by young
Survival rates:		
COYs	Lower	Higher
Adult females	Slightly higher	Slightly lower (CI's overlap)
Adult males	Same	Same (few captured)
Subadult females	None captured	Low
Subadult males	Higher	Lower
Mortality:		
Human-caused (proportion)	Lower	Higher
Natural (proportion)	Higher	Lower (none reported)
Mortality type (provincial database)	Human-caused permitted (hunting)	Human-caused problem wildlife
Mortality type (study bears)	Natural	Human-caused not permitted
Timing of mortalities (study bears)	Spring and summer (small sample)	Fall-incidental to hunting and some bear hunting
Mortality frequency as a function of density	Lower regardless of higher density	Higher mortality even though density is four times lower than in the mountains

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Table 9. Mortality risk model indicating the relative risk of human-caused grizzly bear mortality in the plateau landscape of the Parsnip River study area, British Columbia, Canada during 1990-2003; N = 106. Variables in italics had confidence intervals that did not include 0.

Variables	β	SE	L95%CL	U95%CL	AIC_c	AIC_cD	AIC_cw
Greenness	-0.026	0.013	-0.051	$-3.10E^{-04}$	623.75	0.00	0.58
Mixed wood	-0.330	0.419	-1.151	0.491			
True firs	0.298	0.438	-0.560	1.156			
Pine	1.137	0.265	0.617	1.657			
Shrub	-2.257	1.023	-4.261	-0.253			
Swamp	0.308	0.565	-0.799	1.415			
Urban	2.494	0.494	1.525	3.462			
Distance to highway	$-2.1E^{-05}$	$2.2E^{-05}$	$-6.5E^{-05}$	$2.34E^{-05}$			
Distance to primary logging road	$-1.1E^{-04}$	$7.1E^{-05}$	$-2.5E^{-04}$	$2.97E^{-05}$			
Distance to secondary & decommissioned logging roads	$1.2E^{-04}$	$2.0E^{-04}$	$-2.7E^{-04}$	$5.12E^{-04}$			

mountains (N = 52) during 1990-2003. Assuming that both populations did not change over the 14 years (1990-2003), then the minimum average annual human-caused mortality rate was 5.5% of the plateau populations and 1% of the mountain population (reported kill/14 years/(bear density∗study area size). Adding the study bear mortality (N (plateau) = 98 + 12, N (mountain) = 52 + 3), the minimum average annual human-caused grizzly bear mortality rate was 6% for the plateau and 1% for the mountains.

Similar to our sample, bears on the plateau had the highest number of deaths recorded closest to secondary/decommissioned logging roads (N = 84), followed by primary logging roads (N = 8), and the highway (N = 6). The majority of mountain bears in the Province's database also had the highest number of deaths recorded closest to secondary and decommissioned logging roads (N = 43), followed by primary logging roads (N = 8), and the highway (N = 1). Unlike our sample of radio-collared bears, the majority of plateau bears deaths were animal control measures, and the majority of mountain bear deaths were hunter kills (see Table 7). We have provided a comparison summary of grizzly bear population ecology results for mountain and plateau landscapes in Table 8.

Modeling mortality

Using the BC Province's database to assess risk of human-caused grizzly bear mortality on the plateau, bears on the plateau were 12 times more likely to die in urban areas, followed by three times in pine-dominated stands, than in their reference category of spruce landcover (Table 9 and Fig. 4). Bears were least likely to die in shrub-dominated vegetation types. For the remaining landscape types, confidence intervals for model coefficients overlapped 0,

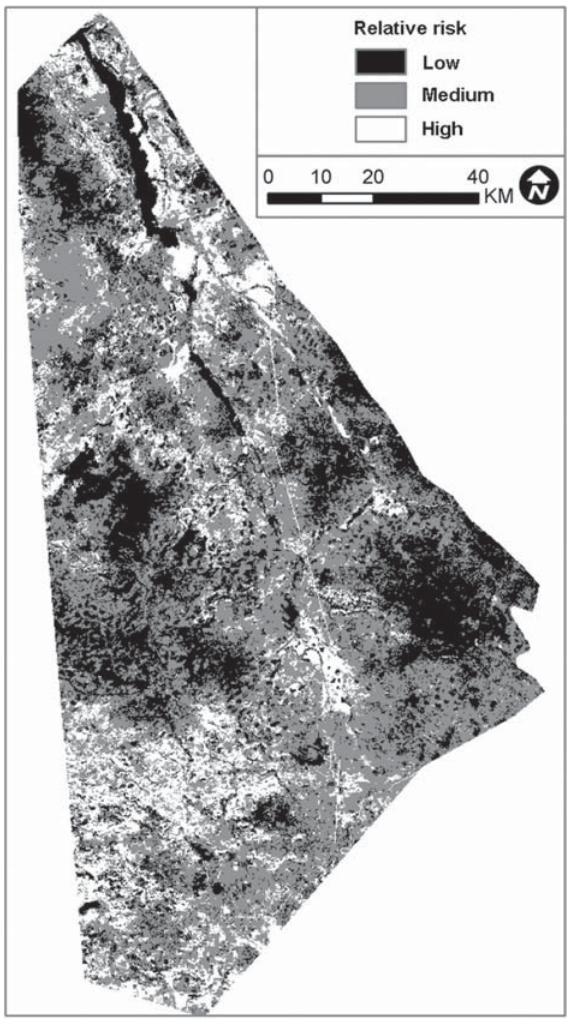


Figure 4. Relative risk of human-caused mortality for grizzly bears inhabiting the plateau landscape of the Parsnip River study area, British Columbia, Canada, calculated using the BC government's compulsory inspection database, 1990-2003 (N = 98). White areas represent an increased relative probability of risk (greater RSF values).

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Table 10. Mortality risk model indicating the relative risk of human-caused grizzly bear mortality in the mountain landscape of the Parsnip River study area, British Columbia, Canada during 1990-2003; N = 55. Variables in italics had confidence intervals that did not include 0.

Variables	β	SE	L95%CL	U95%CL	AIC_c	AIC_cD	AIC_cw
Greenness	-0.054	0.012	-0.078	-0.030	361.84	0.00	1.00
Elevation	-0.004	0.001	-0.006	-0.003			
Distance to primary logging road	$05.90E^{-06}$	$3.1E^{-05}$	$-5.4E^{-06}$	$6.57E^{-05}$			
Distance to secondary & decommissioned logging roads	$02.5E^{-04}$	$7.1E^{-05}$	$-3.9E^{-04}$	$-1.11E^{-04}$			

suggesting poor inference. Grizzly bear mortalities also were more likely in areas with low greenness scores (i.e. less productive vegetation). We were unable to detect whether grizzly bear kills were associated with closer distance to roads because confidence intervals for model coefficients for all road types overlapped 0. The Spearman's Rank correlation between predicted and observed values based on k-fold cross validation for the plateau model was 0.52 (P = 0.1), indicating that this model had overall low internal predictive consistency.

Grizzly bears that lived in the mountains were more likely to die at lower elevations, in areas of low greenness scores, and closer to secondary and decommissioned roads (Table 10 and Fig. 5). A 5-fold cross validation between predicted and observed data provided a mean Spearman's Rank correlation of 0.68 indicating that the mountain risk model had good internal predictive capability and predictions were non-random (P < 0.05).

Discussion

We examined risk factors and population parameters of grizzly bears that might be related to the difference in density between two adjacent landscapes. The higher density (Mowat et al. 2005), higher adult survival, and lower cub survival suggest that density-dependent processes were stronger in the mountain population than in the plateau population. We obtained small sample sizes for age of primiparity, inter-birth interval, and offspring independence. Regardless, the long inter-birth interval and late age of independence of mountain bear offspring support our conclusion that this population is controlled by density-dependent factors. We chose to report on these parameters despite the small sample sizes, because they represent bears that were followed for long periods. We monitored females that never produced cubs in 5-8 years of consecutive monitoring; others lost litters, and the few that kept their cubs did so for ≥4 years. For example, we obtained a fair sample of COY mortality in the mountains showing that although some females were breeding few kept their cubs; this pattern of reproduction and loss results in low sample sizes for parameters that relate to older cubs, such as inter-birth interval and independence, but it is also expected in populations where density-dependent processes are operating. Results of all parameters with

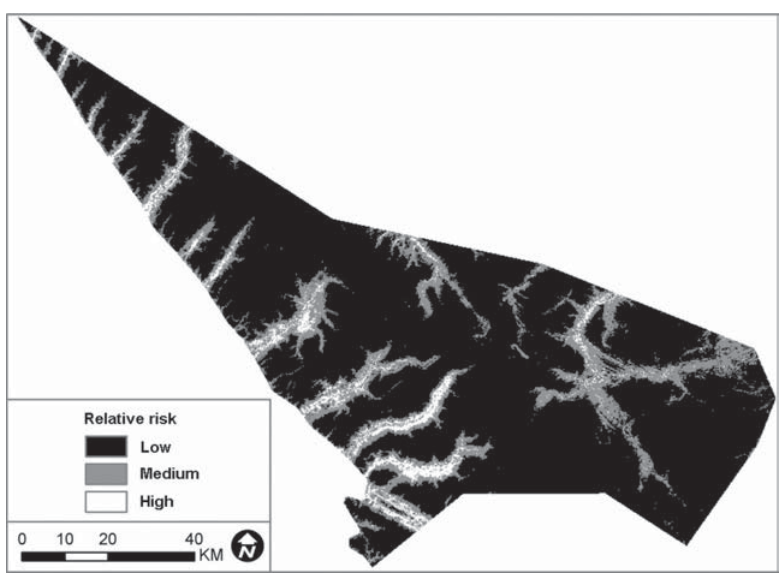


Figure 5. Relative risk of human-caused mortality for grizzly bears inhabiting the mountain landscape of the Parsnip River study area, British Columbia, Canada, calculated using the BC government's compulsory inspection database, 1990-2003 (N = 52). White areas represent an increased relative probability of risk (greater RSF values).

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

low sample sizes were consistent with large differences between landscapes.

For bears, density dependence results in reduced cub production and survival, recruitment, and/or increased dispersal (Taylor 1994, Boyce et al. 2001, Eberhardt 2002). Unlike the plateau, COYs born to mountain females had high mortality, but the cause(s) of COY mortality is unknown. Intraspecific killing of cubs has been reported for bears (Miller 1990b, Taylor 1994, Swenson et al. 1997), and we located one mountain COY that was probably killed by a male grizzly. Also, one adult mountain female's death was attributed to intraspecific killing, and the other was possibly due to intraspecific killing. For density dependence to regulate a population one or more vital rates must decrease with increasing density (Sinclair 1989). For bears, those vital rates are usually intraspecific killing and/or dispersal (McLellan 1994). Our results suggest that density-dependent response in vital rates appears to be more important to mountain than to plateau bear demographics, including poorer nutrition and possibly increased intraspecific killing.

Unlike the mountains where grizzly bears were more likely to die of natural causes, human-caused mortality was the only documented source of bear deaths on the plateau. Forest harvest did not appear to have negative effects on reproductive parameters of grizzly bears and differences in reproductive parameters were in accordance with predictions from a density-dependent response. We found that female bears in our low-density area (i.e. the plateau) were in better condition, had higher cub survival and larger home-range sizes than female bears in the mountains. Our earlier work found that differences in habitat could not account for the differences in density and that plateau bears consumed more high-quality foods, such as meat and berries, than mountain bears (Ciarniello et al. 2007a). Although we did not directly measure bear foods in our study, based on our findings of female plateau bears being significantly heavier, in better condition, and more often accompanied by young, we suggest that the density of plateau bears was not limited by available food resources. Rather, the high recorded study bear mortality and low survival rates of subadult plateau bears suggest that the density of bears on the plateau was limited by human-caused mortality.

Overall, bears had a significantly greater chance of surviving in the mountains than on the plateau, but survival rates varied by sex and age class. Grizzly bear population growth rates are sensitive to adult female survival (McLellan et al. 1999, Boyce et al. 2001). Plateau females had lower survival than their mountain counterparts, but the difference was not significant. Despite intensive trapping efforts, our sample size of adult female bears ≥ 7 years in the mountains was twice that of plateau bears possibly suggesting there were more older female bears in the mountains. We found that more female study bears were poached on the plateau (i.e. animals killed without a legal license and not reported to authorities) than males. Survival of subadult bears that lived on the plateau was low.

During five years of spring and fall trapping sessions, we captured only three males ≥ 7 years of age which lived on the plateau; apparently the majority of subadult males did not survive to become adults. Similar to our findings, Miller (1990a) found that males became rare when hunting pressure was increased in a heavily hunted area of Alaska. We also found that body mass and condition for adult male bears was similar, which we attribute to classifying male bears as 'mountain' or 'plateau' based solely on their capture location. For female bears, the capture location adequately reflected the landscape where they lived, because movement between landscapes occurred only on one occasion. However, two large males in excellent condition, one captured in the mountains and one on the plateau, were known to travel between landscapes. Therefore, for these adult males, their capture location does not necessarily reflect their use of the landscape.

The pattern of bear mortality was consistent between the Province's database and our sample of study animals; more plateau bears died than mountain bears despite the lower density of plateau animals. By contrasting bear mortality locations with bear-use locations, we were able to document that urban areas had the highest risk of human-caused grizzly bear mortality on the plateau, which is consistent with other grizzly bear mortality studies (Schoen et al. 1994, Mattson & Merrill 2002, Nielsen et al. 2004, Schwartz et al. 2006). Our sample of study bears rarely used urban areas and few were problem animals. However, the province's database revealed that when bears used urban areas they experienced high mortality rates (see Table 7). Attraction of animals to attractive sinks (Delibes et al. 2001) or ecological traps (Battin 2004) can result in serious population-level consequences (Kristan 2003).

From field observations, it appeared that the majority of radio-collared bear deaths were associated

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

with the forestry road network; but we could not detect selection for or against road networks on the plateau, possibly because we were unable to separate decommissioned from secondary roads. Schoen et al. (1994:334) found that grizzly/brown bears were not displaced by 'secondary and blocked' roads resulting in 'more frequent bear-human encounters' and higher bear mortality in those areas. Our earlier work revealed that the presence of certain road types may affect grizzly bear use of habitats, but was dependent upon the scale of analysis (Ciarniello et al. 2007b).

In the mountains, bear deaths were associated with secondary and decommissioned logging roads but not primary logging roads. Each year, forestry activities moved further into the mountains by way of the major river valleys leading from the plateau. Increased human access afforded by the forestry road network appeared to allow for a myriad of human activities into formerly pristine habitats, bringing humans and bears into closer contact resulting in higher bear mortality (Schoen et al. 1994). We predict that bear mortality will increase in the mountains if roads are built without strictly managing human access. Indeed, we documented one mountain male shot while feeding in a mountain cutblock.

Our sample of plateau bear deaths coincided with the timing of hunting for other game species, such as moose. During spring, backcountry areas were difficult for people to access due to the snow melt, and in summer, people tended to remain around primary locations (e.g. lakes). Human use of backcountry areas increased in fall during the ungulate hunting season. In Alaska, Miller & Tutterrow (1999) reported that people shooting bears in defense of life and property were most often hunting deer and moose. In our study area, hunting for moose began 10 September and ended 5 November, involving on average about 10,000 hunter days in the study area. This fall period corresponded with the majority of bear deaths, and all bears killed in the fall were on the plateau. Similar to our results, survival was lowest in the fall for bears inhabiting the Greater Yellowstone Ecosystem (Schwartz et al. 2006). We think that some study bears may have been attracted to hunter kills during the fall hyperphagia period making them vulnerable to being shot. Excluding COYs, the primary source of plateau study bear mortality occurred from humans, without a permit, killing bears. Our findings support the hypothesis of Mattson et al. (1996) that grizzly bear deaths were dependent upon the type and frequency of contact between bears and humans; the number of people carrying firearms on the plateau landscape increased substantially in the fall. The density of bears on the plateau probably was affected by human-caused mortality and habitat loss (i.e. urban areas).

Our data do not allow us to determine if the mortality rates we present are sustainable because to do so would require information on trend in bear numbers and human use of the landscape. However, our reported annual mortality rates (plateau 6%, mountains 1%) are considered minimum rates, because they did not account for inflation factors which managers often use to calculate the total mortality rate (e.g. ratio of reported:unreported mortality). Bears should be able to sustain a mortality rate of ~6% (Harris 1986), but any additional mortality might be excessive. If there is a link between urban areas associated with industrial landscapes, human access and bear mortality rates, then it should be safe to assume that as human access continues to increase eventually mortality rates will exceed sustainable levels.

We did not record any female dispersal between landscapes, suggesting that the number of breeding females is not strongly influenced by dispersal. Subadult male dispersal has been cited as one of the main mechanisms regulating grizzly bear populations in North America (McLellan 1994, Schwartz et al. 2006), and we found male sex-biased dispersal from the mountains to the plateau and some adult male movement between the landscapes. We suggest that given the low level of female dispersal from the mountains to the plateau, dispersal from the mountains is inadequate to compensate for grizzly bears lost through human-caused bear mortality on the plateau.

Management implications

Risks associated with the creation of forestry-based towns (i.e. urban areas), and for the mountains the secondary road networks, appear to be a greater threat to interior BC grizzly bears than the direct habitat changes caused by those activities. We believe that society wants grizzly bears on working landscapes, but it is not clear which density most people would find acceptable. From our data, it appears that grizzly bear survival on working landscapes would likely be higher if grizzly bears were dissuaded from entering urban areas, forest harvesting activities were carried out with fewer permanent roads, and ungulate hunters practiced 'bear-smart'

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

hunting techniques. Therefore, we recommend the following:

- Advocate bear-smart management techniques in resource-based urban landscapes and forestry camps, reducing and managing non-natural bear attractants, such as garbage, gardens and fruit trees.
- Provide adequate enforcement and other compliance-inducing methods to reduce poaching of grizzly bears.
- Increase bear-smart content in hunter education. Education courses should emphasize that it is not acceptable to kill a grizzly bear if it takes your game. Further, education should include a component on bear species identification (i.e. black vs grizzly bear). Hunter education courses also should include a component on how to reduce human-bear conflicts while hunting in grizzly bear country.
- Coordinate access planning to minimise the amount and duration of active roads. This may occur through deactivation of forestry roads as well as logging plans that minimize the need for permanent roads, thereby maintaining large roadless areas on the landscape.

Acknowledgements - funding for the Parsnip Grizzly Bear Project was provided by Forest Renewal BC, the Forest Investment Accounts with support from Canadian Forest Products Ltd. and The Pas Lumber. Slocan Forest Products Ltd. and the McGregor Model Forest Association provided additional Project support. L.M. Ciarniello received graduate support from the Natural Science and Engineering Research Council of Canada and Province of Alberta Fellowship. H. Beyer provided GIS work. We thank M. Wood and P. Hengeveld of the Peace-Williston Fish and Wildlife Compensation Program for allowing us to monitor some of their study animals. Field and logistical assistance was provided by J. Paczkowski, E. Jones, G. Watts, I. Ross, C. Mamo, G. Altoft, L. Frey and D.A. Bears. We thank J. Swenson, A. Derocher, C. Cassady St. Clair, F. Schmiegelow, I. Sterling and an anonymous reviewer for constructive comments which improved this manuscript.

References

Anderson, D.R., Burnham, K.P. & Thompson, W.L. 2000: Null hypothesis testing: Problems, prevalence, and an alternative. - Journal of Wildlife Management 64: 912-923.

Battin, J. 2004: When good animals love bad habitats: Ecological traps and the conservation of animal populations. - Conservation Biology 18: 1482-1491.

Ben-David, M., Titus, K. & Beier, L.R. 2004: Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? - Oecologia 138: 465-474.

Boyce, M.S., Blanchard, B.M., Knight, R.R. & Servheen, C. 2001: Population viability for grizzly bears: a critical review. - International Association for Bear Research and Management Monograph Series No. 4, 39 pp.

Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K.A. 2002: Evaluating resource selection functions. - Ecological Modelling 157: 281-300.

Burnham, K.P. & Anderson, D.R. 1998: Model selection and inference: a practical information theoretic approach. - Springer-Verlag, New York, USA, 353 pp.

Ciarniello, L.M. 2006: Demography and habitat selection by grizzly bears (*Ursus arctos*) in central British Columbia. - Ph.D. dissertation, University of Alberta, Edmonton, Alberta, Canada, 215 pp.

Ciarniello, L.M., Boyce, M.S., Heard, D.C. & Seip, D.R. 2005: Denning behaviour and den site selection of grizzly bears along the Parsnip River, British Columbia, Canada. - Ursus 16: 47-58.

Ciarniello, L.M., Boyce, M.S., Heard, D.C. & Seip, D.R. 2007a: Components of grizzly bear habitat selection: density, habitats, roads, and mortality risk. - Journal of Wildlife Management 71: 1446-1457.

Ciarniello, L.M., Boyce, M.S., Seip, D.R. & Heard, D.C. 2007b: Grizzly bear habitat selection is scale dependent. - Ecological Applications 17: 1424-1440.

Delibes, M., Gaona, P. & Ferreras, P. 2001: Effects of an attractive sink leading into maladaptive habitat selection. - American Naturalist 158: 277-285.

DeLong, C. & Tanner, D. 1996: Managing the pattern of forest harvest: lessons from wildfire. - Biodiversity and Conservation 5: 1191-1205.

DeLong, C., Tanner, D. & Jull, J.J. 1993: A field guide for site identification and interpretation for the southwest portion of the Prince George Forest Region, # 24 - British Columbia Ministry of Forests. Crown Publishing Inc. Victoria, British Columbia, 290 pp.

DeLong, C., Tanner, D. & Jull, J.J. 1994: A field guide for site identification and interpretation for the southwest portion of the Prince George Forest Region, # 29 - British Columbia Ministry of Forests. Crown Publishing Inc. Victoria, British Columbia, 141 pp.

Eberhardt, L.L. 2002: A paradigm for population analysis of long-lived vertebrates. - Ecology 83: 2841-2854.

Eberhardt, L.L., Blanchard, B.M. & Knight, R.R. 1994: Population trend of the yellowstone grizzly bear as estimated from reproductive and survival rates. - Canadian Journal of Zoology 72: 360-363.

Gau, R.J., Mulders, R., Ciarniello, L.M., Heard, D.C., Chetkiewicz, C.L.B., Boyce, M., Munro, R., Stenhouse, G., Chruszcz, B., Gibeau, M.L., Milakovic, B. & Parker, K.L. 2004: Uncontrolled field performance of Televilt GPS-Simplex™ collars on grizzly bears in

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

western and northern Canada. - Wildlife Society Bulletin 32: 693-701.

Greenwood, M. 1926: The errors of sampling of the survivorship tables. - Appendix 1 in Report on Public Health and Statistical Subjects 33, London, pp. 23-25.

Harris, R.B. 1986: Modeling sustainable harvest rates for grizzly bears. - In: Dood, A.E., Brannon, R.D. & Mace, R.D. (Eds.); Final programmatic environmental impact statement: The grizzly bear in northwestern Montana. Montana Department of Fish, Wildlife and Parks, Helena, Montana, Appendix K, pp. 268-279.

Hilderbrand, G.V., Jenkins, S.G., Schwartz, C.C., Hanley, T.A. & Robbins, C.T. 1999: The importance of meat, particularly salmon, to the body size, population productivity, and conservation of North American brown bears. - Canadian Journal of Zoology 77: 132-138.

Hooge, P.N. & Eichenlaub, B. 1997: Animal movement extension to Arcview. version 1.1. - Alaska Biological Science Center, U.S. Geological Survey, Anchorage, AK, USA. Available at: http://www.absc.usgs.gov/glba/gistools/animal_mvmt.htm (Last accessed on 10 July 2009).

Johnson, C.J., Nielsen, S.E., Merrill, E.H., McDonald, T.L. & Boyce, M.S. 2006: Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. - Journal of Wildlife Management 70: 347-357.

Jonkel, J.J. 1993: A manual for handling bears for managers and researchers. - United States Fish and Wildlife Service, NS 312, University of Montana, Missoula, Montana, USA, 175 pp.

Kristan, W.B. III 2003: The role of habitat selection behavior in population dynamics: source-sink dynamics and ecological traps. - Oikos 103: 457-468.

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

Mace, R.D., Waller, J.S., Manley, T.L., Lyon, L.J. & Zuuring, H. 1996: Relationships among grizzly bears, roads and habitat in the Swan Mountains, Montana. - Journal of Applied Ecology 33: 1295-1404.

Mattson, D.J., Herrero, S., Wright, R.G. & Pease, C.M. 1996: Science and management of Rocky Mountain grizzly bears. - Conservation Biology 10: 1013-1025.

Mattson, D.J., Knight, R.R. & Blanchard, B.M. 1987: The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. - International Association for Bear Research and Management 7: 259-273.

Mattson, D.J. & Merrill, T. 2002: Extirpations of grizzly bears in the contiguous United States, 1850-2000. - Conservation Biology 16: 1123-1136.

Mattson, D.J. & Merrill, T. 2004: A model-based appraisal of habitat conditions for grizzly bears in the Cabinet-Yaak region of Montana and Idaho. - Ursus 15: 78-91.

McLellan, B.N. 1994: Density-dependent population regulation of brown bears. - In: Taylor, M. (Ed.); Density-dependent population regulation in black, brown, and polar bears. International Association for Bear Research and Management Monograph Series No. 3, pp. 3-14.

McLellan, B.N. 1990: Relationship between human industrial activity and grizzly bears. - International Association for Bear Research and Management 8: 57-64.

McLellan, B.N., Hovey, F.W., Mace, R.D., Woods, J.G., Carney, D.W., Gibeau, M.L., Wakkinen, W.L. & Kasworm, W.F. 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.

McLellan, B.N. & Shackleton, D.M. 1989: Grizzly bears and resource-extraction industries: habitat displacement in response to seismic exploration, timber harvesting, and road maintenance. - Journal of Applied Ecology 26: 371-380.

Miller, S.D. 1990a: Detection of differences in brown bear density and population composition caused by hunting. - International Association of Bear Research and Management 8: 393-404.

Miller, S.D. 1990b: Impact of increased bear hunting on survivorship of young bears. - Wildlife Society Bulletin 18: 462-467.

Miller, S.D., Sellers, R.A. & Keay, J.A. 2003: Effects of hunting on brown bear cub survival and litter size in Alaska. - Ursus 14: 130-152.

Miller, S.D. & Tutterrow, V.L. 1999: Characteristics of nonsport moralities to brown and black bears and human injuries from bears in Alaska. - Ursus 11: 239-252.

Mowat, G.K., Heard, D.C. & Gaines, T. 2004: Predicting grizzly bear (*Ursus arctos*) densities in BC using a multiple regression model. - British Columbia Ministry of Water Land and Air Protection, Victoria, British Columbia, Canada, 16 pp. Available at: http://wlapwww.gov.bc.ca/wld/grzz/#gbpop_harvest (Last accessed on 3 April, 2009).

Mowat, G.K., Heard, D.C., Seip, D.R., Poole, K.G., Stenhouse, G. & Paetkau, D.W. 2005: Grizzly *Ursus arctos* and black bear *Ursus americanus* densities in the interior mountains of North America. - Wildlife Biology 11(1): 31-48.

Nagy, J.A., Hawley, A.W.L. & Barrett, M.W. 1989: Population characteristics of grizzly and black bears in west-central Alberta. - AEC Report V88-R1, Alberta Environmental Centre, Vegreville, Alberta, Canada, 33 pp.

Nielsen, S.E., Boyce, M.S. & Stenhouse, G. 2006: A habitat-based framework for grizzly bear conservation in Alberta. - Biological Conservation 130: 217-229.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Nielsen, S.E., Herrero, S., Boyce, M.S., Mace, R.D., Benn, B., Gibeau, M.L. & Jevons, S. 2004: Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. - Biological Conservation 120: 101-113.

Pollock, K.H., Winterstein, S.R., Bunck, C.M. & Curtis, P.D. 1989: Survival analysis in telemetry studies: the staggered entry design. - Journal of Wildlife Management 53: 7-15.

Schoen, J.W., Flynn, R.W., Suring, L.H., Titus, K. & Beier, L.R. 1994: Habitat-capability model for brown bear in southeast Alaska. - International Association for Bear Research and Management 9: 327-337.

Schwartz, C.C., Haroldson, M.A., White, G.C., Harris, R.B., Cherry, S., Keating, K.A., Moody, D. & Servheen, C. 2006: Temporal, spatial, and environmental influence on the demographics of grizzly bears in the greater Yellowstone ecosystem. - Wildlife Monograph 161: 1-68.

Seber, G.A.F. 1984: Multivariate observations. - John Wiley & Sons, New York, USA, pp. 308-317 and 686.

Servheen, C. 1984: The status of the grizzly bear and the interagency grizzly bear recovery effort. - In: Proceedings of the 64th Annual Conference of the Western Association of Fish and Wildlife Agencies, Victoria, British Columbia, pp. 227-234.

Sinclair, A.R.E. 1989: Population regulation in animals. - In: Cherrett, J.M. (Ed.); Ecological concepts: the contribution of ecology to an understanding of the natural world. Blackwell Scientific Publications, Oxford, United Kingdom, pp. 197-241.

Stringham, S.F. 1990: Grizzly bear reproductive rate relative to body size. - International Association for Bear Research and Management 8: 433-443.

Swenson, J.E., Sandegren, F., Söderberg, A., Bjärvall, A., Franzén, R. & Wabakken, P. 1997: Infanticide caused by hunting of male bears. - Nature 386: 450-451.

Taylor, M. (Ed.) 1994: Density-dependent population regulation of black, brown, and polar bears. - International Association for Bear Research and Management Monograph Series No. 3, 43 pp.

Welch, C.A., Keay, J., Kendall, K.C. & Robbins, C.T. 1997: Constraints on frugivory by bears. - Ecology 78: 1105-1119.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use