*Management and Conservation Article*

# Grizzly Bear Density in Glacier National Park, Montana

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**ABSTRACT** We present the first rigorous estimate of grizzly bear (*Ursus arctos*) population density and distribution in and around Glacier National Park (GNP), Montana, USA. We used genetic analysis to identify individual bears from hair samples collected via 2 concurrent sampling methods: 1) systematically distributed, baited, barbed-wire hair traps and 2) unbaited bear rub trees found along trails. We used Huggins closed mixture models in Program MARK to estimate total population size and developed a method to account for heterogeneity caused by unequal access to rub trees. We corrected our estimate for lack of geographic closure using a new method that utilizes information from radiocollared bears and the distribution of bears captured with DNA sampling. Adjusted for closure, the average number of grizzly bears in our study area was 240.7 (95% CI = 202–303) in 1998 and 240.6 (95% CI = 205–304) in 2000. Average grizzly bear density was 30 bears/1,000 km$^2$, with 2.4 times more bears detected per hair trap inside than outside GNP. We provide baseline information important for managing one of the few remaining populations of grizzlies in the contiguous United States. (JOURNAL OF WILDLIFE MANAGEMENT 72(8):1693–1705; 2008)

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Despite being listed as threatened under the Endangered Species Act since 1975 (U.S. Fish and Wildlife Service [USFWS] 1993), there are no rigorous estimates of grizzly bear abundance for the population as a whole for the Northern Continental Divide Ecosystem (NCDE) in northwestern Montana, USA, including Glacier National Park (GNP). The NCDE population is the largest in the contiguous United States with uninterrupted connection to continuously occupied range to the north. Because of the importance of maintaining this link, the status of bears in the greater Glacier National Park area (GGA), impacts the long-term viability of bears south of Canada (USFWS 1993). Agencies responsible for recovering this population require information on its status to guide management decisions.

From the early 1880s until 1910, when GNP was established, grizzly bears in northwestern Montana were heavily hunted and trapped. The local population likely reached its lowest level during this period (Bailey and Bailey 1918, Keating 1986). As late as 1895, bear trapping was considered the greatest threat to game animals in the region; ≥500 elk (*Cervus elaphus*) and moose (*Alces alces*), and substantial numbers of deer (*Odocoileus* spp.), bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*) were killed each year for bear bait (Bailey and Bailey 1918). Many bears continued to be killed on lands surrounding the park to protect large domestic sheep herds during the first half of the 20th century. After grizzly bears south of Canada were listed as a threatened species in 1975, annual legal harvest in the NCDE was first limited to 25 bears, then progressively fewer animals, before being completely discontinued in 1991 (Dood and Pac 1993, USFWS 1993). It is likely that few bears range exclusively within the confines of GNP throughout their life, or even within each year. Although fairly secure within the center of GNP, bears are exposed to a variety of mortality risks when they move outside park boundaries (K. Kendall, United States Geological Survey, unpublished data). From 1976 to 2000, <9% of the 401 known mortalities that occurred within 40 km of GNP were within the park, which represents 20% of this area.

Increasing trends in grizzly bear sighting rates and informal population estimates in GNP between 1910 and the early 1970s coincided with protection from hunting in GNP (1910), curtailment of predator control within the park (1931), and waning predator control near the park (mid-1950s–1960s; Keating 1986). Fewer predators were killed with the decline of sheep ranching along the park's eastern boundary and agency-sponsored predator control along the park's western boundary. Early (pre-1967) methods used in GNP to estimate grizzly bear population size were informal, often unspecified, and likely unreliable (Baggley 1936). Martinka (1974) estimated population size from density calculations based on annual sightings of unmarked bears in a core area of GNP and extrapolation to the entire park. Because grizzly bear population trends during the 1980s–1990s adjacent to GNP were inconsistent, trends in the park could not be inferred from neighboring areas. Bear numbers increased northwest of GNP in the North Fork of the Flathead River, British Columbia,

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Canada, during 1979–1994 ($\hat{\lambda} = 1.085$, 95% CI = 1.032–1.136; Hovey and McLellan 1996) but decreased to the south in the Swan Mountains from 1987 to 1996 ($\hat{\lambda} = 0.977$, 95% CI = 0.875–1.046; Mace and Waller 1998). However, range expansion suggests population growth in the ecosystem since 1993 (T. Wittinger, United States Forest Service, unpublished data; D. Carney, Blackfeet Nation, unpublished data; J. Jonkel, M. Madel, and T. Manley, Montana Department of Fish, Wildlife, and Parks, unpublished data).

Sampling at baited, systematically distributed barbed-wire hair traps is widely used to estimate bear population abundance (Boulanger et al. 2002, Boersen et al. 2003). Surveys conducted annually in GNP 1983–1997 to document bear sign (tracks, scat, etc.) found that bear rub trees (trees used by bears for rubbing and other forms of marking) were common and distributed throughout the park (Kendall et al. 1992). Most rub trees were identified by presence of bear hair, suggesting that they could be a source of DNA for individual identification and could be used to augment sampling at baited hair traps.

Estimation of density from DNA-based mark–recapture analyses requires adjustment of population estimates to account for violation of closure caused by bear movement on and off the study area during sampling. The proportion of points on the sampling grid from radiocollared bears can be used to scale population estimates assuming that the distribution of collared bears represents overall bear distribution (White and Shenk 2001).

Our objectives for this study were to 1) estimate grizzly bear population size and density for the GGA, 2) explore the use of covariates to improve abundance estimates derived from multiple data sources, and 3) develop methods that use hair trap data to correct closure estimates for nonrepresentative distribution of radiocollared bears.

## STUDY AREA

The GGA encompassed 7,933 km$^2$, straddling the Continental Divide in northwestern Montana along the United States–Canada border. The study area represented the northern third of the NCDE Grizzly Bear Recovery Zone (Fig. 1). The GGA was considered a largely intact natural system (Slocombe 1993). All wildlife species that occurred in the GGA before European settlement were still present, including sympatric grizzly bear and black bear (*U. americanus*) populations. The eastern and western edges of the study area (38% of perimeter) coincided with the approximate limit of occupied grizzly bear range, whereas the population extended beyond the northern and southern boundaries. Topography varied from the glaciated peaks, valleys, and lakes of GNP to the foothills of the Rocky Mountains and the western fringe of the Great Plains. Elevation ranged from 960 m to 3,190 m. Average annual precipitation was 63 cm, much of which was deposited as snow during winter. The Pacific maritime-influenced climate west of the Continental Divide was moister than that found on the eastern side, and the mountains received more precipitation than lower elevations. Vegetation was characterized by coniferous forests, shrub fields, and alpine tundra in the mountains, mixed deciduous–coniferous trees and herbaceous meadows in the valleys, and prairie grasslands and agricultural fields along the eastern boundary. Land management policy and human use in the study area differed by ownership. Glacier National Park (51% of GGA) was largely roadless and managed as wilderness but hosted approximately 1.75 million visitors per year, primarily in the 1% of the Park with roads and visitor services. In the rest of the study area, national (29%) and state (5%) forests were managed primarily for timber harvest and recreation. Blackfeet Tribal lands (8%) principally supported ranching and logging. Corporate timberlands (1%) maximized silviculture, and individually owned private parcels (6%) were mostly rural and low-density residential developments.

## METHODS

### Sampling Methods

We used 2 methods concurrently to collect bear hair for genetic analysis: hair traps and rub trees. We collected bear hair at barbed-wire hair traps systematically distributed on a grid of 125 8 × 8-km cells from mid-May to mid-August in 1998 and 2000 (Fig. 1; Table 1). Traps consisted of one 25-m length of 4-pronged barbed wire nailed to 3–6 trees at a height of 50 cm (Woods et al. 1999). We baited traps with 1 L of scent lure poured on rotten wood and other forest debris piled in the center. The primary liquid scent lure we used at all sites consisted of a 3:3:1 mix of liquid from decomposed fish, aged cattle blood treated with anticoagulant, and glycerin. We placed wool saturated with a secondary lure in a punctured film canister and hung it above the trap. For each of the 5 hair trap sessions, we used a unique secondary lure: 1998—beaver castor, fennel oil, smoky bacon oil, cherry extract, skunk; 2000—shellfish essence, beaver castor, fermented egg, cherry extract, skunk.

We placed one hair trap in each cell for 14 days, after which we collected hair. We defined a sample as all hairs from one set of barbs. We placed each hair sample in a uniquely numbered paper envelope and passed a flame under the barbs to remove any trace of hair. We then dismantled traps and moved them to another site within each cell. We repeated this for each cell for a total of 5 hair trap sampling sessions per year. We divided each 64-km$^2$ cell into 9 equal subcells. We placed each of the 5 traps within a cell in a different subcell and $\geq$1 km from all other hair traps. We based selection of specific trap locations on presence of natural animal travel routes, seasonal habitat quality, and bear sign. All traps were $\geq$200 m from maintained trails and 500 m from developed areas, including campsites.

We also collected bear hair periodically from mid-May to mid-October during 1998 and 2000 from naturally occurring bear rub trees found along maintained trails in GNP (Fig. 1; Table 2). In addition, from 17 August to 17 October 2000, we surveyed rub trees on the Flathead National Forest (FNF) to determine if bear use of rub trees on multiple-use

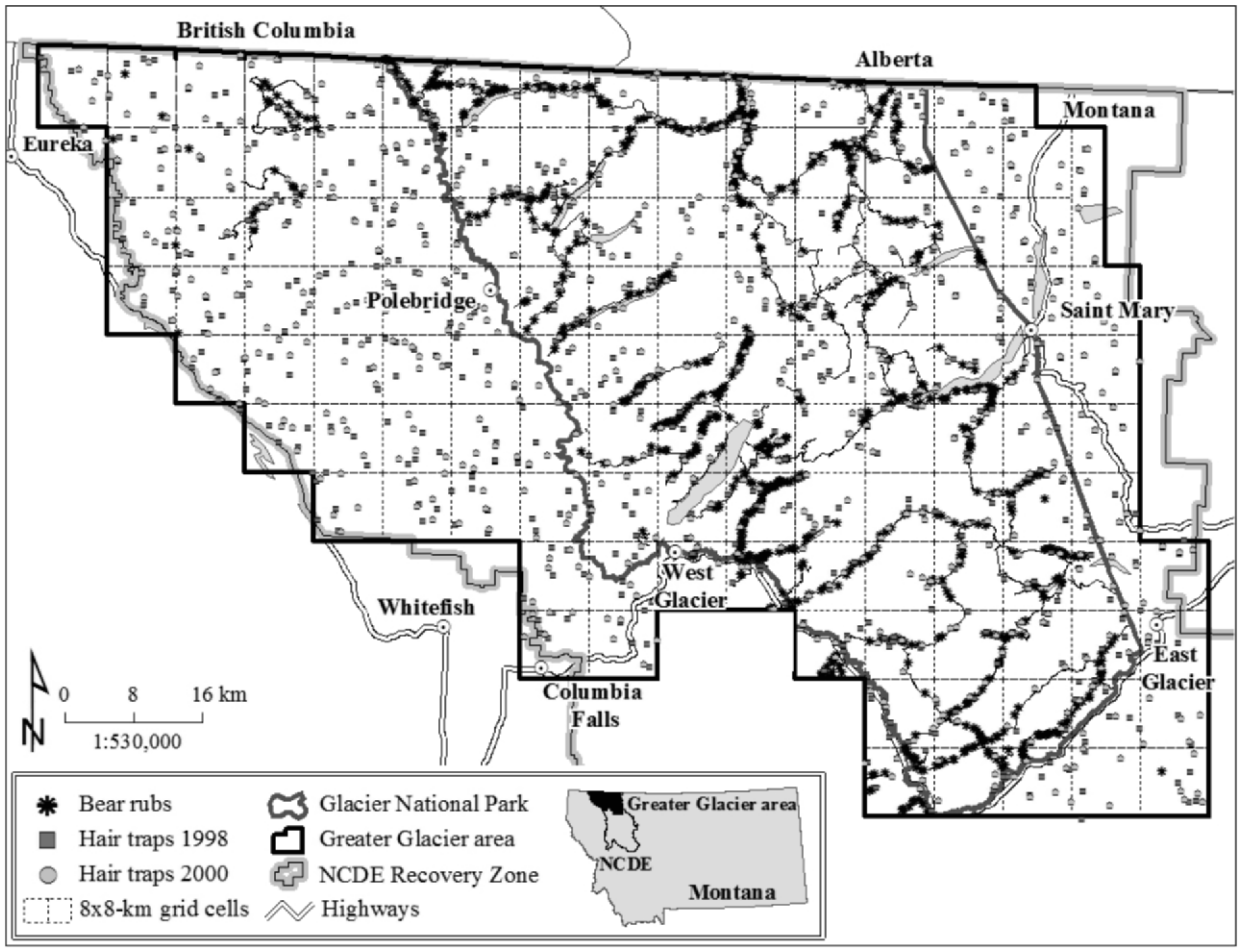


**Figure 1.** Location of bear (*Ursus* spp.) hair traps distributed within an 8 × 8-km grid and bear rub trees surveyed in the greater Glacier National Park study area in northwestern Montana, USA, 1998 and 2000. NCDE = Northern Continental Divide Ecosystem.

lands was similar to that in GNP. We tagged each rub tree with a unique number for identification. To facilitate hair collection, we attached short pieces of barbed wire in a zig-zag pattern to the rubbed surface. We only collected hair that accumulated on the barbed wire; hair snagged on bark was not collected. Rubbing is a ubiquitous behavior of grizzly bears (Green and Mattson 2003); we used no attractant to draw bears to the trails or rub trees. To exclude hair that may have been left the previous year, we only used samples for which the time period of hair deposition was

**Table 1.** Grizzly bear hair trap results from the Greater Glacier Area Bear DNA Project, Montana, USA, 1998 and 2000.

| Yr | Session | Session dates[a] | No. sites | % traps with ≥1 grizzly bear hair sample | Grizzly bear samples/trap[b] | | Total no. grizzly bear samples | No. unique bears | | No. new bears | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | $\bar{x}$ | SD | | F | M | F | M |
| 1998 | 1 | 18–31 May | 124 | 22.6 | 2.6 | 1.9 | 74 | 14 | 13 | 14 | 13 |
| | 2 | 1–14 Jun | 117 | 23.1 | 6.3 | 7.0 | 171 | 18 | 16 | 16 | 14 |
| | 3 | 15–28 Jun | 129 | 24.8 | 3.4 | 3.0 | 109 | 12 | 11 | 9 | 10 |
| | 4 | 29 Jun–12 Jul | 131 | 35.9 | 4.3 | 4.5 | 204 | 35 | 11 | 27 | 10 |
| | 5 | 13–26 Jul | 125 | 35.2 | 4.7 | 4.4 | 206 | 39 | 16 | 25 | 9 |
| $\bar{x}$ | | | 125 | 28.3 | 4.3 | 4.5 | 153 | 24 | 13 | 18 | 11 |
| Total | | | 626 | | | | 764 | | | 91 | 56 |
| 2000 | 1 | 22 May–4 Jul | 123 | 30.9 | 3.8 | 3.1 | 143 | 21 | 25 | 21 | 25 |
| | 2 | 5–18 Jun | 125 | 24.0 | 2.4 | 1.8 | 72 | 18 | 15 | 15 | 12 |
| | 3 | 19 Jun–2 Jul | 125 | 26.4 | 2.6 | 2.0 | 86 | 14 | 22 | 10 | 13 |
| | 4 | 3–16 Jul | 128 | 28.1 | 3.8 | 3.7 | 136 | 19 | 15 | 16 | 9 |
| | 5 | 17–30 Jul | 132 | 31.1 | 3.3 | 3.8 | 136 | 31 | 15 | 23 | 11 |
| $\bar{x}$ | | | 127 | 28.1 | 3.2 | 3.1 | 115 | 21 | 18 | 17 | 14 |
| Total | | | 633 | | | | 573 | | | 85 | 70 |

[a] Session dates reflect the date we installed hair traps for each session. We collected samples 14 days after installation (e.g., in 1998 we collected hair from session 5 traps during 27 Jul–9 Aug).

[b] Of those hair traps that had ≥1 grizzly bear sample.

**Table 2.** Grizzly bear rub tree survey results from the Greater Glacier Area in northwestern Montana, USA. We conducted surveys 18 May–10 October 1998 and 22 May–27 October 2000. Session dates correspond to the 14-day hair trap session intervals (see Table 1) plus 4 additional collection sessions after hair trapping was complete. We combined sessions with low sampling effort for mark–recapture analysis.

| Yr | Session | No. rub tree visits | % rub trees with grizzly bear hair | No. grizzly bear samples/rub tree[a] | | Rub tree effort[b] | Total no. grizzly bear samples | No. unique bears | | No. new bears | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | $\bar{x}$ | SD | | | F | M | F | M |
| 1998 | 1–3 | 31 | 25.8 | 1.9 | 1.4 | 388 | 15 | 0 | 3 | 0 | 3 |
| | 4 | 48 | 10.4 | 1.2 | 0.4 | 620 | 6 | 1 | 2 | 1 | 1 |
| | 5 | 131 | 19.1 | 1.4 | 0.6 | 2,877 | 33 | 6 | 8 | 6 | 6 |
| | 6 | 210 | 19.5 | 1.7 | 1.4 | 4,628 | 71 | 7 | 12 | 6 | 11 |
| | 7 | 471 | 12.7 | 2.0 | 1.5 | 10,742 | 120 | 8 | 22 | 6 | 14 |
| | 8–10 | 505 | 9.1 | 1.7 | 0.9 | 18,124 | 74 | 11 | 13 | 7 | 9 |
| $\bar{x}$ | | 233 | 13.3 | 1.7 | 1.2 | 6,230 | 53.2 | 6 | 10 | 4 | 7 |
| Total | | 1,396 | | | | 37,379 | 319 | | | 26 | 44 |
| 2000 | 1 | 99 | 20.2 | 1.5 | 0.6 | 1,249 | 29 | 0 | 8 | 0 | 8 |
| | 2 | 267 | 20.2 | 1.6 | 0.8 | 3,903 | 87 | 1 | 25 | 1 | 20 |
| | 3 | 384 | 16.9 | 1.6 | 0.9 | 7,072 | 103 | 3 | 30 | 3 | 19 |
| | 4 | 405 | 10.9 | 1.5 | 0.8 | 7,293 | 66 | 6 | 17 | 6 | 7 |
| | 5 | 473 | 12.1 | 2.1 | 1.4 | 8,283 | 119 | 7 | 20 | 5 | 3 |
| | 6 | 525 | 12.4 | 1.6 | 0.9 | 10,305 | 101 | 14 | 26 | 10 | 8 |
| | 7 | 683 | 6.6 | 1.8 | 1.3 | 12,073 | 79 | 12 | 18 | 9 | 1 |
| | 8 | 511 | 3.3 | 2.0 | 1.2 | 7,894 | 34 | 5 | 9 | 2 | 0 |
| | 9 | 558 | 7.5 | 1.6 | 1.1 | 10,921 | 66 | 11 | 13 | 8 | 6 |
| | 10–12 | 452 | 17.7 | 1.7 | 1.0 | 14,605 | 134 | 20 | 26 | 10 | 9 |
| $\bar{x}$ | | 436 | 11.2 | 1.7 | 1.0 | 8,360 | 81.1 | 8 | 19 | 5 | 8 |
| Total | | 4,357 | | | | 83,598 | 818 | | | 54 | 81 |

[a] Of those rub tree visits that had ≥1 grizzly bear sample.
[b] Rub tree effort (RTE) is defined as the cumulative no. of days between successive hair collections for each tree sampled/session. For example, if we surveyed 300 rubs during session 2, each surveyed 20 days earlier, the RTE for session 2 would be $300 \times 20 = 6{,}000$.

known. We assigned rub tree surveys to the 14-day session in which we collected samples.

We compiled capture, telemetry, mortality, and age data for all grizzly bears handled for research or management in the GGA during 1975–2006. We genotyped hair, blood, or muscle samples from these bears when samples were available. Collaring effort and radiocollared bear distribution did not appear to be representative of the distribution of bears. We realized that our grid-based DNA detections of bears provided a snapshot of bear distribution during sampling and could be integrated with the radiocollared bear data to provide better estimates of closure violation and density. To estimate geographic closure during the study, we used radiotelemetry data from individuals that had ≥1 location on the GGA study area between 15 May–15 September within 10 years of our sampling, were <20 years old during our study if we did not know if the bear was still alive, and were genotyped. We used histories of previous live-captures to model heterogeneity in hair trap capture probabilities.

### Genetic Methods

Samples were analyzed at 2 laboratories that specialize in noninvasive genetic samples. We discarded all obvious nonbear (e.g., ungulate) hair samples. Initially, we analyzed all putative bear hair samples with ≥5 follicles; however, over the course of the project genotyping success improved, allowing us to get reliable genotypes from ≥2 follicles. Species was initially determined by a length polymorphism in the mitochondrial control region (Woods et al. 1999). Species was verified with the G10J microsatellite, which has species-specific alleles for grizzly bears and black bears (Mowat et al. 2005; D. Paetkau, Wildlife Genetics International, unpublished report). Finally, an assignment test (Paetkau et al. 1995) was performed with the most complete set of microsatellites available, excluding G10J, which confirmed all species determinations. For every sample, 6 microsatellite loci were analyzed to determine individual identity: G1A, G10B, G10C, G10L, G10M, and G10P (Paetkau et al. 1995). Up to 10 additional loci were analyzed for ≥1 sample from each individual to enable more detailed population genetic analyses. These extended genotypes were used to confirm differences between individuals with similar 6-locus genotypes. Gender was initially determined using the SRY marker (Taberlet et al. 1993) and was verified using a size polymorphism in the amelogenin marker (Ennis and Gallagher 1994). Mixed samples (samples with hair from >1 bear) were reliably identified by evidence of ≥3 alleles at ≥1 locus (Roon et al. 2005*a*).

In addition to the procedures described above, we followed recommendations in Paetkau (2003) and Roon et al. (2005*b*) for detecting and eliminating genotyping error. We replicated genotypes for all 1) individuals identified in one sample, 2) pairs of individuals that differed at only 1 or 2 loci (1- and 2-mismatch pairs), 3) pairs of individuals that differed at 3 loci when ≥1 locus was consistent with allelic dropout, and 4) individuals with samples geographically separated by large distances. We also analyzed additional markers for geographically disparate samples from the same individual. For all samples with sufficient DNA, genotypes

identified by the initial laboratory were independently verified by a second laboratory. We used Program DROPOUT (McKelvey and Schwartz 2005) to provide further evidence that our dataset was free of genotyping errors. We used the observed number of alleles ($A$) and expected heterozygosity ($H_E$) to express genetic variation in our population. We used probability of identity ($P_{ID}$) and of siblings ($P_{SIB}$) to describe the power of our markers to identify individuals (Paetkau and Strobeck 1998). We performed calculations using GENALEX 6 software (Peakall and Smouse 2006).

**Data Analysis**

To estimate total population size, including dependent young, we used Huggins–Pledger closed mixture models (Huggins 1991, Pledger 2000) in Program MARK (White and Burnham 1999; Pledger model updated May 2007; White 2008). We developed one encounter history for each bear for each year. We entered hair trap detections as sessions 1–5, followed by rub tree detections as sessions 6–11 (1998) and sessions 6–15 (2000; Boulanger et al. 2008*a*). For example, the encounter history for a bear detected in the first 3 hair trap sessions and the first 3 rub tree sessions in 1998 would be 11100111000. This approach is permissible because the order of sessions only affects estimates if a behavioral response (e.g., waning response to scent lure) is present in the data (Boulanger et al. 2008*a*). We assumed that any behavioral response to hair traps was negligible because sites were moved between sessions (Boulanger et al. 2006), the scent lure provided no food reward, and a different secondary lure was used each session. We also think a behavioral response in the rub tree sample was unlikely because no attractant was used, and rubbing on trees was a natural behavior.

We obtained estimates of the female, male, and total population size as derived parameters from the Huggins model. Calculation of 95% log-based confidence intervals about those estimates incorporated the minimum number of bears known to be alive on the study area ($M_{t+1}$; White et al. 2002). We calculated variances for pooled estimates from the variance–covariance matrix of the derived N estimates. Biologically plausible models constructed a priori included time variation (t), linear trends (T), and varying capture probability by type of sampling method (type: hair trap or rub tree). We entered the sex of each bear as a group covariate. Number of rub trees sampled and the number of days between successive hair collections for each tree varied for each sampling session. We used a rub tree effort (RTE) covariate to model the time variation caused by varying rub tree sampling intensity. The RTE was the cumulative number of days between successive hair collections for all trees sampled per session. All rub trees sampled in 1998 were inside GNP; 5.3% of the trees sampled in 2000 were outside of GNP (Fig. 1). We predicted an inverse relationship between each bear's mean distance to the closest rub tree and capture probability at rub trees. To model this effect, we included an individual covariate for the distance ($d_{RT}$) and log-transformed distance ($ld_{RT}$) to the nearest cell that contained surveyed rub trees from the mean capture location for each bear. Bears whose mean location was within GNP received a zero for this covariate. This set their rub tree capture probability equal to the mean population (intercept) value for rub tree capture probability. Because capture probability for either sampling method may be a function of proximity to geographically open study area boundaries (Boulanger and McLellan 2001) and because our study area was open on the north and south edges, we evaluated parameters for distance (d), log distance (ld), and quadratic distance ($d^2$) to the north or south boundaries. Lastly, Boulanger et al. (2008*b*) found that detection probability at hair traps was lower for bears that have a history of live-capture than for those that have not been handled; therefore, we tested for an effect of previous live-capture (livecap).

We used the sample size-adjusted Akaike's Information Criterion ($AIC_c$) and $AIC_c$ weights to evaluate relative support for each of our candidate models. We considered the model with the lowest $AIC_c$ score the model that best balanced bias and precision (Burnham and Anderson 2002). We used changes in $AIC_c$ values ($\Delta AIC_c$) to compare model support. We averaged population estimates based on their support by the data as estimated by $AIC_c$ weights to further account for model selection uncertainty (Burnham and Anderson 2002).

During our sampling periods, 62% of the study area boundary was geographically open to bear movement. Therefore, estimates from closed models corresponded to the superpopulation of bears (total no. of full- and part-time residents during the sampling period; Crosbie and Manley 1985) on the grid and surrounding area under the assumption that movement of bears was random across grid boundaries (Kendall 1999). We used the distance of mean capture location to the study area edge (DTE) as an individual covariate to efficiently model low capture rates near the edge caused by closure violation (Boulanger and McLellan 2001). We corrected our population estimates to account for the lack of geographic closure by using data from radiocollared bears that were in the study area during the sampling season (White and Shenk 2001). We calculated the proportion of time spent on the study area for each radiocollared bear; if a bear was collared for multiple years, we used the mean proportion of locations across years. We used data only from grizzly bears with $\geq$15 locations and did not include data from dependent offspring or relocated bears. Higher concentrations of collared bears occurred in locales with chronic bear–human conflicts (often near the study area boundary) and in research areas. To achieve a representative sample of the population, we weighted collared-bear data in proportion to bear density based on the distribution of DNA captures relative to the edge of the sampling grid. For this procedure, we assigned bears detected in hair-snaring efforts in 1998 and 2000 into successive 5-km DTE bins (i.e., 0–5 km, 5–10 km, etc. DTE) for each sex and calculated the relative proportion of bears in each DTE bin. We also estimated DTE for the collared bears based on mean radio locations and binned these into

**Table 3.** Variability of microsatellite markers used to determine individual identity of grizzly bears in the Greater Glacier Area, northwestern Montana, USA, 1998 and 2000.

| Marker | $H_E$[a] | $H_O$[a] | $A$[a] | $P_{ID}$[a] | $P_{SIB}$[a] |
|---|---|---|---|---|---|
| G1A | 0.69 | 0.76 | 6 | 0.13 | 0.44 |
| G10B | 0.76 | 0.78 | 9 | 0.09 | 0.39 |
| G10M | 0.70 | 0.70 | 8 | 0.15 | 0.44 |
| G10P | 0.74 | 0.79 | 7 | 0.10 | 0.40 |
| G10C | 0.65 | 0.66 | 5 | 0.16 | 0.47 |
| G10L | 0.60 | 0.56 | 4 | 0.23 | 0.51 |
| $\bar{x}$ | 0.69 | 0.71 | 6.5 | | |
| Overall probability of identity | | | | 6E − 06 | 0.007 |

[a] $H_E$ = expected heterozygosity; $H_O$ = observed heterozygosity; $A$ = no. of alleles; $P_{ID}$ = probability of identity, $P_{SIB}$ = probability of sibling identity.

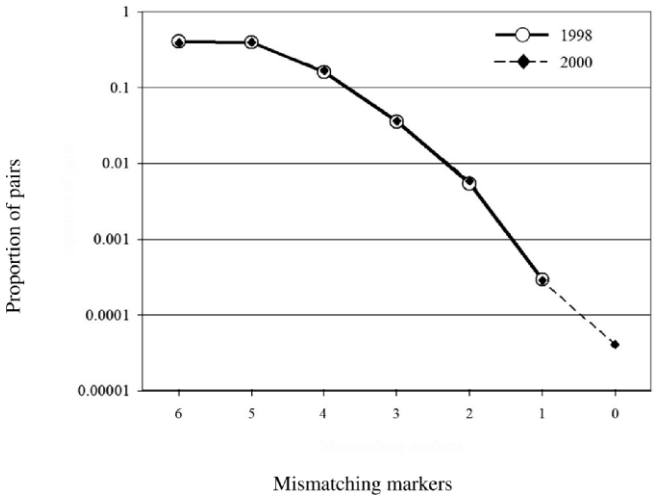


**Figure 2.** Observed distribution of genotype similarity for the 185 and 222 grizzly bears detected in 1998 and 2000, respectively, in the Greater Glacier National Park area in northwestern Montana, USA, for the 6 loci used for individual assignment. Mismatching markers = pairs of individuals that differ at 1, 2, 3 . . . etc. markers. Note that 97% of all grizzly bears detected had ≥9-locus genotypes and, when all available loci were considered, all individuals differed at ≥4 loci.

corresponding 5-km intervals. We then assigned a weight to each radiocollared bear based on the relative proportion of DNA bears in its DTE bin. We then used this weight when estimating the mean proportion of radio locations on the DNA sampling grid, which gave radiocollared bears that were in areas of higher expected bear density more weight in estimates of closure violation (and vice-versa). We calculated estimates for each sex and each year. We also estimated variance using the weighted means procedure. Superpopulation estimates (Kendall 1999) and the proportion of collared bears on the sampling grid have inherent sampling error. We, therefore, used the delta method (Seber 1982) to estimate variance for the average number of bears on the grid during each sampling season under the assumption of no covariance among estimates.

We calculated bear density using our sampled area size of 7,933 km$^2$. Only 2% of the study area was not suitable habitat for bears (e.g., lakes and glaciers); therefore, we retained these areas in sampled area and density calculations.

# RESULTS

## Sampling Effort

During 5 14-day sessions ($\bar{x}$ = 14.13, SD = 1.55), hair trapping yielded 5,582 grizzly and black bear hair samples from 626 sites in 1998 and 5,234 samples from 633 sites in 2000 (Table 1; Fig. 1). We collected grizzly bear hair at 28% of hair traps.

We monitored 660 and 829 rub trees in 1998 and 2000, respectively, along 1,041 km of trails in GNP. We surveyed an additional 78 rub trees on 144 km of trails in the FNF in 2000 (Table 2; Fig. 1) and found that bear use of rub trees was similar to that in GNP. Mean survey frequency was 2.12 visits per tree (SD = 1.31) in 1998 and 5.26 visits per tree (SD = 2.59) in 2000. The higher total rub tree survey effort in 2000 compared to 1998 resulted in the collection of more hair samples: 867 samples in 1998 versus 3,118 samples in 2000 (Table 2). We collected grizzly bear hair during 11.7% of all rub tree visits (1998 and 2000).

## Genetic Analyses

We attempted genetic analysis on all samples meeting our minimum thresholds for number of follicles. Of the 4,848 (44.8%) hair trap samples analyzed, 8.9% did not yield species results, 63.5% were identified as black bear, and 27.5% were identified as grizzly bear. Of the grizzly bear samples, 74.2% ($n$ = 991) were genotyped to individual. We conducted genetic analysis on 2,236 (56.1%) rub tree samples. Of these, 12.2% did not yield species results, 36.9% were identified as black bear, and 50.9% were identified as grizzly bear. Of the grizzly bear samples, 71.1% ($n$ = 809) were genotyped to individual. Fortunately, samples containing DNA from >1 bear were rare: 1.8% of hair trap and 2.0% of rub tree samples were mixed. The only way to obtain individual identities from mixed samples is to analyze single hairs—an expensive process with low success rates. Furthermore, analyzing single hairs does not always avoid mixture because saliva from conspecifics can be the source of mixture (D. Paetkau, unpublished data). We did not attempt individual identification on mixed samples.

The G10J test distinguishes black and grizzly bears on the basis of whether both alleles of an individual are an even number of base pairs (grizzly bear; e.g., 86.90) or odd (black bear; e.g., 101.107). In our population, 11% of our G10J genotypes were 94.odd—a result that typically indicates a black bear (D. Paetkau, unpublished data). A 6–15-locus assignment test excluding the G10J locus confirmed that 94.odd, as well as all odd.odd genotypes were correctly classified as black bears, and all even.even genotypes were correctly identified as grizzly bears.

Mean observed heterozygosity across the 6 markers used to identify individuals was 0.71 (Table 3). The probability that 2 randomly drawn, unrelated individuals would share the same genotype ($P_{ID}$) was 0.000006, and the probability that full siblings would have identical genotypes ($P_{SIB}$) was 0.007 (Table 3). Based on the observed distribution of genotype similarity for the 6 loci used for individual

**Table 4.** Number and percent of individual grizzly bears detected by sampling method in 1998 and 2000 in the greater Glacier National Park area in northwestern Montana, USA, date(s).

| | 1998 | | | | 2000 | | | |
|---|---|---|---|---|---|---|---|---|
| | M | | F | | M | | F | |
| **Sample method** | ***n*** | **%** | ***n*** | **%** | ***n*** | **%** | ***n*** | **%** |
| Hair-trap only | 40 | 48 | 75 | 74 | 27 | 25 | 60 | 53 |
| Rub-tree only | 28 | 33 | 10 | 10 | 38 | 35 | 29 | 25 |
| Both methods | 16 | 19 | 16 | 16 | 43 | 40 | 25 | 22 |
| Total | 84 | | 101 | | 108 | | 114 | |

identifications (Fig. 2), we predicted that one pair of matching genotypes could exist within our dataset, resulting in failure to identify one individual during the course of the project (Paetkau 2003). By extending the genotypes for each individual by up to 9 loci and scrutinizing geographically distant captures, we did identify one such pair. Of the 290 individual grizzly bears represented in this analysis, 97% had $\geq$9-locus genotypes and, when all available loci were considered, all individual bears differed at $\geq$4 loci.

## Population Size and Density

Genetic analysis of the samples from hair traps and rub trees identified 185 and 222 unique grizzly bears in 1998 and 2000, respectively (Table 4). Averaged across 1998 and 2000, 58% of unique individuals identified at hair traps were females compared with 39% females from rub tree data. Sampling at rub trees increased the minimum number of known bears by 24% above that detected with hair traps alone. We successfully genotyped 69 grizzly bears that had been handled for research or management purposes. Of the individual bears identified during hair sampling in 1998 and 2000, 10.3% and 11.3%, respectively, had been live-captured at least once.

Nine models were supported by the 1998 data as indicated by $\Delta AIC_c$ values <2 (Table 5) but none had a high proportion of the model weight. In general, hair trap capture probabilities varied by sex with a linear trend in female capture probabilities. Rub-tree capture probabilities also varied by sex, rub tree effort, and distance of bears from nearest rub tree. Capture probabilities for both data types were also influenced by distance from geographically open study area edge. Capture probabilities contained undefined heterogeneity (as estimated by mixture models) for rub tree data in 9 of 10 of the most supported models.

In contrast to the 1998 data, fewer models were supported by the data from 2000 (Table 6). The most supported models had undefined heterogeneity for both data types with capture probability varying by sex and capture type. There were also linear trends in capture probabilities for sex and capture type. In addition, rub tree capture probabilities varied by effort and distance of bears to the nearest rub tree. For both data types, capture probabilities varied as a function of distance from the open edges of the sampling grid.

Inspection of hair trap capture probability estimates from

**Table 5.** Model selection results from analysis of the 1998 Greater Glacier Area (GGA) in northwestern Montana, USA, grizzly bear population sampled using hair traps (sampling occasions 1–5) and rub trees (occasions 6–11). Models shown account for $\geq$90% of the Akaike weights.[a]

| | | F | | M | | | | No. | |
|---|---|---|---|---|---|---|---|---|---|
| **Model no.** | **GGA 1998 model[b]** | ***N*** | **SE** | ***N*** | **SE** | $AIC_c$ | $\Delta AIC_c$ | $w_i$ | **parameters** | **Deviance** |
| 1[c] | HT: p(sex + $T_F$) RT: π(.) $p_{1\&2}$( + sex + $T_F$ + $T_M$ + RTE + $ld_{rub}$) | 160.8 | 16.19 | 155.3 | 21.88 | 1,337.2 | 0 | 0.143 | 11 | 1,315.14 |
| 2 | HT: p(sex + $T_F$) RT: π(.) $p_{1\&2}$( + sex + $T_F$ + $T_M$ + RTE + $ld_{rub}$) + d | 163.8 | 17.29 | 162.7 | 24.86 | 1,337.4 | 0.13 | 0.134 | 12 | 1,313.25 |
| 3 | HT: p(sex + $T_F$) RT: π(.) $p_{1\&2}$( + sex + $T_F$ + $T_M$ + RTE + $ld_{rub}$) + d + $d^2$ | 166.1 | 18.02 | 166.3 | 25.63 | 1,337.8 | 0.48 | 0.113 | 13 | 1,311.58 |
| 4 | HT: p(sex + $T_F$) RT: π(.) $p_{1\&2}$( + sex + $T_F$ + $T_M$ + RTE + $ld_{rub}$ × sex) | 160.9 | 16.21 | 154.9 | 21.79 | 1,338.1 | 0.78 | 0.097 | 12 | 1,313.90 |
| 5 | HT: p(sex + $T_F$) RT: π(.) $p_{1\&2}$( + sex + $T_F$ + $T_M$ + RTE + $ld_{rub}$) + $d_{NS}$ | 161.9 | 16.56 | 159.5 | 23.42 | 1,338.3 | 1.04 | 0.085 | 12 | 1,314.15 |
| 6 | π(.) $p_{1\&2}$( × type + sex + $T_{HS\text{-}F}$ + $T_{RT\text{-}M}$ + $T_{RT\text{-}F}$) | 156.4 | 15.27 | 149.1 | 19.62 | 1,338.5 | 1.25 | 0.077 | 12 | 1,314.36 |
| 7 | HT: p(sex + $T_F$) RT: π(.) $p_{1\&2}$( + sex + $T_F$ + $T_M$ + RTE + $d_{rub}$) + $ld_{NS}$ | 161.3 | 16.36 | 158.1 | 23.1 | 1,338.8 | 1.50 | 0.068 | 12 | 1,314.62 |
| 8 | HT: p(sex + $T_F$) RT: π(.) $p_{1\&2}$( + sex + $T_F$ + $T_M$ + RTE + $ld_{rub}$) + $d_{NS}$ + $d_{NS}^2$ | 163.4 | 17.06 | 160.0 | 23.35 | 1,338.8 | 1.54 | 0.066 | 13 | 1,312.64 |
| 9 | HT: p(sex + $T_F$ + livecap) RT: π(.) $p_{1\&2}$( + sex + $T_F$ + $T_M$ + RTE + $ld_{rub}$) | 161.3 | 16.35 | 156.7 | 22.52 | 1,3390 | 1.71 | 0.061 | 12 | 1,314.82 |
| 10 | HT: p(sex + $T_F$ + $d_{NS}$ + $d_{NS}^2$) RT: π(.) $p_{1\&2}$( + sex + $T_F$ + $T_M$ + RTE + $ld_{rub}$) | 162.4 | 16.69 | 157.7 | 22.72 | 1,339.5 | 2.21 | 0.048 | 13 | 1,313.30 |

[a] $AIC_c$ = Akaike's Information Criterion adjusted for small sample size; $w_i$ = Akaike wt.

[b] Parameter definitions: HT = hair trap; RT = rub tree. Mixture models were only used with one sample method when listed with these prefixes. RTE = rub tree sampling effort, the cumulative no. of days between successive hair collections for each tree sampled/session. $T_F$,$T_M$ = sex-specific linear trends in capture probability. $d_{rub}$ = distance from each bear's mean capture location to the nearest cell that was sampled with rub trees. $ld_{NS}$ = log-transformed distance from each bear's mean capture location to the N or S border of the study area, whichever is closer. $d^2$ = quadratic distance from each bear's mean capture location to the closest edge of the study area. livecap = effect of previous live-capture on HT capture probability.

[c] Example definition of notation for model 1: HT: sex-specific capture probabilities (p), with a linear trend for F. RT capture probabilities modeled with constant mixture probability. F-specific RT capture probabilities, plus sex-specific linear trends. RT $p_{1\&2}$. also influenced by the log-transformed distance to the closest rub tree–sampled cell and RTE.

**Table 6.** Model selection results from analysis of the 2000 Greater Glacier Area (GGA) in northwestern Montana, USA, grizzly bear population sampled using hair traps (sampling occasions 1–5) and rub trees (occasions 6–15). Models shown account for ≥90% of the Akaike weights. See Table 5 for parameter definitions.[a]

| Model no. | GGA 2000 models | F | | M | | $AIC_c$ | $\Delta AIC_c$ | $w_i$ | No. parameters | Deviance |
|---|---|---|---|---|---|---|---|---|---|---|
| | | *N* | SE | *N* | SE | | | | | |
| 1 | $\pi(.)\ p_{1\&2}(\times \text{type}) + \text{sex} \times \text{type} \times T + RTE + ld_{rub} + ld_{NS}$ | 198.1 | 22.25 | 133.2 | 8.99 | 2,385.2 | 0.00 | 0.420 | 14 | 2,357.11 |
| 2 | $\pi(.)\ p_{1\&2}(\times \text{type}) + \text{sex} \times \text{type} \times T + RTE + ld_{rub} + \text{sex} \times ld_{NS}$ | 202.2 | 25.75 | 133.2 | 9.13 | 2,387.1 | 1.82 | 0.169 | 15 | 2,356.91 |
| 3[b] | $\pi(.)\ p_{1\&2}(\times \text{type}) + \text{sex} \times \text{type} \times T + RTE + ld_{rub}$ | 204.6 | 26.45 | 139.0 | 12.74 | 2,387.2 | 1.92 | 0.161 | 13 | 2,361.05 |
| 4 | $\pi(.)\ p_{1\&2}(\times \text{type}) + \text{sex} \times \text{type} \times T + RTE + ld_{rub} + d_{NS}$ | 199.6 | 24.21 | 135.9 | 11.44 | 2,388.7 | 3.48 | 0.074 | 14 | 2,360.59 |
| 5 | $\pi(.)\ p_{1\&2}(\times \text{type}) + \text{sex} \times \text{type} \times T + RTE + ld_{rub} + d$ | 200.9 | 23.90 | 135.9 | 10.74 | 2,388.8 | 3.56 | 0.071 | 14 | 2,360.66 |
| 6 | $\pi(.)\ p_{1\&2}(\times \text{type}) + \text{sex} \times \text{type} \times T + RTE + ld_{rub} + ld_{NS\text{–}HT}$ | 205.9 | 28.30 | 139.8 | 14.00 | 2,389.1 | 3.90 | 0.060 | 14 | 2,361.00 |

[a] $AIC_c$ = Akaike's Information Criterion adjusted for small sample size; $w_i$ = Akaike wt.

[b] Example definition of notation for model 3: Constant mixture probability. Mixtures modeled are method-specific. Capture probabilities ($p_{1\&2}$) are method-specific for sex, plus sex- and method-specific linear trends. Capture probability also influenced by log-transformed distance to the closest rub tree–sampled cell and RTE for RT $p_{1\&2}$.

the models revealed linear trends among sessions. Male hair trap capture probabilities were relatively constant or decreasing whereas female capture probabilities increased with session in both 1998 and 2000 (Fig. 3). Rub-tree capture probabilities were influenced by effort, with male capture probabilities always higher than females. A bear was unlikely to be detected at a rub tree if its average capture location was >5 km from the nearest cell with rub trees (Fig. 4).

We used 66 radiocollared bears (41 F and 25 M) for the closure correction. The proportion of points on the grid was slightly lower for males in both 1998 and 2000, suggesting that they violated closure more than did females (Table 7). When corrected for this lack of closure, estimated population size for the GGA was 241 grizzly bears (95% CI = 202–303) in 1998 and 241 bears (95% CI = 205–304) in 2000. Mean grizzly bear density was 30 bears/1,000 $km^2$ (95% CI = 27–35). Grizzly bear detections were not distributed equally across the GGA. Considering only the hair trap results (equal sampling effort throughout the study area), we identified 2.4 times more bears per hair trap inside than outside GNP (Fig. 5).

## DISCUSSION

We present the first rigorous estimate of grizzly bear density in the Greater Glacier Area. By using multiple data sources, we obtained a precise estimate (CV = 10%) for this large study area despite fairly low capture and recapture rates. The remarkable consistency of our estimates between years lends credibility to these results and is consistent with the low average annual mortality rate (4.6%) recorded in the GGA during 1998–2000.

Because previous studies used different methods and provided no estimates of precision, there is little value in contrasting our population estimate to historical estimates made in GNP. At 30 bears/1,000 $km^2$, grizzly bear density in the GGA is comparable to levels commonly found in interior North American populations (McLellan 1994, Miller et al. 1997, Schwartz et al. 2003, Mowat et al. 2005). However, comparisons of density across studies must be made cautiously due to differences in age groups included in the estimates and bias caused by lack of geographic closure (White and Shenk 2001, Schwartz et al. 2003). Furthermore, mammalian carnivore density estimates tend to increase with decreasing study area size (Smallwood and Schonewald 1998), presumably because smaller studies tend to target areas where animals are known to occur rather than marginal habitat or areas where populations are sparse (Miller et al. 1997). Larger study areas include more habitat heterogeneity, which is typically associated with substantial variation in animal abundance. Larger areas also have proportionally less edge effect (i.e., include proportionally fewer animals with home ranges overlapping the study area boundary; Miller et al. 1997). The GGA included highly diverse habitats. The eastern edge of the GGA was in the prairie biome where bears primarily inhabited narrow, widely spaced riparian corridors between large agricultural fields. The high relief and topographic complexity of the mountains and valleys of GNP in the center of the study area contrasted with the gentler slopes and lower elevations of commercial forests and small towns on the western edge. Density varied widely across the study area, complicating comparisons of average density to other populations. The notably higher density found inside compared to outside GNP was consistent with the park's high habitat quality (USFWS 1993) and the security of a central protected area (Schwartz et al. 2006). Grizzly bear population density reported for the Flathead River drainage of British Columbia, adjacent to GNP, was 57–80 bears/1,000 $km^2$ (McLellan 1989; study area size = 264 $km^2$). The Flathead study area was selected because of high levels of logging and gas exploration, not because of anticipated high bear density (B. McLellan, British Columbia Ministry of Forests, personal communication). In the Swan Mountains located to the southwest of the GGA, density was 16 bears/1,000 $km^2$ in 1,457 $km^2$ of multiple-use forests and rural lands (Mace and Waller 1998). At 7,933 $km^2$, our study area was 5–30 times larger than adjacent study areas. In addition to real differences in population density, it is likely that differences in study area size as well as differing approaches

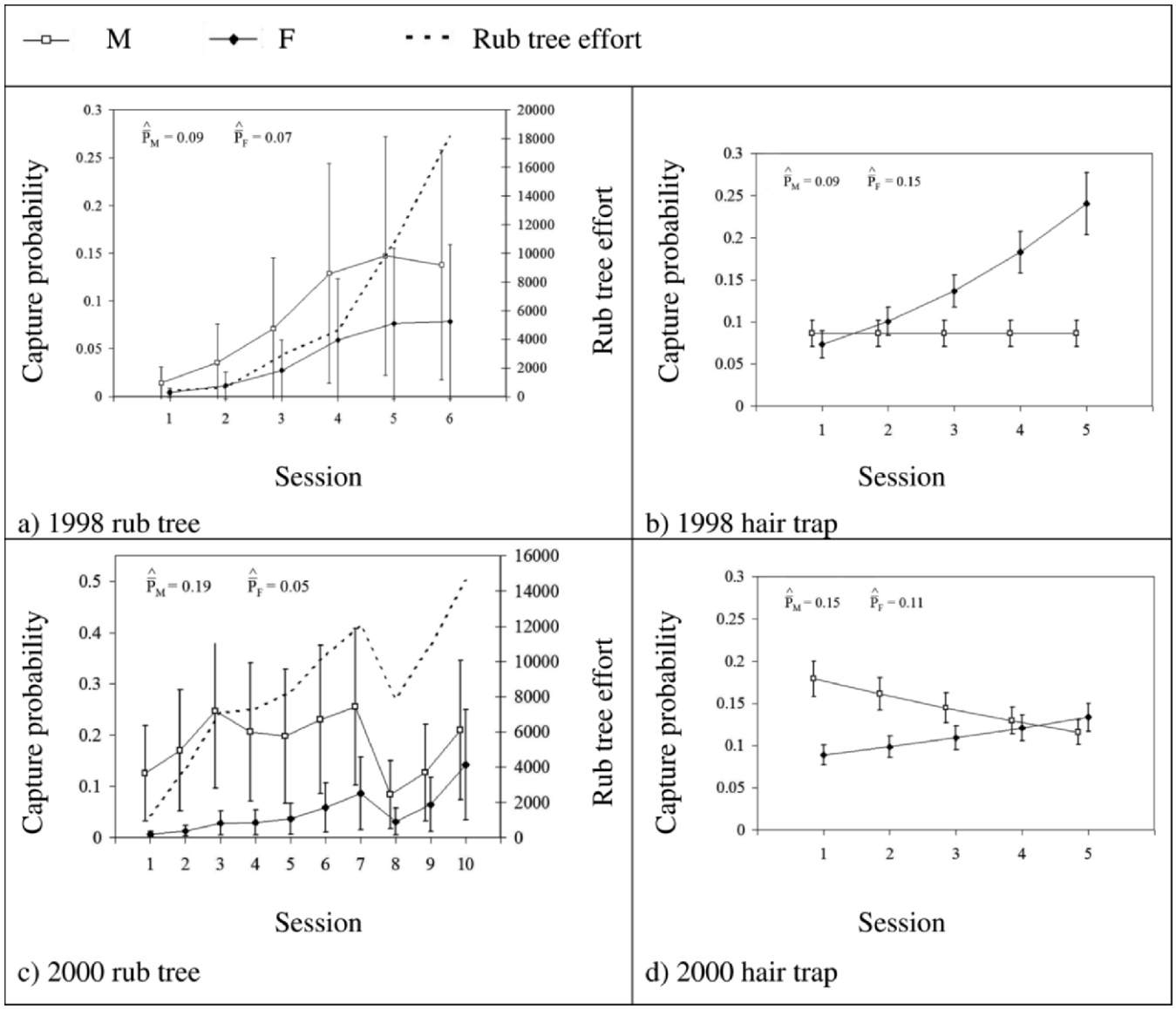


**Figure 3.** Estimates of gender- and session-specific grizzly bear capture probabilities from hair trap and rub tree surveys in the greater Glacier National Park area, Montana, USA, 1998 and 2000. We derived estimates from the most selected models from Tables 5 and 6. Rub tree effort was the cumulative number of days between successive hair collections summed over all trees sampled per session.

to adjusting for lack of closure were responsible for some of the variation in density estimates.

The relative density of bears revealed by hair sampling matched expectations based on the NCDE Grizzly Bear Recovery Zone boundaries and knowledge of population status in adjacent parts of Canada. The east and west study area boundaries coincided with the edge of the recovery zone. We predicted lower bear density in these areas, because the number of bears often declines near the edge of occupied habitat. The higher number of detections along the north and south boundaries supported our assumption that bears moved freely across these study area edges.

Our goal in distributing hair traps was to sample intensively enough to provide an opportunity to detect each bear during each sampling occasion. Our choice of a 64-km$^2$ grid cell for hair trapping was based on grizzly bear home-range sizes in our area. The average seasonal and 14-day minimum convex polygon home ranges of adult females in our area was 231 km$^2$ ($n = 40$, range: 42–1199 km$^2$) and 68 km$^2$ ($n = 95$, range: 2–528 km$^2$), respectively (R. Mace, Montana Department of Fish, Wildlife, and Parks, personal communication). These home-range calculations were based on bears that had $\geq$15 Global Positioning System fixes and were monitored for $\geq$70% of days during the relevant period (i.e., the entire season or each session). These home-range sizes, in conjunction with moving hair traps between sessions, suggest that our sample intensity was sufficient to have given all bears the opportunity to encounter $\geq$1 trap.

A simple proportion of telemetry locations on the study area often is used to adjust abundance estimates for closure violation (White and Shenk 2001). Our data demonstrated that distribution of radiocollared animals does not always represent actual distribution of animals on a study area, especially if live-capture efforts were concentrated in specific

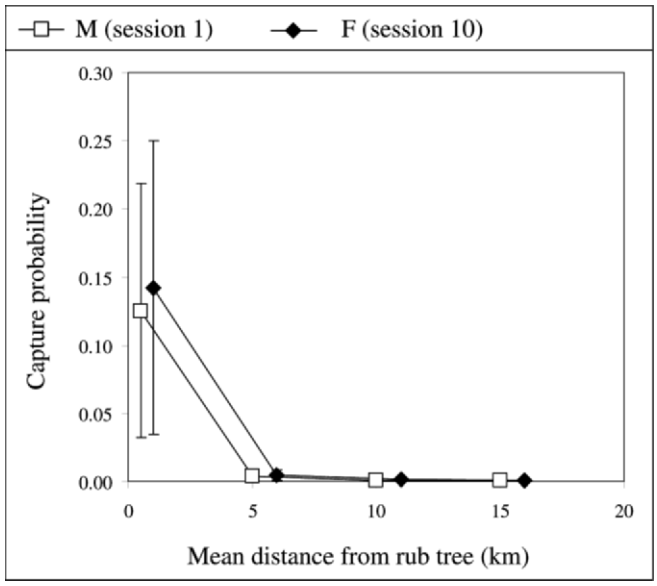


**Figure 4.** Estimated rub-tree capture probability for male and female grizzly bears in the greater Glacier National Park area, Montana, USA in 2000 as a function of the distance from the area sampled with rub-trees; similar trends were found during 1998. Intercept values are offset to allow easier interpretation. Estimates for capture probability are from the sessions with the largest sample sizes, session 1 for males and session 10 for females.

areas. Our weighted mean method to estimate closure violation used the distribution of DNA bears relative to the study area perimeter to reduce potential biases caused by nonrepresentative distribution of radiocollared bears.

Knowing the age classes of animals included in abundance estimates is vital for meaningful comparison of density between populations. We maintain that our population estimates include the total population based on the results of a larger study conducted in the NCDE, which used the same sampling methods. Hair-trap and rub tree sampling conducted in 2004 sampled 7 of 16 (44%) cubs and 12 of 15 (80%) yearlings known to be present (Kendall et al. 2009). This represents the most conclusive evidence to date that DNA-based grizzly bear population estimates include all age classes.

We believe there were 2 primary reasons for the large number of supported models in 1998. First, low capture probabilities and small sample sizes resulted in low power to select models (Fig. 3). Second, most of the candidate models were very similar. The similarity of the population estimates derived from all models bolstered our confidence that the model-averaged abundance estimates in both 1998 and 2000 were reasonable.

In our study, female capture probabilities generally increased over the sampling season for both sampling methods in both years. Increasing female HT capture probabilities have been previously documented (Boulanger et al. 2007), but the underlying causes remain unknown. Females with dependent offspring may range more widely as their young mature, allowing them to encounter more sample sites, or females with young may avoid sites frequented by males during the breeding season. Both of these theories are consistent with the patterns observed for hair trap and rub tree sampling; however, more behavioral data are needed to clarify factors affecting the trends we observed in capture probabilities.

Mark–recapture models assume individual capture probabilities are independent. This condition was violated by sampling dependent offspring, yet we could not remove these individuals from our dataset because we could not determine age through DNA analysis. However, capture of one member of a family group did not ensure that all members were detected. In a larger study that used similar methods conducted in this area in 2004, it was common to detect varying numbers of individuals (1–4) from a family group at hair traps and rub trees (Kendall et al. 2009). Variable detection of bears traveling together would decrease dependence of capture probabilities within groups of mothers and their offspring and would decrease the amount of bias in variance estimates. Simulations suggest inclusion of dependent offspring causes minimal bias to population estimates but potentially a slight negative bias to variance estimates, which is caused by overdispersion of multinomial variances (Miller et al. 1997, Boulanger et al. 2004). At this time, there is no valid approach to estimate

**Table 7.** Model-averaged estimates of total population size and density (including dependent offspring) derived from Huggins–Pledger closed mixture models for grizzly bears in the greater Glacier National Park Area in northwestern Montana, USA, 1998 and 2000.

| | | Super population[a] | | Proportion time on study area | | Population size corrected for lack of geographic closure[b] | | | | Grizzly bear density[c] | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Yr | Sex | Estimate | SE | $\bar{x}$ | SE | Estimate | SE | 95% CI lower | 95% CI upper | Bears/1,000 km$^2$ | CV |
| 1998 | F | 161.7 | 16.68 | 0.78 | 0.05 | 125.4 | 15.25 | 104 | 166 | 15.81 | 12.2% |
| | M | 157.6 | 23.18 | 0.73 | 0.07 | 115.3 | 20.20 | 88 | 171 | 14.53 | 17.5% |
| | Total[c] | 319.4 | 29.51 | 0.75 | 0.11 | 240.7 | 25.31 | 202 | 303 | 30.34 | 10.5% |
| 2000 | F | 201.1 | 24.89 | 0.73 | 0.05 | 146.0 | 20.96 | 116 | 202 | 18.40 | 14.4% |
| | M | 135.3 | 11.02 | 0.70 | 0.07 | 94.6 | 12.40 | 82 | 137 | 11.93 | 13.1% |
| | Total[d] | 336.4 | 30.39 | 0.72 | 0.10 | 240.6 | 24.36 | 205 | 304 | 30.33 | 10.1% |

[a] Mark–recapture population estimate of all bears that were full- and part-time residents on the study area during the sampling period. We did not adjust the superpopulation estimate for lack of geographic closure.
[b] Closure-corrected population estimate is the average no. of bears on the study area during the sampling period.
[c] Density estimates are based on the closure-corrected population estimate in the 7,933-km$^2$ study area.
[d] Total may not equal the sum of F and M due to rounding error.

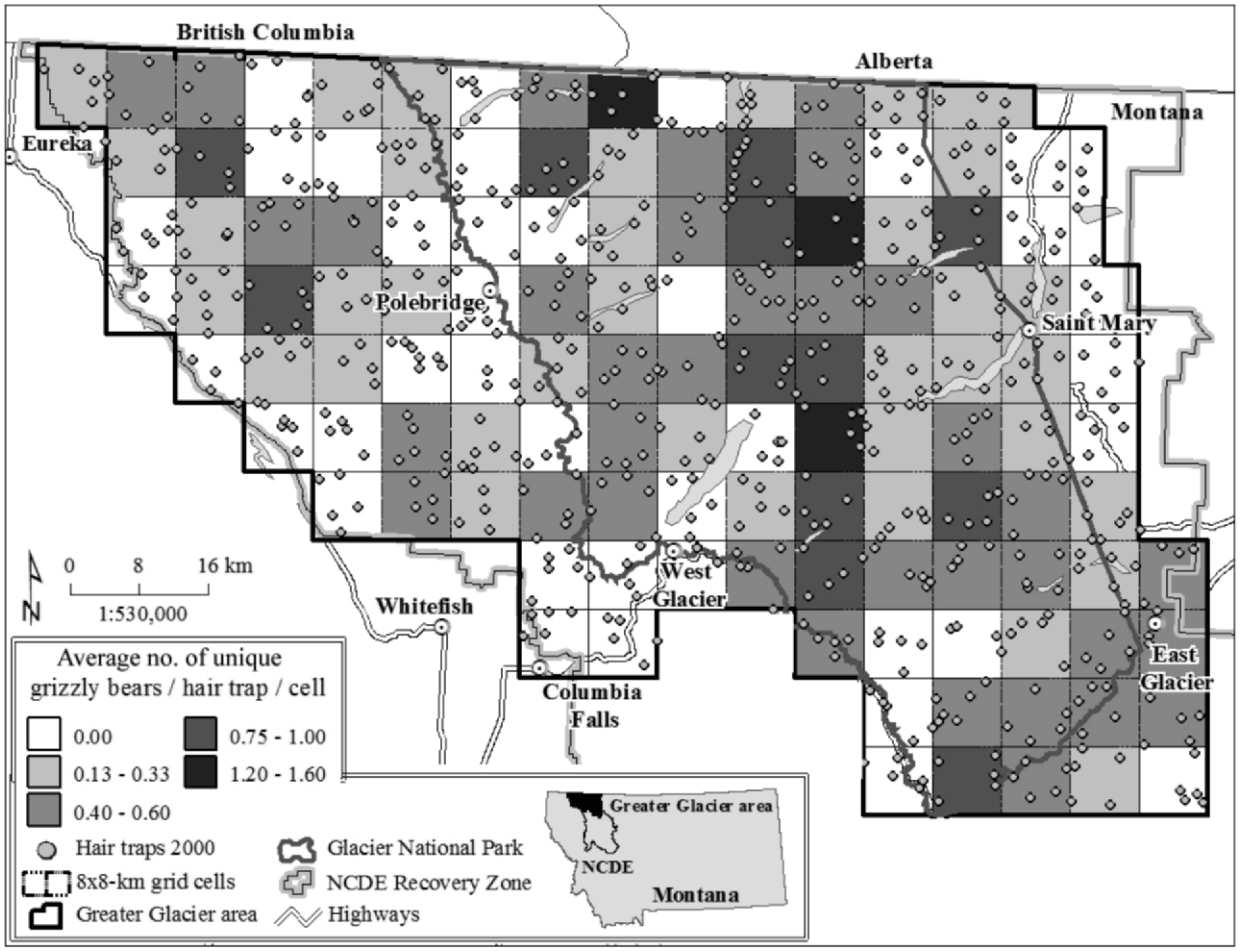


**Figure 5.** Relative density of grizzly bears detected at hair traps systematically distributed in the greater Glacier National Park (GNP) area in northwest Montana, USA, during 15 May–15 August 2000. Density inside GNP was 2.4 times the density outside of the park in the study area. Similar patterns of distribution were found when this area was sampled in 1998 using the same methods. NCDE = Northern Continental Divide Ecosystem.

overdispersion or model fit for closed models (White 2002, Boulanger et al. 2008*b*).

Rub-tree detections were sensitive to the amount of rub tree sampling effort; however, this effect was explained well by the RTE covariate in the Huggins model. The lower number of bears identified at rub trees in 1998 reflected the lower number of trees monitored, longer survey interval, and shorter sampling season compared to 2000. We found rub trees in all types of habitat, in all areas searched. Further, our pilot surveys in the FNF found that patterns of bear use of trails and rub trees on multiple-use national forest land were similar to observations in GNP. Our results suggest that bears' average locations need to be relatively close to rub trees (within 5 km) to have an opportunity to be detected with rub tree sampling (Fig. 4). However, in our study it was not essential for all bears to have nonzero rub tree capture probabilities as long as they were vulnerable to hair trap sampling (Boulanger et al. 2008*a*).

Models using bears detected during multiple sessions of hair trap sampling have been used extensively to estimate grizzly bear population size in North America (Woods et al. 1999, Boulanger et al. 2002). Ours is the first study to use detections from rub trees in a mark–recapture population estimate. Boulanger et al. (2008*a*) used simulation and empirical data from our study to compare estimates made with hair trap–only and joint hair trap–rub tree data. They found that the 2 datasets produced similar estimates, but joint data improved precision as a result of increased sample coverage. Despite minimal sample coverage of rub trees in half of our study area, rub tree detections increased the number of unique individuals above that identified at hair traps by 24%. Our use of covariates in Huggins mixture models also improved precision of our estimates. We developed an individual covariate that incorporated a bear's proximity to areas sampled with rub trees, which effectively modeled heterogeneity caused by uneven rub tree sampling coverage and greatly improved the relative fit of the mark–recapture models. For example, if we removed the distance from rub tree covariate from the most supported models (model 1) in Tables 5 and 6, the resulting models were less supported by 28.4 and 47.1 $AIC_c$ units for 1998 and 2000, respectively. We refined the methods presented in Boulanger et al. (2008*a*) by using a simple covariate to model variation caused when some bears had little or no opportunity to be detected by one of the sampling methods. Our modeling approach could be used to improve estimates

of other populations and species in which mark–recapture data are available from multiple sources. Use of multiple sampling methods can also improve sample coverage for other research objectives such as occupancy modeling, assessing landscape connectivity, and population genetic structure.

The NCDE is one of the last remaining strongholds of grizzly bears south of Canada. We provide data on population status in the northern quarter of the NCDE. The data we present will be useful as benchmarks for monitoring future trends in the size, distribution, and genetic status of the GGA population. Our results highlight the value of large protected core areas. Grizzly bear density in GNP was substantially higher than in surrounding areas. The robust park population is potentially a source of bears for natural range expansion and augmentation of other at-risk populations. As the primary link between the threatened populations in the United States and the larger population in the Canadian Rocky Mountains to the north, the park plays an important role in long-term persistence of grizzly bears south of Canada. Our study provides a snapshot of population status in the GGA; however, comparable data are not available for the remaining 16,000 $km^2$ of the NCDE. This void will need to be filled before recovery status can be evaluated.

## MANAGEMENT IMPLICATIONS

To ensure that desired estimate precision is met, we recommend researchers conduct pilot studies, simulations, and power analyses to guide study design (e.g., cell size, no. of sample sessions, and the need for moving traps between sessions; Miller at al. 1997, Boulanger et al. 2004). We also recommend that bear studies consider collecting hair from rub trees in addition to other sampling method(s). We found that it was less expensive to increase sample size and coverage by adding rub tree surveys than by increasing hair trapping intensity. Rub-trees that are located on trails and other animal travel routes often can be surveyed while field crews are en route to hair traps or performing other duties. In general, use of multiple data sources can cut costs and yield more precise abundance estimates. Because equal sampling effort across the study area is only required for one of the sampling methods, opportunistic data, such as management records, sometimes can be used as secondary sampling type. Covariates (e.g., the distance from rub tree covariate used in our study) provide a simple way to account for variation caused by unequal sampling effort.

The more complex population models we used offer a number of benefits but they will not work for all projects. Inclusion of covariates can more effectively model heterogeneity but more data are needed for model selection as the number of parameters increases. For many studies, small sample sizes or low capture probabilities result in low power to select models. Based on our experience, we recommend several measures to boost capture probabilities and sample sizes. We believe that 1 L of scent lure per hair trap was a minimal attractant and advocate the use of substantially more lure (e.g., $\geq$3 L). It is also important for bear studies to use lure proven to be effective for their population. In our case we needed 12 months of lead time or a heated facility to sufficiently age the fish we used in our scent lure. Hair-trap sites should be selected before the field season by a small number of people armed with bear habitat and activity information, which will ensure that sites are chosen using the best available information and that site selection will be consistent throughout the study area.

Abundance and density estimates should be corrected for lack of geographic closure to facilitate comparison with other populations. Before radiotelemetry data are used to correct estimates for closure violation, locations of the collared animals first should be plotted. If their distribution is not representative of the population, we urge researchers to use a weighted method, such as we developed, for calculating proportion of time on study area. We also advocate clearly stating what population cohorts are included in abundance estimates. Our data suggest that estimates of bear population abundance based on barbed-wire hair trap sampling include all age classes; however, we recommend that this be evaluated by other research projects for their specific methods.

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