# ESTIMATING POPULATION SIZE OF GRIZZLY BEARS USING HAIR CAPTURE, DNA PROFILING, AND MARK–RECAPTURE ANALYSIS

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***Abstract:*** We used DNA analysis to estimate grizzly bear (*Ursus arctos*) population size in a 9,866-km$^2$ area in southeast British Columbia and a 5,030-km$^2$ area in southwest Alberta. We sampled bears by removing hair at bait sites surrounded by a single strand of barbed wire. DNA profiling with microsatellites of the root portion of the hair was used to identify individuals. We collected hair from 109 different bears and had 25 recaptures in 5 10-day trapping sessions in British Columbia. In Alberta we collected hair from 37 bears and had 9 recaptures in 4 14-day sessions. A model in program CAPTURE ($M_h$) that accommodates heterogeneity in individual capture probabilities estimated the population size in British Columbia as 262 (95% CI = 224–313) and in Alberta as 74 (60–100). We believe that hair capture combined with DNA profiling is a promising technique for estimating distribution and abundance of bears and potentially many other species. This approach is of special interest to management biologists because it can be applied at the scale conservation and management decisions are made.

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***Key words:*** Alberta, British Columbia, Canada, density, DNA profiling, grizzly bears, hair removal, mark–recapture, microsatellite analysis, population size, *Ursus arctos*.

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Estimating carnivore abundance is central to their conservation, however, options for estimating carnivore population size are few and often require specific circumstances or assumptions that are difficult to meet. Estimating bear population size is difficult and only has been achieved in conjunction with intensive effort (McLellan 1989, Garshelis 1992, Stirling et al. 1997). Recent efforts to develop bear inventory methods have involved the use of mark–recapture modeling. Researchers have used live capture to mark bears and then recaptured bears using camera stations (Mace et al. 1994), aerial survey (Larsen and Markel 1989, Stirling et al. 1997), and hair removal and DNA fingerprinting analysis (Proctor 1995). Most recently, hair removal and DNA fingerprinting have been used to mark and recapture grizzly bears (Woods et al. 1996, 1999). This latter method has several benefits as live capture of bears is unnecessary, individuals can be identified with a small risk of error, and hair removal sites are faster to set and are checked less often than live–capture sites. Simpler logistics allow a study design that comes closer to meeting the assumptions and sample size requirements of current mark–recapture models.

There are several important assumptions involved with mark–recapture analysis to estimate population size. The most important may be the assumption of population closure, which White et al. (1982) separate into demographic and geographic closure. Demographic closure assumes there are no births or deaths or permanent immigration or emigration during the study. Errors due to demographic changes in population size are likely to be small for bears, especially if the duration of study is restricted to 6–10 weeks. Geographic closure is violated if individuals move on and off the study area between trapping sessions. A positive bias results when animals have home ranges that span the

study area boundary (White et al. 1982, Bondrup-Nielsen 1983, Boutin 1984, Garshelis 1992). The above biases can be minimized by selecting study area boundaries that physically enclose animals on the study area and when average home range size is small compared to the size of the study area. Minimizing the duration of sampling should further reduce this bias (White et al. 1982).

Mark–recapture models also make assumptions regarding the equality of capture probabilities among individuals. White et al. (1982) and Rexstad and Burnham (1991) have incorporated a number of specific mark–recapture models, some of which relax the assumption of equal capture of individuals, into a single program (CAPTURE). They categorize 3 types of capture variation: (1) heterogeneity, where individuals have different capture probabilities for unknown reasons; (2) behavior, where individuals that have been captured once have different capture probabilities than those that have not been captured (trap happy and trap shy response); and (3) time, where there are different mean capture rates among trapping sessions (for example due to the effects of weather or seasonal behavior among sessions). Most mammal studies have detected variation in capture rates, usually heterogeneity (Conner and Labisky 1985, Greenwood et al. 1985, McCullough and Hirth 1988, Hallet et al. 1991, Boulanger and Krebs 1994, Corn and Conroy 1998), and this is likely for grizzly bears as well (Mace and Waller 1997*a*, Woods et al. 1999). The statistical challenge for most mammal biologists using closed mark–recapture models is not to achieve equal catchability, but to select the appropriate model for their data.

With the above limitations in mind, we choose to employ the methods developed by Woods et al. (1996, 1999) to estimate grizzly bear population size for 2 bear populations for which there was considerable management concern. Our objective was to estimate grizzly bear population size using hair removal and DNA profiling for large areas in southern British Columbia and southwest Alberta. Both areas were of the size typically used for bear management decisions. Specifically we wanted to evaluate the logistics of hair removal in the field and investigate study design criteria based on capture results, model selection, and assumptions.

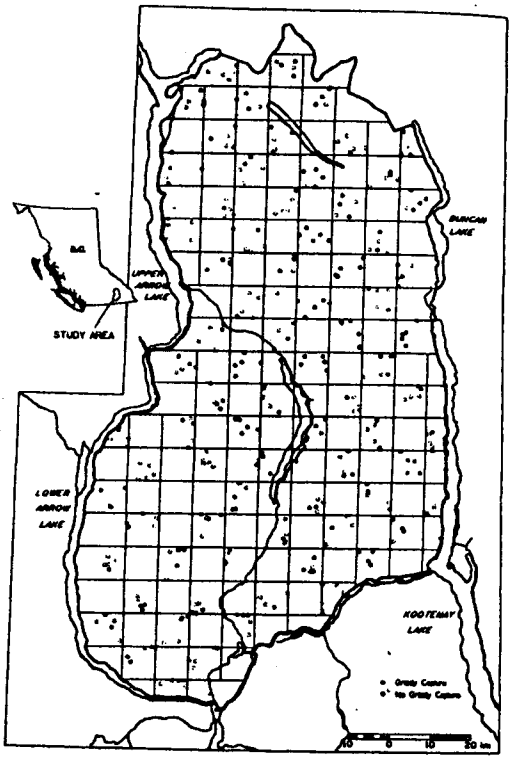


Fig. 1. Study area boundary (thick line), grid system (thin lines), and location of the sample sites (dots) in southeast British Columbia. Solid dots represent sites where grizzly bear hair was collected and hollow dots sites where hair was not collected.

## STUDY AREA

The British Columbia study area was dominated by the central Selkirk Mountains with many peaks exceeding 2,400 m (Fig. 1). The majority of the area was forested. Low elevation forests were typically dominated by western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*), while Englemann spruce (*Picea englemanni*) and subalpine fir (*Abies lasiocarpa*) forests were dominant above 1,400 m. Alpine areas were also common above approximately 2,000 m, as were avalanche chutes. Well developed riparian areas generally occurred only in the large valleys because small river valleys were usually too steep to have riparian zones. Much of the most productive habitat in the larger valleys was settled, flooded by hydroelectric dams or altered in some other way. Logging had occurred throughout the area for the past 100 years and cutblocks with good berry production were common. Three large provincial parks occurred in this area, 2 of which had

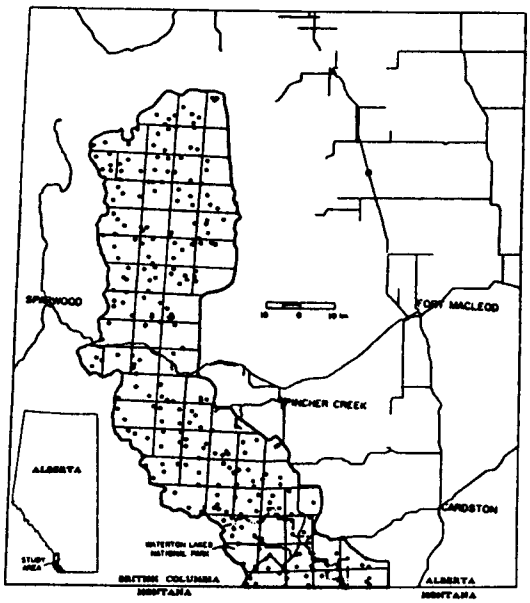


Fig. 2. Study area boundary (thick line), grid system (thin lines), and location of the sample sites in southwest Alberta. Solid dots represent sites where grizzly bear hair was collected and hollow dots sites where hair was not collected.

been logged very little. The study area was bisected north to south by a major highway. Generally, the northern part of the study area was less disturbed than the southern portion.

Our second study area was a 5,030-km$^2$ area in southwest Alberta (Fig. 2). The area included all of Waterton Lakes National Park and several small provincial parks. The western part of the area was dominated by the east slopes of the Rocky Mountains; the east side was predominantly rolling foothills that transformed into open grassland near the eastern edge. Human settlement was scattered throughout the eastern portion of this area and a strip of human settlement ran through the middle of the study area in Crowsnest Pass. Agriculture was extensive at low elevations and was dominated by cattle ranching. Forestry was common only in the northern portion of the study area. The study area was bisected east to west by a major highway; lesser used roads were common. The majority of the area was forested though numerous openings occurred, especially in the eastern part of the area. Low elevation parkland forests were typically dominated by trembling aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), and Douglas fir (*Pseudotsuga menziesii*), while Englemann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forests dominated the montane and subalpine regions above 1,400 m. Alpine areas were common in the west above 2,100 m. Avalanche chutes occurred only in the Rocky Mountains along the western border of the area.

## METHODS

We used a systematic grid design to balance effort across each area and minimize capture variation (White et al. 1982). We subjectively located sites within cells to maximize capture probabilities (Woods et al. 1999). We divided both study areas into 8 × 8-km cells because this was a conservative estimate of the average size of female grizzly bear home ranges in spring in similar nearby ecosystems (J. G. Woods, Parks Canada and B. N. McLellen, British Columbia Ministry of Forests, personal communication; Mace and Waller 1997*b*). All individuals, including bears with small home ranges, must have a non-trivial chance of being caught or underestimates will occur (Pollock et al. 1990). Irregular shaped cells <32 km$^2$ were lumped in the neighboring cell. The resulting 154 cells in British Columbia averaged 64 km$^2$ and varied from 26–94 km$^2$ in size. In Alberta, 73 cells averaged 69 km$^2$ and ranged from 37–96 km$^2$ in size. In British Columbia, we elected to sample every second cell in a checker board fashion because we did not have resources to sample all cells in the study area (Fig. 1). Trapped cells covered 49.3% of the study area. We installed 1 hair removal site in each of 76 cells for approximately 10 days. Each site was visited once at the end of the 10-day trapping session and removed. The next site was installed elsewhere in the cell with the stipulation that new sites be at least 1 km from all previous sites. About half the sites were installed using a helicopter, the rest of the sites were accessed from the ground. Sampling was the same in Alberta except we sampled every cell and used 14-day capture sessions. A second site was installed in about 9 cells that were known to contain grizzly bears in order to increase sample size; we usually moved these sites to new cells in subsequent sessions.

All field crew leaders had considerable experience hunting and watching bears in the areas they worked and were encouraged to select the best sites for catching grizzly bears in each cell. Generally, sites in the first round were in low elevation riparian areas; we moved sites higher in elevation as avalanche chutes and

south facing herbaceous slopes greened up. We made an effort to move sites to berry patches during late July and early August. Some sites were located along well-used pathways, especially where a low pass crossed into an adjoining drainage. A few sites were located near old or current dumps or other areas known to attract bears. On rare occasions there was only 1 or 2 sites that had any hope of catching a grizzly bear in a cell. In these cases, we left the site in the same location or moved it back and forth between the few reasonable sites. Hair removal sites were located a minimum of 200 m from a hiking trail, and 2 km from a campground. Warning signs were posted at 2–4 observable places at all sites.

Hair collection sites consisted of a bait strung approximately 5 m high between 2 trees and a perimeter fence of barbed wire running around ≥3 trees at about 50 cm from the ground (Woods et al. 1999). It is important the wire be placed ≤50 cm above ground and that all places where the wire dips too low or too high be filled with brush to encourage bears to enter at a place where the wire is at the proper height. Sites where vegetation hid the wire appeared to remove more hair than more open sites. We used liquid fish fertilizer and 3 kg of beef fat for bait in British Columbia. Meat baits were rotted for >14 days in barrels left in the sun and hung in gunny sacks between 2 trees >4 m above the ground. Hair removal sites could be installed or removed in <30 min by a 2-person crew. We used fish oil (fish rotted to a liquid) mixed with beaver castor (250 ml/10 L of fish oil) and rotted cow blood as baits in Alberta. We added sodium citrate to the blood as it was collected and put barrels of blood in the sun to rot for >14 days. These were poured on logs placed in the middle of the site. Hair removal sites using liquid bait could be installed or removed in <20 min by a 2 person crew. All hair collected at a single barb was put into a small paper coin envelope. Sometimes we collected hair from places where bears had rubbed or dug about the site, or from below the wire. We let all samples dry at room temperature for 5–20 days before storing them in a freezer. There were only 6 sites of 702 sampled where field personnel felt a bear had visited a site and not left any hair.

All hair samples were inspected under a dissecting microscope to remove unusable samples and sorted into 3 categories: black bear, grizzly bear, and unknown bear species. Black bear samples were identified by the presence of long glossy black guard hairs. Grizzly bear guard hairs were long and brown with grey or silver tips. Unknown samples often contained no guard hair or contained both black and brown guard hair. We performed DNA analysis on all useable samples from Alberta, but in the British Columbia study, we removed black bear samples. Only those samples classified as grizzly bear or unknown were genetically tested for species. This method of subjective sorting was checked during a previous study and 97% of the samples identified as black bear were confirmed by mitochondrial DNA (mtDNA) species analysis (Woods et al. 1999). We also subsampled by site in British Columbia to reduce the number of samples for analysis. All samples were run for sites with <10 samples; for sites with 11–64 samples every second sample was analysed; for sites with >64 samples 32 samples were run.

DNA was extracted from hair roots with chelex (Walsh et al. 1991) and frozen. We put up to 4 roots in an extraction because 4 roots is sufficient for the type of fingerprint analysis being performed (Woods et al. 1999), though more may be optimal (Gossens et al. 1998). Each sample was tested for species by amplifying a section of the control region of mtDNA using PCR and comparing the result to a reference collection (Woods et al. 1999). Black bear samples were removed. The remaining samples were profiled using 6 microsatellite loci (Paetkau and Strobeck 1994, Paetkau et al. 1996, Woods et al. 1999). Any sample that had more than 2 alleles at a locus was assumed to contain DNA from >1 individual and excluded. A nuclear DNA analysis of the SRY locus on the Y chromosome was used to sex individual bears (Woods et al. 1999). We used the sibling match test described in Woods et al. (1999) to measure the conditional probability that the individual in question was a sibling to others already identified because we knew bears often travel in sibling groups with the mother. We accepted new bears when $P < 0.05$.

We used the mark–recapture models in program CAPTURE (Otis et al. 1978, White et al. 1982, Rexstad and Burnham 1991) for estimating population size. Model selection was based on our knowledge of bear biology, the statistical tests available in CAPTURE, and Monte Carlo simulation (Menkens and Anderson 1988). We

Table 1. Hair capture results from the Central Selkirk mountain grizzly bear inventory, British Columbia, 1996 and the southwest Alberta bear inventory, 1997.

| Study site, end date | Session | Trap duration (days) $\bar{x}$ | Trap duration (days) SD | Sites sampled | Sites with hair samples | Hair samples/site $\bar{x}$ | Hair samples/site SD | Hair samples | Grizzly bears | New grizzly bears | Sites where ID failed[a] |
|---|---|---|---|---|---|---|---|---|---|---|---|
| British Columbia | | | | | | | | | | | |
| June 29 | 1 | 10.3 | 1.1 | 76 | 60 | 17.4 | 14.5 | 1,043 | 23 | 23 | 1 |
| July 9 | 2 | 9.7 | 0.6 | 76 | 63 | 18.9 | 15.0 | 1,191 | 19 | 15 | 0 |
| July 19 | 3 | 10.4 | 1.2 | 77 | 67 | 15.4 | 16.5 | 1,029 | 31 | 28 | 1 |
| July 29 | 4 | 10.1 | 1.4 | 76 | 42 | 12.5 | 10.0 | 526 | 35 | 25 | 3 |
| Aug 9 | 5 | 9.2 | 0.8 | 76 | 44 | 10.4 | 9.3 | 456 | 26 | 18 | 3 |
| Total or grand mean | 9.9 | 1.1 | | 381 | 277 | 15.3 | 13.9 | 4,245 | 134 | 109 | 8 |
| Alberta | | | | | | | | | | | |
| June 28 | 1 | 14.6 | 1.9 | 76 | 45 | 4.5 | 4.4 | 201 | 13 | 13 | 3 |
| July 13 | 2 | 14.3 | 1.8 | 81 | 33 | 4.7 | 3.2 | 156 | 13 | 11 | 2 |
| July 27 | 3 | 13.8 | 1.0 | 81 | 39 | 2.9 | 2.3 | 113 | 12 | 9 | 4 |
| Aug 14 | 4 | 13.5 | 1.2 | 82 | 38 | 4.3 | 2.4 | 165 | 8 | 4 | 6 |
| Total or grand mean | 14.0 | 1.6 | | 321 | 155 | 4.1 | 3.3 | 635 | 46 | 37 | 15 |

[a] We collected grizzly bear hair at these sites but failed to identify a bear. ID = identification.

used the simulation procedure in CAPTURE to test the performance of several models using fictitious datasets similar to the 2 we collected. We used an estimated population size of 258 and 84 bears, 1,000 iterations, time variation as estimated by model $M_t$ for our data, and heterogeneity that had the same average capture probability as measured by $M_h$ (all models had capture probability ≈ 0.1 in British Columbia and 0.13 in Alberta). To mimic mild heterogeneity in capture probability we assigned capture probabilities of 0.07, 0.08, 0.09, 0.1, 0.11, and 0.12 evenly among the simulated British Columbia population. For the Alberta population, we used 0.11, 0.12, 0.13, 0.14, 0.15, and 0.16. To mimic strong heterogeneity we assigned capture probabilities as follows (the number of individuals assigned each probability is in brackets): 0.04 (32), 0.06 (52), 0.08 (66), 0.1 (52), 0.14 (32), 0.28 (15), 0.42 (6), and 0.56 (3) for British Columbia; 0.04 (11), 0.07 (17), 0.1 (21), 0.13 (17), 0.16 (11), 0.28 (5), and 0.4 (2) for Alberta.

Table 2. Population estimates from 8 closed mark–recapture models in program CAPTURE for the Central Selkirk grizzly bear population (British Columbia) and southwest Alberta population from DNA analysis of hair collected at bait sites during summer 1996 and 1997, respectively.

| Model | British Columbia $\hat{N}$ | British Columbia SE | British Columbia 95% CI | Alberta $\hat{N}$ | Alberta SE | Alberta 95% CI |
|---|---|---|---|---|---|---|
| $M_o$-Null | 257 | 41.0 | 194–364 | 78 | 19.6 | 52–142 |
| $M_h$-Jackknife | 259 | 23.0 | 221–310 | 72 | 10.1 | 58–98 |
| $M_h$-Chao | 308 | 64.1 | 217–477 | 81 | 22.9 | 54–151 |
| $M_t$-Darroch | 254 | 40.1 | 193–360 | 77 | 18.8 | 52–141 |
| $M_t$-Chao | 256 | 47.2 | 189–380 | 66 | 15.1 | 48–112 |
| $M_{th}$-Chao | 276 | 61.4 | 192–444 | 71 | 18.4 | 50–128 |
| $M_b$-Zippin | failed | | | 47 | 9.5 | 37–147 |
| $M_{bh}$-Removal | 171 | 53.5 | 124–376 | 47 | 9.5 | 37–147 |

## RESULTS

We trapped bears for 5 sessions between 19 June and 9 August, 1996 in southeast British Columbia. Sites were active 10 days on average and 277 of 381 sites (73%) removed ≥1 hair sample. We collected 15 hair samples/site on average and 4,245 hair samples in total (Table 1). We collected ≤116 different envelopes of hair at a site. Twenty sites had the bait pulled down or removed. During the study, British Columbia Wildlife Branch employees moved 1 grizzly bear into the study area, moved 1 bear within the study area, and shot 1 bear in the study area. We ran fingerprints for all 3 of these individuals. We did not include these bears in the mark–recapture analysis because none of these bears were available for capture throughout the study. We added 3 bears to the population estimate to compensate for their removal from the analysis.

We used mtDNA to identify species on 1,308 samples from British Columbia; 608 were grizzly, 661 black bear, and 42 tests failed. We used DNA fingerprinting on 608 confirmed grizzly bear samples; 117 (19%) of these samples did not yield fingerprints at the $P < 0.05$ level. We identified 109 individual bears that were cap-

tured 134 times; 43 bears were females, 33 were males, and there was insufficient DNA remaining to test the other 33 bears for sex. Capture success varied by as much as 50% among sessions and there was little evidence of a decline in new captures through the study (Table 1). The population estimate at the beginning of the sample period using model $M_h$ was 262 with an upper and lower 95% confidence intervals (CI) of 313 and 224 (Table 2). This resulted in a density of 26.6 bears/1,000 km$^2$. The mean capture probability was 0.1 for all models. All plausible models in CAPTURE gave similar population estimates though the Jackknife model ($M_h$) had lower CI. Neither of the behavior models gave sensible estimates (Table 2). None of the goodness-of-fit tests performed in CAPTURE rejected the null hypothesis and the model selection procedure recommended the null model $M_o$. The test for closure rejected the null hypothesis of a closed population ($P$ = 0.03).

In Alberta we trapped bears in 4 sessions between 2 June and 14 August, 1997. Sites were active 14 days on average and 155 of 321 sites removed ≥1 hair sample. We collected 4 hair samples/site on average and 635 hair samples in total (Table 1). Twenty-three samples were not from bears and a further 101 samples contained no roots and were discarded (17% of total). Only 43% of the 612 Alberta bear samples had ≥4 roots while 73% of the British Columbia samples had ≥4 roots. We used DNA fingerprinting of 166 grizzly bear samples and identified 37 individual bears. We were unable to generate a fingerprint for 62 of the 166 samples analyzed (37%) because of insufficient or poor quality DNA. Many of these samples were probably repeats from a previously identified bear because most sites generated >1 sample; however, 15 sites that removed grizzly bear hair did not generate a DNA fingerprint. Hence we know we failed to identify ≥15 bears although some of these individuals may have already been captured in that particular session; other bears may also have been missed. We were able to identify the sex of only 18 bears (13 males and 5 females); there was insufficient template DNA following the fingerprinting work to run the sex test on the remaining individuals.

Captures declined mildly through the study, mostly because samples that failed to generate fingerprints were mainly from the last 2 sessions (Table 1). The population estimate, using Model $M_h$ was 74 with upper and lower 95% CI of 100 and 60. This estimate included 2 bears that were moved during the study (Table 2). Capture probability averaged 16% of the population/session using Model $M_h$. Neither of the behavior models gave sensible estimates; all other models generated similar estimates (Table 2).

We caught more grizzly bears in the northern part of the British Columbia study area (Fig. 1) and most captures in the southern part of the area were in or near 2 provincial parks. Grizzly bears were captured throughout the Alberta study area and several bears made large movements before or during the study. One bear caught in our study area had been captured in 1996 in the Elk valley to the west, another was captured in the Flathead valley, also west of the Alberta study area, in June of 1997. A third bear moved 70 km within the study area. All 3 bears were male.

There were 36 sites that caught >1 bear and 17 sites that captured >2 bears during the British Columbia study. We could tentatively identify related sows and cubs because all cubs should have ≥1 allele in common with the mother. At least 11 of the 17 sites that captured >2 bears detected sows with cubs; only 1 of these groups was recaptured. Two family groups of 4 were captured. Only 2 sites caught >1 bear in Alberta and 1 group of 3 was probably a family group.

We used simulation to assess model performance under data similar to our field data. All models tested except the behavior models ($M_b$ and $M_{bh}$) and Chao's $M_h$ and $M_{th}$ models performed reasonably well under weak heterogeneity, or weak heterogeneity and time variation with biases ≤10% of the true population size. Estimates fell between 95% CI in >91% of cases (Tables 3 and 4). Confidence interval coverage summarizes how often point estimates fell between the CI (Tables 3 and 4). If CIs are unbiased, we expect point estimates to fall between the intervals in 95% of the iterations. The behavior models and Chao's $M_h$ and $M_{th}$ models all showed significant biases usually together with wide CIs or poor CI coverage. The jackknife model ($M_h$) showed slightly reduced CI coverage and a negative bias ≤10% under the mild heterogeneity, and time and mild heterogeneity scenarios. Under strong heterogeneity, only Choa's $M_h$ and $M_{th}$ performed acceptably well. The Jackknife model gave negative biases of ≤24% of the true population and CI cover-

Table 3. Results of Monte Carlo simulations for 8 closed population estimators using the simulation procedure in program CAPTURE. Each simulation was run for 1,000 iterations using a known populations size of 258. We used weak capture variation with mean capture probability as estimated by $M_h$ for our data (0.1), strong capture variation with mean capture probability estimated by $M_h$, weak heterogeneity and time variation as calculated by model $M_t$, and strong heterogeneity and time variation as calculated by model $M_t$.

| | Weak heterogeneity[a] | | | | | Strong heterogeneity[b] | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | $\hat{N}$ | | | 95% CI | | $\hat{N}$ | | | 95% CI | |
| Model | $\bar{x}$ | CV (%) | Bias (%) | Coverage | Width | $\bar{x}$ | CV (%) | Bias (%) | Coverage | Width |
| No time variation | | | | | | | | | | |
| $M_o$-Null | 259 | 18 | 0 | 95 | 189 | 176 | 14 | −32 | 19 | 83 |
| $M_h$-Jackknife | 241 | 9 | −7 | 91 | 87 | 222 | 10 | −14 | 70 | 83 |
| $M_b$-Zippin | 281 | 67 | 9 | 89 | 1,762 | 203 | 56 | −21 | 69 | 629 |
| $M_t$-Darroch | 255 | 20 | −1 | 94 | 185 | 175 | 14 | −32 | 18 | 81 |
| $M_{bh}$-Removal | 267 | 66 | 3 | 83 | 1,577 | 201 | 57 | −22 | 67 | 659 |
| $M_t$-Chao | 252 | 21 | −2 | 94 | 209 | 207 | 18 | −20 | 72 | 145 |
| $M_h$-Chao | 304 | 25 | 18 | 90 | 285 | 243 | 21 | −6 | 92 | 195 |
| $M_{th}$-Chao | 275 | 24 | 7 | 94 | 255 | 234 | 21 | −9 | 91 | 192 |
| Observed time variation | | | | | | | | | | |
| $M_o$-Null | 261 | 19 | 1 | 96 | 192 | 178 | 14 | −31 | 21 | 84 |
| $M_h$-Jackknife | 242 | 9 | −6 | 92 | 87 | 223 | 10 | −14 | 72 | 83 |
| $M_b$-Zippin | 473 | 62 | 83 | 99 | 5,499 | 358 | 67 | 39 | 97 | 3,040 |
| $M_t$-Darroch | 256 | 20 | −1 | 95 | 185 | 175 | 14 | −32 | 18 | 80 |
| $M_{bh}$-Removal | 330 | 74 | 28 | 88 | 3,064 | 287 | 71 | 11 | 84 | 2,061 |
| $M_t$-Chao | 252 | 22 | −2 | 94 | 208 | 205 | 18 | −21 | 70 | 142 |
| $M_h$-Chao | 308 | 25 | 19 | 89 | 289 | 242 | 21 | −6 | 93 | 194 |
| $M_{th}$-Chao | 279 | 25 | 8 | 94 | 261 | 236 | 21 | −9 | 91 | 193 |

[a] An equal number of animals had capture probabilities of 0.07, 0.08, 0.09, 0.1, 0.11, and 0.12.
[b] Probabilities and the number of individuals assigned to that level were: 0.04 (32), 0.06 (52), 0.08 (66), 0.1 (52), 0.14 (32), 0.28 (15), 0.42 (6), 0.56 (3).

Table 4. Results of Monte Carlo simulations for 8 closed population estimators using the simulation procedure in program CAPTURE. Each simulation was run for 1,000 iterations using a known populations size of 84. We used weak heterogeneity with average capture probability as estimated by $M_h$ (0.13), the time variation observed in our dataset as calculated by model $M_t$ and weak heterogeneity, strong heterogeneity with mean capture probability of 0.13, and observed time and strong heterogeneity.

| | Weak heterogeneity[a] | | | | | Strong heterogeneity[b] | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | $\hat{N}$ | | | 95% CI | | $\hat{N}$ | | | 95% CI | |
| Model | $\bar{x}$ | CV (%) | Bias (%) | Coverage | Width | $\bar{x}$ | CV (%) | Bias (%) | Coverage | Width |
| No time variation | | | | | | | | | | |
| $M_o$-Null | 88 | 32 | 5 | 94 | 112 | 70 | 39 | −17 | 80 | 92 |
| $M_h$-Jackknife | 76 | 15 | −10 | 91 | 41 | 64 | 16 | −24 | 63 | 37 |
| $M_b$-Zippin | 75 | 49 | −11 | 85 | 367 | 58 | 44 | −31 | 72 | 239 |
| $M_t$-Darroch | 87 | 33 | 4 | 93 | 107 | 69 | 40 | −18 | 77 | 87 |
| $M_{bh}$-Removal | 72 | 49 | −14 | 82 | 340 | 56 | 45 | −33 | 70 | 227 |
| $M_t$-Chao | 83 | 34 | −1 | 93 | 112 | 69 | 37 | −18 | 84 | 99 |
| $M_h$-Chao | 114 | 48 | 36 | 89 | 202 | 96 | 54 | 14 | 95 | 188 |
| $M_{th}$-Chao | 105 | 67 | 25 | 92 | 197 | 90 | 60 | 7 | 92 | 185 |
| Observed time variation | | | | | | | | | | |
| $M_o$-Null | 90 | 31 | 7 | 96 | 113 | 72 | 37 | −14 | 83 | 96 |
| $M_h$-Jackknife | 77 | 15 | −8 | 93 | 41 | 64 | 17 | −24 | 64 | 37 |
| $M_b$-Zippin | 50 | 28 | −40 | 43 | 69 | 41 | 29 | −51 | 30 | 58 |
| $M_t$-Darroch | 87 | 32 | 4 | 93 | 105 | 69 | 39 | −18 | 77 | 89 |
| $M_{bh}$-Removal | 48 | 27 | −43 | 36 | 59 | 40 | 29 | −52 | 27 | 52 |
| $M_t$-Chao | 83 | 32 | −1 | 94 | 109 | 70 | 40 | −17 | 83 | 103 |
| $M_h$-Chao | 114 | 44 | 36 | 88 | 196 | 98 | 54 | 17 | 94 | 194 |
| $M_{th}$-Chao | 105 | 65 | 25 | 91 | 194 | 97 | 108 | 15 | 93 | 217 |

[a] An equal number of animals had capture probabilities of 0.11, 0.12, 0.13, 0.14, 0.15, and 0.16.
[b] Probabilities and the number of individuals assigned to that level were: 0.04 (11), 0.07 (17), 0.1 (21), 0.13 (17), 0.16 (11), 0.28 (5), 0.4 (2).

age of 60–70%. The population estimates in Table 2 are similar in their ranking to the outcome of simulation results with weak heterogeneity and time variation.

## DISCUSSION

The combination of hair removal and DNA analysis is promising for measuring distribution and abundance of grizzly bears and many other species for which tissue samples can be collected (Raphael 1994, Palsbøll et al. 1997, Foran et al. 1997, Woods et al. 1999). Primers are available for many species, though testing or marker development may be required. The sample population must demonstrate reasonable genetic variation to identify individuals. Identification of individuals using microsatellite profiles may require analysis of a large number of loci for island populations (Paetkau and Strobeck 1994, Paetkau et al. 1998).

Our density estimate of 26.6 grizzly bears/1,000 km$^2$ for the central Selkirk mountains in British Columbia is similar to that observed in the nearby south Selkirk Mountains of British Columbia, Idaho, and Washington, the Swan Mountains of Montana, and the Columbia Mountains of British Columbia (Simpson et al. 1985, Wielgus et al. 1994, Mace and Waller 1997*a*, Woods et al. 1999). McLellan (1989), and Martinka (1974) reported densities more than double those we observed for the Flathead Valley in the southeast corner of British Columbia and Glacier Park, Montana, although both study areas were much smaller and had lower proportions of unusable habitat. The density in the Alberta area was lower than most other estimates in the Rocky Mountains; numbers reported in Banff and Jasper parks during the 1970's and for the east slopes of the Rockies in Montana (LeFranc et al. 1987) were similar to the density reported here.

Except for rare circumstances, a proportion of captured animals will always reside partially off the study area (Boutin 1984, McLellan 1989) causing an overestimate of population size or density. This bias may be greater when baits or lures are used to capture animals. Edge effect is minimized as the ratio of study area size to home range increases (Bondrup-Nielsen 1983, Garshelis 1992). In the British Columbia study area, bear home ranges probably overlapped only about 10% of the boundary because the borders were large lakes and rivers (Fig. 1). Therefore, our estimate probably overestimates bear numbers very little. The Alberta study area was largely closed to the west by the continental divide and to the east by a lack of bears in the prairies (Fig. 2). Another bear DNA inventory was performed along the entire western border contemporary to our work. Although previous radiotelemetry work has demonstrated that bears move across the Rocky Mountain divide (B. N. McLellan, British Columbia Ministry of Forests and R. Quinlan, Alberta Fish and Wildlife, unpublished data), the 2 contemporary studies identified >150 grizzly bears and only 1 bear moved among the 2 study areas during the study period (J. Boulanger and B. N. McLellen, unpublished data). The northern and southern borders were probably not barriers to movement, but were much smaller than the longitudinal borders. We suggest the overestimate caused by transborder movements was also small in the Alberta area.

The closure test in CAPTURE rejected the null hypothesis of population closure in the British Columbia area. This may seem surprising given the above stated closure of the boundaries. However, the closure test cannot differentiate between behavior variation, certain types of time variation, and recruitment (White et al. 1982). We believe this test rejected closure due to the heterogeneity caused by the checkerboard trapping system that we used; we treat this result as evidence for heterogeneity in the dataset. If heterogeneity was extreme, we would expect a significant result from the goodness-of-fit tests in CAPTURE, which did not occur. We conclude the overestimate caused by heterogeneity due to the checkerboard system was small. The checkerboard system may have also caused an underestimate because some individuals may have had such low capture probabilities as to remain undetected.

It is important to define the sample population of any new sampling method. Nuclear DNA results demonstrate that both male and female bears are captured by this method. Bears are unlikely to be randomly sampled based on age or sex, but this observation is common in capture studies (Mace and Waller 1997*a*) and probably relates more to movement patterns, social dominance, and cohort-specific behavior than to sampling bias of the hair removal technique. We demonstrate that cubs are captured with this technique though we do not know if the capture probability for cubs was similar to that of adults.

Model selection is an important part of using mark–recapture models. Considerable work has demonstrated that the model selection procedure in CAPTURE lacks power, especially when sample sizes and capture probabilities are low (Otis et al. 1978; Menkens and Andersen 1988; Pollock et al. 1990; Boulanger and Krebs 1994, 1996). The model selection procedure often selects $M_o$ when power is low. Model $M_o$ is a naive estimator that assumes equal catchability within and among sessions, which is unlikely in wild populations (Pollock et al. 1990). The individual tests in CAPTURE, the population estimates from the various models, and the simulation results suggest that both our datasets contained relatively weak heterogeneity and time variation. Our simulation results suggested that models $M_o$, $M_t$, and $M_h$-Jackknife may be appropriate for the data we collected. We eliminated $M_o$ because of the assumption of equal catchability, and selected $M_h$ over $M_t$ because individual variation in capture probability was likely greater than time variation. The checkerboard design likely caused heterogeneity in capture probabilities in the British Columbia study because bears could move in and out of trappable areas inside the study area. In addition, capture probabilities may vary among sex and age cohorts in all bear populations. Mace and Waller (1997*a*) tested capture biases of grizzly bears using baited camera stations and concluded that adult males had the highest capture probabilities and females with cubs the lowest; we expect the same biases occurred in our data. Further, individuals in family groups do not have independent capture probabilities and $M_h$ is likely to be more robust to deviations from this assumption. Also, simulation results in Otis et al. (1978) and Tables 3 and 4 show that model $M_h$ can deliver generally unbiased results even with moderate time or behavioral variation. We did not select Chao's heterogeneity model because it demonstrated large positive bias under weak heterogeneity (Tables 3 and 4).

Identification failures greatly reduced the number of captures that could be used for capture–recapture modeling in the Alberta dataset. This resulted in wider CIs and may have biased the population estimate. The number of samples with few roots was much higher in the Alberta study and in both study areas the number of hair samples was lower at hair removal sites where identification failed. We believe the low amount of DNA in many of the samples is what caused such disappointingly high identification failures in the Alberta dataset. The east slopes of the Rockies are extremely windy and wind may have blown much of the hair off the barbed wire in Alberta. Gossens et al. (1998) examined the relationship between identification failure and the number of roots in a sample; they found that failure rate declined as the number of roots increased.

## MANAGEMENT IMPLICATIONS

Many aspects of study design need further investigation or require adaptation to a given area. We suggest the use of a grid system and that cell sizes be no larger than the average female home range size for the period of the survey. Smaller cells reduce the chance of an underestimate because fewer individuals will have trivial capture probabilities. We recommend against trapping every second cell as we did in British Columbia. This may cause greater heterogeneity of capture rates and increases the likelihood of individuals having trivial capture probabilities because bears may live in or move through areas where capture success is virtually zero.

We used 4–5 trapping sessions to assess variation in capture probabilities. Fewer sessions would be much cheaper; however, workers must design their sampling to achieve greater capture probabilities than presented here. Generally, fewer sessions reduces model choice so workers considering fewer sessions must make every effort to avoid capture bias in their sample design because they may not be able to use a model that will accommodate behavior or heterogeneity variation; time variation can be accommodated in 2 or 3 session designs.

Capture success can be increased without any further financial cost by leaving sites operational longer; especially in areas where home ranges are large. The benefits of longer trap duration must be weighed against a possible increase in edge effect due to longer overall study period (J. Boulanger, Integrated Ecological Research, personal communication). Leaving sites in the same place through the study would also save costs. However, capture success may decline because sites cannot be moved to follow seasonal habitat selection of bears. Behavioral response may increase also because bears are much more likely to habituate to a site that is left in the same place. We recommend moving sites among trapping sessions.

We found the number of hair samples collected declined and the number of identification failures increased through both of these studies. Our data suggest this problem could be minimized by finishing fieldwork by about 15 July. In addition, future workers could reduce the risk of identification failure by freezing hair immediately after collection and attempting to collect as much hair as possible at a site. In windy areas this may require locating hair removal sites in protected areas, the use of shorter check periods, or spending extra time looking on the ground for more hair. If freezing is impractical, then drying the sample using silica desiccant is an alternative (Foran et al. 1997). Subjectively removing black bear samples before extraction or delivery to the laboratory saved considerable cost and probably reduced the number of grizzly bear captures only marginally.

We suggest that many workers will not be able to rely entirely on the model selection routine in CAPTURE for model selection (Menkens and Andersen 1988). Most workers with sample sizes and capture probabilities similar to ours will have to make a subjective decision based on other information such as results from the individual goodness-of-fit tests in CAPTURE, a non-statistical examination of their data, and results from other studies (Menkens and Andersen 1988, Boulanger and Krebs 1996). Simulation modeling can also provide useful insights in model selection.

Care is required when comparing mark–recapture estimates with other estimates of abundance. Bears that move on and off the study area can cause errors in population estimates and cloud comparison among studies, especially when study areas are small. McLellan (1989) showed how population estimates can vary markedly when corrected for edge effect. Edge effect is likely to cause an overestimate for any attempt to estimate population size and must be given at least subjective consideration in the analysis.

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## LITERATURE CITED

BONDRUP-NEILSEN, S. 1983. Density estimation as a function of live-trapping grid and home range size. Canadian Journal of Zoology 61:2361–2365.

BOULANGER, J., AND C. J. KREBS. 1994. Comparison of capture-recapture estimators of snowshoe hare populations. Canadian Journal of Zoology 72: 1800–1807.

———, AND ———. 1996. Robustness of capture-recapture estimators to sample biases in a cyclic snowshoe hare population. Journal of Applied Ecology 33:530–542.

BOUTIN, S. 1984. Home range size and methods of estimating snowshoe hare densities. Acta Zoologica Fennica 171:275–278.

CONNER, M. C., AND R. F. LABISKY. 1985. Evaluation of radioisotope tagging for estimating abundance of raccoon populations. Journal of Wildlife Management 49:326–332.

CORN, J. L., AND M. J. CONROY. 1998. Estimation of density of mongooses with capture-recapture and distance sampling. Journal of Mammalogy 79: 1009–1015.

FORAN, D. S., K. C. CROOKS, AND S. C. MINTA. 1997. DNA-based analysis of hair to identify species and individuals for population research and monitoring. Wildlife Society Bulletin 25:840–847.

GARSHELIS, D. 1992. Estimating bear population size. Pages 1098–1111 *in* D. R. McCullough and R. H. Barrett, editors. Wildlife 2001: populations. Elsevier Applied Science, London, United Kingdom.

GOSSENS, B., L. P. WAITS, AND P. T. TABERLET. 1998. Plucked hair samples as a source of DNA: reliability of dinucleotide microsatellite genotyping. Molecular Ecology 7:1237–1241.

GREENWOOD, R. J., A. B. SARGENT, AND D. H. JOHN-

SON. 1985. Evaluation of mark–recapture for estimating skunk abundance. Journal of Wildlife Management 49:332–340.

HALLET, J. G., M. A. O'CONNELL, G. D. SAUNDERS, AND J. SEIDENSTICKER. 1991. Comparison of population estimators for medium-sized animals. Journal of Wildlife Management 55:81–93.

LARSEN, D. G., AND R. L. MARKEL. 1989. A preliminary estimate of grizzly bear abundance in the southwest Yukon. Final Report, Yukon Fish and Wildlife Branch, Whitehorse, Yukon, Canada.

LEFRANC, M. N., M. B. MOSS, K. A. PATNODE, AND W. C. SUGG, editors. 1987. Grizzly bear compendium. Interagency Grizzly Bear Committee, Washington, D. C., USA.

MACE, R. D., S. C. MINTA, T. L. MANLEY, AND K. E. AUNE. 1994. Estimating grizzly bear populations size using camera sightings. Wildlife Society Bulletin 22:74–83.

———, AND J. S. WALLER. 1997*a*. Grizzly bear ecology in the Swan Mountains, Montana. Final Report, Montana Fish, Wildlife, and Parks, Helena, Montana, USA.

———, AND ———. 1997*b*. Spatial and temporal interaction of male and female grizzly bears in northwestern Montana. Journal of Wildlife Management 61:39–52.

MARTINKA, C. J. 1974. Population characteristics of grizzly bears in Glacier National Park, Montana. Journal of Mammalogy 55:21–29.

MCCULLOUGH D. R., AND D. H. HIRTH. 1988. Evaluation of the Petersen-Lincoln estimator for a white-tailed deer population. Journal of Wildlife Management 52:534–544.

MCLELLAN, B. N. 1989. Dynamics of a grizzly bear population during a period of industrial resource extraction. I. Density and age-sex composition. Canadian Journal of Zoology 67:1856–1860.

MENKENS, G. E., JR., AND S. H. ANDERSON. 1988. Estimation of small-mammal population size. Ecology 69:1952–1959.

OTIS, D. L., K. P. BURNHAM, G. C. WHITE, AND D. P. ANDERSEN. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62.

PAETKAU, D. W., AND C. STROBECK. 1994. Microsatellite analysis of genetic variation in black bear populations. Molecular Ecology 3:489–495.

———, W. CALVERT, I. STIRLING, AND C. STROBECK. 1996. Microsatellite analysis of population structure in Canadian polar bears. Molecular Ecology 4:347–354.

———, L. WAITS, P. L. CLARKSON, L. CRAIGHEAD, E. VYSE, R. WARD, AND C. STROBECK. 1998. Variation in genetic diversity across the range of North American brown bears. Conservation Biology 12:418–429.

PALSBØLL P. J., J. ALLEN, M. BÉRUBE, P. J. CLAPHAM, T. P. FEDDERSEN, P. S. HAMMOND, R. R. HUDSON, H. JØRGENSEN, S. KATONA, A. H. LARSEN, F. LARSEN, J. LIEN, D. K. MATTLIA, J. SIGURJONSSON, R. SEARS, T. SMITH, R. SPONER, P. STEVICK, AND N. OIEN. 1997. Genetic tagging of humpback whales. Nature 388:767–769.

POLLOCK, K. H., J. D. NICHOLS, C. BROWNIE, AND J. E. HINES. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107.

PROCTOR, M. 1995. DNA fingerprint from black bear hair as a basis for mark–recapture population estimation. Directed studies in ecology. University College of the Okanagan, Kelowna, British Columbia, Canada.

RAPHAEL, M. G. 1994. Techniques for monitoring populations of fishers and American martens. Pages 224–240 *in* S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, editors. Martens, sables, and fishers biology and conservation. Cornell University Press, Ithaca, New York, USA.

REXSTAD, E., AND K. BURNHAM. 1991. User's guide for interactive program CAPTURE. Colorado Cooperative Fish and Wildlife Research Unit, Fort Collins, Colorado, USA.

SIMPSON, K., K. B. HEBERT, AND G. P. WOODS. 1985. Habitats and management of the grizzly bear in the Columbia mountains of British Columbia. Fish and Wildlife Bulletin, British Columbia Ministry of Environment B-35.

STIRLING, S. D., G. C. WHITE, R. A. SELLERS, H. V. REYNOLDS, J. W. SCHOEN, K. TITUS, V. G. BARNES, JR, R. B. SMITH, R. R. NELSON, W. B. BALLARD, AND C. C. SCHWARTZ. 1997. Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark-resight techniques. Wildlife Monographs 133.

WALSH, P. S., D. A. METZGER, AND R. HIGUCHI. 1991. Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. BioTechniques 10:506–513.

WHITE, G. C., D. R. ANDERSEN, K. P. BURNHAM, AND D. L. OTIS. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory LA-8787-NERP.

WIELGUS, R. B., F. L. BUNNELL, W. L. WAKKINEN, AND P. E. ZAGER. 1994. Population dynamics of Selkirk Mountain grizzly bears. Journal of Wildlife Management 58:266–272.

WOODS, J. G., B. N. MCLELLAN, D. PAETKAU, M. PROCTOR, P. OTT, AND C. STROBECK. 1996. DNA fingerprinting applied to mark–recapture bear studies. International Bear News 5:9–10.

———, D. PAETKAU, D. LEWIS, B. N. MCLELLAN, M. PROCTOR, AND C. STROBEK. 1999. Genetic tagging free ranging black and brown bears. Wildlife Society Bulletin 27:616–627.

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