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Original Article

Black Bear Density in Glacier National Park, Montana

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ABSTRACT We report the first abundance and density estimates for American black bears (*Ursus americanus*) in Glacier National Park (NP), Montana, USA. We used data from 2 independent and concurrent noninvasive genetic sampling methods—hair traps and bear rubs—collected during 2004 to generate individual black bear encounter histories for use in closed population mark–recapture models. We improved the precision of our abundance estimate by using noninvasive genetic detection events to develop individual-level covariates of sampling effort within the full and one-half mean maximum distance moved (MMDM) from each bear's estimated activity center to explain capture probability heterogeneity and inform our estimate of the effective sampling area. Models including the one-half MMDM covariate received overwhelming Akaike's Information Criterion support suggesting that buffering our study area by this distance would be more appropriate than no buffer or the full MMDM buffer for estimating the effectively sampled area and thereby density. Our model-averaged super-population abundance estimate was 603 (95% CI = 522–684) black bears for Glacier NP. Our black bear density estimate (11.4 bears/100 km², 95% CI = 9.9–13.0) was consistent with published estimates for populations that are sympatric with grizzly bears (*U. arctos*) and without access to spawning salmonids. Published 2013. This article is a U.S. Government work and is in the public domain in the USA

KEY WORDS abundance, American black bear, bear rubs, density estimation, Glacier National Park, hair trap, mark–recapture, mean maximum distance moved, noninvasive genetic sampling, *Ursus americanus*.

Glacier National Park (NP) retains nearly the full complement of species present prior to the arrival of Europeans, including all native large carnivores. American black bears (*Ursus americanus*), presumably the most numerous of the large carnivore species, are an important component of the faunal community. The Park requires reliable baseline information on population size and trend to decide what actions are likely to be most effective in achieving black bear management goals (Glacier NP Bear Management Plan 2010); however, little was known about the status of this population. Accurate and precise baseline estimates of population parameters such as density are vital to assess current status and monitor changes. This is particularly important as human activity and development continue to increase within and adjacent to Glacier NP's borders, likely leading to increasing human-caused mortality and the potential for fragmentation of bear and other wildlife populations.

Understanding animal density can provide insights into ecological processes and allow prediction of responses to management actions or other changes that may occur at multiple scales (Krebs 1985, Thompson et al. 1998). Such

dynamics are of particular interest to managers of both protected and exploited populations, but are difficult to monitor because most wildlife populations do not exist as islands and animals are free to move across land management boundaries. Despite this, traditional approaches to estimate abundance and density either assume geographic closure or require multiple years of sampling, which dramatically increase monitoring cost. Use of closed population models to estimate the size of geographically open populations requires knowing the effectively sampled area. In the absence of telemetry data that can be used to estimate residency time on the study area (Ivan et al. 2013), effective sampling area is usually defined by buffering the study area by an arbitrarily selected distance related to the observed movements of the animals (Wilson and Anderson 1985). Further, when sampling sites are not arrayed systematically throughout the study area, which is typically the case, heterogeneity in sampling effort can decrease estimate precision.

Recently, spatially explicit capture–recapture (SECR) methods have seen increasing development and application to estimating density for wildlife populations (Efford 2004, Borchers and Efford 2008). Although these models show tremendous promise at circumventing some of the issues with traditional (i.e., closed population abundance estimators with an estimated effectively sampled area), they, too, have assumptions that may be difficult to satisfy for many studies, such as stationary and circular activity centers (Ivan et al.

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2013). Most studies using SECR methods have suffered from small sample sizes and small study areas with a large edge-to-area ratio, which inherently leads to greater violation of geographic closure. This is particularly true for wide-ranging species such as black bears. Spatially explicit capture–recapture models tend to produce lower density estimates than do traditional approaches, so they are often seen as an improvement (e.g., Obbard et al. 2010, Reppucci et al. 2011). Empirical comparisons of these 2 approaches using large datasets should improve our understanding of how reliable either method is for density estimation.

Another recent improvement in the estimation of wildlife population parameters is the use of multiple, concurrent sampling methods (Boulanger et al. 2008; Kendall et al. 2008, 2009; Sawaya et al. 2012). Because all sampling methods are inherently biased in some way, applying ≥ 2 independent methods increases sample coverage by detecting individuals via one method that may be missed by others. In addition to reducing the potential for sampling bias, using multiple sampling approaches can be a more efficient way to increase sampling intensity than increasing sampling effort for a single method. In some systems, multiple sampling approaches may enable concurrent monitoring of multiple species. Such studies can be a cost-effective way to address multiple population management information needs, which is increasingly important in an era of limited funding (Lambeck 1997, Manley et al. 2004). When designing multi-species research and monitoring efforts, however, it is important to ensure an appropriate and adequate sampling design for each species in accordance with research objectives (Yoccoz et al. 2001).

Our objectives were to assist Glacier NP with assessing the status of its black bear population by estimating baseline abundance and density using hair samples for genetic analysis that were collected as part of a larger grizzly bear study (Kendall et al. 2009). Although black bears have smaller ranges than do grizzly bears, we demonstrate that the increase in sampling intensity generated by our 2 concurrent, independent detection methods was sufficient to generate useful estimates of black bear abundance and density. To improve model performance, we developed a more objective way to account for individual and sampling-occasion-specific differences in sampling effort based on the number of sampling points and where each bear was detected. We used an information theoretic-based approach for determining the buffer size most supported by our data in conjunction with Huggins (1991) closed population abundance models, which we then compared with estimates from SECR models that also used measures of site-specific sampling effort (Efford et al. 2013). Our results suggest that adequate sampling scale and intensity may be of greater importance than modeling framework.

STUDY AREA

Our largely mountainous 4,100-km² Glacier NP study area (Fig. 1) straddled the Continental Divide in northwestern Montana, USA. Elevation ranged from approximately 900 m to 3,190 m above sea level with tree line occurring at

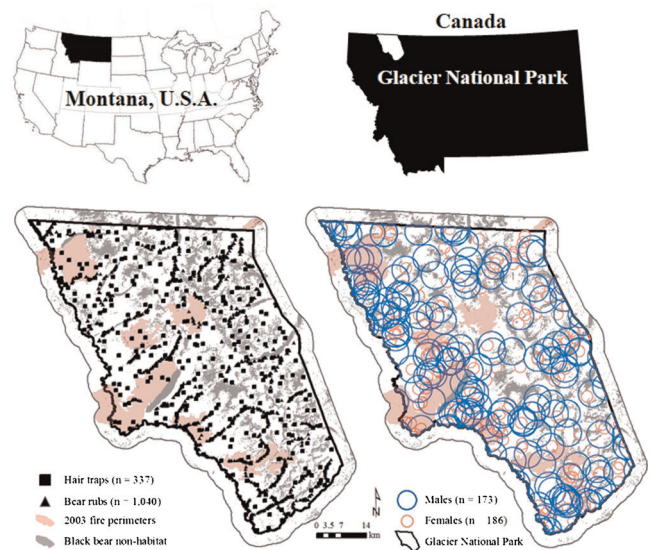


Figure 1. Study area consisting of Glacier National Park, Montana, USA, showing (left) the distribution of bear hair traps and bear rubs surveyed during 15 June to 11 October 2004 and potential black bear non-habitat (gray shading), which excluded areas of rock, permanent snow and ice, and bodies of water >1 ha. Areas burned in stand-replacing wildfires in 2003 (red shading) were also unlikely to provide bear habitat in 2004. (right) Average capture location for each black bear surrounded by a sex-specific idealized home range based on one-half the mean maximum distance moved.

approximately 2,000 m. Glacier NP's topography was shaped during the last ice age by glaciers that carved deep valleys, many of which were filled with large lakes. High elevations had extensive alpine and subalpine meadow and exposed rock and permanent snow and ice fields. Average annual precipitation, much of which was deposited as snow in winter, was 63 cm. The Continental Divide had dramatic effects on local climate and vegetation composition. Areas east of the Divide received less precipitation and had more alpine meadow and prairie grassland than the more heavily forested areas west of the Divide. Higher elevations received more precipitation than valleys.

Black bears in Glacier NP were generally not found in treeless or barren areas. When we subtract areas of rock, snow, ice, and bodies of water larger than 1 ha, we estimated potential black bear habitat in Glacier NP was 3,439 km². During 2003, the year preceding our study, wildfires burned 566 km² in Glacier NP during an unusually active fire season (Fig. 1). Those burned areas created poor bear habitat during 2004. Glacier NP's 1,191 km of maintained trails were used extensively by bears and other wildlife to travel through the thick vegetation and rough terrain in Glacier NP.

Glacier NP was largely roadless and managed as wilderness; however, it received approximately 1.75 million visitors/year during our study. Adjacent to Glacier NP, lands were managed for multiple uses, including timber harvest, hunting, livestock production, and low-density residential development. All areas adjacent to Glacier NP had spring and autumn black bear hunting seasons except Waterton Lakes National Park, Alberta, Canada, which adjoined Glacier NP to the northeast.

METHODS

Field Methods

We used 2 concurrent noninvasive sampling methods to sample the bear population: baited hair traps and unbaited bear rubs (Fig. 1; Table 1; Kendall et al. 2008, 2009). No animals were handled for this research. Hair traps consisted of a single strand of barbed wire stretched 50 cm above ground around 3–6 trees to form a corral. At the center of the hair trap, we piled forest debris approximately 1 m high upon which we poured 3 L of a liquid scent lure that provided no food reward. We also hung an approximately 900-cm² cloth soaked in lure overhead to increase dispersion of the attractant. We established 1 hair trap/7 × 7-km cell for 14 days, after which all hair samples were collected and the trap was moved >1 km to decrease the potential for a waning response to the lure as bears learned that no food was available at hair traps (Boulanger et al. 2008; Kendall et al. 2008, 2009). Hair trapping began 15 June and ran for 4 14-day sessions, ending 18 August 2004.

During 3 June to 11 October 2004, we also surveyed a network of naturally occurring bear rubs found along maintained trails, forest roads, and other obvious animal travel routes. Bear rubs were recognized by evidence of rubbing behavior such as snagged hair, smoothed tree bark, and vegetation-free patches of ground at the base and/or bear trails leading to the rub (Kendall et al. 1992, 2008, 2009; Stetz et al. 2010). We affixed several 30-cm strands of barbed wire to each uniquely numbered bear rub to improve sample quality and collection efficiency. No lure was used to attract bears to these sites or to induce rubbing.

For both methods, a sample was defined as all hairs found on one set of barbs, although we also collected hairs found on lure piles from bears rolling in the lure. All samples were placed in paper envelopes pre-labeled with a uniquely numbered bar code. Locations of hair traps and bear rubs were recorded with handheld Global Positioning Units.

Lab Methods and Hair Sample Sub-Selection Criteria

Hair samples were stored on silica desiccating agent until analyzed at a laboratory that specialized in low-quantity and -quality DNA samples. We followed the protocols of Woods

et al. (1999), Paetkau (2003), and Kendall et al. (2009) to minimize genotyping errors. We initially attempted to extract DNA from all samples with ≥1 guard-hair follicle or 5 underfur hairs, and up to 10 guard hairs plus underfur. Qualifying samples were first analyzed at a single nuclear microsatellite (G10J) to determine species, which we later verified with assignment tests (Paetkau et al. 1995). The G10J marker also provided an index to sample quality; samples that failed at this stage were not likely to produce reliable genotypes and were put aside (Paetkau 2003).

We used 5 additional nuclear microsatellite markers to assign individual identities: G10B, G10H, G10L, MU59, and MU23. Previous genetic analysis of black bears in northwestern Montana indicated that this marker system had an estimated match probability (probability that 2 unique bears share an identical genotype at all 6 markers) of 0.000001. This equates to ≤1 pair of matching genotypes in a sample of 1,400 individual black bears in this region. For sex assignment of bears detected on bear rubs, we initially analyzed 1 sample/individual using the amelogenin marker (Ennis and Gallagher 1994, Pilgrim et al. 2005, Kendall et al. 2009). Based on the large proportion of samples from hair traps producing new genotypes, we ran gender on all hair trap samples, which gave sex determinations on 1–8 samples/individual.

To reduce genotyping costs, we subsampled black bear samples using the G10J locus, which is quite variable in our population (12 alleles detected). Because there is a greater chance of missing-related bears having the same G10J genotype, we analyzed an increasing number of hair samples with the same G10J genotype at the same site. For each hair trap, we used unique G10J genotypes from our species test to select the following number of samples for multi-locus genotyping: 1 sample/G10J genotype assigned to 1–4 samples, 2 assigned to 5–7 samples, 3 assigned to 9–10 samples, 4 assigned to 11–12 samples, and 8 assigned to 20 samples (Table 2). During collection at hair traps, we recorded the relative location of each sample on the wire. We then used this locational information to distribute our selection of samples to maximize detections of different bears (e.g., by avoiding adjacent samples with the same G10J genotype). For example, if 9 hair samples assigned to the

Table 1. Results of black bear hair collection in Glacier National Park, Montana, USA. Hair trap sampling was conducted 15 June to 18 August 2004; bear-rub sampling was conducted 3 June to 11 October 2004.

Session	No. of traps or bear rubs	No. of samples	No. of black bear samples ^a	No. of unique black bears ^b	
				<i>M</i>	<i>F</i>
Hair trap 1	83	1,054	438	60	57
Hair trap 2	84	948	303	46	46
Hair trap 3	86	854	197	16	33
Hair trap 4	84	920	128	16	29
Subtotal	337	3,776	1,066	122	150
Bear rubs	1,040	3,030	791	96	67
Total	1,377	6,806	1,857	173	186

^a The no. of black bear samples includes only those samples for which species determination was attempted and produced unequivocal black bear results and therefore underestimates the number of black bear samples collected.

^b The total number of black bear detected will not equal the sum of the rows as some individuals were detected in multiple sessions and/or sampling methods.

Table 2. Number of black bear hair samples used for multi-locus genotyping based on the number of samples with each G10J genotype per sampling location in our Glacier National Park, Montana, USA, study area in 2004.

Hair samples/G10J genotype/site	Frequency	
	Hair trap	Bear rub
1	369	293
2	8	53
3 ^a	39	19
4	6	6
5		1
8		1
Subtotal	526	493
Total no. of samples	1,019	

^a For example, there were 39 hair traps and 19 bear rub visits where 3 hair samples with the same G10J genotype were selected for multi-locus genotyping.

G10J genotype 187.201 at one trap, we analyzed 3 of them, distributed as well as possible. For bear rubs, we attempted multi-locus genotypes for the following number of samples per visit to each bear rub: 1 sample/G10J genotype assigned to 1–2 samples, 2 assigned to 3 samples, and 3 assigned to 4–5 samples. We did not record sample location information at bear rubs, so sample selection was random for each G10J genotype. Deviation from these criteria occurred when insufficient DNA remained to complete a multi-locus genotype and we substituted other nearby samples. Additionally, we attempted multi-locus genotyping of all samples assumed to be black bear based on visual inspection (jet black guard hairs had approximately 100% probability of being black bear; Paetkau 2003) from each bear rub survey or hair trap because we could not rule out that such samples represented a unique G10J genotype for that sampling point. Our sub-sampling approach was developed based on exploration of other datasets (i.e., Kendall et al. 2008, 2009) and likely resulted in very few missed detections. Genetic results were linked to field data via a relational database system with numerous integrated error-checks (Kendall et al. 2009).

Abundance and Density Estimation

We constructed a single encounter history for each black bear using the 4 hair trap occasions plus 1 occasion that included all detections at bear rubs pooled together. We pooled bear rub detections into a single occasion to eliminate structural zeros due to uneven sampling effort across rubs during the field season. Pooling bear rub detections reduces heterogeneity in capture probabilities and had a minimal effect on abundance estimates in a related grizzly bear analysis (G. White, Colorado State University, unpublished data). We used covariates to improve model fit, including the average distance of each bear to the edge of the sampling grid (DTE) to help model lower detection rates for bears that may spend less time on the grid (Boulanger and McLellan 2001, Kendall et al. 2009). We also developed individual-based sampling effort indices for both hair trap (HTE) and bear rubs (BRE). To quantify sampling effort, we first calculated the sex-

specific mean maximum distance moved (MMDM) for bears caught at >1 location (Dice and Clark 1953). We then calculated the average capture location for each bear (or the only capture location for bears detected a single time), which we buffered by a radius equal to the MMDM and one-half MMDM to define 2 model representations of the home range for each bear. We calculated the occasion-specific hair trap sampling effort for each bear as the count of hair traps located within the full and one-half MMDM idealized home ranges. Bear rub sampling effort was calculated similarly, but used the cumulative amount of sampling effort (i.e., the product of the no. of bear rubs and the no. of days they were available to collect hair within the MMDM and one-half MMDM ranges; Kendall et al. 2008, 2009) instead of a simple count of bear rubs as they were surveyed at varying intervals. This approach follows the theory that detection probability is a function of the distance from the center of an animal's home range (Efford 2004), although here we do not specify the shape of the detection function. We modeled males and females separately to allow for different responses to covariates and generated gender-specific abundance and density estimates.

We performed all standard mark-recapture analyses in Program MARK (v. 6.0, accessed 1 Dec 2010; White 2008) using Huggins closed population models (Huggins 1991) following the approach of Boulanger et al. (2008) and Kendall et al. (2008, 2009). We obtained abundance estimates as derived parameters and calculated 95% log-based confidence intervals about those estimates incorporating the minimum number of bears known to be alive on the study area (White et al. 2001). We evaluated relative support for *a priori* candidate models with the sample-size-adjusted Akaike Information Criterion for small sample sizes (AIC_c). We averaged estimates based on their support in the data, as indexed by AIC_c weights to account for model selection uncertainty (Burnham and Anderson 2002). We used the delta method to calculate confidence intervals on the total abundance estimate (Seber 1982).

Estimating density is often problematic because it is difficult to know the effective sampling area in the absence of radiotelemetry data, especially for animals capable of moving long distances (Efford 2004, Obbard et al. 2010). In addition to the DTE covariate, we investigated which sampling area assumption was best supported by our data by competing models with sampling effort covariates based on the full MMDM and one-half MMDM home ranges and without an effort covariate. We then used the model selection results from Program MARK to inform our estimate of effective sampling area. This approach allowed us to use our detection data to choose from these commonly used buffer values instead of arbitrarily selecting one or reporting multiple estimates (Soisalo and Cavalcanti 2006, Obbard et al. 2010). We therefore increased the study area by a distance equal to the most supported sampling effort covariate (one-half MMDM) to obtain our effective sampling area. We calculated sex-specific density as the model-averaged abundance estimate divided by the sex-specific effective sampling area. We used the delta method to derive

confidence intervals for total abundance and gender-pooled one-half MMDM buffer to estimate total density.

We also explored spatially explicit mark-recapture (Efford 2004, Borchers and Efford 2008) methods to estimate black bear density in Glacier NP. Because of the size of our dataset and the unknown performance of SECR models with bear rub detection data, we limited our analyses to relatively simple models including hair trap only, bear rub only, and combined detections to generate sex-specific density estimates. For all models, density (D) and sigma (σ) were modeled as sex-specific constants; g_0 was modeled as a constant for single-detector datasets, or as a function of sample type for the combined hair trap–bear rub datasets. For all models, we used a half-normal detection function, and a habitat mask buffer of 20 km for males and 15 km for females, with grid-point spacing set to 500 m. Instead of standard binary activity coding, we coded site usage as a measure of sampling effort similar to the covariate explained above, but for each bear rub for each occasion (Efford et al. 2013). This allowed us to use more of our sampling events than with standard closed population models; however, we did collapse bear rub sampling occasions 1–3 and 7–8 due to very low effort. This resulted in 4 hair trap occasions (as with the closed population models above) and 5 bear rub occasions. All SECR analyses were conducted using the R package “secr” (Efford et al. 2013).

RESULTS

Field Sampling and Genetic Analyses

During 15 June to 18 August 2004, we established and collected samples from 337 hair traps distributed in 7×7 -km cells in our Glacier NP study area during 4 14-day sessions (Fig. 1; Table 1). We collected 3,776 bear hair samples from hair traps, 1,066 of which were identified as black bear. From these, we selected 526 samples to attempt multi-locus genotyping. Of these, 75.9% ($n = 399$) produced individual assignments. We also collected bear hair from 4,040 collection visits to 1,040 bear rubs during 3 June to 11 October 2004. The average interval between collection visits was 18.5 days (SD = 10.6 days). From these we collected 3,030 bear hair samples, 791 of which were identified as black bear. We then sub-selected 493 samples to attempt multi-locus genotyping, 67.6% ($n = 333$) of which produced individual assignments. Hair trap samples assigned to 272 individuals (122 M, 150 F) and bear rub samples assigned to

163 individuals (96 M, 67 F) for 359 total unique genotypes (173 M, 186 F; Table 1). Of these 359, 74 (20.6%) were detected by both sampling methods (43 M, 31 F).

Microsatellite marker variability was calculated from 6-locus genotypes from 601 black bears detected during 2004 in our Glacier NP study area plus 10 km beyond the park boundary (excluding Canada). Mean observed heterozygosity across the 6 markers used for individual assignments was 0.831, with an average of 13.2 alleles/locus (Table 3). No locus significantly deviated from Hardy–Weinberg proportions (all $P > 0.07$). The probability of 2 randomly drawn individuals having the same multi-locus genotype (P_{ID}) was 1.09×10^{-8} , while the probability of siblings sharing a genotype (P_{SIB}) was 0.0018 (Table 3). The ratio of genotypes with 2 mismatched markers (2MM) compared with 1MM was approximately 22:1, which is considerably better than the 10:1 ratio suggested by Paetkau (2003) as indicative of an error-free dataset with adequate marker power. We repeated individual assignments with the 4 most variable loci in a larger dataset containing 1,001 black bear genotypes (including those used in this mark-recapture analysis); no discrepancies with our 6-locus genotypes were observed. We used the examining bimodality and difference in capture history tests in Program DROPOUT (McKelvey and Schwartz 2005) to detect and resolve any latent genotyping errors. Neither test found any evidence of errors in our data. Genotyping error rates were estimated at <1%/individual by Kendall et al. (2009), who conducted extensive blind testing of the laboratory and contracted a comprehensive review of methods by Dr. Pierre Taberlet (Universite Joseph Fourier, Grenoble, France). Blind testing also included 115 samples containing hair from >1 known, closely related individuals (e.g., parent–offspring pairs). No errors were detected, suggesting our field dataset is free of spurious individual assignments from hairs mixed from >1 bear. Our observed rate of mixed samples was <2%, consistent with previous studies in this area (Kendall et al. 2009). As we targeted samples with strong single-locus genotypes during the sub-selection process, it is likely that our error rates are even lower for this analysis (D. Paetkau, Wildlife Genetics International, personal communication).

Abundance and Density Estimation

Our model-averaged super-population abundance estimate was 603 (95% CI = 522–684) black bears based on 316-hair trap and 307 bear rub detection events of 359 individuals

Table 3. Variability of microsatellite markers used in assigning individuals identities of black bears in our Glacier National Park, Montana, USA, study area, in 2004. H_E : expected heterozygosity; H_O : observed heterozygosity; A : no. of alleles per locus; P_{ID} : probability of identity; P_{SIB} : probability of identity given siblings.

Marker	H_E	H_O	A	P_{ID}	P_{SIB}
G10J	0.850	0.862	12	0.335	0.038
G10B	0.796	0.812	10	0.369	0.070
G10H	0.899	0.912	21	0.305	0.019
G10L	0.852	0.854	15	0.333	0.034
MU59	0.805	0.807	10	0.363	0.063
MU23	0.743	0.739	11	0.404	0.101
	0.824	0.831	13.2	1.09×10^{-8}	0.0018

within Glacier NP (Table 4). We estimated that there were 268 males and 335 females (95% CIs = 227–310 and 269–400, respectively), which is functionally an even sex ratio (56% F). Models with the effort covariate for both sampling methods measured in the area buffered by one-half MMDM around each bear's average capture location were most supported based on AIC_c values (Table 5). The most supported model with the full MMDM buffer was 262.3 AIC_c units below our best model; models without any sampling effort covariate were 360.8 AIC_c units below our best model. Models with sex and time interactions were more strongly supported than were models with additive effects or no sex effect. The second highest ranked model ($\Delta AIC_c = 1.0$) included DTE, suggesting modest violation of geographic closure.

We used the above model selection results to inform our decision on how large a buffer to use around our sampled area to estimate the effective sampling area for density estimation. Based on a one-half MMDM buffer of 3.8 km, the effective sampling area for males was 5,284 km². Using this area yielded a density estimate of 5.1 (95% CI = 4.3–5.9) males/100 km² (Table 4). For females, the effective sampling area based on a one-half MMDM buffer of 1.6 km was 4,591 km². The corresponding female density estimate was 7.3 (95% CI = 5.9–8.7) bears/100 km². Combined, we

estimated density at 11.4 black bears/100 km² (95% CI = 9.9–13.0) using the more conservative male buffer distance. When we subtracted putative non-habitat (rock, ice, lakes >1 ha) from Glacier NP buffered by male one-half MMDM, density rose to 13.3 black bears/100 km² (95% CI = 11.5–15.0).

Model-averaged capture probabilities showed a negative trend for both male and female black bears across our 4 hair trap sessions, with females having consistently higher capture probabilities (Fig. 2; $F = 0.26$, 0.06; $M = 0.20$, 0.05 for sessions 1 and 4, respectively). Females and males had nearly identical estimated capture probabilities at bear rubs (=0.302 and 0.301, respectively). We did not observe temporal trends in bear rub detection probabilities.

Density estimates from SECR models using the combined detector data were remarkably similar to those derived from combined-data closed population models with a one-half MMDM buffer for both males and females (SECR: male $\hat{D} = 4.8/100 \text{ km}^2$ [95% CI = 4.0–5.7], female $\hat{D} = 7.2/100 \text{ km}^2$ [95% CI = 6.0–8.7]; Fig. 3). Our SECR estimate for the total population density was 12.0 black bears/100 km² (95% CI = 10.0–14.4). Based on SECR results, we estimated that there were 197 (95% CI = 164–234) male and 295 (95% CI = 246–357) female black bears in Glacier NP during our study.

Table 4. Model-averaged estimates of black bear abundance in Glacier National Park, Montana, USA, 2004. Density estimates are based on buffering the sampled area (4,080 km²) by the sex-specific and total one-half mean maximum distance moved (MMDM); 95% confidence intervals incorporate only the variance in abundance estimates. These estimates include areas that are not likely to be used by black bears (rock, ice, lakes >1 ha). $\hat{N}$ = estimated abundance; $\hat{W}$ = estimated effectively sampled area.

No. of bears detected	Abundance			Effectively sampled area				Density		
	$\hat{N}$ (SE)	CV ($\hat{N}$)	95% CI		One-half MMDM (SE; km)	$\hat{W}$ (km ²)	bears/100 km ²	95% CI		
			Lower	Upper				Lower	Upper	
M	173	268.3 (21.1)	7.87%	226.9	309.7	3.78 (0.35)	5,283.9	5.08	4.29	5.86
F	186	334.9 (33.4)	9.98%	269.4	400.5	1.58 (0.18)	4,590.9	7.30	5.87	8.72
Total	359	603.2 (41.4)	6.87%	522.0	684.4	2.88 (0.23)	5,283.9	11.42	9.88	12.95

Table 5. Model-selection results for estimates of black bear abundance in our 4,080-km² Glacier National Park, Montana, USA, study area, 2004. AIC_c , Akaike Information Criterion.

Model ^a	AIC_c	ΔAIC_c	AIC_c wt	Model likelihood	No. of parameters	Deviance
HT:(T + Sex × .5HTE) BR:(Sex × .5BRE)	1,321.918	0	0.518	1	15	1,291.648
HT:(T + Sex × .5HTE + DTE) BR:(Sex × .5BRE + DTE)	1,322.892	0.975	0.318	0.614	16	1,290.586
HT:(T + Sex × .5HTE) BR:(Sex + .5BRE)	1,324.764	2.847	0.1248	0.241	14	1,296.528
HT:(t × Sex × .5HTE) BR:(Sex × .5BRE)	1,328.535	6.618	0.019	0.037	20	1,288.062
HT:(t × Sex × .5HTE + DTE) BR:(Sex × .5BRE + DTE)	1,329.558	7.640	0.011	0.022	21	1,287.036
HT:(t × Sex × .5HTE) BR:(Sex + .5BRE)	1,331.311	9.394	0.005	0.009	19	1,292.883
HT:(t × Sex × .5HTE + DTE) BR:(Sex + .5BRE + DTE)	1,332.388	10.47	0.003	0.005	20	1,291.914
...						
HT:(t × Sex + Sex × HTE) BR:(Sex × BRE)	1,590.781	268.864	0	0	14	1,562.545
HT:(t × Sex × HTE) BR:(Sex × BRE)	1,596.155	274.237	0	0	20	1,555.681
...						
HT:(t × Sex) BR:(Sex)	1,689.354	367.437	0	0	10	1,669.231
HT:(t × Sex + DTE) BR:(Sex)	1,691.058	369.140	0	0	11	1,668.910

^a HT, hair trap; T, linear time; t, time; HTE, hair trap sampling effort; BR, bear rub; DTE, distance to edge of sampling grid; BRE, bear rub sampling effort. For both sampling effort covariates, a prefix of .5 indicates we used one-half mean maximum distance moved (MMDM) buffer around the average capture location to estimate sampling effort; no prefix indicates the full MMDM buffer.

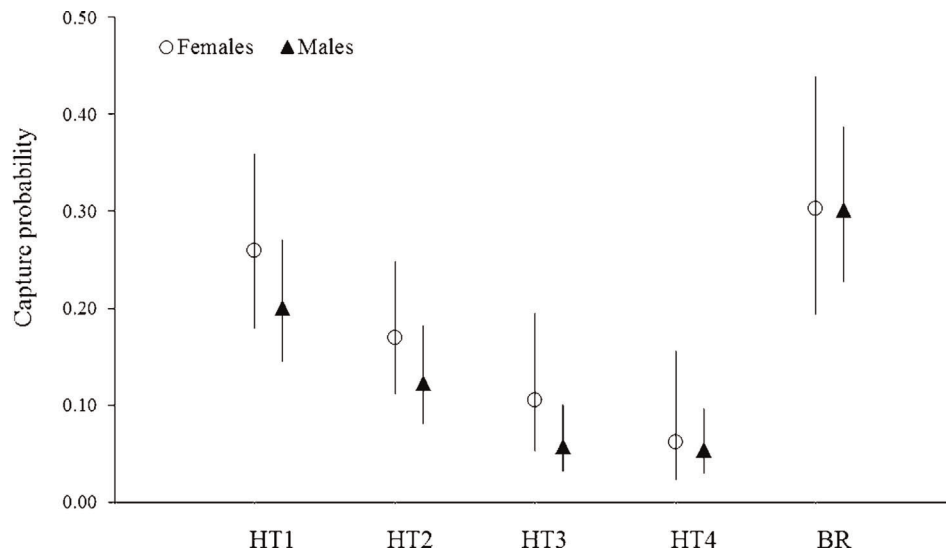


Figure 2. Capture probabilities of black bears from hair traps (HT) and bear rubs (BR) surveyed in our Glacier National Park, Montana, USA, study area. Hair trapping was conducted from 15 June to 18 August 2004; bear rub surveys from 3 June to 11 October 2004.

Hair trap-only SECR models produced slightly higher estimates than combined-data models for both sexes, with male $\hat{D} = 5.5/100 \text{ km}^2$ (95% CI = 3.8–8.0) and female $\hat{D} = 8.2/100 \text{ km}^2$ (95% CI = 5.5–12.1). Female black bears had consistently higher detection rates than males with both detection types as well as the combined detector dataset (Table 6). For both sexes, detection rates were lower for bear rubs than hair traps; however, using detections from traps

and rubs together resulted in more precise density estimates than did either detection method alone (Fig. 3).

DISCUSSION

Population abundance and density estimates are 2 of the parameters of greatest value to wildlife managers, yet they remain difficult to obtain for large carnivores that occur at low densities, are cryptic, and often inhabit regions that are

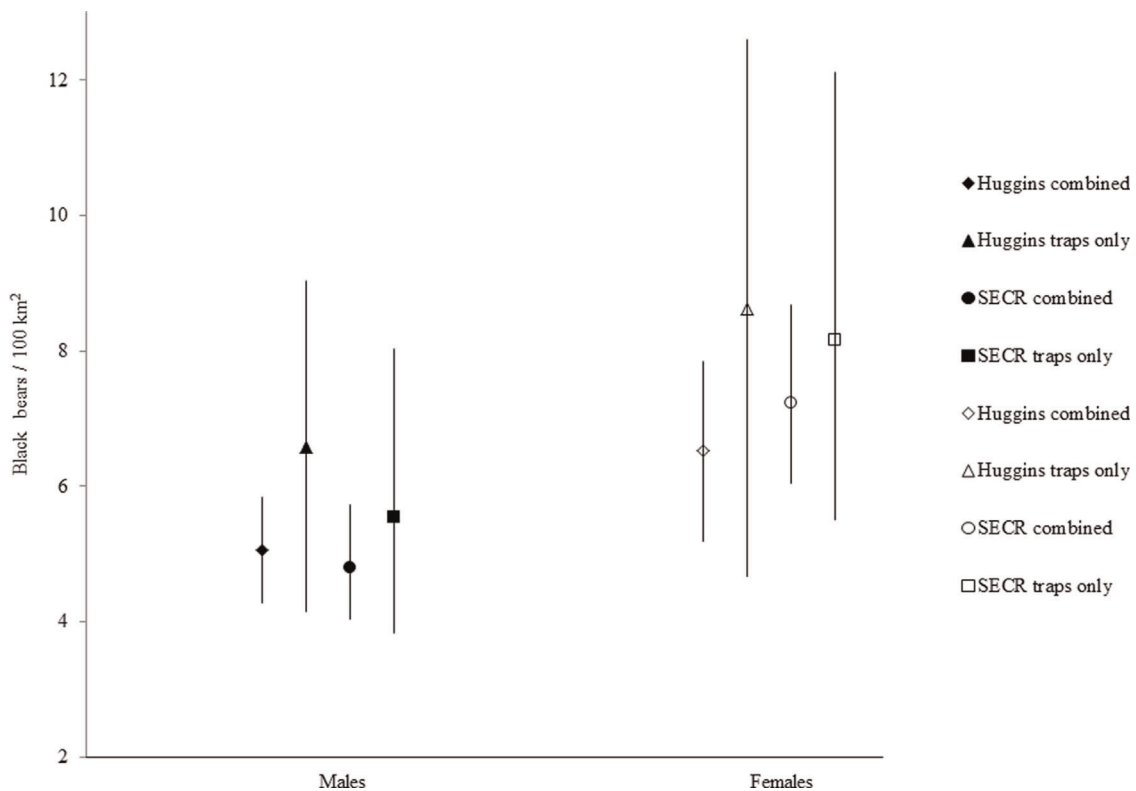


Figure 3. Density estimates of black bears from hair trap-only and combined hair trap and bear rub detection data using Huggins closed population models with a buffer equal to one-half mean maximum distance moved and from spatially explicit capture–recapture (SECR) models with combined and hair trap-only detection data for black bears in Glacier National Park, Montana, USA, 2004. Error bars represent 95% confidence intervals.

Table 6. Black bear detection function estimates from spatially explicit capture–recapture models for our 4,080-km² Glacier National Park, Montana, USA, study area, 2004.

Dataset	$\hat{g}_0^a$	SE ($\hat{g}_0$)	95% CI		$\hat{\sigma}^b$	SE ($\hat{\sigma}$)	95% CI		Home range radius (m)
			Lower	Upper			Lower	Upper	
M combined	0.005	0.001	0.004	0.007	4,511.402	230.655	4,081.506	4,986.578	11,042
M hair trap only	0.004	0.001	0.002	0.007	3,824.449	392.893	3,128.619	4,675.036	9,361
M bear rub only	0.001	<0.001	0.001	0.001	3,423.092	247.648	2,971.103	3,943.841	8,379
F combined	0.021	0.003	0.016	0.027	2,035.703	110.527	1,830.346	2,264.102	4,983
F hair trap only	0.003	0.001	0.002	0.004	1,463.292	114.634	1,255.306	1,705.737	3,582
F bear rub only	0.012	0.004	0.006	0.023	1,934.136	205.329	1,571.723	2,380.115	4,734

^a Detection probability at the activity center.

^b Shape of the half-normal detection function. Home range radius calculated in R as $(qchisq(0.95,2)^{0.5}) \cdot (\sigma)$ (Noss et al. 2012).

difficult to access (Krebs 1985, Turchin 1998, Nichols et al. 2000, Efford 2004). Density in particular is difficult to estimate for geographically open populations, and even more so for wide-ranging species such as American black bears. To account for closure violation when calculating density, it is common to buffer the sampled area by some distance related to the observed movements of individual animals, or to adjust abundance estimates based on the proportion of time a radio-instrumented sample of the population spends on the study area (Soisalo and Cavalcanti 2006, Reppucci et al. 2011). Given the absence of telemetry data, we used our bear detection data and information theoretic methods to guide buffer-size selection among 2 common values. Although this method is perhaps less accurate than using telemetry data, it provides an improvement over arbitrary selection of a buffer size that could allow more reliable comparisons across populations as well as a more repeatable approach for further research on this population.

Recently, spatially explicit density-estimation methods have been developed that avoid the need to apply a buffer to the sampled area to estimate the effectively sampled area. Both maximum likelihood and hierarchical Bayesian approaches claim to produce more accurate and precise estimates of density than do models that do not incorporate locational information. Both spatial approaches have inherent assumptions, however, that may be difficult to meet, such as random distribution of circular home range centers (Kery et al. 2010, Obbard et al. 2010, Ivan et al. 2013). Although not yet proven with all sampling designs, SECR methods may present advantages over buffer-corrected, closed-population abundance estimates in certain systems. This is particularly true for studies that have small sample sizes, and study areas with large edge:area ratios that are small with respect to the study animals' home ranges (Obbard et al. 2010).

Empirical comparisons often report that SECR methods produce much lower density estimates compared with those using abundance estimates and buffers based on observed animal movements (e.g., Obbard et al. 2010, Noss et al. 2012). Conversely, Reppucci et al. (2011) reported that density estimates of Andean cats (*Leopardus jacobita*) in northwestern Argentina in 2007 were, as in our study, nearly identical for a SECR model and standard closed-population abundance estimates with a one-half MMDM buffer. In fact, the choice of closed population model can have equal or

greater influence on density estimates than the choice of buffer size (Reppucci et al. 2011).

Our study differs from most using SECR methods in several ways. Our study area was large relative to the study species' home range. Our sampled area was 66 times larger than 95% kernel home ranges documented near our study area from 11 Global Positioning System-collared male black bears (=61.7 km²; Chilton-Radandt 2006). Further, a large number of individuals were detected ($N = 359$), and we had relatively high sampling effort using 2 concurrent, independent methods. Finally, had we used the full MMDM buffer, our overall density estimate would have only changed from 11.4 to 9.2 black bears/100 km². This relatively small change in density associated with more than doubling the area included in the buffer, reinforces the value of robust abundance estimates that account for variation in capture probability associated with time and gender differences, which are often not included in SECR models because of sample size limitations (Obbard et al. 2010).

Because of the challenges of using spatially explicit models as currently formulated with datasets as computationally demanding as ours, we explored relatively simple SECR models and compared their density estimates with those derived from closed population models. Estimates based on hair trap only or combined hair trap and bear rub detections were similar across model types for both males and females. Our combined-data estimates were slightly lower and consistently more precise than hair trap-only estimates (Fig. 3). This concurrence of results makes us confident that our estimates are likely unbiased. Spatially explicit capture–recapture density estimates from bear rub-only detections were notably lower than hair trap or combined data, which is consistent with previous attempts to estimate abundance with bear rub data (Boulanger et al. 2008) and may be because, at least in part, the rubs we monitored were on trails and roads and they may not have been available to all individuals. Bear rub sampling methods present numerous logistical advantages over other types of noninvasive genetic sampling (Kendall et al. 2009, Stetz et al. 2010), but little is known about bear rubbing behavior and use of rub detection data in SECR models. A better understanding of why bears rub will be helpful in developing and applying SECR methods to these and similar data.

Our findings of 11.4 bears/100 km² establishes the first baseline estimate of black bear density for the Glacier NP,

Montana, and is consistent with published densities for 14 interior populations sympatric with grizzly bears ($=16.4/100 \text{ km}^2$, range = $0.9\text{--}45/100 \text{ km}^2$; [Mattson et al. 2005](#)). It is difficult to place too much confidence in direct comparisons among populations, however, given the range in methods used to determine the effectively sampled area for density estimates and frequent lack of estimates of precision. Studies often do not specify what portion of their population is estimated (e.g., whether or not it includes dependent offspring). Observations made from remote cameras suggest that black bears of all ages are detected in both of our sampling methods; therefore, density estimates should pertain to the entire population. This is consistent with results of a grizzly bear study in this same area ([Kendall et al. 2009](#)), in which bears with ages known from live handling were used to conclude that bears of all sex-age classes were available for detection in hair traps and at bear rubs.

We estimated that black bear density is approximately twice the estimated grizzly bear density in Glacier NP. This is far below published ratios for sympatric, intermountain populations of black:grizzly bears (8–11 times; [Mattson et al. 2005](#)). Qualitative interpretation of detection events suggested that black bears are selecting for lower elevation areas at a coarse scale, because fewer bears were detected near the interior of Glacier NP, generally along and east of the Continental Divide. This is consistent with black bear ecology, because these areas contain more alpine areas and less forest cover. Further, the lower number of black bear detections in Glacier NP's interior coincides with higher numbers of grizzly bear detections ([Kendall et al. 2009](#)). When we removed areas not considered black bear habitat, (i.e., ice, barren, alpine, and open water), black bear density in Glacier NP rose from 11.4 to 13.3 bears/ 100 km^2 .

Noninvasive genetic sampling has been used successfully to estimate black or grizzly bear abundance in numerous studies across North America (e.g., [Woods et al. 1999](#), [Dreher et al. 2007](#), [Kendall et al. 2009](#), [Tredick and Vaughan 2009](#), [Obbard et al. 2010](#)). Although most noninvasive genetic sampling studies are designed to estimate a single parameter for a single species, the data we used in this study were collected as part of a much larger project to estimate grizzly bear abundance for the 32,000- km^2 Northern Continental Divide Ecosystem ([Kendall et al. 2009](#)). We estimate that 90% of the cost of producing the density estimates that we report here (related mainly to field labor and initial genetic analyses) was covered by the original grizzly bear study. With proper design, such as using multiple detection methods, multi-species sampling protocols may substantially increase the efficiency and affordability of producing reliable estimates for multiple populations.

To obtain adequate capture probabilities, black bear DNA-based population abundance studies typically use a denser sampling grid to distribute hair traps than the $7 \times 7\text{-km}$ grid we used (e.g., 1 km^2 , [Tredick and Vaughan 2009](#); however, these populations had considerably smaller home ranges than did black bears in northwestern MT). We were nonetheless able to obtain a precise estimate ($\text{CV}(\hat{N}) = 6.9\%$; Table 4) because our use of a secondary sampling method increased

sample coverage and use of individual covariates helped explain capture probability heterogeneity as a function of sampling effort. Multiple data sources have been used in similar bear studies to improve sampling coverage and precision of estimates ([Dreher et al. 2007](#); [Boulanger et al. 2008](#); [Kendall et al. 2008, 2009](#)). Our sample size was also large enough to model the decline in capture probabilities by sex and time (Fig. 2).

The combined density of black and grizzly bears in our study area suggests high-quality bear habitat for an intermountain region, although some authors have argued that density should not be considered as the sole indicator of habitat quality. Instead, habitat quality should be viewed as a product of density and fitness ([Van Horne 1983](#), [Mosser et al. 2009](#), [Perot and Villard 2009](#)). A single estimate of density, although valuable in establishing baselines to which future research can be anchored, provides little information about population or metapopulation processes. Monitoring population growth rates, immigration–emigration rates, and genetic structure would provide more insight into the role that Glacier NP plays in the greater black bear population. Integrating the results from multiple sampling methods, such as hair traps and bear rubs, has potential for improving the efficiency of monitoring trends in those population parameters. The black bear capture probabilities we observed at bear rubs (0.30 for M and F) may provide an opportunity to monitor black bear population growth rates and other trends as explored for grizzly bears in this region ([Stetz et al. 2010](#)). Use of bear rubs has been documented in other black bear populations (e.g., [Burst and Pelton 1983](#)); however, we recommend pilot studies to estimate capture probabilities before using this approach elsewhere.

MANAGEMENT IMPLICATIONS

Use of multiple independent sampling methods in conjunction with covariates to help explain detection heterogeneity may improve estimates at less cost than increasing sampling intensity. When telemetry data are not available, use of an individual-level sampling effort covariate in a competing models framework can lead to more reliable density estimates. Further, we propose that this approach provides insight into the area used by a geographically open population. SECR methods continue to improve, and we recommend their use when sampling is adequate and matches the biology of the study population.

The combined densities of black and grizzly bears in this area suggests high-quality bear habitat, although information on population growth rates is required to truly evaluate habitat quality. Multi-species analyses offer considerable cost savings over single-species studies, and may improve our understanding of how grizzly bear populations recover or recolonize when black bear populations with significant niche overlap are already established.

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