THE KENAI BROWN BEAR POPULATION ON

KENAI NATIONAL WILDLIFE REFUGE

AND

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ABSTRACT

Field work for a DNA-based, mark-recapture estimate of the Kenai brown bear population on the Kenai National Wildlife Refuge and Chugach National Forest was conducted during 1 June–1 July 2010. Bears were attracted to barbed wire stations deployed in 145 9km x 9km cells systematically distributed across 11,500 km^2. Using two Bell 206B helicopters and four 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 collected 11,175 hair samples during the sessions from both black and brown bears, and another 91 hair samples were collected from other sources. Extracted DNA was used to identify individual bears and develop capture histories as input to mark-recapture models. Combined with data from ADFG-collared bears, at least 211 brown bears were known to be alive on the Kenai Peninsula in 2010. AIC selection of DNA-based mark-recapture models, based on 99 females and 104 males, resulted in an estimate of 428 (95% lognormal CI = 353–539) brown bears (including all age classes) on the study area. Extrapolating the density estimate of 45.1 bears per 1,000 km^2 of available habitat on the study area to the Kenai Peninsula suggests a peninsula-wide population of 624 brown bears (95% lognormal CI = 504–772).

Key words: *Alaska, brown bear, Chugach National Forest, genetics, hair DNA, Kenai National Wildlife Refuge, mark-recapture, Pradel model, population, Program Mark,* Ursus arctos

INTRODUCTION

The grizzly or brown bear (*Ursus arctos*) population on the Kenai Peninsula in south-central Alaska is a keystone species (IBBST2001). Kenai brown bears influence plant distribution and abundance through seed dispersal in feces, transport marine-derived nutrients into terrestrial ecosystems through salmon consumption (Hilderbrand *et al.* 2005), and possibly regulate ungulate populations through neonatal predation under certain conditions (Zager and Beecham 2006). Kenai 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 (ADFG 2000).

The 16-km wide isthmus that separates the 24,300 km^2 Kenai Peninsula from the adjacent mainland presumably restricts brown bear emigration and immigration. Talbot *et al*. (2009) verified that the Kenai brown bear population is indeed insular, significantly differentiated from the nearby Anchorage brown bear population and showing less genetic diversity than mainland Alaskan brown bear populations, based on both microsatellite loci and mitochondrial DNA control region data.

The Kenai Peninsula is also one of the fastest urbanizing areas in Alaska, with ~10,000 new residents added every decade since 1960 (U.S. Census Bureau). Over this same 50-year period, Kenai brown bears killed in defense of life or property (DLP) have increased from <1 per year in the 1960s, to 5 per year in the 1990s, and to 16 per year since 2000 (Suring and Del Frate 2002, ADFG unpubl. data). Legal harvest of brown bears has varied with hunting regulations over this same period, ranging from 0 per year during much of the past decade to 21 individuals in 1993. In 2008 alone, 42 brown bears were reported killed by DLPs, legal harvest, and other human sources (ADFG unpubl. data). The demographic significance of increasing human-caused mortality is uncertain because the population size has not been empirically estimated and, at the time of the study, statistical bounds on estimates of the intrinsic rate of population growth (λ) straddle 1.0 (IBBST 2001, Farley 2010).

In 1998, the Kenai brown bear was designated a population of special concern by the State of Alaska because it "is vulnerable to a significant decline due to low numbers, restricted distribution, dependence on limited habitat resources, or sensitivity to environmental disturbance" (KPBBCS 2000)(NOTE: In Aug 2011, the State eliminated the "species of special concern" list but their previous status is footnoted in Appendix 7 of the Alaska State Wildlife Action Plan). The Interagency Brown Bear Study Team (IBBST), composed of scientists from the Alaska Department of Fish and Game (ADFG), Kenai National Wildlife Refuge, Chugach National Forest, and Kenai Fjords National Park, recognized that a rigorous estimate of the Kenai brown bear population was desirable (IBBST 2001). However, unlike many other areas in Alaska which support brown bears, the Kenai Peninsula is heavily forested, making aerial estimation methods problematic because of low detectability.

Consequently, we chose to use a DNA-based, mark-recapture design to estimate the Kenai brown bear population (Mowat and Strobeck 2000, Poole *et al.* 2001, Kendall *et al.* 2008). Our objectives were to estimate the brown bear population ± 25% of the true number (*N*) on the Kenai National Wildlife Refuge

and Chugach National Forest.   Secondary objectives included determining the sex ratio and the minimum brown bear population occurring within these two Federal conservation units. We conducted our study in June, shortly after brown bears have left mostly high-elevation dens (Goldstein *et al.* 2010) but before most salmon have returned to streams on the Kenai Peninsula (Jacobs 1989). Consequently, we included covariates to test our *apriori* hypotheses that capture rates increased with elevation and were unaffected by proximity to anadromous fish streams at this time of year. We tested for geographic population closure by modeling capture rate as functions of distance to edge of sample frame and distance to apparent open edge (Boulanger and McLellan 2001). We applied the Pradel model (1996) to further test assumptions of both geographic and demographic closure (*i.e.*, negligible change in birth and death rates) during our study.

METHODS

Study area
The Kenai Peninsula juts into the Gulf of Alaska, embraced on the west by the Cook Inlet and on the east by Prince William Sound (Figure 1). Elevations range from sea level to 2,015 m in the Kenai Mountains. Biodiversity is unusually high for this latitude because of the juxtaposition of two biomes on the peninsula: the northern fringe of Sitka spruce-dominated (*Picea sitchensis*) coastal rainforest on the eastern flank of the Kenai Mountains, and transitional boreal forest to the west. The latter forest types include 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. Lichen-dominated tundra replaces mountain hemlock (*Tsuga mertensiana*) and sub-alpine shrub above treeline.

The study area includes 11,700 km^2 of the peninsula on lands administered by Kenai National Wildlife Refuge and Chugach National Forest (Figs. 1,2). The area is 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 Refuge boundaries. The study area includes 127 (1,390 km) of 250 named streams identified on the Kenai Peninsula in the *Catalog of Waters Important for the Spawning, Rearing or Migration of Anadromous Fishes* (http://www.adfg.alaska.gov/sf/SARR/AWC/).

With the exception of the southwest corner of the peninsula (*i.e.,* south of Caribou Hills), the study area effectively includes all known and modeled areas of brown bear habitation on the peninsula (IBBST 2001). On average, 87% (SE = 0.03) of 144,024 telemetry locations from 125 brown bear adult and subadult females radio-collared by the IBBST during 1987-2005 were on the study area (Fig. 3). Excluding all telemetry locations collected after 1 July reduces the data set to 7,413 locations from 114 brown bear females; 11 females (9%) were never on the sample frame during the period when this study was conducted. The proportion of telemetry points on the sample frame, averaged for the 114 females, was 84% (SE = 0.03); 75 of 114 females were on the sample frame during the entire sampling

window. Similarly, of 74 brown bear females for which den sites are known from 1996-2003, 84% denned at least once on the study area (Figure 2).

Study design
We noninvasively collected brown (and black; *Ursus americanus*) bear hairs at barbed-wire stations subjectively placed within 145 9km x 9km cells systematically arrayed across the study area (Figure 4). After an initial 6-day deployment period, we employed a rotating panel design in which five panels of 29 cells each were revisited on five consecutive 5-day trap sessions.   All cells were visited by two-person field crews transported by Bell 206-B Jet Ranger helicopters over 31 consecutive days from 1 June–1 July 2010. Field crews and helicopters were stationed in Soldotna and Moose Pass (Figure 1).

Using expert judgment (see criteria below), we *a priori* selected primary and secondary sites within each cell on which to place hair stations; the final coordinates were frequently adjusted in the field to better reflect *in situ* conditions. If hair samples were not obtained by the end of the third trap session, we either 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 hunting), on rub trees, and from live bears handled during collaring operations incidental to this study.

Site selection for hair sampling stations
Using GIS, we eliminated all lands from sampling that are restricted by ADFG for black bear baiting: no baiting within 1 mile of any residence, including seasonally occupied dwellings, developed recreational facilities or campgrounds; no baiting within 1/4 mile of any publicly-maintained road, trail, or the Alaska Railroad; and no baiting within 1/4 mile from the shoreline of the Kenai, Kasilof and Swanson Rivers (including Kenai and Skilak Lakes).   In total, 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 two locations for hair sampling stations within each cell from digital ortho quads (DOQs):

1) adequate space for helicopter access;
2) ≥200 m from anthropogenic features (trails, cabins, roads);
3) riparian/wetland corridors associated with stream morphology were given first priority;
4) other travel corridors considered were associated with discontinuity between vegetation types, avalanche chutes, shoulders between peaks, and ridges; and
5) other things being equal, trying to ensure spatial separation among sites within the cell.

Hair stations, sampling and processing
Hair was sampled 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 two 30-m long double-stranded barbed wires around ≥ 3 trees or rebar stakes to approximate an equilateral triangle at two

heights (20–30 and 60–70 cm above ground) to increase the likelihood of sampling both adult bears and cubs. Logs, rocks, litter, and other debris were piled in the center of these hair stations to simulate a cache. We used ≥ 3 liters of fermented 3:1 cow blood (The Beef Shop, Centralia, WA) and pure, unprocessed fish oil (Kodiak Fish Meal Company), respectively, as lure per station per visit. Other substances (*e.g.*, fruit extract, spice oils, anise) were used to augment lures. Signs were posted to both warn and inform public who may have accidentally encountered these sites.

All hair was collected with forceps and/or gloves, and placed in coin envelopes; one envelope for each barb cluster. Each coin envelope was bar-coded (Linton Co.) and labeled with station ID, date, barb number, and location (upper strand, lower strand). Barbs were burned with a propane torch to remove any remaining hair after collection. Any hair on the ground below barbed wire strands were collected but not used in the analysis. Immediately before leaving, the simulated cache was freshened with more lure.

Hair was dried overnight in opened envelopes if the samples were wet at time of collection. Hair was stored at room temperature with desiccant. To minimize DNA degradation, hair samples were sent to the lab as soon as possible after field work was completed. All unused hair samples (from both brown and black bears) were archived.

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 by Kendall *et al*. (2009). To reduce costs, samples were excluded from genetic analysis if they contained no guard hairs with roots, and < 5 underfur, or if they were clearly from ungulates based on appearance. We also excluded over 5,000 guard hair samples that were jet black along their entire length, which we felt could be reliably identified as black bear hair in this study area. DNA was extracted from the remaining samples using QIAGEN DNeasy tissue kits, 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, clumps of hair were wound together and placed into the first extraction buffer (buffer ATL). In both cases, a warm water wash was used to remove dirt from the hairs before placing them in the extraction buffer.

DNA extracts were prescreened with the marker *G10J*, both to weed out weak samples and to separate black bear samples 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, MU23) with average heterozygosity > 0.72 in Kenai brown bears, as well as an amelogenin sex marker.

The multilocus microsatellite analyses were performed 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 (clean up) involved those samples which 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. Some of the cleanup was repeated several times before high confidence was developed for all 8 markers based on criteria for signal strength and legibility (samples with low confidence scores at 1 or more markers were excluded from individual identification at the end of the clean up process). In the third (error-checking) phase of genotyping, the remaining samples were subjected to a computerized search for similar pairs of genotypes that might have been created by genotyping error, and the mismatching markers were reanalyzed in these similar pairs. Once the genotypes are completed and checked for errors, a computer search for identical genotypes was performed and individuals defined for each unique 8-locus genotype. Finally, we cross-referenced these genotypes with samples from 2 studies that had previously been conducted by Kenai National Wildlife Refuge in 2005 and 2006.

Comparison with DNA previously collected by ADFG and IBBST
The USGS Alaska Science Center (ASC) maintains a database of 211 genotypes from Kenai brown bear samples that had been collected during past research by ADFG and IBBST, including 39 brown bears known to have telemetry collars and be alive during this study. ADFG agreed to identify genotypes from our study that had been previously "captured".

Microsatellite genotypes in the ASC/ADFG database include 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 are 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, pers. com.)

Excel Microsatellite Toolkit (version 3.3.1, available at http://animalgenomics.ucd.ie/sdepark/ms-toolkit/) was used to generate matches based on the 6 loci shared in common by all individuals in both databases. Matches at additional loci were verified by visual examination. All matches that differed at one allele were examined to verify the differences were not due to PCR artifacts or genotyping error (data not shown). Additionally, sex of matching genotypes was confirmed as one more means of checking error (S. Talbot, pers. com).

Mark-recapture models
Encounter histories were constructed with 6 occasions: 1 for bears known to be alive and on the sample frame (labeled occasion 0), and 5 occasions for the 5 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. Four individual covariates were considered 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). For these variables, we averaged over all captures of an individual. We also considered thresholds of 4.5 and 9 km for DTE, and 4.5, 9, 18 and 27 km for DTOpenE; *i.e.*, the values were truncated when the true value exceeded these values. We modeled trapping effort as the number of days of hair trap availability during each of the 5 occasions.

To assess the potential for use of Pledger heterogeneity models (Pledger 2005) for the 5 trapping occasions, a binomial distribution restricted to the positive integers (zero-truncated) was fitted 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 deemed necessary. If frequencies did not follow a zero-truncated binomial, Pledger models were deemed necessary and were included during subsequent modeling. Subsequent modeling of the combined data set considered detection probabilities for occasion 0 to be sex-specific, since more females than males carried radio collars and were known to be alive and on the study area. The time-varying models considered for occasions 1– 5 were constant capture probabilities across time and time-specific capture probabilities. The basic time-and-individual-varying models considered for occasions 1 – 5 were the time-varying models plus a sex effect and a sex interaction. In addition, the covariates DTE, DTOpenE, ELEV and DTA were added to these models, as well as DTE with thresholds of 4.5 km and 9 km and DTOpenE with thresholds of 4.5, 9, 18, and 27 km. To evaluate time-specific effects on detection probabilities, a fully time-specific model with 5 parameters and a trapping effort model with 2 parameters were used, with values of 826, 717, 767, 731, and 752 hair-snare days for each of the 5 occasions. The Huggins conditional likelihood parameterization (Huggins 1989, 1991; Alho 1990) was used to estimate population size as a derived parameter:

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

All models assume no behavioral effect of capture; *i.e.*, the capture probability of bears that have been detected once does not change for additional detections. Analyses were conducted with Program MARK (White and Burnham 1999) using information-theoretic model selection criteria (AIC$_c$) and model averaging of population estimates (Burnham and Anderson 2002). AICc weights for Pledger models were computed 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 both 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 both apparent survival (φ) and fecundity (*f*) estimated, φ fixed to 1 with *f* estimated, *f* fixed to 0 with φ estimated, and both φ fixed to 1 and *f* fixed to 0.

RESULTS

Field implementation

We originally proposed to sample 190 hair stations deployed in a systematic grid of 8km x 8km cells. However, it became very apparent on Day 1 (1 June) that we would have trouble completing this sample design. Although we were deploying stations in the panel closest to fuel depots, the Moose Pass and Soldotna helicopters logged 6.9 and 7.5 hours in flight time, respectively. On Day 2 (2 June), we decreased the number of hair stations from 190 to 145 by increasing the cell size to 9km x 9km. However, the overall spatial footprint of the panels was not decreased, and it was reflected in flight times of 7.2 and 7.3 hours for the Moose Pass and Soldotna helicopters, respectively. Consequently, on Day 3 (3 June), we completely reshuffled the panels, clustering cells around fixed and mobile fuel depots to reduce daily flight time (Figure 4). We had lost irretrievable time by then, so the initial deployment of stations required 6 (rather than 5) days, thereby extending the sampling period through 1 July.

Despite an unusually rainy and cold June in 2010, the sampling schedule for the panels was sustainable after we established the 9 km x 9 km grid array (Figure 4). A station was never deployed in cell 141 because of persistent snow cover early, and poor weather later in the study. Due to a prolonged period of inclement weather in Prince William Sound, we were unable to sample 6 cells (116,135,136,137,145,146) in the same panel (Figure 4, panel E) during the 2nd revisit; cell 135 was also not sampled during the 4th revisit for the same reason. Visits to a cell were occasionally delayed due to poor weather or an unusually persistent bear but, with the exception of above 6 cells, all cells were sampled before the next scheduled visit.

Hair samples

We collected 11,175 samples of brown and black bear hair from the 144 primary stations and 7 secondary stations. The 1st revisit had the lowest return (1,550 samples) presumably because trap session length varied from 1–9 days due to modifications to the grid design during the first 3 days of deployment. However, the number of samples collected exceeded 2,100 for each of the other 4 revisit sessions, each averaging 5 days.

In addition to hair samples collected at hair stations with lures, 91 samples were collected from rub trees by USFS staff at Quartz Creek and the confluence of the Kenai and Russian Rivers, and by a USFWS technician who collected samples from his permitted black bear baiting station on the Kenai Lowlands. In total, 11,266 hair samples were considered in these analyses.

Genotypes

DNA was extracted from 2,671 of 11,266 samples. This subset included 224 extractions of samples that were visually classified as black bear samples, starting with 50 samples that were extracted specifically to test the visual species identifications, and then adding 174 samples that were extracted at a later date for an occupancy analysis that will be the subject of a future report. Some of these 224 samples failed during genetic analysis, but the successful samples all had odd numbered alleles at G10J,

confirming the accuracy of the visual species identifications as black bears. The prescreen process with marker G10J produced high confidence, even-numbered scores indicating brown bears for 1,226 of 2,671 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 represented by the 1,034 successful brown bear samples, of which 166 were identified from hair collected on the sample frame. Of the 211 unique brown bears (*i.e.*, excluding ADFG bears), 47 were detected in ≥ 2 sessions, 5 were detected in 1 session but also identified in other studies or nonstudy samples, 114 were captured once, 11 were captured only in nonstudy samples, and 34 were not captured but previously identified in other studies or nonstudy samples.

Based on sex and perfect matches at 6–9 loci, 32 of these bears were identified as previously handled bears by ADFG or the IBBST. Six of the previously handled individuals were males, captured by ADFG or the IBBST during radio-collaring operations that targeted females. Five of the 34 radio-collared 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.

Species identity was confirmed 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.

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 roughly 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).

Radio-collared female brown bears
We located 30 radio-collared female brown bears during 5 days of aerial tracking from 26 June–4 July 2010. We combined these locations with telemetry data received from ADFG in March 2012 which represented data collected during the study but previously unavailable. Together the samples of radio-

collared female brown bears provided geographic locations of 39 females known to be alive in June 2010 on the Kenai Peninsula; 5 were not on the sample frame (Figure 6).

Population estimation

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 considered 203 bears (99 females, 104 males) for analysis. Of these 203 individuals, 65 females and 101 males were detected at hair stations, 5 females and 3 males were detected at rub trees, and 29 females were known to be alive and on the sample frame during the study period. Occasion 0 was composed of 41 brown bears known to be alive and on the sample frame during the study, including 34 collared females and 7 bears captured on rub trees [note: 1 sow was both collared and detected on a rub tree].

Capture frequencies of the bears detected on the sample frame (n = 166) were 3 detections (3 females, 5 males), 2 detections (17 females, 21 males), and 1 detection (45 females, 75 males). The zero-truncated binomial fit to these frequencies suggested no lack of fit (P = 0.959 females, P = 0.791 for males). Further, the AICc weight for 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 capture probabilities tended to increase with each successive trap session (Table 4) despite the fact that bears were exposed to traps for approximately the same time period (~ 5 days) during each of the 5 occasions. Consequently, model selection results (Table 2) suggested that a time-specific model was necessary to explain the variation in detection probabilities for occasions 1–5, and that an additive sex effect was needed to explain differences between sexes. These effects resulted in the base model of {sex*p(0), sex+p(t)}. ELEV and DTE covariates were useful predictors of detection probabilities when these covariates were added to the base model {sex*p(0), sex+p(t)}, although DTE did not improve upon the base model. Detection probabilities declined with ELEV (Figure 7) and increased with smaller DTE values (Figure 8); *i.e.*, bears closer to the edge had higher detection probabilities. When DTA and DTOpenE were added to the base model {sex*p(0), sex+p(t)}, as well as truncated values of DTE and DTOpenE, none of the models produced smaller AIC_c values than the base model. Model averaging of the population estimates (Table 3) suggests 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.

The model weights for the 4 Pradel models considered (Table 5) show that 98% of the AICc weight is on the model with φ fixed to 1 and *f* fixed to 0. That is the model best supported assumes no emigration or

immigration, and thus provides further evidence that the hair snare sampling grid can be assumed geographically and demographically closed.

DISCUSSION

This study produced the first empirically-based estimate of brown bear abundance on the Kenai Peninsula, Alaska. As with all population estimates of vertebrates in remote locations, the study design was a compromise among fiscal constraints, logistics, and statistical rigor. The resulting estimate provides a sound foundation for management agencies and others to consider land and resource decisions.   Favorable characteristics of the study area combined with a robust survey sample design along with careful analysis resulted in an estimate that fit the assumptions for mark-recapture remarkably well. Despite these strengths, application of the results will be most effective if certain characteristics of the investigation and of the modeling process are understood. Below we examine the characteristics of our estimate to clarify interpretation of the results.

Study design and modeling considerations
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 x 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 chose 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 the Kenai National Wildlife Refuge and Chugach National Forest, an area that approximates 70% of the known brown bear habitat on the Kenai Peninsula.

The short trap session (5 days), and consequently 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). 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 both the effectiveness of our lures and our study design (because bears begin congregating along streams; Figure 8b). To test for this characteristic of our design, we examined capture rates in relation to salmon streams -- as expected (given our spring trapping), distance to anadromous streams did not significantly improve the model (Table 2).

The shorter trap sessions also limited exposure of samples to the elements which can degrade DNA samples. Our genotyping success was comparatively high (D. Paetkau, pers. comm.). The short trapping session can be particularly important in DNA-sample quality if there is a bias towards samples being collected shortly after deployment when the lure is freshest. Furthermore, keeping the trap session short significantly reduced the cost of the study as the two helicopters and their fuel were the single biggest expense. Finally, the short sampling window provides reasonable assurance of demographic closure (see below).

Per-occasion capture probabilities in our study did not exceed 0.17 for males and 0.11 for females (Table 4). These values were slightly lower than the mean capture probability of 0.19 per 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 low number of trap occasions and the low detection probabilities have two 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.*, that 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, as well as all models that include a component to model individual heterogeneity, performs poorly when the data display little individual heterogeneity and/or 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.

Model selection with AIC is used in our analyses because of the need to recognize uncertainty in which models should be used to make inference about the population size (Burnham and Anderson 2002). A wide range of models is presented in Table 2. The "best" model is the model with the smallest, or minimum, AIC value. However, other models in Table 2 are "close" to the minimum model shown at the top of the list. To account for uncertainty among models, we use model averaging, based on model AIC weights shown in Table 2, to obtain an estimate of population size. If we chose to only present the estimates from the minimum AIC model, we know from theory and simulation that the confidence intervals from this model would be unrealistically narrow because a single model cannot account for the model selection uncertainty. By taking a weighted average of the population estimates, we have accounted for model selection uncertainty in the results presented in Table 3.

Lognormal confidence intervals are presented in Table 3 because of the skewness of the distribution of population estimates. This is a well established approach that accounts for the firm lower bound on the number of animals in the population provided by the number of individuals known to be alive in the population. In contrast, the upper bound is not constrained and results in a long upper tail on the sampling distribution of population estimates.

Population estimate and model assumptions

Based on 203 individual genotypes, we estimated that 428 brown bears were on the Kenai National Wildlife Refuge and Chugach National Forest in June 2010. Although we detected 41% fewer females than males, model-averaged population estimates show essentially the same number by sex (Table 3). The estimate of females is increased considerably by accounting for the females known to be on the study area but never detected at hair stations (34 females and 3 males were known to be alive and on the study area, but never detected at hair stations). Model-averaged population estimates for females and males from just hair stations were 114 and 194, respectively (Table 3). The difference in the estimates from the full analysis that included the bears known to be on the study area but never detected at hair stations, versus the analysis of only hair-snare detections, provides some idea of the bias of the hair-station only data; *i.e.*, not all bears were sampled by hair stations with equal probability. For example, Kendall *et al.* (2009) found 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.*, radio-collared) on the study area and bears detected by rub trees decreased the bias of their final estimate, just as the inclusion here of bears known to be on the study area has decreased the bias of our estimates.

Our evaluation of capture probabilities resulted in a more pronounced adjustment for females. Females of all ages had a lower hair station detection probability than males, as shown by Figures 7 and 8, and demonstrated by radio-collared 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 are 114 and 194, respectively; with inclusion of bears known to be in the population, the numbers increases to 215 and 214. The final estimate for females is 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.*, sows 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, because these 34 bears were undetected, demonstrates the lower capture probability of females. Both of these effects result in increasing the population estimate.

The estimated 50:50 sex ratio that results from our most robust estimate of abundance is unusual in the bear literature. Grizzly and brown bear studies elsewhere have generally estimated more adult females than males, typically 60:40; e.g., Pearson (1975), Craighead et al. (1974). 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. Unpublished ADFG data from 1967-2011 shows that 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. Similarly, an analysis of the age structure of 256 brown bear females captured from 1995–1999 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).

We are confident that the assumption of geographic closure was appropriate for estimating abundance of this population. Distance to edge was originally examined as a covariate to explore the potential violation of geographic closure. Our *apriori* hypothesis was that 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 (Figure 7b). We believe this outcome underscores the fact that the sample frame was bounded by real geographic barriers on ~88% of its 700-km perimeter; *i.e.*, ocean, glaciers, the isthmus (Talbot *et al.* 2009), and the urban interface (Suring *et al.* 1998, Mace et al. 1996), with only the southwest corner of the grid open to significant immigration/emigration from a small area south of Caribou Hills (Figure 4). Bears traveling along these barriers may move along the perimeter because they cannot (in the case of the former) or prefer not (in the case of the latter) 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 (Figure 7b), and the threshold models for DTE were not highly ranked models (Table 2). We explored the influence of the dominant 'open boundary' through a series of models labeled DTOpenE. Models exploring the influence of this edge (DTOpenE) were even less supported than the DTE models based on the AICc weights in Table 2. Finally, the Pradel model which assumes closure was the most supported model with 98% of the AICc weight. Thus, a range of evidence suggests that analysis with models that assume geographic closure was a reasonable choice for the population – potentially more so than in many mark-recapture investigations.

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. Study design which emphasized a short sample period in the spring suggests this would not be 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 as sows 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 Kenai brown bears is much greater than in interior grizzly populations. This attribute makes it more difficult to assume that a single strand would suffice for all sizes.

Multiple captures of different genotypes tended to NOT occur in the Kenai Lowlands in the northeast quarter of the same frame (Figure 5), and thus provides perspective on the spatial distribution of bear density. This area of the sample frame has the lowest elevation as well, and would thus seem somewhat inconsistent with the inverse relationship between ELEV and detection probability (Figure

7a). However, a retrospective analyses of 46 GPS-collared Kenai brown bear females show they move most in June (Figure 8a) and are furthest away from streams in June (Figure 8b). This is consistent with our conceptual model that most Kenai brown bears emerge in the spring from steeped-slope, high-elevation dens (Figure 2) through mid-May (Goldstein et al. 2010), move quickly towards lower-elevation calving areas for moose, and then move towards streams as the early runs of chinook and sockeye salmon enter streams in late June (Jacobs 1989). The exception is sows with cubs of the year, a cohort that will tend to remain at higher elevations near natal sites during early summer (IBBST 2001). 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 4) would explain 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 DTE and ELEV to capture probabilities (Figs. 7a, 7b) make more sense in this light.

Models considered but discarded

As noted earlier, the design of this study and the pattern of recaptures lead to a concern that capture heterogeneity was not being modeled well resulting in poor estimation of precision. We considered several options to address this issue. We carefully considered the Pledger mixture model but ultimately concluded this approach is not appropriate for our circumstances where multiple bears were known to be on the sample frame, but never detected at the hair sampling stations. Data from radio-collared bears makes it clear that numerous bears with no encounters occurred on the grid in June 2010; Consequently their hair station encounter history is all zeros. That is, we included 41 bears known to be alive and on the grid during sampling, of which only 4 were detected at the hair stations; thus, 37 bears had an encounter history of 100000. The Pledger mixture model evaluates this capture history and estimates probability of capture for this set as very near zero. When the count of bears is divided by this estimated capture probability (~ zero) the resulting population estimate will be near infinity. Thus, the Pledger mixture model cannot be applied to the hair-snare encounters in our situation.

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 3 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, 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, SECR models result in an estimate of bear density rather than abundance. Producing an estimate of abundance is accomplished by multiplying the estimated density by the size of the study area. This results in the problem familiar to all practitioners of mark-recapture modeling – determining the size of the sample area. For the SECR models, the issue includes problems associated with bears using the sample area but whose home range center does not occur in the study area. Finally, 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. SECR models developed with limited data generally require biologically unrealistic assumption of a circular area-of-activity. During June, bears on the Kenai are known to move directionally from dens toward moose calving areas 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. (2-13a, b) 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 radio-collared 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 snares to then monitor for use of the grid later. Further, the estimator of Ivan et al. assumes that animals do not change their home ranges after trapping is completed. This assumption is likely not appropriate for our study where bears were moving from den sites during June and likely changing the areas used over the course of the summer.

Management implications

We employed sophisticated models to estimate brown bear abundance on the Kenai Peninsula using a combination of non-invasive DNA sampling and information on radio-collared bears using mark-recapture estimators. Based on an understanding of bear biology, the pattern of recaptures, and the characteristics of the study area, we are confident that our approach did not suffer from confounding issues of geographic closure or demographic closure. However, it is clear from the data that female bears had very low recapture probabilities and it is likely that bears from both sexes had variable recapture probabilities. Therefore, based on an understanding of the performance of our estimators, we suggest that both the point estimate of bear abundance (428 brown bears) and the precision of our estimate (95% lognormal CI = 353–539) are likely biased low. This means that, given the known performance of our estimation approach, the true number of brown bears on our sample area in June 2010 was more likely to be above our point estimate than below. Furthermore, the 'true' 95% CI is likely to be broader than our estimate. These characteristics do not undermine our estimate; rather, we highlight these characteristics so that managers make decisions with a clear understanding of the nature of the estimate.

Our estimate of the Kenai brown bear population is generally consistent with estimates of brown bear density in interior, rather than coastal, Alaska (but see Flynn et al. 2012). Available habitat on the sample frame, after subtracting the Harding Icefield, water bodies, and the anthropogenic footprint, approximates 9,500 km^2, translating to a mean brown bear density of 45.1 per 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 that were characterized by abundant runs of multiple salmon species; these estimates for coastal bear populations ranged from 191–551 per 1,000 km^2. In contrast, brown bear densities (all ages) on 11 study sites in interior Alaska ranged from 10–30 per 1,000 km^2 (Figure 9). Our estimate places the Kenai population within the lower (<50 bears per 1,000 km^2) of two grizzly bear groups in North America based on density (Hilderbrand *et al.* 1999).

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 DTOpenE did not contribute to model fit, we have chosen to not adjust our density estimate.

Our density estimate is more than twice the 20 bears per 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 Sterling Miller: "Miller (pers. comm.; cited in IBBST 2001) 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 (expanding our estimate of 428 bears on the study area to the entire peninsula) and Del Frate's (1999) original value of 13,848 km^2 for available habitat, we estimate a peninsula-wide population of 624 brown bears in June 2010 with a 95% lognormal CI of 504–772 (estimator from Buckland et al. 2001:77). We believe this extrapolation is reasonable given that the sample frame encompasses ~70% of available brown bear habitat on the Kenai Peninsula and that the landcover on the study area and peninsula are similar (Table 1).

However, 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 radio-collared females in 2010 were representative of the larger Kenai 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 radio-collared females, or 38 sows with 43 young (= 1.13 young per adult female). Consequently, the estimate of 624 brown bears on the Kenai Peninsula would translate to approximately 200 adult females, 200 adult males, and 224 dependent young, of which 112 would be males and females each.

We emphasize that the approach Del Frate used to estimate the Kenai brown bear population in 1999 was logical at the time for management purposes and laudably conservation-minded. We caution that these 2 values should not be compared to make inferences regarding population growth, as the earlier value was a reasonable guess and the current value is a model-based estimate using empirical data. Other than increasing DLPs (which is confounded by an increasing human population), we have no empirical data to suggest that the brown bear population on the Kenai Peninsula has increased in the last 2 decades. The only published estimate of λ for the Kenai brown bear population was 1.0128 (95%

CI = 0.9364–1.0588) for 1995–99 (IBBST 2001); the confidence bounds make it difficult to determine the population trajectory but suggest a stable population. However, a recent unpublished λ estimate of 1.039 (95% CI = 1.036–1.043) for 1995–2011 (Farley 2011) suggests that the population may be increasing.

Conclusion

This DNA-based mark-recapture estimation of the Kenai brown bear population was unconventionally short in its duration, with capture sessions of only 5 days. We also increased our sample cell size to 9 km, which resulted in lower trap density. Both decisions were made, in part, to keep the cost of the study within reason.   Despite low capture rates and a strong sex bias in capture probabilities from hair 'trapping', we derived a robust population estimate by including additional data from bears known to alive and on the sample frame during the study (based on telemetry and rub trees). The resulting asymmetric lognormal confidence interval around the population estimate is 17–26% of the mean, achieving our original study objective.

We believe our grid-based approach, complemented with telemetry and rub-tree data, resulted in a credible method for estimating the brown bear population given the size of Kenai National Wildlife Refuge and Chugach National Forest. However, future application of this approach should attempt to use an 8 x 8 km grid, incorporate more secondary sites within cells (perhaps using only a single strand) to improve capture rates as well as more rigorous pursuit of independent samples from rub trees to increase the pre-marked 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 both a lure-based grid design to address closure issues, complemented with break-away hair snares along streams (*e.g.*, Beier et al. 2005, Flynn et al. 2012).

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ADMINISTRATIVE RECORD

9 Oct 2009	IACUC Assurance Form 2009016 approved
29 Apr 2010	ADFG Scientific Permit 10-100 approved
19 May 2010	Final proposal and working plan completed
28 May 2010	NEPA Categorical Exclusion approved
29 May 2010	Wilderness Minimum Requirements Analysis approved
31 May 2010	Aviation Safety Plan approved
1 Jun 2010	Field study implemented on 145 9km x 9km cells
1 Jul 2010	Field study completed
12 Aug 2010	CITES Export Permit 10US18165A/9 approved; hair samples submitted shortly thereafter
18 Jan 2011	Final brown bear DNA results returned from WGI; black bear pending
21 Jan 2011	DNA match requested from USGS/ADFG
5 Feb 2011	Preliminary population estimate by Gary White
26 Mar 2011	DNA match data received from USGS/ADFG
28 Mar 2011	Additional data requested from USGS/ADFG
2 Jun 2011	Match data confirmed by USGS
8 Jun 2011	Photographs from cameras reviewed; additional hair analysis requested for 2 sessions
10 Nov 2011	Draft final mark-recapture modeling by Gary White
14 Nov 2011	Close out USFS Reimbursable Contract #10IA11100400061
27 Jan 2012	Preliminary draft final report (for internal review)
12 Mar 2012	1st draft final report (for external review)
13 Mar 2012	Additional data received from ADFG (Vincent-Lang)
11 Apr 2012	Response from ADFG (Titus)
12 Jul 2012	2nd draft final report (for external review)
14 Aug 2012	Response from ADFG (Van Daele)
6 Sept 2012	3rd draft final report (for external review)
10 Sep 2012	Request external reviews from John Boulanger, Andy Royle and Kate Kendall
13 Nov 2012	4th draft final report (and additional analyses) based on external reviewers
19 Nov 2012	Interagency meeting in Anchorage to discuss reviews and make final recommendations

LITERATURE CITED

ADFG. 2000. Kenai Peninsula brown bear conservation strategy. Alaska Department of Fish and Game, Anchorage, AK. 74 pp.

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.

Boulanger, J., G.C. White, M. Proctor, G. Stenhouse, G. MacHutchon, and S. Himmer. 2008a. Use of occupancy models to estimate the influence of previous live captures on DNA-based detection probabilities of grizzly bears. J. Wildlife Manage. 72:589–595.

Boulanger, J., K.C. Kendall, J.B. Stetz, D.A. Roon, L.P. Waits, and D. Paetkau. 2008b. 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. Can. J. Zool. 79:642–651.

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. J. 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. Corchers and L. Thomas. 2001. Introduction to distance sampling. Oxford University Press, Inc., NY. 432 pp.

Burnham, K. P. and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2nd edition. Springer-Verlag, New York.

Craighead, J.J., J.R. Varney, and F.C. Craighead, Jr. 1974. A population analysis of the Yelowstone grizzly bears. Bull. 40. For. and Conserv. Exp. Stn., School Forestry, University of Montana, Missoula. 20 pp.

Del Frate, G.G. 1999. Units 7 and 15 Brown Bear. Pages 55–71 *in* M.V. Hicks (ed.), 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 Dept. Fish and Game, Juneau, AK.

Farley, S. 2010. Ecological studies of the Kenai Peninsula brown bear. Interagency collaborative project progress report, Project AG-0120-P-08-0042. Alaska Dept. Fish and Game, Anchorage, AK. 19 pp.

Farley, S. 2011. Kenai Peninsula brown bear population demographics. Federal Aid annual research performance report. Alaska Dept. Fish and Game, Anchorage, AK. 6 pp.

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. 106 pp.

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. J. Wildlife Manage. 74:35–42.

Harris, G., S. Farley, G.J. Russell, and J. Selinger. In prep. Sampling bears in locations with high resource density improves capture rates and accuracy while reducing effort. Unpubl. manuscript. 25 pp.

Hilderbrand, G..V., C.C. Schwartz, C.T. Robbins, M.E. Jacoby, T.A. Hanley, S.M. Arthur, and C. Servheen. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Can. J. Zool. 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. 48 pp.

Ivan, J. S., G. C. White, and T. M. Shenk. 2013a. Using auxiliary telemetry information to estimate animal density from capture-recapture data. Ecology in press.

Ivan, J. S., G. C. White, and T. M. Shenk. 2013b. Using simulation to compare methods for estimating density from capture–recapture data. Ecology in press.

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 J. Zool. 86:756–764.

Jacobs, M.J. 1989. An initial population analysis and management strategy for Kenai Peninsula brown bears. M.S. thesis. West Virginia University. 205 pp.

Lukacs, P.M., and K.P. Burnham. 2005. Review of capture-recapture methods applicable to noninvasive genetic sampling. Molecular Ecology 14:3909–3919.

Kendall, KC, JB Stetz, DA Roon, LP Waits, JB Boulanger, and D. Paetkau. 2008. Grizzly bear density in Glacier National Park, Montana. J. Wildlife Manage. 72:1693–1705.

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. J. Wildlife Manage. 73:3–17.

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. J. Applied Ecology 33:1395-1404.

McKelvey, K.S., and M.K. Schwartz. 2004. Providing reliable and accurate genetic capture-mark-recapture estimates in a cost-effective way. J. Wildlife Manage. 68:453–456.

Miller, S.D. Population management of bears in North America. 1990. International Conf. Bear Research and Manage. 8:35—373.

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. 55 pp.

Mowat, G., and S. Strobeck. 2000. Estimating population size of grizzly bears using hair capture, DNA profiling, and mark-recapture analysis. J. Wildlife Manage. 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.

Pearson, A.M. 1975. The northern interior grizzly bear *Urus arctos* L. Can. Wildl. Serv. Rep. Ser. 34. 84 pp.

Pledger, S. 2000. Unified maximum likelihood estimates for closed capture-recapture models using mixtures. Biometrics 56:434–442.

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.

Royle, J.A, K U. Karanth, A. M. Gopalaswamy, and N.S. Kumar. 2009. Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. Ecology 90:3233–3244.

Schwartz, C.C., S. D. Miller, and M. A. Haroldson. 2003. Grizzly bear. Pages 556-586 *in* G.A. Feldhamer, B.C. Thompson, and J.A. Chapman (eds.). Wild Mammals of North America: Biology, Management, and Conservation. Second edition. The Johns Hopkins University Press, Baltimore, MD.

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.

Talbot, S.L., G. K. Sage, and S.D. Farley. 2009. Brown bears of the Kenai Peninsula are genetically isolated from mainland south central and southwestern Alaskan populations (abstract only). U.S. Geological Survey, Alaska Science Center, Anchorage, AK. 2 pp.

Thompson, L.M., F. T. van Manen, and T. L. King. 2005. Geostatistical analysis of allele presence patterns among American black bears in eastern North Carolina. Ursus16:59–69.

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

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.

Table 1. Landcover on the study area and Kenai Peninsula based on a 2006 supervised classification of LANDSAT imagery.

Landcover types	Study area	Kenai Peninsula
	1,174,500 ha	2,433,777 ha
Alpine	16.7%	11.9%
Mixed forest	13.8%	9.6%
Black spruce	11.2%	6.2%
Alder	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	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 (balsam poplar)	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%

Table 2. Model selection results for closed capture population estimators in Program MARK for Kenai brown bears, June 2010. All models were constructed with a sex-specific detection probability for the capture occasion of bears known to be on the study area, labeled as sex*p(0).

Model	AIC$_c$	ΔAIC$_c$	AIC$_c$ Weights	# parameters	-2log(L)
{sex*p(0), sex+p(t)+Elev}	1032.48	0.00	0.7230	9	1014.33
{sex*p(0), sex+p(t)}	1038.10	5.62	0.0435	8	1021.98
{sex*p(0), sex+p(t)+DTE}	1038.51	6.04	0.0353	9	1020.37
{sex*p(0) p(t)}	1039.25	6.77	0.0245	7	1025.16
{sex*p(0), sex+p(t)+min(DTE,9000)}	1039.52	7.05	0.0213	9	1021.37
{sex*p(0), sex+p(effort)	1039.52	7.05	0.0213	5	1029.47
{sex*p(0), sex+p(t)+min(DTOpenE,18000)}	1039.67	7.20	0.0198	9	1021.52
{sex*p(0), sex+p(t)=+min(DTE,4500)}	1039.81	7.34	0.0185	9	1021.66
{sex*p(0), sex+p(t)=+min(DTOpenE,9000)}	1039.82	7.35	0.0184	9	1021.67
{sex*p(0), sex+p(t)=+DTOpenE}	1040.05	7.57	0.0164	9	1021.90
{sex*p(0), sex+p(t)=+DTA}	1040.10	7.62	0.0160	9	1021.95
{sex*p(0), sex+p(t)=+min(DTOpenE,27000)}	1040.11	7.64	0.0159	9	1021.97
{sex*p(0), sex+p(t)+min(DTOpenE,4500)}	1040.12	7.64	0.0158	9	1021.97
{sex*p(0), sex*p(effort)}	1041.39	8.91	0.0084	6	1029.32
{sex*p(t)}	1044.48	12.01	0.0018	12	1020.22
{sex*p(0), sex+p(Elev)}	1049.85	17.38	0.0001	5	1039.80
{sex*p(0), sex+p(.)}	1055.41	22.93	0.0000	4	1047.38
{sex*p(0), sex+p(DTE)}	1055.83	23.36	0.0000	5	1045.78
{sex*p(0), sex+p(min(DTE,9000))}	1056.83	24.35	0.0000	5	1046.78
{sex*p(0), sex+p(min(DTE,4500))	1057.12	24.64	0.0000	5	1047.07
{sex*p(0), sex+p(DTA)}	1057.40	24.92	0.0000	5	1047.35

Table 3. Population estimates and confidence intervals for Kenai brown bears, June 2010, using only hair collected on the sample frame (grid only), and incorporating data from radio-collared 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 incorporate information from $M(t + 1)$ into their calculation.

	Sex	Estimate	SE	M(t+1)	95% Lognormal CI	
					LCI	UCI
Occasion 0	Females	214.6	33.7	99	165.0	301.3
	Males	213.1	30.9	104	167.2	292.2
	Combined	427.6	46.7	203	353.2	539.1
Grid only	Females	114.2	17.1	65	90.4	160.4
	Males	194.1	26.4	101	155.0	261.5
	Combined	308.3	31.8	166	258.3	385.4

Table 4. Capture probabilities (pˆ) for the 5 hair capture occasions for male and female brown bears on the sample frame from the model {sex*p(0), sex+p(t)}, the second best model from Table 2. The values from this model represent the approximate mean estimate that is adjusted by ELEV for model {sex*p(0), sex+p(t)+ELEV} (minimum AICc model)and by DTE for model {sex*p(0), sex+p(t)+DTE} (third best model).

Sex	Occasion	Estimate	SE	95% Lognormal CI	
				LCI	UCI
Female	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
Male	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 5. Model selection results for the Pradel (1996) models used to assess closure of the sample framed.

Model	AICc	ΔAICc	Weights	Num. Par	-2log(L)
{φ(sex*t)=1 p(sex *t) f(sex *t)=0}	830.986	0.0000	0.979	10	809.934
{φ(sex *t) p(sex *t) f(sex *t)=0}	838.980	7.9941	0.018	16	804.301
{φ(sex *t)=1 p(sex *t) f(sex *t)}	843.011	12.0247	0.002	16	808.331
{φ(sex *t) p(sex *t) f(sex *t)}	846.916	15.9296	0.000	20	802.695
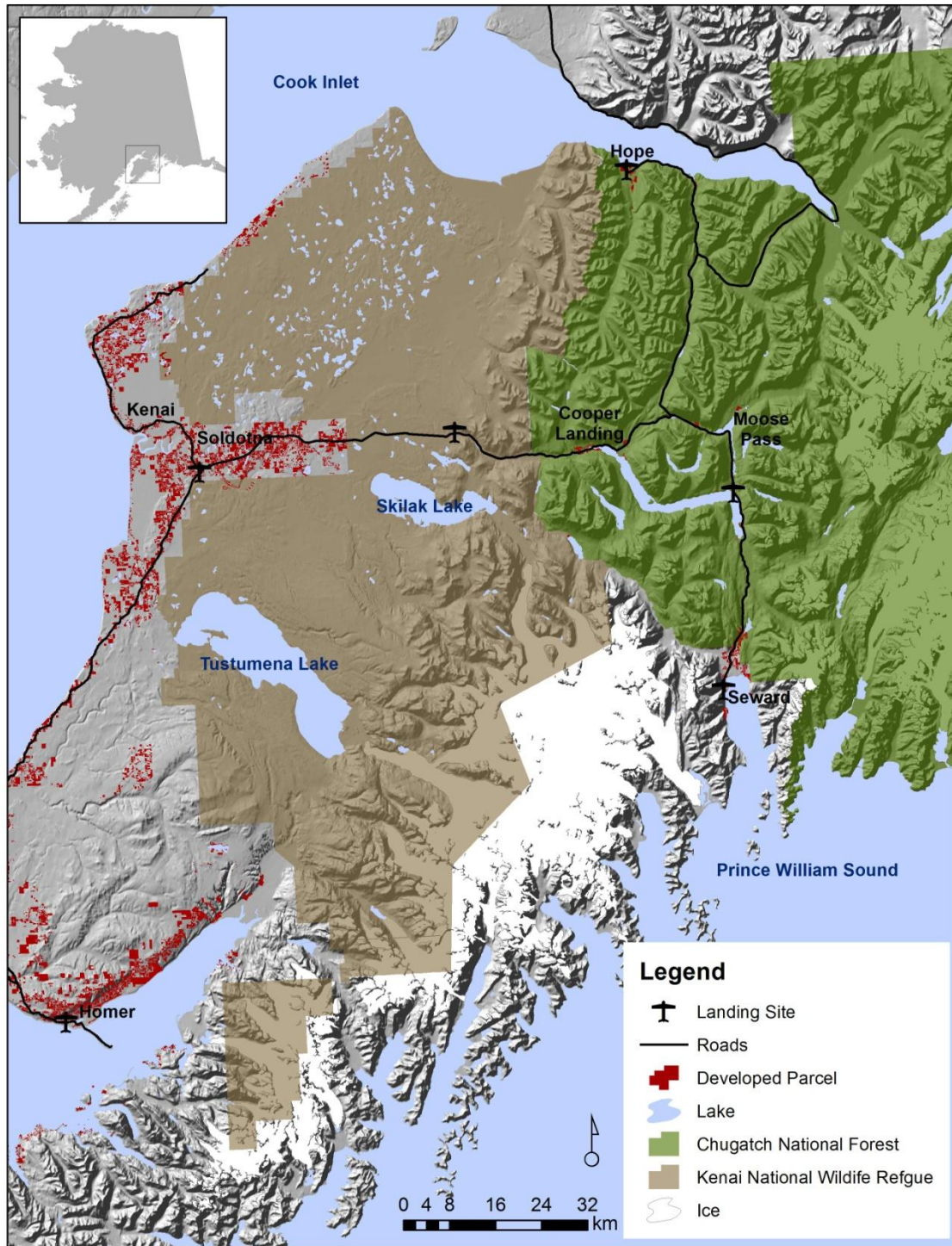
Figure 1. Kenai National Wildlife Refuge and Chugach National Forest, and the 6 fuel depots used during this study: Seward, Soldotna, Homer, Hope, Moose Pass, and the MP63 gravel pit.
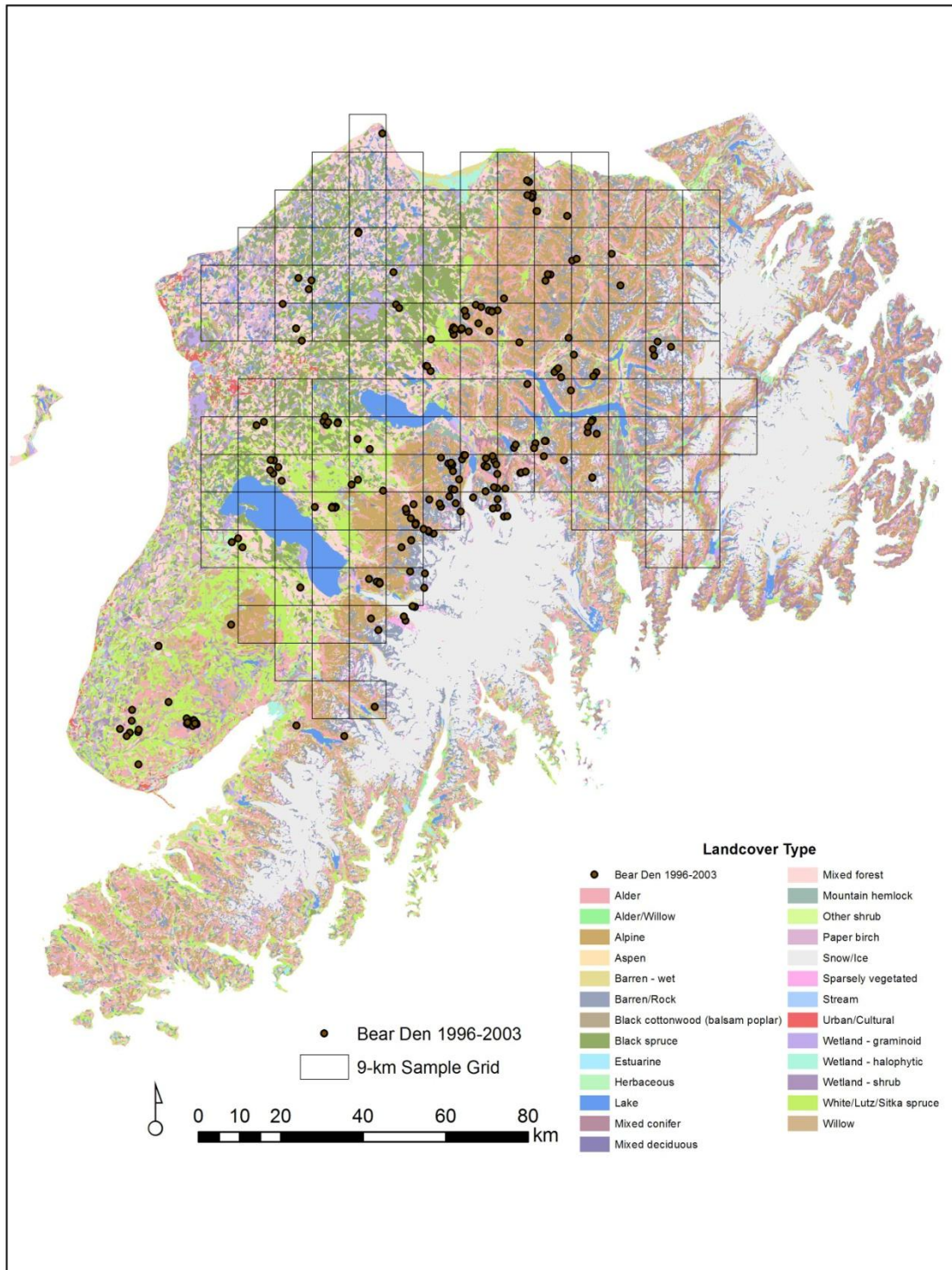
Figure 2. Distribution of dens from 74 brown bear sows during 1996-2003; 84% denned at least once on the study area (Goldstein *et al.* 2010).
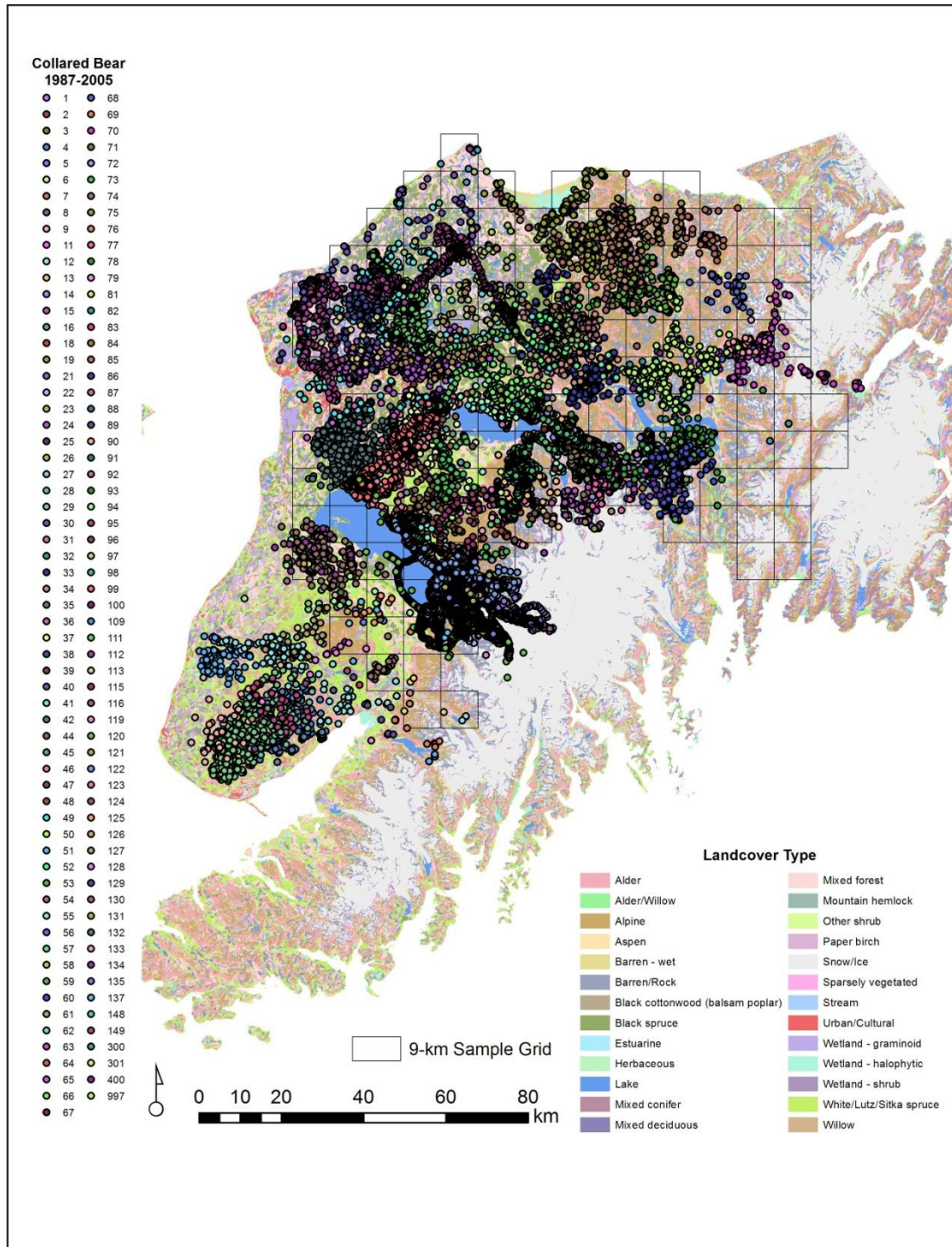
Figure 3. Distribution of 144,024 locations from 125 female brown bears with GPS and VHF collars 1987-2005 (IBBST data). The sample frame encompassed, on average (n = 125), 87% of telemetered locations.
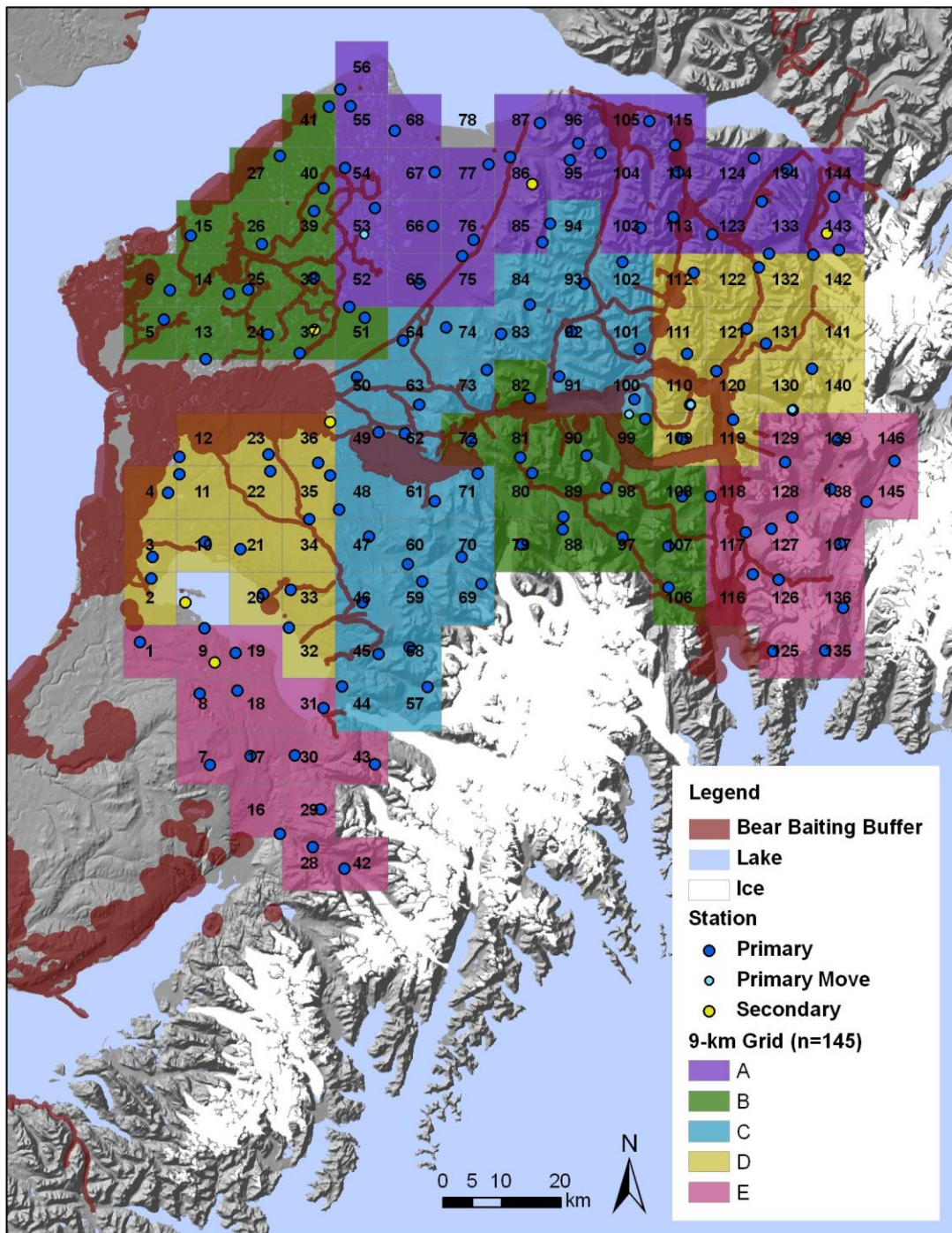
Figure 4. Five panels of 29 9km x 9 km sample cells (n=145) systematically distributed over 11,700 km² (2.9 million acres) of the Kenai National Wildlife Refuge and Chugach National Forest. Hair sample stations were moved or supplemented in 17 cells to increase capture rates.
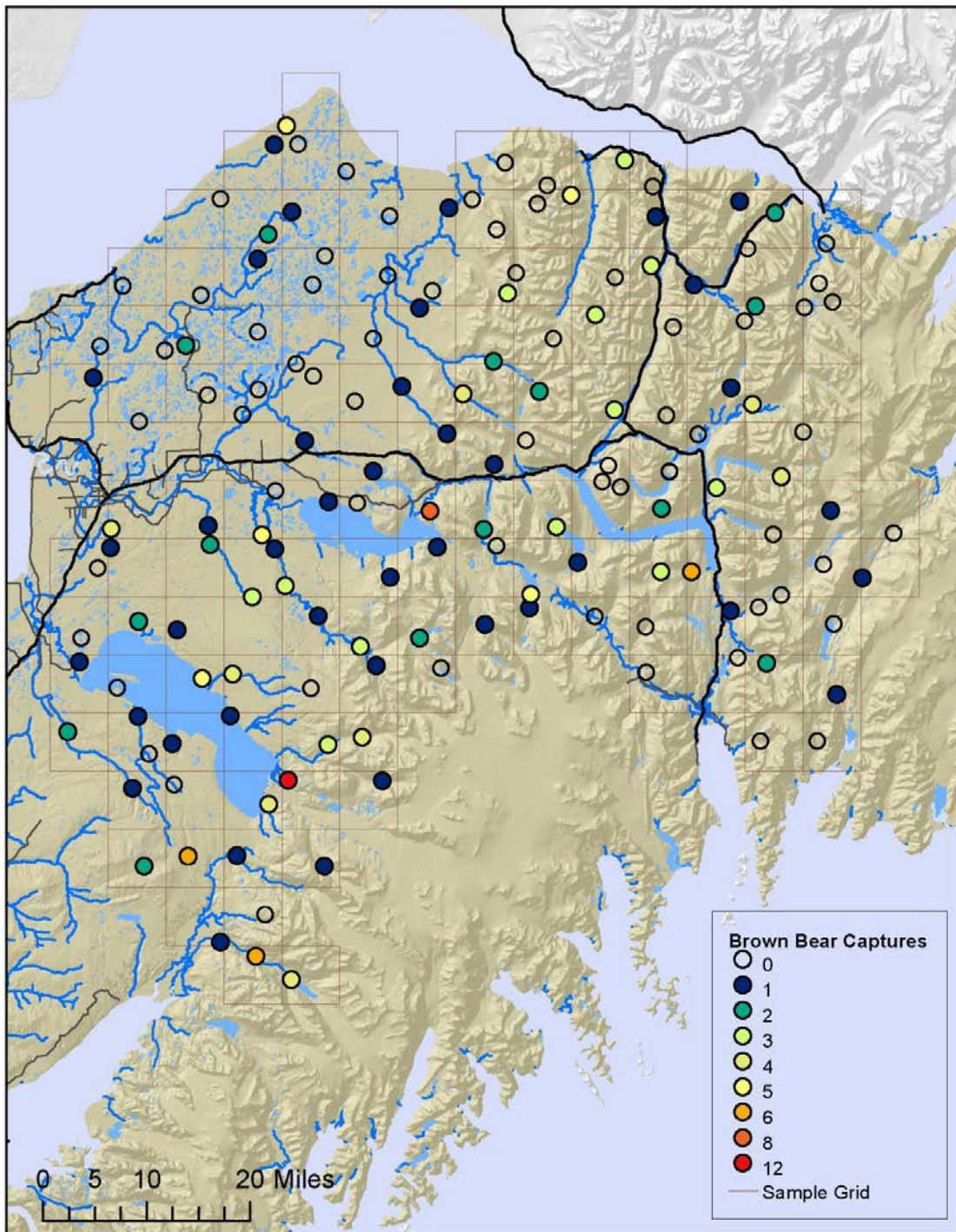
Figure 5. Spatial distribution of brown bear hair captures (unique genotypes) on the sample frame that shows where most detections occurred.
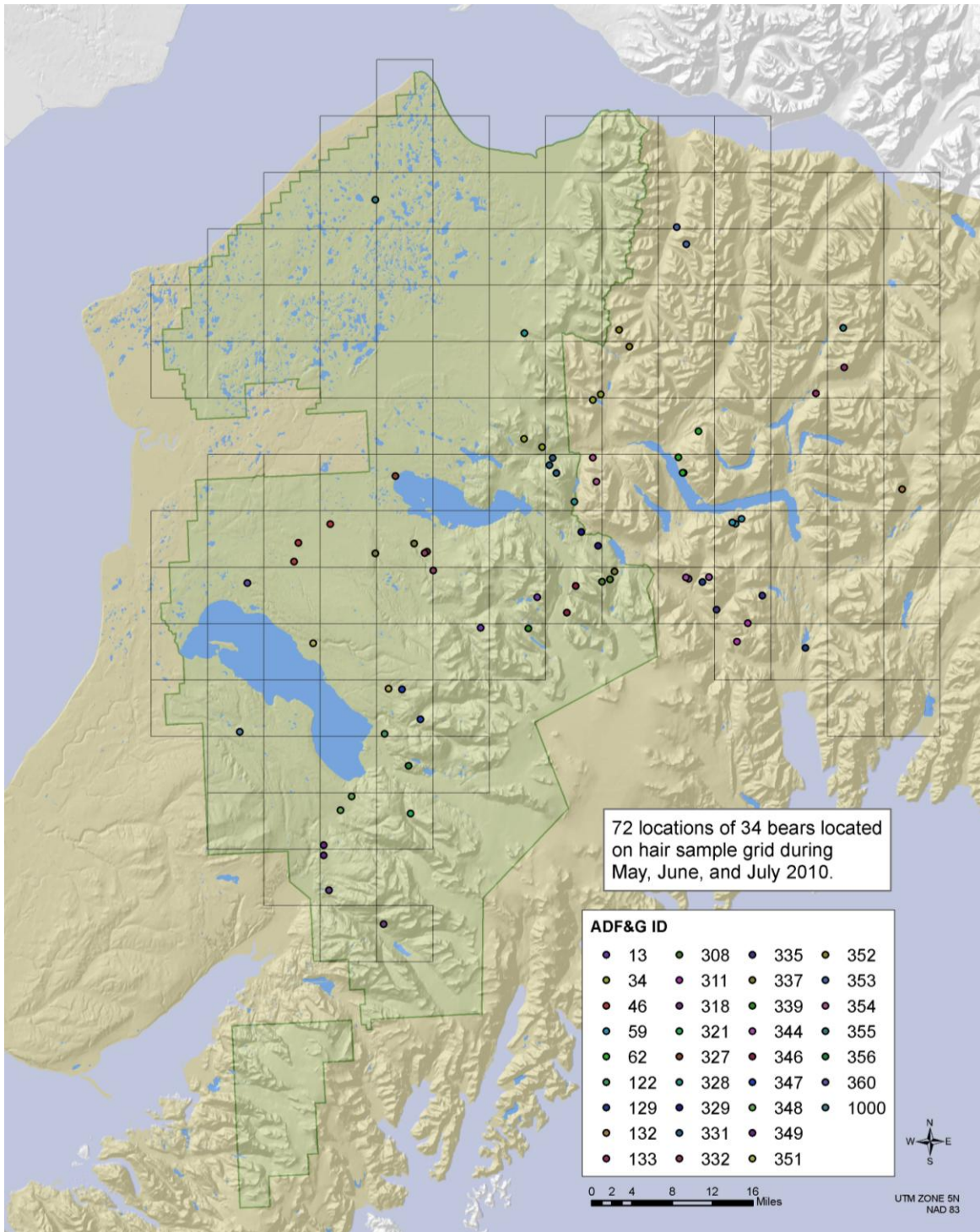
Figure 6. Distribution of 34 collared brown bear sows that were on the study area during May, June, and July 2010. Five other collared sows were alive but outside the study area during this period.
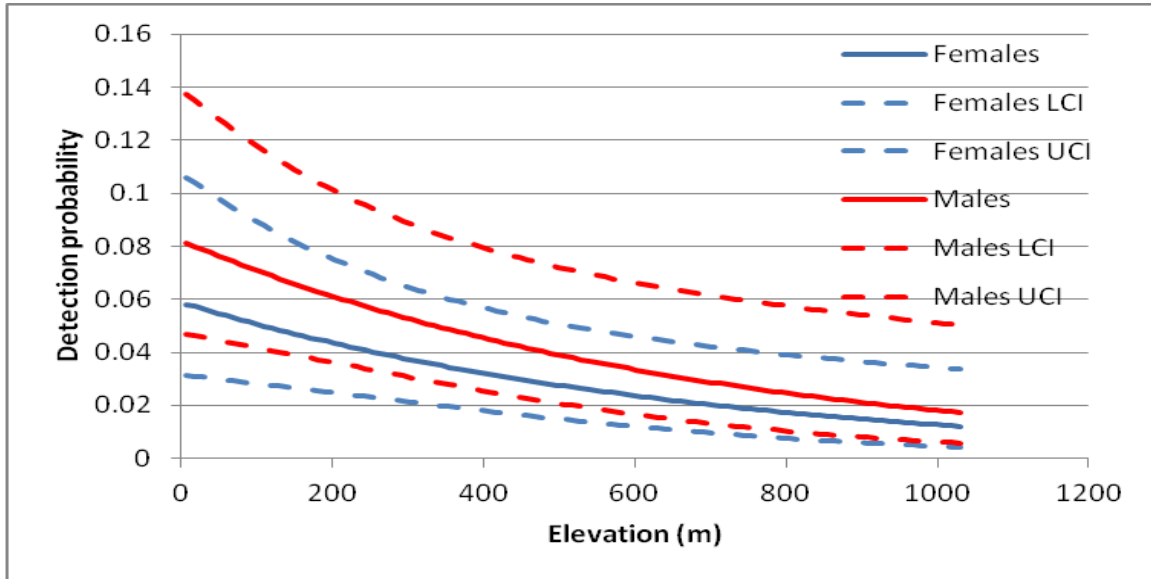
Figure 7a. Plot of detection probabilities for males and females for the first trapping occasion as a function of elevation (ELEV).
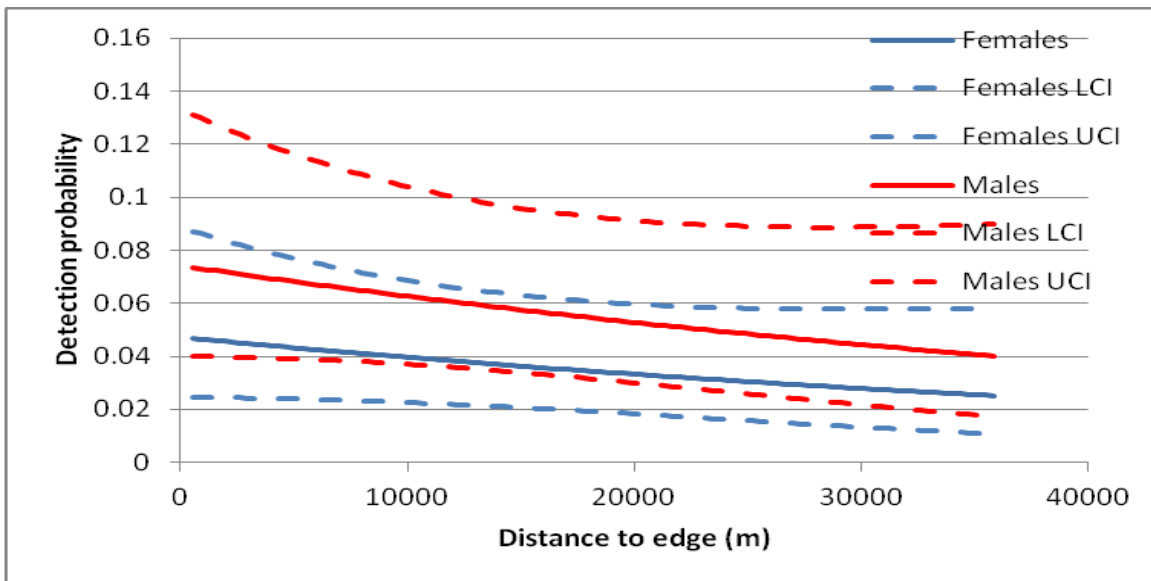

Figure 7b. Plot of detection probabilities for males and females for the first trapping occasion as a function of distance to edge of sample frame (DTE).
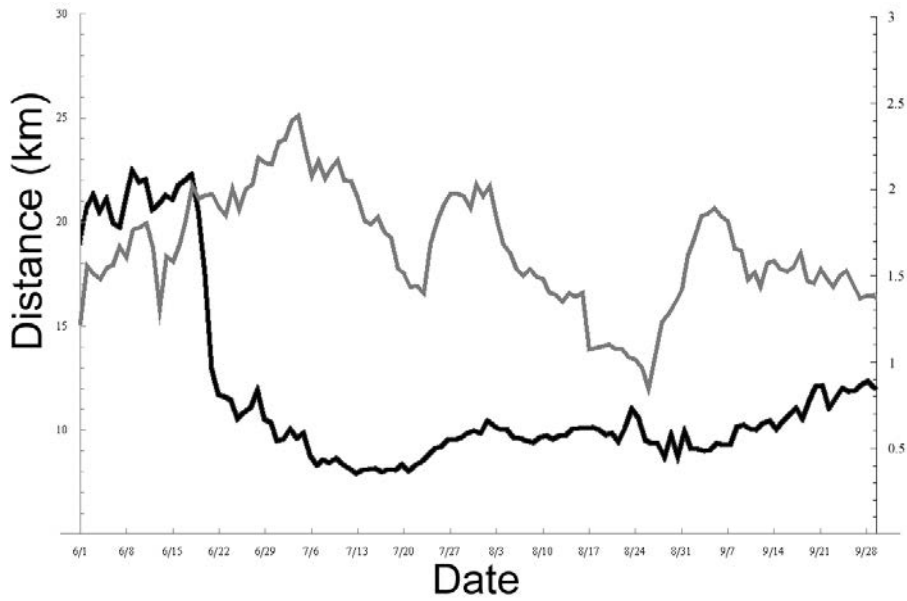
Figure 8a. The black line (right axis) represents the mean distance (km) traveled between successive GPS fix intervals, partitioned into 122 10-day periods for 46 Kenai brown bear sows. The gray line (left axis) quantifies means of the maximum geographical distance (km) between and two of the GPS fixes within each 10-day period. Because GPS fix intervals differ, the distance values are less important than their relative positions (Harris *et al.*, unpubl. ms).

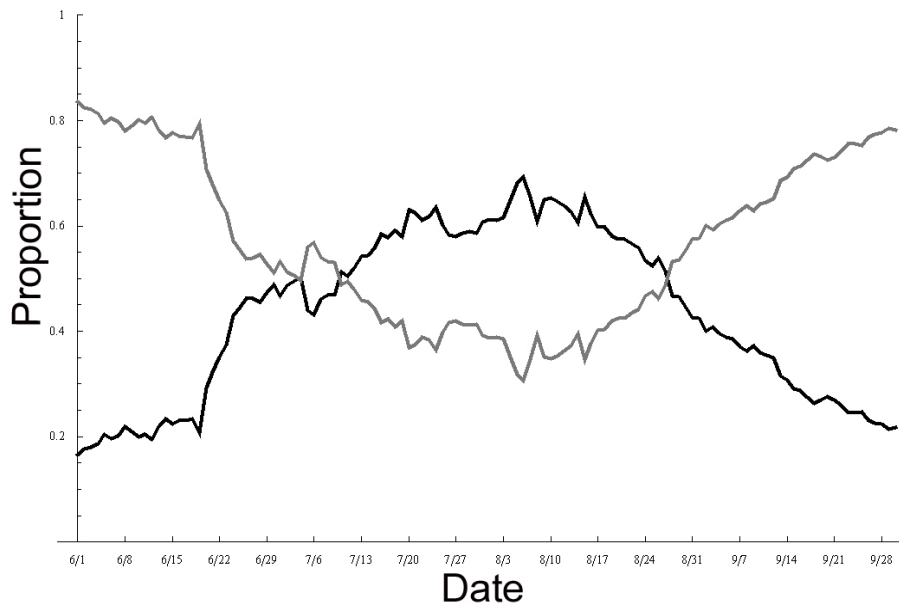Figure 8b. Average proportion of GPS fixes for Kenai brown bear sows close to a stream (<500m, black) and far from a stream (>500m, gray) based on 46 bear-years. Calendar dates represent the start of 122 10-day intervals. Bears are closest to streams during 10-28 July (Harris *et al.*, unpubl. ms).
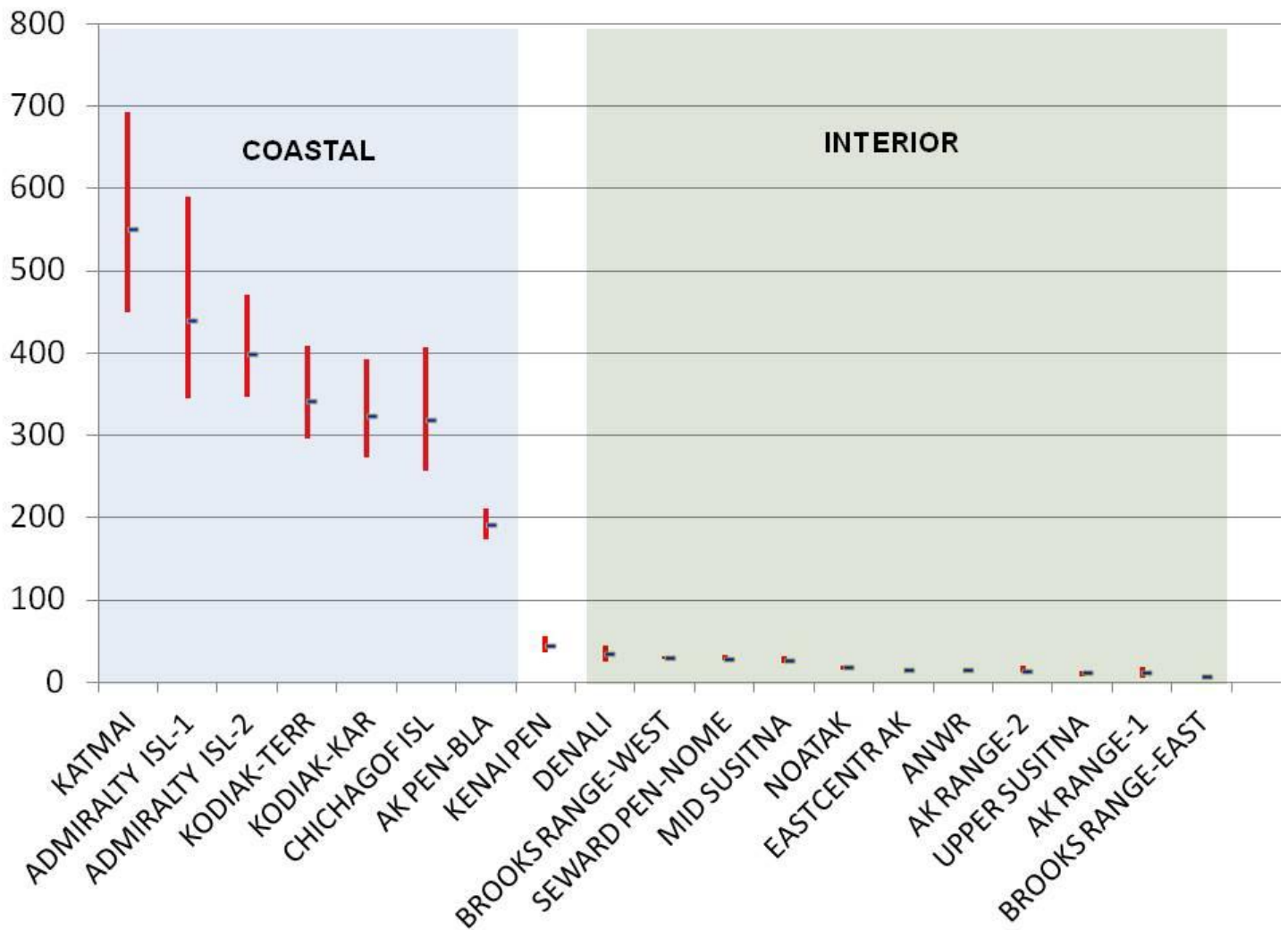
Figure 9. Estimated density of brown bears on the Kenai Peninsula (45.1 per 1,000 km^2) compared to densities of coastal and interior brown bear populations elsewhere in Alaska (per 1,000 km^2; after Miller *et al.* 1997).