The Journal of Wildlife Management 80(2):332–346; 2016; DOI: 10.1002/jwmg.1002

Research Article

Estimation of the Brown Bear Population on the Kenai Peninsula, Alaska

JOHN M. MORTON,[1] *Kenai National Wildlife Refuge, U.S. Fish and Wildlife Service, P.O. Box 2139, Soldotna, AK 99669, USA*
GARY C. WHITE, *Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins, CO 80523, USA*
GREGORY D. HAYWARD, *Alaska Region, U.S. Forest Service, 161 East 1st Avenue, Anchorage, AK 99501, USA*
DAVID PAETKAU, *Wildlife Genetics International, P.O. Box 274, Nelson, BC, Canada V1L5P9*
MARTIN P. BRAY, *Chugach National Forest, U.S. Forest Service, 161 East 1st Avenue, Anchorage, AK 99501, USA*

ABSTRACT The brown bear population on the Kenai Peninsula, Alaska, has not been empirically estimated previously because conventional aerial methods over this heavily forested landscape were infeasible. We applied a rapid field protocol to a DNA-based, mark-recapture approach on a large and tightly bounded sample frame to estimate brown bear abundance. We used lure to attract bears to barbed wire stations deployed in 145 9-km × 9-km cells systematically distributed across 10,200 km^2 of available habitat on the Kenai National Wildlife Refuge and Chugach National Forest during 31 consecutive days in early summer 2010. Using 2 helicopters and 4 2-person field crews, we deployed the stations during a 6-day period and subsequently revisited these stations on 5 consecutive 5-day trap sessions. We extracted DNA to identify individual bears and developed capture histories as input to mark-recapture models. Combined with data from radio-telemetered bears, ≥243 brown bears were alive on the Kenai Peninsula in 2010, but we used only 99 females and 104 males in modeling. We used Akaike's Information Criterion selection and model averaging to estimate 428 (95% lognormal CI = 353–539) brown bears (including all age classes) on the study area. Despite low recaptures rates, we achieved reasonable precision by ensuring geographic and demographic population closure through a spatially comprehensive sample frame and very short sampling window. We reduced bias by including information from rub trees and telemetered females (i.e., occasion 0). Extrapolating the density estimate of 42 bears/1,000 km^2 of available habitat on the study area to the Kenai Peninsula suggests a peninsula-wide population of 582 brown bears (95% lognormal CI = 469−719). Despite a density estimate that is low compared to other coastal brown bear populations in Alaska and genetic evidence that suggests this peninsular population is insular, harvest management has been liberalized since 2012. We recommend this population estimate serve as the benchmark for future management. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS Alaska, brown bear, genetics, hair DNA, Kenai Peninsula, mark-recapture, population, Pradel model, *Ursus arctos*.

The grizzly or brown bear (*Ursus arctos*) population on the Kenai Peninsula in south-central Alaska is a keystone species (Interagency Brown Bear Study Team [IBBST] 2001). Brown bears on the Kenai Peninsula influence plant distribution and abundance through seed dispersal in feces, transport marine-derived nutrients into terrestrial ecosystems through salmon consumption (Hilderbrand et al. 1999*a*), and possibly regulate ungulate populations through neonatal predation under certain conditions (Zager and Beecham 2006). Brown bears are recognized as a source of enjoyment by residents and visitors, as a source of revenue for commercial wildlife viewing and hunting charters, and as a wilderness icon (Alaska Department of Fish and Game [ADFG] 2000).

Received: 3 October 2014; Accepted: 14 September 2015

[1]*E-mail: john_m_morton@fws.gov*

The 16-km wide isthmus that separates the 24,300-km^2 Kenai Peninsula from the adjacent mainland restricts brown bear emigration and immigration (Jackson et al. 2008). Using microsatellite and mitochondrial DNA (mtDNA), Jackson et al. (2008) verified that the Kenai brown bear population is insular, reporting lower mtDNA haplotypic diversity than most other brown bear populations on mainland Alaska but similar to other peninsular populations.

The Kenai Peninsula is also one of the fastest urbanizing areas in Alaska, with approximately 10,000 new residents added every decade since 1960 (http://www.census.gov/population/cencounts/ak190090.txt, accessed 23 Sep 2015). Over these same 5 decades, brown bears killed in defense of life or property (DLP) on the Peninsula have increased from <1/year in the 1960s, to 5/year in the 1990s, and to 16/year since 2000 (Suring and Del Frate 2002, Zulueta 2012). Legal harvest of brown bears has varied with hunting regulations over this same period, ranging from 0/year during much of the past decade to 64 individuals in 2014. In 2013, the year of

highest reported human-caused mortality, 46 brown bears were harvested and 25 were killed by DLPs, of which 23 were adult females (ADFG, unpublished data). The demographic significance of increasing human-caused mortality is uncertain because the population size has not been empirically estimated and, at the time this study was implemented, confidence bounds on estimates of the intrinsic rate of population growth (λ) overlapped 1.0 (IBBST 2001, Farley 2010).

In 1998, the brown bear population on the Kenai Peninsula was designated as a population of special concern by the State of Alaska because it was "vulnerable to a significant decline due to low numbers, restricted distribution, dependence on limited habitat resources, or sensitivity to environmental disturbance" (ADFG 2000:vi). The IBBST recognized that a rigorous estimate of the brown bear population on the Kenai Peninsula was desirable (IBBST 2001). The elimination of the special listing by the State in 2011 and subsequent efforts to liberalize harvests of brown bears in Alaska (Miller et al. 2011) created a sense of urgency among some management agencies. However, unlike many other areas in Alaska that support brown bears, the Kenai Peninsula is heavily forested, making aerial estimation methods difficult because of low detectability. Consequently, the IBBST focused on the potential use of DNA-based mark-recapture methods for estimating brown bears.

Two spatial sampling schemes for collecting bear hair were considered: a stream-based approach that would likely result in higher capture rates (Harris et al. 2013) and a grid-based approach that would likely result in better adherence to mark-recapture model assumptions. In the stream-based approach, hairs are snagged in break-away snares that are set along riparian corridors during salmon runs (Beier et al. 2005). In the grid-based approach, bears are attracted by lures to hair-snagging stations established throughout the sampling area (Mowat and Strobeck 2000, Poole et al. 2001, Kendall et al. 2008). The former approach was initially pursued by the IBBST but dismissed after cost ($\leq$\$2.5 million) and duration ($\geq$3 years) were evaluated and did not meet management goals.

We chose to apply the DNA-based, mark-recapture approach to a grid-based design to estimate brown bear abundance because it was less expensive, more rapid, and more closely met critical assumptions of demographic and geographic closure than the stream-based approach. Our specific study objectives were to estimate the brown bear population with 95% confidence bounds $\pm$ 25% of the true number (N) on the Kenai National Wildlife Refuge (KENWR) and Chugach National Forest (CNF) at an acceptable cost and in a time-frame useful to decision makers. Secondary objectives were to determine the sex ratio and the minimum brown bear population occurring on KENWR and CNF.

STUDY AREA

The Kenai Peninsula juts into the Gulf of Alaska, surrounded on the west by the Cook Inlet and on the east by Prince William Sound (Fig. 1). Elevations range from sea level to 2,015 m in the Kenai Mountains. Climate on the eastern side of the peninsula is maritime influenced, with mean annual temperature and precipitation of 1.3° C and 173 cm, respectively (Seward, AK, http://www.wrcc.dri.edu/, accessed 25 Sep 2015). Climate in the western rain shadow of the mountains is more continental with an active fire regime (Berg and Anderson 2006) and mean annual temperature and precipitation of 1.1° C and 48 cm, respectively (Kenai, AK, http://www.wrcc.dri.edu/, accessed 25 Sep 2015). Biodiversity is unusually high for this latitude because of the juxtaposition of 2 biomes on the peninsula: the northern fringe of Sitka spruce-dominated (*Picea sitchensis*) coastal rainforest in the east, and transitional boreal forest in the west composed of white (*P. glauca*), black (*P. mariana*), and Lutz (*P. X lutzii*) spruces with an admixture of aspen (*Populus tremuloides*) and birch (*Betula neoalaskana*; Table 1). Extensive *Sphagnum* peatlands are interspersed among spruce in the Kenai Lowlands on the northwestern peninsula (Klein et al. 2005). Lichen-dominated tundra replaces mountain hemlock (*Tsuga mertensiana*) and sub-alpine shrub above treeline (Dial et al. 2007).

The study area included 11,700 km^2 of the peninsula on lands administered by KENWR and CNF (Figs. 1 and 2). The area was bounded in the north and northwest by Cook Inlet and Turnagain Arm, in the east by the Sargent Icefield, in the south by the Harding Icefield and Wosnesenski–Grewingk Glacier complex, and in the west by KENWR boundaries. The study area included 127 (1,390 km) of 250 named streams identified on the Kenai Peninsula (http://www.adfg.alaska.gov/sf/SARR/AWC/, accessed 23 Sep 2015). With the exception of the southwest corner of the peninsula (i.e., south of Caribou Hills), the study area effectively included all known and modeled areas of brown bear habitation on the peninsula (IBBST 2001).

METHODS

Hair Sampling

We noninvasively collected brown (and black; *Ursus americanus*) bear hairs at barbed-wire stations subjectively placed within 145 9-km $\times$ 9-km cells systematically arrayed across the study area (Fig. 2). After an initial 6-day deployment period, we employed a rotating panel design in which we revisited 5 panels of 29 cells each on 5 consecutive 5-day trap sessions. Two-person field crews, transported by 2 Bell 206-B Jet Ranger helicopters (Bell, Fort Worth, TX), visited all cells over 31 consecutive days from 1 June to 1 July 2010. Field crews and helicopters were stationed in Soldotna and Moose Pass (Fig. 1).

Using expert judgment (see criteria below), we a priori selected primary and secondary sites within each cell to place hair stations; we frequently adjusted the final coordinates in the field to better reflect in situ conditions. If we did not obtain hair samples by the end of the third trap session, we moved the trap to another site within the cell or added a second trap to the cell. In addition to hair samples collected at stations on the grid, we supplemented sampling with hair collected at a permitted black bear baiting station (for

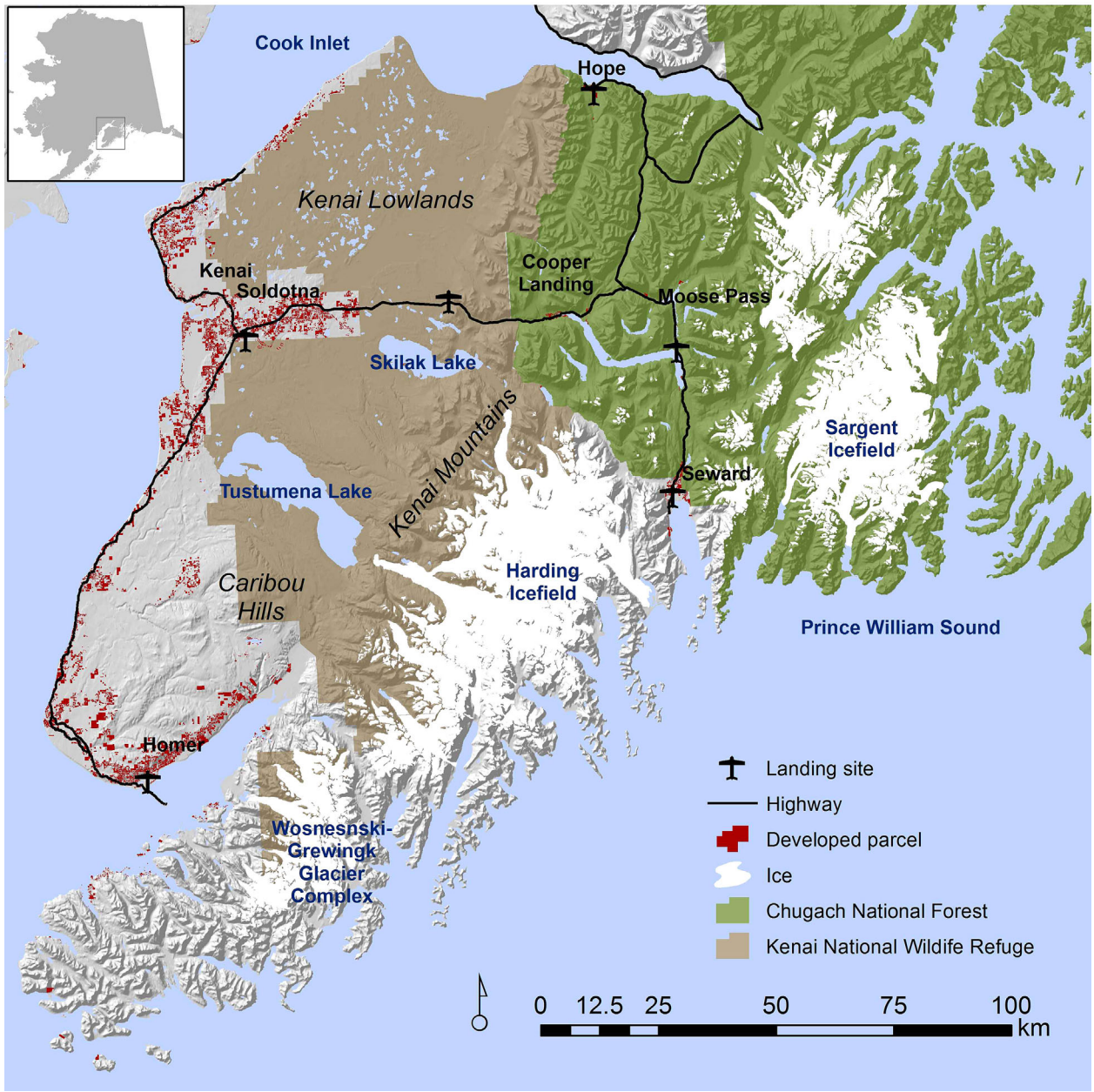

Figure 1. The location of Kenai National Wildlife Refuge and Chugach National Forest in relation to significant topographic features on the 24,300-km^2 Kenai Peninsula, Alaska, USA, and 6 landing sites for refueling 2 helicopters.

hunting), on rub trees, and from live bears handled during collaring operations incidental to this study.

Using a geographic information system, we eliminated all lands from sampling that were restricted by the ADFG for black bear baiting: no baiting ≤1.6 km of any residence, including seasonally occupied dwellings, developed recreational facilities, or campgrounds; no baiting ≤400 m of any publicly maintained road, trail, or the Alaska Railroad; and no baiting ≤400 m from the shoreline of the Kenai, Kasilof, and Swanson rivers (including Kenai and Skilak lakes). These buffered (mostly linear) areas constituted 16% of the study area, mostly in relatively high human use areas.

We used the following ranked criteria to a priori select 2 locations for hair sampling stations within each cell from digital orthoquads (DOQs): 1) adequate space for helicopter access; 2) adequate distance from trails, cabins, or roads; 3) riparian or wetland corridors; 4) other potential travel corridors associated with discontinuity between vegetation associations, avalanche chutes, shoulders between peaks, or ridges; and 5) other things being equal, ensure spatial separation among sites within a cell.

We sampled hair from bears that stepped over or crawled under barbed wire to investigate a simulated cache laced with lure (Mowat and Strobeck 2000). At each station, we strung 2 30-m-long double-stranded barbed wires around ≥3 trees or rebar stakes to approximate an equilateral triangle at 2 heights (20–30 and 60–70 cm above ground) to increase the likelihood of sampling adult and younger bears. We piled logs, rocks, litter, and other debris in the center of these hair stations to simulate a cache. We used ≥3 liters of fermented 3

Table 1. Estimated percent (%) landcover of the 1,174,500-ha study area and 2,433,800-ha Kenai Peninsula based on a 2006 supervised classification of LANDSAT imagery.

Landcover types	Study area	Kenai Peninsula
Alpine	16.7	11.9
Mixed forest	13.8	9.6
Black spruce	11.2	6.2
Alder (*Alnus* spp.)	10.3	9.8
White/Lutz/Sitka spruce	8.9	9.7
Snow/Ice	6.5	20.1
Barren/Rock	6.3	5.2
Lake	5.9	4.0
Wetland—graminoid	3.6	3.6
Mountain hemlock	3.3	2.5
Mixed conifer	2.4	3.8
Paper birch	2.3	1.7
Sparsely vegetated	1.6	1.8
Willow (*Salix* spp.)	1.2	1.7
Barren—wet	1.0	2.1
Herbaceous	0.8	0.9
Stream	0.8	0.7
Wetland—shrub	0.7	1.0
Other shrub	0.6	0.7
Mixed deciduous	0.5	0.4
Alder/Willow	0.4	0.5
Black cottonwood (*Populus trichocarpa*)	0.4	0.3
Urban/cultural	0.3	0.6
Aspen	0.2	0.2
Wetland—halophytic	0.2	0.9
Estuarine	0.0	0.1

parts cow blood (The Beef Shop, Centralia, WA) to 1 part unprocessed fish oil (Kodiak Fishmeal Company, Kodiak, AK) as lure per station per visit. We used other commercial lures (e.g., fruit extract, spice oils, anise) to augment the cow blood-fish oil mixture. We posted signs to warn and inform public who may have accidentally encountered these sites.

We collected all hair with forceps and gloves, and placed samples in coin envelopes using 1 envelope/barb cluster. Each coin envelope was bar-coded (Linton Co., Meridian, GA) and labeled with station identification, date, barb number, and location (upper or lower strand). We burned barbs with a propane torch to remove any remaining hair (i.e., DNA) after collection. Hair was dried overnight in opened envelopes and stored at room temperature with desiccant.

Genetic Analysis

Bear species identification, individual genotyping, and sex determination from DNA in hairs were conducted by Wildlife Genetics International Inc. (Nelson, BC) following quality control methods specified in Paetkau (2003) and validated through blind testing (Kendall et al. 2009). To reduce costs, we excluded samples from genetic analysis if they contained no guard hairs with roots and <5 underfur hairs, or if they were clearly from ungulates based on appearance. We also excluded >5,000 guard hair samples that were jet black along their entire length because we felt they could be reliably identified as originating from black bears. We extracted DNA from the remaining samples using Qiagen DNeasy tissue kits (Qiagen, Valencia, CA), with the target of using 10 guard hair roots if available. For guard hairs, we identified root bulbs under a microscope and used the bottom 5–10 mm of the hair for extraction. For underfur, where dander caught up in the hair can be a significant source of DNA, we wound clumps of hair together and placed them into the first extraction buffer (buffer ATL). In both cases, we used a warm water wash to remove dirt from the hairs before placing them in extraction buffer.

We prescreened DNA extracts with the marker G10J to remove weak samples and to separate black bear from brown bear samples, based on the exclusive presence of odd-numbered allele lengths in the former species and even-numbered alleles in the latter. To identify individuals, we used 7 microsatellite markers (G1A, G10H, G10J, G1D, G10B, MU50, and MU23) with average heterozygosity >0.72 in brown bears from Kenai Peninsula and an amelogenin sex marker.

We performed the multilocus microsatellite analyses in 3 phases. First, an initial pass was made with all 8 markers, including reanalysis of G10J to control for sample handling errors. Samples that produced solid data for <4 loci, including G10J, were excluded from further consideration. The second phase (cleanup) involved those samples that produced incomplete results during the first pass (but were not excluded) and made use of 5 μl of DNA per reaction instead of the 3 μl used during the first pass. We repeated some cleanup several times until high confidence was developed for all 8 markers based on criteria for signal strength and legibility (samples with low confidence scores at ≥1 markers were excluded from individual identification at the end of the cleanup process). In the third (error-checking) phase of genotyping, we subjected the remaining samples to a computerized search for similar pairs of genotypes that could have been created by genotyping error, and the mismatching markers were reanalyzed in these similar pairs. Once the genotypes were completed and checked for errors, we performed a computer search for identical genotypes and individuals were defined for each unique 8-locus genotype. Finally, we cross-referenced these genotypes with samples from 2 unpublished pilot studies previously conducted by KENWR in 2005 and 2006.

We compared genotypes identified in our study with 211 genotypes archived in a database maintained by the United States Geological Survey (USGS) Alaska Science Center (ASC), including 39 brown bears with telemetry collars and alive during this study. Microsatellite genotypes in this database included information from 14 loci: G1A, G10B, G10C, G1D, G10H, G10J, G10L, G10M, G10P, G10X, MU26, MU50, MU59, and C203. Our genotype data included 6 of these markers: G10J, G10B, G1A, G1D, G10H, and MU50. In addition, a subset of samples in our database was typed at additional loci (G10L, G10M, G10C, and G10X), which also were included in the ASC/ADFG database. Thus, the minimum number of loci providing any match statistics was 6, and the maximum possible number of loci was 10; the largest number of loci providing any match was 9 (S. Farley, ADFG, personal communication).

We used the Excel Microsatellite Toolkit (version 3.3.1; Park 2001) to generate matches based on the 6 loci shared in

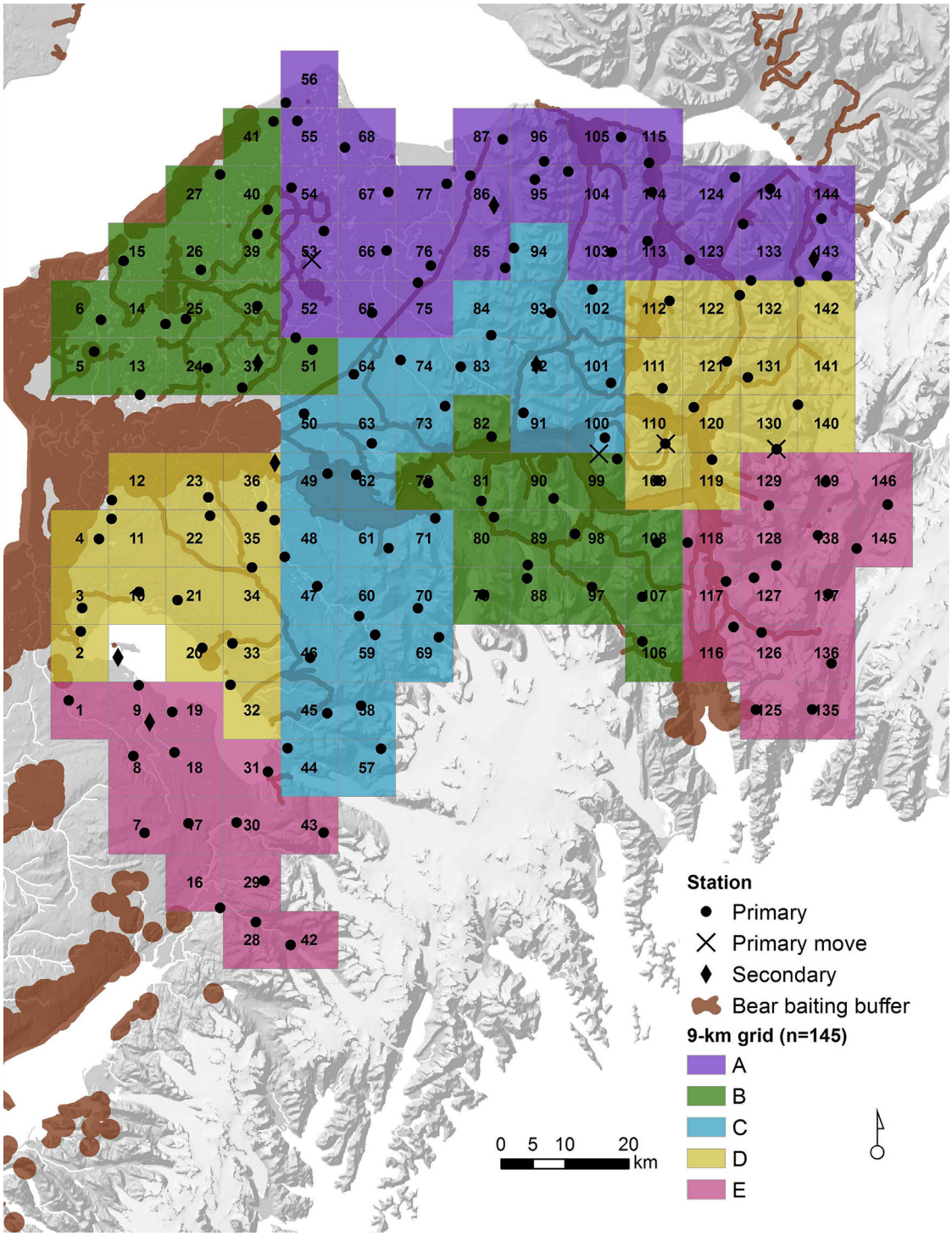

Figure 2. Five panels of 29 9-km × 9-km sample cells ($n = 145$) systematically distributed over 11,700 km^2 of the Kenai National Wildlife Refuge and Chugach National Forest, Alaska, in 2010. Brown bear hair sample stations were moved or supplemented in 17 cells to increase capture rates.

common by all individuals in both databases. We verified matches at additional loci by visual examination. We examined all matches that differed at 1 allele to verify the differences were not due to polymerase chain reaction (PCR) artifacts or genotyping error. Additionally, we confirmed sex of matching genotypes as another means of checking error (S. Talbot, USGS, personal communication).

Mark-Recapture Models

We constructed encounter histories with 6 occasions: 1 for bears alive and on the sample frame (labeled occasion 0), and 5 occasions for the 5 hair trap sessions. Different methods of capture increases the number of unique animals captured (Otis et al. 1978), and hence reduces the bias of the population estimate due to individual heterogeneity. We considered 4 individual covariates in the analysis: average

distance to the edge of the sampling grid (distance to edge), average distance to the open edge of the sampling grid (distance to open edge), average elevation, and average distance to anadromous fish streams. For these variables, we averaged over all captures of an individual. We modeled trapping effort as the number of days of hair trap availability during each of the 5 occasions. We postulated a priori that capture rates would increase with elevation but be unaffected by distance to anadromous fish streams because we conducted our study in June, shortly after brown bears leave dens (Goldstein et al. 2010) but before most salmon return to streams on the Kenai Peninsula (Jacobs 1989). We postulated a priori that capture rates would increase with distance to edge or distance to open edge because bears are likely to spend increasingly more time within the sample frame (Boulanger and McLellan 2001).

To assess the potential for use of Pledger heterogeneity models (Pledger 2005) for the 5 hair trapping occasions, we fitted a binomial distribution restricted to the positive integers (zero-truncated) to capture frequencies for females and males separately. This model tested whether the observed frequencies of female and male captures could have come from a zero-truncated binomial distribution. If so, observed heterogeneity was not strong and Pledger models were not necessary. If frequencies did not follow a zero-truncated binomial, Pledger models were necessary and were included during subsequent modeling. Subsequent modeling of the combined data set considered detection probabilities for occasion 0 to be sex specific because more females than males carried radio collars and were alive and on the study area. The time-varying models considered for occasions 1–5 included constant capture probabilities across time and time-specific capture probabilities. The basic time-and-individual-varying models considered for occasions 1–5 included the time-varying models plus a sex effect and a sex interaction. In addition, we added the covariates distance to edge, distance to open edge, elevation, and distance to anadromous fish streams to these models. We also included distance to edge with thresholds of 4.5 km and 9 km and distance to open edge with thresholds of 4.5, 9, 18, and 27 km (i.e., the values were truncated when the true value exceeded these values). To evaluate time-specific effects on detection probabilities, we used a fully time-specific model with 5 parameters and a trapping effort model with 2 parameters, with values of 826, 717, 767, 731, and 752 hair-snare days for each of the 5 occasions. We used the Huggins conditional likelihood parameterization (Huggins 1989, 1991; Alho 1990) to estimate population size (N) as a derived parameter:

$$\hat{N} = \sum_{i=1}^{M_{t+1}} \frac{1}{1 - \prod_{j=1}^{6} (1 - \hat{P}_{ij})}$$

where M_{t+1} is the number of unique individuals captured and P_{ij} is the probability of detection of the ith individual on the jth occasion.

All models assumed no behavioral effect of capture (i.e., the capture probability of bears that have been detected once does not change for additional detections). We conducted analyses with Program MARK (White and Burnham 1999) using Akaike's Information Criterion adjusted for finite sample sizes (AIC_c) for model selection and model averaging of population estimates (Burnham and Anderson 2002). We computed AIC_c weights of Pledger models for just the grid-based hair data to further assess the need for this mixture model relative to the suite of models considered. To further assess the assumptions of demographic and geographic closure, we constructed 4 models with the Pradel data type (Pradel 1996) in Program MARK using just the 5 hair snare sampling occasions. Models considered were apparent survival (φ) and fecundity (f) estimated, φ fixed to 1 with f estimated, f fixed to 0 with φ estimated, and φ fixed to 1 and f fixed to 0. Lastly, we examined the potential use of spatially explicit modeling approaches for estimating brown bear abundance from out data set. This study was conducted with approval and authorization under the Institutional Animal Care and Use Committee Assurance Form 2009016, ADFG Scientific Permit 10-100, Convention on International Trade in Endangered Species Export Permit 10US18165A/9, a National Environmental Policy Act Categorical Exclusion, and a Wilderness Minimum Requirements Analysis.

RESULTS

Genetic Analyses

We collected 11,175 samples of brown and black bear hair from 144 primary stations (1 cell was never visited because of persistent snow cover or poor weather) and 7 secondary stations. The first revisit had the lowest return (1,550 samples) presumably because trap session length varied from 1 to 9 days because of modifications to the grid design during the first 3 days of deployment. However, we collected >2,100 samples during each of the other 4 revisit sessions, each averaging 5 days. In addition to hair samples collected at stations with lures, we collected 91 samples incidentally from rub trees and a permitted black bear baiting station in the Kenai Lowlands (hereafter referred to as incidental samples). We considered 11,266 hair samples in these analyses.

We extracted DNA from 2,671 samples. We confirmed species identity through a clustering analysis based on 6 microsatellite markers, excluding G10J to ensure independence of tests. Bears with even- and odd-numbered G10J alleles formed 2 discrete clusters, confirming that the G10J data had accurately separated species. The prescreen process with marker G10J had an 80% success rate and produced high confidence, even-numbered scores indicating brown bears for 1,226 samples, which went on to genotyping with 8 markers.

During multilocus genotyping, 1,034 samples produced high-confidence scores for all 8 markers, and were therefore used for individual identification. There were 211 unique multilocus genotypes, of which 166 were identified from hair collected on the sample frame. Of the 211 unique brown

bears (i.e., excluding ADFG bears below), 47 were detected in ≥2 sessions, 5 were detected in 1 session but also identified in previous studies or incidental samples, 114 were captured once, 11 were captured only in incidental samples, and 34 were not captured but previously identified in other studies or incidental samples.

Based on sex and perfect matches at 6–9 loci, 32 of these bears were previously handled by ADFG or the IBBST. Six of the previously handled individuals were males, captured by ADFG or the IBBST during radiocollaring operations that targeted females. Five of the 34 radiocollared brown bear females (15%) known to be on the sample frame immediately before or during June 2010 were matched with genotypes identified by hair sampling.

Genotyping errors normally create pairs of genotype from the same individual that mismatch at 1 marker (Paetkau 2003). Following error-checking there was only 1 such pair among the 211 brown bear genotypes that we recognized, and this pair was solidly confirmed, first through reanalysis of the mismatching marker, and then through analysis of 16 additional markers, several of which mismatched. There were also 8 pairs of multilocus brown bear genotypes that matched at 6 of 8 markers, each of which was confirmed through reanalysis of the mismatching markers. Extensive blind testing has shown that this protocol effectively prevents the recognition of false individuals through genotyping error (Kendall et al. 2009).

In addition to providing reassurances about genotyping errors, the observation of just 1 pair of brown bears whose genotypes matched at 7 of 8 markers indicates a low probability that we sampled any pair of bears with identical 8-locus genotypes. This is because matches at all 8 markers are approximately 10 times less likely than matches at 7 of 8 markers, just as matches at 6 of 8 markers are more common than matches at 7 markers (Paetkau 2003).

Population Estimation

We located 30 radiocollared female brown bears during 5 days of aerial tracking from 26 June to 4 July 2010. We combined these locations with telemetry data supplied by ADFG. Together the samples of radiocollared female brown bears provided geographic locations of 39 females known to be alive in June 2010 on the Kenai Peninsula, of which 5 were not on the sample frame.

All sources of information for brown bears on the Kenai Peninsula in June 2010 identified 243 brown bears, of which 211 were identified genetically and 32 had been handled by ADFG but were not detected during non-invasive hair sampling. After eliminating bears ($n = 40$) for which there were no geographic coordinates, either because they were not located (if collared) or were sampled outside the study area, we used 203 bears (99 F, 104 M) in our analysis. Occasion 0, defined by bears alive and on the sample frame before and during the study, was composed of 41 brown bears including 34 collared females and 7 bears captured on rub trees.

Capture frequencies of the bears detected on the sample frame ($n = 166$) were 3 detections (3 F, 5 M), 2 detections (17 F, 21 M), and 1 detection (45 F, 75 M). The zero-truncated binomial fit to these frequencies suggested no lack of fit ($P = 0.959$ for F, $P = 0.791$ for M). Further, the AIC_c weight of the time-specific Pledger model for the grid-based hair data was only 0.0054, and the 3-parameter Pledger mixture model (no time variation) received no weight, so Pledger models were not considered in subsequent analyses. With only 5 occasions, the level of individual heterogeneity has to be relatively high (i.e., at least a few animals captured on all 5 occasions) before the Pledger mixture models perform reasonably.

Estimates of detection probabilities increased with each successive trap session (Table 2) despite the fact that bears were exposed to traps for approximately the same time period (approx. 5 days) during each of the 5 occasions. Consequently, model selection results (Table 3) suggested that a time-specific model (t) was necessary to explain the variation in detection probabilities (p) for occasions 1–5, and that an additive sex effect was needed to explain differences in detection between sexes. Because all models included a sex-specific detection probability for the initial occasion (0), our base model was {sex×p(0), sex+p(t)}. Elevation was a useful predictor of detection probabilities when added to the base model; distance to edge did not improve upon the base model. Detection probabilities declined with increasing elevation (Fig. 3a) but only marginally so with increasing distance to edge (Fig. 3b). When distance to anadromous fish streams, distance to open edge, truncated values of distance to edge, and truncated values of distance to open edge were added to the base model, none of the models produced smaller AIC_c values than the base model. Model averaging across all models of the population estimates (Table 3) indicated that there were 428 (95% lognormal CI = 353–539) brown bears of all ages on the study area in June 2010, of which 215 were females and 213 were males (Table 4).

The model weights for the 4 Pradel models considered (Table 5) show that 98% of the AIC_c weight was on the model with φ fixed to 1 and f fixed to 0. That the model best supported assumed no emigration or immigration provided further evidence that the grid-based sample frame can be assumed geographically and demographically closed.

Table 2. Estimated capture probabilities ($\hat{p}$) for the 5 hair capture occasions for male and female brown bears on the Kenai Peninsula, Alaska, USA, June 2010, on the sample frame. The probabilities are derived from model {sex×p(0), sex+p(t)} that includes a sex-specific detection probability for the initial capture occasion of bears known to be on the study area and a time-dependent detection probability with an additive effect of sex for all other occasions.

				95% lognormal CI	
Sex	Occasion	Estimate	SE	LCI	UCI
F	1	0.0376	0.0106	0.0215	0.0650
	2	0.0902	0.0198	0.0581	0.1372
	3	0.0783	0.0179	0.0497	0.1213
	4	0.1061	0.0224	0.0696	0.1585
	5	0.1101	0.0230	0.0724	0.1639
M	1	0.0595	0.0156	0.0353	0.0986
	2	0.1381	0.0272	0.0928	0.2005
	3	0.1208	0.0249	0.0799	0.1785
	4	0.1610	0.0302	0.1101	0.2294
	5	0.1667	0.0310	0.1144	0.2365

Table 3. Model selection results for closed capture population estimators in Program MARK for brown bears on the Kenai Peninsula, Alaska, USA, June 2010. We constructed all models with a sex-specific detection probability (p) for the capture occasion of bears known to be on the study area, labeled as sex × p(0). We used 4 covariates in the analysis: average distance to the edge of the sampling grid (DTE), average distance to the open edge of the sampling grid (DTOpenE), average elevation (Elev), and average distance to anadromous fish streams (DTA). We used Akaike's Information Criterion adjusted for finite sample sizes (AIC_c) for selection of models, where K is the number of parameters and $-2\log(L)$ is the likelihood estimate.

Model	AIC_c	ΔAIC_c	AIC_c weights	K	$-2\log(L)$
{sex×p(0), sex+p(t)+Elev}	1,032.48	0.00	0.723	9	1,014.33
{sex×p(0), sex+p(t)}	1,038.10	5.62	0.044	8	1,021.98
{sex×p(0), sex+p(t)+DTE}	1,038.51	6.04	0.035	9	1,020.37
{sex×p(0), p(t)}	1,039.25	6.77	0.025	7	1,025.16
{sex×p(0), sex+p(t)+min(DTE,9000)}	1,039.52	7.05	0.021	9	1,021.37
{sex×p(0), sex+p(effort)	1,039.52	7.05	0.021	5	1,029.47
{sex×p(0), sex+p(t)+min(DTOpenE,18000)}	1,039.67	7.20	0.020	9	1,021.52
{sex×p(0), sex+p(t)=+min(DTE,4500)}	1,039.81	7.34	0.019	9	1,021.66
{sex×p(0), sex+p(t)=+min(DTOpenE,9000)}	1,039.82	7.35	0.018	9	1,021.67
{sex×p(0), sex+p(t)=+DTOpenE}	1,040.05	7.57	0.016	9	1,021.90
{sex×p(0), sex+p(t)=+DTA}	1,040.10	7.62	0.016	9	1,021.95
{sex×p(0), sex+p(t)=+min(DTOpenE,27000)}	1,040.11	7.64	0.016	9	1,021.97
{sex×p(0), sex+p(t)+min(DTOpenE,4500)}	1,040.12	7.64	0.016	9	1,021.97
{sex×p(0), sex×p(effort)}	1,041.39	8.91	0.008	6	1,029.32
{sex×p(t)}	1,044.48	12.01	0.002	12	1,020.22
{sex×p(0), sex+p(Elev)}	1,049.85	17.38	0.000	5	1,039.80
{sex×p(0), sex+p(.)}	1,055.41	22.93	0.000	4	1,047.38
{sex×p(0), sex+p(DTE)}	1,055.83	23.36	0.000	5	1,045.78
{sex×p(0), sex+p(min(DTE,9000))}	1,056.83	24.35	0.000	5	1,046.78
{sex×p(0), sex+p(min(DTE,4500))	1,057.12	24.64	0.000	5	1,047.07
{sex×p(0), sex+p(DTA)}	1,057.40	24.92	0.000	5	1,047.35

DISCUSSION

Our study produced the first empirically based estimate of brown bear abundance on the Kenai Peninsula. Motivated by the need to estimate bear abundance quickly and to consider model assumptions, our study design was similar to that used by Poole et al. (2001) to estimate the grizzly bear population on the Prophet River in British Columbia. They used a sample frame of 103 9-km × 9-km cells on an area slightly smaller than our study area. They used 1 station within each cell with a single barbed-wire enclosure, but increased capture rates by moving stations between each of the 5 trap occasions and by adding new lures. We worked to increase our capture rates by using 2 barbed-wire strands, using commercial lures in addition to the cow blood and fish oil lure, and adding secondary stations or moving stations within cells but only when the primary site performed poorly. We also improved our population estimate by using supplemental DNA sources: ad hoc sampling of rub trees (Boulanger et al. 2008) and telemetry data (Boulanger et al. 2002). We chose to tradeoff intensive sampling with smaller cells, which may have allowed for the detection and modeling of individual heterogeneity (Boulanger et al. 2002), for a more extensive sample frame that encompassed virtually all of the known brown bear habitat on KENWR and CNF, an area that approximates 74% of the known brown bear habitat on the Kenai Peninsula.

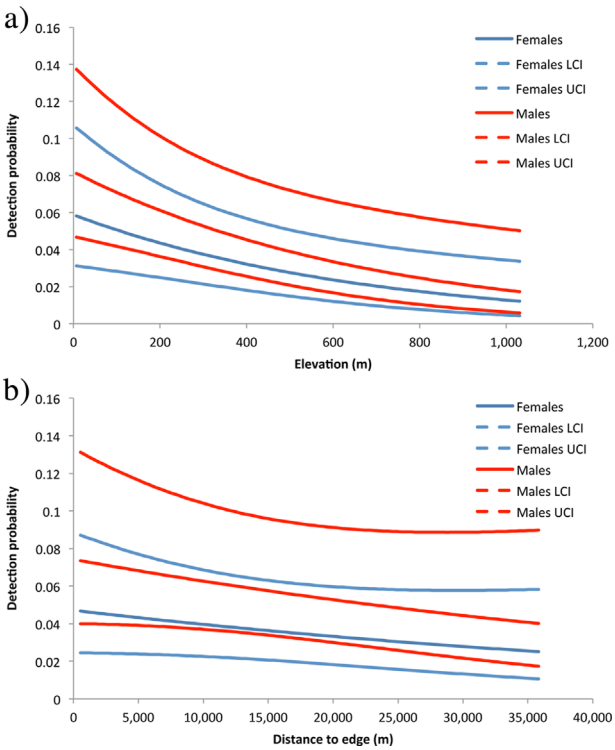

Figure 3. Detection probabilities for male and female brown bears on the Kenai Peninsula, Alaska, USA, June 2010, for the first hair trapping occasion as a function of a) elevation (ELEV) and b) distance to edge of sample frame (DTE).

The short trap session (5 days) and the constrained sampling window (June) makes our study unique in the published literature. Poole et al. (2001) and Kendall et al. (2009), for example, used trap sessions of 12–14 days. However, both of these populations were inland grizzlies, not salmon-dependent brown bears (Hilderbrand et al. 1999*a*). Consequently, although we recognized that shorter trap sessions might reduce capture rates, we were concerned that extending the study into July when most salmon return to the Kenai Peninsula would reduce the effectiveness of our lures and our study design (because bears begin congregating

Table 4. Population estimates and confidence intervals for brown bears on the Kenai Peninsula, Alaska, USA, June 2010, using only hair collected on the sample frame (hair snares), and incorporating data from radiocollared females and hair from rub trees (occasion 0). M_{t+1} is the number of bears detected or known to exist on the sample frame. The 95% lognormal confidence intervals (LCI and UCI) incorporate information from M_{t+1} into their calculation.

					95% lognormal CI	
Data used	**Sex**	**Estimate**	**SE**	M_{t+1}	**LCI**	**UCI**
Occasion 0 and hair snares	F	214.6	33.7	99	165.0	301.3
	M	213.1	30.9	104	167.2	292.2
	Combined	427.6	46.7	203	353.2	539.1
Hair snares only	F	114.2	17.1	65	90.4	160.4
	M	194.1	26.4	101	155.0	261.5
	Combined	308.3	31.8	166	258.3	385.4

Table 5. Model selection results for the Pradel (1996) models used to assess closure of the sample frame for brown bears on the Kenai Peninsula, Alaska, USA, June 2010. The parameter φ is apparent survival, p is probability of detection, and f is new recruits per animal previously in the population. We used Akaike's Information Criterion adjusted for finite sample sizes (AIC_c) for selection of models, where K is the number of parameters and $-2\log(L)$ is the likelihood estimate.

Model	**AIC_c**	**ΔAIC_c**	**Weights**	**K**	**$-2\log(L)$**
$\{\varphi(\text{sex}\times t)=1\ p(\text{sex}\times t)\ f(\text{sex}\times t)=0\}$	830.99	0.00	0.98	10	809.93
$\{\varphi(\text{sex}\times t)\ p(\text{sex}\times t)\ f(\text{sex}\times t)=0\}$	838.98	7.99	0.02	16	804.30
$\{\varphi(\text{sex}\times t)=1\ p(\text{sex}\times t)\ f(\text{sex}\times t)\}$	843.01	12.02	0.00	16	808.33
$\{\varphi(\text{sex}\times t)\ p(\text{sex}\times t)\ f(\text{sex}\times t)\}$	846.92	15.93	0.00	20	802.70

along streams; Suring et al. 2006). To test for this characteristic of our design, we examined detection probabilities in relation to salmon streams; as expected (given our spring trapping), proximity to anadromous streams did not significantly improve the model (Table 3).

The shorter trap sessions also limited exposure of samples to the elements, which can degrade DNA samples. Our prescreen success rate was 80%, the upper end of rates which typically vary from 55% to 80% for grizzly or brown bear hair samples (D. Paetkau, Wildlife Genetics International, unpublished data). The short trapping session can be particularly important for DNA-sample quality if there is a bias toward samples being collected shortly after deployment when the lure is freshest. Furthermore, keeping the trap session short significantly reduced the cost of the study because the 2 helicopters and their fuel were the single biggest expense. The inflated cost of a longer season would have precluded conducting the field study (and any estimate of bear abundance) because of budget limitations. Finally, the short sampling window provides reasonable assurance of demographic closure (see below).

Precision and Bias

Several design and analysis considerations specifically addressed the desire for a precise estimate with limited bias while acknowledging demands for limited budget and an estimate based on a single field season. Per-occasion capture probabilities in our study did not exceed 0.17 for males and 0.11 for females (Table 2). These values were slightly lower than the mean capture probability of 0.19/session reported by Poole et al. (2001) and generally lower than the observed capture probabilities of 0.1–0.25 reported by Kendall et al. (2009). The small number of trap occasions and the low detection probabilities have 2 negative consequences. First, these features result in less precise estimates of abundance. Second, these characteristics make it difficult to apply recently developed Pledger models. We expect individual heterogeneity of capture probabilities to exist in the population (i.e., each animal has its own innate detection probability), and Pledger models have been demonstrated as the superior choice for estimating abundance when capture probabilities are heterogeneous. Unfortunately, the Pledger model, and all models that include a component to model individual heterogeneity, performs poorly when the data display little individual heterogeneity and capture probabilities are low. Therefore, application of Pledger models was not appropriate for our data even though we suspect the models fit the underlying capture process.

Our evaluation of capture probabilities resulted in a more pronounced adjustment for females. Although we detected 41% fewer females than males, model-averaged population estimates show essentially the same number by sex (Table 4). Females of all ages had a lower hair station detection probability than males (Fig. 3a and b) as demonstrated by radiocollared subadult and adult females known to be in the population but never detected at hair stations. The model-averaged estimates for females and males from just grid-based detections were 114 and 194, respectively; with inclusion of bears known to be in the population, the numbers increased to 215 and 214. The final estimate for females was almost twice the estimate from grid-based data, whereas the estimate for males increases only 9%. Females were under-represented in the grid-based sampling presumably because some cohorts may behave differently (e.g., females with cubs of the year tend to move little during June) and because males have almost twice the home range (950 km^2) as females (401 km^2) on the Kenai Peninsula (Jacobs 1989). Further, the presence of 34 females in the analysis that were not detected at hair stations increases the number of females known to be alive and, coincidentally,

demonstrates the lower capture probability of females. Both of these effects result in increasing the population estimate. Kendall et al. (2009) reported that only 61% of females and 35% of males known to be on their study area in northern Montana were detected by hair traps. However, the inclusion of data from previously handled bears (e.g., radiocollared) on the study area and bears detected by rub trees decreased the bias of their final estimate, just as the inclusion in our study of bears known to be on the study area decreased the bias of our estimates.

The estimated 50:50 sex ratio that resulted from our most robust estimate of abundance is unusual in the bear literature. Grizzly and brown bear studies elsewhere generally have estimated more adult females than males, typically 60:40 (Craighead et al. 1974, Pearson 1975). One possible interpretation is that our population estimate is still biased low for females, even after adjusting the modeled estimate with data from collared bears and rub trees. Alternatively, it is also likely that adult female mortality on the Kenai Peninsula may be skewed high. From 1967 to 2011 of 122 adult brown bears killed by humans from sources other than hunting (i.e., DLPs, illegal take, road kills, and management kills), 69% were females (ADFG, unpublished data). Similarly, an analysis of the age structure of 256 brown bear females captured from 1995 to 1999 suggested that 2- to 6-year-old females were underrepresented in the hypothetical age distribution, a finding that "is troubling because, in other brown bear studies, weaned sub-adult bears usually account for >20% of a population" (IBBST 2001:20).

Geographic and Demographic Closure

The spatial extent of the sample frame and the short sampling period were attributes of our study design that helped ensure reasonable geographic and demographic closure for modeling. Distance to edge was originally examined as a covariate to explore the potential violation of geographic closure. We assumed detection probabilities would be lower for bears near the edge because they are likely to spend time outside the sample frame (Boulanger and McLellan 2001). However, this was not observed and, in fact, detection probabilities were higher closer to the sample frame edge (Fig. 3b). This outcome underscores that the sample frame was bounded by real geographic barriers on 88% of its 700-km perimeter (i.e., ocean, glaciers, the isthmus, and the urban interface; Mace et al. 1996; Suring et al. 1998, 2006; Jackson et al. 2008), with only the southwest corner of the grid open to significant movement to, and from, a small area south of Caribou Hills (Figs. 1 and 2). Bears traveling along these barriers may move along the perimeter because they cannot or prefer not to move through it. As a consequence, these bears encounter more stations near the edge of the sample frame.

Regardless of the explanation, evidence for an edge effect is weak (Fig. 3b), and the threshold models for distance to edge were not highly ranked models (Table 3). We explored the influence of the dominant open boundary through a series of models labeled distance to open edge. Models exploring the influence of distance to open edge were even less supported than the distance to edge models based on AIC_c weights (Table 3). Indeed, a retrospective analysis (unpublished data) of 40 global positioning system (GPS)-collared female brown bears that were monitored in 1996–2004 ($n = 3{,}687$ locations; Fig. 4) indicated that 5 bears were never on the study area during June of those years although all were adjacent to (but outside) the open boundary (distance to open edge). Finally, the Pradel model that assumed closure was the most supported model with 98% of the AIC_c weight. Thus, a range of evidence suggests that analysis with models that assume geographic closure was a reasonable choice for this population.

Demographic closure is another potential concern for mark-recapture estimates. Violation of demographic closure might occur if a proportion of the population were to die during the study. Our study design, which emphasized a short sampling period in spring, minimizes the likelihood of this being a problem. A second violation of the demographic closure assumption could occur if cubs of the year were sampled more frequently as the study progressed or perhaps not at all. However, we doubt the former was the case because females with young of the year tend to stay near their natal sites, particularly early in the summer when this study was conducted. In the case of the latter, we chose to use 2 barbed wires strung at different heights as a reasonable way to ensure that cubs were sampled. Although inclusion of cubs in estimates using single barbed wire has been suggested in various studies (Boulanger et al. 2004, Kendall et al. 2009), and Boulanger et al. (2006) did not show large differences in estimates from single- versus double-strand enclosures, we also recognized that the size range of brown bears on the Kenai Peninsula is greater than in interior brown bear populations. This attribute makes it more difficult to assume that a single strand would suffice for all sizes.

Multiple captures of different genotypes generally did not occur in the Kenai Lowlands in the northwest quarter of the sample frame (Fig. 5), and thus provides perspective on the spatial distribution of bear density. This area of the sample frame has the lowest elevation, and would thus seem somewhat inconsistent with the inverse relationship between elevation and detection probability (Fig. 3a). However, a retrospective analysis of 46 GPS-collared brown bear females on the Peninsula reported they move most in June and are farthest away from streams in June (G. Harris, U.S. Fish and Wildlife Service, unpublished data). This is consistent with our conceptual model that most brown bears emerge in the spring from steeped-slope, high-elevation dens through mid-May (Goldstein et al. 2010), move quickly toward lower-elevation calving areas for moose (*Alces alces*), and then move toward streams as the early runs of chinook (*Oncorhynchus tshawytscha*) and sockeye (*O. nerka*) salmon enter streams in late June (Jacobs 1989). The exception is females with cubs of the year, a cohort that remains at higher elevations near natal sites during early summer (IBBST 2001, Suring et al. 2006). This gradual movement across the study area, combined with the observed lower detection probabilities for the early occasions and higher detection probabilities in the later occasions (Table 2) would explain

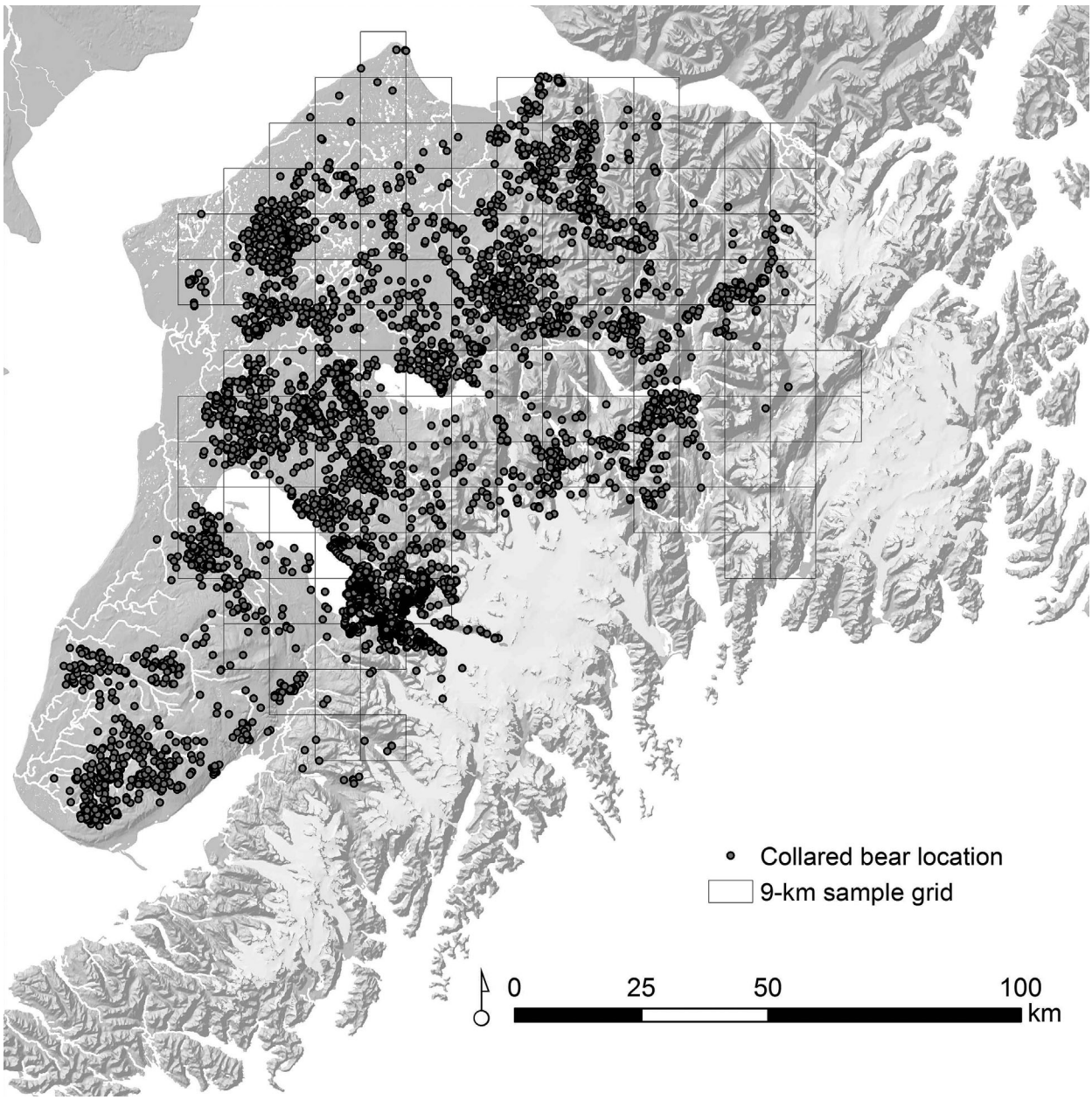

Figure 4. Distribution of 144,024 telemetered locations from 125 female brown bears with global positioning system (GPS) and very high frequency (VHF) collars on the Kenai Peninsula, Alaska, 1987–2005 (IBBST, unpublished data). The 11,700-km^2 sample frame used in our study encompassed 87% of locations.

why we found higher detection probabilities at lower elevations. Bears were at lower elevations during the later occasions of the survey, providing higher detection probabilities. The observed weak relationships of distance to edge and elevation to capture probabilities (Fig. 3a and b) make more sense in this light.

We think our grid-based approach, complemented with telemetry and rub-tree data, resulted in a credible and relatively fast method for estimating the brown bear population given the large size of the study area and lack of alternative population estimation methods (e.g., aerial surveys). These features met the information needs of managers for a timely, reliable, within-budget estimate of abundance. Our abundance estimate is likely biased low but precision was reasonable. The tradeoff with employing a larger cell size and shorter sampling duration was lower detection probabilities and the difficulties of modeling heterogeneity variation (Proctor et al. 2010). Future application of this approach should attempt to use smaller grid cells and incorporate more secondary sites within cells (perhaps using only a single strand) to improve capture rates and incorporate more rigorous pursuit of independent samples from rub trees to increase the premarked sample (i.e., occasion 0) and thereby reduce sex bias in capture probabilities. Capture rates and measurement of capture heterogeneity could also be improved with a hybrid approach that employs a lure-based grid design to address closure issues, complemented with break-away hair snares along streams (Beier et al. 2005, Flynn et al. 2012).

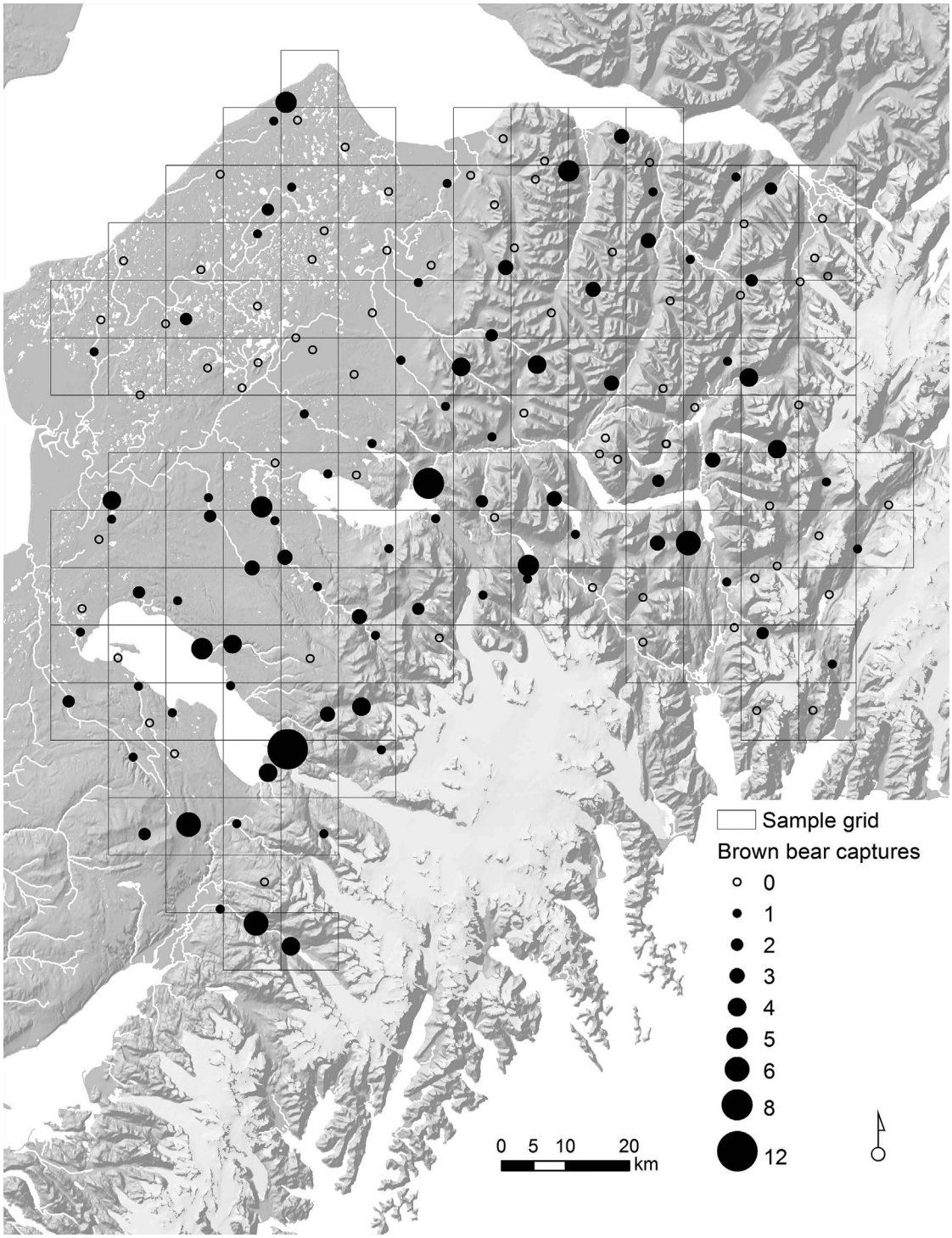

Figure 5. Spatial distribution of brown bear hair captures (unique genotypes) on the sample frame on the Kenai Peninsula, Alaska, USA, June 2010.

Models Considered but Discarded

Spatially explicit capture-recapture (SECR) models represent a recent development in estimators that is especially suitable when geographic closure is a concern. We did not use SECR models for 2 reasons. Foremost, SECR models would not have accommodated data for the bears known to be alive and on the grid but never detected in hair samples. As discussed above, the improvements in estimates of capture probabilities achieved by including these bears in the study are substantial. Without information provided by these bears, our estimates would suggest an extremely skewed sex ratio (with males dominating). Second, we rejected SECR models because of issues estimating σ (a parameter associated with home range size) based on our capture histories. To rigorously estimate σ, SECR models use recapture histories, representing movements of bears among snare sites. Our data included only 54 pairs of distances from which to estimate movements. Further, σ should be

estimated separately for male and female bears because of the well-documented differences in home range size of the sexes. Spatially explicit capture-recapture models developed with limited data generally require the biologically unrealistic assumption of a circular area of activity. During June, bears on the Kenai are known to move directionally from dens toward moose and Dall sheep (*Ovis dalli*) calving areas, and subsequently toward streams with early run salmon, suggesting a circular activity area is not a reasonable assumption. For these reasons, we rejected SECR models as a stronger approach to estimating bears from the data collected in this study.

Ivan et al. (2013*a*,*b*) also describe an alternative spatial modeling approach to examine mark-recapture data. In contrast to the SECR approach, the method defines explicit study boundaries and thus eliminates the problem of estimating abundance (from the density estimate) encountered with SECR models. However, this estimator requires that animals be monitored for use of the sample frame before and after the lure is removed. Typically this monitoring requires that animals be radiocollared when captured on the sample frame and then monitored after the capture-recapture portion of the study is completed. In our case, we were not specifically capturing animals on our sample frame, and so do not have a legitimate sample of the bears detected via hair stations to then monitor for use of the grid later. Further, the Ivan et al. estimator assumes that animals do not change their home ranges after trapping is completed. This assumption is likely inappropriate for our study where bears were moving from den sites during June and likely changing the areas used over the course of the summer.

Population Inferences

To put our estimate of bear abundance into ecological and management context, we calculated the density of brown bears on the study area. Available habitat on the sample frame, after subtracting the Harding Icefield, water bodies, and the anthropogenic footprint, approximated 10,200 km^2, translating to a mean brown bear density of 42/1,000 km^2. To put this in perspective, Miller et al. (1997) reported brown bear densities (all ages) on 7 study sites in southern coastal habitats of Alaska, characterized by abundant runs of multiple salmon species, ranged from 191 to 551/1,000 km^2; in contrast, brown bear densities (all ages) on 11 study sites in interior Alaska ranged from 10 to 30/1,000 km^2 (Fig. 6). Our estimate placed the Kenai Peninsula population on the low end of coastal brown bear densities elsewhere in Alaska, perhaps attributable to restricted access to salmon on some rivers because of shoreline development and intense sport fishing (Hilderbrand et al. 1999*b*).

We considered calculating a density estimate for a core area (rather than the entire sample frame) by placing a buffer along open portions of the sample frame. Boulanger and McLellan (2001) did exactly that based on their findings from a Pradel model that fidelity rate was low and addition rate was high within 10 km of the edge of their sample frame. However, because our best Pradel model assumed no emigration or immigration, and because the inclusion of distance to open edge did not contribute to model fit, we chose not to adjust our density estimate.

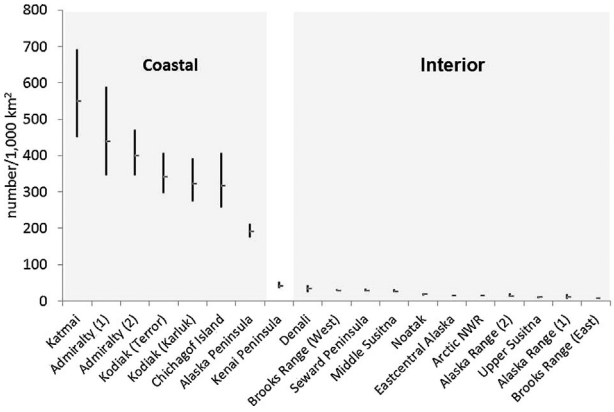

Figure 6. Estimated (with 95% CIs) density of brown bears on the Kenai Peninsula (42.0/1,000 km^2) in June 2010 compared to densities of coastal and interior brown bear populations elsewhere in Alaska (per 1,000 km^2; after Miller et al. 1997).

We also considered using the proportion of locations from GPS-collared female brown bears on and off the grid from monitoring in previous years for the purpose of extrapolating a peninsula-wide population estimate (White and Shenk 2001). However, habitat use and movements by adult females are unlikely to be representative of other sex and age cohorts. Furthermore, bear capture occurs mostly in remote areas of the Kenai Peninsula and subsequent telemetered locations are likely to be biased toward a population that uses the study area rather than areas closer to the urban interface. Consequently, rather than introduce known biases, we deemed it more appropriate to assume that habitat quality on and off the grid was similar (Table 1).

Our density estimate is more than twice the 20 bears/1,000 km^2 that was assumed when Del Frate (1999) suggested that the brown bear population on the Kenai Peninsula was 250–300 individuals. His assessment was based on previous work by Miller (cited in IBBST 2001:19) who "... suggested that the density of brown bears on the Kenai was probably lower than the 27.1 bears per 1000 km^2 that he reported for his middle Susitna study area [1987]." Based on our estimated density and Del Frate's (1999) original value of 13,848 km^2 for available habitat, we estimated a peninsula-wide population of 582 brown bears in June 2010 with a 95% lognormal confidence interval of 469–719 (estimator from Buckland et al. 2001:77).

We think our extrapolation is reasonable given that the sample frame encompasses 74% of available brown bear habitat on the Kenai Peninsula, and that landcover on the study area and peninsula are similar (Table 1). Similarly, 84% of 74 brown bear females for which den sites are known from 1996 to 2003 denned on the study area (Goldstein et al. 2010). Furthermore, on average, 87% (SE = 0.03) of 144,024 telemetry locations from 125 brown bear adult and subadult females radiocollared by the IBBST during 1987–2005 were on the study area (Fig. 4). As stated above, this percentage is likely biased high because of the skewed distribution of capture locations, but it is indicative of the spatial robustness

of the sample frame. Lastly, the absolute value of the sample frame area is so large relative to available area that adjustments of the extrapolated value do little to significantly change the peninsula-wide population estimate.

Our population estimate includes dependent young. If we assume that 1) dependent young were as likely to be captured as adults; 2) the reproductive demographics of the 39 radiocollared females in 2010 were representative of the larger population of adult females; and 3) sexes were equally represented among dependent young, then we can approximate the number of independent males and females on the Kenai Peninsula. In 2010, Farley (2010) documented litter sizes for 38 of 39 radiocollared females, or 38 females with 43 young (1.13 young/adult female). Consequently, the estimate of 582 brown bears on the Kenai Peninsula would translate to approximately 188 adult females, 188 adult males, and 206 dependent young, of which 103 would be males and females each.

We emphasize that the approach Del Frate (1999) used to estimate the brown bear population in the mid-1990s was logical at that time for management purposes. We caution that these 2 values should not be compared to make inferences regarding population growth, as the earlier value was based on expert opinion and the current value is a model-based estimate using empirical data. However, a recent unpublished λ estimate of 1.039 (95% CI = 1.036–1.043) for 1995–2011 (Farley 2011) suggests that the population was increasing during this interval.

Despite uncertainty about the population status, recreational and subsistence harvest of brown bears has been liberalized since 2007 on the Peninsula. For many years prior to 2007, the only mechanism for legal harvest of brown bears was a limited fall drawing that was contingent on a human-caused mortality cap of reproductive-aged females not being exceeded. In 2007, the federal subsistence harvest of brown bears was authorized (albeit only 2 bears) and shortly thereafter a spring drawing hunt was allowed by ADFG regardless of whether or not a drawing hunt had been held the previous fall. In 2012, recreation harvest was changed from a limited drawing to a general registration hunt. In 2013, hunting regulations were further liberalized by increasing harvest season length, allowing the take of brown bears at bait stations, allowing take of 1 bear per regulatory year (rather than every 4 years), and eliminating a previous annual harvest cap based on the number of reproductive-aged females. In 2014, an annual human-caused mortality cap that cannot exceed 70 bears or 17 adult females was re-established. This increase in hunting pressure on brown bears on the Kenai Peninsula is consistent with liberalized brown bear regulations over large areas of Alaska that have been pursued with the goal of increasing ungulate populations (Miller et al. 2011).

We are concerned about the long-term conservation of brown bears on the Kenai Peninsula. Mortality of 70 bears for a population estimated to be 582 brown bears is 12%, more than twice the value that Miller (1990) recommended for all sources of human-caused mortality. Furthermore, the absence of significant inbreeding and population substructuring reported by Jackson et al. (2008) are likely fragile demographic statistics because this brown bear population is peninsular with lower mtDNA haplotypic diversity than most other brown bear populations in Alaska (Jackson et al. 2008). Many of the concerns expressed by Kendall et al. (2009) for a similarly sized grizzly bear population in northwestern Montana are relevant including the need for a more rigorous monitoring program.

MANAGEMENT IMPLICATIONS

Our peninsula-wide estimated population of 582 brown bears in June 2010 with a 95% lognormal confidence interval of 469–719 provides a lower bound for management of this population. Human-caused mortality has increased through time even as a recent estimate of λ at 1.039 (95% CI = 1.036–1.043) for 1995–2011 (Farley 2011) indicates that the population was increasing prior to recent liberalization of recreational hunting harvests. Future decisions on the management of this population should be based on our benchmark population estimate.

ACKNOWLEDGMENTS

We thank ADFG for sharing telemetry and genetics data. J. Boulanger, K. C. Kendall, T. L. McDonald, G. Pendleton, N. Roberts, J. A. Royle, K. Titus, L. J. Van Daele, and 2 anonymous ADFG personnel reviewed earlier versions of this report. M. I. Goldstein helped with the original proposal. Field personnel were M. L. Bowser, S. E. Bradley, T. D. Eskelin, J. Heydinger, N. J. Lester, A. Neurock, B. Parsons, S. D. Parkin, R. Ruffner, C. Whitaker and R. S. Zulueta. Technical support was provided by T. A. Burke, R. D. Ernst, E. A. Jozwiak, M. W. Laker, D. R. Magness and T. C. Mullet. D. M. Perez and D. J. Handley assisted with radio dispatching and flight monitoring. J. Benson led WGI lab efforts. A. J. Loranger and M. E. Novy provided managerial support. This study was funded by the U.S. Fish and Wildlife Service and U.S. Forest Service. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of any government agencies.

LITERATURE CITED

Alaska Department of Fish and Game [ADFG]. 2000. Kenai Peninsula brown bear conservation strategy. Alaska Department of Fish and Game, Anchorage, USA. http://www.adfg.alaska.gov/static/research/plans/pdfs/kbbcs2.pdf. Assessed 23 Sep 2015.

Alho, J. M. 1990. Logistic-regression in capture recapture models. Biometrics 46:623–635.

Beier, L. R., S. B. Lewis, R. W. Flynn, G. Pendleton, and T. V. Schumacher. 2005. A single catch snare to collect brown bear hair for genetic mark-recapture studies. Wildlife Society Bulletin 33:766–773.

Berg, E. E., and R. S. Anderson. 2006. Fire history of white and Lutz spruce forests on the Kenai Peninsula, Alaska, over the last two millennia as determined from soil charcoal. Forest Ecology and Management 227:275–283.

Boulanger, J., K. C. Kendall, J. B. Stetz, D. A. Roon, L. P. Waits, and D. Paetkau. 2008. Multiple data sources improve DNA-based mark-recapture population estimates of grizzly bears. Ecological Applications 18:577–589.

Boulanger, J., and B. McLellan. 2001. Closure violation in DNA-based mark-recapture estimation of grizzly bear populations. Canadian Journal of Zoology 79:642–651.

Boulanger, J., M. Proctor, S. Himmer, G. Stenhouse, D. Paetkau, and J. Cranston. 2006. An empirical test of DNA mark-recapture sampling strategies for grizzly bears. Ursus 17:149–158.

Boulanger, J., G. Stenhouse, and R. Munro. 2004. Sources of heterogeneity bias when DNA mark-recapture sampling methods are applied to grizzly bear (*Ursus arctos*) populations. Journal of Mammalogy 85:618–624.

Boulanger, J., G. C. White, B. N. McLellan, J. Woods, M. Proctor, and S. Himmer. 2002. A meta-analysis of grizzly bear DNA mark-recapture projects in British Columbia, Canada. Ursus 13:137–152.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling. Oxford University Press, New York, New York, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, New York, New York, USA.

Craighead, J. J., J. R. Varney, and F. C. Craighead, Jr. 1974. A population analysis of the Yellowstone grizzly bears. Bulletin 40. Forest and Conservation Experiment Station, School Forestry, University of Montana, Missoula, USA.

Del Frate, G. G. 1999. Units 7 and 15 brown bear. Pages 55–71 *in* M. V. Hicks, editor. Management report of survey-inventory activities, 1 July 1996–30 June 1998; Federal Aid in Wildlife Restoration, Project W-24-5 and W-27-1; Study 4.0. Alaska Department of Fish and Game, Juneau, USA.

Dial, R. J., E. E. Berg, K. Timm, A. McMahon, and J. Geck. 2007. Changes in the alpine forest-tundra ecotone commensurate with recent warming in southcentral Alaska: evidence from orthophotos and field plots. Journal of Geophysical Research 112:G04015.

Farley, S. 2010. Ecological studies of the Kenai Peninsula brown bear. Interagency collaborative project progress report, Project AG-0120-P-08–0042. Alaska Department of Fish and Game, Anchorage, Alaska, USA.

Farley, S. 2011. Kenai Peninsula brown bear population demographics. Federal Aid annual research performance report. Alaska Department of Fish and Game, Anchorage, USA.

Flynn, R. W., S. B. Lewis, L. R. Beier, G. W. Pendleton, A. P. Crupi, and D. P. Gregovich. 2012. Spatial use, habitat selection, and population ecology of brown bears along the proposed Juneau Access Improvements Road Corridor, Southeast Alaska. Final wildlife research report, ADF&G/DWC/WRR-2012-04. Alaska Department of Fish and Game, Juneau, USA.

Goldstein, M. I., A. J. Poe, L. H. Suring, R. M. Nielson, and T. L. McDonald. 2010. Brown bear den habitat and winter recreation in south-central Alaska. Journal of Wildlife Management 74:35–42.

Harris, G., S. Farley, G. J. Russell, M. J. Butler, and J. Selinger. 2013. Sampling designs matching species biology produce accurate and affordable abundance indices. PeerJ 1:e227.

Hilderbrand, G. V., T. A. Hanley, C. T. Robbins, and C. C. Schwartz. 1999*a*. Role of brown bears *(Ursus arctos)* in the flow of marine nitrogen into a terrestrial ecosystem. Oecologia 121:546–550.

Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, M. E. Jacoby, T. A. Hanley, S. M. Arthur, and C. Servheen. 1999*b*. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Canadian Journal of Zoology 77:132–138.

Huggins, R. M. 1989. On the statistical analysis of capture experiments. Biometrika 76:133–140.

Huggins, R. M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. Biometrics 47:725–732.

Interagency Brown Bear Study Team [IBBST]. 2001. A conservation assessment of the Kenai Peninsula brown bear. Alaska Department of Fish and Game, U.S. Fish and Wildlife Service, National Park Service, and USDA Forest Service. http://www.fws.gov/uploadedFiles/Farley_SF_et_al_2001.pdf. Accessed 27 Sep 2015.

Ivan, J. S., G. C. White, and T. M. Shenk. 2013*a*. Using auxiliary telemetry information to estimate animal density from capture-recapture data. Ecology 94:809–816.

Ivan, J. S., G. C. White, and T. M. Shenk. 2013*b*. Using simulation to compare methods for estimating density from capture-recapture data. Ecology 94:817–826.

Jackson, J. V., S. L. Talbot, and S. Farley. 2008. Genetic characterization of Kenai brown bears (*Ursus arctos*): microsatellite and mitochondrial DNA control region variation in brown bears of the Kenai Peninsula, south central Alaska. Canadian Journal of Zoology 86:756–764.

Jacobs, M. J. 1989. An initial population analysis and management strategy for Kenai Peninsula brown bears. Thesis, West Virginia University, Morgantown, USA.

Kendall, K. C., J. B. Stetz, J. Boulanger, A. C. Macleod, D. Paetkau, and G. C. White. 2009. Demography and genetic structure of a recovering grizzly bear population. Journal of Wildlife Management 73:3–17.

Kendall, K. C., J. B. Stetz, D. A. Roon, L. P. Waits, J. B. Boulanger, and D. Paetkau. 2008. Grizzly bear density in Glacier National Park, Montana. Journal of Wildlife Management 72:1693–1705.

Klein, E., E. E. Berg, and R. Dial. 2005. Wetland drying and succession across the Kenai Peninsula Lowlands, south-central Alaska. Canadian Journal of Forest Research 35:1931–1941.

Mace, R. D., J. S. Walker, T. M. Manley, L. J. Lyon, and H. Zuuring. 1996. Relationship among grizzly bears, roads, and habitat in the Swan Mountains Montana. Journal of Applied Ecology 33:1395–1404.

Miller, S. D. Population management of bears in North America. 1990. International Conference on Bear Research and Management 8:35–373.

Miller, S. D., J. W. Schoen, J. Faro, and D. R. Klein. 2011. Trends in intensive management of Alaska's grizzly bears, 1980–2010. Journal of Wildlife Management 75:1243–1252.

Miller, S. D., G. C. White, R. A. Sellers, H. V. Reynolds, J. W. Schoen, K. Titus, V. G. Barnes, Jr., R. B. Smith, R. R. Nelson, W. B. Ballard, and C. C. Schwartz. 1997. Brown and black bear density estimation in Alaska using radio-telemetry and replicated mark-resight techniques. Wildlife Monographs 133:1–55.

Mowat, G., and S. Strobeck. 2000. Estimating population size of grizzly bears using hair capture, DNA profiling, and mark-recapture analysis. Journal of Wildlife Management 64:183–193.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical-inference from capture data on closed animal populations. Wildlife Monographs 62:1–135.

Paetkau, D. 2003. An empirical exploration of data quality in DNA-based population inventories. Molecular Ecology 12:1375–1387.

Park, S. D. E. 2001. Trypanotolerance in West African cattle and the population genetic effects of selection. Thesis, University of Dublin, Ireland.

Pearson, A. M. 1975. The northern interior grizzly bear *Urus arctos* L. Canadian Wildlife Service Report Series 34, Ottawa. http://parkscanadahistory.com/wildlife/report-34.pdf. Accessed 27 Sep 2015.

Pledger, S. 2005. The performance of mixture models in heterogeneous closed population capture-recapture. Biometrics 61:868–873.

Poole, K. G., G. Mowat, and D. A. Fear. 2001. DNA-based population estimate for grizzly bears *Ursus arctos* in northeastern British Columbia, Canada. Wildlife Biology 7:105–115.

Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. Biometrics 52:703–709.

Proctor, M., B. McLellan, J. Boulanger, C. Apps, G. Stenhouse, D. Paetkau, and G. Mowat. 2010. Ecological investigations of grizzly bears in Canada using DNA from hair, 1995–2005: a review of methods and progress. Ursus 21:169–188.

Suring, L. H., K. R. Barber, C. C. Schwartz, T. N. Bailey, W. C. Shuster, and M. D. Tetreau. 1998. Analysis of cumulative effects of brown bears on the Kenai Peninsula, southcentral Alaska. Ursus 10:107–117.

Suring, L., and G. Del Frate. 2002. Spatial analysis of locations of brown bear killed in defense of life or property on the Kenai Peninsula, Alaska, USA. Ursus 13:237–245.

Suring, L. H., S. D. Farley, G. V. Hilderbrand, M. I. Goldstein, S. Howlin, and W. P. Erickson. 2006. Patterns of landscape use by female brown bears on the Kenai Peninsula, Alaska. Journal of Wildlife Management 70:1580–1587.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139.

White, G. C., and T. M. Shenk. 2001. Population estimation with radio-marked animals. Pages 329–350 *in* J. J. Millspaugh and J. M. Marzluff, editors. Design and analysis of wildlife radiotelemetry studies. Academic Press, San Diego, California, USA.

Zager, P., and J. Beecham. 2006. The role of American black bears and brown bears as predators on ungulates in North America. Ursus 17:95–108.

Zulueta, R. S. 2012. Residential perceptions of brown and black bears and human-bear conflict mitigation on the Kenai Peninsula of Alaska. Thesis, University of Wisconsin, Madison, USA.

Associate Editor: Scott McCorquodale.