QUANTIFICATION OF BLACK BEAR USE OF SALMON STREAMS

INTRODUCTION

Bears (*Ursus* spp.) frequent the riparian areas of streams when anadromous Pacific salmon (*Oncorhynchus* spp.) arrive annually to spawn. A large literature exists on the fishing and social behavior of brown bears (*U. arctos*) where salmon concentrate (Egbert and Stokes 1974, Quinn and Buck 2000, Reimchen 2000, Ruggerone *et al.* 2000, Gende *et al.* 2001, Quinn and Buck 2001, Quinn *et al.* 2003, Gende and Quinn 2004, Gende *et al.* 2004a), and on the effect of salmon on brown bear reproduction (Hilderbrand *et al.* 1999b, Hilderbrand *et al.* 2000). Researchers have also examined brown bear-mediated transfer of marine nutrients to the terrestrial ecosystem (Hilderbrand *et al.* 1999a, Gende *et al.* 2004b) and brown bear behavior across scales larger than localized fishing spots (Ben-David *et al.* 2004). Fewer studies exist on black bears (*U. americanus*) in areas where spawning salmon are abundant. There have only been a few observational studies of black bear fishing behavior (Frame 1974, Reimchen 1998b, a). Some larger studies have incorporated data on the use of salmon by black bears (Jacoby *et al.* 1999, Gende *et al.* 2001) and Chi (1999) studied black bear, brown bear and human intra- and inter-specific interactions in areas with high salmon concentrations. Like brown bears, black bears may also facilitate nutrient transfer from marine to terrestrial ecosystems, and salmon may also affect bears' reproduction, behavior and movement across the landscape. My goal was to quantify black bear use of riparian areas of anadromous salmon spawning streams (hereafter, salmon streams).

Salmon streams and black and brown bears occur in high densities on the 6.8-million hectare Tongass National Forest of Southeast Alaska (Willson *et al.* 1998, Whitman 2001), which is one of the most productive timber forests in the United States (United States Forest Service 1997). Conservation of salmon runs and the wildlife that relies on them, for both intrinsic value and the local economy, depends on good forestry practices, most notably riparian management. On the Tongass, if streams are deemed important for particular wildlife species (*e.g.*, brown bears), management guidelines call for an increase in the width of riparian buffers without logging from 30.5 – 152.4 m (100 – 500 feet) for all Class I streams (streams with anadromous fish) and some Class II streams (streams with resident fish, United States Forest Service 1997). Specific data on wildlife use of individual streams that occur within timber sales are necessary to trigger extended protection.

Genetic tagging (*sensu* Palsboll *et al.* 1997) is a relatively new tool that has been effective in the estimation of population sizes of bears (*e.g.,* Woods *et al.* 1999). It has the potential to be a straightforward method that wildlife managers can use to quantify the use of salmon streams by bears. Genetic *tracking* of brown bears, through the opportunistic collection and subsequent individual identification of shed hair, was first used to determine that five brown bears remained in the Pyrenees Mountains (Taberlet *et al.* 1997). Genetic tagging uses genetic identities, derived from non-invasively collected tissue samples (*e.g.,* hair, feathers, scat) that are systematically collected in a mark-recapture format to estimate demographic parameters such as survival rates and population size. Genetic tagging has been widely used to study black and brown bears (Woods *et al.* 1999, Poole *et al.* 2001, Boersen *et al.* 2003, Belant *et al.* 2004), but also cougars (Ernest *et al.* 2003), whales (Palsboll *et al.* 1997) elephants (Eggert *et al.* 2003) and martens (Mowat and Paetkau 2002). Recently, Boulanger *et al.* (2004) used genetic tagging of brown bears on salmon streams to estimate overall population size and related parameters. The main benefit of genetic tagging is increased sample size compared to more traditional marking methods, through increased capture and recapture probabilities. In the present study, the large number of black bears that frequent salmon streams, based on observations of biologists and hunting and wildlife viewing guides, would be impractical to quantify using traditional methods of capture. Genetic tagging may also lower behavioral heterogeneity in recapture probability (Boersen *et al.* 2003), which is common in studies involving physical trapping of bears. I refined and used the technique of genetic tagging in the high density, ephemeral populations of black bears on salmon streams in Southeast Alaska. I used genetic tagging to estimate abundance and other population parameters that describe the nature in which black bears use these streams.

Study system

The study was conducted on Kuiu Island (1963 km^2, 134°10' W, 56° 45' N) in the Alexander Archipelago of Southeast Alaska (Figure 1) during salmon runs in the summer and fall of 2000 and 2002. The temperate rainforest on Kuiu Island is dominated by Sitka spruce (*Picea sitkensis*) and western hemlock (*Tsuga heterophylla*), and is managed by the Tongass National Forest. Northern Kuiu Island (673 km^2) has been subjected to commercial clear-cut logging since the 1940’s, and 40% of northern Kuiu, where all study streams occur (Figure 2), is in various seral stages of second growth (R. Lowell, pers. comm.). The Alaska Department of Fish and Game (ADF&G) recognizes 34 class I anadromous salmon spawning streams on northern Kuiu Island (W. Bergmann, pers. comm). Four species of salmon spawn from May through November on Kuiu Island: Sockeye (*Oncorhynchus nerka*), chum (*O. keta*), pink (*O. gorbushcha*) and coho salmon (*O. kisutch*). The riparian areas of the streams are dominated by Sitka spruce and western hemlock, and also by salmonberry (*Rubus spectabilis*), red and Sitka alder (*Alnus rubra, A. sinuata*), blueberry (*Vaccinium* spp.) and Devil's club (*Oplopanax horridum*). Black bears, which occur at high densities on the island (Chapter 1), river otters (*Lontra canadensis*), the Alexander Archipelago wolf (*Canis lupus ligoni*), mink (*Mustela vision*) and bald eagles (*Haliaeetus leucocephalus*) are all known to prey on spawning salmon on Kuiu Island. Brown bears do not occur on Kuiu Island.

General approach

I used genetic tagging to document black bear use of the riparian areas of salmon streams by sampling hair from barbed wire snags (hereafter, fences) placed on bear trails. From the hair samples, I derived genetic individual identities that I employed in mark-recapture models to estimate the number of bears that used the riparian areas over the course of the run. In most previous genetic tagging studies of bears, fences have been set up in a corral-like fashion (e.g., Woods *et al.* 1999) over a grid-based landscape, with attractive bait and lures. In two notable exceptions, barbed wire fences were set up on bear trails in the riparian areas of cutthroat trout spawning streams (Hardoldson *et al.* in press) and on brown bear salmon streams in British Columbia (Boulanger *et al.* 2004) to estimate the number of brown bears using the regions. Compared with these other studies, I placed fences at higher densities of 8 – 65 per km of stream, and I surveyed a very small area (0.20 to 2.0 km per stream). In addition, I did not seek to estimate total population size *per se*, but to estimate the total number of black bears visiting particular stream lengths.

Mark-recapture analyses

I used mark-recapture models to document how and how many black bears used the salmon streams. I captured (genetically tagged) bears initially, and recaptured them (genetically reidentified) in subsequent encounter occasions. I used the pattern of captures and recaptures to estimate the parameters (*e.g.,* recapture probability, population size) in each mark-recapture model. Each set of models (*i.e.,* Cormack-Jolly-Seber (CJS), POPAN and closed-captures) was defined by probabilistic equations incorporating a combination of parameters. The number of parameters differed within a set of models, as I either held parameters constant or allowed them to vary with encounter occasion and other factors such as stream size and fence density. For CJS and POPAN models, I used the model selection procedure, Akaike's Information Criterion adjusted for small sample size (AIC_c) to compare different models within a set. AIC_c is based on a combination of the model's fit to the data and parsimony, measured by the number of estimable parameters. AIC_c uses distance and information theory to determine the distance, or difference, between the models and the true underlying distribution. $AIC_c = -2\ln \text{likelihood} + 2K + 2K(K+1)/(n - K - 1)$, where K is the number of estimable parameters in the model and n is the effective sample size (Burnham and Anderson 2002) . I used program MARK (White and Burnham 1999) to perform all parameter estimation and model selection. I used MARK to compute the natural log likelihood of each model as the parameters were estimated using maximum likelihood. The smallest AIC_c within a set of models indicated the best fitting model in the set. I used program CAPTURE within MARK to select the appropriate closed-capture population estimation models, based on the data's consistency with each model's assumptions. I then used CAPTURE to generate population estimates from the selected models.

Assumption of equal catchability

Mark-recapture studies were initially based on the assumption of equal catchability, *i.e.,* marked and unmarked animals have an equal probability of being captured and recaptured. In this case, bears should have an equal probability of being genetically tagged and re-identified. However, the assumption of equal catchability is often not met in natural systems (Pledger 2000). Behavior, time and inherent heterogeneity affect the likelihood of an individual being captured and recaptured (White *et al.* 1982, Pledger 2000). Heterogeneity may be due to sex, age, home-range or some unknown individual characteristic. Boulanger and McClellan (2001) recommended that open population models, which do not allow for individual heterogeneity, should not be used for grizzly bear mark-recapture studies as it is likely that there are age and sex-specific capture probabilities that could result in a negative bias in population estimates. This may also be true for black bears on salmon streams, as it is known that age and sex affect the behavior of black bears on streams (Frame 1974, Chi 1999) and may influence their use of particular trails. As a consequence, I used closed-capture models (Otis *et al.*1978, Pledger 2000) that allowed for heterogeneity to estimate the number of bears visiting salmon streams.

While I took capture heterogeneity into account in the analysis, I took some precautions to reduce heterogeneity in the field. For example, there were likely individual behavioral differences in use of specific trails due to social dominance. Therefore I placed fences on most bear trails in the riparian areas. There was unlikely to be a trap-shy behavioral response as bears habitually climb under sharp logs and brush against overhanging limbs on bear trails. This assertion was supported by observation and remote photography of bears moving under fences and the lack of new trails around fences. I intended to reduce a trap-happy behavioral response by using neither bait nor lure.

Assumption of closure

Geographic closure has been identified as an important assumption of mark-recapture (Garshelis 1992), and specifically in brown bear genetic tagging studies (Boulanger and McLellan 2001). Violation of this assumption in closed-capture models will result in a negative bias in capture probability and an overestimate of population density. However there will be no bias in the estimate of the super-population size (Kendall 1999), *i.e.,* the total number of animals using the study area over the course of the study, if movement in and out of the study area is random with respect to marks. The super-population includes all animals sampled in an area, but this estimate cannot be used to calculate density for the study area at a given time (Garshelis 1992, Kendall 1999, Boulanger and McLellan 2001). In the present study, I did not know whether bears stayed on a salmon stream for the duration of the spawning run. Yet my intent was to estimate the number of bears that visited the riparian areas of streams, not to estimate the size of a biological population defined within a geographic area. Thus the estimates in this study provided by closed-capture models were the total number of bears visiting each stream over the study period. I also used the open population model POPAN (Schwarz and Arnason, 1996) primarily as a comparison model, and to estimate “recruitment” of bears to the stream, which is not included as a parameter in closed-capture models.

Because I used primarily closed-capture models, I must also assume that there is demographic closure. Genetic tagging occurred on streams for four to nine weeks between July and September, according to the length of individual runs. I assumed that no adult bears died during this interval. However, hunting seasons started on September 1^{st}, and during 2002, four bears were killed on Saginaw Creek and one on Rowan Creek before the end of sampling.

Correct identification of animals

The supposition that marks are unique is so basic an assumption in individual-based mark-recapture that it usually remains unstated. However, violation of this assumption can have significant ramifications for bias, and is more likely when using genetic marks (Mills *et al.* 2000). If individuals were represented by greater than one genetic identity (multiple marks per individual) or spurious individuals were generated, there would be a negative bias in recapture probability, resulting in an overestimate of population size. This problem would have been a result of data quality compromised by laboratory or scoring (interpretation of the genotype) errors, but could be reduced by various quality control measures (Paetkau 2003, McKelvey and Schwartz 2004a, b, Paetkau 2004). An opposite problem could have resulted from the fact that genetic identities were probabilistic, due to shared genetic information between individuals. If different animals were identified as the same genetic individual (same mark for different animals) there would be an underestimate of population size and variance (termed a *shadow effect*, Mills *et al.* 2000), due to a positive bias in recapture probability. To reduce the appearance of genetic shadows, the genetic characteristics that I used to identify the animal were sufficiently numerous and had sufficient variability to identify animals with a high degree of confidence.

METHODS

Field methods

In 2000, I used genetic tagging to quantify the number of bears using four salmon streams on Kuiu Island: Saginaw, Security, Portage and Cabin creeks. Samples were also collected from Kadake Creek, but these were not used to estimate number of bears, but used to augment the analysis of capture heterogeneity. In 2002, I sampled Saginaw, Portage, Cabin, Rowan and Skinny Rowan creeks (Figure 2, Table 1). Portage, Cabin and Skinny Rowan creeks had spawning reaches of less than 500 m. I sampled the entire spawning reaches on these smaller streams, whereas on the larger Saginaw, Rowan and Security creeks, I sampled from 1.6 to 2.0 km sections. The total spawning reach on these larger creeks was approximately three to five km. I sampled two sections on Kadake Creek. The lower sampling reach (3.2 km) included the tidal area, and the upper segment (0.5 km) was roughly 6 km upstream. Kadake Creek was the largest stream sampled (27 – 50 m across), and had a tidal bay of 4 km^2 with strong pink, coho and chum salmon runs of 100,000’s of individuals. In the lower section, salmon were only accessible to black bears in the shallower riffles (pers. obs., and see Gende *et al.* 2004). The upper segment of Kadake Creek was comparable in channel width and depth to Saginaw, Security and Rowan creeks.

I placed fences on all prominent bear trails in the riparian areas, and positioned them at a height to avoid sampling cubs-of-the-year. The density of fences ranged from 8.6 per km on Kadake Creek to 65.0 per km on Cabin Creek (2000). Fences were 53.4 ± 1.3 cm high. In Southeast Alaska, only cubs-of-the-year are dependent on their mothers. Therefore, I assumed that all samples from fences came from independent bears that were at least 1.5 years old. I visited fences weekly, and in general took one hair sample from each fence per week (encounter occasion). To avoid mixed samples *i.e.*, samples from multiple capture events, I did not take samples from barbs packed full with hair. I took multiple samples from a fence only if the samples were separated by greater than an approximate bear-width (*i.e.*, five barbs), and therefore most likely represented different capture events. This eliminated the cost of processing samples from the same capture event, but likely reduced capture probability. I cleaned and discarded unsampled hair from fences. I stored hair samples from individual barbs in separate paper envelopes that were kept dry and out of UV light to prevent further degradation of DNA.

Laboratory methods

Sample choice and extraction

I extracted DNA from hair samples using the Qiagen DNeasy and Qiagen DNeasy 96 well plate extraction kits (http://www1.qiagen.com/), according to the manufacturer’s protocols. To avoid sampling from multiple capture events, I included hair strands in an extraction that were from the same clump (a clump was often formed by dried blood or skin). In addition, I only included hairs that were similar in length, texture and color. I eliminated samples if they consisted of more than one clump of hair, indicating that the sample may have been from multiple capture events, or if there were not enough suitable follicles. Initially, I used ten hairs per extraction, following the suggestion by Goossens *et al.* (1998) that extraction from ten follicles greatly reduced the occurrence of allelic dropout (*i.e*., false homozygotes, see below), which is common when small quantities of DNA are amplified in polymerase chain reaction (PCR). However, it became evident that reliable genotypes could be derived from extractions with fewer follicles, and thus I extracted from samples that had at least one good follicle. It is likely that fewer than ten follicles (Goossens *et al.* 1998) were sufficient to produce reliable genotypes due to the advent of better extraction methods. For example, I used an RNA carrier (SIGMA, http://www.sigmaaldrich.com) to increase the quantity of DNA eluted during the final extraction step. I also used a more sensitive *taq* polymerase formulated for low quantity DNA templates (Titanium *taq*, CLONTECH, http://www.bdbiosciences.com/clontech/) in the PCR. The ability to use fewer hairs in the extraction likely reduced the probability that an extracted sample consisted of multiple capture events.

Microsatellite amplification

I used seven microsatellite loci developed for black bears (Table 2) to amplify each individual DNA sample using PCR (Paetkau and Strobeck 1994, Paetkau *et al.* 1995). I also amplified the amelogenin gene for each sample for sex identification using primer sequences developed for *Bovis* (Ennis and Gallagher 1994). I carried out all

PCR's in 15 µl reaction volumes, on a Peltier 200 or 220 thermocycler (Table 3). The concentration of the DNA template was generally < 1 ng/µl (Taberlet *et al.* 1996), and therefore I could not quantify the extract using standard fluorometry; I used five µl of DNA template per reaction. I started all PCR's with a one-minute hot start at 95°C, followed by a cycling sequence: the DNA was denatured for 30 seconds at 95°C, primers were bound to the template at the primer-specific annealing temperature for 30 seconds, and fragments were built at 72°C for 30 seconds. I repeated this sequence for 30 to 45 cycles, depending upon the efficiency of the reaction. I followed the cycling sequence with a 72°C extension for ten minutes.

I variously diluted PCR products with deionized water based on the efficiency of the reaction (no dilution to 1:200). I ethanol precipitated PCR products to remove non-bounded primers, and combined the precipitated PCR products with either a formamide-LIZ or -ROX (Applied Biosystems (ABI)) ladder (total volume, 20 µl), which was used to calibrate fragment size estimation. I fluorescently-labeled the forward primer (OPERON and ABI) in all PCR's, allowing size estimation of the fragments using capillary electrophoresis on an ABI 3700 or 3730 automated sequencer at the Nevada Genomics Center at the University of Nevada, Reno.

Analysis

Probability of identity

Probability of identity (P_{ID}) was calculated as a measure of the reliability of genetically derived individual identities. P_{ID} is the probability that two random individuals in a population have the same genetic identity (Taberlet and Waits 1998, Waits *et al.* 2001). A sufficiently low P_{ID} was necessary to avoid the shadow effect (Mills *et al.* 2000). P_{ID} must be determined on a population basis, as the number of microsatellite loci required to determine individual identity is negatively correlated with genetic variation in the population. To determine the appropriate number of loci to use, I calculated P_{ID} using various numbers of loci for northern Kuiu Island, where all study streams occurred. P_{ID} was estimated using genotype frequencies expected from a population in Hardy-Weinberg equilibrium (Paetkau and Strobeck 1994). The unbiased probability of identity, P_{ID_UNB}, was corrected for small sample size (Paetkau *et al.* 1998). P_{ID_SIB} (Waits *et al.* 2001) was used to estimate the probability that two full siblings in the population share the same multi-locus genotype, and was a more conservative estimate of P_{ID}. I used P_{ID_UNB} and P_{ID_SIB} to provide the lower and upper bounds for the number of loci required for individual identification (Waits *et al*. 2001). All P_{ID} calculations were performed in GIMLET version 1.3.3 (Valiere 2002) using a tissue data set from harvested black bears (*n* = 117) from northern Kuiu Island.

It was necessary to determine if there was genetic substructure within northern Kuiu Island to determine if the P_{ID} estimated for northern Kuiu Island would be applicable to all study streams. If substructure was found, then P_{ID} would need to be calculated for each individual stream. This is not preferred, as P_{ID} would then be calculated with much smaller, watershed-based data sets. A more accurate and precise estimate of P_{ID} could be calculated using the 117 tissue samples available for northern Kuiu Island. Genetic substructure was evaluated by testing for heterozygote excess in the population (Hartl and Clark 1997). If there was heterozygote excess, Wright’s inbreeding coefficient, F_{IS} would be significantly lower than expected, indicating population substructure. I used F-STAT (Goudet 2001) to calculate F_{IS}. I also calculated P_{ID} from watershed-based tissue sample data sets: Rowan (n = 33 individuals), Saginaw (n = 35) and Security (n = 25). Tissue samples were also available from Port Camden Bay, the location of Portage and Cabin creeks, and from Kadake Bay; these bays are large with respect to the streams, however, and the genetic variation may be no more representative than that of northern Kuiu Island.

Data quality

Confidence in data quality was essential, as all mark-recapture analyses used in this study were based on the correct identification of individuals (Mills *et al.* 2000). Rigorous quality control of genotyping data was necessary due to prevalence of genotyping error in studies using degraded and low quantity DNA (Gagneux *et al.* 1997, Taberlet and Waits 1998, Mills *et al.* 2000, Waits and Leberg 2000, Waits *et al.* 2001, Miller *et al.* 2002, McKelvey and Schwartz 2004a, b, Paetkau 2004). For example, allelic dropout is common when PCR is used to amplify only a few copies of DNA (Waits and Leberg 2000), and considered one of the “most severe” (McKelvey and Schwartz 2004a) problems with this kind of sampling. Allelic dropout occurs when the larger allele of a heterozygous sample is not well amplified due to competition between the alleles during replication in the PCR (Taberlet *et al.* 1996, Gagneux *et al.* 1997, Goossens *et al.* 1998, Waits and Leberg 2000). Smaller alleles replicate faster than larger alleles and thus due to initial sampling of the alleles from a heterozygous sample in the first cycles of PCR, the smaller allele may be replicated exponentially more times, resulting in allelic dropout.

Additional problems in data quality could be due to other PCR errors, including ambiguity in the signal, or scoring mistakes (Paetkau 2003).

A rigorous multiple-tubes approach (multiple PCR's per sample) has been recommended (Taberlet *et al.* 1996) to confirm genotypes generated from low quality and quantity DNA. Taberlet *et al.*'s (1996) approach required three identical PCR's per sample to confirm genotypes, and required additional PCR's if the first three were not identical. Samples have not routinely been amplified using multiple PCR's in large-scale bear genetic tagging projects, but samples are generally variously reamplified when genotypes are of poor quality or ambiguous, or are unique or differ from other multilocus genotypes at one or two loci (Woods *et al.*, 1999, Poole *et al.* 2001, Boersen *et al.* 2003, Belant *et al.* 2004). While authors in recent literature (Paetkau 2003, Paetkau 2004, McKelvey and Schwartz 2004ab) have debated procedures necessary to standardize data quality methods, my laboratory work was done prior to these publications, and I employed my own data quality procedures.

My data quality efforts included both lab and analytic procedures. First, I made efforts to increase the quantity of DNA in the extract by using an RNA carrier, and to increase the quality of the PCR product using a more efficient *taq* polymerase, specifically designed for low quantity DNA. To facilitate finding genotyping errors, I wrote a sorting program, IDENTITY, in Visual Basic 6.0 (Appendix I; available at www.consgenetics.unr.edu/~peacock) to flag pairs of genetic individuals that differed from one another at a single locus. I re-examined and/or reamplified such pairs of "individuals" from the samples from 2000 at the locus in question. I also reamplified samples from 2000 that had homozygous, rare, ambiguous or poor quality genotypes. I simply reamplified all samples from 2002 two to three times to confirm genotypes (repeating PCR's for entire 96-sample trays was easier and less error prone than isolating and reamplifying specific samples as was done in 2000). Where differences in genotypes of the same sample were irreconcilable (regardless of the error-checking approach), I eliminated the sample from analysis. I also eliminated obviously mixed samples (*i.e.*, "polyploid" genotypes). I made the assumption that elimination of samples was random with respect to date of capture and individual identity.

Capture histories

I created a capture history that showed the distribution of capture (1) and non-capture (0) events (*e.g.,*11000010), for each genetically identified individual. I grouped capture histories for each of the data sets (stream-years; Appendix V) for stream-based analyses. I pooled all capture histories from streams that I sampled in 2002 to evaluate the effect of stream, stream size and fence density on recapture probability, and stream and stream size on the fidelity of bears to the stream reaches.

Recapture probability, fidelity and recruitment

I estimated recapture probability (p) and apparent survival (φ, fidelity) for each stream-year ($n = 10$) using the open Cormack-Jolly-Seber (CJS) model (Cormack 1964, Jolly 1965, Seber 1965, Brownie 1987, Lebreton *et al.* 1992). In this model, animals survived between encounter occasions with the probability φ_i. φ could not be estimated for the last interval, as it was confounded with p, the probability that a bear, marked previously, was reidentified in a subsequent interval. $1 - \varphi$ included animals that either died or left the study area. I assumed that no animals died in the four to nine weeks of the sampling period, thus φ represented the probability that an animal remained on the stream for the interval of interest.

I ran all pre-defined CJS models in MARK: $\varphi(.)p(.)$; $\varphi(.)p(\mathrm{t})$; $\varphi(\mathrm{t})p(.)$ and $\varphi(\mathrm{t})p(\mathrm{t})$, where (.) indicated that the parameter was held constant over the encounter occasions (for p) or intervals (for φ), and (t) indicated that the parameter was estimated for each occasion or interval. I also evaluated the effect of a time trend (T) on φ and p. (T) differed from (t) in that it allowed for estimation of a constant trend through time but did not estimate the parameter for different occasions or intervals. (T) required less power in the data set as fewer parameters were estimated, thus (T) models would have been selected preferentially to (t) models if the deviance of the model from the saturated model (most complex) was equal.

I ran another set of CJS models with data pooled from all streams sampled in 2002. I ran all pre-defined models, in addition to all variations involving $\varphi(\mathrm{g})$ and $p(\mathrm{g})$, where the parameters varied by group (stream). I also examined models that included the effects of density of fences (3 levels of density: 15 fences/km; 30 fences/km and 45 fences/km) on recapture probability, and size of the stream (2 levels of size: < 500 m and > 500 m of spawning habitat available to bears) on recapture and fidelity probabilities.

I presented model-averaged estimates of all parameters. Model-specific parameters are averaged with respect to the AICc weight of each model in the set.

Mark-recapture analyses did not include multiple recapture events within encounter occasions, yet this information provided insight into the temporal pattern of bear activity on the streams. I investigated the temporal effect on the pattern of recapture, by regressing the frequency of recapture, including bears recaptured within intervals on different fences, against the encounter occasion in which animals were recaptured. This regression analysis used frequency of recapture events, and did not use any information on time-specific estimations of recapture probability.

I did not incorporate sex as a group covariate in mark-recapture models, due to sample size. However, to investigate a potential cause of heterogeneity in capture probability, I examined the use (frequency of capture and recapture) of the eleven stream reaches and different parts of three streams by male and female bears. Again, this analysis did not incorporate estimates of recapture probability.

To observe the dynamic nature of the group of bears in the riparian areas, I estimated the probability of entry (*pent*), *i.e.,* the probability that a new bear arrived on the stream (recruitment), using the POPAN model (Schwarz and Arnason 1996), which is a reparameterization of the open CJS (Cormack 1964, Jolly 1965, Seber 1965).

Abundance

MNA

I used IDENTITY to determine the minimum number known alive (MNA; the number of bears genetically identified) that used each reach of stream in each year. I used IDENTITY to compare genotypes at each locus for each pair of samples, and to tally the number of matched and mismatched single locus-genotypes between a pair of samples. The program considered two samples that matched at at least five locus-genotypes (see **RESULTS**, *Probability of Identity*), with no mismatches, to represent the same bear. I used IDENTITY to compare all pairs of samples in this way. Ultimately, I used the program to identify the number of bears using the reach of stream (MNA) from the total samples collected. MNA not only did not take into account capture probability, but it also contained all the additional negative bias due to heterogeneity in capture (Mills *et al.* 2000). While MNA is likely a biased number, I estimated MNA to provide a baseline index, to be examined where capture probability was too low to provide an abundance estimate.

Population size estimation

I used closed capture models (Otis *et al.* 1978, Norris and Pollock 1995, Pledger 2000) to estimate the total number of bears using the sampled reaches of salmon streams. I used program CAPTURE within MARK to compare the models: the null model, M_o, where capture probability was constant, M_h, where capture probability varied with individual, M_b, where capture probability was a function of a behavioral response to capture, and M_t, where capture probability varied over time. I also compared combinations of the models: M_{bh}, M_{th}, M_{tb} and M_{tbh}. Otis *et al.* (1978) described the model selection procedure in detail; it consisted of likelihood ratio tests of each model with respect to M_o, and goodness-of-fit tests of each model. Based of the outcome of these tests of the assumptions of the different models, I used CAPTURE to choose the most appropriate model to estimate population size (Otis *et al.* 1978). I presented the probability of the selected model and its corresponding population estimate. When the model that most appropriately described the pattern in capture and recapture had no associated population estimator (M_{tb}, M_{th} and M_{tbh}, Otis *et al.* 1978), I used the next most appropriate model to estimate population size. Since small sample size may have resulted in indistinguishable population estimates from different closed capture models, including the selected model, for comparison I produced population estimates from six models (M_o, M_h, M_b, M_t, M_{th} and M_{bh}) with different assumptions regarding capture probability.

I also used POPAN to estimate the size of the super-population (Kendall 1999), which represented the total number of bears visiting each stream. White and Burnham (1999) suggested that the POPAN parameterization is particularly robust in the estimation of population size.

RESULTS

Effort

I collected 1554 hair samples from seven streams in 2000 and 2002 (Table 4), resulting in ten stream-year data sets for estimation of fidelity and recapture probability and nine data sets for population estimation. I compiled 11 data sets to assess differential use of streams by male and female bears, as an examination of one possible cause of heterogeneity in capture probability.

I collected a subset (38%) of the available samples that were on the fences. Of the collected hair samples, I determined that 71% were suitable for extraction. Of the samples that I extracted, I successfully amplified 77% of the samples at five to seven microsatellite loci.

Probability of identity

Northern Kuiu Island did not have heterozygosity excess ($F_{IS} = 0.03$), at a Bonferroni-adjusted alpha value of 0.007 (140 randomizations), indicating no significant population substructure. P_{ID_UNB} varied from 0.0001 to 0.000018 for five to seven loci, sufficiently low to have confidence in the identification of individuals from the data (Taberlet and Luikart 1999, Waits *et al.* 2001). PI_{SIB} for northern Kuiu Island ranged from 0.022 to 0.0102 for five to seven loci, indicating that one to two of 100 multi-locus genotypes from full siblings may have resulted in a genetic shadow with this number of loci. I also calculated P_{ID} for three watersheds in which four of the study streams occurred, however their values did not differ substantially from P_{ID} calculated for the black bears from all of northern Kuiu Island (Figure 3). Therefore, I used P_{ID} calculated for northern Kuiu Island as the criterion and used samples that were identified at at least five loci for subsequent analyses.

Stream use by black bears

Recapture probability

Black bear recapture probability (p) on the salmon streams estimated by Cormack-Jolly-Seber (CJS) ranged from 0.03 ± 0.02 on Portage Creek in 2000 to 0.42 ± 0.09 on Skinny Rowan Creek in 2002. $\varphi(.)p(.)$ was selected as the best model in eight of ten stream-year data sets, however AICc weights of these top $\varphi(.)p(.)$ models were generally low and ranged from 0.08 – 0.89 (Table 5, Appendix VI). A trend effect (T) on recapture probability was present in all other models with ΔAICc < 2.0 in all stream-year data sets (Appendix VI).

The effect of density of fences on recapture probability was present in eight of the ten top models (models with ΔAICc < 2.0), using data pooled from all five streams sampled in 2002 (Figure 4). Recapture probability was highest for the single stream (0.40 ± 0.07, Cabin Creek) with an intermediate level density of fences (30 per km). Recapture probability was higher on streams (n = 2) with high density of fences (45 fences per km, 0.25 ± 0.06) than on streams (n = 2) with low density of fences (15 fences per km, 0.12 ± 0.02), and was higher for streams with < 500 m of salmon spawning habitat (n = 3, 0.32 ± 0.05) than > 500 m (n = 2, 0.12 ± 0.02; Figure 5). Three of the top models (ΔAICc, 0.46 to 0.65) included an effect of stream size on recapture probability. Recapture probability did not vary significantly among streams as this grouping variable (stream) did not appear in any of the top models by itself in this pooled data set from 2002.

More bears were recaptured within the week in which they were first captured and in the subsequent week after initial capture, than in any other subsequent week (Figure 6). Polynomial regressions of the number of recapture events on encounter occasion were significant for six (p < 0.0001 – 0.048) of the nine stream-year data sets (Table 6).

Stream use by male and female bears

Fewer females used eight of eleven stream reaches than would be expected by chance (Figure 7), assuming the sex ratio on northern Kuiu Island was even. The number of female bears that visited tidal areas of three streams in 2000 was lower than expected, and lower than the number visiting upstream, forested areas (1-tailed t-test, p = 0.01, Figure 8).

Fidelity

The probability of a bear remaining on the stream from one week to the next (φ), ranged from 0.61 ± 0.06 on Saginaw Creek in 2000 to 0.96 ± 0.09 on Lower Kadake Creek in 2000 and 0.96 ± 0.24 on Cabin Creek in 2002 (Table 5, Appendix VI). Thus, for example on Saginaw Creek in 2000 there was a 39% chance of an individual bear not being on the stream one week after having been there the week before.

Eight of the ten top models in the pooled 2002 data set had a trend (T) in φ (Figure 9). Model-averaged φ estimates, for all streams combined, decreased from 0.90 ± 0.05 during the first interval to 0.75 ± 0.06 during the last estimable interval. Stream size had a weak effect (ΔAICc, 1.9 to 2.03, Figure 10) on the probability of a bear remaining on the stream for a given interval; fidelity was slightly higher on smaller streams.

Recruitment

The probability of entry parameter (*pent*, POPAN) ranged from 0.03 ± 0.03 on Rowan Creek to 0.12 ± 0.08 on Portage Creek in 2000 and 0.12 ± 0.02 in 2002. For example in 2000 on Saginaw Creek, recruitment was estimated at 0.10 ± 0.008 (Table 7), meaning that in every week, there was a 10% chance that a bear on the stream had entered since the last week. On average, every week, 9% ($\overline{X}$ = 0.09 ± 0.02) of the bears using a stream were new visitors. Bears stayed on average 1.2 ± 0.7 weeks (Portage 2000 and Rowan creeks) to 2.7 ± 2.5 weeks (Skinny Rowan Creek) on the sampled reaches of stream (Table 8, Figure 11).

Abundance

MNA

On streams where I surveyed 200 to 500 m of spawning habitat (*n* = 5 stream-years), 14 to 29 bears were genetically identified on each stream over the course of the study (four to nine weeks, Table 9). Where between 1.6 and 2.0 km of spawning habitat was surveyed (*n* = 4 stream-years), 68 to 107 individual bears were identified on each stream over approximately two months. On these larger streams, an average of 23 ± 4 bears per 500 m were identified over two months.

Population size estimation

I used program CAPTURE to select the most appropriate closed capture population estimation models (Table 10). Heterogeneity in capture probability was apparent in seven of the nine stream-year data sets. The effects of behavior or time appeared in four of the selected models. I estimated the number of bears using each stream using the selected model (Table 9). The coefficients of variation around the population point estimates ranged from 9% on Rowan Creek to 34% on Skinny Rowan Creek. I also produced estimates from a total of six different closed capture models (M_o, M_b, M_h, M_t, M_{th}, M_{bh}), and in four of the six cases, standard errors of the largest and smallest estimates overlapped (Table 11).

MNA ranged from 21 to 87% of the closed-capture population estimates ($\overline{X}$ = 52 ± 11%). On the smaller streams with less than 500 m surveyed, the average estimated number of bears per 500 m ranged from 47 bears on Skinny Rowan Creek (nine weeks) to 95 bears on Cabin Creek (four weeks) in 2000 (Table 12). On the larger creeks, the number of bears using 500 m of stream ranged from 22 on Rowan Creek in 2002 (eight weeks) to 97 bears on Security (nine weeks) and Saginaw (eight weeks) creeks in 2000.

The number of bears using Saginaw Creek (2000) was also estimated for sequential four week periods (Figure 12). While 60 ± 7 to 188 ± 45 black bears were estimated to use Saginaw Creek during sequential four-week periods, a total of 348 ± 35 were estimated to use the stream reach over the entire eight-week period. This indicated a turnover in the identities of individual bears over the two month period.

MNA ranged from 17 to 81% of the estimated number of bears visiting the streams ($\overline{X} = 48 \pm 11\%$) using the open POPAN population estimation model (Table 9). There was no consistent difference between the open and closed model estimates of the number of bears visiting the streams.

DISCUSSION

Probability of Identity

Mills *et al.* (2000) recommended a P_{ID_UNB} of less than 0.01 to avoid the shadow effect for population size estimation studies using genetic tagging. Woods *et al.* (1999) recommended a P_{ID_SIB} of < 0.05, for distinguishing between brown bear siblings in a genetic tagging study. I concluded that the upper ($P_{ID\_SIB} = 0.02 – 0.003$) and lower ($P_{ID\_UNB} = 0.0002 – 0.000018$) bounds of identification confidence in the northern Kuiu Island data set were adequate for individual identification and population estimation purposes.

Quantification of black bear use of salmon streams

From the 2002 data, 225 different bears were genetically identified over the course of nine weeks on a total of 4.8 km of five streams, which represents approximately 23% of the black bear population on northern Kuiu Island (Chapter 1). Using estimated numbers from the closed capture models, 345 bears used these reaches of streams, representing approximately 35% of the northern Kuiu Island population. This is not surprising, as I purposely chose to sample the most productive fishing streams for bears, based on anecdotal information.

I estimated a high density of bears using small reaches of streams: 22 to 120 bears (on the different streams) were estimated to use 500 m of riparian areas over the course of two months. As an example, I estimated that 38 ± 8 and 73 ±15 bears used 200 m of Cabin Creek in 2000 and 2002, respectively, over the course of four and eight weeks. This particular stream had small chum, and even smaller pink and coho salmon runs. Over the last decade the annual chum salmon escapement in Cabin Creek has averaged 1,800 individuals (W. Bergmann, pers. comm.). The minimum number of bears that used Portage Creek in 2000, which had approximately 300 m of spawning habitat, was 28 bears (four weeks). When the spawning habitat was reduced to about 200 m due to a beaver pond in 2002, 14 bears were identified (eight weeks). The number of bears using particular stream reaches was not consistent between years. For example, on Saginaw Creek in 2000, I estimated that 348 bears visited the stream over eight weeks, whereas in 2002, I estimated that 115 bears visited Saginaw Creek in nine weeks.

Small sections of salmon streams in this study minimally supported high densities of black bears, suggesting the importance of this irruptive food resource for black bears on Kuiu Island. Enumeration of black bears on average salmon streams (as opposed to prize fishing spots for bears, *e.g.,* Anan Creek) has not previously been accomplished, with the exception of a study in Bag Harbor (chum salmon run of 2,000 to 6,000 individuals) on Moresby Island, British Columbia (Reimchen 1998b). Reimchen (1998b) observed one to six bears using the salmon stream every night for four nights over 700 m of stream. However the total number of bears using the stream over the course of the salmon run is not known. In south-central Alaska on Olsen Creek, which may be most comparable to Saginaw, Rowan and Security creeks in terms of salmon escapement (~26,000 chum and ~27,000 pink individuals annually), Frame (1974) identified 18 black bears using a 600 m tidally influenced reach of stream over the course of three months. During daylight hours, Chi (1999) used visual observations to document 16 male and 12 female individual black bears over three months fishing at two waterfalls on 400 m of Anan Creek on the mainland of Southeast Alaska. In the subsequent year of study, she observed 26 individual bears. Using my MNA data, which is most comparable to the data in these studies, I detected between 35 and 59 ($\overline{X} = 33 \pm 13$ SD) bears per 500 m of stream reach ($n = 9$ stream-years) over the course of two months, which is higher than these other censuses (Frame 1974, Reimchen 1998b, Chi 1999). The only study to indicate the rigor used for individual identification was Chi (1999), and thus I will only further comment on this study for comparison. The difference in number of bears documented on each of the streams on Kuiu Island compared to Anan Creek, could be due to several reasons. My study included bears that used the streams during the day and the night, and Reimchen (1998b) suggested that 98% of all black bear activity on salmon streams (where black and brown bears are not sympatric) occurred during darkness. Although brown bears congregate and fish generally > 1 km away from the Anan Creek waterfalls (Chi 1999), brown bear presence may influence black bear numbers and activity. It is not likely that more black bears use the streams on Kuiu Island than at Anan Creek due to salmon accessibility. Anan Creek is unique in Southeast Alaska, as 250,000 pink salmon run in the stream annually, and salmon are very accessible to black bears at the waterfalls as evidenced by high fish capture rates (Chi 1999). I suggest that the genetic tagging on Kuiu Island may have increased the detection of individuals, allowed for the collection of effective night time "observations," offered a more rigorous assessment of individual identity and reduced observer effects on bears, all of which could have contributed to higher census numbers of black bears on streams. I also suggest that the number of individuals documented to use salmon streams is not a result of data quality issues. I assert this due to the data quality control measures taken in this study (including two to three amplifications per sample in 2002), coupled with the fact that although recapture probability was low (potentially indicating spurious individuals) and abundance estimates were high, animals *were* recaptured at high rates within the initial capture interval, which is uninformative for mark-recapture analysis (but informative for bear biology). My subsequent use of estimation procedures using mark-recapture allowed for the incorporation of detection probability and variation in detection probability to produce a less biased (than visual observation and genetic MNA) assessment of the number of bears using salmon streams.

Black bear use of salmon streams

The pattern of recapture of black bears on the salmon streams highlights the dynamic nature of black bear use of this habitat. Recapture probability on most streams was low to moderate (0.03 ± 0.02 to 0.42 ± 0.09, $\overline{X} = 0.20 \pm 0.12$ (SD). The data suggest that while the density of black bears remains high over the course of the salmon run, there was substantial turnover of individual bears on particular streams. In all data sets, bears used streams on average for less than three weeks. When animals were recaptured, they were most likely to be recaptured within the initial interval or one or two weeks after initial tagging. Thus relatively low recapture rate was more likely due to the biological phenomenon that black bears use these streams for periods of time shorter than the course of the sampling, rather than the inability of the method to produce recaptures.

The data from Saginaw Creek (2000) provide a good example of the dynamic nature of the group of bears on a salmon stream. The probability of a bear remaining on Saginaw Creek from one week to the next ranged from 0.42 ± 0.26 to 0.71 ± 0.19. On average, fidelity was 61%, thus after three weeks the turnover of individual bears was 77% ($1 - 0.61^3$). The probability that a bear was not on the stream the week before it was sampled, was approximately 0.10 ± 0.002. When bears were recaptured they were most often recaptured in the next encounter (38%); 76% of recapture events occurred within the interval or in the first or second week following initial capture.

Seven of the nine genetic tagging data sets on black bear use of salmon streams showed heterogeneity in capture probability. Heterogeneity in capture was to be expected as it is almost ubiquitous in mark-recapture studies of mammals (Sequin *et al.* 2003), especially with brown bears (Boulanger and McLellan 2001). Individuals may differ in capture probability in the riparian areas of streams due to dominance status, which can be a function of age, sex or individual variation in behavior. Social status is known to affect fishing behavior in brown bears (Fagen and Fagen 1996, Gende and Quinn 2004). In direct contrast with previous studies of brown bear behavior, Frame (1974) did not observe black bears defending fishing areas or holding territories. In contrast, Chi (1999) found that 36% of intraspecific interactions of black bears at Anan Creek were aggressive; 65% of these resulted in the displacement of one of the bears. Thus it is likely that social status affects black bear behavior on the study streams on Kuiu Island. This behavior could be expressed by differential use of trails, differential use of the stream in terms of the duration that the individuals stay, or a myriad of other aspects of black bear ecology and behavior (Table 13). Differential behavior will result in different capture and recapture probabilities among individuals or types of bears (*e.g.*, single females, females with cubs, subadults, males), and ultimately will influence population estimation model selection.

Of the possible aspects of bear behavior that could produce heterogeneity in capture, I can only attempt to address differential use of the stream by male and female bears. However, because sample sizes were small, using sex as a group variable in mark-recapture analyses would have resulted in imprecise estimates of the effect of sex on recapture probability, fidelity and the probability of entry. However, I used this information to document differential use of the study streams by male and female black bears, which may suggest why heterogeneity appears in most of the selected closed capture population models. In eight of eleven data sets, females represented less than 50% of the individuals using the stream (If anything, black bear sex ratio on Kuiu Island favors females, as hunting is heavily skewed towards males, Chapter 1). Less than expected use of streams by females may be due to the threat of infanticide in areas of high bear density (Hessing and Aumiller 1994). For example, on Saginaw Creek in 2000, where only 33% of the individuals using the stream were female, I observed an adult bear killing two sibling cubs while the mother was fishing approximately 100 m away. Alternatively, females did not use streams less, but had systematic lower capture probability. Whether the data result from lower capture probability or lower incidence of females, both behaviors indicate that male and female bears were behaving differently on these streams. However, in contrast to other data sets, on Portage Creek, 64% of the individuals were females, and 72% of the visits recorded at the stream (capture events) were by females (heterogeneity in capture was not found on Portage Creek).

If particular streams are used differentially by male and female bears, heterogeneity in capture, caused by different capture probabilities of males and females, may appear in mark-recapture data sets on those streams. In addition, I documented male and female bears to differentially use sections of three streams. I found that females used tidal areas less than would be expected by chance, and less than upstream, forested areas. This habitat use pattern exhibited by female bears, may be due to the distance to escape cover (trees) for dependent young from tidal fishing spots. If I did not distribute fences randomly with respect to this sexual segregation, heterogeneity in capture could have been generated.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Genetic tagging as a method for the enumeration of bears on salmon streams

I suggest that genetic tagging is an effective method to quantify black bear use of salmon streams. I have estimated how many bears use these streams, and that they use the streams in a dynamic fashion. While recapture probability was low to moderate across the total sampling period, it was high when capture probabilities were truncated to the average stay of a bear on the stream. This was corroborated by the pattern of recapture events with respect to encounter occasion. I believe better estimates of local abundance could be produced by a study designed with shorter intervals to increase capture probability. In addition, overall sample size should be increased to obtain more precise estimates. This could be accomplished in several ways. Primarily, I advise collecting and identifying > 1 sample per fence. While this will inevitably produce more uninformative recaptures within encounter occasions, it will also only increase recapture probability and sample size (number of bears identified). Secondly, recapture probability and sample size could be increased by increasing the density of fences, as suggested by the results of this study. If sample size is increased sufficiently in the above ways, a robust design (Pollock 1982) approach (*i.e.,* temporally nested sampling) could be used to better document the fluctuating group of bears, by separately estimating fidelity (secondary sampling) and recapture probability (primary sampling). Quantification of black bear use of salmon streams using traditional methods such as physical capture or observation would have been substantially more labor and cost intensive across such a large landscape of streams. It also would have been likely unfeasible to capture the number of bears necessary on single streams to generate meaningful stream-based abundance estimates, or to identify (with visual observations) enough animals with a sufficient degree of rigor (pers. obs.).

A large number of black bear adults use riparian areas of spawning salmon streams, indicating the importance of intact riparian areas and salmon runs to the black bear population on Kuiu Island, and likely throughout Southeast Alaska. While bears have been studied and populations enumerated where fish, bears and humans congregate, (*e.g.,* McNeil River, Anan Creek) the number of bears, and the nature of their use of ‘average’ anadromous salmon streams has not before been documented for black bears. Just recently, Boulanger *et al.* (2004) documented use of “average” streams by brown bears using genetic tagging. There are thousands of such streams across the Pacific Northwest used by anadromous salmon species for spawning, especially on the Tongass National Forest. This study highlights the importance of even small reaches of small and average salmon runs to black bears. Black bears in this study tended to use the smaller streams in higher densities than larger streams, likely due to the accessibility of salmon in smaller streams (Gende *et al.* 2004a) indicating the need to manage streams that have low escapement (< 1,500 salmon) in addition to streams that are managed based on their contribution to the commercial fishery.

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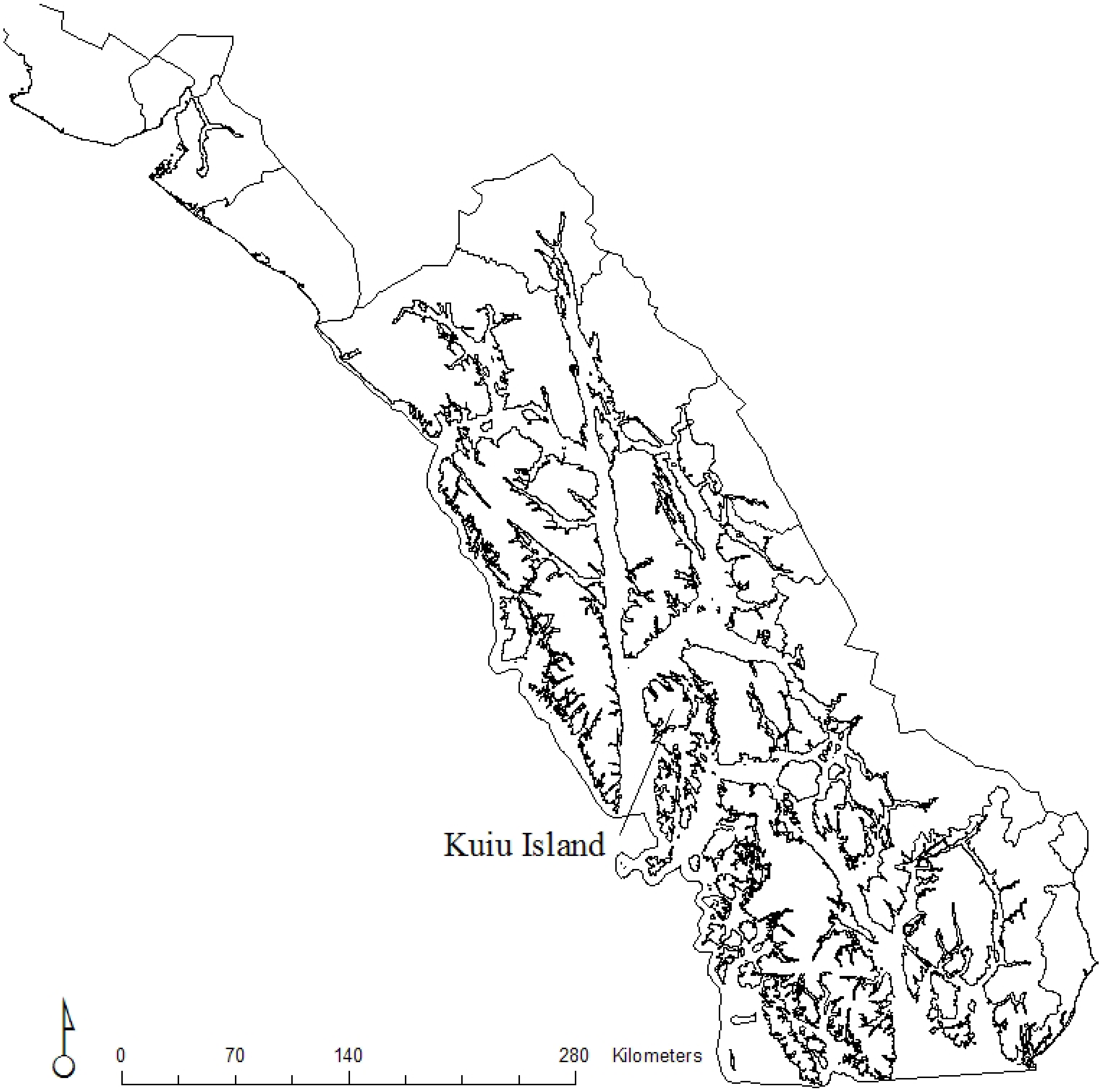

Figure 1. Kuiu Island and the Alexander Archipelago of Southeast Alaska.

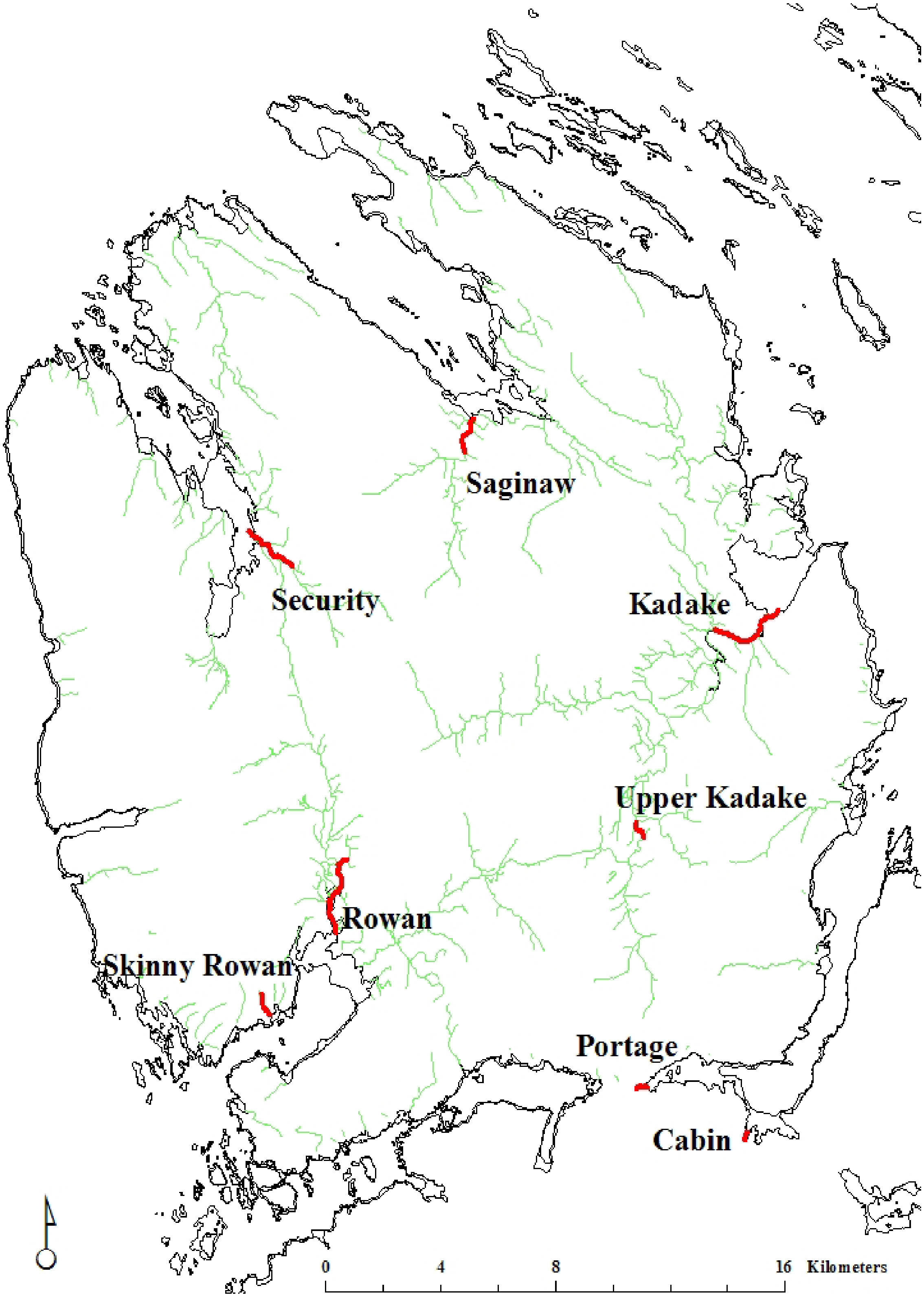

Figure 2. Study streams (red bold) and other Class I anadromous streams (green) on northern Kuiu Island.

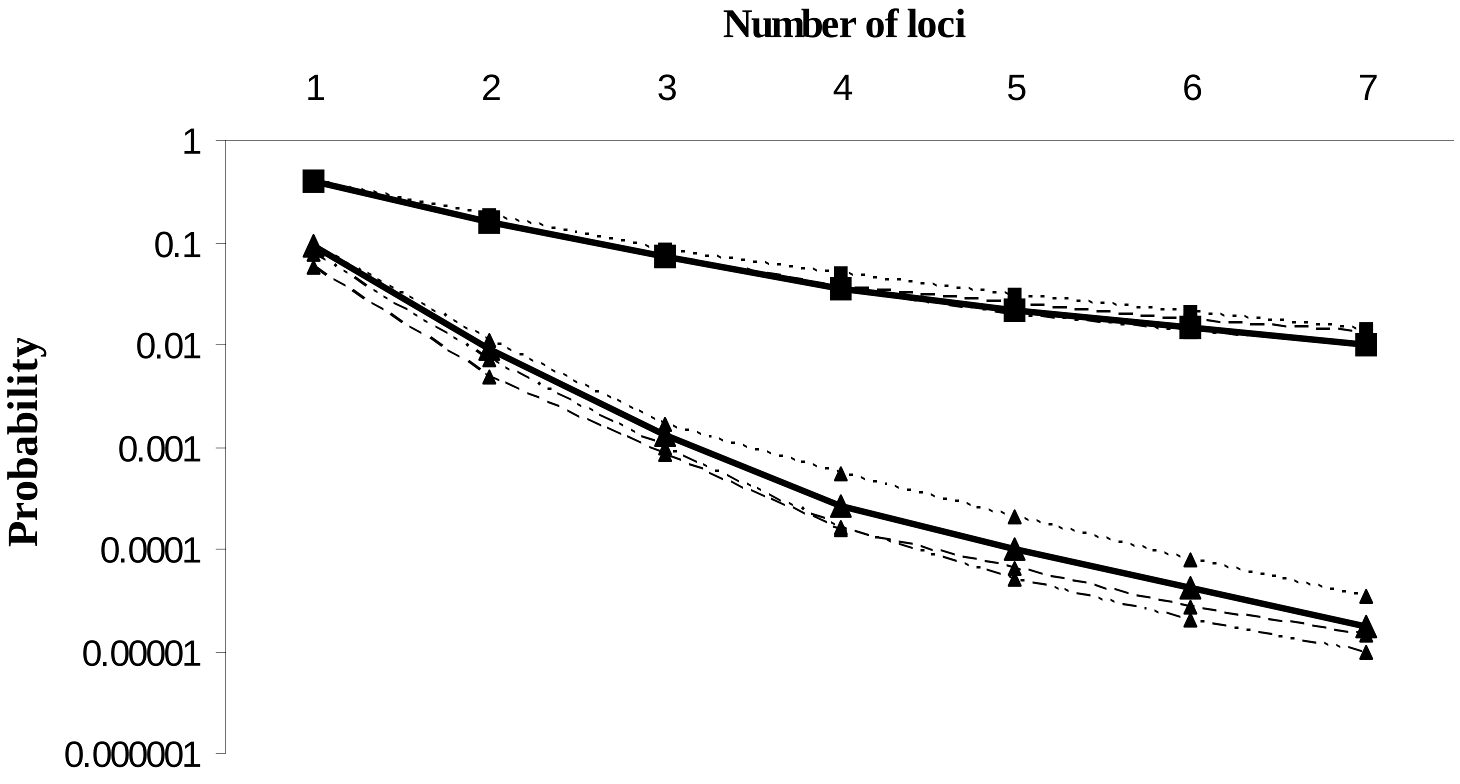

Figure 3. Probability of Identity (P_{ID}) for black bears on northern Kuiu Island. Squares are P_{ID_SIB} and triangles are $P_{ID\_UNB.}$ Bold solid lines show values for northern Kuiu Island (*n* = 117 bears). Dotted lines show values for the Rowan watershed (*n* = 33), dashed lines show values for the Security watershed (*n* = 25), and dashed-dotted lines show values for the Saginaw watershed (*n* = 35).

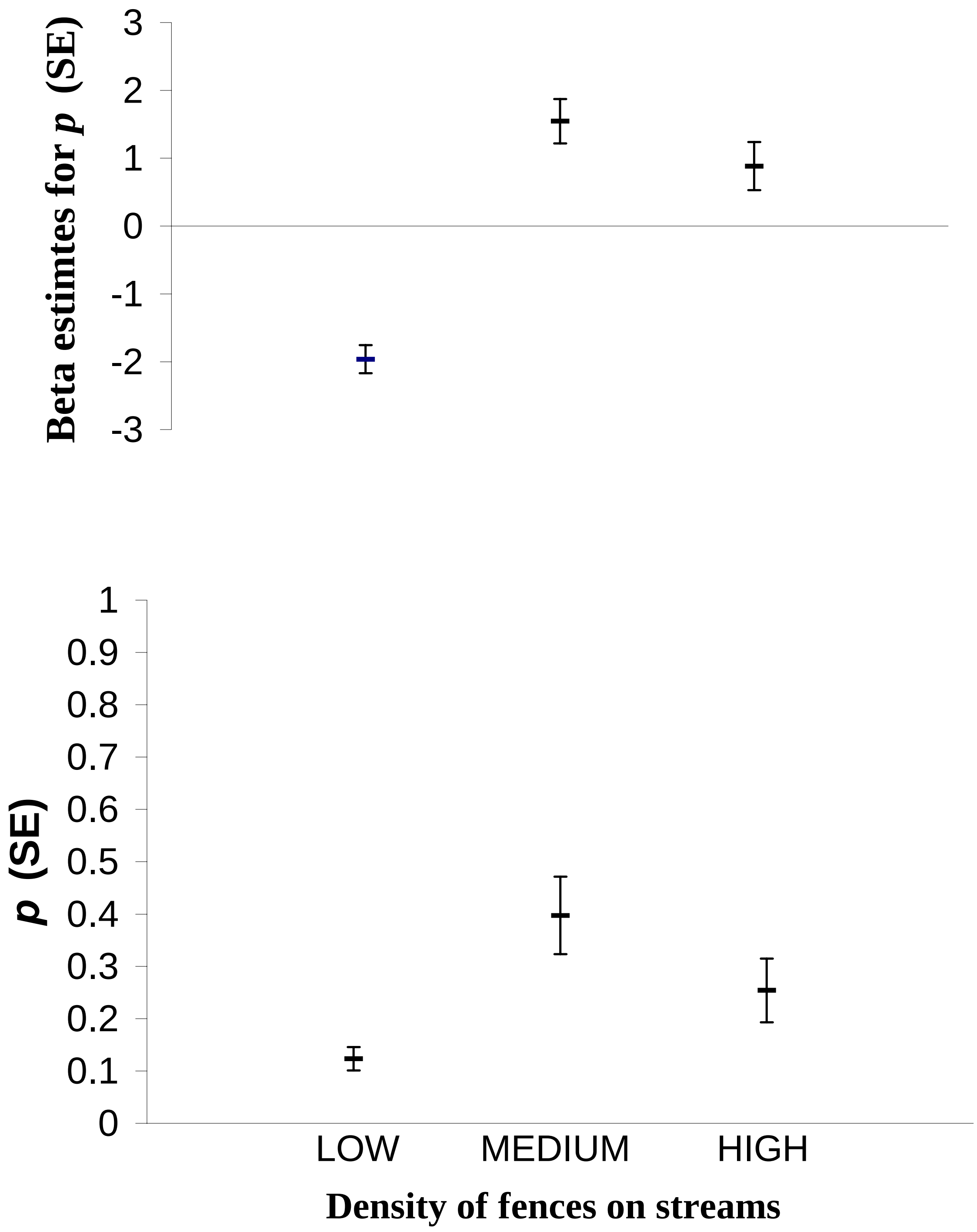

Figure 4ab. Beta (a) and real (b) estimates of recapture probability of black bears on salmon streams on Kuiu Island with respect to density of fences. Beta and model-averaged real estimates were generated from CJS models using mark-recapture data from all streams sampled in 2002 (*n* = 5). Error bars are ± SE.

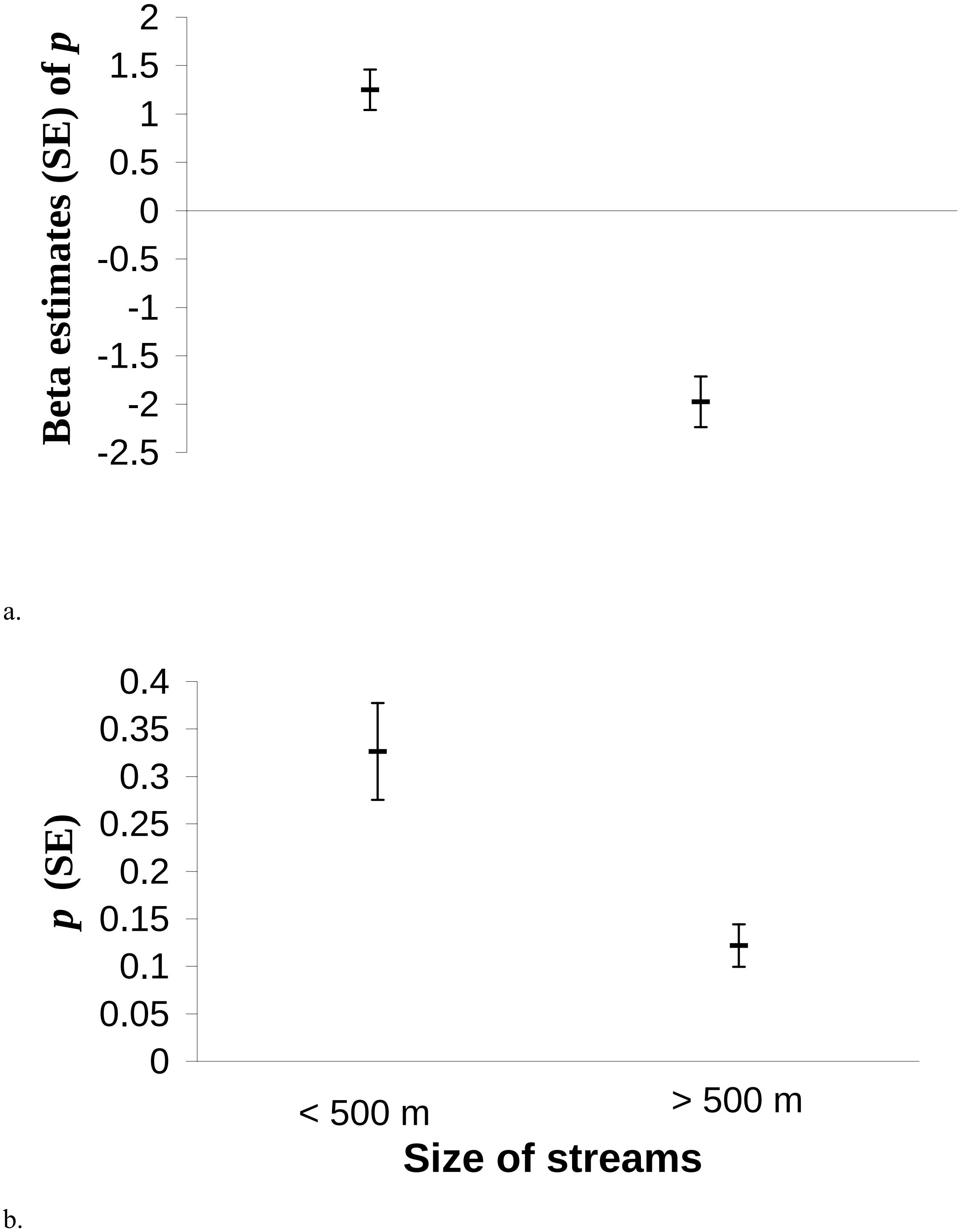

Figure 5ab. Beta (a) and real (b) estimates for recapture probability of black bears on salmon streams on Kuiu Island with greater (*n* = 3) and less (*n* = 2) than 500 m of salmon spawning habitat. Error bars are ± SE.

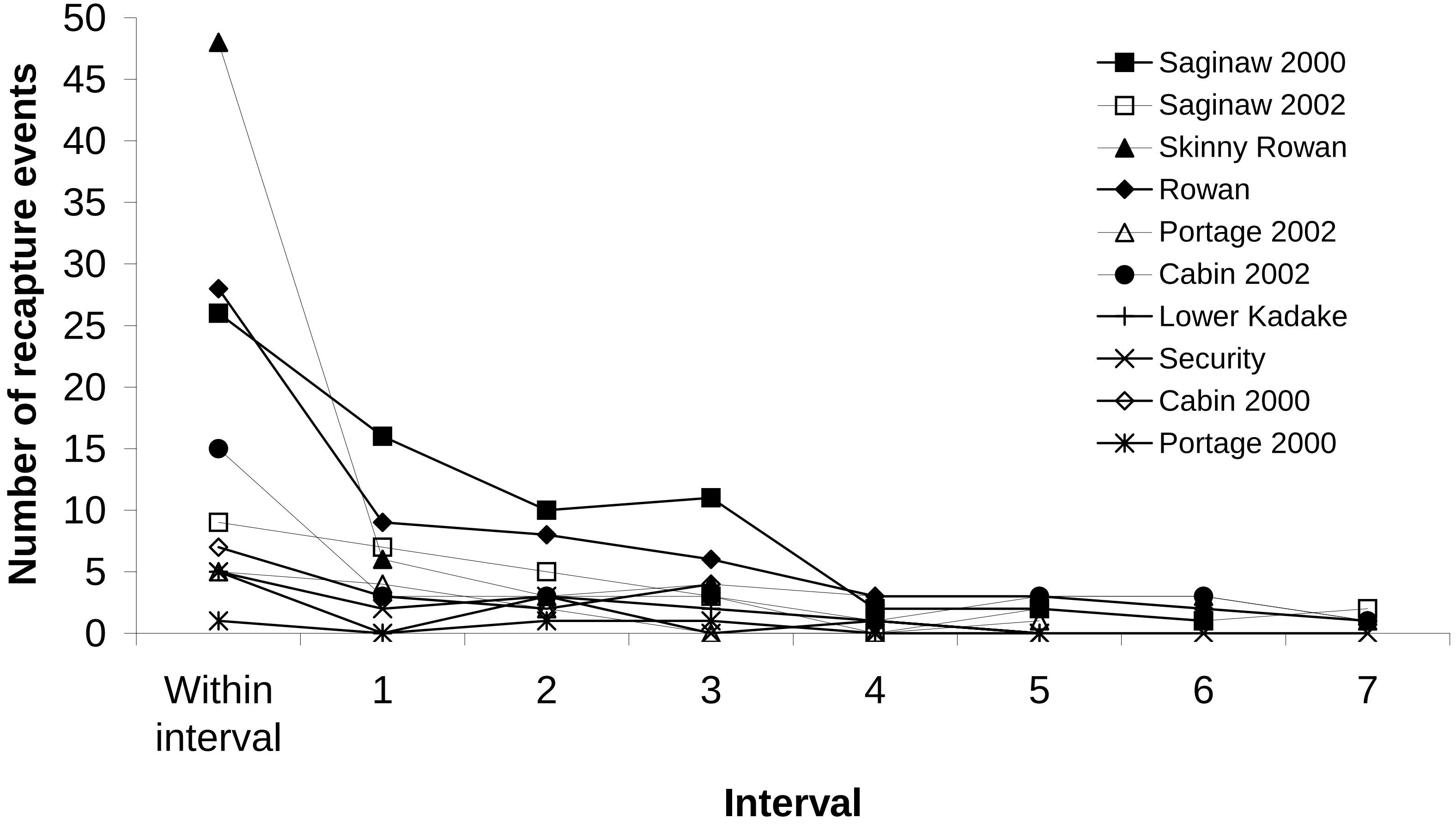

Figure 6. The number of recapture events of black bears on salmon streams on Kuiu Island within the interval of first capture, and in intervals subsequent to initial capture.

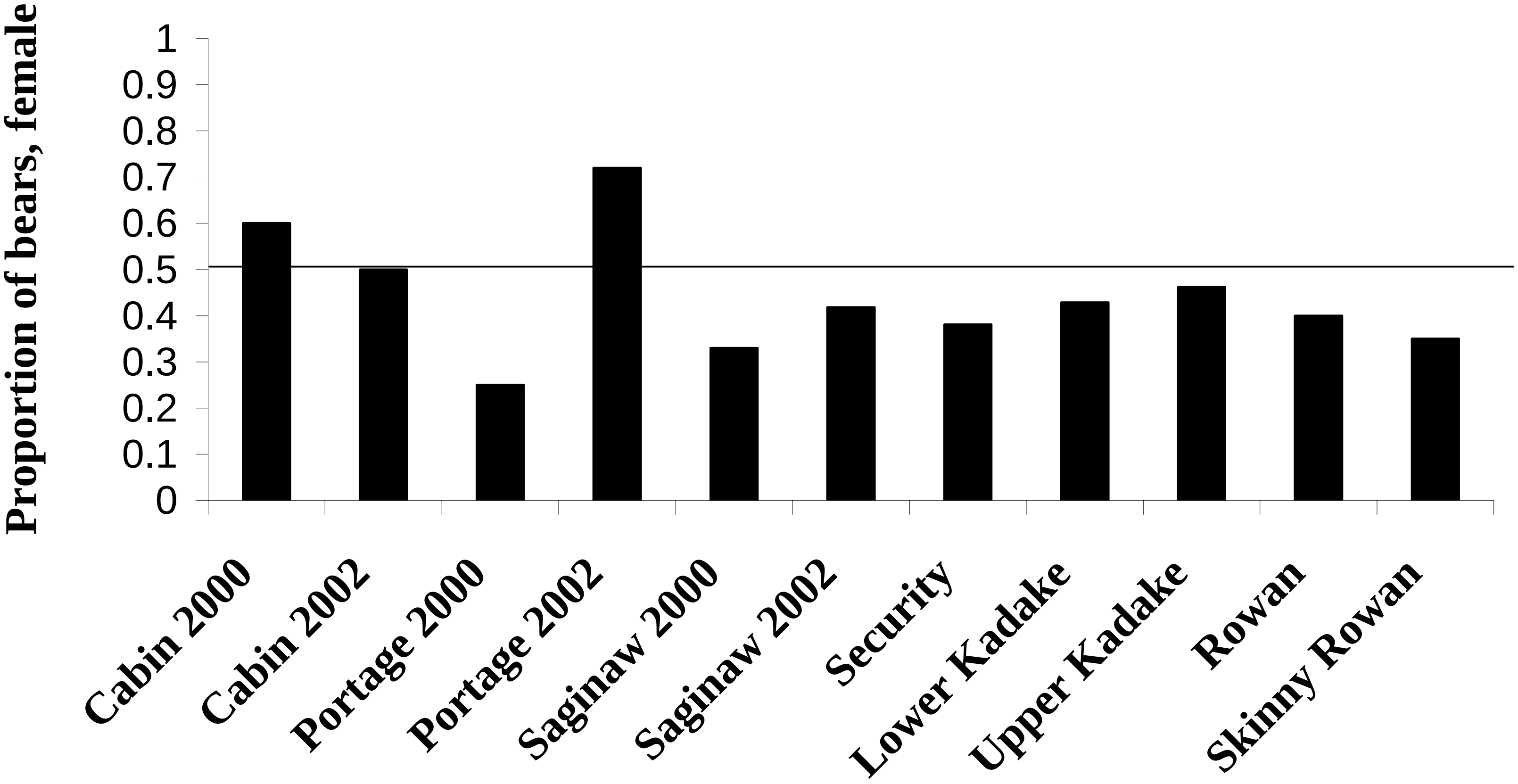

Figure 7. Proportion of individual black bears (MNA) that visited salmon streams that were female. The line indicates 0.5, which would be the expected proportion by chance, assuming the sex ratio of black bears on northern Kuiu Island was even.

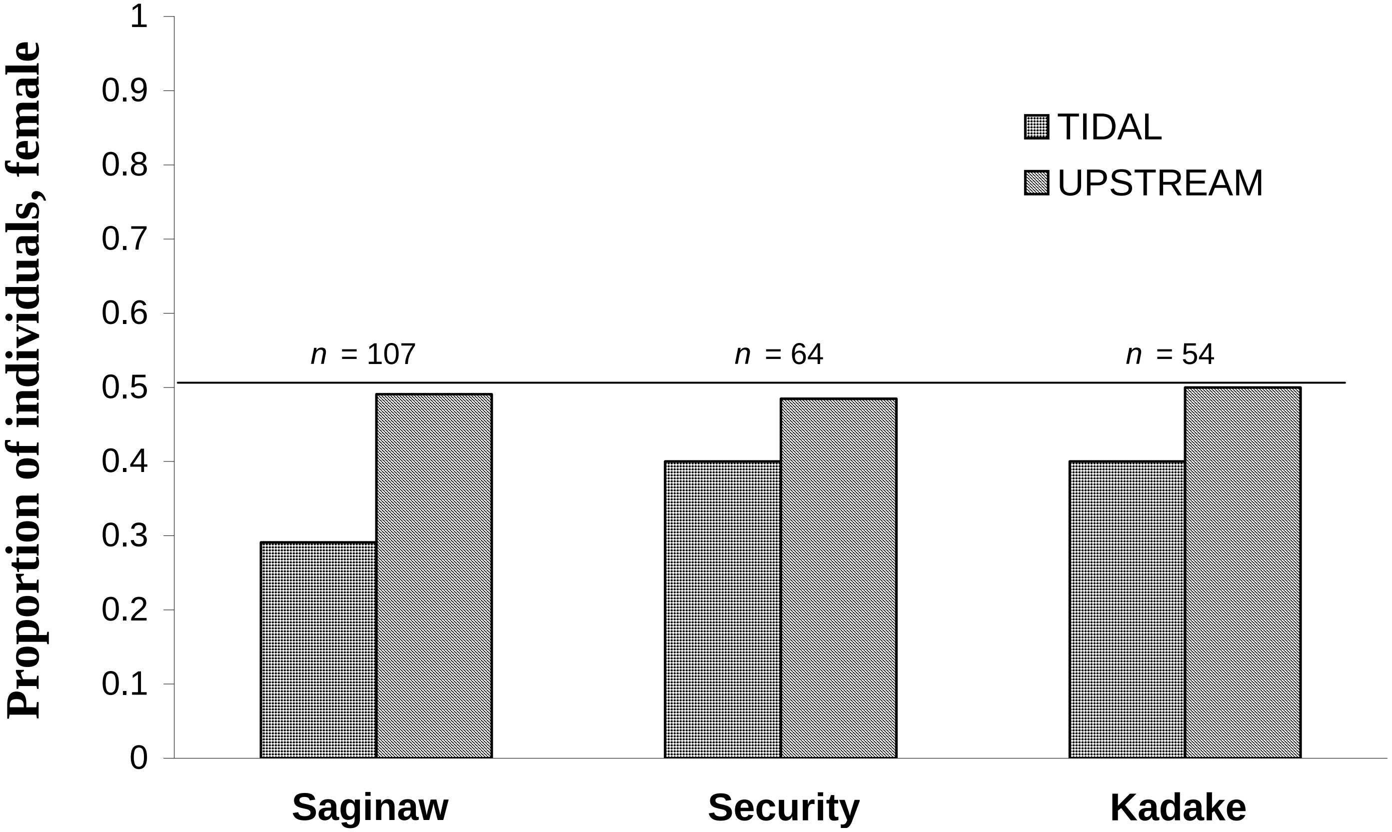

Figure 8. Proportion of individual black bears (MNA) using tidal and upstream portions of three streams in 2000. The line indicates 0.5, which would be the expected proportion by chance, assuming a sex ratio on northern Kuiu was even. 1-tailed t-test, *p* = 0.01. Sample sizes are total number of samples that had genetic individual and sex identities.

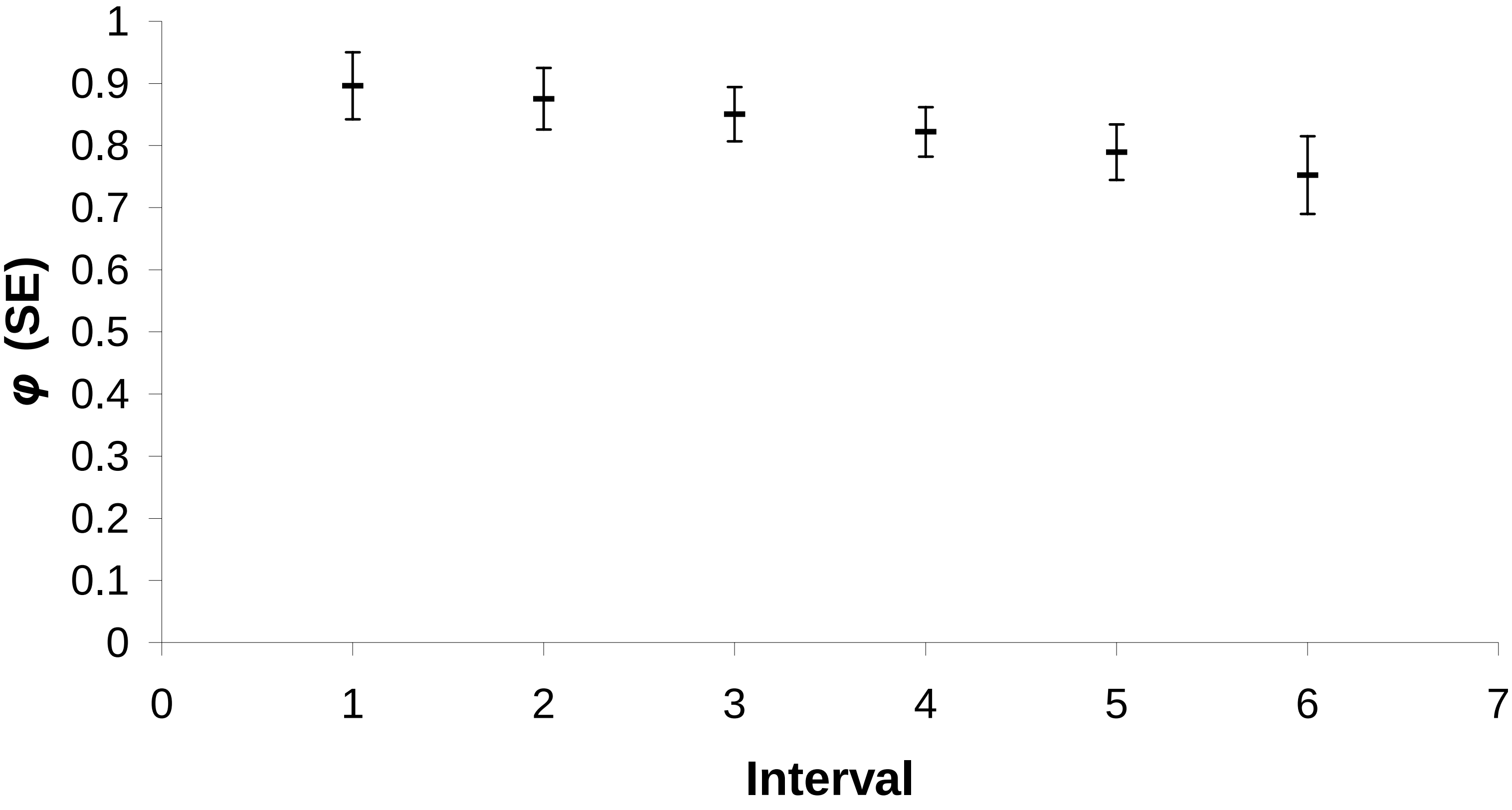

Figure 9. Probability of bears staying on streams from one week to the next (*φ*), over the course of encounter occasions. Estimates of *φ* are model-averages from CJS models incorporating pooled data from all streams sampled in 2002 (*n* =5). Trend effects of *φ* are found in eight of the ten models with ΔAICc < 2.0. Error bars are ± SE.

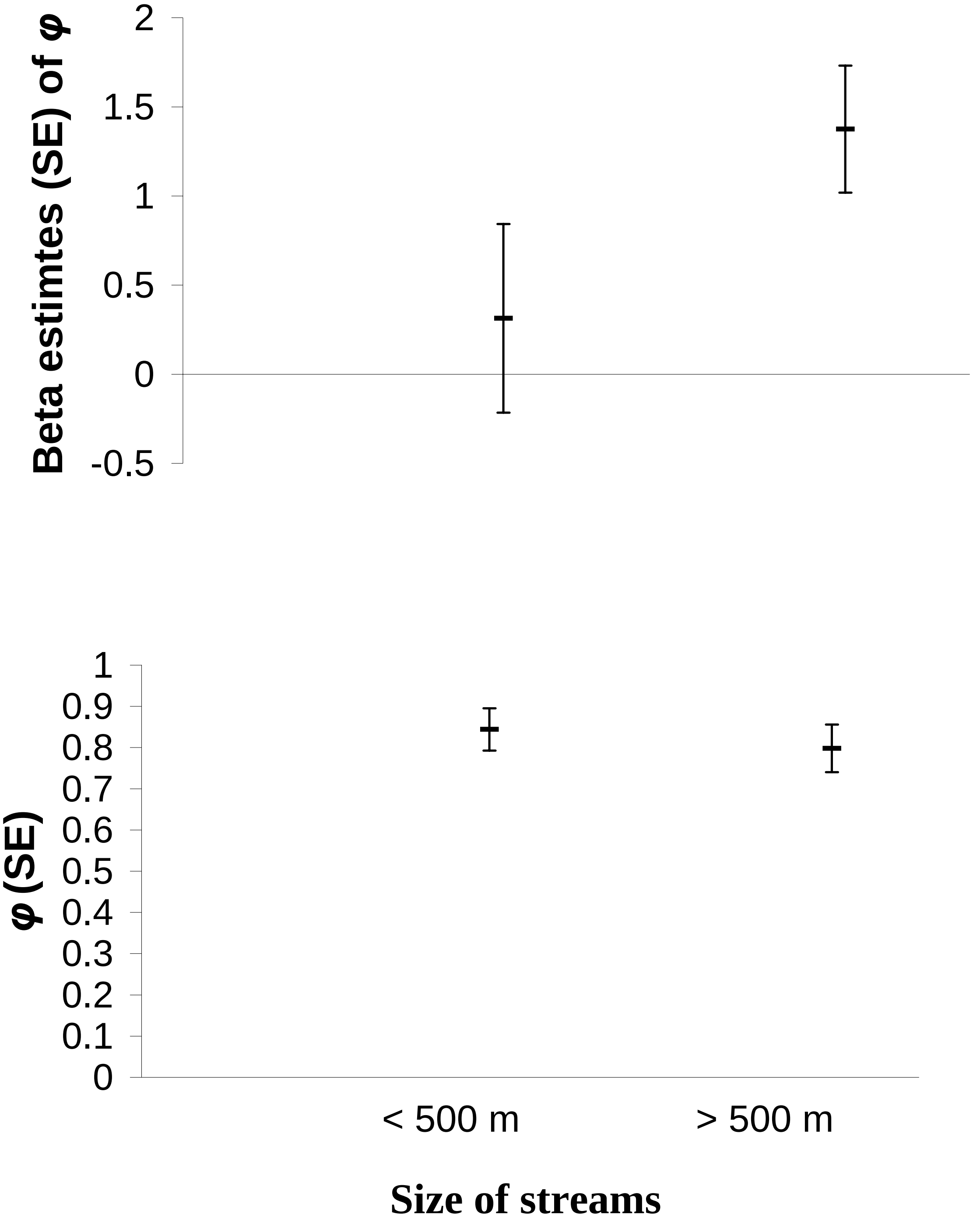

Figure 10. Apparent survival (*φ*) of black bears on salmon streams that have < 500 and > 500 m of available salmon spawning habitat over the course of seven weeks for all stream data sets (*n* =5) from 2002 combined. This effect on black bear fidelity was weakly supported and occurred in models with ΔAICc from 1.9 – 2.0.

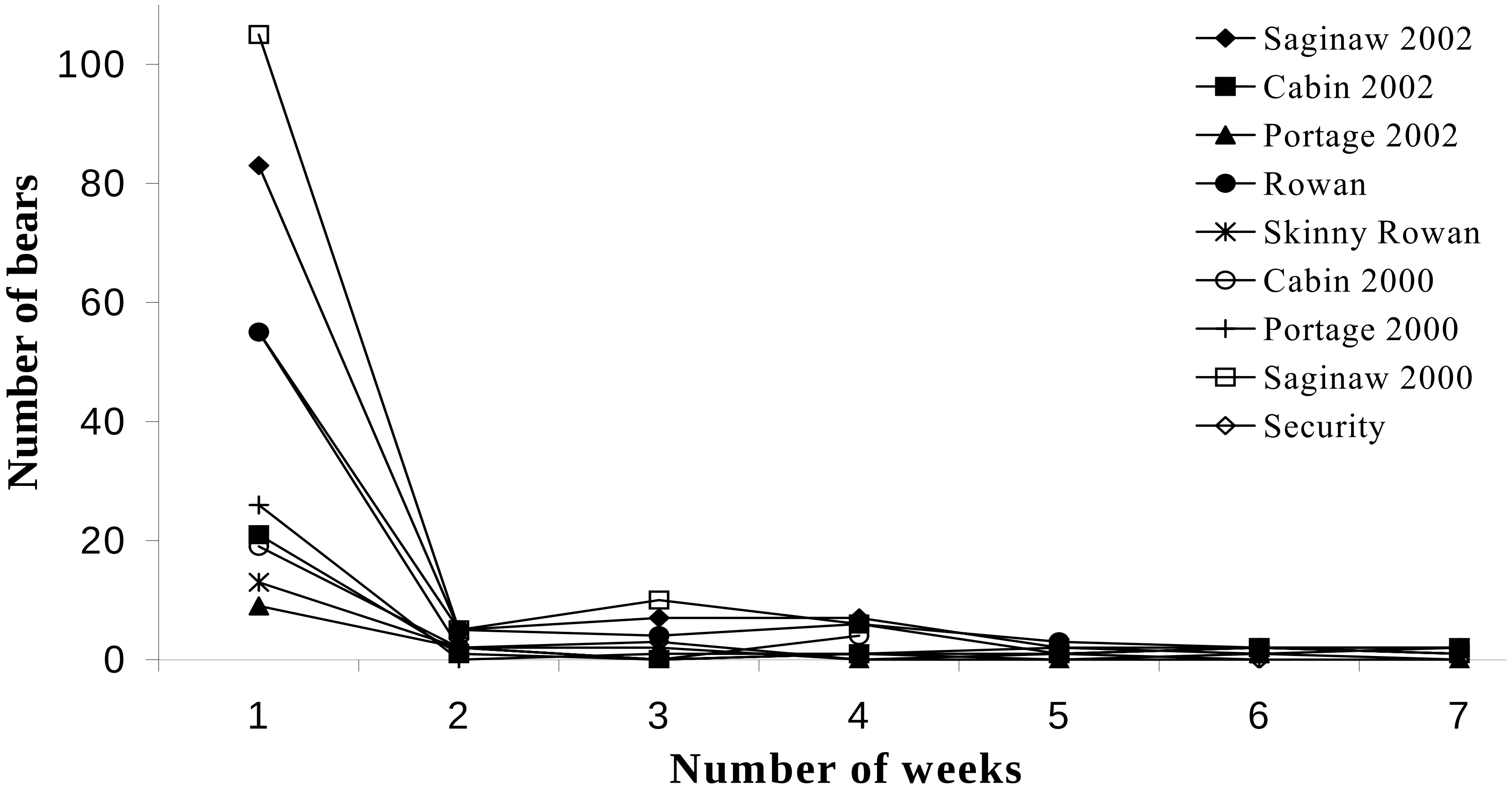

Figure 11. The minimum number of identified black bears (MNA) that stayed for varying number of weeks on salmon streams on Kuiu Island.

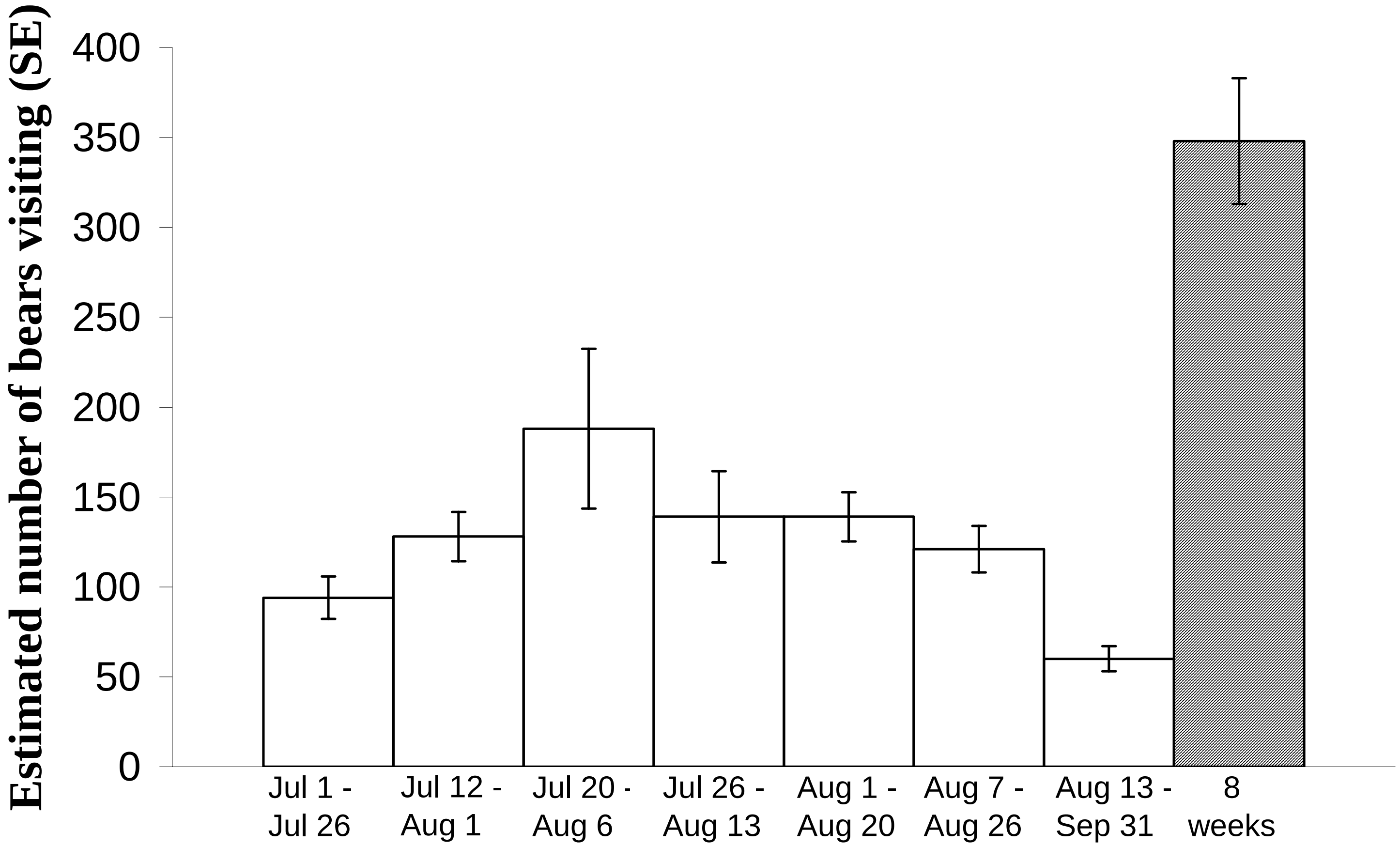

Figure 12. The estimated total number of bears visiting Saginaw Creek in 2000 over sequential four-week time periods, and over the entire eight week period. Numbers of bears were estimated using the M_h model in CAPTURE. Error bars are ± SE.

Table 1. Characteristics of study streams on northern Kuiu Island, Southeast Alaska. All streams are class I anadromous streams. Salmon escapement data are approximate data, and collected for management, not research, purposes (W. Bergmann, pers. comm.).

Stream	Average annual salmon escapement, 1994- 2000	Approximate mean depth (cm)**	Approximate bank full width (m)*	Channel type*	Comments
Saginaw	58,000 ± 17,000 (pink) 950 ± 500 (chum)	40	21	Flood plain	Riffle-pool mix
Security	32,900 ±7,500 (pink)	40	25	Flood plain, large estuarine channel	Riffle-pool mix
Rowan	1600 ± 500 (chum) 44,100 ± 14,000 (pink)	50	24	Palustrine/beaver ponds, large estuarine channel	Some deep pools (> 2 m in depth)
Skinny Rowan	1,500 ± 400 (pink)	25	5	Narrow channel	Riffle-shallow pools. Some water falls (~ 1 m)
Portage	1,100 ± 300 (chum)	25	8	Palustrine/beaver ponds, large estuarine channel	No substantial pools
Cabin	1,800 ± 700 (chum)	25	8	large estuarine channel	No substantial pools

* USFS data

** in riffles, and when fish are available to bears

Table 2. Primer pairs used to amplify microsatellite loci (Paetkau and Strobeck 1994, Paetkau *et al.* 1995). Sequences are given in the 5' to 3' direction.

Locus	GenBank accession number	Repeat motif	Forward sequence	Reverse sequence	Dye	Allele range (bp)
O	U22090	$(GT)_n$	CCTTGGCTACCTCAGATGG	GCTTCTAATCCAAAGATGCATAAAGG	5-FAM	164-190
J	U22087	$(GT)_n$	GCTTTTGTGTGTGTTTTTGC	GGATAACCCCTCACACTCC	6-HEX	80-97
L	U22088	$(GT)_n$	GTACTGATTTAATTCACATTTCCC	GAAGATACAGAAACCTACCCATGC	5-FAM	134-172
Ct‡	U22085	$(GT)_n$	AAAGCAGAAGGCCTTGATTTCCTG	**GTTT**GTGGACATAAACACCGAGACAGC	6-HEX	103-123
M	U22089	$(GT)_n$	TTCCCCTCATCGTAGGTTGTA	GATCATGTGTTTCCAAATAAT	NED	209-223
D	U22094	$(GT)_n$	GATCTGTGGGTTTATAGGTTACA	CTACTCTTCCTACTCTTTAAAGAG	NED	180-184
X	U22093	$(GT)_n$	CCCCTGGTAACCACAAATCTCT	GCTTCTTCAGTTATCTGTGAAATCAAAA	PET	141-169

‡ the “t” symbolizes that a tail sequence (GTTT) was added to the 5' end reverse primer in order to decrease the effect of 2-basepair stutter.

Table 3. PCR conditions for microsatellite primer pairs and the sex determining region of the amelogenin gene. Numbers are volume (µl). All reactions were run with 0.6 µl of BSA‡ (20 mg/ml; SIGMA). All reactions are 15 µl total volume, and thus remainder volume not listed here is in dH_20 or DNA template. For PCRs using extracted DNA from hair, 5 µl of DNA template (< 1 ng/ µl) was used. For PCRs using extracted DNA from tissue, 2 µl of template (10 ng/ µl) was used.

Locus	ABI† $MgCl_2$ (25mM)	ABI† Buffer Cetus II	CLONTECH Titanium *taq* buffer	DNTPs (10mM)	Betaine (SIGMA)	Primer mix (10µM)	CLONTECH Titanium *taq* polymerase	cycles	T_a ††
J§§O	1.2	1.5	-	0.5	3.0	0.7/0.3	0.2	45	58
L	1.5	1.0	-	0.5	-	0.5	0.2	30	60
Ct	0.9	1.5	-	0.5	-	0.5	0.2	45	62
M	0.9	1.5	-	0.5	-	0.4	0.2	45	50
X	-	-	1.5	0.6	-	0.7	0.2	45	58
D§§	-	-	1.5	0.5	3.0	0.6	0.3	45	58
SE47/48	0.9	1.5	-	0.5	-	0.3	0.2	35	58

†Applied Biosystems, Inc.

‡ Bovine Serum Albumin

††Annealing Temperature, °C

§ used in tissue PCRs for PI calculation; not used in individual identification. §§ used in individual identification, not in PI calculation

Table 4. Effort data for study streams on Kuiu Island in 2000 and 2002. Numbers in parentheses are percentages of previous column.

Stream-year	Length surveyed (km)	Fences	Density of fences per km	Weeks	Possible samples	Samples taken	Samples extracted	Samples amplified
Rowan 2002	2.0	28	14.0	8	683	247 (36)	168 (68)	141 (84)
Saginaw 2000	1.8	32	17.8	8	903	343 (38)	254 (74)	180 (71)
Saginaw 2002	1.8	28	15.6	9	701	217 (31)	140 (65)	113 (81)
Security 2000	1.6	19	11.9	9	556	207 (37)	134 (65)	101 (75)
Skinny Rowan 2002	0.5	16	32.0	9	163	149 (91)	138 (93)	95 (69)
Portage 2000	0.3	11	36.7	6	178	66 (37)	39 (59)	30 (77)
Portage 2002	0.2	6	30.0	8	84	33 (39)	27 (82)	25 (93)
Cabin 2000	0.2	13	65.0	4	256	87 (34)	45 (52)	37 (82)
Cabin 2002	0.3	14	46.7	8	230	86 (37)	76 (88)	62 (82)
Kadake 2000	3.7	32	8.6	6	292	119 (41)	84 (71)	69 (82)
Total					**4049**	**1554 (38)**	**1105 (71)**	**853 (77)**

Table 5. Apparent survival (φ; probability of a bear remaining on the stream from one interval to next) and recapture probability (p) estimates of black bears on salmon streams, over the course of the study periods. Estimates are from the dot models: $\varphi(.)p(.)$. ~ indicates that the parameter was not estimated, but approximately 1.0.

Creek	AIC_c weight	Model likelihood	p (± SE)	φ (± SE)
Saginaw 2000	0.08	1.0	0.32 ± 0.07	0.61 ± 0.06
Saginaw 2002	0.08	1.0	0.10 ± 0.04	0.80 ± 0.09
Security 2000	0.07	0.7	0.07 ± 0.05	0.70 ± 0.20
Lower Kadake 2000	0.08	1	0.07 ± 0.06	0.96 ± 0.24
Portage 2000	0.87	1.0	0.03 ± 0.02	~ 1.0
Portage 2002	0.16	1.0	0.36 ± 0.16	0.74 ± 0.14
Cabin 2000	0.49	1.0	0.26 ± 0.07	~ 1.0
Cabin 2002	0.29	1.0	0.18 ± 0.06	0.96 ± 0.09
Rowan 2002	0.13	1.0	0.16 ± 0.04	0.81 ± 0.07
Skinny Rowan 2002	0.01	0.1	0.42 ± 0.09	0.81 ± 0.08

Table 6. Polynomial regressions for the number of recapture events of black bears on salmon streams versus the encounter occasion in which the animal was recaptured post initial capture, including within the initial capture occasion.

Stream	Equation	R^2	*p*
Rowan	$Y = 23.3 - 8.5X + 0.8X^2$	0.85	**0.008**
Saginaw 2000	$Y = 9.5 - 3.1X + 0.3X^2$	0.93	**0.001**
Saginaw 2002	$Y = 24.7 - 7.5X + 0.6X^2$	0.96	**0.004**
Cabin 2000	$Y = 7 - 0.5X + 1.5X^2$	1.0	**< 0.0001†**
Cabin 2002	$Y = 11.5 - 4.5X + 0.5X^2$	0.68	0.059
Portage 2000	$Y = 0.67 - 1.3X + 0.1X^2$	0.31	0.57
Portage 2002	$Y = 5.1 - 1.9X + 0.2X^2$	0.91	**0.003**
Skinny Rowan	$Y = 35.7 - 16.6X + 1.8X^2$	0.70	**0.048**
Lower Kadake	$Y = 3.7 - 1.0X + 0.1X^2$	0.41	0.452

† the shape of the curve is not asymptotic, but parabolic.

Table 7. Probability of entry (*pent*), or probability of a bear arriving on a stream (recruitment), having not been there one week prior, estimated using the POPAN model.

Creek	Model	AICc weight	pent
Cabin 2000	$\varphi(.)p(.)\mathit{pent}(.)N(.)$	0.24**	0.15 ± 0.07
Cabin 2002	$\varphi(.)p(.)\mathit{pent}(.)N(.)$	0.75	0.08 ± 0.03†
Portage 2000	$\varphi(t)p(.)\mathit{pent}(.)N(.)$	0.07***	0.12 ± 0.08
Portage 2002	$\varphi(.)p(.)\mathit{pent}(.)N(.)$	0.95	0.12 ± 0.02
Skinny Rowan	$\varphi(t)p(t)\mathit{pent}(.)N(.)$	0.62	0.09 ± 0.02†
Saginaw 2000	$\varphi(.6)p(.2)\mathit{pent}(.)N(.)$	0.88	0.10 ± 0.002
Saginaw 2002	$\varphi(t)p(.)\mathit{pent}(.)N(.)$	0.54	0.05 ± 0.03†
Security	$\varphi(.7)p(.07)\mathit{pent}(.)N(.)$	0.90	0.11 ± 0.007
Rowan	$\varphi(t)p(.)\mathit{pent}(.)N(.)$	0.20*	0.03 ± 0.03

*the best model, $\varphi(.)p(.)\mathit{pent}(.)N(.)$ (AICc weight = 0.80) produced an erroneous estimate of *pent*.

**the best model $\varphi(.)p(.)\mathit{pent}(t)N(.)$ (AICc weight = 0.68) was not able to estimate 2 of the 3 *pent* parameters.

***the best model $\varphi(.)p(.)\mathit{pent}(.)N(.)$ (AICc weight = 0.96) was not able to estimate pent.

† weighted average

Table 8. Average number of weeks that individual black bears remained on salmon streams on Kuiu Island.

Stream	Average number of weeks	SD
Portage 2000	1.2	0.7
Portage 2002	1.8	1.4
Cabin 2000	1.6	1.1
Cabin 2002	2.3	2.3
Saginaw 2000	1.5	1.1
Saginaw 2002	1.6	1.3
Rowan	1.9	1.7
Skinny Rowan	2.7	2.5
Security	1.2	0.7

Table 9. Minimum number known alive (MNA, number of individual bears genetically identified) and population estimates of black bears on salmon streams from POPAN and closed-capture models. Closed capture estimates are generated from the selected model. – indicates that the parameter was inestimable. M_o is the null model. M_t indicates a model that allows for recapture probability varies with time, M_b indicates a model where there is a behavioral effect on recapture probability, M_h indicates a model with heterogeneity in capture probability and M_{bh} indicates a model that has heterogeneity and behavior effects. M_{tbh} is a combination model.

Stream	MNA	POPAN		Closed captures		
		Number of bears visiting ± SE	CV	Selected model (probability)	Number of bears visiting ± SE	CV
Cabin 2000	21	39 ± 9	23%	M_{tbh} (1.0)*	38 ±8**	21%
Cabin 2002	29	47 ± 9	19%	M_h (1.0)	73 ±15	20%
Portage 2000	26	144 ± 30	21%	M_{tbh} (1.0)*	-	-
Portage 2002	14	21 ± 6	29%	M_o (1.0)	21 ± 5	24%
Skinny Rowan	22	27 ± 3†	11%	M_{th} (1.0)	47 ± 16	34%
Saginaw 2000	107	212 ± 15	7%	M_h (1.0)	348 ± 35	10%
Saginaw 2002	82	254 ± 54†	21%	M_{bh} (0.92)	115 ± 20	17%
Security	64	378 ± 45	12%	M_o (1.0)	309 ± 115	37%
Rowan	78	155 ± 30	19%	M_{bh} (1.0)	89 ± 8	9%

† weighted average

* No estimator is available for M_{tbh}

** estimate from next most probable model, M_h (0.89)

Table 10. Closed-capture model selection for mark-recapture data of black bears for ten stream-year data sets. No goodness of fit tests (GOF) were performed on M_t, as expected values of the chi-square test were too small in all data sets. – indicates that expected values were too small, and the test was not performed. The most likely model was selected based on the fit of the data to the different models, as revealed by the GOF tests. M_t indicates a model that allows for recapture probability varies with time, M_b indicates a model where there is a behavioral effect on recapture probability, M_h indicates a model with heterogeneity in capture probability and M_{bh} indicates a model that has heterogeneity and behavior effects.

Stream	GOF of the models					Selected model (probability)
	M_h	M_b			M_{bh}	
		Overall	First capture†	Recapture††		
Cabin 2000	**0.04**	0.66	-	0.64	0.20	M_{tbh} (1.0)
Cabin 2002	0.14	0.25	0.53	0.14	0.37	M_h (1.0)
Portage 2000	0.50	0.38	0.10	0.85	0.25	M_{tbh} (1.0)
Portage 2002	0.22	0.71	-	0.71	0.77	M_o (1.0)
Skinny Rowan	**0.00**	**0.02**	**0.06**	**0.06**	0.31	M_{th} (1.0)
Saginaw 2000	0.46	0.39	0.72	0.17	0.46	M_h (1.0)
Saginaw 2002	0.28	0.11	0.54	**0.04**	0.74	M_{tbh} (1.0)
Security	0.11	0.44	-	0.44	0.2	M_o (1.0)
Rowan	**0.08**	0.38	0.62	0.21	0.53	M_{bh} (1.0)

† contribution of the first capture homogeneity over all intervals

†† contribution of the recapture homogeneity over all intervals

Table 11. Number of black bears using salmon streams, estimated from closed-capture models ± SE. Estimate in **bold** is from the selected model.

Stream	M_o	M_t	M_b	M_h	M_{th}	M_{bh}
Cabin 2000†	38 ± 8	36 ± 7	-	**48 ± 8‡**	69 ± 32	-
Cabin 2002†	41 ± 6	40 ± 6	88 ± 120	**73 ± 15**	86 ± 32	88 ± 120
Portage 2002†	**21 ± 5**	20 ± 4	-	23 ± 6	15 ± 2	15 ± 2
Skinny Rowan	25 ± 2	24 ± 2	35 ± 17	39 ± 8	**47 ± 15**	22 ± 0.3
Saginaw 2000	190 ± 21	189 ± 21	164 ± 32	**348 ± 35**	346 ± 72	164 ± 32
Saginaw 2002	201 ± 37	199 ± 36	115 ± 20	238 ± 34	216 ± 51	**115 ± 20**
Security†	**309 ± 116**	302 ± 111	-	215 ± 30	303 ± 112	277 ± 518
Rowan	131 ± 17	130 ± 16	89 ± 8	204 ± 29	180 ± 39	**89 ± 8**

† SE of largest and smallest populations estimates overlap

‡ M_{tbh} was selected as the most probable, however an estimator is not available for this model, and so the estimate provided is from the next most likely model M_h that had a probability of 0.89.

Table 12. Estimated number of black bears using 500 m reaches of spawning salmon streams on Kuiu Island. Estimates are provided from the most appropriate closed capture model

Stream	Length surveyed (km)	Weeks	Closed capture population estimate	Number of bears/500 m
Cabin 2000	0.2	4	38 ±8	95
Cabin 2002	0.3	8	73 ±15	120
Portage 2002	0.2	8	21 ± 5	53
Saginaw 2000	1.8	8	348 ± 35	97
Saginaw 2002	1.8	9	115 ± 20	32
Security	1.6	9	309 ± 115	97
Rowan	2.0	8	89 ± 8	22
Skinny Rowan	0.5	9	47 ± 16	47

Table 13. Aspects of bear behavior and ecology that may result in behavioral, temporal and heterogeneity effects in genetic mark-recapture analyses of black bears on salmon streams. Combined phenomena could result in combined effects in models.

Phenomenon	Effect on capture and recapture	Effect in model
Differential§ use of trails	Placement of fence results in differential capture	Heterogeneity
Differential fidelity to stream	Duration spent on stream results in differential capture, recapture	Heterogeneity, behavioral*
Flux in bear numbers as a result of flux in salmon numbers†	More bears on stream results in higher capture during flux period.	Temporal
A type§ of bear avoids peak of run	Types of bears have differential capture with respect to time	Temporal, heterogeneity
Fidelity on stream varies with time†	At peak salmon numbers, bears spend more or less time on stream, resulting in differential capture, recapture	Temporal
Satiation of bears with salmon, other food becomes available	Bear numbers decrease, capture, recapture probability declines	Temporal
Spatial sexual segregation†	If fences are not distributed randomly with respect to sexual segregation, capture and recapture probabilities would differ according to sex	Heterogeneity
Stream dominated by one type of bear†	One type has higher capture, recapture	Heterogeneity
Wary ↔ curious bears differ in reaction to fence	Curious, bold bears have higher capture, recapture	Heterogeneity, behavioral

* Not an actual behavioral response to a trap, but a heterogeneity response masked as trap-happy behavior

† Phenomenon detected in present study

§ Differential with regard to types of bears or individuals. Type could be sex, age, dominance or reproductive condition, *etc.* If difference is attributed to sex of bears, and sex is incorporated into model, the difference could be treated as a group effect.

Elizabeth Peacock

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Reno, OU = Ecology,
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