LINEAR DENSITY ESTIMATION FOR POPULATION MONITORING OF GRIZZLY BEAR ALONG THE TAKU RIVER, BRITISH COLUMBIA

FINAL REPORT: 5 NOVEMBER 2006

Prepared for:
Taku River Tlingit First Nation
Atlin, BC

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ABSTRACT

Grizzly bears (*Ursus arctos horribilus*) seasonally congregate to forage on Pacific salmon (*Oncorhynchus* spp.) along the Taku River in remote northwestern British Columbia, Canada. We took advantage of this seasonal activity to develop a noninvasive DNA sampling design that overcomes key challenges facing capture-recapture population monitoring in remote regions. A linear array of hair snares along the river corridor was monitored within two study areas: Upper River (UR) and Lower River (LR). DNA analyses of hair identified individual grizzly bears, and the capture and recapture histories of these individuals were used in closed population models. Resulting annual abundance estimates (±SE) in the LR were 19.8 (±11.1), 19.5 (±9.0) and 25.0 (±3.8) and abundance estimates for the UR were 52.3 (±32.5), 62.6 (±11.9) and 84.2 (±30.7) for the sampling years of 2000, 2001 and 2003, respectively. We used estimated bear movement distances along the river corridor to calculate a linear density estimate, which ranged from 0.34 – 0.44 grizzly bears/kilometer and 1.08 – 1.45 grizzly bears/kilometer for the LR and UR, respectively. The consistent difference in population densities was unexpected and potential causes are explored. The linear density methodology alleviates significant logistical barriers to using robust techniques for population monitoring in remote landscapes.

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INTRODUCTION

Wide-ranging and low density carnivores, such as grizzly bears (*Ursus arctos horribilus*), wolverines (*Gulo gulo*) and wolves (*Canis lupus*), are often species vulnerable to anthropogenic impacts (Cardillo et al. 2004; Johnson et al. 2005), but estimating and monitoring their population size can be logistically and financially challenging (Thompson 2004). Even committed field sampling provides only relatively sparse data, supporting few analytical approaches. Populations of the largest carnivore species remain primarily in remote landscapes, where challenges to monitoring are the most pronounced and the difficulty and expense of monitoring is high. Still, it is increasingly recognized by the scientific community, and society at large, that these same large carnivores are flagship species for our remaining wild places and important indicators of landscape and ecosystem conditions (Soulé et al. 2003; Soulé and Terborgh 1999). The challenge for the scientific and management community is to develop effective and efficient methods to meaningfully monitor these species, within the reality of increasingly limited budgets and capacity.

Innovations in genetic analyses that enable individual identification from small samples of DNA have revolutionized wildlife population analysis. It is now possible to non-invasively identify individuals through field collections of hair or scat, and, with the appropriate sampling design, to use those identities within capture-recapture analyses to estimate population size (Lukacs and Burnham 2005). These advancements provide new opportunities to estimate and monitor populations of species that have been difficult or costly to observe or capture, including large carnivores such as grizzly bear (Apps et al. 2004; Kendall et al. 2008; Mowat et al. 2005; Poole et al. 2001; Romain-Bondi et al. 2004), lynx (*Lynx canadensis*; McKelvey 2006; Palomares et al. 2002) and wolverine (Flagstad et al. 2004). Still, significant logistical and financial challenges remain, including the trade-off between sampling intensity and study area size, with all the attendant implications for meeting modeling assumptions, model selection, and parameter estimate precision (Boulanger and McLellan 2001; Boulanger et al. 2004b; Boulanger et al. 2002; Long and Zielinski 2008). Abundance estimation with the classic capture-recapture sampling design requires uniform sampling effort across the length and breadth of the study area (Otis et al. 1978), regardless of any habitat-related density variation in the target species. In large roadless areas, where extensive helicopter time would be needed to establish and revisit sampling grids for large carnivores, this requirement has a large associated cost and, therefore, limits the use of noninvasively collected DNA for population monitoring and estimation of large carnivores (Mowat et al. 2005; Mowat and Strobeck 2000; Poole et al. 2001).

There is a need for alternative population monitoring options that provide meaningful measures of carnivore status in remote landscapes. We used non-invasive DNA sampling of grizzly bears within a modified capture-recapture design that relaxes some of the most limiting and expensive aspects of classic approaches by removing one spatial dimension of sampling. Non-invasive sampling along a linear sampling frame leads to an estimate of abundance along that line, and an associated linear density estimate. In particular, we sampled grizzly bears during seasonal congregations along salmon migratory and spawning habitats, and used capture-recapture analytical tools to estimate the number of bears per river kilometer. The linear metric of density appropriately accounts for detection probability and sampling effort, reflects the distribution of bears concentrated along the salmon spawning streams, and provides a robust alternative to area-based density estimates that would be extremely difficult and expensive in these landscapes. For areas where the cost and logistical challenges would otherwise limit the ability to collect the information to develop population estimates, this linear approach allows an efficient and effective sampling design that can be applied where there are predictable, seasonal congregations of animals.

MATERIALS AND METHODS

Study System

We sampled grizzly bears within the Taku River watershed in northwestern British Columbia, Canada. The Taku River is a transboundary watershed, with its headwaters, major tributaries and upper mainstem in northwestern British Columbia, Canada, and its lower mainstem and estuaries in the panhandle of southern Alaska, U.S.A (Figure 1). The Taku River and its associated tributaries support wild populations of six Pacific salmon species: sockeye (*Oncorynchus nerka*), Chinook (*O. tshawytscha*), coho (*O. kisutch*), chum (*O. keta*), pink (*O. gorbuscha*), and steelhead (*O. mykiss*). Grizzly bears were sampled within British Columbia, along the mainstem Taku River and the lower portions of large tributaries of the river. The study area spans a suite of major ecosystem types, defined by coastal influences in the lower, southwestern reaches of the river system, and arctic and boreal influences along the upper reaches of the mainstem and along most of the major tributaries.

We examined bear abundance in two distinct parts of the watershed: the Upper River (UR) and Lower River (LR) study areas. There was no physical boundary that would impede bear movement between these study areas. The lower, southwestern portion of the study area (Lower River) is a large river floodplain, with extensive cottonwood forest, and multiple dynamically changing river channels. Salmon spawning habitats that receive focused use by grizzly bears are primarily located within backwater channels and sloughs, and the small tributaries that feed them. These small tributaries and sloughs are used by fall run chum and Coho salmon for spawning habitat, and bears congregate there in early fall, as described by local and indigenous knowledge (e.g., Heinemeyer et al. 2003).

The more interior and eastern portions of the study area (Upper River) are dominated by boreal climates, vegetation and topography, with spruce and lodgepole pine forests. The river valley narrows into a single dominant channel, with occasional back channel sloughs. The Taku River is formed by the confluence of two major rivers (Nakina and Inklin Rivers), which are themselves formed by the confluence of sizeable tributaries. Sockeye, Chinook and pink salmon either migrate through or spawn within the Taku River and its large tributaries in the upper portions of the study area. During early and mid summer, grizzly bears use the Upper River study area for both focused fishing where salmon are vulnerable, and to travel to and between these fishing areas.

Sampling Design and Field Collections

We non-invasively collected hair samples from grizzly bears in 2000, 2001 and 2003. We stratified sampling temporally and spatially, to focus effort where seasonal salmon abundance – and assumed bear abundance – was highest. The UR study area was sampled during the early and mid summer (June-August) to coincide with the highest abundance of sockeye, Chinook and pink salmon. The LR study area was sampled during the fall (September-October) to coincide with the return of fall run chum and Coho.

Within each of the two study areas, sampling sites were selected to distribute sampling effort within areas of bear use (e.g., bear trails, fishing sites); these areas were primarily along the single river corridor of the UR study area and along sloughs and associated small channels and tributaries of the LR study area (Figure 1). We attempted to sample the extent of the river valley corridor, but we did not sample habitats above the river valley. Sampling intensity across the two study areas and all years was approximately consistent, between 0.7 and 1.5 sampling sites per km. The total river distance sampled on the LR study area was 54.8 km in all three years, but the sampled area on the UR study area expanded after 2000 such that the distances sampled were 39.2 km in 2000, and 54.6 km in both 2001 and 2003 (Figure 1).

During the initial sampling year (2000), barbed wire was attached to existing or potential bear rub trees, and the trees were baited with a standardized lure consisting of long-distance general carnivore scent lure, fish oil and beaver castor. During the second and third years of the study (2001 and 2003), we also established barbed wire "corrals" near each rub tree sampling set, so that a corral and a rub tree were associated with each sample site. Corrals were 3 – 4 m diameter, with a single strand of barbed wire suspended ~50 cm above the ground (Woods et al. 1999) with the same scent lure mix in the center of the corral on an existing woody structure (e.g., log, stick, brush).

Once sampling sites were established, they were checked 2 – 5 times per sample season (year), with re-luring and snare maintenance at each check. Sample site checks were scheduled for every 7 – 10 days, with some variation due to logistical and weather conditions. To maximize the likelihood that sampled hair came from one individual, a single clump of hair on a single barb constituted a sample. The selected hair clumps were removed with tweezers and placed into paper envelopes, which were labeled and stored within plastic storage containers with silica desiccant. Multiple samples could be collected at a single sampling station (e.g., corral), such that we would obtain 2 -3 samples of hair that appeared to be from the same bear from a station. In some cases, differences in hair indicating potentially different bears were noted, and multiple samples from each potential bear were collected. Hair clumps that contained six or more guard hairs were preferred. This procedure was repeated at each of the two sampling stations for each sample site, with potentially unique bears noted between stations.

Sample Preparation and DNA Analyses Methods

Due to financial limitations, not all samples collected during the field season could be sent in for DNA analyses, and a process of subsampling was used to reduce the analysis set. We initially eliminated black bear hair that could be confidently identified (Mowat and Strobeck 2000) and then selected at least one hair sample from each successful check of sampling sites. At sample sites where unique samples were identified as potentially from different bears, we visually re-evaluated samples and selected at least one sample from each potential bear for DNA analysis. Sorting and selection of samples for analyses were completed following each field season, and selected hair samples were sent to Wildlife Genetic International (WGI) for DNA extraction and analysis.

When possible, 10 guard hair roots per sample were used for the DNA extraction. Underfur was used if sufficient guard hair material was not available. The first step of the genetic analysis was a pre-screen using a single nuclear microsatellite marker (G10J) to determine species and to assess each sample for adequate DNA concentration. Individual identification of grizzly bear samples was based upon G10J, as well as microsatellite loci G1D, G1A, G10B, G10X, and MU59 (Paetkau 2004; Woods et al. 1999). Once the genotypes were completed and checked for errors (described in Paetkau 2003), a computer search for identical genotypes was performed and individuals were defined for each unique genotype. Analysis of gender for one sample from each identified individual was based on the amelogenin gene (Chen et al. 1999).

Samples from two individuals that shared alleles at all 6 microsatellite markers would have appeared to have come from the same individual; this has been termed the "shadow effect" and would cause bias in mark-recapture analyses, falsely decreasing the apparent number of unique individuals (Mills et al. 2000). In our samples, two individuals with no mismatches at any of the six loci used for screening would appear to be the same genetic individual. Out of 332 fully genotyped samples from the watershed, there were 12 pairs of individuals whose genotypes with these six markers were mismatched by two alleles (2MM pairs; Paetkau 2003) and 3 pairs of individuals that were mismatched at only one allele (1-MM pairs). These frequencies led to an expected number of 0MM-pairs (errors) of less than

one. Thus, it was probable that the individuals identified did not duplicate genotypes from other individuals, i.e., that there were no genetic "shadows."

Genotyping error is another source of bias that can mistakenly increase the apparent number of individuals, and decrease the estimated detection rate (McKelvey and Schwartz 2004). The hypothesis that our data had a low genotyping error rate was supported by independent tests conducted by the Rocky Mountain Research Station DNA Analysis Laboratory using statistical analyses of the microsatellite results (McKelvey and Schwartz 2005).

Population Analysis

Data preparation. Individual bear encounter histories were summarized from the data, based on detections in each sampling session. For the population analyses, an individual bear was simply recorded as 'detected' for the sampling session, even if it had been identified at multiple sampling sites within that session.

Location data from individual bears that were detected at more than one sampling site in a single sampling session contributed to within-session movement distance estimates, while bears that were detected more than once in one year contributed to intra-annual movement distance estimates. Twenty-nine and 18 bears from the UR and LR study areas, respectively, contributed to intra-annual movement distances within each study area. We also noted maximum movement distances that bears moved within single years between sampled sites.

Modeling framework. Based on the encounter histories from bear DNA in the discrete sampling sessions per year, we estimated grizzly bear abundance, $\hat{N}$, for the UR and LR study areas separately for each year (6 total estimates). We used Huggins mixture closed population models to estimate $\hat{N}$ using program MARK (White and Burnham 1999). Huggins models use the encounter histories of detected animals to estimate the mean and variance of detection probability (*p*) and re-detection probability (*c*) for all animals in the population, then estimate mean and variance for $\hat{N}$ based on estimates of *p* and *c* (Huggins 1989). Models can set *p* and *c* to be identical (i.e., *p* = *c*) or, if there are more than two trapping occasions, *p* and *c* may differ. They should be equal unless there is a behavioral "trap response" that causes animals to be trap-happy or trap-shy (Otis et al. 1978). Mixture models can represent heterogeneity of detection probability in the population, because the model structures include *p* and *c* parameters for two groups of individuals (Pledger 2000) whose proportion in the population is represented by the mixture parameter (*pi).*

Accurate estimates of $\hat{N}$ depend on accurate estimates for *p*, but the actual probability that an individual in the population is detected can vary by individual, by sex and across different sampling sessions (e.g., because of differences in sampling effort or weather). We structured 16 (eight pairs) of biologically motivated models for estimating $\hat{N}$ (Table 1); these models reflected plausible effects that could cause *p* or *c* to vary, and potentially allowed for heterogeneity of capture with inclusion of the mixture parameter, *pi*. The first model in each pair estimated *pi* and also included an additive parameter by which the two groups of individuals differed in *p* and *c*. The second model of each pair had *pi* set to 1; models with this fixed *pi* value did not incorporate capture heterogeneity. The simplest model (Model "*p*=*c*(.)*pi*(fixed)") had only one parameter to estimate: the per-session detection probability for all animals in all sampling sessions. We included some models where *c* could be estimated separately from *p*; these models represent a potential trap response, although we note that there was no food reward at sampling sites.

We used Akaike's Information Criterion corrected for small sample size (AICc) and the associated Akaike weights (Burnham and Anderson 2002) to evaluate the models' relative fit to the detection history data. Based on Akaike weights for different model structures, we assessed the effects of sex, sampling effort, capture heterogeneity, trap response, and temporal variation on detection probability. We estimated abundance ($\hat{N}$) and its associated standard error based on model averaged estimates, which were combined estimates from each model, weighted according to the Akaike weights (Burnham and Anderson 2002). Prior to model averaging, in a few cases we chose not to include models that had yielded implausible abundance estimates. Specifically, models with separate parameters for c appeared not to have adequate data to estimate p and c reliably; in some cases those models had absurdly high $\hat{N}$ estimates over 10,000 bears. Other models that were not considered in model averaging had standard error values of zero, an indication that the model had more parameters than could be supported by the data.

We tested for capture heterogeneity using Akaike weights (Burnham and Anderson 2002) to compare models that included capture heterogeneity (the eight "*pi*(.)" models) to models with no capture heterogeneity (the eight "*pi*(fixed)" models). We expected that there would be little evidence of capture heterogeneity if the summed Akaike weights for the eight models with the *pi*(fixed) structure was markedly greater than 0.5.

Testing for Closed Population. One assumption common to all closed population models is that there is virtually no birth, death, emigration or immigration during sampling. Over the short time span of sampling a single reach in a given year, grizzly populations are effectively closed to births and deaths (e.g., Boulanger and McLellan 2001). While we expected bears to remain near seasonally abundant food sources, we used two independent methods to test the assumption that bears did not move in and out of the population during the sampling period: evaluation of the movement rates documented through the sampling and testing using Pradel open population models (Pradel 1996) in program MARK (White and Burnham 1999). Details of these evaluations are provided in Appendix I.

Linear density estimates

We estimated linear density based on the population abundance estimate divided by the estimate of effective linear distance sampled. The estimate of the "effective" sampling extent recognizes that an animal slightly outside the sampling area at the start of sampling may enter the sampling area during sampling. The "mean maximum distance moved" method (Anderson et al. 1985; Karanth and Nichols 1998) was developed for sampling grids with area measures (e.g., km^2), but we apply a similar approach to our linear system. Observed animal movements lead to a boundary strip estimate, $\hat{W}$, that, when added to each side of the sampled linear distance, provides an estimate of "effective" distance sampled. The estimated $\hat{W}$ is half of the mean maximum distance moved, $\hat{\bar{d}}$, based on observed movements of individuals detected multiple times. Thus, a bear as far away as $\hat{W}$ from the outside snare was available for sampling because a typical movement could take it into the sampling area.

Movement distances between sample sites were calculated from predicted movement paths using a least-cost path (LCP) movement model (e.g., Adriaensen et al. 2003; Larkin et al. 2004) developed within ArcGIS sofware (ESRI, Redlands, CA), with movement decisions influenced by distance and topography. This model predicts movements primarily follow the river corridor, with some "shortcuts" across level or shallow area; these predictions are similar to observed high-use "bear trails" in the study area (K. Heinemeyer, pers. obs.). The LCP modeling provides a prediction of the actual movement

distances between snares that is likely more accurate than either straight line distances or strict river distances.

The linear density estimator, $\hat{D}$, also incorporates uncertainty (sampling variance) about the boundary strip distance in the estimate of variance for effective linear distance sampled (for area-based estimates, see Anderson et al. 1985; Dice 1938; Otis et al. 1978). We calculated mean maximum distance moved, $\hat{\bar{d}}$, and sampling variance of the maximum distance moved within a study area and year. The seasonal timing of sampling and the geomorphology of UR and LR study areas differed, so we used an unpaired t-test to test for categorical differences in $\hat{\bar{d}}$ for bears detected in the two study areas. After finding significant differences in mean maximum movement distance according to study area, we estimated the boundary strip variance, $\hat{\text{var}}(\hat{W})$, as one-quarter the sampling variance of $\hat{\bar{d}}$ for each study area.

The effective linear distance sampled ($\hat{A}(W)$) was calculated by adding the boundary strip distance to both sides of the linear sampling area. The variance for this estimated effective linear distance sampled, $\hat{\text{var}}(\hat{A}(W))$, comes only from sampling uncertainty of the distances that bears move during the sampling period, so it is the same as the variance of the boundary strip distance.

Grizzly bear linear density, $\hat{D}$, can be estimated as the estimated abundance divided by the estimated effective sampling distance:

$$\hat{D} = \hat{N} / \hat{A}(W)$$

The variance estimate for $\hat{D}$ incorporates uncertainty from both the abundance estimator and the estimate of distance effectively sampled.

$$\hat{\text{var}}(\hat{D}) = \hat{D}^2 \left[\frac{\hat{\text{var}}\,\hat{A}(W)}{\left[\hat{A}(W)\right]^2} + \frac{\hat{\text{var}}(\hat{N})}{\hat{N}^2} \right]$$

RESULTS

Field sampling

In the three years of the study, there was variation in sampling effort (e.g., number of sampling sites, number of sessions) as well as in the number of samples containing useful DNA, and the number of bears detected (Table 2). Having two complementary set types (rub tree and barbed-wire corrals) may have improved the sample of grizzly bears in 2001 and 2003. In 2001 and 2003, the total number of genotyped grizzly bear samples was approximately evenly divided between set types, with 144 from rub trees, and 121 from barbed wire corrals. In 2000, when only rub trees were used to collect hair, more individual males than females were detected, with a ratio of 1.92M:1F. In 2001 and 2003 there were more females detected, with ratios of 0.9M:1F and 0.57M:1F, respectively. In 2001 and 2003 combined, 12 females were detected only at rub tree sets, 14 were detected at only corral sets, and 22 were detected from both types of set; 12 males were only detected at rub tree sets, while 6 were detected at only at corral sets, and 14 were detected at both set types.

Population Analyses

Observed movement distances. Within sampling years and single study areas, the range for the maximum observed distances moved by individual grizzly bears was from 0 to 15,969 m, with a mean of 2,892 m (S.E. = 474 m). For grizzly bears detected in single study areas and single years, the mean

number of detections per bear was 2.2 (S.D. = 1.4). In the UR, $\hat{\bar{d}}$ was 3,446 m (n=29, S.E. = 666 m), and $\hat{\bar{d}}$ was 2000 m in the LR (n=18, S.E. = 578 m). The difference between these groups was significant (T = 1.638, d.f. = 44.5, P = 0.054), so the buffer width, $\hat{W}$, for estimating effective linear distance sampled was 1.72 km in the UR (S.E. = 0.33) and 1.00 km in the LR (S.E. = 0.289).

After adding of the buffer distance of 1.00 km (S.E. = 0.29 km), the LR effective sampling distance was 56.8 km in all years. With the slightly longer buffer distance of 1.72 km (S.E. = 0.33 km) added to each end of the UR, the effective distances sampled there were 42.6 km in 2000, and 58.0 km in 2001 and 2003.

At least a few bears moved seasonally between study areas during the course of this study, but the two study areas appeared to be closed during sampling sessions. Seven individuals were observed to have moved from the UR to the LR study areas in single years, while four individual bears were detected at both study areas over the time span of more than one year. Even using all detections per year in both study areas, the mean maximum movement distance was 4.02 km (S.E. = 0.59 km), which is comparable to the $\hat{\bar{d}}$ value for the UR study area. This suggests to us that over the time period of sampling in both study areas the majority of bears do not move long distances.

Population model rankings and detection probability estimates. Except for LR 2000, the simplest model structure, p=c(.)pi(fixed), generally had a high Akaike weight (Table 3). For the LR in 2000, all models with two parameters for detection probability had equally high Akaike weights, yielding identical detection probability and abundance estimates. This unusual result was likely due to the limited sampling in 2000 in the LR, with only two sampling sessions of roughly equal effort, and relatively few recaptured bears. In several cases, models with a separate parameter for estimation of *c*, the re-detection probability, yielded abundance estimates or standard error estimates that were unreasonably high. In those cases, our data probably had too few animals that were detected multiple times to yield reliable parameter estimates for *c*.

Within single study areas and years, model fit was generally not improved by the inclusion of an additive parameter representing effort. Using model-averaged estimates, single-session detection probabilities ranged from quite low (0.10 in UR 2000) to quite high (0.86 in one session on LR 2000; Table 4). Based only on the sampling sessions in 2001 and 2003, when effort was relatively high, the per-session detection probability was 0.26 (S.E. = 0.47). Per-session detection probabilities on the UR in 2000 may have been low because of the minimal sampling effort (Table 2).

Adding parameters to reflect capture heterogeneity did not improve model fit over simpler models; almost universally, models that estimated a mixture parameter that accounted for capture heterogeneity, *pi*, had lower Akaike weights than models in which *pi* was fixed as 1, and the sum of Akaike weights for models with pi(.) structure was less than 0.5 in all years (Table 3).

Both the evaluation of movement distances and the comparison of Pradel open population models indicated that the population of bears within each study area was essentially closed during the sampling sessions. Details of approaches used and the results are provided in Appendix I.

Abundance and linear density. There was a consistent difference in density between the UR and LR (Figure 2). Based on model averaging, the abundance of grizzly bears estimated for the UR study area varied from of 52.3 in 2000 (S.E. = 32.5), to 62.6 in 2001 (S.E. = 11.9), and 84.2 in 2003 (S.E. = 30.7). Accounting for differences in the effective distance sampled, linear density estimates can be compared directly across years (Figure 2), at 1.22 bears/km in 2000 (S.E. = 0.76), 1.08 bears/km in 2001 (S.E. = 0.21), and 1.45 bears/km in 2003 (S.E. = 0.53). The number of bears estimated in the LR was markedly

lower than found in the UR. The LR abundance estimates were 19.8 in 2000 (S.E. = 11.1), 19.5 in 2001(S.E. = 9.0) and 25.0 in 2003 (3.8). Linear density estimates for the three years were 0.35 bears/km in 2000 (S.E. = 0.19), 0.34 bears/km in 2001 (S.E. = 0.16), and 0.44 bears/km in 2003 (S.E. = 0.67).

From these estimates alone, linear density in each of the study areas appeared relatively stable from year to year. However, uncertainty around the point estimates reduces the ability to discern small changes in true linear density. In particular, there would be low power to detect a trend in the UR because of the high variance around the UR 2000, which probably resulted from low sampling effort that year. Similarly, sampling variance around the point estimates on the LR makes any trend statistically undetectable. Most of the uncertainty in linear density estimates came from abundance estimates, with less than 1% of the uncertainty due to movement distance estimates.

DISCUSSION

Non-invasive sampling for individual genotyping is increasingly recognized as a valuable and robust method for estimating wildlife abundance (Kendall and McKelvey 2008; Petit and Valiere 2006), and it has been used to assess grizzly bear populations in a diversity of landscapes (e.g., Boulanger et al. 2004a; Boulanger et al. 2008; Gervasi et al. 2008; Kendall et al. 2008; Mowat et al. 2005; Poole et al. 2001; Romain-Bondi et al. 2004), though the logistical and financial cost of undertaking classic capture-recapture studies has limited its utility. We have been able to take advantage of seasonal congregations of grizzly bears along a salmon system to develop an effective and efficient sampling design that overcomes several of the challenges of conventional capture-recapture field studies. The number of grizzly bears detected per 1000 trap-nights ranged from 15.2 – 33.2, and compares favorably to other hair-snare efforts. Based on eight grizzly bear studies, Romain-Bondi (2004) summarized the number of grizzly bears detected per 1000 trap-nights, which ranged from 0.19 to 28.61.

While sampling in areas of seasonal bear concentrations is not new (Boulanger et al. 2004a; Haroldson et al. 2005), our use of a linear metric appropriately applies the results of population abundance estimation to the study system, and provides a meaningful and standardized population measure for assessment and monitoring. The study design is efficient not only because effort is focused within areas of high bear density, but also because, in remote and mountainous areas such as our study area, efficient access is often limited to following waterways by boat or foot, or other similar linear routes (e.g., ridgelines).

It has been found that the abundance of bears within a salmon system is correlated to the abundance of fish, particularly within a local system (Boulanger et al. 2004a). We did not attempt to correlate salmon abundance with bear abundance for two reasons. Our sampling covered a broad area of the Taku River including travel routes and a diversity of potential feeding or fishing areas, and measuring localized abundance associated with some sampling sites would likely not have captured the overall salmon resource availability that bears within the system are likely responding to. Additionally, the Taku River supports 5 anadromous salmon species, and each of the two study areas themselves support 2-3 species simultaneously. The salmon returns to the Taku River system are large, and represent the largest wild salmon system in the SE Alaska-BC transboundary region, and bear response to salmon is likely not significantly limited by annual variation in runs of any single species. Even during the 2001 sampling year, which had with the lowest returns of salmon, the system still supported nearly 200,000 returning salmon (Boyce and Andel 2003; Table 5). It is interesting to note that 2003 supported a very large salmon return of >400,000 fish, and that the estimated density of bears on both the UR and LR were not significantly higher than previous years. Additional research linking system-wide bear numbers within years to salmon abundance would improve our ability to detect changes in bear abundance by potentially accounting for some of the variation. Still, we feel that in systems that

support multiple species of salmon with overlapping distributions and spawning areas, there is likely a sufficiently abundant and high value resource (even in low salmon years) that will consistently attract a large portion of the resident bears. Still, in low years, bears may not stay within the salmon system for the same duration, and consistent sampling should occur across the breadth of the salmon availability to ensure consistent sampling of individual grizzly bears when they are present.

We do not know the spatial distribution of the sampled bear population during other times of the year, when salmon are not a primary food source. In southwestern Alaska, grizzly bears were shown to shift their seasonal home ranges to move to salmon streams (Collins et al. 2005). Bears in the Taku system likely use habitats outside of the valley bottom study areas during non-salmon seasons, but may show a high fidelity to the study area when salmon are available, as has been observed along reaches of the Taku River (P. Timpany, pers. comm.) and in other salmon systems (Sellers and Aumiller 1992; P. Timpany, pers. comm.). Use of the study area to access salmon is likely critical to the productivity and abundance of the resident bear population (Hilderbrand et al. 1999), and monitoring bear abundance and density during this time provides an efficient population monitoring opportunity.

While we expect that a large proportion of the resident bears utilize the study area during the sampling window, there may be some important exceptions. For example, it has been shown that female grizzly bears with young of the year may avoid bear congregation areas to avoid the risk of infanticide (Ben-David et al. 2004; Rode et al. 2006; Suring et al. 2006; Wielgus and Bunnell 1995). While it is likely that some females may avoid using the entire river corridor within the study areas when with cubs of the year, others likely still use the river to travel to foraging areas and to access salmon. Females with cubs are, in some cases, dominant bears at fishing sites (Gende and Quinn 2004), but others may become subdominant and potentially use lower quality salmon fishing sites that are not frequented by male grizzly bears (Rode et al. 2006; Suring et al. 2006) or they may alter foraging patterns (e.g., scavenge salmon carcasses, prey on less desirable salmon, move away from stream to consume fish; Gende and Quinn 2004). Thus, it is likely that a large portion of females within the Taku system still uses the river corridor for foraging or to traveling to fishing sites, but may avoid the best quality fishing areas to avoid males. This continued but selective use of salmon rivers by females with cubs is supported by the positive association of females with cubs to areas with a higher density of salmon streams on the Kenai Peninsula; at a finer scale, these females are found closer to streams with lower salmon productivity (Suring et al. 2006). Similarly, Collins, Kovach et al. (2005) reported a lack of correlation between reproductive status and distance to salmon streams in southwestern Alaska. If females with cubs tend to use alternative fishing sites within our study areas, our sampling regime would likely have encompassed these areas or the travel routes to them.

Grizzly bear population on the Taku River

Grizzly bear densities were estimated to be between 2 to 4 times higher in the UR study area than in the LR study area. This result is surprising, as the coastal habitat influences in the LR study area results in its classification as higher quality habitats than the more interior UR study area, based on habitat capacity rankings provided by Hamilton and Austin (2004). We do not know why there are so few grizzly bears in the LR. Salmon-feeding grizzly bear populations may be vulnerable to loss of salmon resources (Collins et al. 2005; Hilderbrand et al. 1999) or other seasonally abundant and high quality food sources (e.g., trout spawning; Haroldson et al. 2005). Boulanger (2004a) found that bear abundance along salmon spawning streams changed, potentially in response to salmon availability, and concluded that the bear population may be vulnerable to loss of salmon resources. Over the last 20 years, the wild chum salmon runs have dramatically declined in the Taku River (Tobler 2002); these salmon have historically been heavily used by bears and other carnivores in the LR during late summer and fall.

But spawning coho salmon are currently very abundant in the lower Taku River, and coho overlap in timing and habitat with the chum salmon. While it may be assumed that grizzly bears in the LR are using the abundant coho salmon as an alternative to the chum salmon, this has not been confirmed and there may be differences in the availability of coho salmon (e.g., if they use different micro-habitats that create more difficult fishing conditions for bear; Gende et al. 2004).

In addition to notable decline in chum salmon abundance, it is possible that increased bear-human encounters and potential conflicts result in higher mortality rates and/or displacement of bears in the lower Taku River. A small in-river commercial salmon fishery on the Canadian side of the international border was established in 1980, and results in substantially higher human presence, use and infrastructure within portions of the LR. Additionally, there is significant mineral exploration activity in the lower Taku River, with associated increase in human presence and infrastructure. Finally, the fall grizzly bear hunting season overlaps with the time when bears would be concentrated along fishing sites within the LR and are relatively accessible by boat.

The linear densities that we recorded for grizzly bears in the Taku watershed are baseline measures for monitoring changes into the future. Perhaps the linear densities on the UR are a conservative indication of what bear densities could be supported in the LR. If so, then increasing grizzly bear densities in the LR should be a management goal. We urge conservation efforts to support recovery of the Lower Taku River grizzly bear population, with the success of those efforts to be measured against estimates presented here.

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TABLES

Table 1. Summary of models evaluated in the Huggins closed population capture-recapture analyses. Some models included additive parameters for effort or sex. All models labeled "*pi*(.)" estimated a mixture probability, *pi*, that represents the proportion of two groups of bears whose difference in detection probabilities is estimated via an additive beta parameter. Models with "*pi*(fixed)" indicate one estimated detection probability for all bears as a single group. The total number of parameters in models with session-specific detection rates depended on the number of sampling sessions.

Model	***No. of parameters***	***Description***
p=*c*(.)*pi*(fixed) *p*=*c*(.)*pi*(.)	1 3	Equal per-session detection probability for all animals in all sampling sessions
p=*c*(+sex)*pi*(fixed) *p*=*c*(+sex)*pi*(.)	2 4	Detection probability includes a sex-based parameter
p(.)*c*(.)*pi*(fixed) *p*(.)*c*(.)*pi*(.)	2 4	Redetection probability could be different then initial detection probability
p=*c*(+effort)*pi*(fixed) *p*=*c*(+effort)*pi*(.)	2 4	Detection per session is influenced by trap effort, the total number of site-days for each session
p=*c*(+snares)*pi*(fixed) *p*=*c*(+snares)*pi*(.)	2 4	Detection is influenced by the total number of sites in each session
p=*c*(+days)*pi*(fixed) *p*=*c*(+days)*pi*(.)	2 4	Detection is influenced by the length of each sampling session, in days
p=*c*(t)*pi*(fixed) *p*=*c*(t)*pi*(.)	t t+2	One detection probability for each of t sessions
p=*c*(t+sex)*pi*(fixed) *p*=*c*(t+sex)*pi*(.)	t+1 t+3	One detection probability for each of t sessions, with a sex-based parameter for all sessions

Table 2. Summary of sampling effort and results on Upper and Lower River study areas in the Taku River, British Columbia. Measures of trap effort include the number of sites, the average time that each site was set for snaring bear hair, and the total number of days that sites were open for snaring hair (site-days). Summarized results include the number of grizzly bear samples of high enough quality to identify individuals (detections) and the number of unique grizzly bears identified in each session.

Reach, Year, and Session	*No. Sites*	*Avg. Set Time*	*Site-days*	*No. Detections*	*No. Grizzly Bears*
Upper River 2000					16
Session 1	11	6	67	4	4
Session 2	23	8	180	8	7
Session 3	11	9	94	8	7
Upper River 2001					40
Session 1	57	17	970	13	11
Session 2	50	11	528	16	11
Session 3	50	12	528	17	17
Session 4	74	18	1500	25	18
Upper River 2003					38
Session 1	64	11	708	13	12
Session 2	74	12	836	18	15
Session 3	60	11	662	10	9
Session 4	44	11	486	17	12
Lower River 2000					14
Session 1	56	9	520	17	13
Session 2	56	8	464	7	5
Lower River 2001					11
Session 1	74	16	1168	10	8
Session 2	68	8	564	5	5
Lower River 2003					20
Session 1	71	8	582	4	3
Session 2	70	7	494	7	6
Session 3	69	12	819	10	7
Session 4	70	7	520	17	12
Session 5	68	4	306	8	7

Table 3. Akaike weights for grizzly bear abundance models for Lower River (LR) and Upper River (UR) study areas within the Taku River, British Columbia. Akaike weights are based on AICc values within single years and study areas. Models marked with asterisks were not included in model averaging because the estimates they yielded were entirely implausible (i.e., abundance greater than 10,000). *p*(.)*c*(.) models are not included for LR 2000 and LR2001, when there were only two trapping sessions.

Model	***LR 2000***	***LR 2001***	***LR 2003***	***UR 2000***	***UR 2001***	***UR 2003***
***p*=*c*(.)*pi*(fixed)**	0.009	0.163	0.101	0.219	0.109	0.208
***p*=*c*(.)*pi*(.)**	0.003	0.048*	0.036	0.074	0.014	0.045
***p*=*c*(+sex)*pi*(fixed)**	0.010	0.049	0.116	0.086	0.089	0.176
***p*=*c*(+sex)*pi*(.)**	0.010*	0.013*	0.040	0.028	0.032	0.033
***p*(.)*c*(.)*pi*(fixed)**	--	--	0.199*	0.107*	0.336*	0.092
***p*(.)*c*(.)*pi*(.)**	--	--	0.069*	0.010*	0.119*	0.017
***p*=*c*(+effort)*pi*(fixed)**	0.114	0.080	0.037	0.095	0.055	0.092
***p*=*c*(+effort)*pi*(.)**	0.114*	0.080*	0.013	0.031	0.002	0.020
***p*=*c*(+snares)*pi*(fixed)**	0.003	0.080	0.049	0.084	0.066	0.090
***p*=*c*(+snares)*pi*(.)**	0.000*	0.080*	0.017	0.027	0.024	0.019
***p*=*c*(+days)*pi*(fixed)**	0.114	0.080	0.0376	0.124	0.044	0.131
***p*=*c*(+days)*pi*(.)**	0.114*	0.021*	0.013	0.040	0.016	0.028
***p*=*c*(t)*pi*(fixed)**	0.114	0.080	0.098	0.043	0.034	0.022
***p*=*c*(t)*pi*(.)**	0.114*	0.021*	0.032	0.013	0.004	0.004
***p*=*c*(t+sex)*pi*(fixed)**	0.108	0.021	0.108	0.015	0.027	0.018
***p*=*c*(t+sex)*pi*(.)**	0.027	0.021*	0.034	0.004	0.009	0.003

Table 4. Model averaged detection probabilities for each study area and year. Estimated values of *p* are given for each session. The estimate for p* is the overall probability that an individual would be detected in at least one of the sampling sessions.

	Lower 2000	***Lower 2001***	***Lower 2003***	***Upper 2000***	***Upper 2001***	***Upper 2003***
p, session 1	0.86	0.39	0.24	0.10	0.21	0.15
p, session 2	0.57	0.31	0.30	0.12	0.20	0.16
p, session 3	n/a	n/a	0.32	0.12	0.21	0.14
p, session 4	n/a	n/a	0.40	n/a	0.24	0.14
p, session 5	n/a	n/a	0.32	n/a	n/a	n/a
p*	0.94	0.58	0.85	0.30	0.62	0.47

Table 5. Estimated abundance of salmon within the Taku River system (Boyce and Andel 2003) during the years of sampling the grizzly bears. These are Taku watershed-wide estimates and do not indicate the number of salmon available at any particular bear sampling area, but, generally, the Upper River study area focused across areas within the distribution and spawning habitats of sockeye, Chinook and pink salmon (totals for these 3 species provided at bottom of table) and the Lower River study area primarily supports coho and chum salmon distribution and spawning, particularly within the backwater and slough habitats most intensively sampled for bears.

Species	**2000**	**2001**	**2003**
Sockeye*	87298	144071	167691
Chinook*	30529	42980	36435
Pink**	6529	9134	15491
Coho*	64700	104394	183038
Chum**	423	250	262
UR Salmon Estimate	*124356*	*196185*	*219617*
LW Salmon Estimate	*65123*	*104644*	*183300*

*Population escape estimates into spawning habitats within the Taku River

** Counts of fish captured in the Canyon Island fish wheel monitoring near the US-Canada border on the Taku River

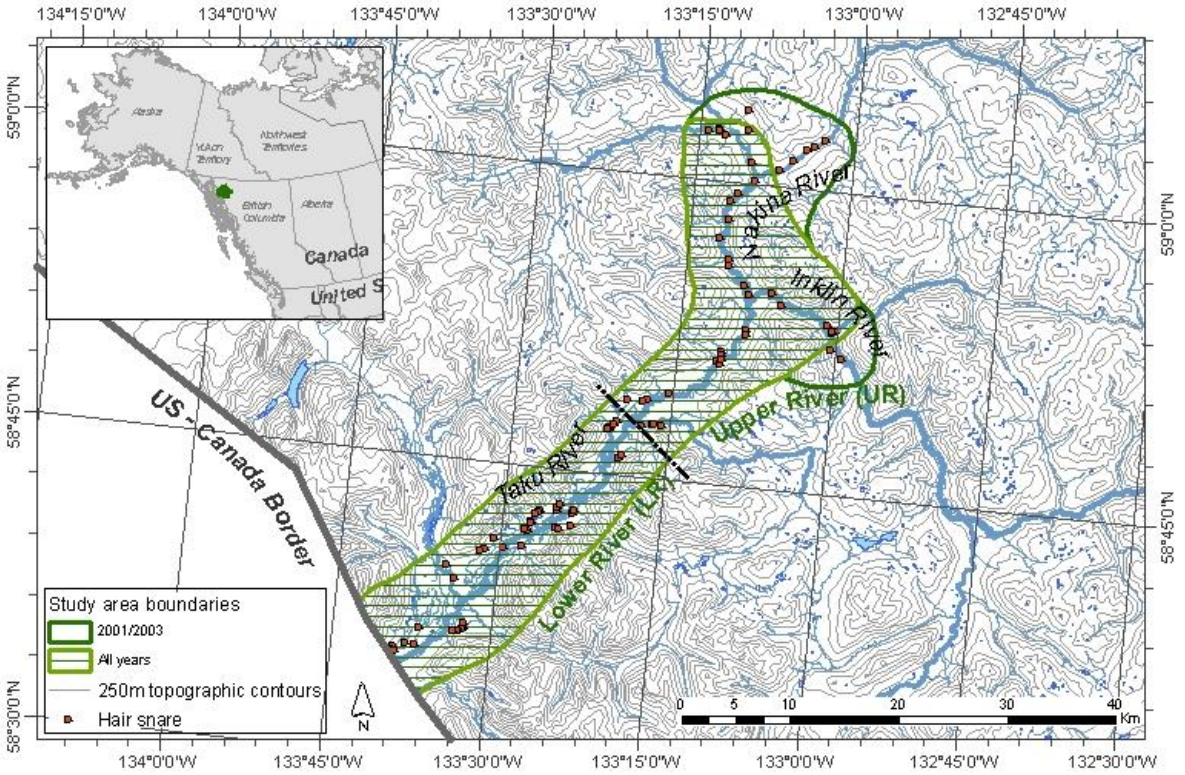

Figure 1. The study area in the Taku River watershed in northwestern British Columbia. The Upper River study area was expanded slightly in 2001 and 2003. Snare locations are shown as brown dots.

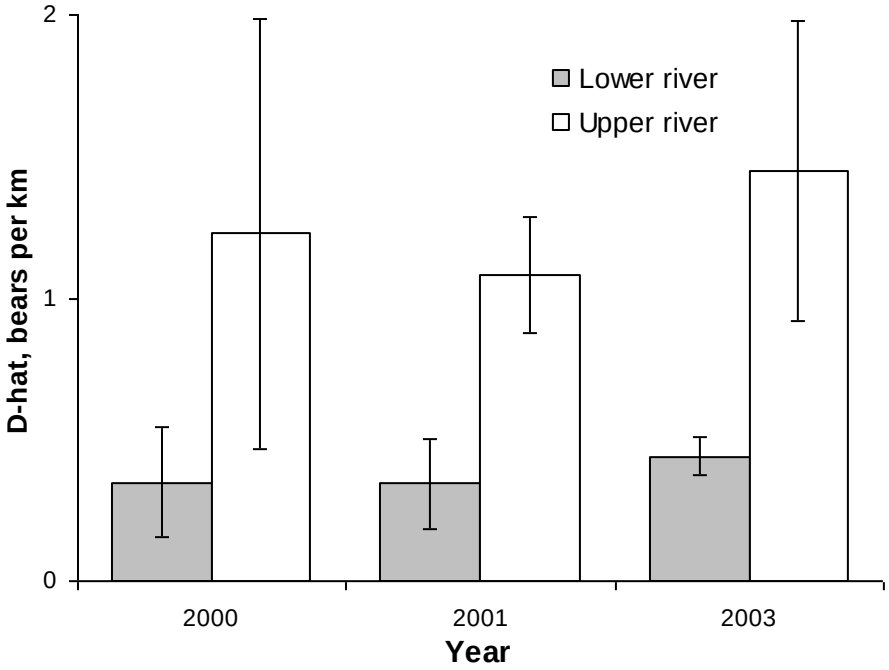

Figure 2. Linear density estimates for sampled reaches in the Lower River (grey bars) and Upper River (white bars) study areas, in units of bears per km. Error bars represent one standard error.

APPENDIX I: Additional Details Regarding the Testing for Closed Population

Introduction and Methods

We used two methods to test the assumption that the Taku River grizzly bear study population can be considered "closed" during the sampling periods (i.e., virtually no births, deaths, immigration or emigration during the sampling period). First, using data from multiple sampling sessions collected within single years and study areas, we tested the fit of encounter history data to Pradel open population models (Pradel 1996) in program MARK (White and Burnham 1999) with and without movement parameters (Boulanger et al. 2004a). Pradel models can only be used when there are three or more sampling occasions; this limited the applicable data to those from the Upper River in 2001 and 2003 and from Lower River in 2003. Pradel models potentially have variation in immigration rate (*f*), and fidelity rate (fidelity is one minus the emigration rate). Assuming that survival during sampling is 100%, apparent survival ("phi") becomes an estimate of fidelity. The simplest model representing complete population closure is one with 100% fidelity (i.e., no emigration), one parameter for detection probability, and no immigration. We denote this model "phi(1)p(.)f(0)"; it has only one parameter to estimate, for detection probability. We used likelihood ratio tests (Lebreton et al. 1992) to determine whether the additional parameters for movement (phi and f) were significantly supported by encounter history data (Cooch and White 2006). If there was no significant improvement in model fit from including a parameter for movement, then we concluded that the population was closed.

As a second way to examine the likelihood that the closed population assumption could be violated by animals moving in and out of the system, we calculated the median of maximum distances moved by individual bears detected more than once, and evaluated those distances relative to the sampling extent. If animals tended to move distances that are large relative to the sampling area, we would assume that there could be a reasonable expectation that bears were moving in and out of the study area on a regular basis; conversely, if movements were small relative to the study area extent, we assume it supports the assumption that animals were not regularly moving in and out of the study area.

Results

Comparison of Pradel models indicated that the population was essentially closed. Models with parameters for emigration or immigration did not significantly improve model fit over the simplest model representing a completely closed population in either UR 2003 ($P > 0.5$ in all cases) or LR 2003 ($P > 0.1$ in all cases). For UR 2001 only, the inclusion of one parameter for immigration, in model "*phi*(1)*p*(.)*f*(.)", was supported over model "*phi*(1)*p*(.)*f*(0)" (Chi-square = 4.3; d.f. = 1; P = 0.038). In that model, however, the actual estimate of immigration rate, f, appeared low (f = 0.22, S.E. = 0.12).

Detected movements also indicate that the sampled populations were essentially closed during the annual sampling seasons. At 2.00 km for the Lower River, and 3.45 km for the Upper River, the $\hat{\bar{d}}$ for grizzly bears during sampling at single study areas are less than 10% of the total river lengths sampled (between 39 and 55 km). Those $\hat{\bar{d}}$ estimates alone suggest that roughly 90% or more of the bears that were in the sampling area in the first sampling session in a study area would have still been in the sampling area on the last session in that study area. Sampling at the LR study area was always at least three weeks later than at the UR study area, so the few observed movements between study areas are not violations of population closure for abundance estimates.