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Current harvest management of grizzly bears *Ursus arctos* in British Columbia (B.C.), Canada, is based primarily on modeling of habitat capability/suitability. No research has been conducted in the northern half of B.C. to verify these habitat-based estimates. We estimated grizzly bear population size in a 8,527 km^2 study area in northeastern B.C. that included the east slopes of the northern Rocky Mountains (Northern Boreal Mountains ecoprovince) and the boreal plains (Taiga Plains ecoprovince) using hair removal to sample bears, microsatellite profiling to identify individuals, and mark-recapture models. We placed bait sites encircled by barbed wire in a grid of 103 9 × 9 km (81 km^2) cells. In each cell a different bait site was set for 12 days in each of five sessions. We collected 2,062 hair samples from 332 sites and detected grizzly bears at 113 sites. DNA profiling of grizzly bear samples identified 98 different bears; 44 of these individuals were females, 47 were males, and the remaining seven individuals could not be sexed. Forty-one grizzly bears were caught at >1 site. We used a closed mark-recapture model to obtain a naive population estimate of 148 grizzly bears (95% confidence interval (CI): 124-182). We reduced this estimate by 6.8% to account for closure bias, which resulted in an adjusted population estimate of 138 grizzly bears (95% CI: 114-172) within the study area (16 bears/1,000 km^2; 95% CI: 13-20). Within the two biophysical ecoprovinces we estimated a density (corrected for closure) of 29 bears/1,000 km^2 (95% CI: 23-37) for the Northern Boreal Mountains and 10 bears/1,000 km^2 (95% CI: 7-18) for the Taiga Plains. The current habitat-based capability ratings for grizzly bears in the boreal ecoprovinces of B.C. are supported by our results in the Taiga Plains, but are lower than densities we obtained in the Northern Boreal Mountains by about half. With further testing, habitat-based estimates of grizzly bear density in B.C. could be adjusted using the results of DNA-based population estimates.

Key words: British Columbia, density, DNA, genetic tagging, grizzly bear, microsatellites, population estimate, Ursus arctos

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Recent developments in techniques to estimate grizzly bear *Ursus arctos* population size have included use of remote hair capture to sample populations, DNA analysis to identify individuals, and mark-recapture modeling to estimate population size (Woods, Paetkau, Lewis, McLellan, Proctor & Strobeck 1999, Mowat & Strobeck 2000). These techniques appear to provide an accurate, less costly and less invasive alternative to population estimates derived from intensive capture and radio-collaring efforts (i.e. McLellan 1989, Miller, White, Sellers, Reynolds, Schoen, Titus, Barnes, Smith, Nelson, Ballard & Schwartz 1997). Currently, population management of grizzly bears in British Columbia (B.C.), Canada, is based primarily on estimates of carrying capacity, which are based on modeling of habitat capability and suitability and extrapolating population size using density estimates from previous research (Fuhr & Demarchi 1990). No research has been conducted in the northern half of the province to verify these habitat-based extrapolations.

We derived a DNA-based population estimate for grizzly bears for a portion of the Prophet River area in northeastern B.C. This area included the east slopes of the northern Rocky Mountains (Northern Boreal Mountains ecoprovince) and the boreal plains (Taiga Plains ecoprovince; Demarchi 1995). Industrial activity is increasing in the area and hunting by residents and outfitters is popular. Grizzly bear populations in northeastern B.C. are among the least studied and current density estimates are among the most contentious in the province. Our primary objective was to estimate grizzly bear population size for management needs and to provide a comparison to numbers predicted from the habitat based method currently in use. Secondary objectives were to examine the distribution of grizzly bears across the study area and to assess the usefulness of the methods and study design followed.

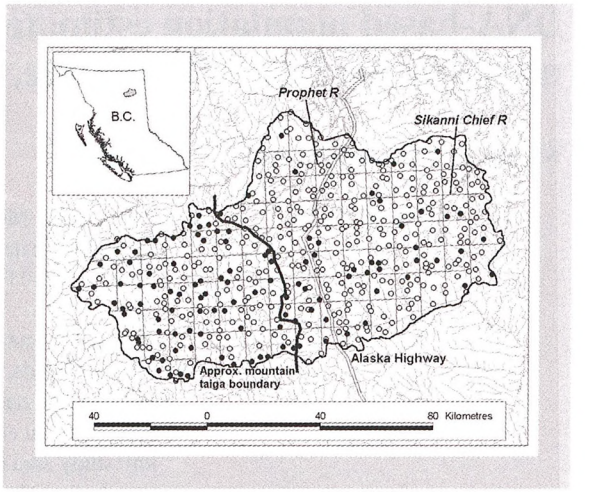

Figure 1. Prophet River grizzly bear DNA inventory study area, grid cells and site locations in 1998. Sites that detected grizzly bears are shown in solid circles, sites that did not are shown in open circles. The mountainous area was found west of the mountain-taiga boundary.

Material and methods

Study area

We based study area selection on a number of interrelated factors, including geographic closure, cell size, session length, access and cost (see Survey design, below). We selected an 8,527 km^2 study area stretching from the continental divide of the northern Rocky Mountains (elevations up to 3,000 m a.s.l.), to the rolling boreal forest east of the Alaska Highway (elevations from 450 m a.s.l.; centred at 57°40'N, 123°20'W; Fig. 1).

Two systems of ecosystem classification are used in B.C. to model grizzly bear carrying capacity and predict density. Biophysical mapping defines units based largely on elevation, climate and vegetation (Demarchi 1995). Ecoprovinces are large continental ecosystems, whereas ecosystem divisions are delineated at a more detailed level at the ecoregion (provincial) and ecosection (regional) scale. Our study area was divided into the Northern Boreal Mountains ecoprovince, which covered the western one-third (3,114 km^2), and the Taiga Plains ecoprovince, which covered the eastern two-thirds (5,413 km^2). The Eastern Muskwa Range and Muskwa Foothills ecosections lie within the Northern Boreal Mountains ecoprovince, and the Muskwa Plateau ecosection and a very small portion of the Fort Nelson Lowlands ecosection are found within the Taiga Plains ecoprovince. Grizzly bear habitat capability is applied at the ecosection level.

Biogeoclimatic zones, each with a distinct pattern of vegetation and soil, are an ecosystem classification system that assumes climate is the principle factor influencing ecosystem development (Meidinger & Pojar 1991). Biogeoclimatic zones are further divided into subzones based on relative precipitation and temperature within the zone. The study area covers three biogeoclimatic zones; boreal white and black spruce (BWBS; moist warm (mw2) and wet cool (wk3) subzone/variants) in the lower elevation boreal forest; spruce-willow-birch (SWB; moist cool (mk) subzone) in the foothills; and alpine tundra (AT) in higher elevations (Meidinger & Pojar 1991). The alpine tundra and spruce-willow-birch zones essentially align with the

Northern Boreal Mountains ecoprovince, and the boreal white and black spruce zone aligns with the Taiga Plains ecoprovince.

Winters in the study area are long and cold, and the growing season is relatively short. Mean July and January temperatures for Fort Nelson, 100 km north of the study area in the boreal white and black spruce zone, are 16.7 and -22.0°C, respectively, with an average of 449 mm of precipitation annually, 191 mm of which falls as snow (Environment Canada climate normals, unpubl. data).

Frequent fire disturbances have resulted in a mosaic of successional coniferous, primarily lodgepole pine *Pinus contorta*, and deciduous, primarily trembling aspen *Populus tremuloides*, forests throughout the study area (MacKinnon, Pojar & Coupé 1992). Black spruce *Picea mariana* and white spruce *P. glauca* stands are found throughout the boreal white and black spruce zone, along with scattered stands of subalpine fir *Abies lasiocarpa*. Willow *Salix* spp. and alder *Alnus* spp. often cover open areas. The more mountainous spruce-willow-birch zone is characterized by white spruce and subalpine fir at lower elevations, grading to deciduous shrubs, mainly scrub birch *Betula* spp. and willow at higher elevations. Upper elevation valleys often have a mosaic of shrubs, grassland and wetlands. Treeline is generally at 1,300-1,400 m a.s.l. Alpine tundra vegetation includes dwarf willows, herbs, mosses and lichens. Several plant species that are important foods of bears further south do not occur in this area, such as western springbeauty *Claytonia lanceolata*, glacier lilies *Erythronium grandiflorum*, and wild parsley *Lomatium* spp., or are uncommon, such as sweet-cicely *Osmorhiza* spp. and angelica *Angelica* spp. (Fuhr & Demarchi 1990, MacKinnon et al. 1992). Two of the most commonly eaten grizzly bear plant foods, sweet vetch *Hedysarum* spp. and cow parsnip *Heracleum sphondylium* occur throughout the region.

The only permanent human residents within the study area were found at a lodge along the Alaska Highway, which bisects the study area from south to north. Various oil and gas leases also housed more ephemeral human residents. Oil and gas and forestry development had resulted in a sparse system of all-weather and winter access roads and seismic lines centred along the Alaska Highway and extending over much of the eastern half of the study area. There was one road and many horse and all terrain vehicle trails in the western third of the study area. Spring and fall grizzly hunting was permitted and controlled by quota. Hunters were encouraged to shoot males; the shooting of females accompanied by young was prohibited.

Survey design

Following methods outlined in Woods et al. (1999) and Mowat & Strobeck (2000), we used a systematic grid design to distribute sampling effort across the study area. We selected a 9 × 9 km cell size (81 km^2) in order to balance between the smallest likely home range size in that northern habitat (females with cubs in west central Alberta: mean = 252 km^2, N = 4; Nagy & Haroldson 1989) and enable coverage of the area. We selected study area boundaries to maximize geographic closure. Geographic closure, potentially the most important assumption of mark-recapture models, is violated if there is movement of individuals on and off the study area among trapping sessions (White, Andersen, Burnham & Otis 1982). We hoped to minimize movement by selecting the height of land between major drainages as the boundary, and by selecting a large area. The resulting study area boundary followed the height of land and enclosed complete drainages on all sides except where it crossed the main branches of the Prophet River in the north and the Sikanni Chief River in the southeast (see Fig. 1). We recognise that there were no real physical or behavioural barriers to bear movement along the study area boundary except perhaps to the west where the height of land generally exceeded 2,000 m a.s.l.

We divided the study area into 103 cells. Irregular shaped cells <40.5 km^2 in size along the boundary were lumped in with a neighbouring cell, resulting in a mean cell size of 82.8 km^2. We installed one capture site in each cell for approximately 12 days, and trapped five sessions, ensuring that each new site in a cell was located >1 km from all previous sites and that all five sites were roughly evenly spaced throughout each cell. We started the fieldwork in late May 1998 when we felt all bears would be out of their dens, based on the timing of emergence by grizzly bear populations in other areas (B. McLellan, B.C. Ministry of Forests, Revelstoke, B.C., pers. comm.). Females with cubs are typically the last age and sex cohort to leave their dens (Mace & Waller 1997). A 12-day trapping session was used to ensure that the study was completed by 1 August 1998. Stone sheep *Ovis dalli stonei* hunting started 1 August, after which time there was potential for conflict between hunters and bears at bait sites. Also, in late July and early August bears tend to move to berry patches, which can alter movement patterns and reduce catchability (Mowat & Strobeck 2000).

Field methods

We used a Bell 206B helicopter, a truck, and an ATV for access to sites. In the helicopter we used a Global Positioning System (GPS)-Geographic Information

System (GIS) linked computer navigation and mapping program to facilitate navigation and site placement (Poole, Mowat & Pritchard 1999). We selected sites based on our subjective interpretation of the best bear habitat in that cell. Both crew leaders were experienced in site selection from previous grizzly bear DNA studies. We placed sites near natural travel corridors whenever possible (e.g. alpine passes, valley bottoms and animal trails). Site selection in the mountains ranged from river valley bottoms to high passes between drainages. In the boreal forest, site selection was often restricted to road and seismic line access or suitable helicopter landing locations. Very few sites were set adjacent to all weather roads. We posted several warning signs at all sites where there was a risk of human encounter.

Hair collection sites consisted of liquid bait poured on a 1-1.5 m high mound of logs, stumps, moss and boughs. The mound was placed in the middle of a perimeter fence of 20-30 m of barbed wire running around three or more trees at about 50 cm from the ground (Woods et al. 1999, Mowat & Strobeck 2000). For bait we used about 250 ml of rancid fish oil and 3-4 litres of rotten beef blood. For the last two trapping sessions we added 30-40 g of beaver *Castor canadensis* castor wrapped in cloth and hung 2 m up in a tree within the site. The beaver castor was added in an attempt to provide a novel scent to enhance site attractiveness to previously captured bears. Change of bait part way through the study will not affect the statistical analysis of the data, because the change was uniform for all sites and several mark-recapture models accommodate this type of variation (White et al. 1982, Rexstad & Burnham 1991). However, if capture success varies strongly among sessions, the commonly used heterogeneity model (Jackknife) cannot be used.

When sites were removed, all hair from each barb was placed in a small paper envelope, air dried for one day, then frozen (-18°C) in a zip-lock bag containing 5-10 g of granular silica. Silica is a desiccant, which minimizes DNA degradation (Foran, Minta & Heinemeyer 1997).

DNA analysis

Using a dissecting microscope, all hair samples were sorted into three categories: black bear *U. americanus*, grizzly bear and unknown species. Samples which contained no roots or which were obviously not bear were removed. We identified black bear samples by the presence of glossy black guard hairs with a solid black tip, and grizzly bears by brown guard hairs with grey or silver tips. Unknown samples often contained both black and brown guard hair, or no guard hair at all. This method of subjective sorting has been checked during a previous study where 98% of the samples identified as black bear were confirmed by genetic testing (Woods et al. 1999). Normally, only those samples classified as grizzly bear or unknown would be tested for species using a genetic marker (Woods et al. 1999). However, because of reports of a number of very dark grizzly bears in the area, at least one sample from each site was genetically tested for species.

DNA analysis was conducted at the Wildlife Genetics International laboratory in Edmonton, Alberta, Canada. For samples with ≥6 roots we used chelex-based extraction (Walsh, Metzger & Higuchi 1991) on six roots, and stored the remaining roots. On samples with ≤5 roots, DNA from all roots was extracted using the tissue extraction protocol for QIAamp™ kits (Qiagen Inc., Ontario, Canada). We conducted species tests on each sample by amplifying a section of the control region of mitochondrial DNA (mtDNA) and comparing the results to a reference collection (Woods et al. 1999). We genotyped all grizzly bear samples using the same six microsatellite loci as Woods et al. (1999), which are known to be highly variable in grizzly bears (Paetkau & Strobeck 1994, Paetkau, Calvert, Stirling & Strobeck 1995). Genotyping failures were unacceptably high for the samples extracted using chelex (73%), thus we re-extracted 306 samples using QIAamp and re-ran the genotypes. We ran nuclear DNA analysis of the Amelogenin locus on individual grizzly bears to classify their sex using the primers SE47 and SE48 as described in Ennis & Gallagher (1994).

We used the sibling match test described in Woods et al. (1999) to measure the conditional probability that the full sibling of a given individual would have the same genotype, because we knew young bears often travel in sibling groups with the mother. We accepted new bears when they had unique genotypes and the P-values for the sibling match test were < 0.05. We declared two samples to be from the same bear when the genotype they had in common (i.e. excluding loci that were incomplete for one animal) had a P-value for the sibling match test < 0.05. If this criterion could not be met, one sample was eliminated. Several samples with 4-locus genotypes and $P < 0.05$ were also eliminated because they matched more than one other genotype at those four loci. In practical terms, a sample had to have a genotype at four or more loci to meet our criterion, and a pair of samples had to have genotypes for at least four common loci to be recognized as coming from the same individual.

We minimized typing errors by following the pre-

Table 1. Grizzly bear hair capture results from the Prophet River area in 1998. One hundred and three cells were sampled during each capture session.

Session	Start date	Duration (days) Mean (SE)	Sites with hair samples (%)	No. of samples	Hair samples/site Mean (SE)	Grizzly bears	New grizzly bears	Sites where ID failed
1	25 May	11.8 (0.10)	13 (12.6)	84	6.5 (1.70)	22	22	0
2	06 June	12.4 (0.12)	27 (26.2)	121	4.5 (0.67)	36	30	3
3	18 June	12.2 (0.11)	21 (20.4)	78	3.9 (0.54)	18	9	3
4	30 June	12.4 (0.13)	33 (32.0)	175	5.3 (0.57)	42	25	2
5	12 July	11.8 (0.14)	19 (18.4)	87	4.6 (0.80)	24	12	2
Grand mean		12.1 (0.06)	22.6 (21.9)		4.9 (0.35)			
Total			113	545		142	98	10

cautions outlined in Woods et al. (1999). Of 420 samples identified to individuals, 399 had genotypes that were not unique (i.e. were found in more than one sample). Since it is very unlikely that errors will be reproduced, or will cause a match to another genotype, we assumed that these 399 samples did not contain genotyping errors. Of the remaining 21 samples, any that differed from another genotype at one or two loci were confirmed by reanalysis. In addition, any genotype that differed from another genotype at only one locus was reanalysed, even if multiple samples were found with that genotype. The checking process found five cases where errors were made between the raw data and the data file (scoring errors), and five cases of amplification errors, including four cases of allelic dropout (Taberlet, Griffin, Goossens, Questiau, Manceau, Escaravage, Waits & Bouvet 1996). In the final data set, there were five pairs of individuals with genotypes that differed at only one locus.

Data analysis

We used the mark-recapture models in the program CAPTURE to estimate population size (White et al. 1982). Model selection was based on a subjective review of capture results, the model selection tests performed by CAPTURE, previous simulation results (Otis, Burnham, White & Andersen 1978, Mowat & Strobeck 2000), and our knowledge of bear behaviour. We also estimated population size within the two ecoprovinces in the study area. Each ecoprovince formed a continuous portion of the greater study area and we used the captures within each ecoprovince to estimate specific densities. We compared grizzly bear detection rates among biogeoclimatic subzones and between ecoprovinces using likelihood ratio contingency analysis. Spatial analysis was conducted using ArcView (Environmental Systems Research Institute, Redlands California). Distances moved by sex classes of bears were compared between ecoprovinces and sexes using t-tests.

Results

Hair collection and analysis

We set and monitored 515 sites between 25 May and 1 August 1998 (see Fig. 1). Sites were active an average of 12.1 days (Table 1). We collected 2,062 hair samples from 332 sites (range: 1-28 samples/site). We ran mtDNA species checks on 1,139 samples; 544 were grizzly, 453 black bear, one contained DNA from both bear species, 25 samples were from wolves *Canis lupus*, and 116 tests failed primarily because of insufficient DNA, or they were not bear or wolf. Subjective identification of samples correctly identified 94.5% of black bear samples and 81.3% of grizzly bear samples, as verified by genetic testing (Table 2).

We identified grizzly bear hair at 113 sites (see Fig. 1 and Table 1). During the first session, the proportion of sites that detected grizzly bears (mean: 22.6%) was

Table 2. Comparison of species identification of bear hair using macroscopic sorting and DNA species testing, Prophet River grizzly bear inventory in 1998.

Sorting Id[a]	N	Species identification based on mtDNA (%)			
		Black bear	Grizzly bear	Both bears	Unknown[b]
Black bear	128	121 (94.5)	6 (4.7)	0	1 (0.8)
Grizzly bear	433	45 (10.4)	352 (81.3)	1 (0.2)	35 (8.1)
Unknown	578	287 (49.7)	186 (32.2)	0	105 (18.2)

[a] Hair samples were sorted into black bear, grizzly bear and unknown based on gross hair morphology and colour.
[b] Unknown samples included wolf, species other than bear or wolf, and species test failures.

Table 3. Grizzly bear population estimates from eight closed mark-recapture models in program CAPTURE from DNA analysis of hair collected at bait sites during summer 1998 for the Prophet River area.

Model	$\hat{N}$	SE	95% CI
M_o-Null	151	14.9	126-187
M_h-Jackknife	190	19.6	159-237
M_h-Chao	174	25.9	137-243
M_t-Darroch	148	14.1	124-182
M_t-Chao	154	19.6	127-207
M_{th}-Chao	166	26.2	131-239
M_b-Zippin	193	69.0	124-438
M_{bh}-Removal	193	69.1	124-438

slightly lower and the number of grizzly bear hair samples per site (mean: 4.9) was slightly larger than in the following sessions (see Table 1). We identified black bear hair at 203 sites, with proportionately more detections in the eastern half of the study area. The number of sites at which black bear was detected was relatively constant for the first four sessions (39-47 sites/session), but dropped to 30 sites in the fifth session. Wolf hair was identified at 14 sites distributed throughout the study area.

DNA fingerprinting was performed on the 544 confirmed grizzly bear hair samples (see Table 1; the single sample that contained both grizzly bear and black bear DNA was not genotyped). Four hundred and twenty samples (77%) generated 98 genotypes with a sibling match probability of <0.05; 44 of these individuals were females and 47 were males. We could not assign sex to the remaining seven individuals due to inadequate amounts of template DNA. We identified 10 family groups (females with offspring, or siblings) based on exclusion (the principle that all offspring must share at least one allele with each parent), although we had low power of exclusion because we analyzed only six loci. There were 10 sites that removed grizzly bear hair but where we were unable to identify an individual (see Table 1). The 98 grizzly bears were caught 159 different times during our study. However, for mark-recapture modeling, a bear caught at two different sites in the same session counts as one capture; we captured bears 142 times in the five capture sessions. Forty-one grizzly bears were caught at >1 site. Individual sites generally caught 1-3 bears; two sites caught four bears and one site captured seven bears. To our knowledge, no grizzly bears were removed from the study area during the study.

Population size

We examined eight closed mark-recapture models and selected Darroch's time model (M_t-Darroch) to obtain a naive population estimate for our study area of 148 grizzly bears (95% confidence interval (CI): 124-182; Table 3). We selected Darroch's time varying model because there was obvious variation in capture success among sessions ($\chi^2 = 17.2$, df = 4, P = 0.002; Fig. 2), and little evidence of heterogeneity variation ($\chi^2 = 0.60$, df = 1, P = 0.44) or behaviour response ($\chi^2 = 0.93$, df = 1, P = 0.34) based on the goodness of fit tests in CAPTURE. In addition, previous simulation and analysis suggest that M_t is robust to mild heterogeneity (Otis et al. 1978, Mowat & Strobeck 2000). The model selection routine in CAPTURE also suggested M_t; we selected M_t-Darroch over M_t-Chao because we did not consider capture probabilities to be sparse enough to require the Chao model (Chao 1989). The mean capture probability was 0.19 per session.

We considered the naive estimate to be biased high because the majority of the study area boundary was not topographically closed. In addition, the closure test in CAPTURE rejected closure at P = 0.05. We estimated population size for males and females separately to investigate the potential impact of closure bias on the combined estimate. The population estimate for males (71 bears) was nine bears higher than the estimate for females (62 bears). Added together, these estimates by sex are slightly lower than the unadjusted estimate for the entire study (133 versus 148). Closure bias for females was likely smaller than for males because females have smaller home ranges (see summary in LeFranc, Moss, Patnode & Sugg 1987). The true sex ratio in the population was likely to approximate 50:50 or favour females (see Table 9 in LeFranc

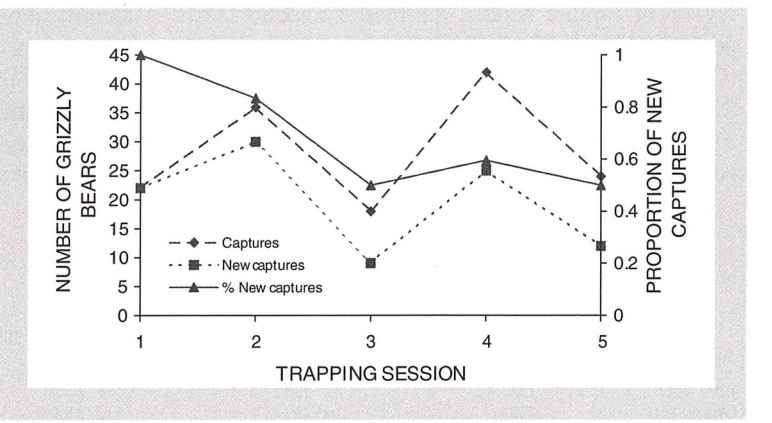

Figure 2. Total number of grizzly bears captured per trapping session, the number of new bears captured per session, and the proportion of captured bears which were new bears in each of five capture sessions on the Prophet River study area in 1998.

Table 4. Distance moved (km) by recaptured grizzly bears according to ecoprovince and sex class in the Prophet River area in 1998.

Ecoprovince	Sex class	N	Mean	SE	Range
Taiga Plains[a]	Male	8	21.9	6.55	7.5-64.8
	Female	4	11.2	3.59	3.8-18.7
	Family group	2	17.1	5.75	11.3-22.8
Northern Boreal Mountains[b]	Male	18	15.8	1.60	8.2-37.4
	Female	15	10.9	1.34	5.1-20.9
	Family group	8	5.4	0.88	2.0-10.6

[a] Difference between sexes in the Taiga Plains: t = 1.09, df = 1, P = 0.30
[b] Difference between sexes in the Northern Boreal Mountains: t = 2.31, df = 1, P = 0.028

et al. 1987), because males generally have higher mortality rates than females especially in hunted populations where females with cubs are protected (McLellan, Hovey, Mace, Woods, Carney, Gibeau, Wakkinen & Kasworm 1999), as was the case in our study area. Males probably had higher overall capture probabilities due to their larger home ranges and movements (Mace, Minta, Manley & Aune 1994). Therefore, we reasoned that the difference between the male and female population estimates was probably largely due to closure bias in the male segment of the population. To partially account for closure bias, we reduced the overall population estimate by 6.8% to correct for the greater abundance of males shown in the estimates for each sex cohort. We derived the correction factor by dividing nine (the estimate for males was nine bears larger than for females) by 133 (the total population estimate for both sexes). We consider this a conservative measure of the bias caused by lack of closure because we conservatively assumed that the actual sex ratio was even, which is unlikely (McLellan et al. 1999). This correction for lack of closure resulted in an adjusted population estimate of 138 grizzly bears (95% CI: 114-172 or roughly ±21% of the estimate) within the study area (16 bears/1,000 km^2; 95% CI: 13-20).

Population density among ecosystems

We were more likely to detect grizzly bears in sites set in the more mountainous Northern Boreal Mountains than in the flatter Taiga Plains (χ^2 = 39.2, df = 1, P < 0.001; see Fig. 1). We estimated population size independently within the two ecoprovinces using Darroch's time model. The naive population estimate for the Northern Boreal Mountains was 96 grizzly bears (95% CI: 80-122) and for the Taiga Plains it was 58 bears (95% CI: 40-99). These numbers appear accurate because together they approximate the unadjusted estimate for the entire study area (154 versus 148). Sample sizes were too small to analyse either region by sex to investigate closure bias. However, we used the correction that was suggested for the entire study area (6.8%) as a rough guide to obtain adjusted population estimates and density for each region: Northern Boreal Mountains 89 grizzly bears (95% CI: 73-115), 29 bears/1,000 km^2 (95% CI: 23-37); Taiga Plains 54 grizzly bears (95% CI: 36-95), 10 bears/1,000 km^2 (95% CI: 7-18).

Bear movements

Forty-one bears (including eight family groups) were captured more than once during the study. Within each ecoprovince, there was a tendency for males to move greater distances than single females, however, a significant difference was obtained only for the mountainous region (Table 4). Family groups tended to move smaller distances than non-family groups in the mountainous regions. Between regions, males and females again tended to move greater distances in the boreal plains, however, the differences were not significant (P > 0.39). Although a few bears were captured near the boundary between the mountains and plains regions, no individual bears were captured in both the mountainous and plains regions during the study. One male grizzly captured well within the boreal plains during the second session was recaptured 65 km to the west near the interface between regions during the forth session, and subsequently was recaptured at two sites back in the boreal plains in the fifth session. Two males moved 23 and 37 km from within the mountainous region to near the interface between the regions during the study, but again did not cross.

Discussion

The grizzly bear population size in B.C. is currently extrapolated from estimates taken from detailed population research projects and applied to similar biogeoclimatic variants within ecosections (Fuhr & Demarchi 1990). These estimates of undisturbed habitat capability may then be stepped down based on current suitability, for example if the area in question is disturbed

Table 5. Grizzly bear population estimate for the Prophet River study area based on current (August 1999) habitat capability modeling.

Ecoprovince	Ecosection	Biogeoclimatic variant	Area (km²)	Habitat capability class[a]	Estimate[b]
Northern Boreal Mountains					48.7
	EMR	AT	670[c]	5	0
	EMR	SWBmk	206	3	5.4
	MUF	AT	663	4	4.0
	MUF	SWBmk	1406	3	36.6
	MUF	BWBSmw2	109	3	2.8
Taiga Plains					61.5
	MUP	SWBmk	4	3	0.1
	MUP	BWBSmw2	4734	4	28.4
	MUP	BWBSwk3	643	2	32.8
	FNL	BWBSmw2	32	4	0.2
Entire study area					110.2

[a] Density (bears/1,000 km²) in Class 1: 76-100; Class 2: 51-75; Class 3: 26-50; Class 4: 6-25; Class 5: 0-5.
[b] Population estimates were derived based on the low value of the density range in all classes (current government policy; T. Hamilton, B.C. Ministry of Environment, Lands and Parks, Victoria, B.C., pers. comm.).
[c] Approximately 60 km² of lake and glacier (with a density of 0 bears) removed.

by humans or to account for harvest. Each combination of biogeoclimatic variant and ecosection is assigned one of five density classes; density (bears/1,000 km²) in Class 1 = 76-100; Class 2 = 51-75; Class 3 = 26-50; Class 4 = 6-25; Class 5 = 0-5 (Fuhr & Demarchi 1990). Estimates may change through use of the low, mid-point or high values within each density range and through changes to the capability class assigned to biogeoclimatic subzone/variants within each ecosection. Current government policy is to use the low end of all density ranges when applying habitat capability ratings (T. Hamilton, B.C. Ministry of Environment, Lands and Parks, Victoria, B.C., pers. comm.). This policy generated a habitat capability estimate for our study area of 110 grizzly bears (Table 5).

The current habitat-based estimate predicts similar overall densities to our estimates for the Taiga Plains (11 versus 10 bears/1,000 km², respectively), but only about half of our estimate for the Northern Boreal Mountains (16 versus 29 bears/1,000 km², respectively). Although additional data should be obtained to verify our results, some modification to increase the habitat capability ratings could be considered in light of these results. Any modifications should be conservative given the possibility that our estimate is biased high. Changes could include applying the mid-point of the density estimates, or revising the ratings assigned to various biogeoclimatic zones. Use of the midpoint of the density ratings provided an overall population estimate (192 bears) above the upper confidence interval of our population estimate, and generated a lower estimate for the mountainous area (77 bears) and a much higher estimate for the Taiga population (115 bears) compared to our results.

If habitat capability ratings were to be revised, the combined habitat estimates for the alpine tundra and spruce-willow-birch biogeoclimatic zones within the Northern Boreal Mountains could be doubled to better reflect our results; this could be obtained by changing the habitat capability class for the SWBmk variant from 3 to 2. Although our estimates within the Taiga Plains agree with the habitat based estimates, the low end of capability class rating 2 for the boreal white and black spruce wk3 variant within the Muskwa Plateau ecosection (MUP) appears to inflate the grizzly bear density (adding 33 bears to the estimate from only 643 km²), whereas the low end of rating 4 for the boreal white and black spruce mw2 variant appears to considerably underestimate bear density (see Table 5). We found no supporting evidence for separating the habitat based density estimates for these two variants; to better reflect our estimates the habitat based estimates within the Taiga Plains could be changed to approximately 0.02 bears/km² (the upper range of the class 4 rating).

The annual resident and non-resident harvest of grizzly bears for the study area between 1986 and 1996 was roughly 8-9 bears (MELP hunter harvest summary statistics). The First Nation's harvest of grizzly bears in the study area was negligible (B. Wolf, Prophet River Indian Band, pers. comm.). Assuming similar bear densities over the past decade and a half, the harvest rate for our study area has averaged roughly 6% per year to 1996, slightly higher than the provincial policy of 4-5% for managing grizzly bear harvest in this area.

There have been few studies conducted on grizzly bears that inhabit habitats similar to the foothills and boreal forests of the eastern Prophet River area. All of the Prophet study area is located in the Cold Boreal Plains grizzly bear zone. Banci (1991) estimated the density in this zone to be roughly 3.3 bears/1,000 km². Our

study would suggest this number is grossly conservative, especially for the western part of the zone. In the adjacent Subarctic Mountains and Plains grizzly bear zone the estimated density is 15.4 grizzly bears/1,000 km^2 (Banci 1991), which more closely approximates our overall estimate for the study area. The nearest studies on grizzly bears east of the Rocky Mountains were conducted in the west-central portion of Alberta, located in the Cold Boreal Plains grizzly bear zone but in three different ecoprovinces. Estimated densities of grizzly bears in these study areas ranged from 4.6 bears/1,000 km^2 in the Berland-Wildhay rivers region, 7.4/1,000 km^2 in the areas of the South Wapiti River, and 7.4-9.6/1,000 km^2 in the Swan Hills study (Nagy & Gunson 1990), slightly lower or similar to our density estimate for the boreal plains portion of the Prophet River study (CI: 7-18 bears/1,000 km^2). All three of these areas were in proximity to much higher human density and probably received much greater human use than our study area. However, it is worth emphasizing that the boreal plains portion of our study had much greater road density than the boreal mountains, where there was only one road, and this increased access may have resulted in greater bear mortality than in the mountains to the west.

There is currently no other estimate of grizzly bear density in the Northern Boreal Mountains ecoprovince of B.C. However, for the same ecoprovince in southern Yukon Larsen & Markel (1989) presented a preliminary estimate of 13-22 bears/1,000 km^2 and Pearson (1975) estimated density that ranged within 37-44 bears/1,000 km^2. To the south, Russell, Nolan, Woody & Anderson (1979) estimated bear density to be 10-12 bears/1,000 km^2 in Jasper National Park, which lies in the northern portion of the Southern Interior Mountains ecoprovince. It would seem that there may be a large variation in bear density in the northern mountains and that the relatively high density we report for the mountainous part of our study (29 bears/1,000 km^2) is not unprecedented in that ecoprovince (Pearson 1975). We caution that all of the above-noted densities were derived from intensive capture and collaring studies, and rarely include measures of precision. Different methodologies and assumptions in each study suggest that these densities may not be directly comparable to those which we used in the Prophet River area.

Although it would appear one could use the model selection routine in CAPTURE for this dataset, interpretation of the results was complicated by the fact that the proportion of new captures increased during sessions four and five (see Fig. 2). Whereas this result may simply be due to sampling variation, the movement of male bears off the study area during sessions four and five after the breeding season could also explain it, and is supported by the closure test in CAPTURE, which was rejected. Alternatively, it is possible that the addition of beaver castor in sessions four and five caused an increase in the capture of new bears that were not interested in the fish and blood baits used exclusively during sessions 1-3. This explanation is less likely because we would expect all bears to respond positively to a new bait, not just bears which had not been previously captured.

We estimated that topography may have been severe enough to force bears to align their home range boundaries with the study area boundary for about 20% of the study area perimeter (along the height of the Rocky Mountains on the western end of the study area). This suggests the possibility for an important closure bias in this study. We calculated the maximum trappable area by extending all border cells out to their full size except for those cells that we felt had closed borders (in the western mountains). Density was reduced by 20% when we used the maximum trapped area to calculate density. Individuals residing partially on the study area have reduced capture probabilities so the capture bias is likely to be less than the 20% we estimated based on the maximum trappable area. Although the distribution of grizzly bear captures across our area was not homogenous, we feel that lacking a more objective correction for closure the difference between male and female population sizes is the best, though possibly conservative, estimate of closure bias we have for this data set. Recent modeling supports our contention that our correction for closure may be conservative (Boulanger & McLellan 2001).

Our field techniques generally followed techniques used in previous studies, however, we used mounds of sticks, branches and stumps, topped with moss for bait-placement, rather than the conventional practice of suspending bait on a rope between trees (Woods et al. 1999, Mowat & Strobeck 2000). We suspect these mounds may have helped to entice bears past the barbed wire because they resembled a carcass covered by a bear, both in size and smell. Also, the bait was 1-2 m off the ground, which encouraged air flow, and the moss helped keep the bait moist and smelly during the relatively warm and dry summer. We were able to smell the bait at many sites after 12 days. Use of mounds and liquid baits also enabled consistency among bait sites throughout the study; many alpine sites were placed in areas where it would have been impossible to suspend bait from trees. We cannot assess whether the addition of beaver castor during the last two sessions aided our goal of increasing recaptures. It is interesting to note that

total captures went up dramatically in the fourth session and the proportion of repeat captures increased in both the fourth and fifth sessions.

Grizzly bears in the Taiga Plains may have been more difficult to capture than the bears in the Northern Boreal Mountains. Capture probabilities in the Taiga Plains and Northern Boreal Mountains (0.14 versus 0.21, respectively) support this hypothesis. We feel this was primarily because of the limited options on the Plains for accessible sites (generally roads, seismic lines or abandoned well sites) and a paucity of obvious travel corridors. Grizzly bears were often detected in the mountains on travel corridors in saddles, passes, and animal trails along rivers and valleys; similar features were less obvious and perhaps less abundant in the boreal forest.

We used the same technician as used by Woods et al. (1999) to sort out black bears samples, and her ability to identify black bear hair was similar for both studies. Success of species identification and genotyping for the Prophet River data set were higher than other studies we have conducted (Mowat & Strobeck 2000). This may have resulted from careful handling of samples between the field and the laboratory (drying and freezing samples with silica) or use of the QIAamp method to ultimately extract most samples. Genotyping failures were unacceptably high for the samples initially extracted using chelex, although we do not know the cause of these failures. It appears that the species test presented by Woods et al. (1999) will also identify wolves. We report here the first instances of verified capture of wolves at hair snagging bait sites.

Management implications

We suggest that the capability ratings currently in use for the boreal biogeoclimatic zones within the northern ecoprovinces of B.C. significantly underestimate density in the mountainous portions of the Prophet River area. These capability ratings could be adjusted if the Prophet River area is representative of the biogeoclimatic zones and ecoprovinces elsewhere in the northern part of the province. A second DNA-based estimate of grizzly bear population size in another location in the northern boreal portion of B.C. would provide an additional set of data to support the refinement of the habitat-based capability ratings.

We demonstrate that adequate capture success for grizzly bears can be achieved using liquid baits, however, we do not know how important it is to add a novel bait or baits during a study. We concur with Woods et al. (1999) and Mowat & Strobeck (2000) that removing obvious black bear samples before extraction can reduce DNA analysis costs. QIAamp extraction may improve genotyping success in some laboratories (J. Boulanger, Integrated Ecological Research, Nelson, B.C., pers. comm.).

We corrected for closure bias in our study but our population estimate may still have been high. Application of mark-recapture to calculate population density will always involve a subjective component until there is an objective method to correct for closure bias. Large study areas, boundaries that provide topographic barriers, and short study duration will all minimize closure bias and should be considered in study design.

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