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We collected hair samples from bears and used microsatellite genotyping to identify individual bears on three study areas near the Canadian Rocky Mountains. We estimated density of grizzly bears *Ursus arctos* in eight different ecosystems across five study areas, including the reanalysis of two previously published data sets. We also estimated black bear *U. americanus* density for two ecosystems in one study area. Grizzly bear density was lowest in boreal and subboreal plateau areas, moderate in the Rocky Mountain east slopes and highest in the Rocky Mountain west slopes. Presumably these gross differences are related to ecosystem productivity. In the Rocky Mountain west slopes, grizzly bear density was lower in populations that were partially isolated from the continuous bear population to the north. Presumably, these differences have more to do with human impacts on habitat and survival than ecosystem productivity, because productivity in partially isolated areas was similar to productivity in adjacent continuous populations. We show that large differences in bear density occur down to the ecoregion scale; broader ecosystem classes such as Banci's (1991) grizzly bear zones, ecoprovinces or ecozones would include areas with major differences in density and are therefore too coarse a scale at which to predict grizzly bear density. There appears to be little movement across ecoregion boundaries further suggesting that this may be an appropriate scale at which to extrapolate density. Differences in density across finer-scale ecosystems are likely due to seasonal movements and not population level differences in density. Average bear movements were longer in less productive ecosystems. Female grizzly bears did not appear to leave their home ranges to fish for salmon *Oncorhynchus* spp., and extra-territorial movements by males appeared to be rare, in both ecosystems which supported spawning salmon.

Key words: carrying capacity, closure, ecosystems, movements, population size, Ursus americanus, Ursus arctos

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The conservation of grizzly bears *Ursus arctos* is a high profile wildlife management issue in North America. The issue encompasses both concern about land use practices, and the impact of hunting and other human caused mortality. Estimates of grizzly bear abundance were few until the recent development of genetic tagging techniques (Taberlet et al. 1997, Woods et al. 1999). DNA-based inventories have been applied in many areas of western Canada to facilitate harvest management decisions. However, these inventories are expensive, and they are unlikely to be applied in all areas where grizzly bears occur. In contrast, there is much less conservation concern for black bear *U. americanus* populations in western North America, although the species is harvested in large numbers, and no empirically derived estimates of abundance exist for the species in the provinces of British Columbia or Alberta.

Estimates of density have direct use for harvest management in both British Columbia and Alberta, especially for grizzly bears, which are managed under a quota system. Human caused mortality of adult bears is the primary factor limiting grizzly bear populations in western North America (McLellan et al. 1999); hence, controlling harvest and other human-caused mortality is a major conservation objective. Precise estimates of abundance are required because allowable harvests from bear populations are very small (Taylor 1994). In both British Columbia and Alberta, managers use habitat based population extrapolations to estimate carrying capacity for grizzly bears and then adjust these numbers subjectively based on human impacts on habitat suitability (Fuhr & Demarchi 1990, Nagy & Gunson 1990). However, estimates of carrying capacity are unavailable for many of the ecosystems where grizzly bears occur.

Banci (1991) identified 14 grizzly bear zones in western Canada based on climate and landform (Wiken 1986), which presumably reflect variation in both primary productivity (which we equate to food in this paper) and life history strategies for bears. Finer scales of ecosystem classification are available, couched within the same system; from coarsest to finest they are: ecozones, ecoprovinces and ecoregions (Wiken et al. 1996). We treat the idea that bear density varies among ecosystems as a hypothesis. To this end, we conducted several DNA-based inventories, reviewed other studies of grizzly bear density in interior North America, and compared density among ecosystems.

The objectives of our study were to estimate population density of grizzly bears in five interior ecosystems in three study areas and estimate black bear density in two interior ecosystems in one study area. For two earlier studies (Mowat & Strobeck 2000, Poole et al. 2001), we recalculated density in order to generate estimates for four additional ecosystems. We wanted to compare grizzly bear abundance among ecosystems in and around the Rocky Mountains. We assess which scale of ecosystem mapping delineates measurable differences in grizzly bear populations. This information is useful in assessing conservation status (Banci 1991) and for extrapolating density to predict harvest.

Methods

Study areas

Yellowhead

This 5,352-km^2 area contains two distinctly different habitats separated by an ecozone boundary. The mountainous habitat in Jasper National Park (ranging to 3,000 m a.s.l.) is typical of the Rocky Mountain east slopes and is the largest portion of the study area. To the east, the topography is rolling and the habitat more typical of the boreal region to the north and east (Franklin et al. 2001). The Yellowhead study area contains a variety of habitats including alpine and subalpine meadows, wet meadow complexes, and forests dominated by conifers in the west with a greater deciduous component further east of the Rocky Mountains. No salmon *Oncorhynchus* spp. are available to bears in this area.

People live throughout the study area, both in and outside the park, although human residents (and use) are much fewer in the park relative to the public land to the east. Human use includes forestry, coal mining, oil and gas exploration and development, transportation corridors, trapping and commercial outfitting outside the park. In the park human use includes one major transportation corridor and a single paved road; other use is mainly non-motorized recreation.
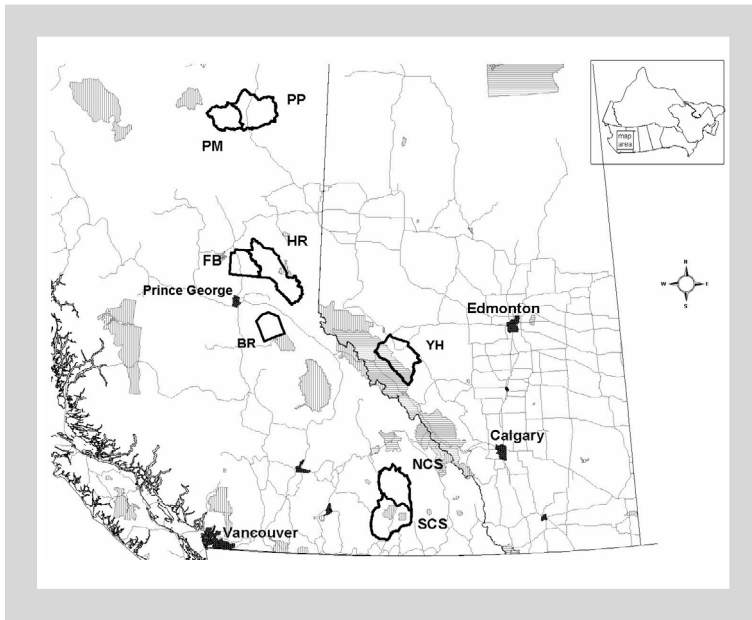
Figure 1. Location of the study areas (outlined in heavy black). PP = Prophet plateau, PM = Prophet mountains, HR = Parsnip mountains, FB = Parsnip plateau, BR = Bowron River, YH = Yellowhead, NCS = northcentral Selkirk Mountains and SCS = southcentral Selkirk Mountains. Parks are stippled gray, highways are thin black lines and provincial and international boundaries are thicker black lines. Cities are black.

and varies greatly in extent among drainages; the headwaters of most watersheds are undeveloped wilderness. There are no permanent residents in the mountains.

Herrick Creek, to the south, has fall chinook salmon *O. tshawytcha* spawning runs. Spawning fish reach natal streams in mid-August or September and are available in < 10% of the mountain study area. Total numbers of spawning adults enumerated within Herrick Creek and associated tributaries have ranged from approximately 500 to 4,000 fish annually. In fall 2000, 679 fish were counted, and the run size was estimated at 2,000-2,500 fish (B. Toth, unpubl. data).

Bowron

The Bowron River study area covers 2,494 km^2 and is a broad valley that separates a more rugged mountainous area in the east from less rugged topography in the west; however, no ecoregion boundaries occur in the area. Low elevations are covered with subboreal forest, while moderate elevations are predominantly subalpine forest. Only very small patches of alpine exist in the western portion of the study area, while larger and more continuous patches occur in the east due to the more mountainous topography. Likewise, avalanche chutes are rare in the eastern portion of the study area, but common in the west. Most of the area is covered by an extensive road system although roads in the steep eastern portion are few and often impassable. Extensive logging occurred in the subboreal zone during the 1980s in an effort to control an insect outbreak. The center of the study area contained a 640-km^2 clearcut which was largely continuous.

There are both chinook and sockeye salmon *O. nerka* runs in the Bowron River. Total spawning escapement of chinook within the Bowron system was estimated at 5,636 for 2001, with an estimated mean annual escapement of 6,168 for the previous 10-year period (D. Michie, unpubl. data). Sockeye salmon enter the Bowron River slightly later than the chinook and the majority migrate directly through the mainstem and spawn south of the study area in Bowron Lakes Provincial Park. Total spawning escapement of sockeye within the Bowron River in 2001 was estimated to be 5,842 (N. Todd, unpubl. data) with a mean annual escapement of 8,990 for the previous 10-year period (1987-1996).

Parsnip

The Parsnip River study area covers 9,452 km^2 and is divided into plateau and mountain areas for analysis based on an ecoregion boundary (Demarchi et al. 1990; Fig. 1). In the 3,016-km^2 plateau area, elevations range from about 800 to 1,100 m a.s.l. In the 6,436-km^2 mountainous area elevations range from valley bottoms at about 800 m to peaks of 2,700 m.

The plateau portion of the study area primarily supports subboreal conifer forests, and lakes and wetlands are abundant. Industrial development is extensive including a major highway and a network of forest roads and scattered human settlement. A substantial proportion of the plateau forests has been logged over the past 30 years and supports new and regenerating cutblocks.

In the mountainous portion of the study area, subalpine conifer forests dominate at lower elevations. Large avalanche chutes measuring in the square kilometers are common. Rolling meadows and open basins are common in the subalpine. Higher elevations contain a combination of barren rock, ice or alpine tundra communities.

Industrial development in the mountains is less than on the plateau, although all major and some minor watersheds have logging roads along at least part of the valley bottom. Logging is generally at lower elevations

Prophet River

The Prophet River study area is located in the boreal region of northeastern British Columbia and is described by Poole et al. (2001). We divided the study area into mountains and plateau areas for population estimation based on an ecoprovince division (Poole et al. 2001).

Central Selkirk Mountains

The Selkirk Mountains study area is located in the temperate mountains of southeastern British Columbia and is described by Mowat & Strobeck (2000). We divided the area north-south for population estimation based on evidence from Proctor et al. (2002) who used genetic methods to show that there was little north-south movement of bears in the study area, and Mowat & Strobeck (2000) who found greater detection success in the north than in the south. The majority of the 9,866-km^2 study area is in a single ecoregion; a sliver of area along the southern boundary fell within a dryer ecoregion.

Hunting and recreational activity

Recreational use in all study areas varied seasonally and included hunting, fishing, camping, and all-terrain vehicle use, except in Jasper Park in the Yellowhead study area. Grizzly bear hunting was controlled by quota in both Alberta and British Columbia. Hunter effort is controlled by limiting the number of hunters through a lottery system. Hunters were encouraged to shoot males and the shooting of a bear accompanied by another bear was prohibited to protect females with young. Black bears were hunted during spring and fall with a bag limit of two per hunter. All grizzly bears killed (including problem bears killed by government employees) were submitted to government wildlife staff for data and sample collection.

Field methods

We followed the field methods outlined by Woods et al. (1999) and Mowat & Strobeck (2000). Briefly, we used a systematic grid design to distribute hair capture sampling effort across each study area. One hair removal site was set in each cell, and sites were moved within each cell for each subsequent trapping session. Sites were baited with rotten blood, fish or meat, and hair samples were removed from bears as they passed by the single strand of barbed wire surrounding the site. A novel scent such as beaver castor, catnip, skunk essence or fennel oil was added during each recapture session to reduce the chance that bears would become disinterested in bait sites in later trapping sessions.

In the Yellowhead area, we trapped three hair capture sessions between 19 May and 9 July 1999 (Table 1). Intensive live capture effort using both aerial darting and leg snares was conducted before and during our hair removal work. Bears were attracted to open areas (to facilitate aerial darting) and snare sites with large baits. Grizzly bears were live captured between 28 April and 20 June 1999 with much greater effort during April to mid-May. Live capture effort was carefully distributed across the study area, and home range data were available for a number of bears (Nielsen et al. 2002; J. Boulanger & G. Stenhouse, unpubl. data.).

In the Parsnip study area, we trapped four hair capture sessions between 30 May and 2 August 2000 (see Table 1). We conducted additional hair sampling at 10 sites along three salmon spawning streams in the mountains along the southern boundary, between 16 August and 4 September 2000. River sites were checked every 4-5 days and were not moved between sessions. River sites differed from upland sites in that they were not baited; 1-3 strands of wire were strung across sand bars or trails to remove hair from passing bears. In the north end of the Parsnip area, grizzly bears had been radio collared and tracked for three years previous to our study (Ciarniello et al. 2001). Using aerial darting and leg-snare capture techniques, 37 grizzly bears and 23 black bears had been live captured previous to our

Table 1. Study areas, field methods and sampling design used in the five studies reported on in this paper.

Study area	Study area size (km^2)	Year of survey	Cell size (km^2)	No of sessions[1]	Session duration (days)	Sample dates	Bait
South Central Selkirks	5226	1996	64	5	10	19 June- 9Aug.	Meat & fish oil
North Central Selkirks	4640	1996	64	5	10	19 June- 9Aug.	Meat & fish oil
Prophet plateau	5413	1998	81	5	12	25 May- 1 Aug.	Blood & fish oil
Prophet mountains	3114	1998	81	5	12	25 May- 1 Aug.	Blood & fish oil
Yellowhead	5352	1999	81	4[2]	14	19 May- 9 July	Blood & fish oil
Parsnip plateau	3016	2000	64	4	14	30 May- 2 Aug.	Blood & fish oil
Parsnip mountains	6436[3]	2000	64	4	14	30 May- 2 Aug.	Blood & fish oil
Bowron River	2494	2001	64	3	14	2 Aug.-22 Sept.	Meat, blood & fish oil

[1] Sites were moved among sessions in all studies except for sites along the Bowron River (N = 27 of 159 sites sampled).
[2] The first session was live trapping and subsequent sessions were hair capture.
[3] The study area size for black bears was 3,636 km^2.

fieldwork. During the period immediately preceding our hair removal work, three grizzly bears and 10 black bears were live captured.

In the Bowron area, we trapped three 14-day hair capture sessions between 2 August and 22 September 2001 (see Table 1). These sites were systematically distributed throughout the study area, and we refer to these as upland sites. Concurrently, we trapped five one-week sessions along the river between 4 August and 21 September 2001. River sites were placed along bear travel routes adjacent to reaches which were known spawning areas for chinook salmon. At a few reaches no adequate trail set could be established so we built a bait site and baited it with blood and fish oil.

Field methods for the Prophet River and Central Selkirk Mountains study areas were similar to the above and are described in Mowat & Strobeck (2000) and Poole et al. (2001) and summarized in Table 1.

Genetic analysis

DNA analysis was conducted by University of Alberta (Edmonton, Alberta, Canada) and Wildlife Genetics International (Nelson, British Columbia, Canada) following methods described in Woods et al. (1999) and Paetkau (2003). Species was confirmed using a length polymorphism in the mitochondrial DNA (mtDNA) control region (Paetkau & Strobeck 1996). Alternatively, species assignment was based on the results of the microsatellite marker G10J, where black bears have exclusively odd-numbered alleles and brown bears have exclusive even-numbered alleles, at least in our study areas. This method is more efficient than a mtDNA-based species test because it also provides information on individual identity. Furthermore, G10J amplifies in a greater proportion of samples than any other nuclear marker that we used, so eliminating samples that fail to amplify with this marker is an efficient way to eliminate samples that have no prospect of producing multi-locus, nuclear genotypes.

In order to identify individual bears, each grizzly bear sample was analysed at six microsatellite markers (G1A, G10B, G1D, G10J, G10L and G10M) using primers and methods described by Paetkau et al. (1998). For the Parsnip and Bowron areas, another six markers (G10C, G10H, G10P, G10X, MU50 and MU59; Paetkau et al. 1998, Taberlet et al. 1997) were screened on a small number of samples, and rejected due to lower variability or less robust amplification. For black bears we screened 12 microsatellite markers (G10C, G10H, G10J, G10L, G10X, G1A, G10B, G1D, G10M, G10P, MU50 and MU59) and used the five former markers for individual identity for the reasons given above.

We attempted to increase genotyping success and decrease typing errors by using at least 10 guard hairs in a sample. If < 5 guard hairs were available, then we added up to 30 underfur hairs to the sample. Roots were clipped from guard hairs, but entire underfur hairs were used for extraction. Occasionally, samples from adjacent barbs were combined if both samples had few hairs. No roots were available for some river sites and in this case we put all available hair into the extraction. We did not extract adjacent samples, or samples separated by a single barb, because they are usually from the same bear (J. Boulanger & S. Himmer, unpubl. data). We preferred to analyze every third sample in a group of consecutive samples, but this varied depending on sample quality. We analyzed at least one sample from each group of samples at a site unless there were more than eight groups, in which case we usually chose the best samples from about eight groups. We analyzed all samples from the Yellowhead area. Samples with hair from more than one individual have 3-4 alleles at one or more loci (Paetkau 2003) and were excluded.

We declared two samples to be from the same bear when the genotype they had in common (i.e. excluding the loci that were incomplete for either animal) had a P value for the sibling match test of < 0.05 (Woods et al. 1999). Genotyping errors were minimized by following the error testing procedures outlined in Woods et al. (1999) for the Yellowhead study and Paetkau (2003) for the Parsnip and Bowron areas. Once the process of identifying individuals was complete, one sample from each individual was selected for gender determination. Gender was identified using a length polymorphism in the Amelogenin gene that differentiates the X and Y chromosomes (Ennis & Gallagher 1994). Primers were modified to discourage the amplification of human DNA (D. Paetkau, unpubl. data).

Statistical analysis

We used the mark-recapture models in the software programs CAPTURE and MARK to test for capture variation and estimate population size (Otis et al. 1978, White & Burnham 1999). Because most collared grizzly bears had been darted from the air rather than snared, it is unlikely that their previous live capture caused those individuals to avoid baited hair traps. A positive behavioural response was unlikely for hair captured bears because there was no available food reward at a site, and traps were moved each session. Likewise, we tried to reduce negative behavioural response (trap apathy) by adding novel scents during each recapture session. Therefore, we did not consider behaviour models during model selection. Time variation is easily detected in the absence

of a behavioural response except when sample sizes are small. Heterogeneity of capture probabilities among individuals is more difficult to detect and can cause significant bias. We examined the tests in CAPTURE for evidence of heterogeneity, while considering that these tests have low power when sample sizes are small (Otis et al. 1978, Boulanger & Krebs 1996). We also tested for capture variation among sexes using program MARK when sample size permitted. If heterogeneity was suggested we used one of the three heterogeneity models in CAPTURE for analysis. Data were often too sparse to test for capture variation conclusively and usually, in these cases, there was inadequate data to utilize a heterogeneity model with confidence (Manning et al. 1995). The only models available for these small data sets were time varying models, which would generate conservative results if heterogeneity was indeed present (Otis et al. 1978, Manning et al. 1995).

We used Chao's time and heterogeneity model when sample sizes were small because these models are designed for sparse data (Chao 1989, Chao & Jeng 1992) and, the Jackknife heterogeneity model is negatively biased with low sample size (Otis et al. 1978). We used Darroch's time model when sample sizes were large. When both time and heterogeneity variation were indicated we used Chao's time and heterogeneity model. When model choice was uncertain, we used the simulation routine in CAPTURE to compare the performance of the candidate models to aid model selection (Mowat & Strobeck 2000). Inhospitable habitat (rock, ice and lakes) was subtracted from study area size to calculate all densities.

Closure bias

Population estimates are typically biased upwards when the assumption of geographic closure is not met (White et al. 1982). We assessed the possibility of closure bias by visually examining capture locations with respect to the study area boundary. In addition we examined the closure test result generated in the program CAPTURE while recognizing the test is prone to Type 2 errors in the presence of time and behaviour variation (Otis et al. 1978, White et al. 1982). Thirdly, we examined the relationship between the capture distance from the edge of the grid and density for signs of lack of closure (Boulanger & McLellan 2001). Finally, we subjectively assessed the possible size of closure bias by comparing likely home range sizes to the study area size.

We used three different methods to correct for closure bias. The boundary strip correction was based on the idea that the area trapped is larger than the outer perimeter of the grid. In this case we increased the size of

the grid to attempt to enclose the entire 'trappable area' or superpopulation (Dice 1938, Kendall 1999). Average spring-early summer home range size was taken from the literature or local unpublished data (e.g. Ciarniello et al. 2001). We calculated the radius of a circle equal to the average home range sizes. We then extended the effective census area beyond the perimeter of the study area by this distance to correct density estimates for closure bias (Dice 1938; see White et al. 1982 for a discussion of various similar methods).

Another way to approach the problem of closure is to weight each animal captured by a measure of its residency on the study area as determined by radio telemetry (Kenward et al. 1981). In the Yellowhead area, there were sufficient locations (mean N = 198, range: 49-689) to estimate residency for 27 bears during 1999-2002. These 27 bears spent 89.3% (SE = 3.8) of their time on the study area during the period of sampling. We multiplied the point estimate and confidence intervals by 0.893, which equates to the time based correction given by Kenward et al. (1981). This simplistic correction factor does not incorporate the sampling error or the variability in measuring residency among animals.

Finally, we used a simplification of the method presented by Boulanger & McLellan (2001) to correct for closure based on the average distance each individual was detected from the edge of the grid. We calculated core population correction estimates by excluding a subset of bears based on their distance from the edge of the study area using 1-km interval increments (Boulanger & McLellan 2001). We then looked for a decline and leveling off in density with distance from edge, and chose the distance from edge based on where density began to level off.

We used the core correction method for the Parsnip, Bowron and Prophet study areas. Boulanger & McLellan (2001: Fig. 4) present similar calculations for the combined Prophet River data. We did separate estimates for each sex because we felt each sex cohort was likely to demonstrate different closure bias. Where possible, we apply several closure correction methods for each area to allow comparison among methods.

Results

Yellowhead

We captured 41 grizzly bears 51 different times during the three hair capture sessions. Live-capture crews captured 23 different grizzly bears 24 times; one live-captured bear moved off the study area, and one bear died during handling. We captured 14 grizzlies during both

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Table 2. Capture success and population estimation results for the five study areas reported on in this paper.

Study area	No of bears caught	No of captures	Average capture probability	Model used	Naïve population size		Closure correction method[1]
South Central Selkirks	38	45	0.09	$M_{th\text{-}Chao}$	97	(61- 192)	None
North Central Selkirks	74	91	0.08	$M_{th\text{-}Chao}$	223	(138- 416)	None
Prophet plateau	32	42	0.13	$M_{t\text{-}Chao}$	63	(42- 122)	Core
Prophet Mtns	67	100	0.21	$M_{t\text{-}Darroch}$	96	(80- 122)	Core
Yellowhead	48	71	0.16	$M_{th\text{-}Chao}$	107	(71- 198)	Radio
Parsnip plateau, grizzly	21	24	0.12	$M_{t\text{-}Chao}$	50	(29- 122)	Boundary strip
Parsnip Mtns, grizzly males	76	106	0.22	M_{o}	120	(97- 156)	Core
Parsnip Mtns, grizzly females	140	193	0.22	$M_{t\text{-}Darroch}$	221	(188- 268)	Core
Parsnip plateau, black bear	194	216	0.06	$M_{th\text{-}Chao}$	892	(565-1509)	Core
Parsnip Mtns, black bears	85	90	0.08	$M_{t\text{-}Chao}$	363	(200- 758)	None
Bowron River	53	74	0.32	$M_{t\text{-}Darroc}$	76	(63- 104)	None

[1] see Methods for a description of each closure correction method.

live capture and hair removal work. Most live captures occurred before we began hair removal work, although live capture effort continued, at lower intensity, into our second hair removal session. Of the 49 bears captured on the study area during summer 1999, 29 were female and 20 were male (41M:59F). Detection success at hair sites was higher in the more mountainous ecozone to the west (22%; N = 162) than in the flat subboreal ecoregion to the east (16%; N = 38).

To increase sample size, we combined the live capture and hair capture data sets for analysis by creating a fourth capture session; the new session began 28 April and ran until the beginning of our first hair removal session (19 May). When corrected for closure using radio telemetry data, the population estimate was 96 bears (95% confidence interval (CI): 63-177), which generates a density estimate of 17.9 bears/1,000 km² (CI: 12-32; Table 2). Home ranges were very large in this area, and the boundary strip method generated a much lower density (Table 3).

Parsnip

DNA fingerprinting resulted in identification of 239 grizzly bears and 275 black bears (see Table 2). The grizzly bear sex ratio for the plateau and the mountains combined was 35M:65F (N = 237). The sex ratio of DNA-identified black bears was 45M:55F (N = 194) on the plateau and 41M:59F (N = 85) in the mountains.

Bear movements

During the Parsnip study, 86 grizzly bears were detected more than once (up to four times). Within the mountains, the average movement by males was over twice that for females (Table 4). No recaptures of males occurred on the plateau. Only one grizzly bear crossed the boundary between the mountain and plateau regions, a male that moved from well inside the mountains to well inside the plateau and back again during the study. One long-distance movement was detected; a male bear that moved 111 km from the Sukunka River valley in the northeastern corner of the study area to the

Table 3. Grizzly and black bear naïve and closure corrected densities estimated by genetic sampling and mark-recapture analysis for 11 populations in western Canada during 1996-2001. Closure correction methods are described in Methods. Densities in *italics* were deemed most appropriate for the study area. The closure test examines the null hypothesis that the population described by the data set was closed (Otis et al. 1978).

Study area	Naïve density		Boundary strip corrected density		Core corrected density		Radio telemetry corrected density	Closure test result
South Central Selkirks	*19*	*(12- 37)*	13	(8- 26)	n.a.		n.a.	0.13
North Central Selkirks	*48*	*(30- 90)*	36	(22- 68)	n.a.		n.a.	0.08
Prophet plateau	11	(7- 18)	7	(5- 14)	*10*	*(7- 16)*	n.a.	0.60
Prophet Mtns	31	(26- 39)	19	(16- 24)	*23*	*(20- 29)*	n.a.	0.02
Yellowhead	20	(13- 37)	9	(6- 16)	n.a.		*18 (12-33)*	0.04
Parsnip plateau, grizzly	*17*	*(10- 40)*	12	(7- 28)[1]	No evidence of closure bias		n.a.	0.50
			9	(5- 23)[2]				
Parsnip Mtns, grizzly	54	(46- 68)	43	(37- 54)	*49*	*(43- 59)*	n.a.	0.39
Parsnip plateau, black bear	296	(187-500)	208	(132-352)	*257 (173-458)[3]*			
					212	(156-405)[4]	n.a.	0.40
Parsnip Mtns, black bears	*100*	*(55-210)*	70	(38-145)	73	(43-149)	n.a.	0.62
Bowron River	*31*	*(26- 42)*	22	(19- 32)	No evidence of closure bias		n.a.	0.71

[1] We subjectively reduced the buffer length based on movement information and topography.
[2] This estimate is based on a continuous buffer.
[3] This estimate was based on a biological decision to use a 1-km buffer.
[4] For this estimate we selected the distance from edge based on the apparent decline in edge effect (3 km for females and 5 km for males; Fig. 2) as described in Methods.

Table 4. Distance moved (in km) between capture locations for grizzly and black bears by ecoregion and sex in the Parsnip river area of British Columbia in summer 2000.

Ecoregion	Species	Sex	N	Mean	SE	Range
Mountains	Grizzly	♂[a]	45	13.1	2.38	1.6 - 110.7
	Grizzly	♀	75	5.3	0.57	0.8 - 38.1
Plateau	Grizzly	♂[a]	0			
	Grizzly	♀	3	4.6	1.92	1.1 - 7.7
Mountains	Black	♂[b]	7	8.1	1.33	4.6 - 12.9
	Black	♀	5	4.3	0.40	3.1 - 5.4
Plateau	Black	♂	16	4.6	0.50	2.2 - 8.3
	Black	♀	6	2.7	0.49	1.6 - 4.8

[a] In addition, one male grizzly bear was detected moving from the mountains to the plateau (34.0 km), and back to the mountains (28.6 km).

[b] One male black bear that moved 40 km across the mountains to the edge of the plateau was excluded because we felt it was not a territorial movement.

McGregor River in the southern end of the study area between sessions 1 and 3.

Black bear movements in the Parsnip-Herrick study were shorter than those of grizzlies, and as for grizzlies, females did not move as far as males (see Table 4). One male black bear moved 40 km across the entire mountainous portion of the study area. Three black bears were detected moving across the mountain-plateau boundary, although all three movements were within 2.4 km of the boundary.

Population estimation for Parsnip grizzly bears

We captured 21 grizzly bears during hair sampling on the plateau. During our study, three radio-collared bears spent > 50% of their time on the plateau portion, hence the total number of grizzly bears known to be on the plateau during our study was 24 (see Table 2).

Few bears were captured near the boundary on the plateau, and core correction and the closure test in CAPTURE did not demonstrate any evidence of closure bias (Fig. 2A, see Table 3). Closure bias may have been small, or the small sample size may have rendered the bias undetectable. Total captures were only 14 for the smallest core area, 7 km from the boundary. We felt the core closure correction technique was unreliable for the plateau grizzly bears due to the small sample size. Our only option to correct for closure bias for grizzly bears on the plateau was to use the boundary strip method (see Table 3). To estimate corrected male and female density on the plateau, we assumed that the naïve estimate of 50 bears had the same 35M:65F ratio that we recorded over the entire grid area. We did not buffer the sampling grid at the boundary between the plateau and mountain portions of the grid because both radio telemetry and DNA data indicated almost no movement of bears across this boundary during the June-July period (see Table 3). This subjectively correct-

ed boundary strip resulted in a 33% higher density over a continuous buffer. We believe the uncorrected population density is most accurate for the plateau (16.6 bears/1,000 km^2; CI: 10-40).

We identified 216 different grizzly bears in the mountain portion of the Parsnip study area during hair sampling (see Table 2). We calculated separate population estimates for males and females in order to reduce capture variation and allow for more realistic correction for closure bias. During hair sampling, eight of 12 radio-collared grizzlies were detected, giving an overall detection probability of 0.67, which is similar to the overall detection probability of hair sampled bears (0.63).

The boundary strip correction method resulted in reductions of 15 and 29% for female and male grizzly bears in the mountains, respectively, compared to the naïve density estimates (see Table 3). Mountain grizzly bear population size declined measurably using a 1-km interior boundary to correct for closure bias for females and a 2-km boundary for males, and then changed little using smaller core populations (Fig. 2B). We used the 1-km core population estimate to calculate density for females and the 2-km estimate to calculate density for males, resulting in a density of 49 bears/1,000 km^2 (CI: 43-59), a reduction of 7 and 12% from the naïve density estimates for female and male grizzly bears, respectively. We believe the core corrected density is the most accurate of the two closure correction methods.

Population estimation for Parsnip black bears

We caught 194 black bears 216 times on the plateau (see Table 2). Changes in population estimates with increasing distance from the study area boundary suggest the use of the 3-km core estimate for female black bears and the 5-km estimate for males on the plateau (Fig. 2C). However, this means closure bias of 22% for females and 55% for males, which is highly unlikely given the large study area (see Table 3), and relatively small home ranges of black bears in wet ecosystems (Pelton 1983, Kolenosky & Strathearn 1987). Given the small number of recaptures in this data set, stochastic events may have lead to declines in the estimates with distance from the study area boundary. Therefore, we used the 1-km buffer and combined sexes to estimate population size for the plateau as 753 black bears (CI: 506-1,344), which yields a density of 257 bears/1,000 km^2 (CI: 173-458).

We captured 85 black bears 90 times during the four capture sessions in the mountains (see Table 2). We combined sessions 3 and 4 to estimate population size because capture success was extremely low in the last ses-
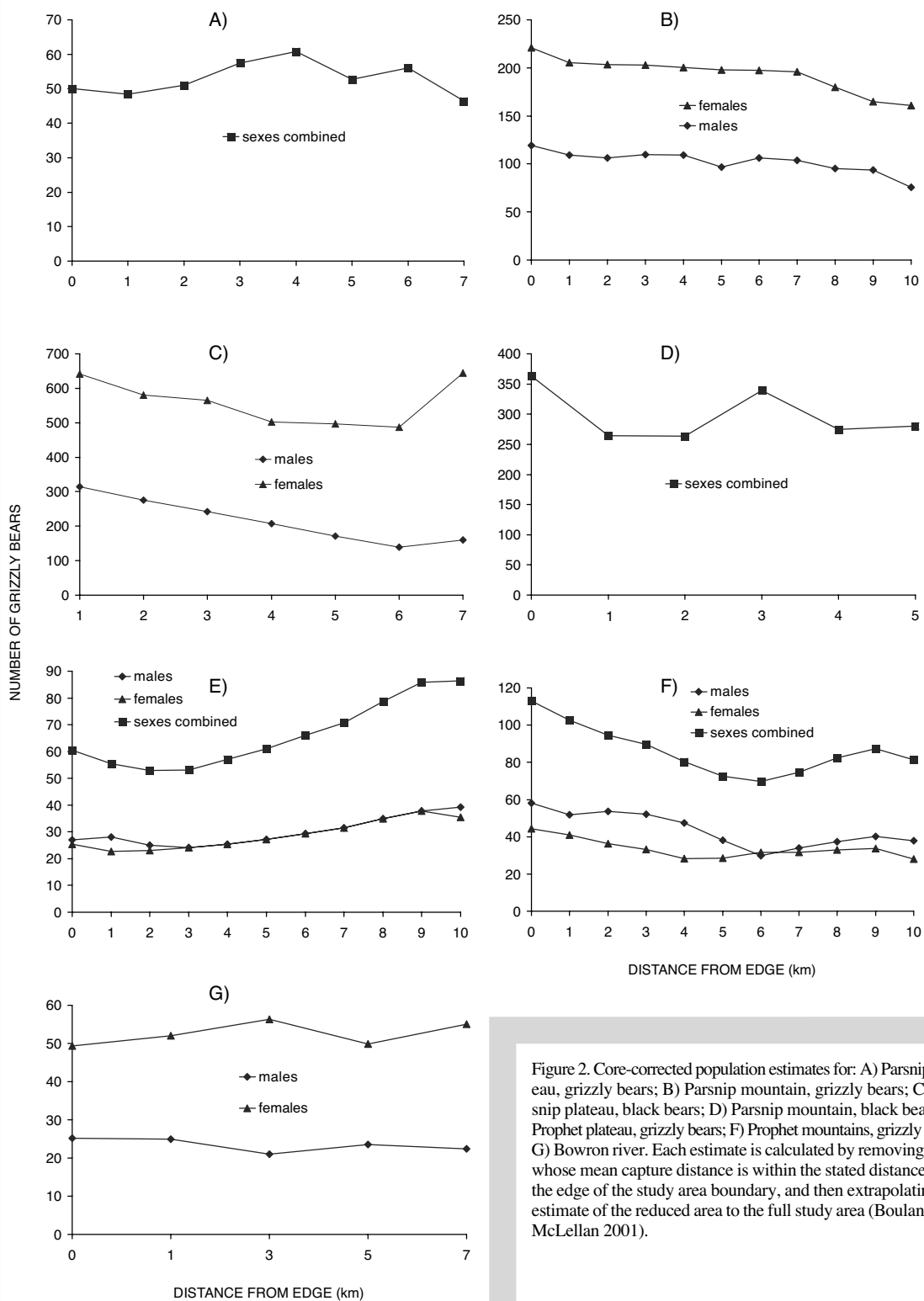
Figure 2. Core-corrected population estimates for: A) Parsnip plateau, grizzly bears; B) Parsnip mountain, grizzly bears; C) Parsnip plateau, black bears; D) Parsnip mountain, black bears; E) Prophet plateau, grizzly bears; F) Prophet mountains, grizzly bears; G) Bowron river. Each estimate is calculated by removing bears whose mean capture distance is within the stated distance from the edge of the study area boundary, and then extrapolating the estimate of the reduced area to the full study area (Boulanger & McLellan 2001).

sion and time variation was obvious. Core-corrected estimates generated a sharp initial decline in population size by excluding bears within 1 km of the border; the estimates were roughly equal for the next four core calculations (Fig. 2D). Using the 1-km core corrected estimate suggested a closure bias of 28%, and here again the low numbers of recaptures makes this number suspect. The boundary strip method generated similar reductions in density (see Table 3). We elected not to correct for closure because recaptures were few; black bear density was 100 bears/1,000 km^2 (CI: 55-210) in the mountains.

Fall sampling along salmon streams

During fall hair sampling, grizzly bear hair was collected at seven of 10 sites. Black bear hair was detected at only one site, which did not detect a grizzly bear. We identified 15 grizzly bears (9 M, 6 F), and four bears were recaptured within the fall samplings, all on the same creeks as originally detected. At four sites we removed grizzly bear hair, but we were unable to identify an individual. Hair samples from the fall were generally of lower quality than the summer samples; more hairs were required to score all six loci. We combined the third and fourth capture sessions to calculate grizzly bear population size along these creeks because only one bear was captured during the last session. We estimated that 21 grizzly bears (CI: 16-44) used the 47 km of creek that we trapped in fall (5 bears/10 km) which is only a small portion of the bears resident in the nearby area.

Of the 15 fall-captured bears, 11 (6 M, 5 F) had been detected previously. The distance between their last summer capture location and their fall capture location was greater for males ($\bar{x}$ = 18.6 km, range: 4.0-48.3 km) than for females ($\bar{x}$ = 4.8 km, range 0.3-7.5 km). Two male grizzly bears made long-distance movements of 35 and 48 km.

Bowron
Grizzly bear movements

We detected 36 grizzly bear movements and grouped these based on whether the movement was within the upland, along the river, or between the upland and the river in either direction (Table 5). No movements > 13.5 km were detected from upland to the river (N = 13) even though 12 grizzly bears moved < 13.5 km from the upland to the river, which was 24% of all grizzly bears known to be in the study area. This pattern of movement suggests that only local residents used salmon streams.

Grizzly bear population size and density

Mark-recapture databases were generated from: 1)

Table 5. Direction and distance moved (in km) between capture locations for grizzly bears in the Bowron River drainage fall in 2001.

Type of movement	Sex	N	Mean	SE	Range
Upland to river	♂	4	10.4	2.7	2.5 - 13.5
	♀	9	9.4	1.3	2.5 - 13.4
Along river	♂	3	8.4	3.8	4.6 - 16
	♀	11	5.9	1.3	0.7 - 14
Within upland	♂	2	9.0	1.7	7.3 - 10.6
	♀	7	5.1	1.4	1.6 - 12.2

upland sites, 2) river sites and 3) upland and river sites combined. Sessions 2-3 and 4-5 were combined for river sites in order to align the data with the three upland sessions (see Table 2). There were 47 captures of 41 bears in the upland, 34 captures of 26 bears along the river, and 74 captures of 53 bears in the combined data. The use of distance from edge to exclude bears caught near the study periphery did not suggest any degree of closure violation (Fig. 2G), a result that is not surprising because few bears were caught near the study area boundary.

Population size for the upland was 109 (CI: 67-221) and 47 (CI: 33-85) for the river. The population estimate using the combined data was 76 (CI: 63-104; see Table 2). The estimate for females ($\hat{N}$ = 49; CI: 41-70) was double that for males ($\hat{N}$ = 25; CI: 21-39), and the combined density of grizzly bears in the study area was 30.9 bears/1,000 km^2 (range: 25.7-42.3). Based on the movement data we assumed our river sites were trapping bears that lived in the two rows of cells (roughly 16 km) on each side of the river. The estimated density for this area using the river sites only was 27.2 bears/1,000 km^2 (range: 19.1-49.2). There was about six grizzly bears per 10 km of river, a similar number to that observed along Herrick Creek in the Parsnip fall sampling, about 100 km further north. Boundary strip closure correction suggested a much greater reduction in density (see Table 3).

Closure correction for Prophet River grizzly bears

For the boreal plains portion of the Prophet River study area, there was a small decline in the estimated core-corrected population size of grizzly bears up to 2 km inside the study area, but the population estimates increased using data from 3 to 9 km inside the boundary (Fig. 2E). We used the 2-km corrected estimate to estimate population size for the boreal plains because this is where the initial decline stopped. Population size was estimated at 53 (CI: 39-89) and density was 10 bears/1,000 km^2 (CI: 7-16); virtually identical to the density presented by Poole et al. (2001).

Using the core population correction for the moun-

Table 6. Grizzly bear densities in and near the Rocky Mountains of North America.

	Density (bears/1,000 km^2)	95% CI	Study area size (km^2)	Reference
Rocky Mountain west slopes and adjacent ranges				
Flathead Valley, B.C.	46-80		130	McLellan (1989)
Flathead Valley	48	30-92	3233	Boulanger et al. (2002)
Parsnip mountains, B.C.	49	43-59	6436	This study
Northern Central Selkirk Mountains, B.C.	48	30-90	4640	Recalculated from Mowat & Strobeck (2000)
Glacier National Park, Montana	32		1044	Martinka (1974)
Bowron River, B.C.	31	26-42	2494	This study
Central Purcell Mountains, B.C.	25	22-40	1650	Boulanger et al. (2002)
Central Columbia Mountains, B.C.	26	13-39	4096	Boulanger et al. (2002)
Rocky Mountain east slopes				
Northern Canadian Rocky Mountains, B.C.	23	20-29	3114	Recalculated from Poole et al. (2001)
Jasper-Cadomin, Alberta	18	12-33	5352	This study
Kananaskis, Alberta	16		254	Wielgus & Bunnell (1994)
Southwest Alberta	15	12-20	5030	Mowat & Strobeck (2000)
Discontinuous populations in the Rocky Mountain west slopes				
South Selkirk Mountains, B.C.	23		235	Wielgus et al. (1994)
Southern Central Selkirk Mountains, B.C.	19	12-37	5226	Recalculated from Mowat & Strobeck (2000)
Swan Mountains, Montana	16		1457	Mace & Waller (1998)
South Selkirk Mountains, WA, ID	14		100	Wielgus et al. (1994)
Boreal and subboreal plains				
Parsnip plateau, B.C.	17	10-40	3016	This study
Prophet River boreal plains, B.C.	10	7-13	5518	Recalculated from Poole et al. (2001)

tainous portion of the Prophet River study area, there was a sizable decline in population size up to 6 km inside the study area and estimates increased from 6 to 9 km inside the boundary (Fig. 2F). We used the 6-km corrected estimate to estimate grizzly bear population size for the Prophet mountains because this is where the initial decline stopped. We combined two sexes for estimation because sample sizes were very low for individual sexes with data 6 km in from the boundary. The final estimate was 70 grizzly bears (CI: 63-91), which generated a density of 22.5 bears/1,000 km^2 (CI: 20-29), 22% lower than the density presented by Poole et al. (2001).

Central Selkirk Mountains grizzly bear densities

Grizzly bear density in the southern half of the Central Selkirk Mountains was 19 bears/1,000 km^2 (CI: 12-37) and 48 bears/1,000 km^2 (CI: 30-90) in the north. Again the boundary strip closure correction suggested much lower densities, but Mowat & Strobeck (2000) suggested the outer boundary was largely closed to bear movement, and Proctor et al. (2002) demonstrated that there was little movement, among subpopulations within the study area. There were very few bear captures near the north-south boundary.

Discussion

Grizzly bear density

There are marked differences in grizzly bear density among biomes that are broadly defined by the Rocky

Mountains (LeFranc et al. 1987; Table 6). Densities are highest in the Rocky Mountain west slopes, followed by the east slopes, with the lowest densities observed in the boreal and subboreal plains on either side of the mountains. Small study areas are often placed in higher quality habitats than surrounding areas (Smallwood & Schonewald 1996); therefore some of the densities reported for small study areas are likely higher than would be found over a larger surrounding landscape. Densities of coastal bear populations are usually much higher than observed in the continental interior (MacHutchon et al. 1993, Miller et al. 1997), although Boulanger et al. (2002) reported a density similar to the Rocky Mountain west slopes for a coastal area of southwest British Columbia. Densities in the boreal and tundra regions of Alaska are highly variable; some areas have densities similar to the Rocky Mountain west slopes, while others are lower than documented in the subboreal plains (Miller et al. 1997).

Bear density is moderate to low in all the discontinuous populations that have been studied along the southern edge of the bear's range (LeFranc et al. 1987; see Table 6). Densities in these discontinuous populations are likely limited by the effects of habitat loss and ongoing human impacts, not lower habitat productivity. All four densities from discontinuous populations in Table 6 are from areas in the west slopes of the Rocky Mountains and all have habitat qualities similar to adjacent areas to the north. For example, grizzly density in the north part of the Central Selkirk Mountains, where the grizzly bear distribution is continuous with populations to the north and east, was approximately dou-

ble that in the south despite similar habitat. Capture data and genetic analysis have shown that the southern half of the Central Selkirk population is partially isolated from surrounding populations (Mowat & Strobeck 2000, Proctor et al. 2002). Habitat quality may be secondary to human impact in predicting bear density in the southern discontinuous portion of the grizzly bear's distribution.

Further north along the interior mountains, bear densities are consistently higher on the windward side of the continental divide than in the rain shadow on the leeward side to the east, likely a result of the reduced rainfall and hence reduced vegetative production in the rain shadow of the large interior mountains (Hamer & Herrero 1987, Hamer et al. 1991). The single study area with estimated bear density > 20 bears/1,000 km^2 on the east side of the continental divide is in the Prophet River area of the Northern Rocky Mountains where rainfall is higher than on the Rocky Mountain east slopes further south. Grizzly densities are low in the boreal and subboreal plains in British Columbia and Alberta (LeFranc et al. 1987, this study). Many of these areas have also been heavily impacted by humans, which may partially explain the consistently low densities. However, the boreal plains of the Prophet River were only mildly impacted by people (Poole et al. 2001), and densities were low here too.

At what scale do landscape factors affect bear density? This question is important because density extrapolations are often used to predict harvest levels and using the correct scale for extrapolation will reduce errors in harvest management. Large differences in bear density occur right down the ecoregion level of classification. This is demonstrated by the large differences in density among the adjacent Parsnip mountain and plateau areas, where density varied > 4-fold on either side of an ecoregion boundary (see Table 6). Bear densities also differed across coarser ecosystem levels, as shown by the difference in density across the ecoprovince boundary in Prophet and the differences in detection success between ecozones in the Yellowhead study area. Broader-scale ecosystem classes such as Banci's (1991) grizzly bear zones, ecoprovinces or ecozones (also termed ecodomains; Bailey 1997) encompass areas with major differences in density and are clearly too coarse a level at which to predict or extrapolate grizzly bear density. All three of these mapping scales combine areas of Rocky Mountain west and east slopes or subboreal (or boreal) plains, where densities can vary > 5-fold. In contrast, ecoregions map areas of relatively homogenous topography and climate and appear to better group areas of similar bear density.

We could not compare finer levels of ecosystem classification with our data because in most cases they occur at finer resolution than our density data. For example, ecoregions are further divided into ecodistricts (termed ecosections in British Columbia; Demarchi et al. 1990), but our study areas often contained 3-6 different ecodistricts making any comparison of density tenuous. Further, our movement data suggested that individual bears move among ecodistricts (G. Mowat, unpubl. data), and it is more appropriate to assign density to units that include the year-round life history of the population (Miller et al. 1997). Ecodistrict scale effects to bear density are probably best measured by stand level effects on habitat quality, rather than broad scale correlates to density.

Black bear density

The pattern of black bear densities is opposite to that of grizzly bears, with estimated black bear density about three times greater in the Parsnip plateau than in the mountains. Even in the mountains, black bears were mainly captured in valley bottoms. The low number of captures in the mountains in the third and fourth trapping sessions resulted from our tendency to move hair capture sites higher in elevation through the study. Black bears were rarely detected near the treeline, possibly due to competitive exclusion by grizzly bears. Grizzly bears also appeared to exclude black bears from near the Herrick salmon streams when salmon were running. This pattern has also been observed along coastal salmon streams (Miller et al. 1997, Jacoby et al. 1999). Conversely, black bears were detected regularly along the Bowron River where a larger number of salmon were spread across a much longer stretch of river.

Little research has been done on black bear population characteristics in British Columbia or Alberta. Densities varied from about 320 to 800 bears/1,000 km^2 in a small area of high quality in northeast Alberta, an area most comparable to our plateau study area (Young & Ruff 1982). Given the reported home range sizes and the presence of three dumps on the study area, actual density was likely similar to, or less than, our Parsnip Plateau area because these authors did not correct for lack of closure, and this bias would likely have been large. Jonkel & Cowan (1971) reported densities 2-5 times higher than what we document in the Parsnip Mountains for an area in northern Montana which is most similar to our mountain study area. Again, the actual density of the greater landscape was likely much lower given the study area size, bear home range sizes and the fact that no correction was made for closure. Miller et al. (1997) estimated black bear density to be 89 bears/1,000 km^2

(CI: 77-103) in a relatively flat, partially forested area of interior Alaska. This is much lower than the black bear density we found on the Parsnip plateau; however, black bears in their study area existed in creek bottoms and forested strips, similar to our mountain population. Also, grizzly bear density was considerably higher in the Alaska study area than in the plateau portion of our area. Miller et al. (1997) reported black bear densities similar to our plateau estimate in two areas of coastal Alaska. Kolenosky & Strathearn (1987) reported densities of 200-1,300 black bears/1,000 km² in the Pacific Northwest, with the highest density reported for coastal Washington. Our data support the suggestion by Miller et al. (1997) that black bears occur at higher densities than grizzlies in the interior, and that black bears are most abundant where grizzly bears are rare or absent.

Movements

Movement between mountainous and plateau ecosystems in spring and early summer appears to be rare, which is consistent with movements of radio-collared bears in this area (Ciarniello et al. 2001) and results in the Rocky Mountains further north (Poole et al. 2001). Females did not move as far as males, which is expected given their smaller home ranges (Nagy & Haroldson 1989, Ciarniello et al. 2001), and is also consistent with results from the Northern Rocky Mountains (Poole et al. 2001). Black bear movements were smaller than those of grizzly bears, which suggests that they have smaller home ranges. Converse to grizzly bears, black bear movements in the mountains were greater than on the plateau, which suggests that black bear ranges are smaller in the flatter plateau area.

Female grizzly bears did not appear to leave their home ranges to catch salmon along the Herrick or Bowron rivers. Given the relatively small home ranges of bears in the Parsnip mountains, it seems likely that two males made extra-territorial movements to fish for salmon in Herrick Creek; long-distance movements of males may have gone undetected in the Bowron because our sample size was small. Movement distances to the river for Bowron females were double those observed in the Parsnip mountains, suggesting that female home ranges in the relatively flat part of the Bowron mainstem are larger than in the very rugged Parsnip mountains to the east. Ciarniello et al. (2001) found that bears living on the flatter plateau portion of their study area had much larger home ranges than bears residing in the mountainous portion. Miller et al. (1997: Table 2) also found that males moved farther than females to fish in an interior salmon stream, and movement distances and density were similar to those reported in this paper.

Mattson & Reinhart (1995) documented grizzly bears feeding on spawning cutthroat trout *Oncorhynchus clarki* in the Yellowstone ecosystem. They show that females made greater use of streams and that most bears that had > 5% of their home ranges touching a spawning stream used trout. Some females may have made extra-territorial movements to streams. In interior Alaska, Miller et al. (1997) found that < 40% of resident bears moved to a nearby salmon stream; however, bear use of salmon in this interior Alaska stream was high. These authors also studied two areas on the northern coastal plains of Alaska with periodically abundant salmon, but bears used these streams little. Most bears in coastal ecosystems move to streams when salmon are running (MacHutchon et al. 1993, Schoen et al. 1994); however, Schoen & Beier (1990) documented that 14% of the bears they had radio-collared never moved to streams during the salmon season. Often the bears that did not use salmon streams were females with young cubs. Even bears that used salmon streams were located away from streams, usually in the alpine, 15% of the time during the salmon season. Using radio isotope analysis, Hilderbrand et al. (1996) also demonstrated that most coastal bears rely heavily on salmon in the fall, while a few bears do not use salmon at all. In a following paper, Hilderbrand et al. (1999) demonstrated that salmon are important to bears at both the individual and population level because meat in the diet was correlated with body size, litter size and density.

Closure

The boundary strip method generated more conservative estimates of density than the radio telemetry or core-closure corrections. We subjectively adjusted the boundary strip calculations for the Parsnip areas based on our observation of essentially no bear movements along the plateau-mountains boundary and the presence of glaciers along portions of the boundary. The population estimate would have been even more conservative had we not made these adjustments. Indiscriminate application of a boundary correction factor could greatly overestimate closure bias if portions of a boundary are indeed closed or uninhabited by the study species (Boutin 1984). Perhaps residency is heterogeneous along study area boundaries because only a portion of all bears are sampled, and application of a continuous boundary strip overestimates the amount of permeable boundary. If this is true, then this bias is likely to be greater with lower capture probabilities, because individuals along the boundary would be more lightly sampled.

In contrast, the modest reduction in predicted population size for the Parsnip mountains, using concentric

increases in distance from edge, suggests that lack of closure only biased population estimates within about 1 km from the study area boundary. Corrected estimates for buffers 2-7 km inside the study area were similar, so the choice of the buffer distance had little effect on the corrected density. Buffers of > 7 km predicted lower population sizes, especially for females; these effects are more likely due to the reduction in sample size than closure bias.

Boulanger & McLellan (2001) suggested closure-correction of 17-25% below naïve estimates for the entire Prophet River area. They used a core correction distance of 10 km to estimate density for the entire study area. This distance appears overly conservative when compared to the home ranges observed for bears living in the Parsnip mountains where home range diameters averaged about 6 km for females and 15 km for males (Ciarniello et al. 2001).

Poole et al. (2001) demonstrated that the majority of the bears in the Prophet study area resided in the mountains; however, the centre of the study area was in the boreal plains (Fig. 3). Capture probabilities were lower on the boreal plains, which likely explains why Boulanger & McLellan (2001: Figs. 1 and 3) found a reduction in fidelity and capture probabilities at large distances from the edge. At about 20 km from the edge, bears caught on the plateau became the majority in the mark-recapture sample and at 25 km from the edge, only one mountain caught bear remained in the sample (see Fig. 3). This demonstrates the sensitivity of the core correction technique to variation in the distribution and capture probabilities of individuals in the sample.

In all analyses we attempted to calculate separate closure corrections for each sex because we expected less closure bias for females due to their smaller home ranges. Closure bias generally influenced female estimates
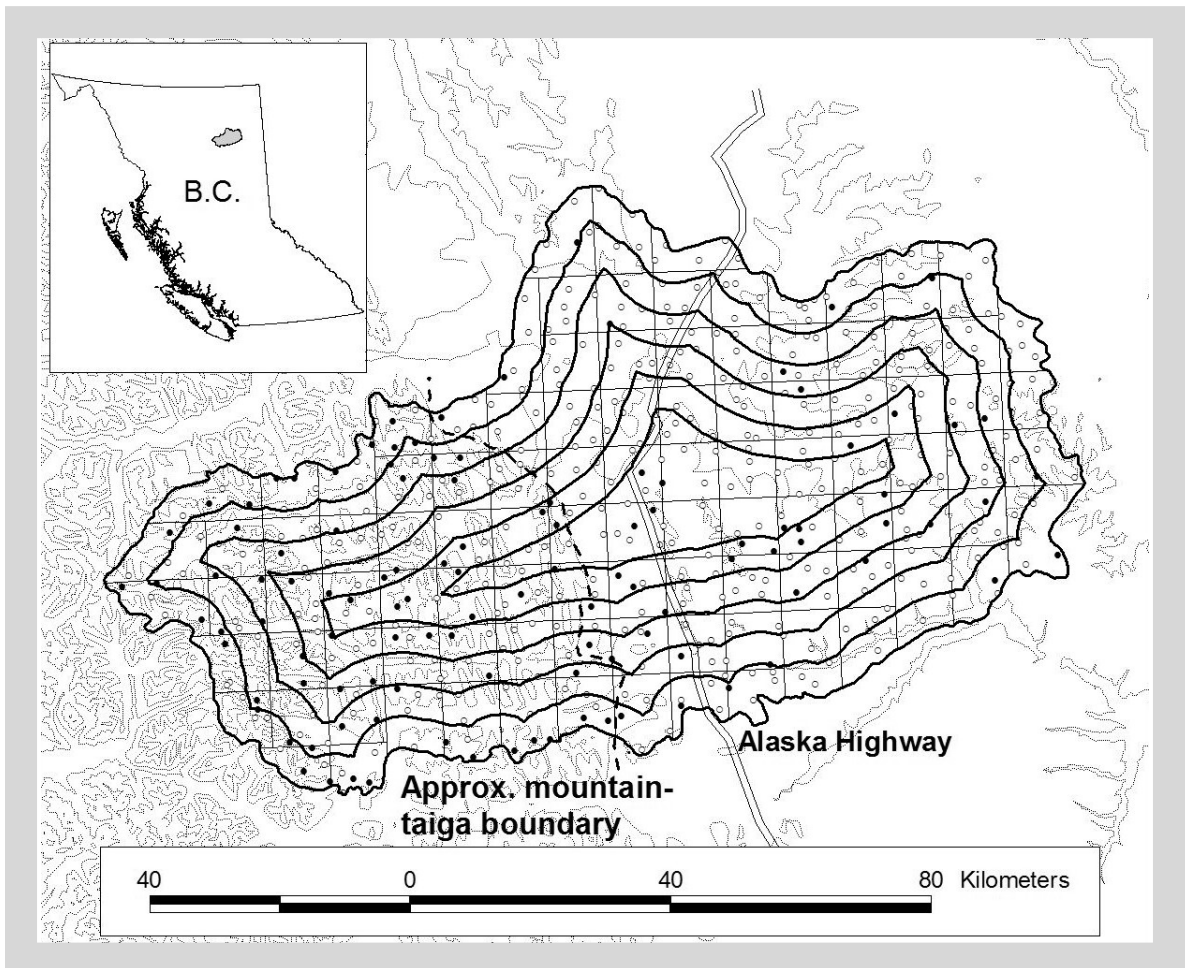

Figure 3. Sites at which grizzly bears were detected (●) and sites at which grizzly bears were not detected (○) in relation to 5-km wide strips from the study area boundary for the Prophet River grizzly bear DNA inventory (Poole et al. 2001).

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closer to the boundary, although the differences were often subtle. Conversely, the reduction in sample size that results from dividing and excluding samples reduces power and could lead to spurious results. Heterogeneity models are more sensitive to sample size than simple time models (Otis et al. 1978, Manning et al. 1995, Kendall 1999). The jackknife model in particular tends to be biased low when recaptures are few (Otis et al. 1978). Sequentially reducing sample size could yield reduced estimates due to model bias that could be mistaken for closure bias. The core population correction method appears to be a more accurate method to correct for closure than the boundary strip method, but its application will be limited by sample size, as is the case for the similar nested grid method (Otis et al. 1978). The core correction method, like the boundary strip, could also generate large errors if applied indiscriminately.

The radio-telemetry method can also provide accurate estimates of density, but a large and representative sample of bears must be collared during the study (Eberhardt 1990, Garshelis 1992). This is difficult not only because collaring is expensive but also because live capture effort and success are rarely random with respect to the residency of bears.

Kendall (1999) argued that closure violation would add heterogeneity to capture probabilities, necessitating the use of models that accommodate this form of capture variation. We suspect individuals with very low capture probabilities (who presumably have only a small portion of their home range on the study area) are few when the grid is large relative to home range size, which explains why we rarely detected heterogeneity in our data. However, when the mean capture probability is low, differences between the mean probability and those of edge bears may be small, making it difficult to detect the heterogeneity caused by edge bears, especially when sample size is low. It seems likely that bears that have only a very small portion of their home range on the study area have capture probabilities so low that, if they are undetected during the study, they are not accounted for in the population estimate; which is perhaps the desirable result if the goal is to estimate mean population size for only the area studied.

Closure bias should be considered for all estimates of population density. In a mark-recapture setting statistical tests may help detect lack of closure, but test results should not replace knowledge of the study area. For example, closure test results for the Central Selkirk Mountains study areas suggested lack of closure, but this result was likely due to the poor capture success along the study area boundary which declined through the study, because we moved our sites to higher elevations that were closer to the center of the study area. Indiscriminant application of all three of the closure correction methods discussed here could result in a less accurate estimate of density than the naïve estimate. It appears that the boundary strip method often overcorrects for closure, at least with low capture probabilities. Subjective reduction of the buffer length based on topography and population distribution can reduce this bias. The core correction method may also overcorrect for closure when sample sizes are small or capture distribution and success are spatially heterogeneous. The radio-telemetry method can generate biased corrections for closure bias if the radio-collared sample is not randomly drawn from the study population. We had radio-collared individuals for both Parsnip study areas but were unable to use them for this reason. Correcting for closure bias should be based on a detailed knowledge of the study area, capture data, species biology and careful examination of the appropriateness of each technique.

DNA-based inventory along salmon streams

Large numbers of bears can be sampled with relatively little effort along salmon streams in the interior. We generated a precise estimate of the number of bears using approximately 40 lineal kilometers of river (tributaries not included) with about 18 crew days (two people) of effort and the use of a truck and a boat. A much less precise estimate of the number of bears in the upland was generated with 24 crew days of effort and 35 hours of helicopter time and much greater truck costs. By our crude estimates the upland sampling covered roughly one third more area than the river sampling for roughly four times the cost.

The problem with sampling along streams during salmon runs is calculating bear density. We spent considerable effort attempting to document movement distances and still our results for males were weak, because we caught few males overall and none on the western periphery of our study area. Even in areas where bears are more abundant and the population distribution more homogenous, it will be difficult to get robust measures of bear movement distances. Field costs to measure movement distances could be reduced if sampling were restricted to only those upland areas beyond the distance bears are known to move to the river. In the Bowron study for example, it was unnecessary to sample the upland within 10 km of the river to determine if bears were moving beyond their normal home ranges.

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