University of Nevada, Reno

Population, Genetic and Behavioral Studies of Black Bears *Ursus americanus* in Southeast Alaska

A dissertation submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in Ecology, Evolution and Conservation Biology

by

Elizabeth Peacock

Dr. Mary Peacock – Dissertation Advisor

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ABSTRACT

I studied population, genetic and behavioral aspects of black bear (*Ursus americanus*) in the temperate rainforest of Southeast Alaska. At a landscape level, I used population genetics to investigate black bear movement in the Alexander Archipelago and mainland of Southeast Alaska. I found that geographic structure defined by salt water and glaciers curtails black bear movement, to the extent that most regions have significantly genetically differentiated black bear populations. I found that black bears in Southeast Alaska cluster into seven genetic types. I also found that two larger, nuclear genetic clusters of black bears in Southeast Alaska correspond, geographically, to the two ancient mitochondrial lineages of black bears. This perhaps indicates that the nuclear genome retains a genetic signature of the secondary contact of these two lineages. I also studied black bear vagility on a much smaller scale – at the level of riparian areas of salmon spawning streams. I used genetic tagging to demonstrate that the group of bears using these streams is in demographic flux throughout the course of the salmon stream, and that a high number of individual bears use these streams. The persistence of intact salmon streams in Southeast Alaska likely contributes to high black bear population density. In a final aspect of my dissertation research, I used tetracycline biomarking to estimate the population size of black bears on Kuiu Island to be 1.5 bears/km^2. This estimate is among the highest recorded bear densities.

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INTRODUCTION TO THE DISSERTATION

The coastal rainforest of Southeast Alaska and British Columbia constitutes 25% of the world's remaining temperate rainforest. The forest in Southeast Alaska is important as it remains largely intact, and enjoys more legal protection than temperate rainforests in South America, Canada and the Pacific Northwest of the United States. Attention to conservation and wildlife management is elevated in the region, as the forest occurs on the over 1,000 islands of the Alexander Archipelago and a narrow strip of coastal mainland, where insular endemics may be more vulnerable to habitat destruction and fragmentation. Furthermore, demand for natural resources is high as consumptive and non-consumptive resource use is the keystone of the region's economic viability. Industrial logging and commercial fishing have occurred for over 50 years on the Tongass National Forest, which comprises 80% of Southeast Alaska. Recreational use including hunting, sport fishing and wildlife viewing is increasing on the Forest and other federally-managed land, which together comprise 95% of the region.

The American black bear (*Ursus americanus pugnax*) occurs on the southern islands of the Alexander Archipelago at high densities, likely due to intact anadromous Pacific salmon (*Oncorhynchus* spp.) runs and productive forests. Since the temperate rainforest of Southeast Alaska remains largely conserved, I was able to study black bears in a natural context, at different landscape and temporal scales. Most aspects of this dissertation have direct management and conservation implications for black bears on the Tongass National Forest. This work also contributes to the field of Ursid ecology, specifically, but to animal behavior in general. While I've made specific contributions to

the understanding of black bears in the salmon dominated ecosystem, in a more general light, I have examined how a solitary species behaves in the face of ephemeral, high density gatherings of conspecifics. The dissertation also contributes specifically to the phylogeography of mammalian species on the Alexander Archipelago, but also more generally to how animals navigate fragmented systems.

Two mitochondrial lineages of the black bear, which diverged at the beginning of the Pleistocene 1.8 million years ago, co-occur in Southeast Alaska. I have shown that two groups of the black bears, defined by nuclear microsatellite variation, correspond geographically to these two mitochondrial lineages. I suggest that the geographical interface of these two groups occurs near the Cleveland Peninsula on mainland, on Mitkof Island, and on Prince of Wales Island. In addition, results from several analyses suggest that there is a general, historical movement of bears southward along the coast.

I described the dispersal patterns of black bears among the islands and mainland of Southeast Alaska using nuclear, microsatellite genetic markers. I found that the geographic structure of the region curtails black bear dispersal, as geographical distance does not satisfactorily predict genetic distance. Salt water crossing distance explained a fair degree of variation in genetic distance, however other factors such as the direction of crossing may play an additional role. I detected asymmetrical movement of black bears among islands of the Alexander Archipelago, which could be possibly due to ecological differences between islands, such as differences in population density, instigating dispersal behavior. Alternatively, or in addition, directional tidal currents could have produced asymmetrical migration, by affecting the success of dispersal. Finally, large ice fields, of greater than approximately 150 km were substantial barriers to black bear

movement, and intervening salt water bays on the mainland of Southeast Alaska, mitigated, but did not prevent black bear movement.

At a smaller scale, I studied the black bears on Kuiu Island in the Alexander Archipelago. I used tetracycline biomarking to estimate the population size of black bears on Kuiu Island to establish base line data for effective wildlife management. This technique proved to be an effective tool, in terms of labor and cost, to estimate population size of a harvested, yet elusive, mammal. With two independent data sets, I estimated the population size of black bears on Kuiu Island to be roughly 1.5 bear/km^2, which is one of the highest recorded bear densities in the world.

I also estimated the number of bears that used reaches of salmon streams using genetic tagging – a form of mark-recapture using genetic identities as tags. I detected large numbers of black bears using small sections of the streams over the course of the salmon runs. However, there was high turn over in the identities of individual black bears using the salmon streams. In all data sets, I detected heterogeneity in capture probability, which is likely due to behavioral differences of the bears on salmon streams. One plausible explanation of heterogeneity in capture, could be due to male and female bears using the streams differently. I found that on most streams, females were detected on the streams less than expected. In addition, I found that females used tidal areas of streams less than upstream, forested stretches of streams. Both of these findings may suggest that there maybe sexual segregation on streams, and that not all female black bears in the population use salmon streams.

ESTIMATION OF BLACK BEAR POPULATION SIZE ON KUIU ISLAND, ALASKA USING TETRACYCLINE BIOMARKING SUPPLEMENTED WITH GENETIC METHODS

INTRODUCTION

Bears (*Ursus* spp.) in Southeast Alaska (Figure 1) are valued for hunting and viewing, and also for their role in the ecosystem, as they mediate transportation of marine nutrients to the terrestrial ecosystem through predation on spawning salmon (Schwartz and Franzmann 1991, Willson *et al.* 1998). The high density populations of brown bears (*U. arctos*) have been well studied (Hilderbrand *et al.* 1996, Miller *et al.* 1997, Paetkau *et al.* 1998a, Gende and Willson 2001, Ben-David *et al.* 2004), and their harvest is conservatively managed at a level of 4% of the size of each population (Whitman 2001). There have been no population-level studies of American black bears (*U. americanus*) in Southeast Alaska. Yet, black bears in the region are of interest to wildlife managers and biologists, as they also occur at very high densities, may also function in nutrient transport, and their hunting and viewing has been increasingly important to local economies. Two studies that have occurred on black bears in Southeast Alaska have focused on viewing (Chi 1999) and denning (Erickson *et al.*1982).

Black bear harvest has increased most dramatically on Kuiu Island (Figure 2, 134°10' W, 56° 45' N), due to large trophies and reporting of high densities by the popular hunting press; harvest has increased 46% on Kuiu Island in the Alexander Archipelago of Southeast Alaska during the 1990's (Figure 3). Hunting has increased to

the extent that local wildlife managers have begun to question whether current hunting levels are sustainable, and a harvest cap of 120 bears per year was established for Kuiu Island in 2000 through regulatory action. Sustainably managing bear populations can only be done successfully with adequate information on population size and trend.

Brown bear population size in Alaska has been estimated using Capture-Mark-Resight (CMR, Miller *et al.* 1997), in which animals are physically captured, marked with a radio-collar and then resighted. CMR studies on Admiralty Island in the Alexander Archipelago have produced density estimates of 0.26 ± 0.03 adult bears/km^2 (mean ± SE, Miller *et al.* 1997). Brown bears are known to use non-forested alpine areas, where individuals can be resighted. This prerequisite for CMR does not occur for black bears in the temperate rainforest of Southeast Alaska, as black bears do not readily use the small amount of alpine habitat that is available on the Archipelago's black bear islands (*e.g.,* Kuiu, Kupreanof, Mitkof and Prince of Wales).

My objective was to estimate the density and adult survival rate of black bears on Kuiu Island using tetracycline biomarking (Garshelis and Visser 1997), a method in which bears are remotely marked with tetracycline-laced baits, and which does not require resighting individuals. Garshelis and Visser (1997) first used tetracycline biomarking successfully to estimate the size of very large populations (15,000 – 25,000 animals) across expansive areas in Michigan and Minnesota (43,000 – 83,000 km^2).

METHODS

I used tetracycline biomarking to estimate the size of the black bear population on northern Kuiu Island (673 km^2) in 2000 and 2002. I altered methods described by Garshelis and Visser (1997) slightly to accommodate a smaller sample size and the higher density of bears. Baits were laced with the antibiotic tetracycline and distributed; when a bait was taken by a bear, the tetracycline was incorporated in the newly-forming bone tissue (Johnson 1964). As the recovery sample, hunters provided bear bones that were examined under an ultraviolet microscope for the fluorescent biomark.

Since bears were marked remotely, the number of bears marked was likely higher in comparison to methods in which bears must be captured. Disadvantages of the tetracycline method include the fact that bears could be recaptured only once (*i.e.,* recovered), bears did not have individual marks, and the population had to be hunted to supply the recapture sample. In addition, little is known about the marked animals (*e.g.,* sex, age, reproductive history). I augmented the tetracycline method with genetic information regarding sex identity, from a sample of the animals that took baits, which aided in an investigation of possible biases in the population estimate.

Field methods

I used tetracycline-laced baits to mark individual black bears on Kuiu Island, north of the Bay of Pillars and Port Camden isthmus (Figure 4), in 2000 and 2002. The isthmus is a 1.5 km wide land bridge that connects northern and southern Kuiu Island. I chose this study area due to its insular nature, which maximized geographic closure, and because logging roads facilitated bait distribution.

In late June 2000, I distributed tetracycline baits on northern Kuiu Island over the course of four days. I distributed baits (n = 188) at 1.6-km intervals along the coast and road system and left them out for an eight day period (Figure 5a). In 2002, I made methodological changes to decrease a possible bias resulting from the manner in which I distributed baits in 2000, and to increase precision in the population estimate. I divided northern Kuiu Island into 1.6 km^2 grid cells, and systematically placed baits as close to the centers of these cells as possible (Figure 5b). I did not place baits in cells that were entirely composed of rock or ice, or where helicopter access was dangerous. To increase precision, I distributed 29% more baits (n = 263) than in 2000, over the course of five days. Crews first revisited baits eight days after I distributed the initial baits. However, because of initial low visitation, possibly associated with cooler weather, I left out baits for an additional one to five weeks, depending on how quickly the bait was taken.

Baits consisted of nine, 500 mg tetracycline capsules embedded in 0.5 kg of suet and bacon. This dose of tetracycline is sufficient to mark bears up to 225 kg (20 mg/kg, Taylor and Lee 1994, Garshelis and Visser 1997). Only approximate weights are known for the Kuiu Island black bears, since few non-urban black bears have been weighed in Southeast Alaska. I assumed the maximum weight of an adult male black bear to be approximately 215 kg and the average weight of independent black bears to be approximately 115 kg (R. Lowell, L. Beier, pers. comm.). Therefore, the dosage of the tetracycline baits used on Kuiu Island was sufficient to mark the bears.

I used scent flags soaked in a fish-shrimp soup to attract bears to the baits. I enclosed baits in wood-panel boxes (30 cm x 10 cm x 10 cm in 2000 and 22.5 cm x 10 cm x 10 cm in 2002), and attached them at a height of 2 m on trees. I chose to use a box

and the box height to diminish the possibility of non-target species accessing the bait. If a non-target animal took the bait, the presence of the box would cause the animal to leave enough sign to reveal its identity. I hung a barbed-wire strand around each box to collect a hair sample of the individual taking the bait (Figure 6). I used hair samples to genetically determine sex and individual identity of a proportion of bears that took baits.

Crews inspected the immediate vicinity of the bait station for uneaten tetracycline capsules. If more than half of the capsules remained, I considered the bait not taken, as the dosage ingested would be less than that required (20 mg/kg) to mark an average-sized bear (115 kg). I assumed that all bears marked with tetracycline were independent subadults or adults, because I considered the likelihood that a sow would share a small, 0.5-kg bolus of meat with a cub-of-the-year to be low. I assumed the number of baits taken by bears to be the number of tetracycline marks then in the population. The number of marks in the population does not equal the number of marked bears, as bears could take multiple baits. Therefore, I calculated the number of marked bears by reducing the number of marks in the population by a rate of double-marking.

Bone and tooth examination

All hunters that killed a black bear in Southeast Alaska were required to register the bear by Alaska Department of Fish and Game (ADF&G) officials. I requested that hunters submit toe bone (metatarsal) samples from their harvested bears from the fall of 2000 through the spring of 2003 from the entirety of Kuiu Island. I requested bone samples, as tetracycline is incorporated more readily in the bone than in teeth, due to the rate of deposition of new material (Garshelis and Visser 1997). When hunters did not

provide a toe bone, I used a premolar tooth for analysis. I also collected samples from bears harvested from Kupreanof Island from spring 2002 to spring 2003 to further address the assumption of geographic closure. I only requested bone samples from western Kupreanof Island, but I obtained biomark data from bears harvested from the remaining areas of Kupreanof by screening the teeth submitted for age analysis.

I analyzed bones and teeth for biomarks at the Minnesota Department of Natural Resources (1201 East Highway 2, Grand Rapids, MN 55754) and Matson's Laboratory LLC (P.O. Box 308, Milltown, MT 59851). I cut cross sections of the bone, approximately 100 +/- 20 microns in width (Matson and Kerr 1998), and longitudinal sections of tooth samples using a double-bladed diamond saw. I examined the sections for tetracycline fluorescence (Figure 7) under an ultraviolet microscope (40-100x; Leitz Laborlux S, Bartels and Stout, Inc.). Because marked bears harvested in the fall of 2002 and spring of 2003 could have been marked either in 2000 or 2002, Matson's Laboratory LLC prepared half of the tooth for age analysis (by counting cementum annuli), and the other half for tetracycline analysis. The lab examined concurrently the tetracycline and age preparations to determine the year of marking (Matson and Kerr 1998), and also aged all marked and unmarked harvested bears from the study area.

Genetic laboratory methods

I genetically examined hair samples collected from the barbed wire associated with bait boxes to: 1) determine the sex of the animal that took the bait to address a potential bias due to unequal capture and recapture probabilities of the sexes; and 2)

determine the genetic identities of the animals that took baits to assess the rate of double-marking.

I extracted DNA from 130 hair samples, which represented 65% of the baits taken in 2002. I extracted DNA from the follicles of the hairs using the QIAGEN DNeasy 96-well plate extraction kit. To determine sex of the genetic sample, I amplified the DNA extract using polymerase chain reaction (PCR) at a sex-specific locus on the ameliogenin gene (Poole *et al.* 2001), using the primers SE47 (with fluorescent label VIC) and SE48 (Table 1); primer sequences are published in Ennis and Gallagher (Ennis and Gallagher 1994). If the sample was male, I observed two fragments, a 187 base pair (bp) fragment and a 239 bp fragment. Only the 239 bp fragment was present in females.

I used a suite of seven microsatellite loci (Paetkau and Strobeck 1994, Paetkau *et al.* 1995, Paetkau *et al.* 1998a) for individual identification of the hair samples that I collected from baits in 2002 (Table 1). I ran all PCR's on a Peltier Thermal Cycler 225 or 200 (MJ Research) in 15 µl volumes (Table 2). The concentration of the DNA extract was generally < 1 ng/µl, and therefore I was not able to quantify the concentration of the extract using standard fluorometry. Instead, I used 5 µl of DNA template in each PCR. 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, dependent 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 product with either a formamide-LIZ or -ROX (ABI) ladder (total volume, 20 µl), which were used to calibrate fragment size estimation. I fluorescently labeled the forward primer in all PCR's (OPERON and ABI), allowing for 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.

To determine the probability of identity (see below) for the northern Kuiu Island population, I also extracted DNA from 117 representative tissue samples of known northern Kuiu Island individual bears, and amplified the extract at seven microsatellite loci.

Analysis

Estimation of number of marked bears

In most mark-recapture studies the number of marks in the population is known; in this study I estimated this value. To avoid an overestimate of the number of marked animals, I reduced the number of baits taken by bears by an estimate of the rate of double-marking. I used two methods to assess the rate of double-marking.

Bone method

Empirical evidence from known marking events suggested that multiple tetracycline marks could be detected in individual bears if baits were taken at least 24

hours apart (Garshelis & Visser 1997). I divided the total number of marks (including double marks) detected in the harvest, by the total number of marked bears (a double marked bear is one marked bear) in the harvest to estimate the number of marks/marked bear (double-marking estimate). I divided the number of baits taken by this double-marking estimate to calculate the number of individual bears marked in the population (Garshelis and Visser 1997).

Hair method

Because bears may ingest multiple baits in less than 24 hours, I also estimated the rate of double-marking by comparing individual genetic fingerprints of the hair samples that were associated with bait boxes in 2002. I compiled genotype data at each microsatellite locus to produce a multilocus genotype (*i.e.,* genetic fingerprint) for each successfully amplified hair sample (n = 103). I wrote the program IDENTITY in Visual Basic 6.0 to sort and compare each genetic fingerprint (Appendix I). IDENTITY compared the genotypes at each locus for each pair of samples sequentially, and tallied the number of matched and mismatched locus-genotypes between a pair of samples. If two samples matched at at least five genotypes (see discussion on *probability of identity* below), and had no mismatches, I considered the samples to represent a single individual. IDENTITY compared all pairs of genetic fingerprints in this way. I used this program to ultimately identify the number of unique genetic individuals within the set of hair samples.

To ensure that genetic individuals were equivalent to real individuals, I calculated the probability that two individuals had the same genetic identity, *i.e.,* the probability of identity (PI), for the northern Kuiu Island black bear population (Taberlet and Luikart

1999, Waits *et al.* 2001). A low PI (< 0.01) was required to assume that one genetic individual represents one real individual (Mills *et al.* 2000). I calculated unbiased PI using equations for small sample size (Paetkau *et al.* 1998b, Valiere 2002). I discounted the number of baits taken by bears, by the number of baits taken per genetic individual. This resulted in the number of marked bears in the population.

I assumed that the estimation of double-marking using hair samples was more accurate and precise than the method using detection of double-marks in the bones. The hair method included bears that took multiple baits within a 24 hour period, and was based on a larger sample size (n = 103 hair samples *vs.* 30 bones). Therefore, I derived the population and survival estimates from the estimated number of marked bears using the hair-sample method.

Estimation of the number of recovered bears

I increased the number of marked harvested bears (recoveries) slightly due to consideration of the decreased uptake of tetracycline in teeth, with respect to bone. The number of marks recovered in teeth was divided by 0.9 (Garshelis and Visser 1997), to obtain the estimated number of marks in teeth.

Density estimate

I used the Lincoln-Petersen model corrected for small sample size (Chapman 1965) to estimate population size:

$$\hat{N} = \frac{(M+1)(C+1)}{(R+1)} - 1$$

where *M* was the number of animals marked, *C* was the number of animals harvested, and *R* was the number of harvested animals with marks (recovered). I used the tetracycline mark data from 2000 and 2002 for northern Kuiu Island in separate Lincoln-Petersen models. I used bears killed in the harvest regulatory year 2000 (fall 2000 and spring 2001) as the recovery sample for the 2000 marks, and bears killed in regulatory year 2002 as the recovery sample for the 2002 marks. Thus, these two models used only the recoveries from the first year post marking.

The Lincoln-Petersen model assumes geographic closure, an assumption that was most likely not supported, thus the population estimates from these models should be considered as super-population estimates (Kendall 1999).

I also ran additional Lincoln-Petersen models by reducing the number of marked bears available for recovery by an estimate of annual immigration of unmarked individuals to Kuiu Island. I calculated the annual immigration rate for each data set (2000 and 2002) separately, from data regarding the *emigration* of marks; I assumed that immigration and emigration were equal. I calculated the ratio of the number of marked bears harvested on southern Kuiu and Kupreanof islands to the total number of bears marked bears harvested in the years post marking. Thus for the 2000 data set, I divided this figure by three, to calculate an estimate of an annual emigration rate. In this assessment of emigration of marked individuals, I did not include the differential probability of marked bears being available outside the study area.

I calculated density estimates by dividing the population estimate by island area, 673 km^2. This area was the entirety of Kuiu Island, north of the Bay of Pillars and Port Camden isthmus, including higher elevation rock. I considered all of the area bear habitat

for this analysis, as there was little concrete information on black bear habitat use in Southeast Alaska (but see Erickson *et al.* 1982). The density estimates, based on the area of northern Kuiu Island, are likely biased high due to this closure violation.

Survival estimate

I used a Brownie recovery model with the mark and recovery data of 2000 and 2002 tetracycline marks (Brownie and Pollock 1985) to estimate the survival *(S)* and recovery *(f)* rates of independent black bears marked on Kuiu Island (Appendix II). I used data from all bears recovered from 2000 to 2002 in this analysis. In this study, the age and sex of all marked individuals was unknown, and therefore I assumed recovery and survival rates to be independent of these parameters. This assumption was likely to be violated. For example, if capture and recovery samples were skewed in the same direction, for example toward older males, the survival estimate would have been biased toward the survival rate for older males. I assumed that the mark did not affect survival rate, and the survival of marked animals were independent of one another. I also made the basic assumptions of mark-recapture that are also inherent in the Brownie recovery model such as equal catchability (*i.e.,* the sample was representative of the target population) and no mark loss within the time period of the study.

To estimate survival, two encounter occasions were required after marking (Brownie *et al.* 1985). Marked bears that survived the first interval may or may not have been sampled in the second encounter occasion, as recovery probability was less than one. Therefore, to estimate both survival and recovery rates, a third encounter occasion was needed. Data from animals recovered in this third session, but not in the second,

were used to estimate survival. Therefore, with these tetracycline data, I estimated a survival rate for the interval from the fall of 2000 to the fall of 2001. I used only data from the capture of 2000 marks to estimate survival, as there have not been enough encounter occasions of 2002 marks to estimate survival during later intervals. However, I included data from the recovery of 2002 marks in this model to estimate recovery rate with higher precision. A more precise estimate of recovery rate would result in a more precise estimate of survival, as recovery rate is used in the estimation of survival (Brownie *et al.* 1985), whether or not I used recovery of 2002 marks *per se* to estimate survival.

Recovery rate in the Brownie model was equivalent to $Kc\lambda$, where K was the probability that an animal was shot, c was the probability that an animal was retrieved and λ was the probability that a harvested bear was registered (Brownie *et al.* 1985). I assumed that $\lambda = 1$, as there was an incentive to register the bear, since skull size could not be officially recorded without registration through ADF&G. Therefore $f = Kc(1)$, where Kc represented the reported harvest. The probability that an animal died from natural causes was $(1 - S) - f$. In the case presented here, 'natural' causes included: 1) mortality not associated with hunting; 2) bears shot and not retrieved, hereafter referred to as "wounding mortality"; and 3) the probability that a mark did not appear in the bone or tooth of a bear that took a bait (see discussion on biases in the data set below). Therefore, $1 - [(1 - S) - f]$ was the estimate of survival of black bears from fall 2000 to fall 2001, without harvest . Note, this is not an estimate of "true" survival, *i.e.*, survival in the absence of hunting, as it is not known whether black bear hunting on Kuiu Island is compensatory or additive.

I ran Brownie recovery models with *f* varying according to year. I examined models: *f*(.)*S*(.); *f*(t)*S*(.); *f*(1_2, 3)*S*(.) and *f*(1,2_3)*S*(.). In the latter two models, I held the recovery rate constant for the first (1_2) and last two intervals (2_3), respectively, allowing it to differ from recovery rate in the remaining interval (3 and 1, respectively). I included these models as the legal harvest differed between the years (Figure 3). I used program MARK (White and Burnham 1999) to generate maximum likelihood estimates of the parameters and variance, and used Akaike's Information Criterion (AIC) corrected for small sample size (Anderson *et al.* 2001) to rank the ability of the different models to explain the data. I used model-averaging to produce the annual survival and recovery rate estimates.

RESULTS

Estimation of the number of marked bears

In 2000, 144 of the 188 distributed baits were taken (76.6%), and 138 were taken by bears. One bait was taken by a red squirrel and I found unconsumed tetracycline capsules at the other five bait stations. In 2002, 73 – 76% of the 263 distributed baits were taken by bears (n = 191 – 201); ten of the taken baits may or may not have resulted in a marked bear. At nine of these ten bait stations, there was no animal sign. It seems likely that a smaller animal would have left sign, as the box would have been more difficult for them to open. I suggest that these nine baits were most likely consumed by bears. At the tenth bait station, I found four tetracycline capsules, thus I considered this bait to be taken by a bear, as fewer than half of the capsules were found. Because the total

number of baits taken in 2002 was somewhat ambiguous, I modeled two scenarios, one with 201 and one with 195 baits taken by bears (the latter assuming that ½ of the baits from the ambiguous bait stations were taken by other animals).

The rate of double-marking during the 2000 baiting effort, using the occurrence of double marks that appeared in the recovered bones, was 5%; one sample had two marks out of the 20 marked bears harvested from 2000 to 2002. The estimate of double-marking during the 2002 baiting effort was 10%; one out of ten marked bears harvested had two 2002 marks. This estimate for the 2002 marking was based only on the first year of recaptures after marking. This high percentage of double 2002 marks may be an overestimate due to low sample size, as there was no reason to expect that double-marking should be greater in 2002 than 2000. In 2002, I did not place baits along roads, but systematically near the center of grid cells, which would have likely decreased double-marking. Thus, it is likely that as more bears are recaptured with 2002 marks, this estimate of double-marking will decrease.

Unbiased PI, calculated from the 117 representative northern Kuiu Island tissue samples, was sufficiently low to identify known individuals with only five microsatellite loci (PI = 0.002 – 0.0001 for five loci, depending on the actual five loci used for identification; Figure 8). Therefore, I used samples that successfully amplified at five to seven loci. From the individual identification of hair samples (n = 103) from the taken baits, I estimated that an average of 1.062 baits were taken by each baited bear, a double-marking estimate of 6.2%. Most bears that took multiple baits, took baits adjacent to one another (Figure 9). I used the estimate of double-marking derived from the hair samples, to estimate the number of marked bears. I estimated the number of marked bears in the

summer of 2000 to have been 129.4. In the summer of 2002, 188.5 or 182.9 bears had 2002 marks, if 201 or 195 baits were taken, respectively.

I successfully amplified 89 hair samples associated with bait boxes in 2002 at both enough microsatellite loci for individual identification and at the sex identification locus. This sample represented 44% of baits taken. Of these samples, 54% of the identified individuals were male (n = 48) and 46% were female (n = 41).

Estimation of the number of recovered bears

I found 32 marks in 503 bone and tooth samples from Kuiu and western Kupreanof islands. Two samples had double marks from the same marking year; one sample had a mark from both 2000 and 2002. I found 27 marks from bears harvested on northern Kuiu Island, and five marks from bears harvested outside of the study area on southern Kuiu Island (n = 2) and Kupreanof Island (n = 3; Table 3). Of 10 known marked northern Kuiu bears (based on examination of bone samples), I found eight marks in corresponding teeth, a detection rate for teeth of 80%. This detection rate for teeth was similar to what Garshelis & Visser (1997) found empirically (90%) from 207 samples. Using this 90% detection rate (due to higher sample size), I increased the number of recovered bears in the Lincoln-Petersen models using 2000 marks from 9 to 9.1, because one mark was found in a tooth sample (1/0.9 detection rate = 0.1 additional bears marked).

Imprecise kill locations for bears harvested in 2000 (n = 2) and 2002 (n = 3) were recorded for bears killed in Port Camden and Bay of Pillars (Figure 4). These five bears were unmarked. Whether these bears were taken from the north or south side of these

bays would determine whether they were taken from the study area (northern Kuiu Island) or from outside the study area on southern Kuiu Island. I assumed that half of these numbers (1 bear in 2000 and 1.5 in 2002) were taken from northern Kuiu Island, and used these harvest numbers for population estimation.

Density

I estimated the population size for northern Kuiu Island using the 2000 marks to have been 1019 bears with a coefficient of variation (CV) of 0.31, using recovery data from regulatory year 2000 (fall 2000 and spring 2001, Table 5). Based upon this population estimate, I estimated the density to have been 1.51 bears/km^2. Population point estimates using the 2002 marks and recovery data, were 983 (1.46 bears/km^2) and 1013 (1.51 bears/km^2), derived from both the low (195) and high (201) estimates of total baits taken by bears, respectively, with CV's of 0.31 (Table 4). Using marked bears recovered outside of the study area, I calculated the rate of emigration of marks of 6.6% for the 2000 marks and 10% for the 2002 marks. If I use this mark emigration rate to reduce the number of marked bears available as a surrogate for immigration of unmarked individuals, density point estimates range from 1.31 to 1.51 bears/km^2.

Survival

Of 129 bears marked in 2000, 21 were recovered from 2000 through 2002, while ten of the 189 bears marked in 2002 were recovered in 2002 (Table 5). The best Brownie model (AICc weight = 0.36) held recovery rates constant (Table 6). The model-averaged estimate of annual survival from fall 2000 to fall 2001 was 0.67 ± 0.18 SE (Table 7),

which included mortality due to legal recovery (f(2000) = 0.079 ± 0.02, f(2001) = 0.072 ± 0.02 , f(2002) = 0.060± 0.02). Using a estimate of f (0.068 ± 0.014) from the best model, the estimate of 'natural' mortality, $1-S-f$, was 0.26 ± 0.2 (complied SE), which included mortality due to natural causes and wounding loss. Wounding loss results in the reported harvest to be roughly 70% of actual harvest, based on reports from hunting guides (R. Lowell, pers. comm.). Thus recovery rate with incorporated wounding loss was roughly 9.7% (0.068/0.7) and therefore adult survival from fall 2000 to fall 2001 without incorporating harvested animals was approximately 75%.

DISCUSSION

Density

This study is the first to estimate a population density of black bears in Southeast Alaska. The estimate of 1.51 bears/km^2 (both the 2000 and 2002 estimates) is among the highest published black bear density across the entire distribution of the species. Incorporating immigration of unmarked individuals, which would dilute the proportion of marks available, the point estimates range from 1.31 to 1.51 bears/km^2.

At the southern extent of the coastal rainforest, Lindzey & Meslow (1977b) documented an increase in the density of black bears (determined by a census of known individuals) on Washington's Long Island (21 km^2) from 1.14 bears/km^2 to 1.57/km^2 from 1973 to 1975. By 1982, the density on this small island had remained at 1.0/km^2 for several years (Lindzey *et al.* 1986). Urban black bears, in relatively small areas, approach the densities found on Kuiu and Long islands. Beckmann and Berger (2003) concluded

that the density of black bears (a minimum census density of known bears) in the urban areas of the Lake Tahoe region was 1.2/km^2. This urban black bear density is probably representative of other black bear populations in urban areas or around landfills, where human food serves as an attractant. Higher densities of bears can occur in areas of seasonally high food concentrations, such as on salmon-spawning streams (Miller *et al.* 1997, Chapter 3). In other systems, without a seasonal concentration of food or significant access to human food, Martorello *et al.* (2001) used photographic mark-recapture to estimate relatively high black bear densities of 0.80 bears/km^2 in eastern North Carolina and 0.71 bears/km^2 in the Great Smoky Mountains National Park. Belant *et al.* (2004) estimated black bear density, using genetic tagging, on two of the Apostle Islands in Lake Superior to be 0.6 and 0.5 bears/km^2. Much lower black bear densities occur in the Susitna Valley of interior Alaska, where the density is estimated at 0.065 bears/km^2 (Miller *et al.* 1997), and in the wildland areas around Lake Tahoe where Beckmann and Berger (2003) established a black bear density of 0.032 bears/km^2.

Survival

I estimated the annual survival rate for the adult black bears marked on Kuiu Island to be 0.67 ± 0.18 SE. This estimate probably has a negative bias due to the small data set, as additional encounter occasions can only reveal more survivors, although the marked population likely accurately represents the population (see discussion of biases in the data set below). In addition, this estimate of survival is relatively imprecise, due to the small sample size, and should be interpreted cautiously.

Annual adult survival in non-hunted populations in the southeast of the United States ranges from 0.69 to 1.00 ($\overline{X}$ = 0.89, Freedman *et al.* 2003). The lowest survival estimates for a non-hunted population, 0.69 and 0.77 for females and males, respectively, are reported for black bears in North Carolina (Lombardo 1993), where there was significant mortality due to traffic. Beck (1991) estimated adult survival to be 0.70 and 0.96 for male and female bears, respectively, in a protected area of Colorado, which was surrounded by hunting. Survival increased from 0.58 to 0.98 in the Pisgah bear sanctuary in North Carolina after management actions decreased poaching (Sorensen and Powell 1998); hunting was allowed outside the sanctuary. Martorello (1998) estimated survival of adult females to be 0.90 in a hunted population in North Carolina. In Alberta, adult survival of an unprotected bear population was 0.84, which the authors suggested was comparable to other unprotected populations (Hebblewhite *et al.* 2003).

Despite my concerns regarding the precision and bias of this survival estimate, it is the only estimate of survival for black bears in Southeast Alaska, and I think it is relevant to discuss this fairly low survival estimate. In addition, since population growth rate in black bears is often most sensitive to annual adult survival (Freedman *et al.* 2003, Hebblewhite *et al.* 2003), it is important to speculate on why the survival estimate on Kuiu Island is low. After accounting for legal harvest and estimated wounding loss, the survival of marked bears was approximately 0.75, *i.e.*, 25% of the adult population on north Kuiu died due to natural causes. Wildlife viewers, pilots and hunting guides on northern Kuiu Island have observed wolves (*Canis lupus ligioni*) killing adult bears. I frequently found black bear hair in wolf scat on Kuiu Island (Peacock, unpublished data). The most common prey species of wolves in Southeast Alaska is Sitka blacktail deer

(*Odocoileus hemionus sitkensis*; Person *et al.* 1996), yet deer abundance is very low on Kuiu Island (Kirchhoff 2000). The beaver (*Castor canadensis*) was the only other species whose frequency of occurrence in wolf scat on Prince of Wales Island was greater than 10%. Wolves may also eat salmon, mustelids, small mammals and birds, but not in significant amounts (Person *et al.* 1996). The rate of occurrence of black bear hair in wolf scat, low deer numbers and anecdotal observations of predation events, suggest that annual survival of adult black bears on Kuiu Island may be influenced by wolf predation.

Bias in the data set

The high black bear population and low survival estimates reported in this study requires a rigorous analysis of the possible biases. In addition, in a mark-recapture study where the number of marks is not known but estimated, it is especially important to address the criteria used in estimating the number of marked bears, as an over or underestimate of the animals marked will lead to biases in the demographic estimates.

Negative bias

In 2000, I distributed baits only along the coastline and road system due to accessibility. Because the recovery sample (hunter harvest) was also skewed towards sites with easier access, I expected a negative bias in the 2000 estimate. In 2002, I sought to reduce this potential bias by distributing the baits according to a systematic grid. Therefore, I assumed that hunters, while still inclined towards roads and the coastline, had an equal probability of capturing a marked or unmarked bear. However, I detected no negative bias in the 2000 estimate when compared with the 2002 estimate (both estimates

were identical, 1.51 bears/km^2). Thus, bears or hunters may move around more than I had expected. Another possibility is that population size decreased between the two years, and that the first estimate did actually contain a negative bias. However, there is no way to address the possibility of a decreasing population trend with the data from this study alone.

A negative bias due to heterogeneity of behavior of marked and unmarked bears could have resulted if bears that were more likely to take human-distributed baits, were also more susceptible to hunters. Heterogeneity in capture and recapture probability has been detected in other studies of bears (Boulanger and McLellan 2001), and is possibly why most mark-recapture studies produce underestimates of population size (Garshelis and Visser 1997).

Hunters took male bears disproportionately on northern Kuiu Island during the years of this study: 82% and 75% in 2000 and 2002, respectively. In 2002, males took 54% of the baits. The sex ratio in the population was unknown, though probably was biased towards females as males were targeted in the harvest. Therefore, there may be a negative bias due to heterogeneity in capture and recapture between the sexes.

Positive bias

An overestimate of the number of marks in the population would inflate the population estimate. I took precautions to not overestimate the number of marks in the population. An overestimate of the number of marks could result from: 1) taken baits that did not result in a marked bear; 2) an underestimate of double-marking and/or 3) immigration of unmarked individuals.

Baits taken not resulting in marked bears

The first assumption regarding this bias is that if tetracycline is ingested, a mark will be detected. Garshelis and Visser (1997) estimated the probability that a mark appeared in the bone as 1 when a captured bear was fed or injected with tetracycline (n = 36). They estimated that the probability that a mark appears in the tooth, if detected in a bone, as 0.9 (n = 207). I adjusted for probability of detection in teeth, by increasing the number of marks recovered according to this detection probability.

Assuming that marks will be detected if they are ingested, I must next evaluate whether a taken bait results in the ingestion of the bait by a bear. I determined the number of baits taken by bears after taking into account baits taken by other animals (n = 1). I also did not consider taken baits from which more than half of the capsules were found in the vicinity of the bait. The bait was relatively small, and therefore the bait was most likely eaten immediately. Therefore, it was improbable that any uneaten capsules were dispersed outside the immediate vicinity of the bait station. The area near each taken bait for uneaten tetracycline capsules was searched by two to three crew members. In 2002, no animal sign was found at ten bait stations where baits were taken. Although I expected that a smaller animal would leave more sign than a bear, I explored the implications of this ambiguity by running models with the conservative estimate (all ambiguous baits were taken by bears) of the number of baits taken, and a smaller estimate assuming that ½ of the ambiguous bait stations were taken by other animals.

Underestimate of double-marking

I used two methods to estimate double-marking: genetic individual identification of a proportion of the bears that took baits (51%) and the rate of appearance of double marks in the bones. Using the method which assesses the double-marking rate in bone, I estimated a rate of 5 – 10% double-marking from a sample of 30 marked bones. From the genetic identification of 103 baited bears in 2002, I calculated an estimate of 6.2% double-marking. This latter estimate would include bears that took multiple baits within 24 hours. Due to the fact that genetic identity is only a probability of identity, and not an exact identity, any error in this estimate of double-marking due to this factor would tend to lean towards an overestimate of double-marking. A review of the tendency of genetic identification that would lean towards an underestimate of double-marking, due to genetic data quality, is given in Chapter 3. With the similarity in the estimation of double-marking using these two independent methods (three data sets), I suggest that I have not underestimated the extent of double-marking.

Immigration of unmarked individuals

In 2000 and 2002, the estimates of 1019 bears and 1013 bears, respectively, should be considered super-population estimates (Kendall 1999). The super-population estimate includes all bears using the northern Kuiu Island area over the period of the study, if we assume that immigration and emigration were random with respect to the mark. These numbers are biased, if we ask how many animals are on northern Kuiu Island at a particular time (*e.g.*, the time of the 2000 baiting). Therefore, the estimates are

only biased if our "frame of reference" (Kendall 1999) is the study area, not the super-population, which Kendall (1999) asserts may be more ecologically relevant.

If I use the northern Kuiu Island study area as my "frame of reference," the estimates produced by reducing the number of marked bears available will better reflect the number of bears on northern Kuiu Island at a particular time. I detected the first emigration events in spring 2001, when I found marks in two bears harvested on southern Kuiu. By spring 2003, I had found 20% of the recaptured 2000 marks (n = 20) outside of northern Kuiu Island (two on southern Kuiu Island and two on Kupreanof Island). By the first spring after the 2002 marking, I had found 10% (n = 1) of the recovered 2002 marks (n = 10) outside of the study area, on Kupreanof Island. If I assume that emigration of marked bears and immigration of unmarked bears were equal, the population size estimation may be inflated due to the immigration of unmarked individuals from Kuiu Island. Therefore, I included Lincoln-Petersen estimates that incorporate estimates of the rates of immigration of marked individuals, based on empirical data on the rate of emigration of marks. However, genetic data suggest that movement of black bears between Kuiu and Kupreanof Islands was asymmetrical. The number of migrants per generation, incorporating an unknown microsatellite locus mutation rate, was 16.12 (95% CI =15.37 – 16.77) from Kuiu to Kupreanof and 10.69 (95% CI = 9.6 – 11.36) from Kupreanof to Kuiu (Chapter 2). Thus, immigration of unmarked individuals from Kupreanof may have been slightly lower than emigration of marked individuals from Kuiu Island. The next closest population of black bears is on Prince of Wales Island (11 km over salt water from Kuiu Island), however based on genetic information, it is unlikely that unmarked bears immigrated from Prince of Wales (Chapter 2).

This closure assumption was not made for the survival estimate, as the model estimated the survival of all animals marked on Kuiu Island in 2000; where the bears were harvested was irrelevant.

Precision of the data set

The coefficients of variation (0.30 – 0.31) of these black bear population estimates and standard error of the survival estimate (0.67 ± 0.18 SE) are greater than in studies in which bears can be recaptured or resighted multiple times. However, when I regressed standard error of recent North American black bear density estimates against estimated density, the precision associated with the estimate presented in this study is consistent with these other studies (Figure 10). Precision can only be influenced by the success of the baiting effort and the number of animals harvested. Baiting success in this study was high, approximately 70% in both years, in comparison to other tetracycline studies, where 31% of the baits were taken by bears in Michigan and 34% in Minnesota (Garshelis and Visser 1997). It would be difficult to increase baiting success, while keeping the rate of double-marking low, as grid cells (1.6 km^2) were already relatively small. I expected that the precision of the estimate produced by the 2002 baiting effort would be greater than that of the 2000 estimate because 32% more baits were distributed. However, despite 30% more bears marked in 2002 than in 2000, 30% fewer bears were harvested in 2002 and therefore the precision of the estimate was left virtually unchanged by these factors.

Other marking methods can produce higher precision of the survival and population estimates, however these methods were not feasible on Kuiu Island. CMR

cannot be used in the temperate rainforest, as black bears cannot be resighted. Genetic tagging, where barbed wire hair snagging sites (fences) are visited multiple times, can result in lower variation, but would be very difficult to implement on the remote Kuiu Island. Due to the density of bears on the island, the density of fences used in a genetic tagging study would have to be very high to obtain a modest recapture probability. Fences would have to be distributed at the density of tetracycline baits, 1 per 1.6 km^2 and be visited multiple times to increase precision. It cost roughly $50,000 (not including labor costs) to visit every square mile of northern Kuiu Island two times in 2002 for this tetracycline study. Visiting these sites multiple times would be financially and logistically prohibitive. However, an estimate using one genetic sample of hair-snagged individuals and the genetic identities of the tissue samples in the harvest (Lincoln-Petersen model) would presumably give the same population estimate with the same variation and with the same field cost, but such an approach would have higher analysis costs than tetracycline analysis ($40 – 60/genetic sample *vs*. $3.15/tetracycline sample).

The high density of black bears on Kuiu Island is perhaps due to the confluence of several important factors: access to spawning salmon, absence of brown bears and a heterogeneous topographical and vegetation matrix. Access to spawning salmon is known to increase brown bear population production (Miller *et al.* 1997, Hilderbrand *et al.* 1999), and this is likely true for black bears as high quality fall foods correlate with higher reproduction (*e.g.*, Rogers 1987). However, in other areas of Alaska where black bears occur with spawning salmon runs, densities are not as high. On the Kenai Peninsula, Miller *et al.* (1997) estimated the densities of black bears in two different areas to be 0.15 and 0.20 bears/km^2. They suggested that the black bears in these study areas do

not use salmon due to competitive exclusion by brown bears. Other black-bear-only islands in Southeast Alaska where there are abundant salmon streams may also support high black bear densities (Prince of Wales, Kupreanof and Mitkof islands). However, anecdotal observations from biologists and hunting guides suggest that densities on these islands are not as high as on Kuiu Island.

The mountainous topography of Kuiu Island produces avalanche paths, which maintain swaths of land in early seral stages that provide abundant berries (*Vaccinium* spp. and *Rubus* spp.), which in turn likely influences bear population density. In addition to avalanches maintaining berry production at high levels in some areas, new clear-cuts on northern Kuiu Island also provide high berry abundance. Erickson *et al.* (1982) also noted that black bears on Mitkof Island in Southeast Alaska used early seral stage clear-cuts in greater proportion than their availability. Black bears on Long Island, WA also have strong association with early seral stage clear-cuts (Lindzey and Meslow 1977a, b, Lindzey *et al.* 1986), and the authors have shown that the bear density fluctuates with variation in berry production. Early vegetative seral stages subsequent to clear-cutting enhance berry production, however as succession progresses, these clear-cuts enter a stem-exclusion stage, where berry production is reduced. Lindzey *et al.* (1986) documented a reduction in recruitment and an increase in mortality and dispersal as carrying capacity was reduced when berry production declined. Likewise, the high black bear population density on Kuiu Island estimated in this study may be influenced by the abundance and seral stages of clear-cuts. However, the majority of industrial logging on Kuiu Island occurred in the mid 1980's resulting in clear-cuts just beginning to approach stem-exclusion stage and reduced berry production, and thus population density may

respond accordingly. While to date there are no comprehensive studies on habitat use by black bears in Southeast Alaska, I expect the black bear density is likely to fluctuate in relation to habitat quality, which is influenced by timber management policy.

Devil's club berries (*Oplopanax horridus*), which are associated with moist old-growth forests, were singled out as an important summer and fall food for black bears on the Kenai Peninsula on the central coast of Alaska (Schwartz and Franzmann 1991). Black bears used old-growth forests in proportion to their availability on Mitkof Island in Southeast Alaska (Erickson *et al*. 1982), and 13 out of 13 dens examined were associated with old-growth, decadent trees. These authors concluded that "There can be little doubt… that the assured providing of suitable dens for black bears is a serious concern if the near-elimination of old forests… is a management objective" (Erickson *et al*. 1982). Thus while clear-cuts may produce an ephemeral increase in black bear density, the vegetative matrix, which includes old-growth forest, intact riparian areas of salmon streams and avalanche slopes, likely provides a more consistent, heterogeneous and productive environment resulting in a high black bear density.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Garshelis and Visser (1997) have shown that the tetracycline biomarking method is effective at estimating size of large populations (15,000 – 25,000) in areas of 43,000 km^2 (MI) and 83,000 km^2 (MN). I suggest that this method is also effective in a small (673 km^2), dense population. This study benefited from a relatively high harvest rate, and a well coordinated bear registration effort by ADF&G, ensuring high compliance of

hunters providing samples (95 – 100%). If future researchers are considering employing tetracycline biomarking in a small population, the small sample size should be offset by a combination of high rate of sample submission by hunters, harvest and baiting success.

This study has produced point estimates of the density of black bears on Kuiu Island. These estimates are among the highest recorded across the species range, suggesting high productivity of the environment. However, the population estimate generated in this study represents a snapshot in time, yet effective population management requires an understanding of temporal trends in population size. It is unknown whether this high black bear density is an ephemeral effect of the current seral stage of clear-cuts on northern Kuiu Island. Because little is known about black bear habitat use in Southeast Alaska, and consumptive use of the black bears and the forest on Kuiu Island continues, further population and habitat studies should be conducted to inform future management actions.

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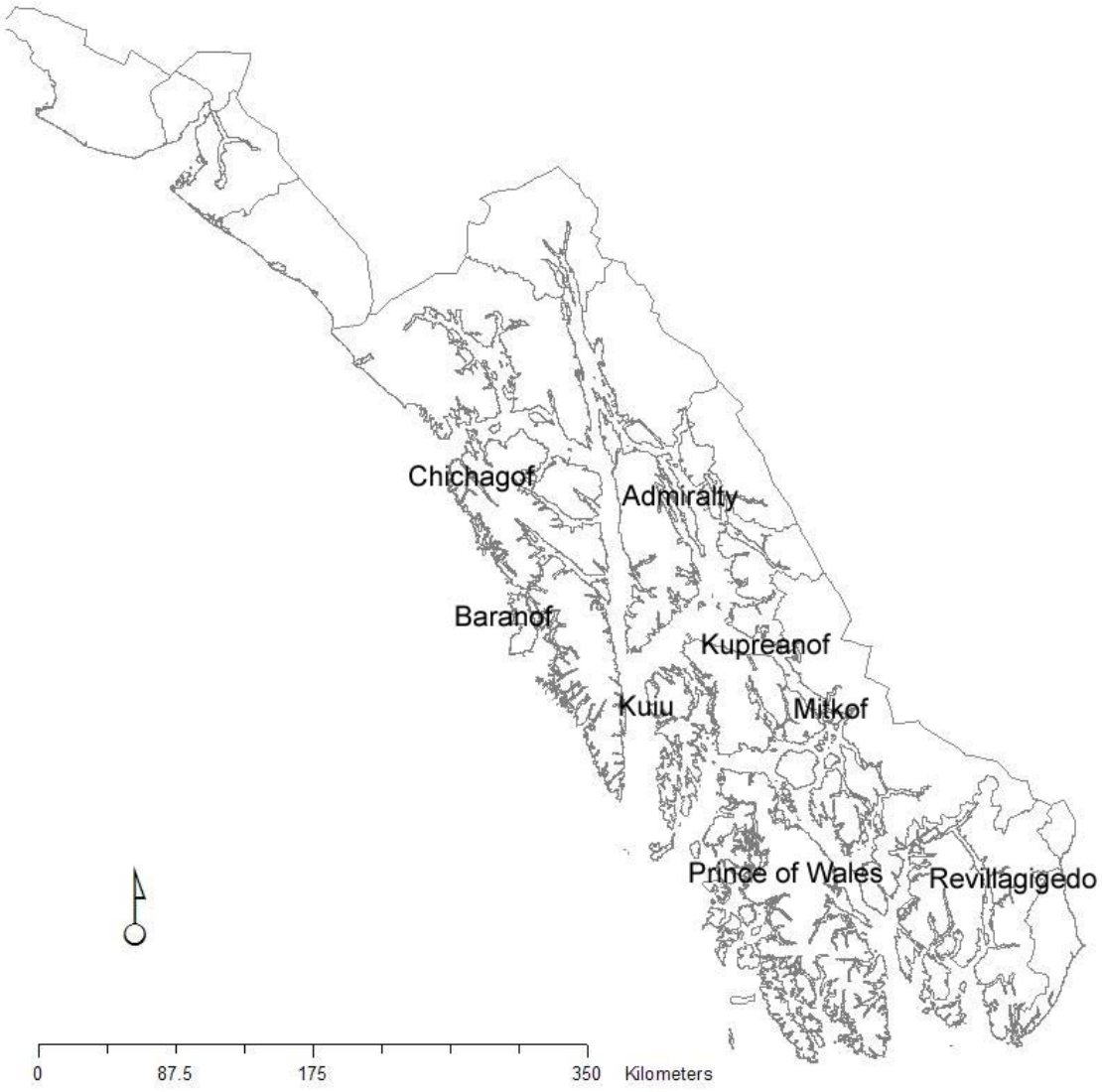


Figure 1. The islands of the Alexander Archipelago of Southeast Alaska.

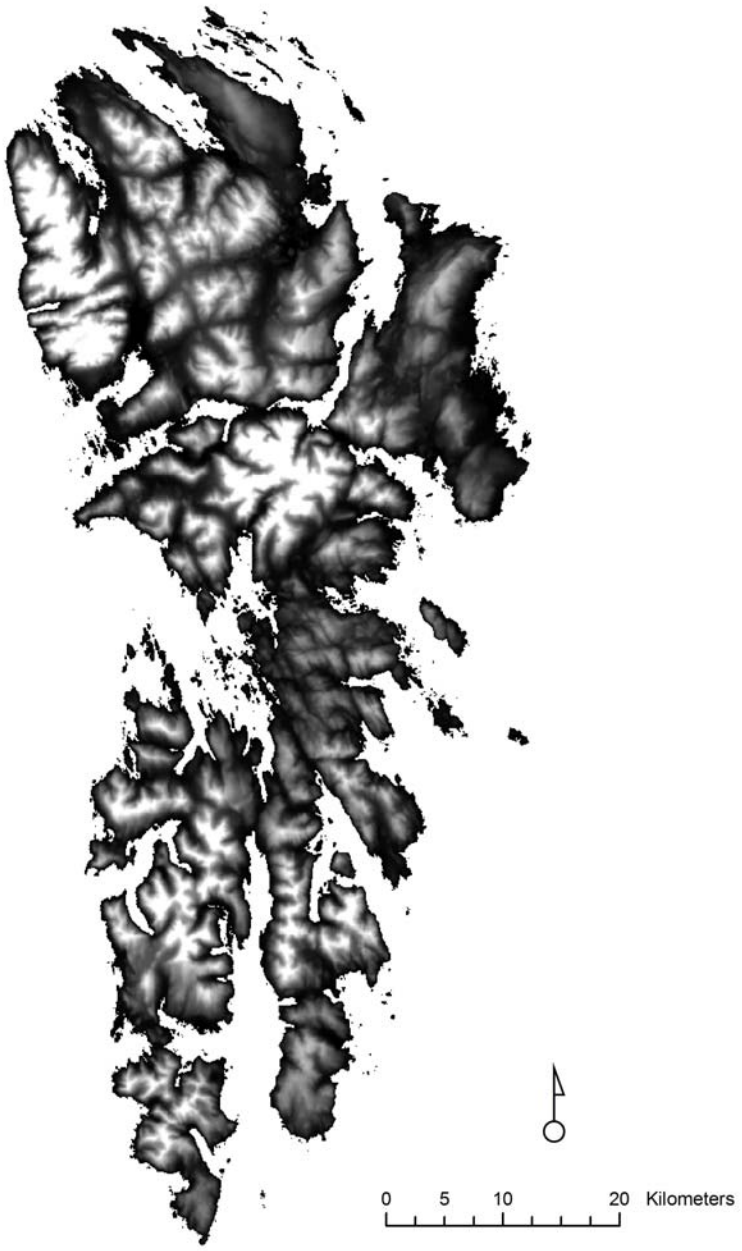


Figure 2. Kuiu Island (1963 km^2) of the Alexander Archipelago, in Southeast Alaska (Digital Elevation Model, provided by USFS).

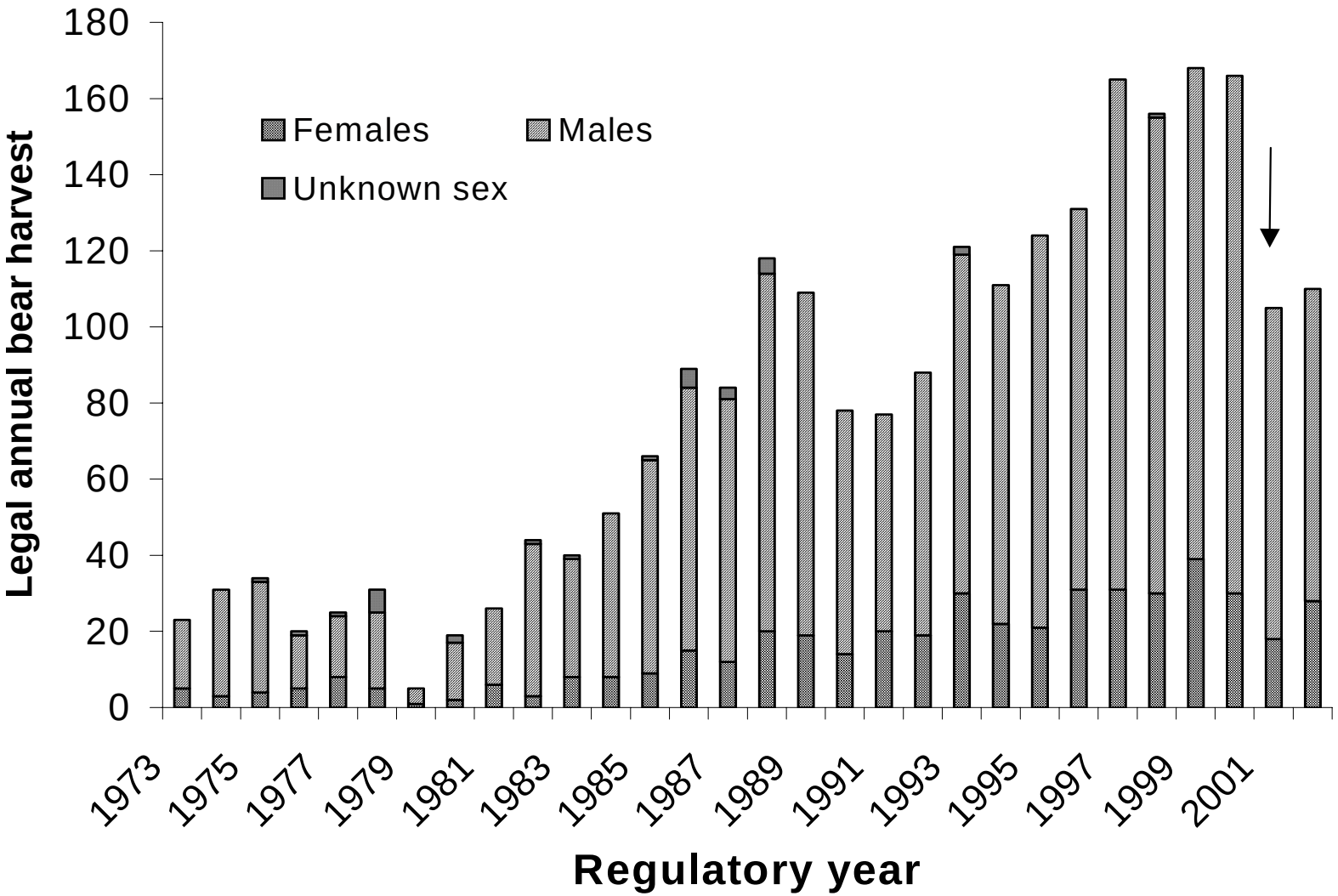


Figure 3. Annual legal black bear harvest on Kuiu Island, Alaska. Data from Alaska Department of Fish and Game. Arrow shows the commencement of the annual harvest cap of 120 bears/regulatory year.

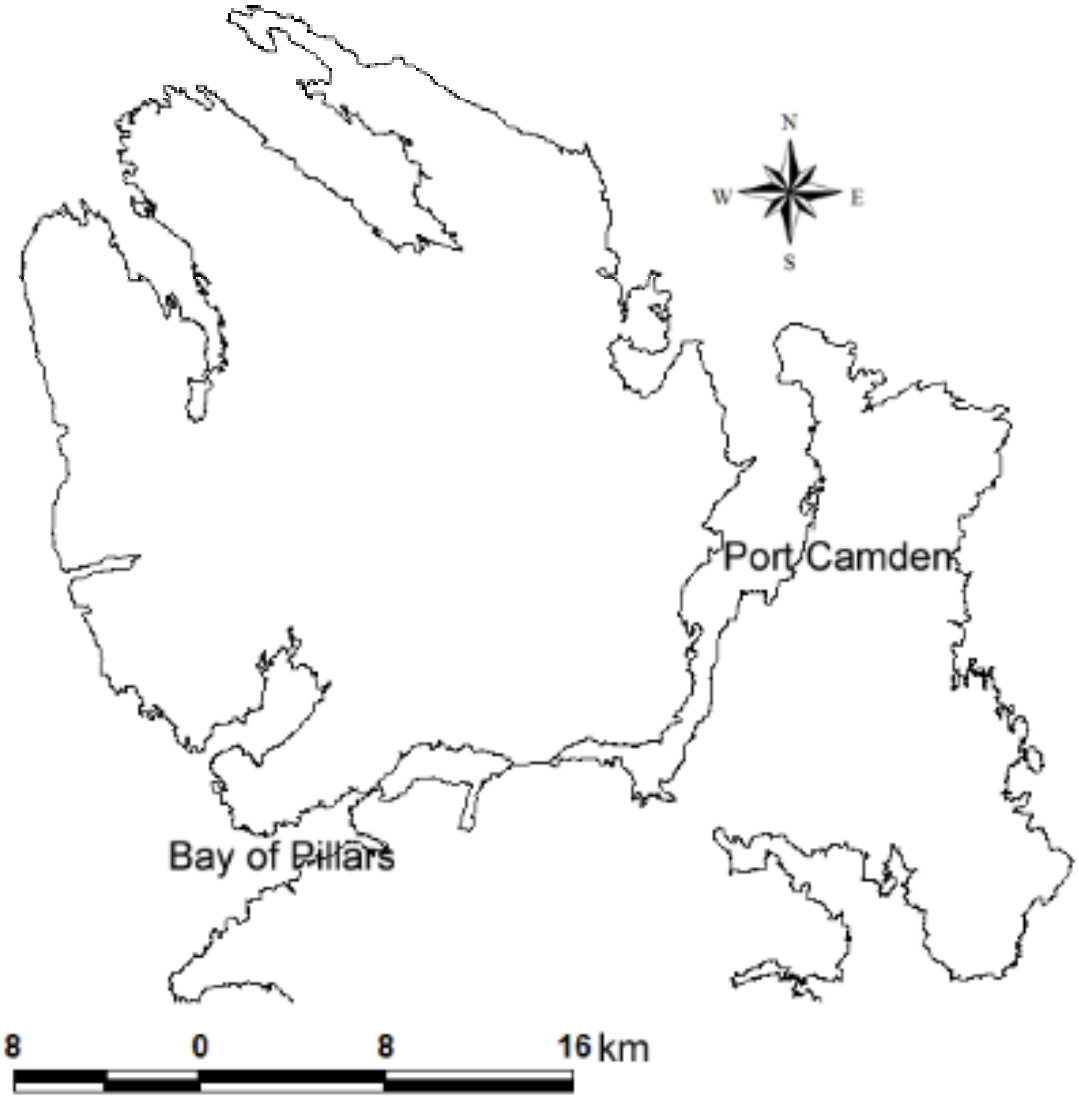
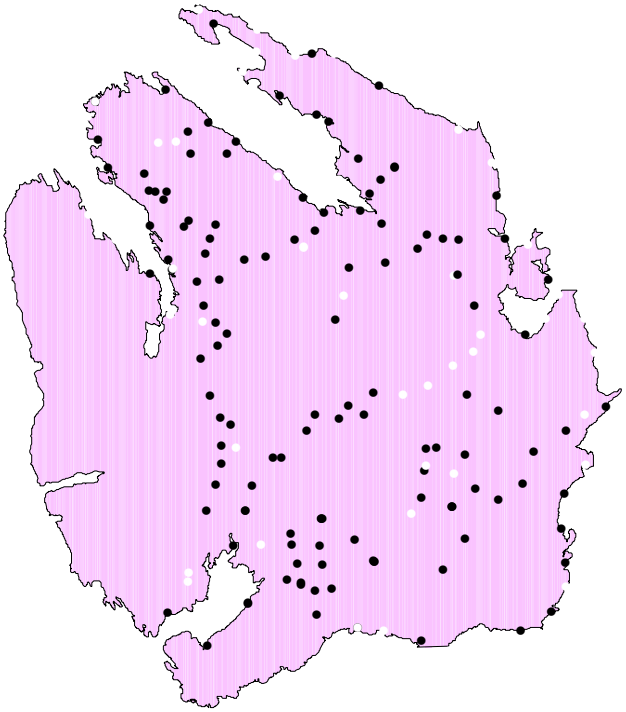
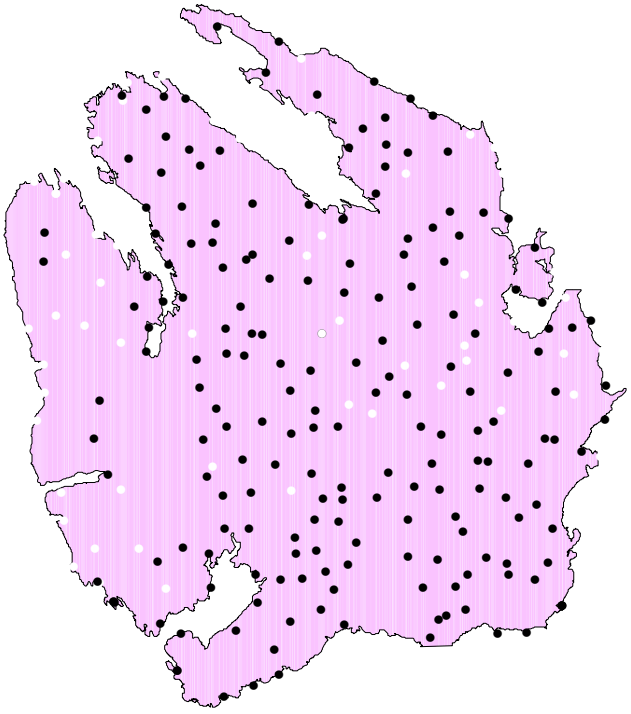


Figure 4. Northern Kuiu Island (673 km^2), Alaska.



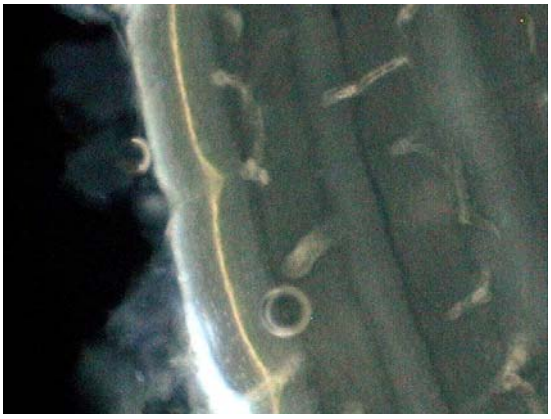
a.



b.

Figure 5. a. Distribution of tetracycline baits in 2000 on northern Kuiu Island. Black dots represent baits taken by bears; white dots represent baits not taken by bears. b. Distribution of tetracycline baits in 2002.

Figure 6. Clockwise from top left: An intact 2000 bait showing barbed wire for hair snaring and scent flag; an intact bait in old-growth hemlock forest; a bear smelling a scent flag with bait in background; remains of taken bait.



a.

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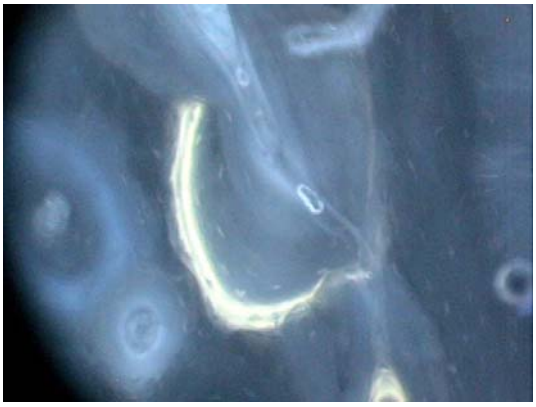

c.

Figure 7. a. 40X image of tetracycline mark in Kuiu bear toe bone. b. 40X image of tetracycline marks, partially remodeled in haversian systems of a toe bone. c. 100X image of a double mark in a toe bone. Images provided by D. Garshelis.

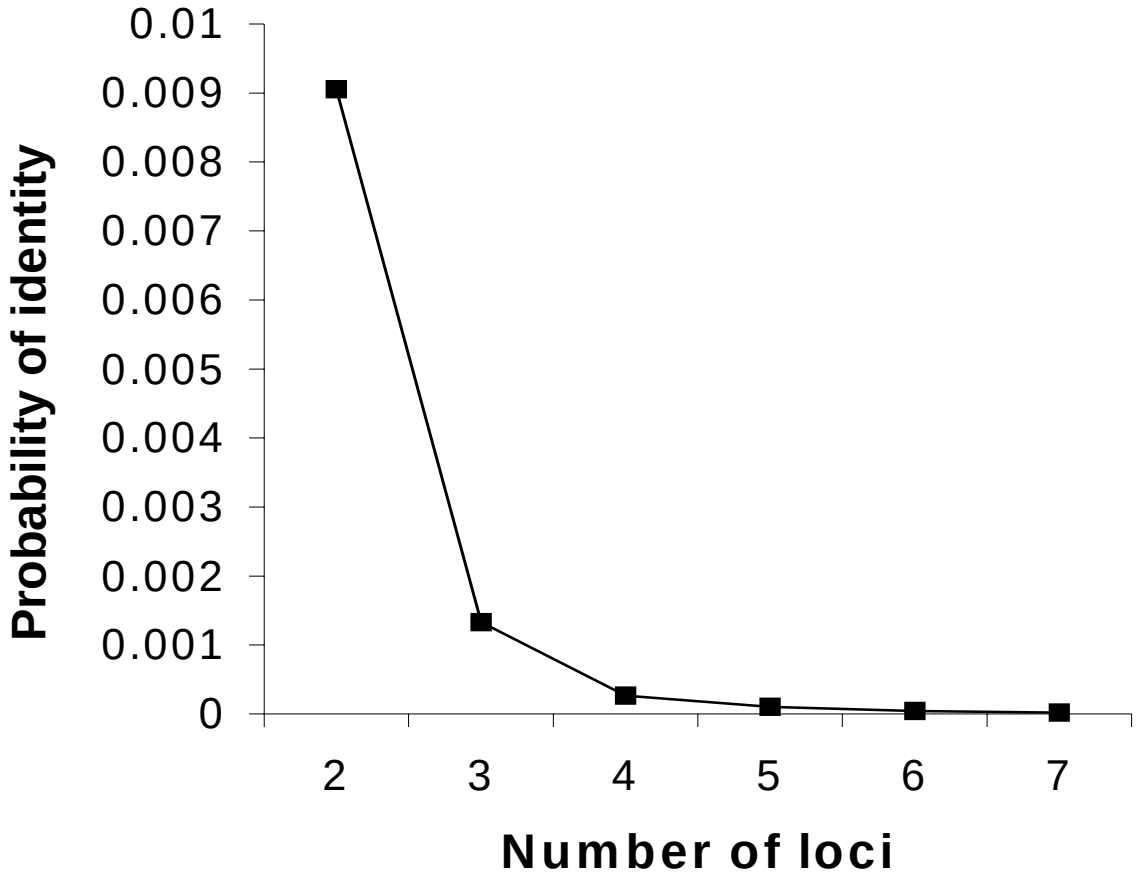

Figure 8. Unbiased probability of identity for northern Kuiu Island black bears, calculated with microsatellite genetic data from 117 tissue samples.

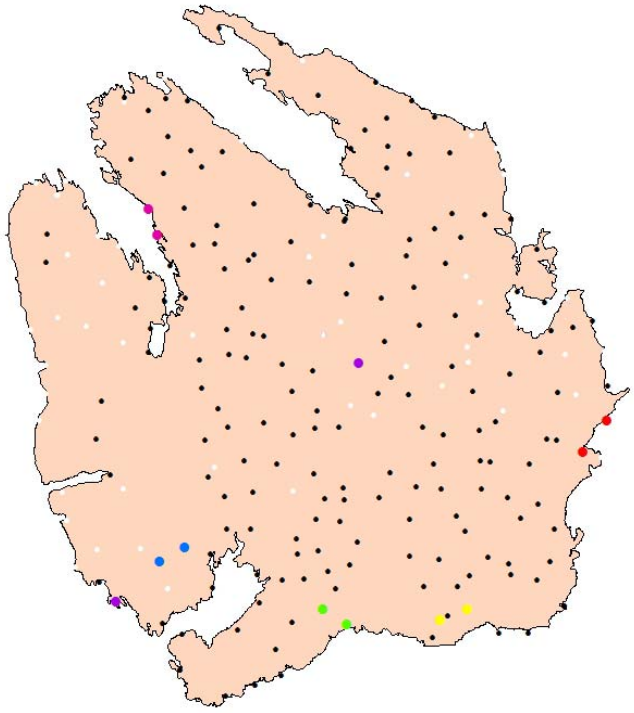

Figure 9. Multiple tetracycline baits taken by the same individual bears in 2002. Each pair of baits with the same color (n = 6) were taken by the same bear. Baits in black were each taken by a single bear, baits in white did not result in a marked bear.

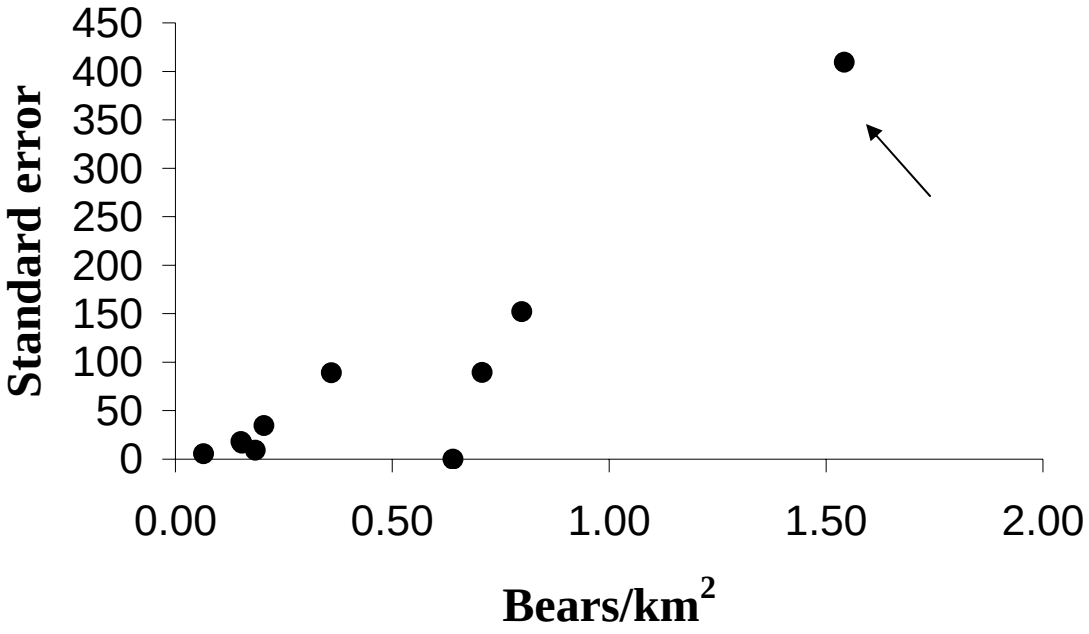

Figure 10. Standard error associated with North American black bear density estimates produced since 1997. Arrow indicates the density and standard error estimated for the Kuiu Island black bears using tetracycline biomarking.

Table 1. 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 2. 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	GenBank Accession Number	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 ††
OJ	U22087 U22090	1.2	1.5	-	0.5	3.0	0.7/0.3	0.2	45	58
L	U22088	1.5	1.0	-	0.5	-	0.5	0.2	30	60
Ct‡‡	U22085	0.9	1.5	-	0.5	-	0.5	0.2	45	62
M	U22089	0.9	1.5	-	0.5	-	0.4	0.2	45	50
X	U22093	-	-	1.5	0.6	-	0.7	0.2	45	58
D	U22094	-	-	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
‡‡ the "t" symbolizes that a tail sequence (gttt) was added to the 5' end reverse primer in order to decrease the effect of 2 base pair stutter.

Table 3. Summary of harvested bears that were marked on northern Kuiu Island with tetracycline, and unmarked during three regulatory harvest years (2000 – 2002) from Kuiu and Kupreanof Islands.

	Northern Kuiu		Southern Kuiu		Western Kupreanof	
Year†	# of samples* (% compliance)	# of bears marked	# of samples	# of bears marked	# of samples	# of bears marked
2000	79 (100%)	9 (1 double)	84	2	5	0
2001	57 (100%)	5	48	0	67	1
2002‡ (2000 marks)	54 (95%)	2	54	0	53	1
2002‡ (2002 marks)	54	9 (1 double)	54	0	53	1

† regulatory year. For example, year 2000 includes harvest seasons fall 2000 and spring 2001.

* these include samples from Port Camden and Bay of Pillars, whose precise location is unknown (n = 2, 3 and 3 from 2000, 2001 and 2002, respectively).

‡ One bear harvested in 2002, had a mark from 2000 and a mark from 2002.

Table 4. Lincoln-Petersen population estimates of black bears on Kuiu Island, Alaska using tetracycline biomarking. Estimates are based on bears marked, which is reduced from baits taken by an estimate of 6.2% double-marking. Yearly emigration rate for 2000 was calculated by the number of recoveries of 2000 marks outside northern Kuiu Island divided by total number of recoveries averaged from the three years of data. Emigration for 2002 was calculated by the number of recoveries of 2002 marks outside northern Kuiu Island divided by the total number of 2002 marks recovered. In 2002, the two estimates of baits taken by bears (195 vs. 205) are a liberal and conservative estimate of how many baits with no sign were taken by non-target species.

Year	Baits taken	Emigration	M	C†	R	N est.	SE	95% CI of N	N est./km^2	Lower 95% CL	Upper 95% CL
2000	138	-	129.4	78	9.1	1019	316	538	1.51	0.71	2.3
2000	138	0.066	120.3	78	9.1	948	293	499	1.41	0.67	2.2
2002	195	-	182.9	52.5	9	983	299	510	1.46	0.70	2.2
2002	201	-	188.5	52.5	9	1013	309	526	1.51	0.72	2.3
2002	195	0.100	163.4	52.5	9	879	266	454	1.31	0.63	2.0
2002	201	0.100	168.4	52.5	9	905	275	469	1.34	0.65	2.0

† number of captures includes all captures from northern Kuiu in addition to ½ of imprecise locations (*n* = 2 and 3 for 2000 and 2002, respectively). Imprecise locations are for a few bears from Port Camden and Bay of Pillars, which bisect the study area.

M – number of bears marked; C – number of bears harvested; R – number of bears recaptured. N est. – population point estimate.

Table 5. Mark and recovery data of tetracycline marked black bears used for Brownie survival model.

Year marked	Bears marked	Bears recovered		
		2000	2001	2002
2000	129	11	7	3
2001	0		0	0
2002	189			10

Table 6. Selected Brownie recovery models for black bears marked on northern Kuiu Island in 2000.

Model	AICc	ΔAICc	AICc Weight	Likelihood	# Parameters	Deviance
S(.)*f*(.)	239.93	0.00	0.36	1	2	1.74
S(.)*f*(1, 2_3)	240.23	0.30	0.31	0.86	3	0.01
S(.)*f*(12_3)	240.98	1.04	0.21	0.59	3	0.75
S(.)*f*(t)	242.28	2.35	0.11	0.31	4	0.0

Table 7. Estimates of survival and recovery rate (model averaged) for black bears marked with tetracycline on Kuiu Island in 2000.

Parameter	Estimate ± SE
Survival rate fall 2000 - fall 2001	0.67± 0.18
Recovery rate summer 2000 - fall 2000	0.079 ± 0.02
Recovery rate 2000 - 2001	0.072 ± 0.02
Recovery rate 2001 - 2002	0.060 ± 0.02

GLACIERS, MOUNTAINS AND SALT WATER: ASSESSING BARRIERS TO MOVEMENT OF A VAGILE SPECIES

INTRODUCTION

Biogeography of the Alexander Archipelago

The Alexander Archipelago of Southeast Alaska (54°– 60° N, 130°– 140° W; Figure 1, 2) is home to 24 endemic species and subspecies of mammals (MacDonald and Cook 1996). The current distribution of inter- and intraspecific biodiversity is the consequence of past and present forces operating on a landscape of more than 1,000 oceanic islands and a narrow strip of mainland, bounded to the east by the glaciated Coast Mountains. Some species are ubiquitous throughout the region (*e.g., Castor canadensis, Mustela vision*, MacDonald and Cook 1996) while others have smaller distributions. These distributions result from patterns of colonization after the last Wisconsin glaciation (22,000 – 10,000 years before present (ybp)[1], Klein 1963, Stuiver *et al.* 1998, Conroy *et al.* 1999), the location of a possible ice-free Wisconsin refugium (Heaton *et al.* 1996, Heaton and Grady 2003), ecological processes (*e.g.*, competitive exclusion and range contraction due to climate warming, Klein 1963, Mann and Hamilton 1995, Conroy *et al.* 1999) and differential dispersal abilities (Conroy *et al.* 1999, Bidlack and Cook 2002). For example, northern flying squirrels (*Glaucomys sabrinus*) that occur only on the mainland and islands south of Sumner Strait, have high dispersal within the Prince of Wales complex, which includes Prince of Wales Island and the smaller islands to its west. However, there is no current gene flow across Clarence Strait between the Prince of

Wales complex and the mainland, hence the endemic subspecific status of the Prince of Wales complex group (*G. s. griseifrons*, Bidlack and Cook 2002). Frederick Sound presents another boundary, across which occur disjunct distributions of several mammalian species (MacDonald and Cook 1996). The endemic subspecies of gray wolf (*Canis lupus ligoni*), likely a post-glacial colonizer (Leonard 2002), does not occur north of Frederick Sound, on Admiralty, Baranof and Chichagof (ABC) islands. Wolves are able to disperse to Admiralty Island from the mainland, but populations may not persist due to competitive exclusion by the high density brown bear population (D. Person, pers. comm., Conroy *et al.* 1999). The naturally-fragmented landscape of Southeast Alaska is also an interface between sub-specific genetic lineages for several mammalian taxa including dusky shrews (*Sorex monticolus*, Demboski and Cook 2001), and martens (*Martes americana*, Dembowski *et al.* 1999).

Bears on the North Pacific coast

The Ursidae offer another example of interesting distributions at the specific and intra-specific level in Southeast Alaska. Brown bears occur on the ABC islands, while black bears occur on Pleasant Island and the islands south of Frederick Sound. The two species of bears are sympatric on the mainland of Southeast Alaska. Heaton *et al.* (1996) and Talbot and Shields have (1996) suggested, based on paleontological and mitochondrial DNA (mtDNA) evidence, that the brown bears on the ABC islands may be a paleoendemic lineage (500 – 750,000 years old) persisting during the Wisconsin in an ice-age refugium, possibly on Prince of Wales Island (Heaton and Grady 2003). Some of the most compelling evidence of a refugium is recent mtDNA evidence from brown bear

fossils found in Blowing in the Wind Cave on Prince of Wales (Barnes *et al.* 2002) suggesting that the now-extinct Prince of Wales brown bear was a member of the ancient ABC clade.

Investigation of black bear genetic variation is central to the debate regarding the location of a Wisconsin refugium on the North Pacific coast of North America (Byun *et al.* 1997, Byun *et al.* 1999, Demboski *et al.* 1999, Stone and Cook 2000). Two ancient North American black bear clades have been reported by several authors (Paetkau and Strobeck 1996, Byun *et al.* 1997, Wooding and Ward 1997, Stone and Cook 2000), and Wooding and Ward (1997) found that two black bear mtDNA lineages diverged 1.8 million years ago, at the beginning of the Pleistocene. Byun *et al.* (1997) suggested that a coastal mtDNA lineage persisted in the now submerged Hecate refugium (Mandryk *et al.* 2001), between Haida Gwaii and the British Columbia mainland, and post-glacially recolonized Haida Gwaii. Dembowski *et al.* (1999) argued that the pattern of converging coastal and continental black bear lineages was not compelling support for the existence of a Hecate refugium, because sampling had been limited (Byun *et al.* 1997) and the coastal black bear mitochondrial lineage had also been found in the interior of the continent (Cronin *et al.* 1991, Paetkau and Strobeck 1996, Byun *et al.* 1997, Wooding and Ward 1997). In addition, Stone and Cook (2000) determined that the coastal black bear lineage extends northward to the islands south of Frederick Sound in the Alexander Archipelago and to Windham Bay on the Alaskan mainland, with the exception of one bear from the coastal mtDNA lineage having been sampled on the Chilkat Peninsula. Stone and Cook (2000) suggested that the geographical transition between this coastal and a continental lineage occurs in Southeast Alaska, as they determined that the

continental mtDNA lineage exists on the Southeast Alaskan mainland from the Juneau area south to Windham Bay.

Modern black bears of the coastal mtDNA lineage in Southeast Alaska may have expanded from a refugium in Southeast Alaska, perhaps on Prince of Wales Island, colonized from the Hecate refugium or arrived from south of the continental ice field (Stone and Cook 2000). The continental mtDNA lineage may also have colonized from areas south of the ice sheet, or from eastern North America (Stone and Cook 2000). Regardless of how black bears arrived at their present distribution – expansion within or recolonization of the Archipelago – their movements required the navigation of shifting configurations of salt water, land and ice. During the last glacial maximum (25,000 – 19,000 ybp), the continental shelf of Southeast Alaska was mostly covered by glaciers, punctuated by small ice-free areas (Mann 1986, Mann and Hamilton 1995, Heaton *et al.* 1996). Klein (1963) suggested that when the glaciers began to retreat in the coastal areas by 19,000 ybp, the extent of the aerially-exposed landforms remained largely the same until the expansive continental ice field melted and sea levels began to rise significantly by 12,000 ybp. This suggests at some points during the late Pleistocene, rapidly recolonizing fauna and flora enjoyed narrower salt water channels, and possibly land bridges among islands and the mainland. Whether larger islands and land bridges existed in Southeast Alaska during early deglaciation would have been dependent on the local interacting effects of isostatic rebound (Mann and Hamilton 1995), local tectonism, and forebulge. A forebulge effect, where periglacial land is laterally displaced and uplifted, would have resulted in exposed land during periods of lower sea levels, such as in the Hecate Strait (Josenhans *et al.* 1995, Mandryk *et al.* 2001). However, whether between

coastal glacial melting and eustatic sea level rise, the ice-free land of the Alexander Archipelago was exposed or drowned is unclear (Mann and Hamilton 1995). Currently, the Alexander Archipelago lies within the expanse of the continental shelf, most islands are separated by channels 50 – 200 m deep (Mann 1986), and much of the coastal geography and distribution of islands of the Archipelago have not significantly changed in the last ~9,000 years.

Employing genetic markers more rapidly evolving than mtDNA, such as nuclear microsatellite loci, it may be possible to explore how bears have navigated the changing mosaic of salt water, mountain ranges and glaciers in Southeast Alaska since deglaciation. While Talbot and Shields (1996) determined that two mtDNA lineages of brown bears converged in Southeast Alaska, Paetkau *et al.* (1998a) used 17 microsatellite loci to estimate nuclear gene flow between populations dominated by the different mtDNA lineages: the putative paleoendemic ABC island brown bears and brown bears on the mainland of Southeast Alaska. They concluded that gene flow occurs between the ABC island and mainland brown bears, suggesting current mixing between populations in which the different mtDNA lineages occur (Paetkau *et al.* 1998a).

Purpose of study

The main purpose of the present study was to investigate the relative permeability of physical barriers, such as salt water, narrow coastal fringe and glaciated mountain ranges to black bears in Southeast Alaska. I examined historical nuclear gene flow to assess the cumulative effective dispersal of black bears in the region since deglaciation, and determined if genetic differentiation reflects the current geographic mosaic of land

and salt water. I also investigated the extent of mixing between populations in which the coastal and continental mtDNA lineages (Stone and Cook 2000) co-occur. If the extent of mixing between the mtDNA lineages is minimal, then nuclear DNA variation may still reflect the patterns of expansion of the two mtDNA lineages.

METHODS

Overview of methodological approach

I evaluated current and historical movement[2] of black bears among the islands and mainland of Southeast Alaska using various methods of analyzing microsatellite variation. Microsatellite loci are non-coding, biparentally inherited and rapidly evolving nuclear genetic markers that can be used to detect both historical and contemporary animal movement (Manel *et al.* 2003). Although direct demographic measures of movement may seem more straightforward (*e.g.*, following radio-tagged individuals), rare dispersal events, though biologically important, are often difficult to detect with non-genetic methods (Paetkau *et al.* 1998a). Furthermore, it is usually unknown whether movements detected with mark-recapture or radio-telemetry culminate in successful mating. In addition, non-genetic estimates of dispersal only reflect movement over the course of the study. Genetic data can provide estimates of both current dispersal and the integrated effects of movement over thousands of past generations. I first analyzed the genetic variation for each sampling region in Southeast Alaska to determine whether the data set contained enough power to detect movement among sampling regions. As an initial examination of genetic differentiation (Slatkin 1985) among black bears in

Southeast Alaska, I used Wright's pairwise F_{ST} (Wright 1969, Weir and Cockerham 1984). This statistic has been traditionally used to ascertain average genetic differentiation that evolved over many generations, by comparing allele frequencies within and among sampling regions. Where insignificant F_{ST} values were found among sampling areas, the regions were combined for subsequent analyses.

In addition to estimating gene flow from F_{ST}, a maximum-likelihood approach using optimal coalescent-trees (Beerli and Felsenstein 1999) was used to estimate gene flow. These procedures have different assumptions regarding the inference of gene flow. I used this coalescent approach to estimate one-way migration rates, theta (a measure of genetic variability) and effective population size for all sampling regions.

I evaluated contemporary black bear movement from genetic data using natal population assignment methods (Paetkau *et al.* 1995, Pritchard *et al.* 2000, Paetkau *et al.* 2004). Genetic assignment tests are most similar to studies of movement using radio-telemetry or mark-recapture as they are individually based, however genetic sampling often allows for greater sample size. To address vagility of black bears across geographical barriers, I used Paetkau *et al.*'s (1995) test to assign individuals to sampling regions. I also used Pritchard *et al.*'s (2000) method to assign individuals to genetically-relevant population clusters. Both of these techniques assign individuals to populations based on the genetic likelihoods. However, in Pritchard *et al.'s* (2000) approach, the populations themselves are concurrently defined by allele frequency distributions. Pritchard *et al.'s* (2000) program STRUCTURE avoids the assumption of subpopulation boundaries by using a Bayesian clustering algorithm to group individuals.

Sampling methods

Alaska Department of Fish and Game (ADF&G) staff obtained frozen tissue samples (n = 807) when hunters sealed (reported) harvested black bears. I chose 289 representative samples to genetically characterize the black bears of Southeast Alaska. I included samples from the major black bear islands of the Alexander Archipelago: Kuiu (1962 km^2; n = 39); Kupreanof (2813 km^2; n = 35); Prince of Wales (6675 km^2; n = 37); Mitkof (546 km^2; n = 8); and Revillagigedo (2965 km^2; n = 22) islands (Figure 2). I also incorporated samples from the mainland of Southeast Alaska: The Yakutat region (n = 19) is separated from the rest of Southeast Alaska by the Fairweather Range and its associated glaciers. South of the Fairweathers, the Chilkat Peninsula (n = 34) is separated from the Skagway (n = 22) region by the Chilkat Mountains at the Davidson Glacier. The Skagway region was bounded to the south by Eldred Rock, an area where steep mountains descend immediately into Lynn Canal. I sampled the Juneau region (n = 30) from Eldred Rock to the north side of the Taku Inlet, the central mainland (from the Taku Inlet south to the Cleveland Peninsula, n = 35), and the southern mainland (the coastal fringe south of the Cleveland Peninsula to Misty Fjords, n = 8). I used a slightly reduced data set (n = 263) for the analyses in STRUCTURE.

Laboratory methods

I isolated DNA from samples using the Qiagen DNeasy extraction kit (http://www1.qiagen.com/) according to the manufacturer's protocols, and amplified the DNA extract using polymerase chain reaction (PCR) at seven microsatellite loci (Table 1, 2, Paetkau and Strobeck 1994, Paetkau *et al.* 1995). I ran all PCR's on a Peltier Thermal

Cycler 225 or 200 thermocycler (MJ Research) in 15 µl volumes, beginning 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, and 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 then ethanol-precipitated PCR products to remove non-bounded primers, and combined the precipitate with either a formamide-LIZ or -ROX (ABI) ladder (total volume, 20 µl), which was used to calibrate fragment size estimation. I fluorescently labeled the forward primer in all PCR's (OPERON and Applied Biosystems, Inc.), allowing for size estimation of the fragments using capillary electrophoresis on an ABI 310, 3700 or 3730 automated sequencer at the Nevada Genomics Center at the University of Nevada, Reno.

Analytic methods

Genetic variation

I calculated genetic variation using F-STAT version 2.9.3.2 (Goudet 2001). I calculated allelic richness (R_S), a measure of allele number adjusted for sample size, for each sampling region at each locus. I used Nei's gene diversity index (Nei 1987) to calculate expected heterozygosity (H_E) for each region, and Wright's coefficient of inbreeding, F_{IS}, for each region and locus (Weir and Cockerham 1984). The proportion of randomizations of alleles among individuals within regions that gave larger or smaller F_{IS}

than observed was used to evaluate whether the population had heterozygote deficiency or excess. Significantly large or small F_{IS} indicates a departure from random mating within sampling locations.

I used Garza and Williamson's (2001) M-ratio and program to test for black bear population bottlenecks on the islands of the Alexander Archipelago (Appendix III).

Genetic differentiation

I calculated Weir and Cockerham's (1984) pairwise F_{ST} in F-STAT (Goudet 2001) to assess population differentiation among the black bear sampling regions of Southeast Alaska. I tested for significance of the differentiation with the log likelihood G-statistic (Appendix III, Goudet *et al.* 1996).

Historical gene flow

F_{ST} can overestimate the degree of gene flow if the assumptions of the island model are violated, such as migration-drift equilibrium (Wilson *et al.* 2004). In these cases, F_{ST} should not be used (Whitlock and McCauley 1999) to infer the rate of gene flow – the effective number of migrants per generation, N_em (Slatkin 1985). The inference of gene flow from F_{ST}, requires satisfaction of the assumptions of the island model, which include equal migration rates among subpopulations, and equal effective subpopulation sizes. The relationship between genetic variation and gene flow is traditionally encapsulated in the formula: $N_em = (1- F_{ST}) / 4 F_{ST}$ (Wright 1931). One main pitfall of this relationship is that migration rate cannot be evaluated independently from N_e (Whitlock and McCauley 1999). Consequently, N_em between two populations may be

estimated as equal, but in actuality migration is quite different, due to differences in N_e. The assumptions of N_e equivalence among subpopulations and symmetrical migration are violated in most natural populations. Whitlock and McCauley (1999) suggest that estimates of gene flow from F_{ST} may only be correct "within a few orders of magnitude." Wilson *et al.* (2004) found that F_{ST}-derived dispersal estimates of brook char were two orders of magnitude greater than estimates produced from a gene coalescence-based method (Beerli and Felsenstein 1999), and an order of magnitude greater than mark-recapture estimates. Thus different methods of estimating gene flow produce different estimates, likely due to the varying assumptions of the different models. For example, the coalescence-based model includes the assumptions of equal mutation rate among loci and constant population sizes.

In addition to estimating gene flow from F_{ST} , I have used the alternative gene-coalescence (Kingman 1982) approach to estimate average gene flow among populations of black bears in Southeast Alaska. A genealogy illustrates the coalescent process: the copies of an allele in a set of samples can be traced back through generations of a hypothetical genealogy to its likely origin in the population by way of mutation or immigration. Geneologies are created by sampling from a Fisher-Wright population, which has a constant number of individuals that randomly mate (Beerli 1998). There are generally many possible genealogies to explore that are consistent with the present distribution of alleles in a population. Beerli and Felsenstein's (1999) approach and program, MIGRATE (Beerli 2003), used Markov chain sampling methods to search the genealogical space for the genealogy with the maximum likelihood given the data.

MIGRATE avoids the assumptions of equal migration and N_e in the estimation of gene flow, as the program estimates these parameters themselves. From the most probable genealogy, $4N_em_{ji}$ is estimated for each population pair, where m_{ji} is the number of migrants/generation from population j to i. The program also estimates Θ ($4N_e\mu$), which reflects the capacity of a population to generate and maintain genetic variation (Paetkau and Strobeck 1994, Beerli and Felsenstein 1999), where μ is mutation rate. Increases in μ and N_e are expected to increase genetic variation in a region; immigration, out-breeding and growth in population size act to increase N_e. I solved for N_e, assuming a mutation rate range from 1×10^{-3} to 1×10^{-4} mutations per locus per generation (D. Paetkau, pers. comm.). I calculated one-way migration rates such that $M_{ji} = m_{ji}/\mu$. m_{ji} represents the actual numbers of migrants per generation, but only if one assumes a mutation rate. I present M_{ji}, which represents migrants per generation, incorporating an unknown migration rate. These M_{ji} values can be compared in a relative sense, but do not represent actual numbers of migrants.

Seven G4 processors were clustered at the Conservation Genetics Center at the University of Nevada – Reno to run MIGRATE (Beerli 2003). Each MIGRATE run took approximately ten days; four runs were performed to increase precision of the estimates of Θ and $4N_em_{ij}$, with each successive run starting with the previous run's final estimates of Θ and $4N_em_{ij}$. The first run was started with values of $4N_em$, calculated from F_{ST} (Beerli 2003). Pairwise population migration rates were estimated only between adjacent sampling regions due to processor speed and capacity and biological relevance.

Comparison of methods to evaluate gene flow

I evaluated the difference between the gene flow estimates using Wright's (1931) and Beerli and Felsenstein's (1999) approaches, due to the indications that gene flow estimates derived from F_{ST} are biased (Whitlock and McCauley 1999, Wilson *et al.* 2004). Simulations (Beerli 1998) showed that gene flow estimates from F_{ST} are biased, whereas estimate from the coalescence-method were more accurate. I calculated N_em from F_{ST} and from MIGRATE'S $4N_em_{ji}$. Because $4N_em_{ji}$ was estimated for both directions of movement between a pair of populations, I present both directions of gene flow.

Tree Building

Three phylogenetic trees were estimated using Cavalli-Sforza population chord-distance (Cavalli-Sforza and Edwards 1967) calculated with the POPULATIONS program. (Langella 2002). Cavalli-Sforza genetic distance was used as it is appropriate for hypervariable genetic markers (Takezaki and Nei 1996), and as it assumes no particular mutational model. The neighbor-joining algorithm was used to build the trees (Saitou and Nei 1987), which were drawn using TREEVIEW version 1.6.6 (http://taxonomy.zoology.gla.ac.uk/rod/treeview.html). I evaluated the extent of support for nodes in the tree from 5,000 bootstrap replicates. The first tree treated the eleven black bear sampling regions in Southeast Alaska as operational taxonomic units (OTU). Population clusters identified by STRUCTURE were used as the OTU's in a second tree. I also built a third tree with four *a priori* defined OTU's: the mainland cluster, the island cluster, the southern mainland and Yakutat.

Genetic distance between sampling regions

D_{LR}, the genotype likelihood ratio genetic distance (Paetkau *et al.* 1997), was calculated between each pair of adjacent sampling regions using the calculator at http://www2.biology.ualberta.ca/jbrzusto/Doh.php. D_{LR} is based on the expected frequencies of an individual's assignment (Paetkau *et al.* 1995) to its sampling region of origin and to the other sampling region in the pair. D_{LR} can be interpreted as the order of magnitude relative likelihood that an individual was born in a region where it was sampled compared with the other region in the pair (Paetkau *et al.* 1997). I computed D_{LR} for each pairwise comparison of sampling regions. I constructed assignment plots for each pair of sampling regions by graphing the negative log likelihood of each individual being born in the population where it was sampled, against its likelihood of being from the second population in the pair. The likelihoods of individuals sampled from the second population in the pair, being from this population versus the first population is represented in the same graphical space for comparison (*e.g.,* Belant *et al*. 2004). D_{LR} is estimated as the average graphical distance of the individuals from one population to the 45 degree line dividing this graphical space (Paetkau *et al.* 2004).

Current gene flow

Frequentist assignment test

The original conception of the assignment test by Paetkau *et al*. (1995) used the expected frequencies of an individual's multilocus genotype in each population, which were based on each population's allele frequency distribution. This method assumed Hardy-Weinberg equilibrium frequencies of genotypes at each locus; expected multi-

locus genotype frequencies were products across all loci. Individuals were assigned to populations where the probability of this multilocus genotype was the highest. Paetkau *et al.* (2004) refined the methods of Paetkau *et al.* (1995) by sampling multilocus gametes (haploid), as opposed to genotypes (diploid), to account for admixture linkage, which results from the migration process. I used GENECLASS 2 (Piry *et al.* 1999), which employs the methods in Paetkau *et al.* (2004), to assign individuals to each sampled region.

Bayesian clustering

I used the likelihood of multilocus genotypes in a given population to assign individuals to the population clusters defined by Pritchard *et al.'s* (2000) program STRUCTURE. The primary assumption of the STRUCTURE model is that there is Hardy-Weinberg and linkage equilibrium within populations; genetic clusters (*i.e.,* populations) are defined by optimizing fit to these equilibrium expectations. This Bayesian clustering method grouped individuals into populations and simultaneously calculated individual assignments to those groups, which were described by allele frequency distributions that satisfied the assumptions of Hardy-Weinberg and linkage equilibrium (Appendix III). The program inferred q, each individual's proportional membership (assignment) to each of K clusters. I allowed for admixture in STRUCTURE'S estimation procedure, and provided no initial information regarding sampling origin. The assignment approach of Paetkau *et al.* (1995) is relevant as the genetic clusters (Pritchard *et al.* 2000) may not always correspond to modern populations, and especially to wildlife management units, which are often defined geographically.

RESULTS

Genetic variation

Genotype frequencies over all loci in all black bear sampling regions in Southeast Alaska were consistent with Hardy-Weinberg equilibrium (1540 randomizations) with the exception of Yakutat, where randomizations suggested that F_{IS} was smaller than expected at the table-wide α (p = 0.00065, Table 3). Within the Prince of Wales Island population, F_{IS} values were found to be significantly high at two loci (G10L and G10X), but over all loci the F_{IS} value was significant only at the nominal α-level (p = 0.01). These two loci were not found to have significantly large F_{IS} values in any other sampling region, suggesting that large F_{IS} values do not necessarily suggest the heterozygote deficiency is a result of laboratory conditions (allelic dropout), but rather biological factors may be at work in the Prince of Wales population.

Nei's expected heterozygosity (H_E) in the sampling regions ranged from 0.55 (Kuiu Island) to 0.79 (southern mainland; Table 3). Within the islands of the Alexander Archipelago, average H_E for the black bear populations ranged from 0.55 (Kuiu Island) to 0.68 (Kupreanof Island). H_E for the mainland sampling regions ranged from 0.62 (Yakutat) to 0.79 (southern mainland), and the mean was higher (0.74 ± 0.03) than it was for island populations (0.62 ± 0.03; p = 0.005, 1-tailed t-test), as expected.

Maximum likelihood estimates of Θ ($4N_e\mu$) ranged from 0.23 on Kuiu Island and in the southern mainland (95% CI: 0.21 – 0.25, Kuiu; 0.18 – 0.30, southern mainland) to 0.63 on the Chilkat Peninsula (0.57 – 0.71, Table 4). Θ was generally higher for mainland (0.23 – 0.63) than island sampling regions (0.23 – 0.33; p = 0.06, 1-tailed t-test), as

expected. Estimates of N_e ranged from 79 – 794 (Yakutat) to 159 – 1585 (Chilkats) black bears (Table 4) assuming mutation rates of 10^{-4} – 10^{-3}.

The black bear populations of the Yakutat region, Kupreanof, Mitkof, Prince of Wales and Revillagigedo islands showed no evidence of bottlenecks using the M-ratio test; average M-ratios were 1.0 for all sampling regions. However, a significant population bottleneck was detected for the Kuiu Island black bear population. Kuiu Island had an M-ratio of 0.70, and the significance value ranged from $p = 0.001$ to 0.003, depending on the specific parameters of the simulations.

Genetic differentiation

Pairwise F_{ST} values ($n = 55$) were calculated between all pairs of 11 black bear sampling regions in Southeast Alaska (Table 5); values ranged from 0.007 (Mitkof Island – Kupreanof Island) to 0.292 (Yakutat – Kuiu Island). In subsequent gene flow analyses, I treated Mitkof and Kupreanof islands as a single population of bears. All other pairwise comparisons were significant (G-test) at the Bonferroni-corrected α value (0.0009; $n = 28$) or nominal level (0.05; $n = 7$), except between the Chilkat Peninsula and Skagway ($F_{ST} = 0.02$; $p = 0.17$). I did not test for significance ($n = 19$) for pairwise comparisons involving Mitkof Island or Yakutat due to low sample size. However, pairwise F_{ST} values between Yakutat and other sampling regions in Southeast Alaska were very high (0.12 to 0.29), suggesting significant genetic differentiation of the Yakutat region from the rest of Southeast Alaska. Pairwise F_{ST} values involving Mitkof Island were generally low, likely due to its proximity to the mainland (~ 10 – 100 m at low tide). Pairwise F_{ST} values were

higher between sampling regions that would require a salt water crossing than between sampling regions connected by land (p = 0.0007, 1-tailed t-test).

Historical gene flow

Estimates of migration rate (migrants per generation incorporating an unknown mutation rate (*i.e.,* not *actual* numbers of migrants), M_{ji}) between sampling regions were calculated from maximum-likelihood estimates of $4N_em_{ji}$ and Θ_i, obtained from the fourth run (Beerli 2003) of MIGRATE (Table 6). The estimates of M_{ji} were high between adjacent mainland sampling regions (average pairwise M_{ji} = 9.2 ± 4.9 (SD)), ranging from 1.6 from the southern to the central mainland to 18.2 migrants/generation from Skagway to the Chilkat Peninsula. In comparison, migration rate was lower between adjacent sampling regions that were separated by salt water (average pairwise M_{ji} = 5.2 ± 4.6; p = 0.01, Mann-Whitney test). Migration rate between these regions ranged from 0.07 migrants per generation (Revillagigedo Island to Prince of Wales Island) to 16.1 (Kuiu Island to Kupreanof Island).

I also calculated effective numbers of migrants per generation between adjacent sampling regions from estimates of each region's average pairwise F_{ST}. These estimates of gene flow were consistently higher than those generated from maximum-likelihood estimates from MIGRATE (Figure 3).

Genetic distance, D_{LR}, ranged from 0 (Kupreanof Island – Mitkof Island) to 11 (Kuiu Island – Yakutat; Table 5). Average D_{LR} between adjacent mainland sampling regions was 2.2 ± 0.9 (SE), and between regions separated by one water crossing D_{LR} was 3.2 ± 2.5. For example, the D_{LR} between Kuiu and Prince of Wales islands was 7.0,

estimating that a bear sampled from Kuiu Island was seven orders of magnitude more likely to be from Kuiu Island than Prince of Wales Island, and vice versa (Paetkau *et al.* 1997). D_{LR} were positively associated with straight-line distance between the geographic centers of the sampling regions, for all pairwise comparisons (R^2 = 0.31, Figure 4). D_{LR} was also regressed on minimum salt water crossing distance for population pairs separated by one salt water crossing (R^2 = 0.71, Figure 5) and on geographic land distance (*i.e.,* as the bear walks) for pairs of mainland populations (R^2 = 0.40, Figure 6).

Current gene flow

Frequentist assignment test

Assignment to sampling regions of origin ranged from 95% of the individuals at Yakutat to 25% on Mitkof Island (Table 7). Assignment plots (n = 55) of genotype log likelihoods for pairs of sampling regions graphically displays the log likelihoods of each individual's assignment (Appendix IV).

Bayesian clustering

STRUCTURE identified seven population clusters of black bears in Southeast Alaska. The likelihood of the data given seven clusters, 1, was unambiguously highest compared to the likelihood for any other number of clusters (Table 8); the distribution of the probability of the data given the number of clusters was unimodal (Figure 7) and was nine orders of magnitude greater than the next most likely clustering pattern (K = 8). The seven clusters (cluster names are indicated in *italics* to distinguish them from names of sampling regions) had geographic affinities (Figures 8a, 9, Appendix IV), however

individuals within sampling regions were assigned to various clusters. The *Kuiu Complex Cluster* included individuals sampled from Kuiu Island (average proportional membership of individuals (q) sampled from Kuiu Island to the *Kuiu Complex Cluster*, q = 0.93, Table 9), Kupreanof Island (q = 0.61) and Mitkof Island (q = 0.46) islands. The black bears from the Chilkat Peninsula (q = 0.57) and Skagway (q = 0.37) grouped together in the *Northern Southeast Alaska Cluster*. Bears sampled from Revillagigedo Island were associated with the *Southern Southeast Alaska Cluster* (q = 0.86), as were bears from the southern mainland (q = 0.46). Gene pool groupings of the remaining black bears were consistent with the *a priori* sampling regions: Yakutat (q = 0.87); Juneau (q = 0.55); central mainland (q = 0.59) and Prince of Wales Island (q = 0.72). Individuals from each sampling region were assigned to other genetic clusters with probabilities ranging from 1 to 28%. For example, some individuals sampled from the Juneau and central mainland regions were also assigned to the *Yakutat Cluster* (q = 0.14, 0.28 respectively). Only 42% of the black bears in Southeast Alaska (110 of 263) could be assigned with probability >90% to any cluster (Appendix IV).

When I assumed the existence of only two genetic clusters, individuals from sampling regions north of and including the central mainland grouped together in the *Mainland Cluster* (q = 0.83 – 0.97, Table 10, Figures 8b, 10, Appendix IV). Individuals sampled from the islands contributed to the *Island Cluster* (q = 0.82 – 0.98). Animals from the southern mainland were assigned variously to the *Mainland Cluster* (q = 0.43) and *Island Cluster* (q = 0.57).

The neighbor-joining tree (Figure 11) of all sampling regions in Southeast Alaska had bootstrap values ranging from 37 – 67% (54.3 ± 10.9). The optimal tree based on the

seven clusters of black bears (Figure 12) had slightly higher bootstrap values, which ranged from 36 – 74% (60.8 ± 16.9). The third tree including the *Mainland* and *Island clusters*, the putative area of lineage convergence (southern mainland) and Yakutat had bootstrap values of 97% at both nodes (Figure 13).

DISCUSSION

Genetic variation

There was no significant departure from Hardy-Weinberg equilibrium over all loci within any black bear sampling region of Southeast Alaska, with the exception of Yakutat, suggesting that these ten sampling regions are not composites of smaller subpopulations (Figure 2). In Yakutat, F_{IS} was significantly negative. The sample from Yakutat may be in disequilibrium as Yakutat is a relatively small region (289 km^2), surrounded largely by glaciated mountain ranges (with the exception of the Alsek River corridor), and may support a relatively small, isolated black bear population. Thus, random mating in Yakutat may be more likely to produce a population out of equilibrium than a larger population. Alternatively, there could be current population admixture.

Genetic variation of black bears in Southeast Alaska was relatively high (H_E = 0.55 to 0.79) and consistent with estimates from other parts of the species' range, in which H_E varies from 0.31 in White River, Arkansas (Csiki *et al.* 2003) to 0.80 in Banff National Park, Alberta (Paetkau and Strobeck 1994) [3]. The H_E of black bear populations in Southeast Alaska is comparable to genetic variation of black bears on the coast and oceanic archipelago of British Columbia where H_E was estimated to range from 0.62 to

0.79 (Marshall and Ritland 2002). The statistically lower average H_E estimated for the islands of the Alexander Archipelago versus mainland regions probably reflects greater isolation from gene flow, however the sets of H_E estimates overlap (0.55 to 0.68 in the island populations versus 0.62 to 0.79 in mainland populations). H_E of these island black bear populations is similar to that estimated for brown bears on nearby Admiralty Island (0.63), and on Baranof-Chichagof Islands (0.50, Paetkau *et al.* 1998a), using markers from the same set of microsatellite loci. H_E for black bears on two of the Apostle Islands in Lake Superior, ≥ 2 km from nearest land, is higher (0.77, Belant *et al.* 2004), perhaps indicating a difference between oceanic and lentic water as barriers to bear movement. H_E in *Ursus* is also lower on more isolated oceanic islands. For example, H_E in black bears on Newfoundland Island, 16 km from mainland Canada, is only 0.41 (Paetkau and Strobeck 1994), and in brown bears on Kodiak Island, 35 km from the mainland, H_E is 0.27 (Paetkau *et al.* 1998a).

The lowest H_E in Southeast Alaska estimated in this study was found on Kuiu Island (0.55). The relatively low genetic variation most likely reflects the island's geographic isolation and the fact that the black bear population has undergone a bottleneck (M-ratio, 0.70, $p = 0.02$). On Prince of Wales Island, the black bear population has relatively low H_E (0.59) but no detected bottleneck. Genetic variation of the bears on Prince of Wales Island may be maintained, relative to that on Kuiu Island, through the island's size and the numerous, close and smaller islands to the west. Garza and Williamson (2001) used data from Paetkau *et al.* (1997) and detected bottlenecks for more isolated populations of bears, such as the brown bears on Kodiak Island (M-ratio, 0.69), and black bears on Newfoundland Island (M-ratio, 0.64).

The Yakutat region showed relatively low H_E (0.62) and allelic richness (an average of 1.5 to 2 alleles/locus) for a continental population of bears. Lower genetic variation in Yakutat is perhaps due to restricted gene flow as a result of the surrounding massive ice fields, the Fairweathers to the south and Malaspina glacier to the northwest. In addition, H_E is known to decrease at the edge of the species range in both black bears (in coastal Louisiana, $H_E = 0.43$, Csiki *et al.* 2003) and brown bears (Paetkau *et al.* 1998b). This is also consistent with Marshall & Ritland's (2002) data on genetic variation in black bears on the coastal fringe of British Columbia.

Estimates of theta (Θ) in all regions of Southeast Alaska (0.23 to 0.63) are similar to estimates for the Newfoundland Island black bear population (0.24 to 0.53 per locus), but lower than estimates for continental populations of black bears (1.81 to 4.69 per locus; Paetkau & Strobeck 1994). Θ for the Newfoundland Island population is low despite a census size of 3,000 to 10,000 black bears, reflecting the population's decreased capacity to maintain genetic variation due to 12,000 years of isolation from the mainland (Paetkau & Strobeck 1994). Although Kuiu and Newfoundland islands have similar estimates of Θ, Kuiu Island's census size is probably lower (3,000 bears, Chapter 1) and probably sustains its genetic variation by immigration from Kupreanof Island. Estimates of Θ for the islands and mainland regions of the coast of British Columbia are an order of magnitude greater than those estimated here for Southeast Alaska's black bear populations (Marshall and Ritland 2000). This difference may reflect different census population sizes or time since black bear colonization.

Genetic differentiation

F_{ST}

F_{ST} analyses suggest that black bears in Southeast Alaska exhibit substantial population substructure, to be expected from a region characterized by geographic insularity. All pairwise F_{ST} values involving Yakutat are high (> 0.12), indicating the region's isolation from the rest of Southeast Alaska. There is approximately 250 km of rock and ice between the Yakutat region and the sampling area on the Chilkat Peninsula, and 160 km between Yakutat and the Skagway region. The genetic differentiation of Yakutat suggests that the 3,000 to 4,500 m peaks of the Fairweather range and associated ice fields pose a significant barrier to black bear gene flow. It should be noted, however, that black bears in Yakutat may not be isolated from black bear populations in the Alsek and Tatshenshini River Valleys of British Columbia, because black bear samples from Canada were not used in this study.

With the exception of ice fields, pairwise F_{ST} values between black bear sampling regions in this study separated by land, are generally low (< 0.1), as are pairwise F_{ST} values from regions separated by rivers and bays (*e.g.,* Taku Inlet). In contrast, pairwise F_{ST} involving salt water crossings are relatively high (> 0.1). This conclusion holds with the exception of pairs of sampling regions separated by narrow channels (*e.g.,* Rocky Pass, 0.25 km at its minimum breadth between Kuiu and Kupreanof islands). Mitkof Island, which has pairwise F_{ST} values of < 0.01 with the adjacent mainland and neighboring island, is so close to the mainland that the intervening area is navigable by humans on foot during low tide. Thus, while pairwise F_{ST} values suggest that salt water is in general more of a barrier to black bear movement than mountainous land, some

narrow, sheltered areas of salt water do not appear to pose a significant barrier to movement.

The largest pairwise F_{ST} value estimated for continental populations of polar bears (*U. maritimus*) is 0.10 between Foxe Basin in Hudson Bay and the Chukchi Sea, which are separated by ~ 4,000 km (Paetkau *et al.* 1999). By comparison, 43% of the pairwise F_{ST} values (n = 55) between black bear sampling regions of Southeast Alaska were > 0.1, highlighting the effect of geographic structure and animal behavior on genetic differentiation. Waits *et al*. (2000) found significantly differentiated populations of brown bears within Scandinavia, with F_{ST} values ranging from 0.02 – 0.14. An F_{ST} of 0.14 between two Scandinavian populations connected by 180 km of land was the same level of differentiation found between black bear populations on Prince of Wales and Kupreanof Islands, which are minimally separated by 8.6 km of salt water.

Historical gene flow – gene coalescence method

Historical effective dispersal as estimated by MIGRATE between populations separated by land is only slightly higher than those separated by salt water (nine versus five migrants per generation). Again, these migration rate per generation include an unknown microsatellite mutation rate, and therefore are not actual numbers of migrants per generation. This difference is most likely minimized due to high gene flow over short salt water crossings. For example, there are 16 migrants/generation from Kuiu Island to Kupreanof Island and 11 in the opposite direction. An estimated 13 black bears per generation migrate from Prince of Wales Island to the southern mainland, and 16 from Revillagigedo Island to the southern mainland. The estimate of this latter migration rate is

likely elevated by ADF&G black bear management actions. From 1994 to 1998, ~52 urban bears were relocated to the mainland from Revillagigedo Island (D. Larson, pers. comm.).

In contrast, there is reduced gene flow across more substantial bodies of salt water. Low migration rates (< 1 migrant/generation) were estimated between Prince of Wales and Kuiu islands (1 crossing of 10.6 km), Revillagigedo and Prince of Wales islands (17.7 km), and the southern mainland and Mitkof/Kupreanof (multiple water crossings).

On the mainland there is moderate gene flow (six to eight migrants/generation) between Yakutat and the Chilkat Peninsula, in comparison with migration rates between other black bear populations separated by land. There is also movement between the Skagway and Juneau areas (10 – 11 migrants/generation), indicating that the narrow reach of coastal black bear habitat serves as a connection between the areas. In comparison, MIGRATE results suggest more significant movement (13 and 18 migrants/generation) between the Chilkat Peninsula and the Skagway-Haines area, indicating the Davidson glacier area and the Chilkat Range are not significant barriers for bears. In contrast, no physical barrier exists between the central and southern mainland sampling regions; the boundary was arbitrarily set at the Cleveland Peninsula. Yet, pairwise gene flow estimates between the southern and central mainland are relatively low – one and four migrants/generation for the two directions. These low historical nuclear gene flow estimates between the southern and central mainland likely maintain the genetic signature of the two mtDNA lineages that occur in either area; this region is

likely the geographic interface of the two ancient lineages (Stone and Cook 2000, see below).

The direct comparison between N_em estimates derived from F_{ST} and estimates produced from MIGRATE in this study shows that F_{ST} consistently generated higher estimates of gene flow (Figure 3). These differing estimates likely result from the differing assumptions of the derivation of the estimates; both methods contain assumptions that are likely violated in the field. For example, the coalescence-based approach, among other assumptions, assumes that population sizes do not fluctuate and mutation rates are equal among loci. However, MIGRATE provides data that address key assumptions of the derivation of gene flow from F_{ST}: equal effective population sizes and symmetrical migration. One mechanism driving the tendency of F_{ST} to predict higher levels of gene flow than MIGRATE may be the violation of these assumptions. Asymmetries in migration rates between sampling regions are apparent (95% CI do not overlap) in all pairwise comparisons (n = 14) of adjacent sampling regions except between Kuiu and Prince of Wales islands. For example, migration from the central mainland to Mitkof/Kupreanof is estimated to be six times greater than in the opposite direction. Asymmetrical migration rates might be due to local tidal patterns, which could influence the relative success of dispersal in different directions, or differences in the ultimate ecological factors instigating dispersal behavior. For instance, Kuiu Island, which receives five fewer migrants per generation from Kupreanof Island than travel in the opposite direction, has a higher bear density than Kupreanof Island and may provide a source of immigrants to the less productive Kupreanof.

Historical gene flow – genetic distance

D_{LR}, the genetic distance measure associated with Paetkau *et al*.'s (1997) assignment test, suggests that salt water passages and expansive ice fields (≥ 150 km) provide the most significant barriers to gene flow. According to Paetkau *et al.* (1998) the D_{LR} of 5.28 between brown bear populations on Baranof/Chichagof and Admiralty islands implies "very limited if not absent" gene flow across the 7 km of Chatham Strait. I estimated that there is also very limited gene flow between Prince of Wales and Kuiu islands *(*D_{LR} = 7.1) and Revillagigedo and Prince of Wales Islands (5.7) which are separated by distances of 10.6 (Sumner Strait) and 17.7 km (Clarence Strait), respectively. Even the central mainland and Mitkof Island, which are separated by roughly 100 m at low tide by the aptly named Dry Strait, have a D_{LR} of 2.2, suggesting that an animal sampled on the central mainland is over two orders of magnitude more likely to be from the mainland than from Mitkof Island.

Minimum salt water crossing distance among sampling regions separated by a single water crossing explains a substantial proportion of variation in genetic distance (71%). Additional genetic variation may be explained by time since land connections were sundered between now insular populations.

Linear regression suggests that the variation in genetic distance between mainland populations is not explained well (31%) by geographic land distance, indicating that the intervening bays and narrow coastal fringes may disrupt the pattern of isolation-by-distance that would occur across a landscape, homogenous to migration. It is likely that in addition to geographic distance, either differential dispersal success or ecological factors,

both of which could produce asymmetrical migration, may contribute to variation in genetic distance.

Current gene flow

Both the maximum-likelihood and the F_{ST} estimates of population differentiation provide indirect measures of gene flow, integrated over the time since black bears recolonized Southeast Alaska, with diminishing sensitivity to increasingly older events. Assignment tests are individually based estimates of dispersal in the current generation. The assignments of individuals to the different sampling regions in Southeast Alaska suggest that there is contemporary bear movement across glaciers, mountains, narrow strips of habitat along the coastal fringe, bays, rivers and salt water passages. Three regions – Skagway, the southern mainland and Mitkof Island – appear not to be genetically isolated as fewer than half of the individuals sampled there were assigned back to these regions. In all other sampling regions the majority of black bears were assigned to the regions in which they were sampled, although some current movement was also detected among these more isolated regions.

Bayesian clustering

By considering the sampling regions as populations, it is only possible to determine what the migration rate is over the specific obstacles to movement (*e.g.*, Taku Inlet, Wrangell Narrows) that separate the *a priori* defined populations. In contrast, the Bayesian clustering approach (Pritchard *et al.* 2000) is designed to reveal the location of the actual barriers to movement, which may not be obvious to the researcher. Results

from the STRUCTURE analysis suggested that there are seven clusters, or gene pools, of black bears in Southeast Alaska (Figure 9).

Some clusters are bounded by obvious geographic features. For example, the well supported *Yakutat Cluster* does not extend beyond the Fairweather range to the south. This suggests that the Fairweather range with peaks of 3,000 to 4,500 m and expansive ice fields, is a barrier to bear movement. The *Kuiu Complex Cluster* is geographically bounded by Sumner Strait to the south and Frederick Sound to the north. One hundred percent of black bears from Kuiu Island were assigned to the *Kuiu Complex Cluster*, and 90% of the bears were assigned with high confidence ($q > 0.9$). Not a single bear on Kuiu Island, separated from Kupreanof Island by only 0.25 km of an inland passage, was assigned to another cluster. The inside waters of Rocky Pass and the Wrangell Narrows between Kuiu and Kupreanof islands and Kupreanof and Mitkof islands do not serve as significant barriers, most likely as they are not characterized by heavy currents or rough water. Similarly, only one bear on Revillagigedo Island was not assigned to the *Southern Southeast Cluster*, this not is surprising given the short water crossing distance between Revillagigedo and the mainland of 0.8 km.

Individuals from the other sampling regions were not assigned in great proportion to the cluster of their geographic home, but were assigned to multiple clusters, indicating the presence of ongoing population admixture in these geographic regions. For example, only 70% of the individuals sampled from the Chilkat Peninsula were assigned to the *Northern Southeast Alaska Cluster*. Similarly, 71% of bears in the Juneau region were assigned to the *Juneau Cluster*, and 74% of the central mainland bears were assigned to the *Central Mainland Cluster*. In Skagway, only 44% of individuals were assigned to the

Northern Southeast Alaska Cluster (q = 0.37), yet the average proportional membership for Skagway bears to the *Yakutat Cluster* was 28%. The mainland clusters (*Northern Southeast Alaska, Juneau* and *Central Mainland*) have identifiable geographic centers, but their indistinct geographic edges suggest a degree of black bear movement along the coast of Southeast Alaska. The narrow beach fringes and mountainous topography of the coastal mainland habitat mitigates, yet does not prevent movement of black bears.

Implications for the geographical interface of the two mitochondrial lineages

The nuclear DNA data suggest the black bear population in Southeast Alaska is characterized by a modest degree of movement throughout the archipelago, with a high degree of genetic similarity within some areas (Yakutat, Kuiu Island and Revillagigedo Island, Figure 9). However, despite some current mixing, the existence of the two ancient lineages of black bears initially recognized with mtDNA data (Byun *et al.*, 1997, 1999, Dembowski *et al*. 1999, Wooding and Ward 1997, Stone and Cook 2000) is still evident in the more rapidly evolving microsatellites of the nuclear genome. When STRUCTURE was constrained to assign black bears to two clusters (Figure 10), the average individual proportional membership (q) to one cluster, for individuals from the central mainland northward (n = 123), ranged between 0.83 and 0.97. Individuals from the islands and the mainland south of the Cleveland Peninsula (n = 139), were assigned to the other cluster with average q ranging from 0.82 – 0.98. This stark division is geographically concordant with the separation between the mtDNA lineages of black bears found by Stone and Cook (2000) in Southeast Alaska.

Stone and Cook (2000) analyzed samples of black bears from Southeast Alaska (eight sequences of cytochrome b and 43 samples used in an RFLP analysis), and found that bears from the island populations and the southern mainland belonged to the coastal mtDNA clade, whereas animals sampled north of Windham Bay (central mainland, Figure 2) were grouped in the continental mtDNA clade. The most northerly extent of continuous assignment of individuals in the present nuclear DNA study to the mainland cluster also occurs at Windham Bay. Interestingly, there was also a single animal from the Chilkat Peninsula in the present study that was assigned to the island cluster and a single animal sampled in the Chilkat Peninsula by Stone and Cook (2000) was assigned to the coastal mtDNA clade, indicating some northward of the coastal clade.

In this study, 17% of the individuals from the central mainland were assigned to the *Island Cluster*, and 83% to the *Mainland Cluster*. In the southern mainland nearly equal proportions of animals were assigned to the *Mainland* and *Island Clusters*. The presence of the *Island Cluster* on the southern mainland is most likely the result of the movement of animals for management, as there is no evidence of the mainland cluster on Revillagigedo Island, 0.8 km from the southern mainland. There is also some evidence of mixing of the island and mainland clusters on Prince of Wales and Mitkof islands, as only 82% of the individuals on these islands belong to the *Island Cluster*. Thus, while there is a pattern of bimodal clustering which for the most part reflects the geographic delineation of the mtDNA data, this study suggests that the region of mixing between the lineages exists between the central mainland (including Mitkof Island) and southern mainland, and on Prince of Wales Island. It is evident in this study, that the nuclear data retains the signature of secondary contact between ancient lineages, suggesting that there has not

been enough gene flow in the area since the time of recolonization to geographically homogenize the population with respect to the two lineages.

When individual black bears are assigned to two nuclear genetic clusters, it is evident that more animals sampled in southern Southeast Alaska are assigned to the mainland cluster than the other way around (Figure 10). If the mainland and island nuclear DNA clusters are comparable to the continental and coastal mtDNA lineages, respectively, as suggested by their geographical congruence, this suggests a general expansion southward of the continental mtDNA black bear clade.

Results from MIGRATE, which reflect historical patterns of gene flow, also support the contention of a predominant southward flow of black bears. Estimated asymmetries of migration rates between adjacent mainland sampling regions suggest more southward dispersal than northward: there is greater migration southward from the Skagway area to the Juneau region (12 vs. ten migrants/generation in the opposite direction), Juneau to the central mainland (12 vs. six migrants/generation), and from the central mainland to both the southern mainland (four vs. two migrants/generation) and Mitkof/Kupreanof (six vs. 0.8 migrants/generation). All of these differences are statistically significant (95% confidence intervals do not overlap in any of these comparisons), the biological meaning of a difference in two to six migrants/generation between regions is unknown. However, that the same direction of asymmetrical movement is reflected in these four pairwise comparisons is suggestive of a trend.

Prince of Wales Island

Black bears from Prince of Wales Island were assigned to six of the seven Southeast Alaskan population clusters identified by STRUCTURE, highlighting the genetic diversity maintained on the island. Prince of Wales Island individuals were assigned to clusters that genetically characterize areas as far north as Yakutat, although the ambiguity of these assignments was relative high due to the island being in a zone of admixture. In addition, Prince of Wales black bears were assigned to both the *Island* (82%) and *Mainland Clusters* (18%). The maintenance of high black bear genetic diversity on Prince of Wales could be due to a combination of the island's large size, high rates of successful current and/or past dispersal, or Prince of Wales could be a source of genetic diversity seeding the rest of Southeast Alaska. There is a modest amount of current dispersal to and from Prince of Wales Island, as indicated by the frequentist assignment test. However, other less geographically isolated islands maintain higher genetic isolation than does Prince of Wales Island. For example, Revillagigedo Island is separated from the mainland by only 0.8 km, but is more isolated genetically than Prince of Wales; 87% of animals sampled from Revillagigedo Island were assigned to Revillagigedo whereas only 68% of bears were assigned back to Prince of Wales. Kuiu Island is separated from the mainland by two salt water crossing steps of 0.25 and 0.1 km, and 87% of Kuiu individuals were assigned to Kuiu Island. Only 75% of the bears from Prince of Wales Island were assigned to the *Prince of Wales Cluster* (66% of the individuals with $q >$ 0.9.), despite the island being 6 km from the mainland and approximately 11 km and 9 km from Kuiu and Kupreanof islands, respectively. However, via multiple crossings (6 to 7) of 1.5 to 3.5 km, a bear could cross from the northeast corner of Prince of Wales Island

using several small islands to reach Zarembo Island and eventually the mainland; this stepping-stone route may allow for increased gene flow for Prince of Wales Island. Thus, Prince of Wales Island is characterized by probably greater geographic isolation but less genetic isolation. The current high level of genetic diversity may have resulted from Prince of Wales Island being less isolated from the mainland during periods of lower sea level between 19,000 and 10,000 ybp. Alternatively or concomitantly, as Prince of Wales Island includes the range of black bear genetic variation found in the entirety of Southeast Alaska, the island may have been an origin (Cann *et al.* 1987) of the modern Southeast Alaskan black bears.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Salt water provides a significant barrier to dispersal for black bears, as indicated by higher D_{LR} and F_{ST} values between areas separated by salt water compared with greater distances over land in the absence of terrestrial dispersal barriers. Salt water is more of a barrier to movement and isolates populations to a greater degree than would be predicted by a pure isolation-by-distance model. However, distance across salt water cannot fully predict the degree of isolation. Ecological factors, tidal patterns and the protected nature of inside passages may all contribute to the extent of gene flow and to cryptic population boundaries. Large expanses of ice (≥ 150 km) also effectively isolate black bear populations, whereas expansive salt water bays and major river systems, such as the Taku Inlet, do not. However, the mosaic of narrow beach fringe, steep mountains,

smaller glaciers and intervening bays does shape gene flow patterns for black bears on the mainland of Southeast Alaska.

If wildlife management units are based on populations that differ significantly in allele frequencies, all Southeast Alaska regions sampled in this study would be considered separate black bear management units, except for the grouping of Chilkat with Skagway bears into one management unit, and Kupreanof with Mitkof islands' bears. However, additional genetic information about population bottlenecks, effective population size and current movement patterns can also be profitably applied to wildlife management. For example, the dynamic relationship within the islands of the Kuiu complex suggests that Kuiu Island may act as a source, and thus black bear population dynamics on Kupreanof Island are likely controlled to a degree by those on Kuiu Island. In addition, although two genetic clusters are apparent and distinguish the Juneau and central mainland bears, movement does occur across the Taku Inlet, and likely contributes to high genetic variation within both areas.

In addition, black bear management may benefit from recognizing that Southeast Alaska is the area of convergence between the two divergent mitochondrial lineages of black bears. Despite a degree of modern gene flow between areas in which these lineages occur, the island populations still represent the northern most extent of the coastal lineage of black bears, which began diverging from the continental lineage some 1.8 million years ago.

FOOTNOTES

[1] all dates are calibrated (calendar) years before present (ybp). Calibrated dates are directly from reference, or converted from radiocarbon dates using the INTCAL98 data set from Stuiver *et al.* 1998.

[2] I use the terms *movement*, *gene flow*, *migration* and *dispersal* interchangeably. I use these terms to indicate average historic effective (bears survive and reproduce) movement from one region to another; I do not use the term migration in a traditional ecological context, *e.g.,* annual migration of geese.

[3] Throughout the discussion, I will compare estimates of H_E, Θ and D_{LR} of black bear populations in this study to other populations of *Ursus.* These measures are dependent on the variability of certain microsatellite loci. The values may be comparable if markers from the same set of microsatellite loci are used, and if we assume that the loci in the set mutate at the same rate and that they mutate at the same rate across species. However, this is unknown. These loci were developed for black bears, presumably to maximize variability in black bear populations, and thus the comparisons of genetic measures of variation may be less valid across species.

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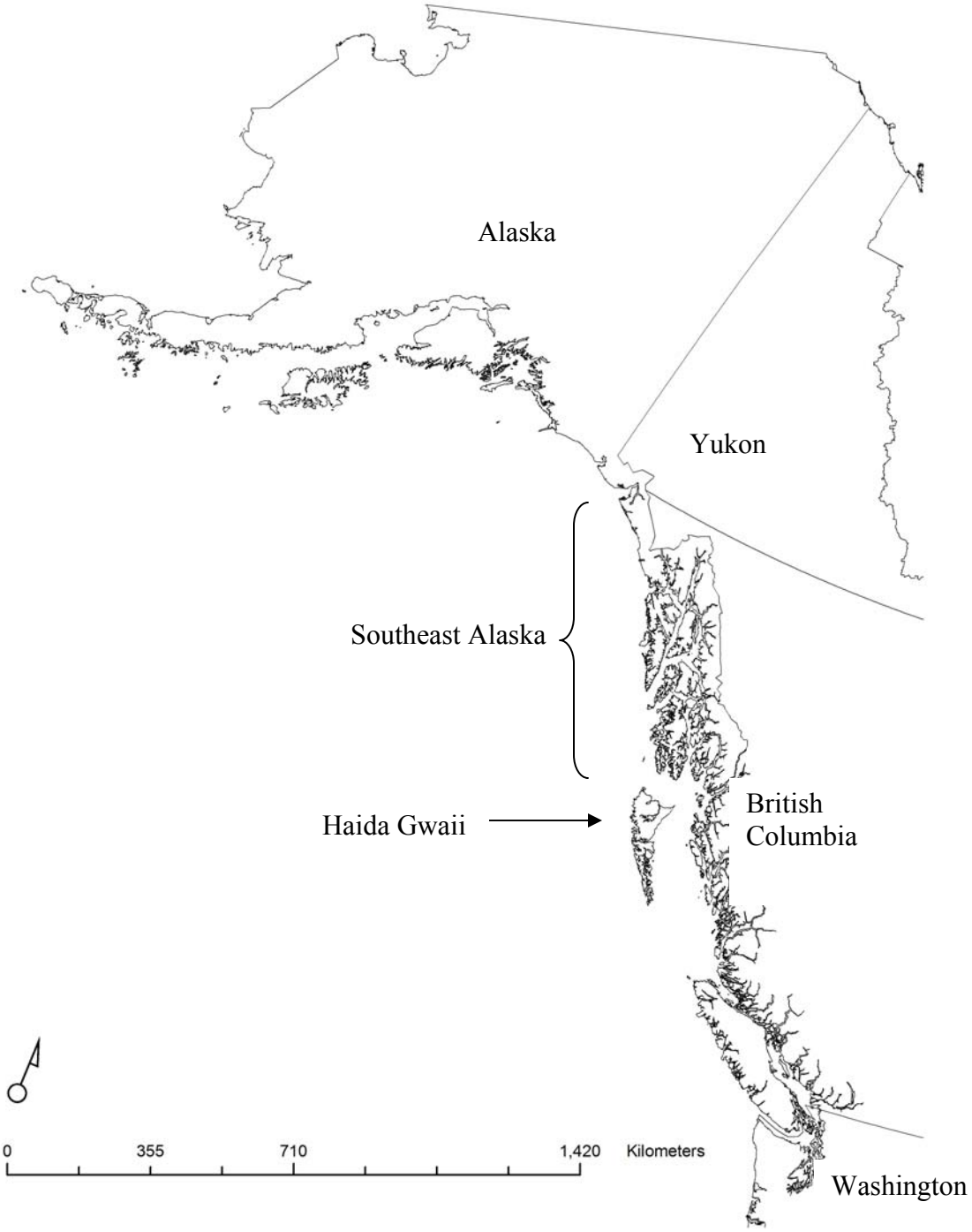

Figure 1. The North Pacific coast of North America.

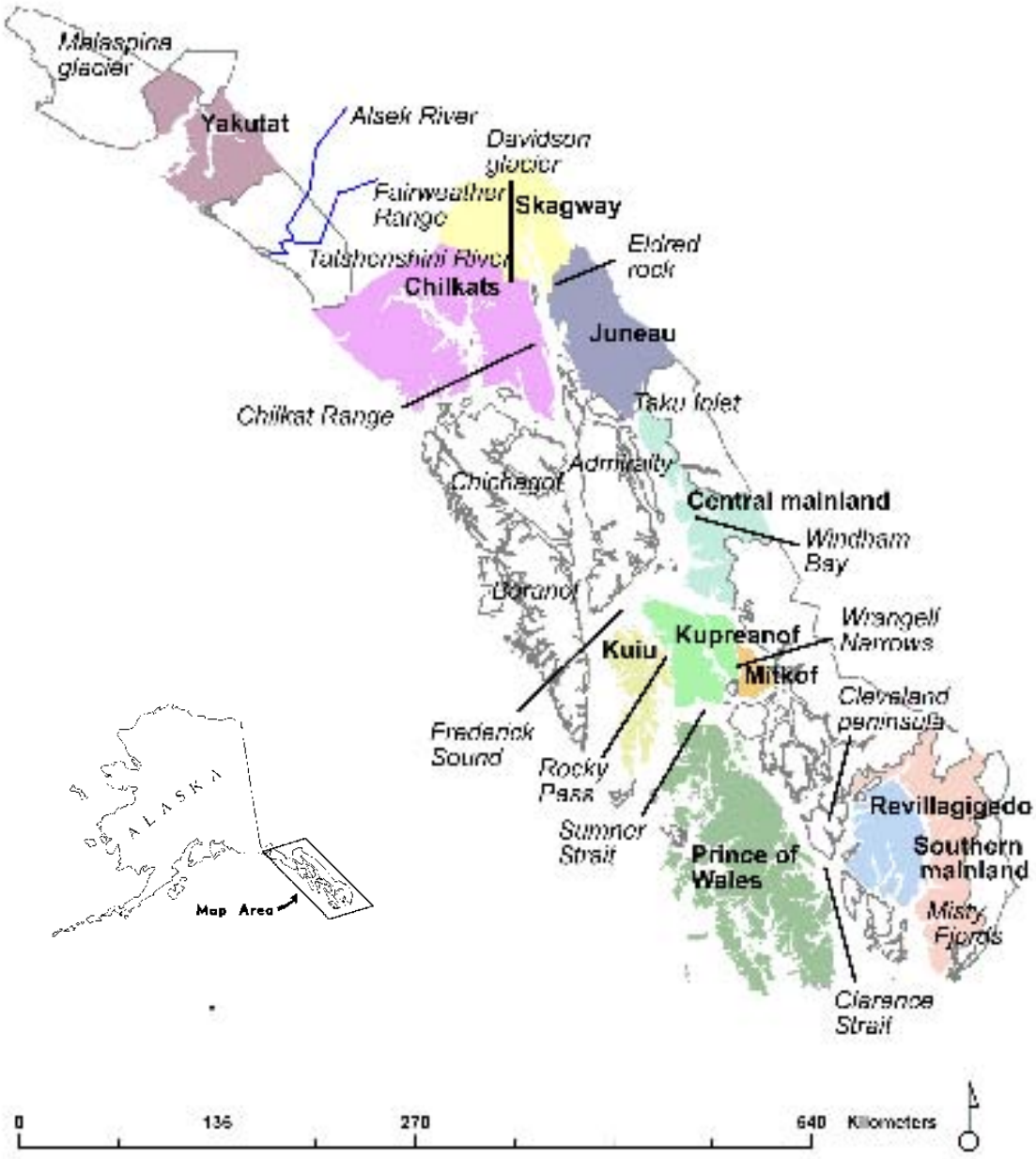

Figure 2. Black bear sampling regions (bold) and place names in Southeast Alaska.

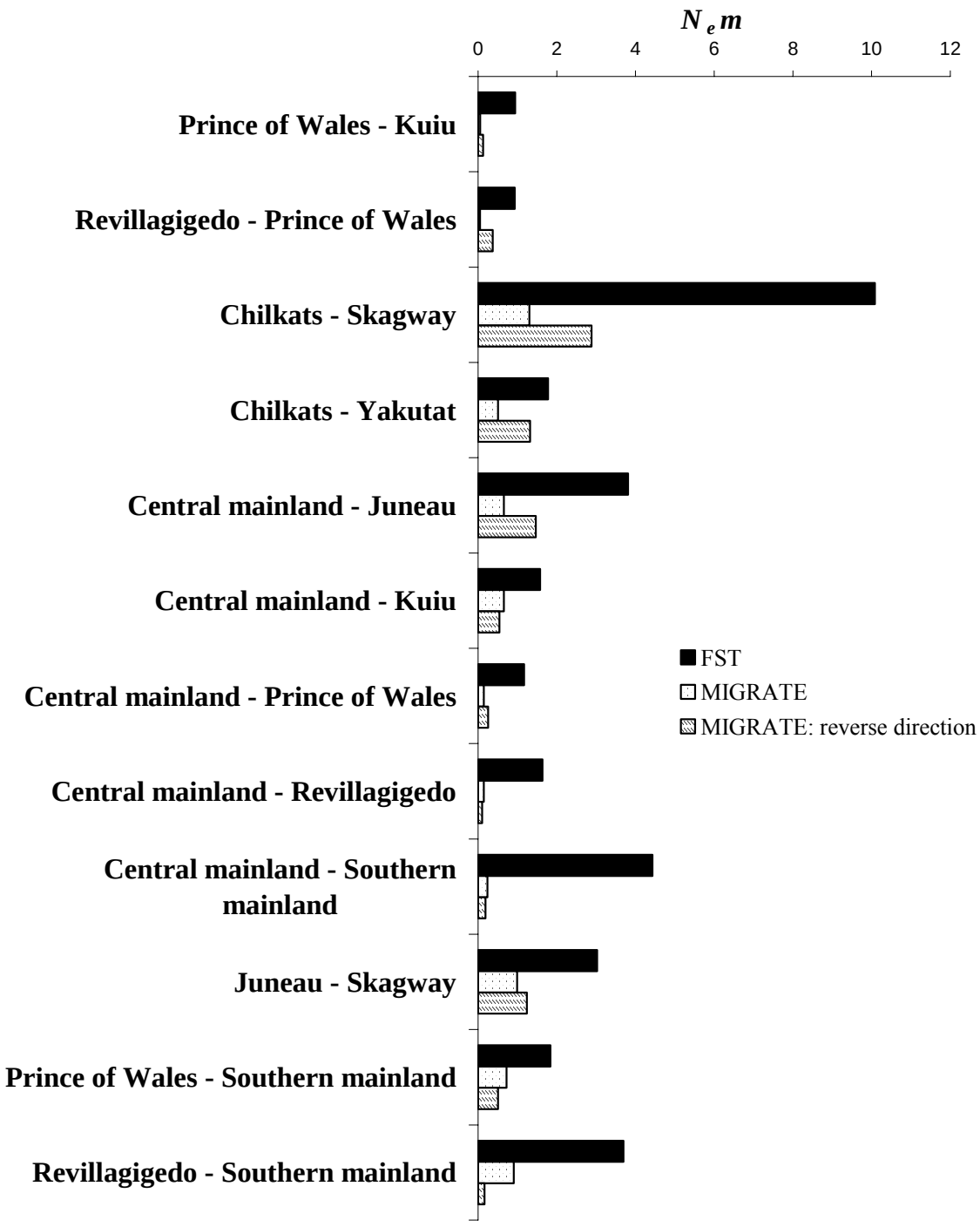

Figure 3. Comparison of F_{ST}-derived and maximum-likelihood coalescence-derived (MIGRATE) estimates of the effective number of migrants/generation (N_em) between a subset of the sampling regions. The gene flow estimate derived from F_{ST} is a pair-wise value; the estimates derived from MIGRATE are unidirectional.

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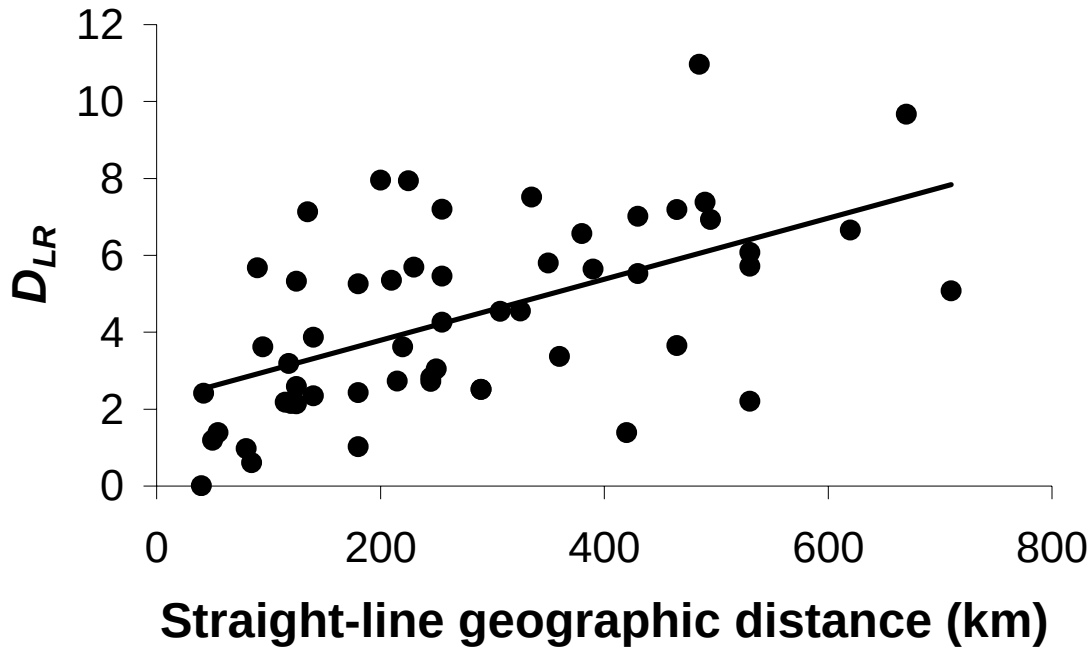


Figure 4. Genetic distance (D_{LR}) regressed on straight-line geographic distance between the geographic centers of sampling regions: y = 0.008x + 2.2; R^2 = 0.31, p = 0.000.

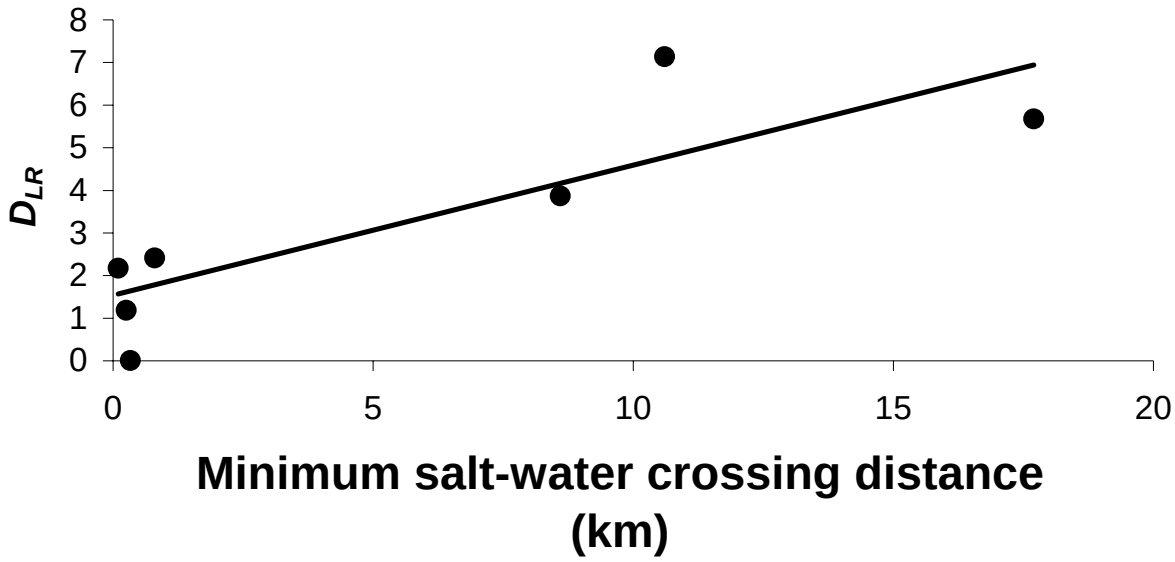


Figure 5. Genetic distance (D_{LR}) regressed on the minimum salt water crossing distance between pairs of sampling regions, separated by one crossing: y = 0.31x + 1.5; R^2 = 0.71, p = 0.017.

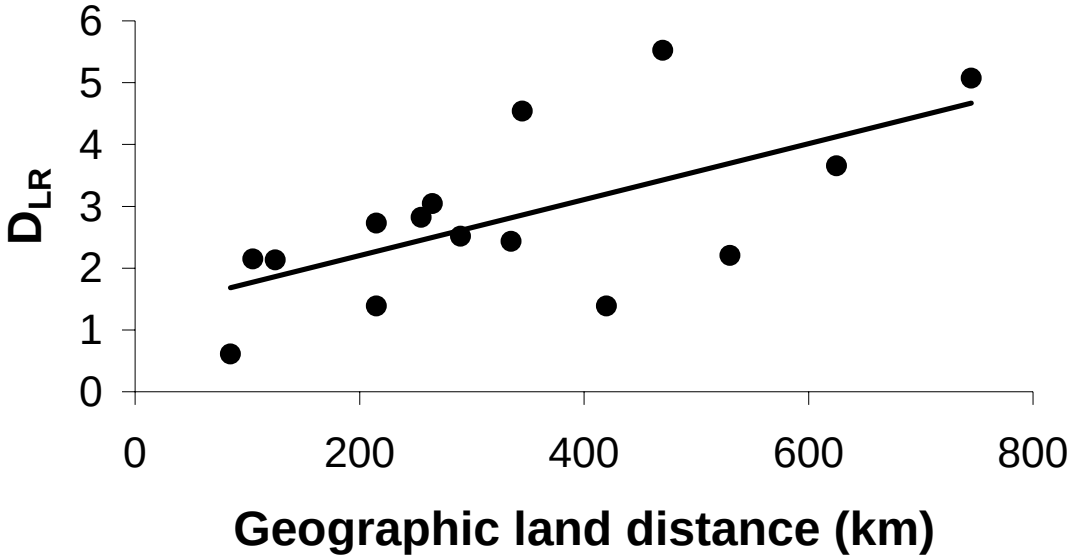


Figure 6. Genetic distance (D_{LR}) regressed on geographic land (not straight-line) distance between centers of mainland sampling regions. y = 0.0045x + 1.30; R^2 = 0.4.

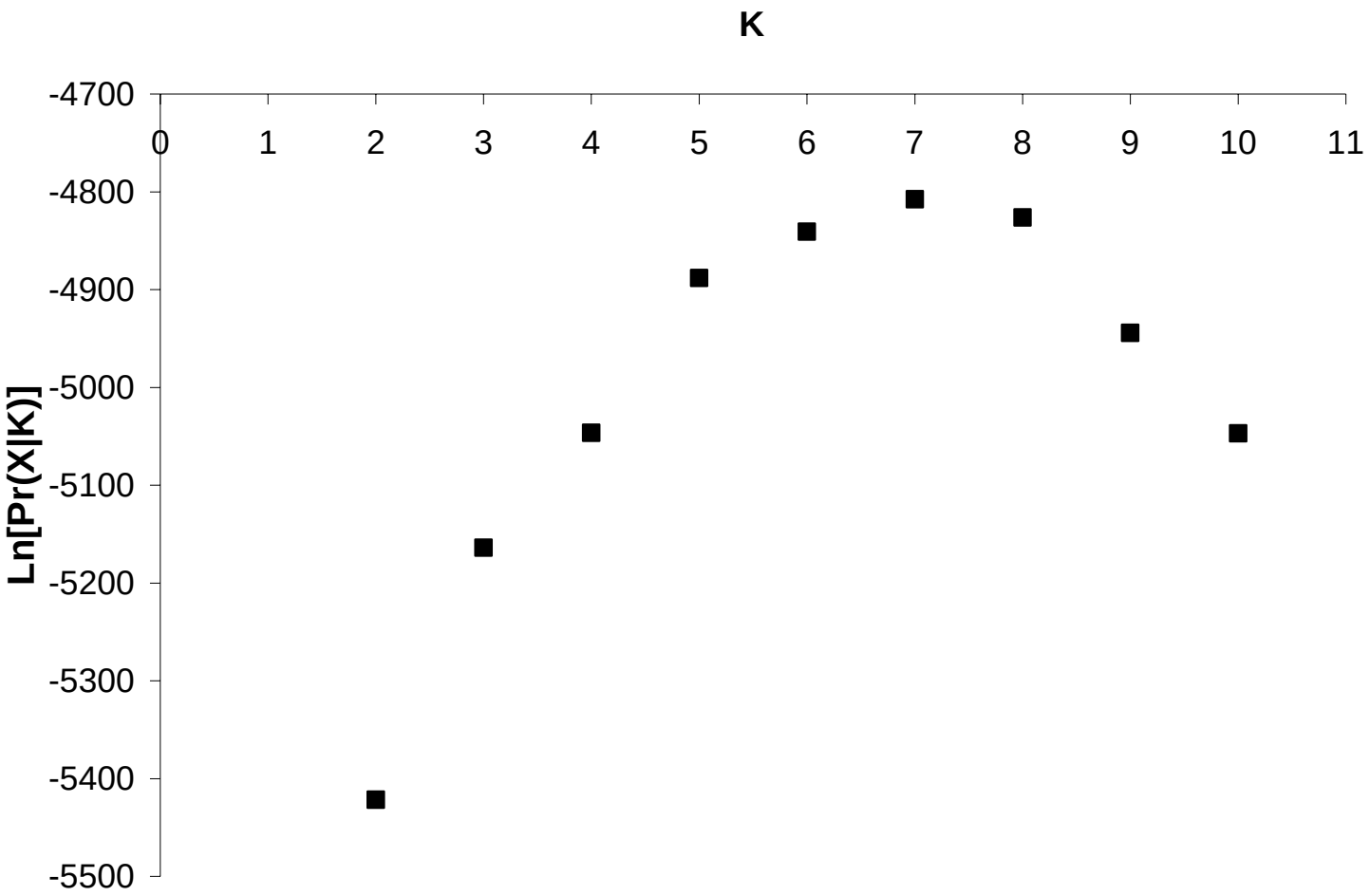
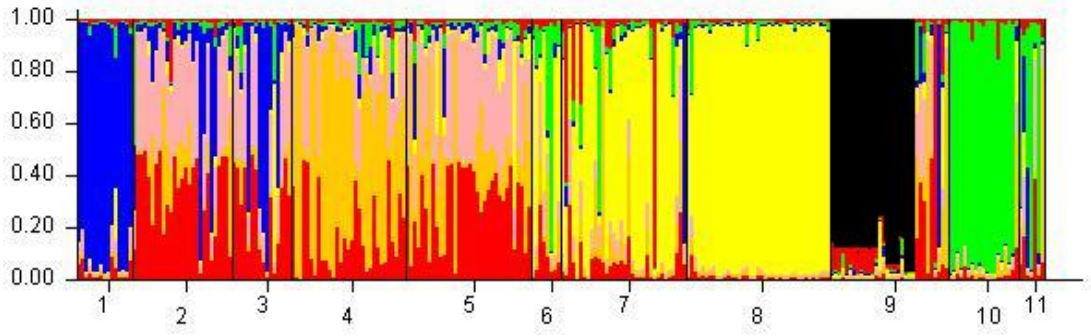
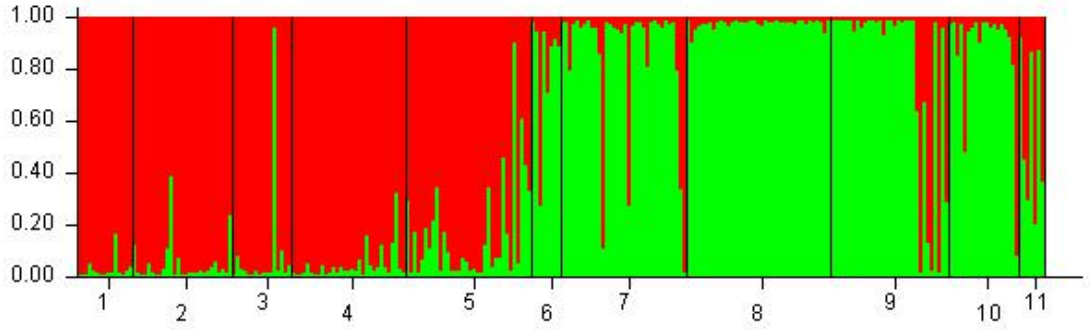


Figure 7. The negative natural log of the probability of the data, given the number of population clusters (K) chosen for Southeast Alaskan black bears.



a.



b.

Figure 8. STRUCTURE plot for a. seven clusters (represented by different colors) and b. two clusters of black bears in Southeast Alaska. Individual samples are organized (each represented by a single vertical line) on the X-axis according to sampling region: 1 – Yakutat; 2 – Chilkat Peninsula; 3 – Skagway; 4 – Juneau; 5 – Central Mainland; 6 – Mitkof; 7– Kupreanof; 8 – Kuiu; 9 – Prince of Wales; 10 – Revillagigedo; 11 – Southern Mainland. The Y-axis is probability of an individual assigning to each of the seven clusters. The colors correspond to the following clusters. In 8a: blue, *Yakutat Cluster*; orange, *Juneau Cluster*; pink, *Central Southeast Cluster*; red, *Northern Southeast Cluster*; yellow, *Kuiu Complex Cluster*; black, *Prince of Wales Cluster* and green, *Southern Southeast Cluster*. In 8b: red, *Continental Cluster* and green, *Island Cluster*.

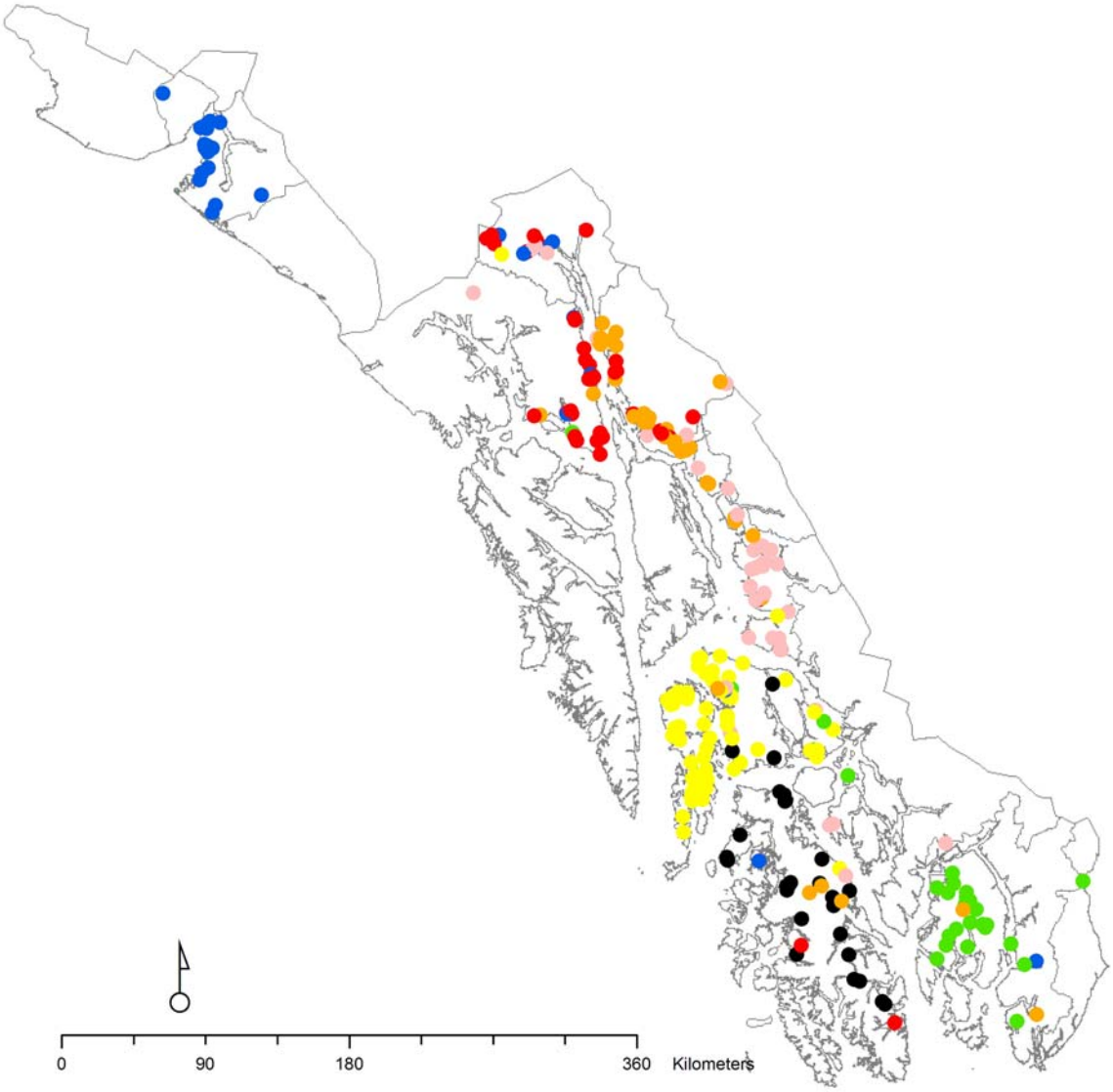


Figure 9. Assignment of individual black bears to the seven genetic clusters in Southeast Alaska, identified by STRUCTURE. Clusters are represented by different colors; dots indicate where the bears were sampled. Colors represent: blue, *Yakutat Cluster*; orange, *Juneau Cluster*; pink, *Central Southeast Cluster*; red, *Northern Southeast Cluster*; yellow, *Kuiu Complex Cluster*; black, *Prince of Wales Cluster* and green, *Southern Southeast Cluster*..

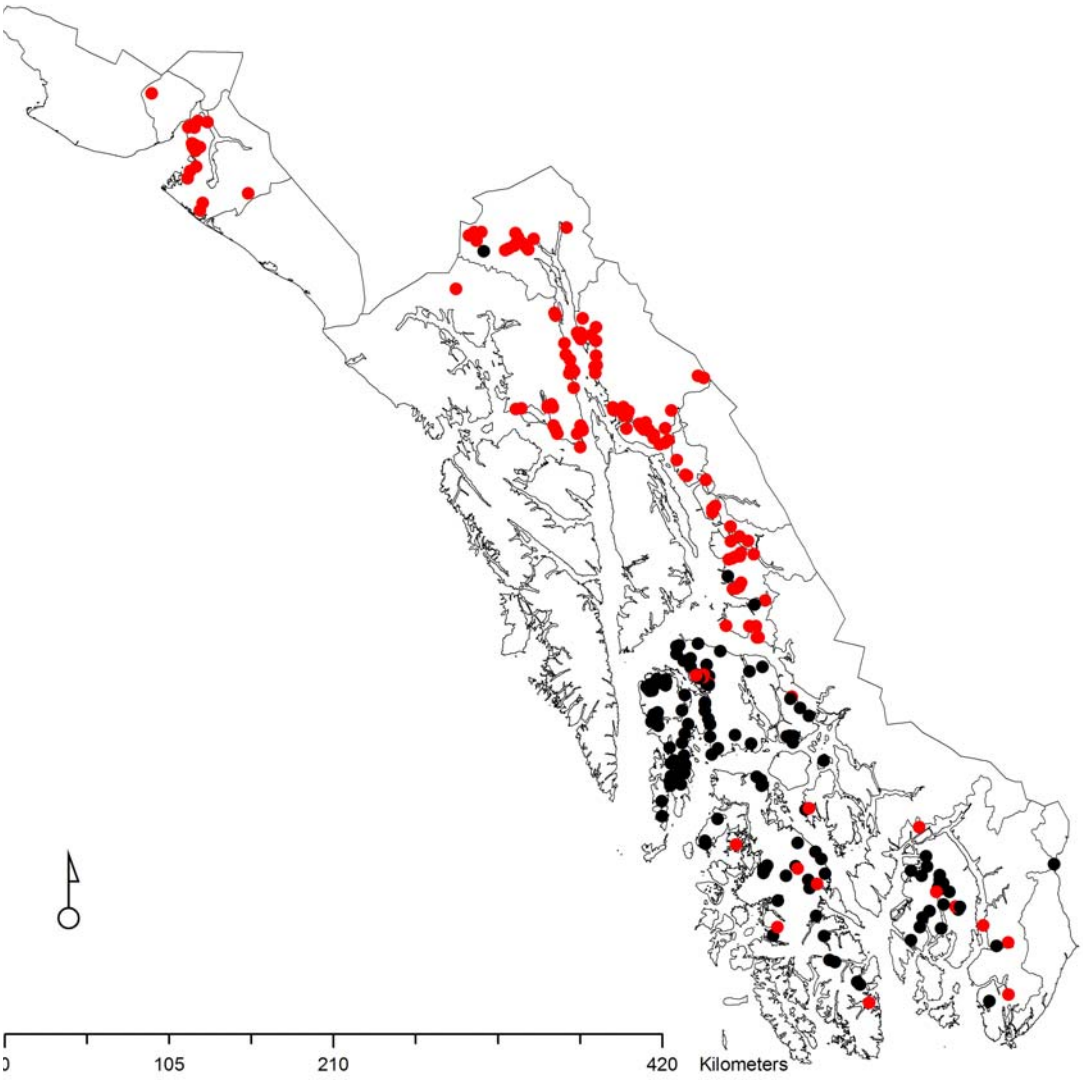


Figure 10. Assignment of individual black bears to the *Island* (black dots) and *Mainland* (red dots) *Clusters* in Southeast Alaska, identified by STRUCTURE.

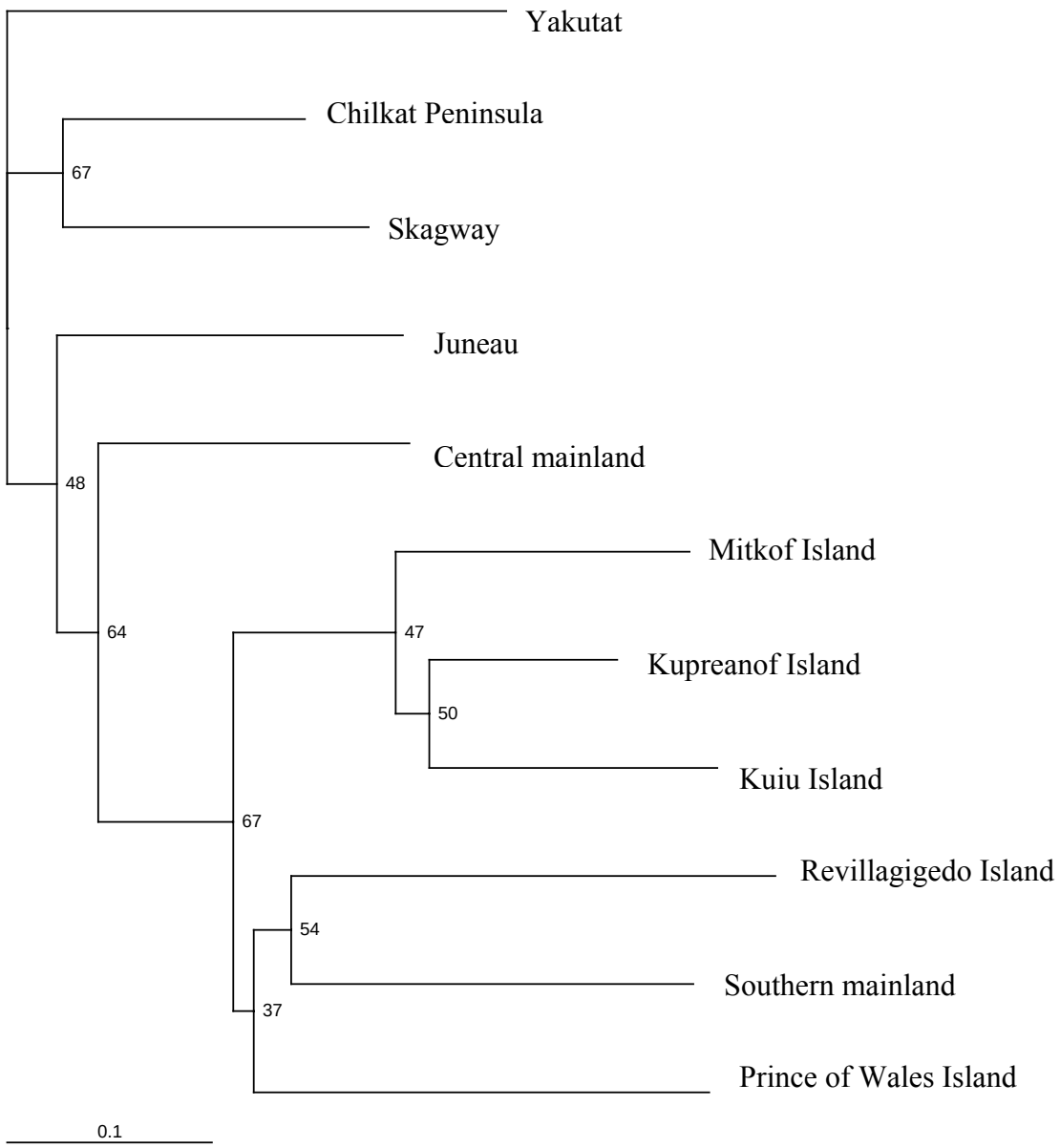


Figure 11. Rooted (Yakutat) neighbor-joining tree of Southeast Alaskan black bear sampling regions based on Cavalli-Sforza distance (scale bar shown). Bootstrap values are given at the node (5,000 replicates).

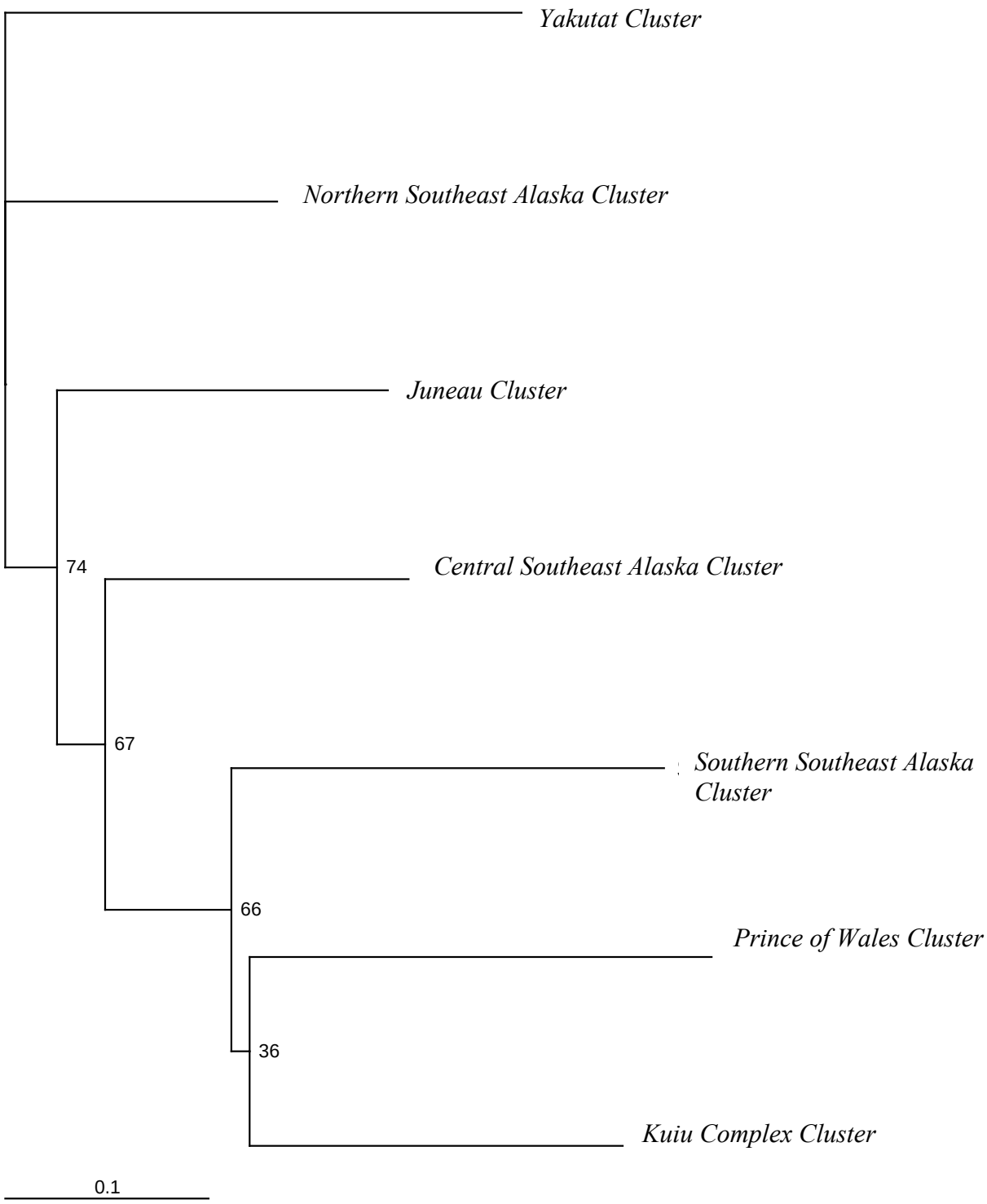


Figure 12. Rooted (Yakutat) neighbor-joining tree based on Cavalli-Sforza distance (scale bar shown) of genetic clusters of Southeast Alaska. Bootstrap values are given at the node (5,000 replicates).

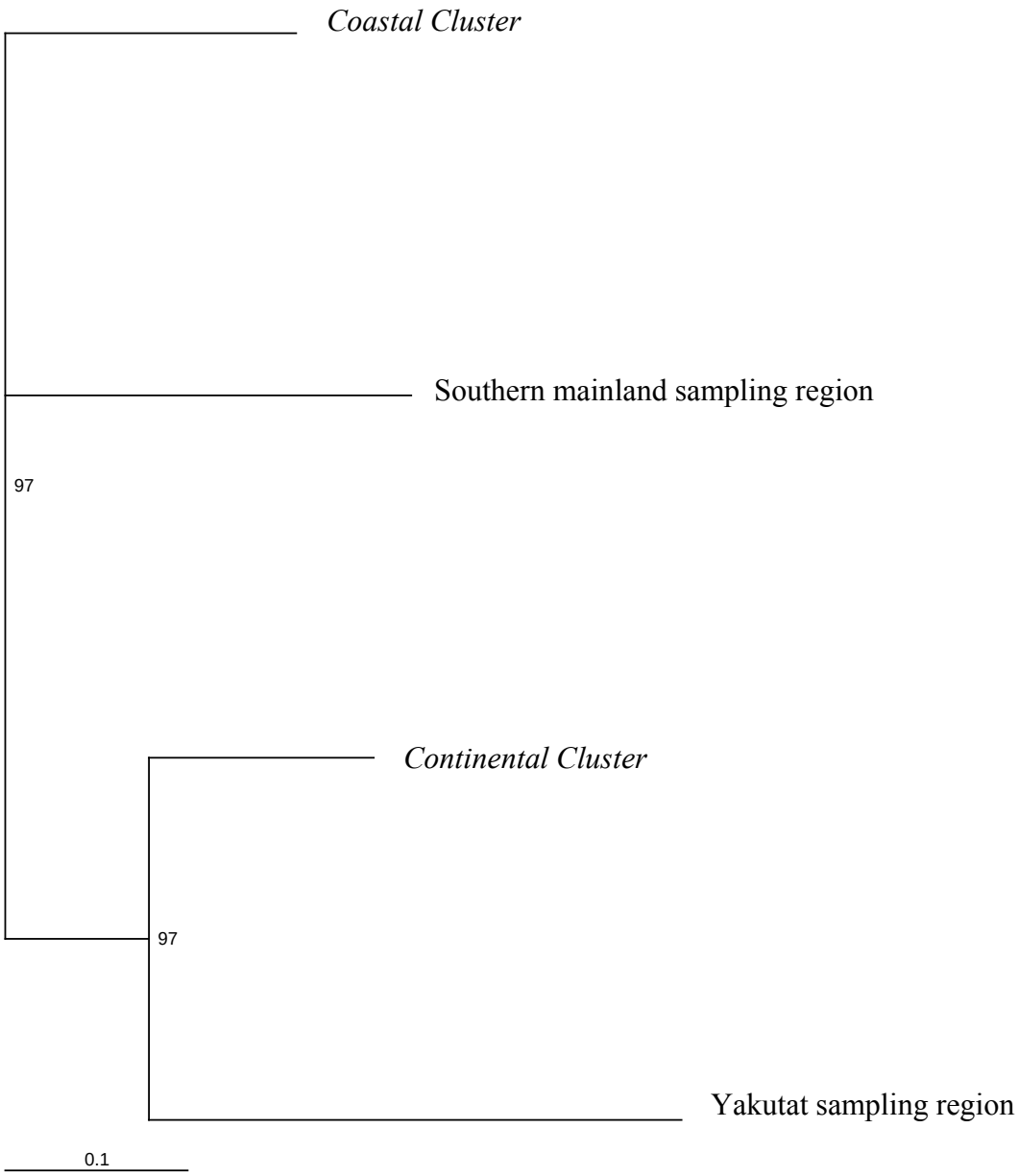


Figure 13. Rooted (Yakutat) neighbor-joining tree based on Cavalli-Sforza distance of four groupings of individuals of Southeast Alaska. Bootstrap values are given at the node (5,000 replicates).

Table 1. Primer pairs used to amplify microsatellite loci (Paetkau and Strobeck 1994, Paetkau *et al.* 1995). Sequences are given in the 5' – 3' direction.

Locus	GenBank accession number	Repeat motif	Forward sequence	Reverse sequence	Dye	Allele range (bp)
G10O	U22090	$(GT)_n$	CCTTGGCTACCTCAGATGG	GCTTCTAATCCAAAGATGCATAAAGG	5-FAM	164-190
G10L	U22088	$(GT)_n$	GTACTGATTTAATTCACATTTCCC	GAAGATACAGAAACCTACCCATGC	5-FAM	134-172
G10Ct‡	U22085	$(GT)_n$	AAAGCAGAAGGCCTTGATTTCCTG	**GTTT**GTGGACATAAACACCGAGACAGC	6-HEX	103-123
G10M	U22089	$(GT)_n$	TTCCCCTCATCGTAGGTTGTA	GATCATGTGTTTCCAAATAAT	NED	209-223
G10X	U22093	$(GT)_n$	CCCCTGGTAACCACAAATCTCT	GCTTCTTCAGTTATCTGTGAAATCAAAA	PET	141-169
G1A	U22095	$(GT)_n$	GACCCTGCATACTCTCCTCTGATG	GCACTGTCCTTGCGTAGAAGTGAC	6-HEX	177-197
G10B	U22084	$(GT)_n$	GCCTTTTAATGTTCTGTTGAATTTGGTTTG	GACAAATCACAGAAACCTCCATCC	5-FAM	158-172

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

Table 2. PCR conditions for microsatellite primer pairs. 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 is in dH_20 and 2 µl of template (10 ng/µl).

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 ††
G10O	1.2	1.5	-	0.5	3.0	0.7	0.2	45	58
G10L	1.5	1.0	-	0.5	-	0.5	0.2	30	60
G10Ct‡	0.9	1.5	-	0.5	-	0.5	0.2	45	62
G10M	0.9	1.5	-	0.5	-	0.4	0.2	45	50
G10X	-	-	1.5	0.6	-	0.7	0.2	45	58
G1A	1.8	1.5	-	0.5	-	0.75	0.3	30	58
G10B	-	-	1.5	0.5	-	0.5	0.2	30	60

†Applied Biosystems, Inc.
‡ Bovine Serum Albumin
††Annealing Temperature, °C

Table 3. Genetic variation information for black bears at each locus in all sampling regions of Southeast Alaska: CH – Chilkat Peninsula; CM – Central mainland JN – Juneau; KP – Kupreanof Island; KU- Kuiu Island; MK – Mitkof Island; POW – Prince of Wales Island; RV – Revillagigedo Island; SK – Skagway; SM – Southern mainland; YK – Yakutat. N, number of samples; A number of alleles observed; A_R allelic richness; F_{IS}, Wright's inbreeding coefficient; H_E, expected heterozygosity.

	CH	**CM**	**JN**	**KP**	**KU**	**MK**	**POW**	**RV**	**SK**	**SM**	**YK**	Average
G1A												
N	17	23	20	29	39	1	21	17	7	6	1	
A	-	-	-	-	-	-	-	-	-	-	-	
R_s	5.0	5.0	5.0	5.0	5.0	2.0	7.0	6.0	5.0	5.0	2	
H_E	0.779	0.796	0.745	0.661	0.479	-	0.707	0.8	0.821	0.883	-	0.741
F_{IS}	0.019	0.181	0.194	-0.095	0.197	-	-0.212	0.191	-0.043	0.245	-	
G10B												
N	32	34	31	34	39	7	34	22	21	8	18	
A	5	8	6	7	5	5	8	7	5	5	4	
R_S	4.06	7.19	5.64	6.87	5.0	1.81	7.41	6.50	3.88	4.93	1.637	
H_E	0.645	0.729	0.776	0.761	0.666	0.81	0.69	0.798	0.707	0.83	0.632	0.786
F_{IS}	-0.259*	0.031	-0.163	-0.082	-0.04	-0.059	0.099	-0.026	-0.077	-0.054	-0.23	
G10C												
N	27	34	30	35	39	8	35	18	17	8	18	
A	11	9	11	12	5	5	8	7	10	5	3	
R_S	10.17	7.93	9.64	11.57	5.0	1.60	6.98	6.83	7.88	4.50	1.532	
H_E	0.884	0.831	0.84	0.745	0.34	0.607	0.761	0.683	0.912	0.795	0.525	0.673
F_{IS}	0.036	-0.098	0.167†	0.233†	0.095	-0.029	-0.09	0.187	0.29†	0.213	-0.483	

	CH	**CM**	**JN**	**KP**	**KU**	**MK**	**POW**	**RV**	**SK**	**SM**	**YK**	Average
G10L												
N	23	29	21	31	39	4	31	17	12	7	14	
A	10	8	8	5	4	4	5	6	7	7	8	
R_S	9.06	7.67	7.86	5.0	4.0	1.75	4.69	6.00	5.80	6.68	1.802	
H_E	0.797	0.747	0.821	0.759	0.614	0.75	0.590	0.798	0.792	0.929	0.802	0.676
F_{IS}	0.128	0.031	0.13	-0.02	-0.085	0	0.454††	0.041	0.158	0.385†	0.021	
G10M												
N	29	35	31	35	39	8	34	21	20	8	18	
A	6	6	7	6	5	6	5	7	4	3	4	
R_S	5.42	5.98	6.13	5.97	5.0	1.68	4.23	6.59	3.35	2.74	1.592	
H_E	0.748	0.787	0.742	0.658	0.562	0.679	0.413	0.646	0.696	0.42	0.587	0.653
F_{IS}	0.077	0.093	0.088	0.089	-0.095	0.079	-0.14	-0.105	-0.149	-0.191	-0.326	
G10O												
N	33	35	33	34	39	7	35	20	21	6	17	
A	5	6	6	3	3	2	6	3	6	4	5	
R_S	4.28	5.54	5.58	3.00	3.0	1.50	5.14	3.00	3.73	4.0	1.686	
H_E	0.651	0.717	0.741	0.482	0.457	0.476	0.489	0.553	0.419	0.833	0.678	0.591
F_{IS}	-0.024	0.083	-0.022	0.145	-0.234	-0.5	0.183	0.005	0.205	0.4	-0.388*	
G10X												
N	28	31	31	33	39	8	33	19	18	6	15	
A												
R_S	7.83	7.98	7.80	7.39	5.0	1.533	4.46	4.79	4.60	6.0	1.513	
H_E	0.762	0.844	0.551	0.681	0.712	0.527	0.477	0.371	0.794	0.867	0.512	0.661
F_{IS}	-0.172	-0.033	0.005	-0.067	-0.116	-0.186	0.492††	-0.134	0.021	0.038	-0.042	

	CH	CM	JN	KP	KU	MK	POW	RV	SK	SM	YK	Average
Overall H_E	**0.752**	**0.779**	**0.745**	**0.678**	**0.547**	**0.642**	**0.589**	**0.664**	**0.735**	**0.794**	**0.623**	**0.683**
Overall F_{IS}	**-0.02**	**0.04**	**0.06**	**0.02**	**-0.05**	**-0.09**	**0.09**	**0.04**	**0.06**	**0.18†**	**-0.23****	

* significantly smaller F_{IS} than expected at nominal significance level (0.05); † significantly larger F_{IS} at nominal level.
** significantly smaller F_{IS} than expected at table-wide significance level (0.0009); †† significantly larger F_{IS} at table wide level.

Table 4. Estimates of Θ and N_e from each black bear sampling region in Southeast Alaska.

Sampling Region	Lower 95% CI	MLE Θ	Upper 95% CI	N_e min*	N_e max†
Yakutat	0.28	0.32	0.36	79.4	794.2
Chilkat Peninsula	0.57	0.63	0.71	158.5	1585.4
Skagway	0.35	0.39	0.43	97.4	974.0
Juneau	0.39	0.43	0.47	107.4	1074.1
Central mainland	0.43	0.47	0.52	117.8	1178.2
Mitkof-Kupreanof islands	0.30	0.33	0.36	82.1	821.1
Kuiu Island	0.21	0.23	0.25	57.2	571.7
Prince of Wales Island	0.24	0.27	0.29	66.5	664.8
Revillagigedo Island	0.29	0.32	0.37	80.7	806.8
Southern mainland	0.18	0.23	0.30	57.5	575.2

* calculated with $\mu = 1 \times 10^{-3}$ mutations per locus per generation
†calculated with $\mu = 1 \times 10^{-4}$ mutations per locus per generation

Table 5. Pair-wise F_{ST} (above diagonal) and genetic distance (D_{LR}) (below diagonal) values for black bear sampling regions in Southeast Alaska. F_{ST} values which are significant at the Bonferroni-corrected alpha value (0.0009) for multiple comparisons are symbolized by §. Those values which are only significant at the uncorrected alpha value (0.05) are symbolized by *. † symbolizes significance tests that could not be run due to low sample size (in terms of numbers of samples or loci).

	Chilkat Peninsula	Central mainland	Juneau	Kupreanof Island	Kuiu Island	Mitkof Island	Prince of Wales Island	Revillagigedo Island	Skagway	Southern mainland	Yakutat
Chilkats		0.067§	0.049§	0.117§	0.215*	0.096†	0.199§	0.158§	**0.0242**	0.091*	0.123†
Central mainland	2.4		0.062§	0.076§	0.137§	0.068†	0.177§	0.132§	0.072*	0.053§	0.136†
Juneau	1.4	2.1		0.119§	0.221§	0.088†	0.212§	0.130§	0.076*	0.093§	0.163†
Kupreanof	4.3	3.6	5.4		0.046§	0.007†	0.14§	0.142§	0.127§	0.087§	0.211†
Kuiu	7.2	5.3	7.9	1.2		0.061†	0.209§	0.252§	0.219*	0.165§	0.292†
Mitkof	2.5	2.2	2.7	0.0	1.0		0.157†	0.095†	0.142†	0.059†	0.233†
Prince of Wales	5.6	5.7	5.8	3.9	7.1	3.2		0.211§	0.239*	0.120§	0.235†
Revillagigedo	7.0	5.5	6.6	5.3	8.0	2.3	5.7		0.178*	0.063§	0.270†
Skagway	0.6	2.8	2.1	4.6	7.5	3.4	7.2	6.9		0.067§	0.123†
Southern mainland	3.7	2.5	3.8	3.6	5.7	1.0	2.6	2.4	2.2		0.140†
Yakutat	3.0	5.5	4.5	7.4	11.0	6.1	6.7	9.7	2.7	5.1	

Table 6. One-way migration rates (M_{ji} = migrants/generation, incorporating microsatellite mutation rate) between black bear sampling regions in Southeast Alaska as estimated by MIGRATE.

Pair of sampling regions	Lower 95% CI	M_{ji}	Upper 95% CI
Yakutat → Chilkats	6.13	6.34	6.47
Chilkats → Yakutat	8.00	8.31	8.54
Chilkats → Skagway	13.28	13.39	13.40
Skagway → Chilkats	17.85	18.20	18.41
Skagway → Juneau	11.21	11.55	11.80
Juneau → Skagway	9.93	10.19	10.38
Juneau → Central mainland	12.05	12.44	12.73
Central mainland → Juneau	5.69	6.14	6.54
Juneau → Mitkof/Kupreanof	8.92	9.75	10.52
Mitkof/Kupreanof → Juneau	5.13	5.57	5.98
Central mainland → Mitkof/Kupreanof	5.56	6.35	7.12
Mitkof/Kupreanof → Central mainland	0.50	0.79	1.15
Central mainland → Kuiu*	3.10	3.71	4.34
Kuiu → Central Mainland	4.08	4.58	5.06
Central mainland → Southern mainland	3.31	4.08	4.67
Southern mainland → Central mainland	1.23	1.61	2.02
Central mainland → Prince of Wales	3.84	4.63	5.43
Prince of Wales → Central mainland	1.74	2.17	2.61
Central mainland → Revillagigedo	1.39	1.81	2.24
Revillagigedo → Central mainland	0.56	0.86	1.20
Mitkof/Kupreanof → Kuiu	9.96	10.69	11.36
Kuiu → Mitkof/Kupreanof	15.37	16.12	16.77
Mitkof/Kupreanof → Prince of Wales	8.20	9.09	9.93
Prince of Wales → Mitkof/Kupreanof	2.70	3.36	4.05
Mitkof/Kupreanof → Revillagigedo	0.74	1.08	1.47
Revillagigedo → Mitkof/Kupreanof	2.15	2.76	3.43
Mitkof/Kupreanof → Southern mainland	3.12	3.90	4.49
Southern mainland → Mitkof/Kupreanof	0.46	0.82	1.28
Kuiu → Prince of Wales*	1.35	1.92	2.58
Prince of Wales → Kuiu	0.61	0.96	1.39
Prince of Wales → Revillagigedo	4.08	4.58	5.06
Revillagigedo → Prince of Wales	0.35	0.70	1.18
Prince of Wales → Southern mainland	12.50	12.64	12.25

Pair of sampling regions	Lower 95% CI	M_{ji}	Upper 95% CI
Southern mainland → Prince of Wales	6.73	7.61	8.46
Revillagigedo → Southern mainland	16.05	15.78	14.98
Southern mainland → Revillagigedo	1.16	2.05	2.49

Table 7. Frequency-based assignment of individual black bears to sampling regions in Southeast Alaska.

	Yakutat	Chilkats	Skagway	Juneau	Central mainland	Mitkof Island	Kupreanof Island	Kuiu Island	Prince of Wales Island	Revillagigedo Island	Southern mainland	*N*	% of individuals that were assigned to sampling origin
Yakutat	18				1							19	95%
Chilkats	1	21	3	3	3	2					1	34	62%
Skagway	2	7	9	2	1	1						22	41%
Juneau	1	4	1	23	4	1						34	68%
Central mainland		2		4	27			1			1	35	77%
Mitkof						2	5	1				8	25%
Kupreanof			1	1	1	4	19	6	2	1		35	54%
Kuiu					1	3	1	34				39	87%
Prince of Wales	2	2		3	1	2	2		25			37	68%
Revillagigedo					1		1			19	1	22	86%
Southern mainland			1	1	2	1					3	8	38%

Table 8. Likelihood of the Southeast Alaskan black bear genetic data (X) assuming different numbers of clusters (K) as estimated by STRUCTURE.

K	Ln Pr(X|K) (SD)	Pr (K)
2	-5422 (12)	2×10^{-267}
3	-5164 (15)	2×10^{-155}
4	-5047 (17)	2×10^{-104}
5	-4888 (18)	2×10^{-35}
6	-4840 (20)	4×10^{-15}
7	-4807 (23)	1.0
8	-4826 (25)	8×10^{-9}
9	-4944 (31)	5×10^{-60}
10	-5407 (35)	1×10^{-104}

Table 9. Average proportional membership (q) of black bear individuals from sampling regions to the seven genetic clusters in Southeast Alaska. Bold values highlight the most likely cluster to which individuals were assigned.

Sampling region	*Cluster*						
	Yakutat	*Northern Southeast*	*Juneau*	*Central Southeast*	*Kuiu Complex*	*Prince of Wales*	*Southern Southeast*
Yakutat	**0.87**	0.04	0.02	0.02	0.02	0.01	0.02
Chilkats	0.14	**0.57**	0.11	0.10	0.02	0.02	0.04
Skagway	0.28	**0.37**	0.05	0.19	0.06	0.01	0.03
Juneau	0.03	0.22	**0.55**	0.13	0.03	0.01	0.03
Central mainland	0.04	0.04	0.23	**0.59**	0.06	0.04	0.03
Mitkof Island	0.02	0.04	0.10	0.14	**0.46**	0.09	0.22
Kupreanof Island	0.01	0.01	0.08	0.09	**0.61**	0.09	0.06
Kuiu Island	0.01	0.01	0.01	0.02	**0.93**	0.01	0.02
Prince of Wales Island	0.04	0.06	0.08	0.04	0.03	**0.72**	0.03
Revillagigedo Island	0.01	0.02	0.04	0.02	0.02	0.02	**0.87**
Southern mainland	0.11	0.02	0.13	0.19	0.05	0.03	**0.46**

Table 10. Average proportional membership (*q*) of black bear individuals from sampling regions to two genetic clusters in Southeast Alaska.

Sampling region	*Continental cluster*	*Island cluster*
Yakutat	0.97	0.03
Chilkats	0.95	0.05
Skagway	0.91	0.09
Juneau	0.95	0.05
Central mainland	0.83	0.17
Mitkof Island	0.18	0.82
Kupreanof Island	0.14	0.86
Kuiu Island	0.02	0.98
Prince of Wales Island	0.12	0.82
Revillagigedo Island	0.12	0.88
Southern mainland	0.43	0.57

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 = -2ln 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 1st, 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: $\varphi(.)p(.)$; $\varphi(.)p(t)$; $\varphi(t)p(.)$ and $\varphi(t)p(t)$, 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 $\varphi(g)$ and $p(g)$, 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 ± 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 ± 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 ± 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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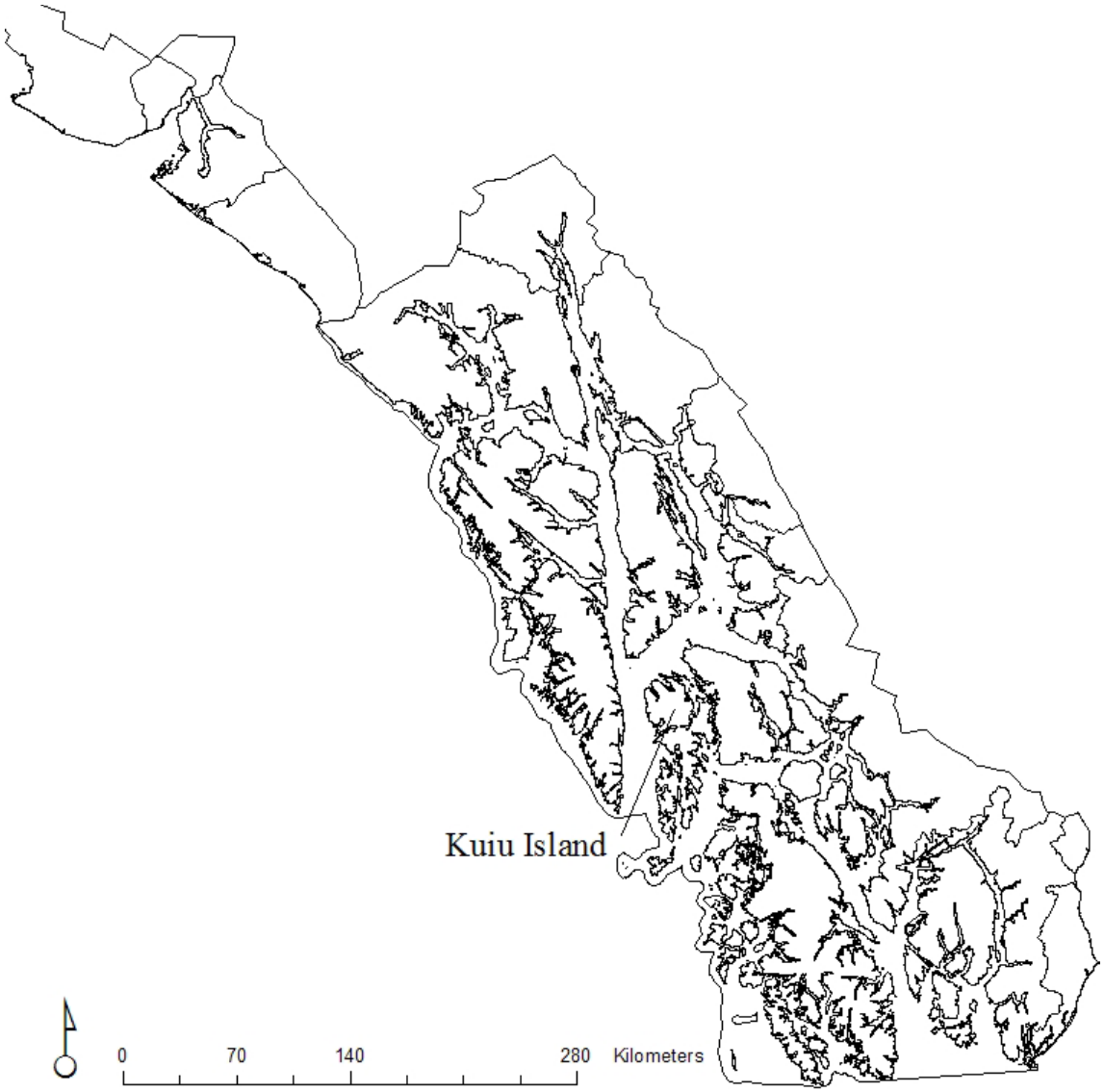


Figure 1. Kuiu Island and the Alexander Archipelago of Southeast Alaska.

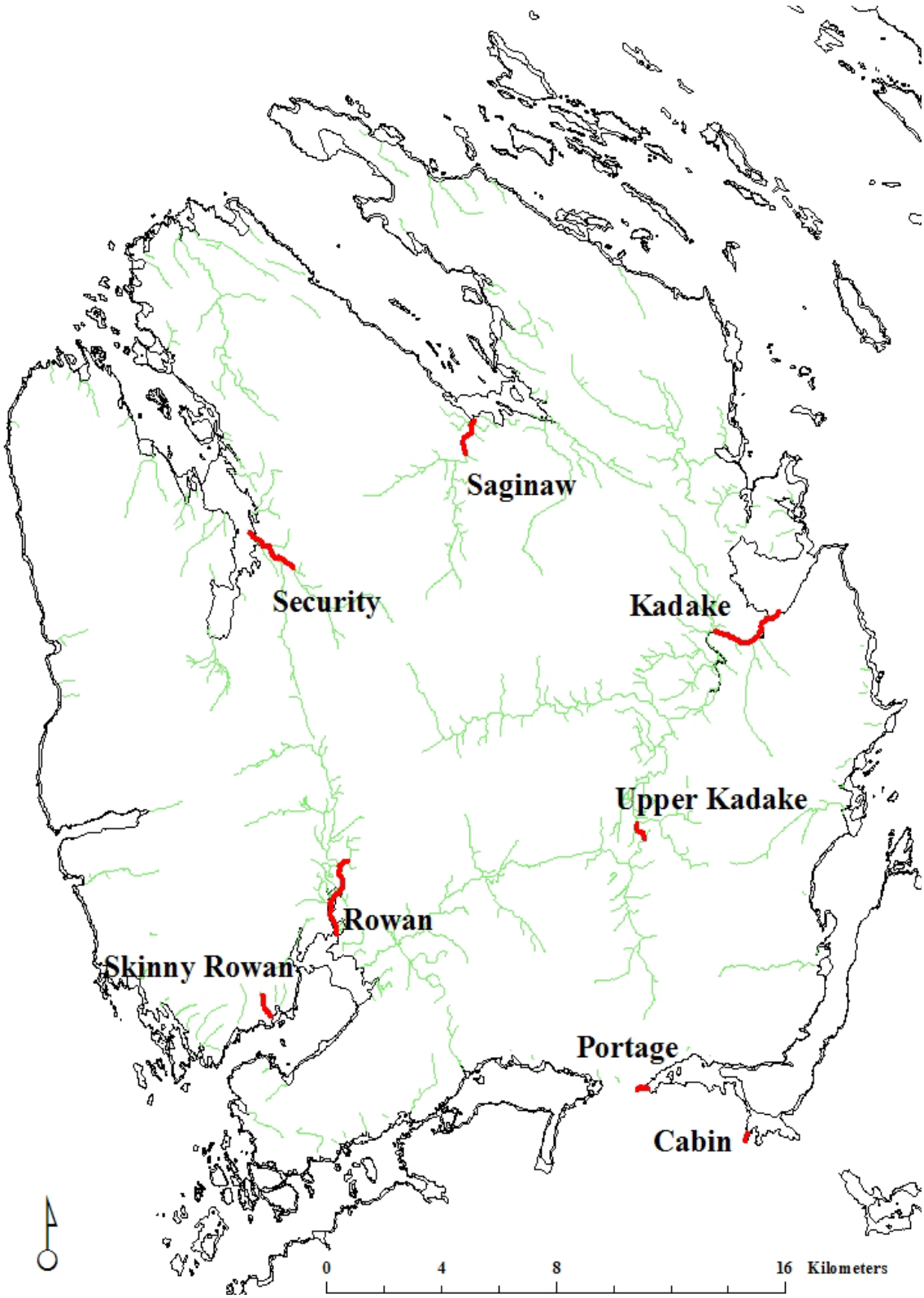


Figure 2. Study streams (red bold) and other Class I anadromous streams (green) on northern Kuiu Island.

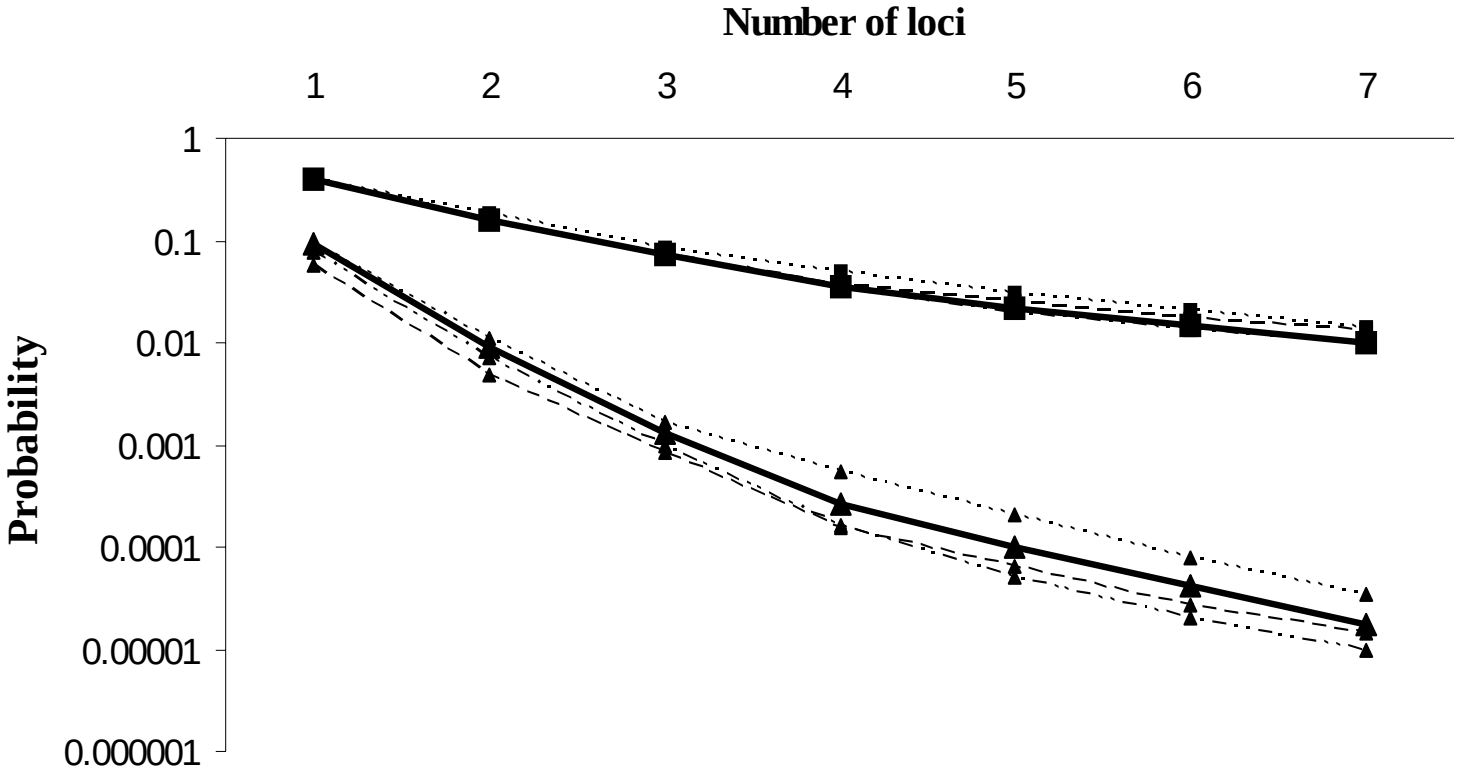


Figure 3. Probability of Identity (P_{ID}) for black bears on northern Kuiu Island. Squares are P_{ID_SIB} and triangles are P_{ID_UNB}. Bold solid lines show values for northern Kuiu Island (n = 117 bears). Dotted lines show values for the Rowan watershed (n = 33), dashed lines show values for the Security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

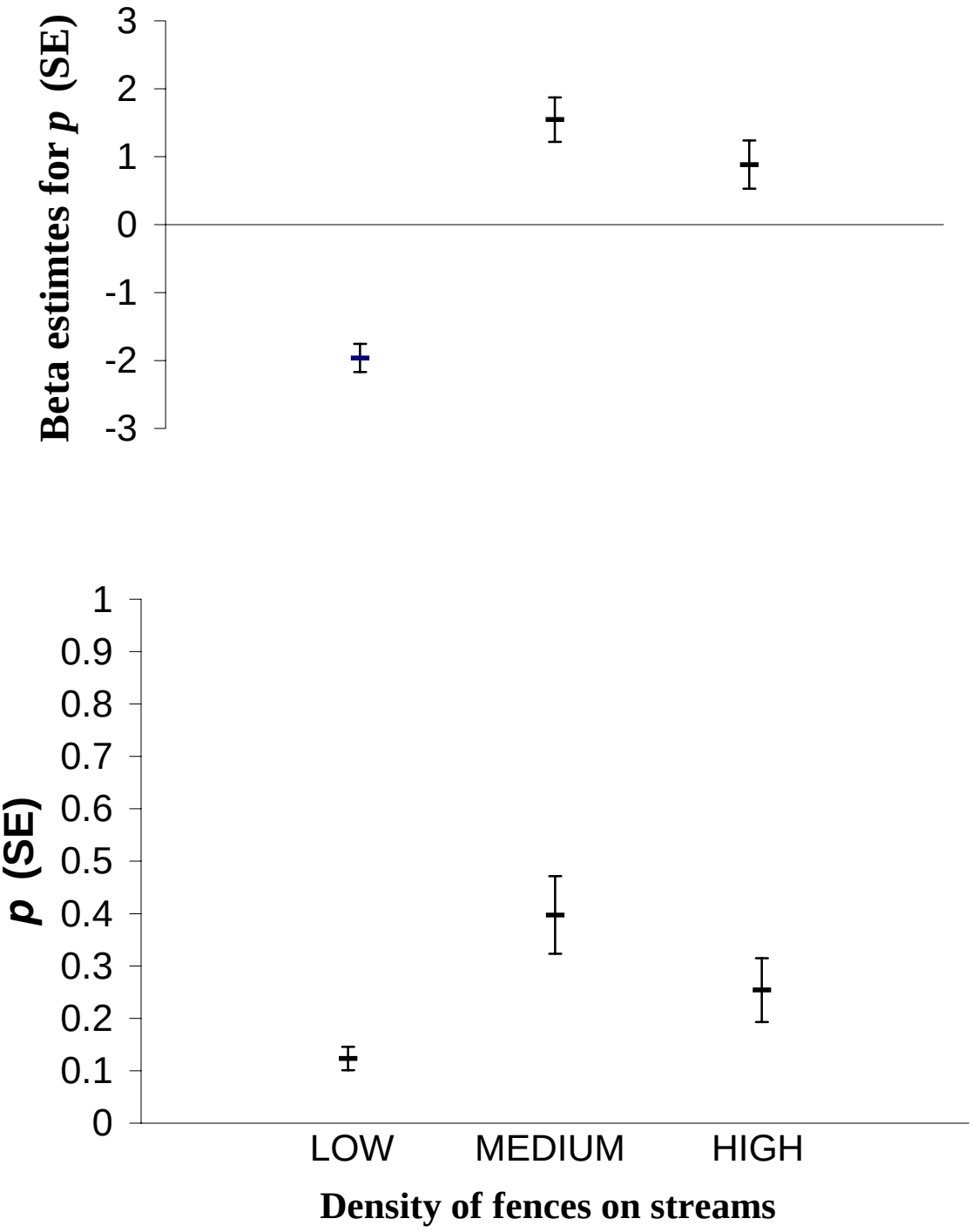
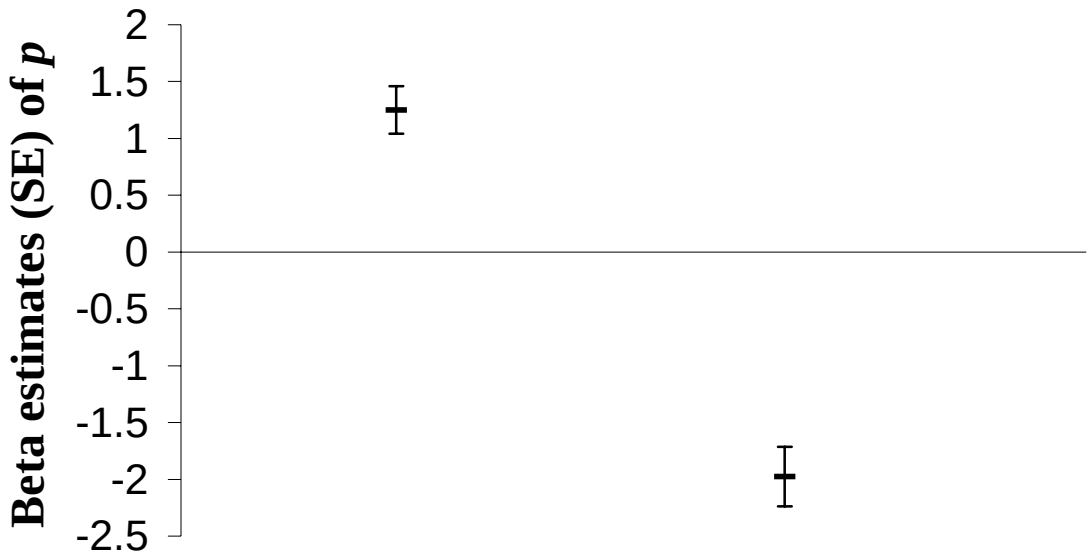
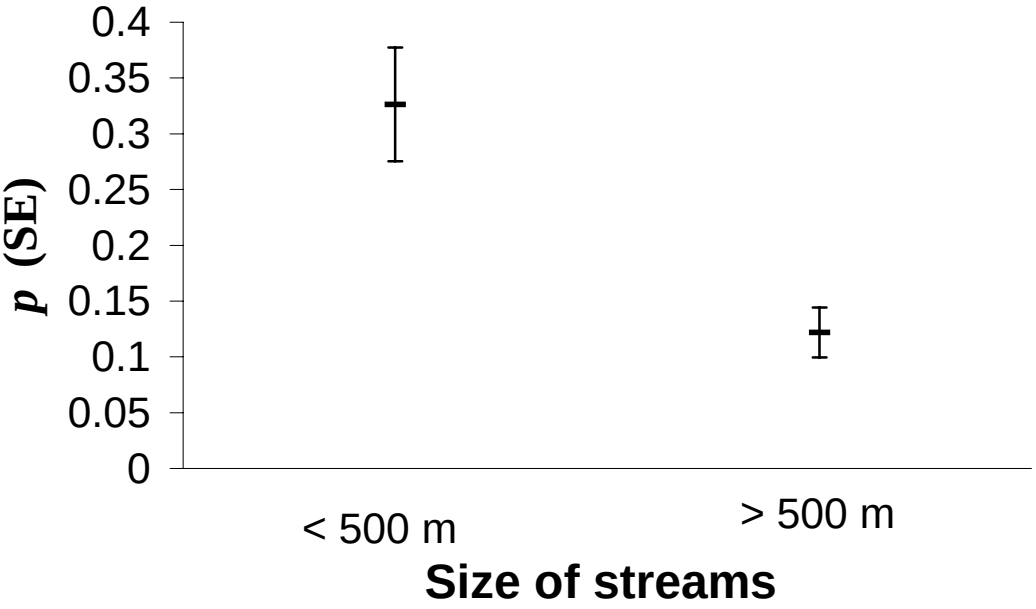


Figure 4ab. Beta (a) and real (b) estimates of recapture probability of black bears on salmon streams on Kuiu Island with respect to density of fences. Beta and model-averaged real estimates were generated from CJS models using mark-recapture data from all streams sampled in 2002 (n = 5). Error bars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



a.



b.

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.

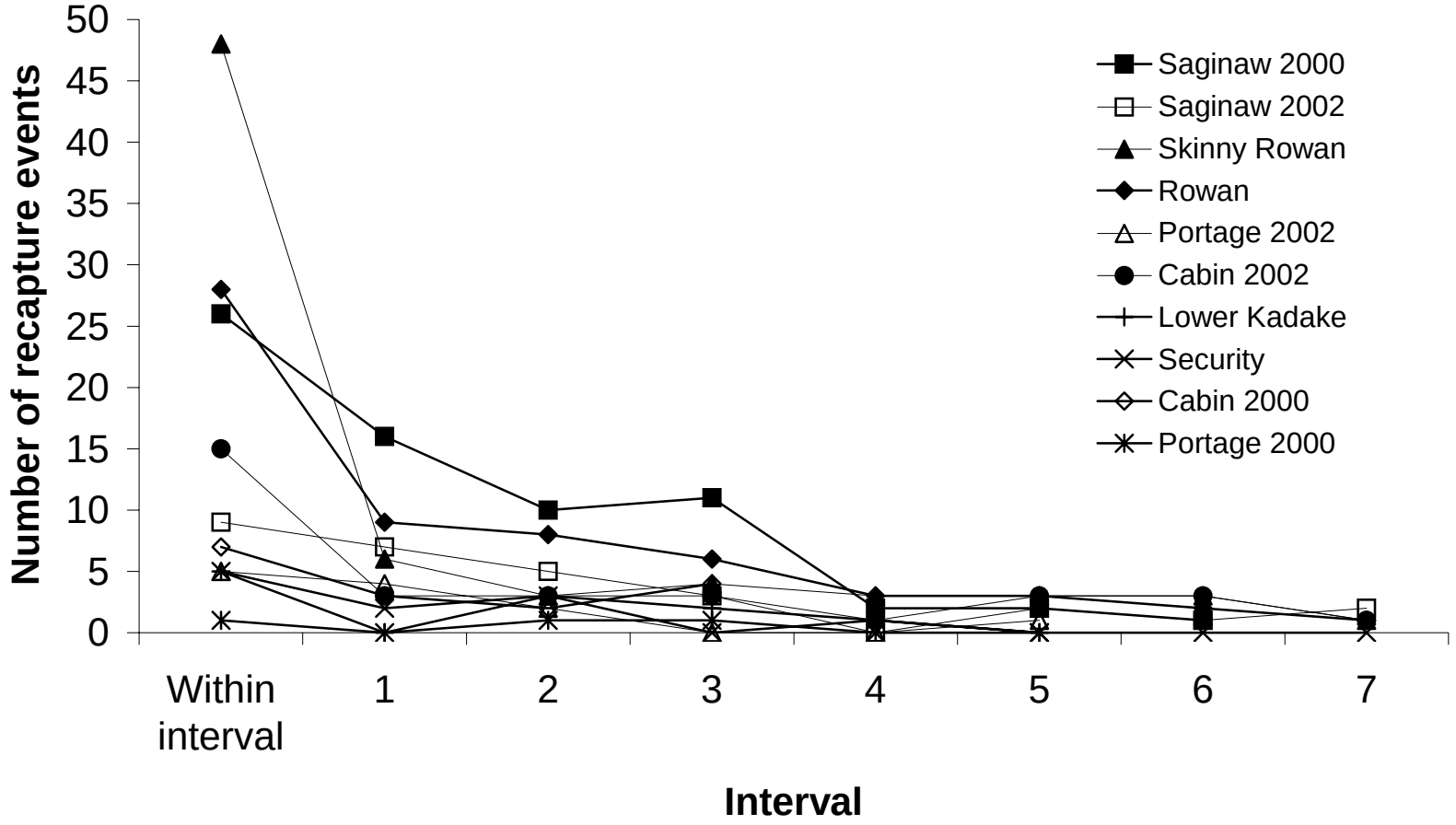


Figure 6. The number of recapture events of black bears on salmon streams on Kuiu Island within the interval of first capture, and in intervals subsequent to initial capture.

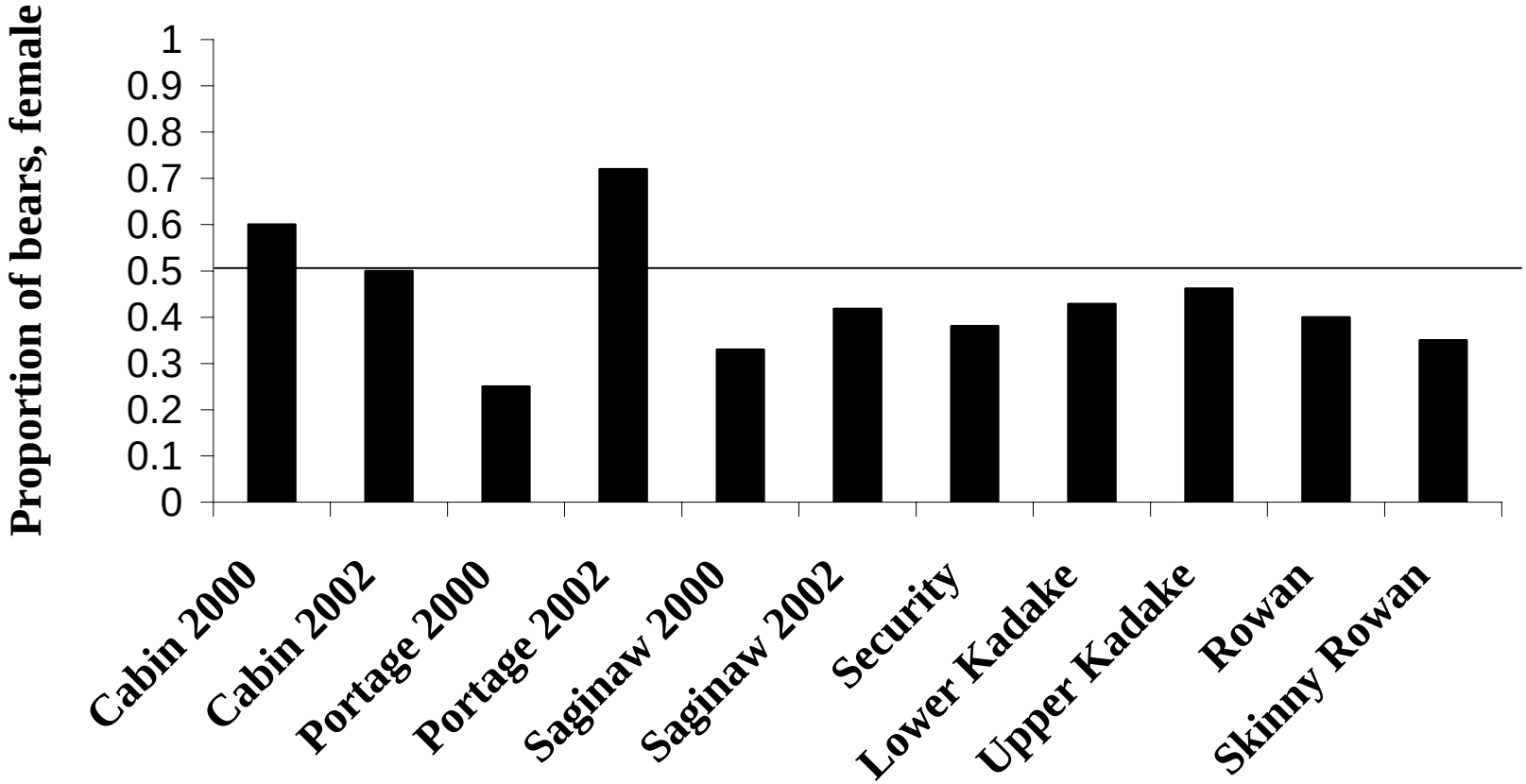


Figure 7. Proportion of individual black bears (MNA) that visited salmon streams that were female. The line indicates 0.5, which would be the expected proportion by chance, assuming the sex ratio of black bears on northern Kuiu Island was even.

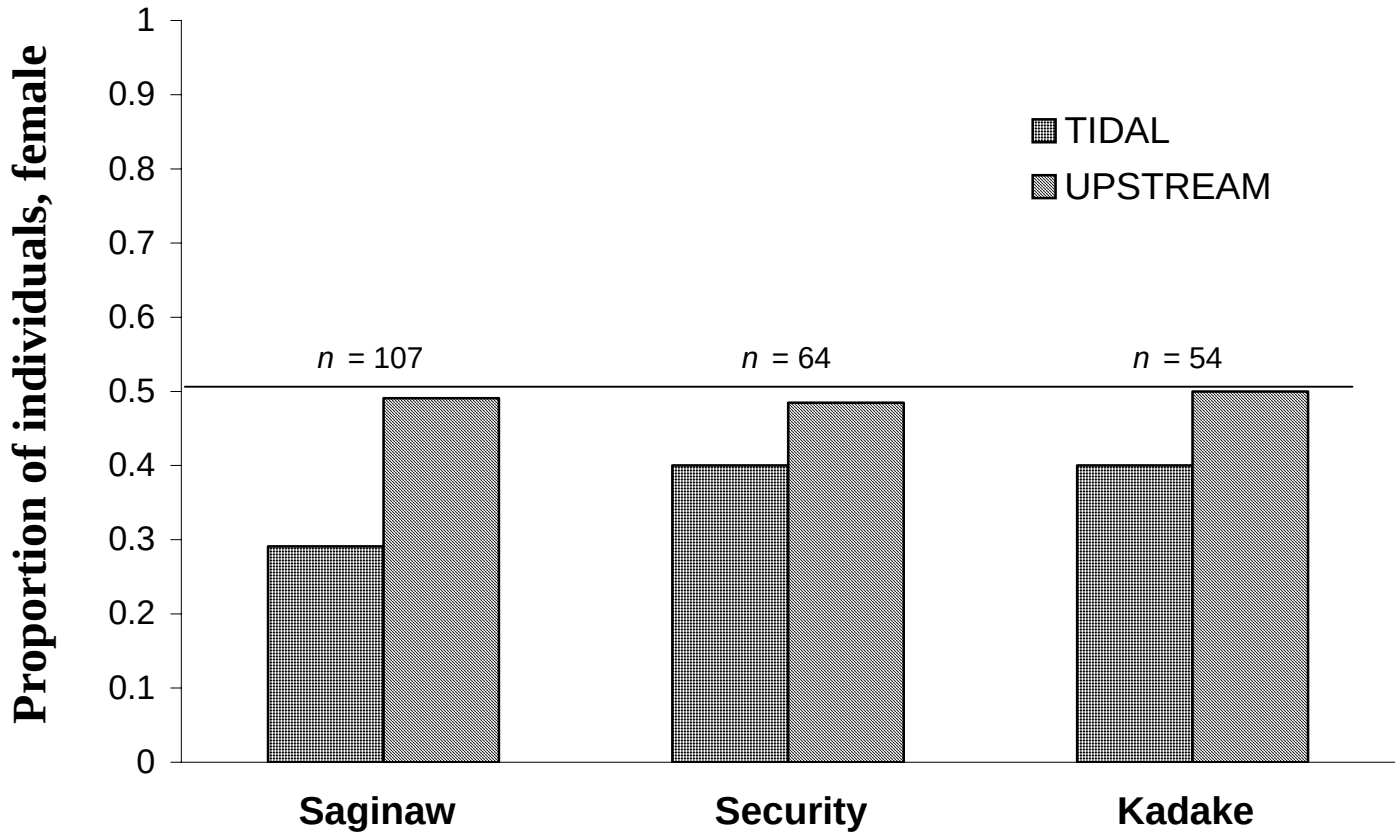


Figure 8. Proportion of individual black bears (MNA) using tidal and upstream portions of three streams in 2000. The line indicates 0.5, which would be the expected proportion by chance, assuming a sex ratio on northern Kuiu was even. 1-tailed t-test, $p = 0.01$. Sample sizes are total number of samples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

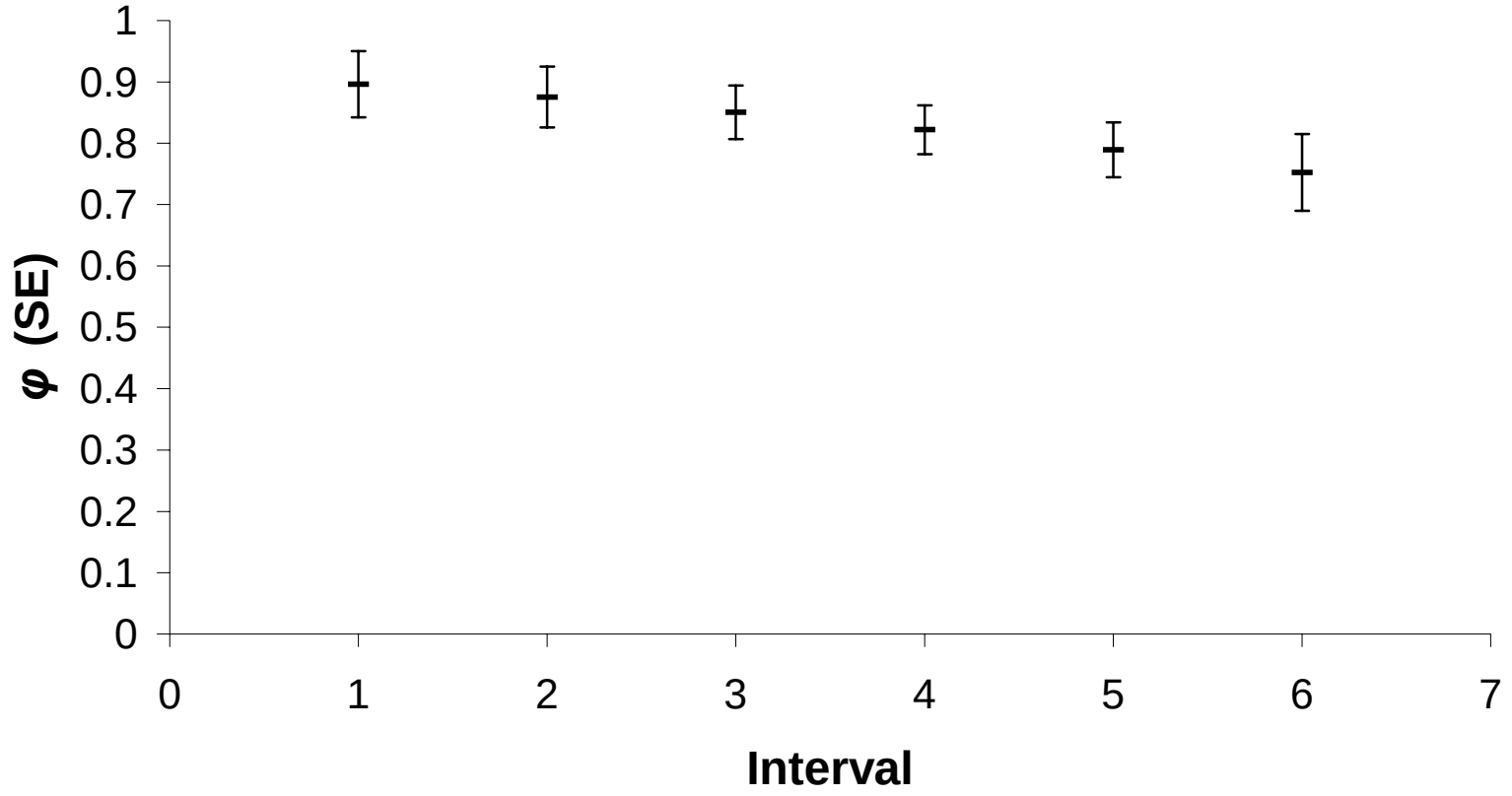


Figure 9. Probability of bears staying on streams from one week to the next (φ), over the course of encounter occasions. Estimates of φ are model-averages from CJS models incorporating pooled data from all streams sampled in 2002 (n =5). Trend effects of φ are found in eight of the ten models with ΔAICc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

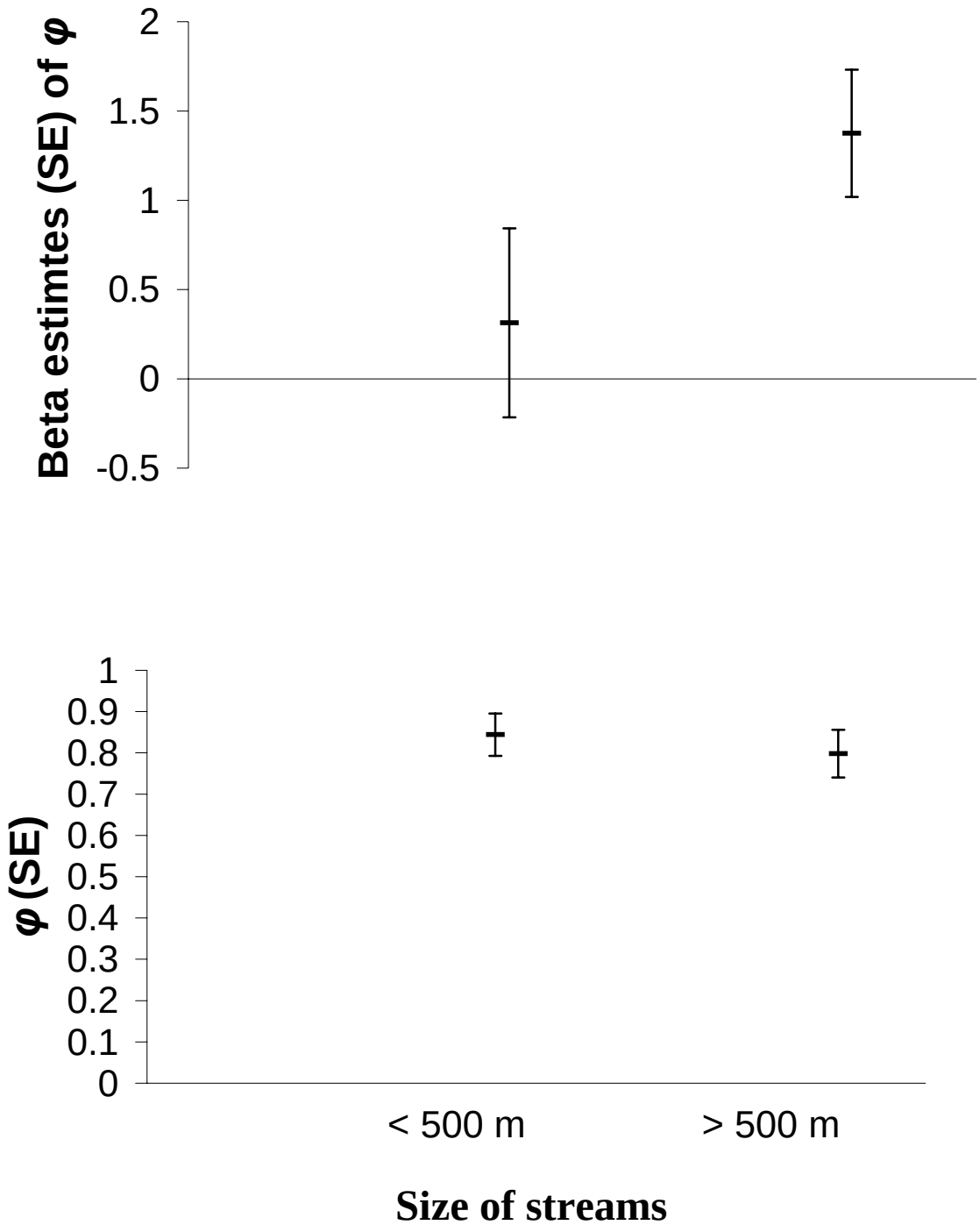


Figure 10. Apparent survival (φ) of black bears on salmon streams that have < 500 and > 500 m of available salmon spawning habitat over the course of seven weeks for all stream data sets (n =5) from 2002 combined. This effect on black bear fidelity was weakly supported and occurred in models with ΔAICc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

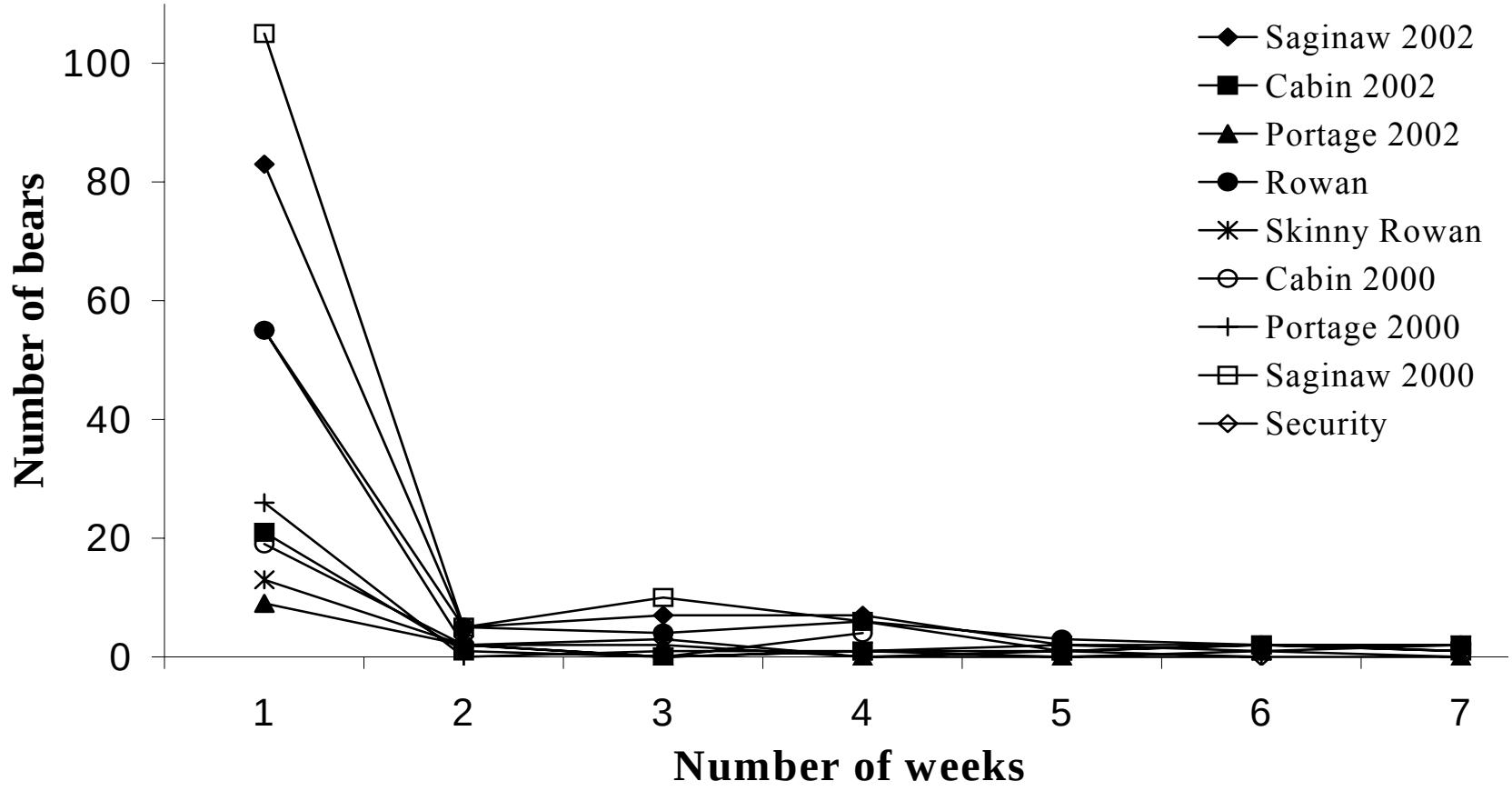


Figure 11. The minimum number of identified black bears (MNA) that stayed for varying number of weeks on salmon streams on Kuiu Island.

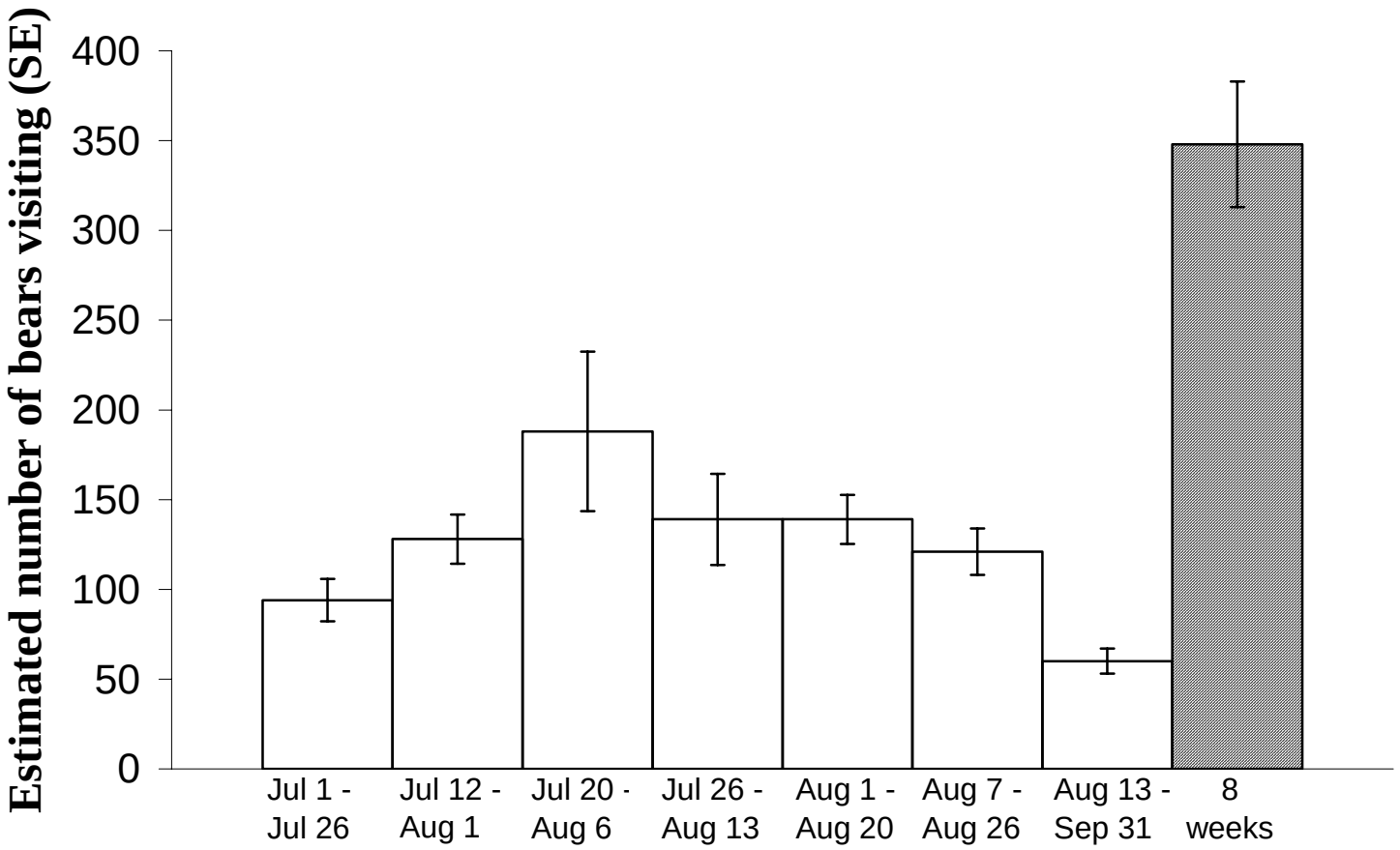


Figure 12. The estimated total number of bears visiting Saginaw Creek in 2000 over sequential four-week time periods, and over the entire eight week period. Numbers of bears were estimated using the M_h model in CAPTURE. Error bars are ± SE.

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

*the best model, $\varphi(.)p(.)pent(.)N(.)$ (AICc weight = 0.80) produced an erroneous estimate of *pent*.
**the best model $\varphi(.)p(.)pent(t)N(.)$ (AICc weight = 0.68) was not able to estimate 2 of the 3 *pent* parameters.
***the best model $\varphi(.)p(.)pent(.)N(.)$ (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.

APPENDIX I

PROGRAM IDENTITY

```
Option Explicit
Dim FileName As String
Dim SaveFile As String
Dim filetmp() As String

Private Sub CmdMain_Click()

Dim Identity As Integer
Dim NumLoci As Integer
Dim Diff As Integer
Dim MisMatch As Integer
Dim NumSamp As Integer
Dim Ct As Integer
Dim Loc As Integer
Dim No As Integer
Dim Yes As Integer
Dim Fld As String
Dim LineNum As Integer
Dim LineNumA As Integer
Dim LineNumB As Integer
Dim LineStr As String
Dim I As Integer
Dim Identfld As Integer
Dim Samefld As Integer
Dim Maybefld As Integer
Dim ErrorCode As String
Dim lp As Integer
Dim lp2 As Integer
Dim DiffLoc As String
Dim B(500, 24) As String
Dim Temp() As String

Identity = Val(IdentityBox.Text)
MisMatch = Val(MisMatchBox.Text)
NumLoci = Val(NumLociBox.Text)
NumSamp = Val(NumSampBox.Text)

Identfld = NumLoci + 1
Samefld = NumLoci + 2
Maybefld = NumLoci + 3
```

```
Diff = Identity - MisMatch

If Identity = 0 Then
        ErrorCode = "Identity field not entered." + Chr(10)
End If
If MisMatch > Identity Then
        ErrorCode = ErrorCode + "Mis-Match must be less than Identity field." + Chr(10)
End If
If NumLoci = 0 Then
        ErrorCode = ErrorCode + "You must enter the number of Loci in data file." +
Chr(10)
End If
If NumSamp = 0 Then
        ErrorCode = ErrorCode + "You must enter the number of samples in data file!" +
Chr(10)
End If
If FileName = "" Then
        ErrorCode = ErrorCode + "You didn't choose a file!!" + Chr(10)
End If
If SaveFile = "" Then
        ErrorCode = ErrorCode + "You didn't name an output file." + Chr(10)
End If
If ErrorCode <> "" Then
        MsgBox ErrorCode, 16,
Else

Open FileName For Input As #1
LineNum = 0
For LineNum = 0 To NumSamp
        Input #1, LineStr
        Temp = Split(LineStr, Chr(9))
        For I = 0 To NumLoci
                B(LineNum, I) = Temp(I) 'brings in the data into array B
        Next I
        B(LineNum, Identfld) = ""
        B(LineNum, Samefld) = ""
        B(LineNum, Maybefld) = ""
Next LineNum
        B(0, Identfld) = "Identity"
        B(0, Samefld) = "Same"
        B(0, Maybefld) = "Maybes"
Close #1

Ct = 2
Loc = 1
```

```
B(1, Identfld) = 1
For LineNumA = 1 To NumSamp
        For LineNumB = 1 To NumSamp
        No = 0
      Yes = 0
      DiffLoc = ""
      If LineNumA <> LineNumB Then
        For Loc = 1 To NumLoci
        If B(LineNumB, Loc) <> B(LineNumA, Loc) And B(LineNumA, Loc) <> "--"
        And B(LineNumB, Loc) <> "--" Then
                No = No + 1
                DiffLoc = DiffLoc + B(0, Loc)
        End If
        If B(LineNumB, Loc) = B(LineNumA, Loc) And B(LineNumA, Loc) <> "--"
        Then
                Yes = Yes + 1
                End If
        Next Loc
        If No <= MisMatch And No > 0 And Yes >= Diff Then
                B(LineNumA, Maybefld) = B(LineNumA, Maybefld) + "_" +
                B(LineNumB, 0) + "(" + DiffLoc + ")"
        End If
        If No = 0 And Yes >= Identity Then
                B(LineNumA, Samefld) = B(LineNumA, Samefld) + "_" + B(LineNumB,
                0)
        If B(LineNumB, Identfld) <> "" Then
                B(LineNumA, Identfld) = B(LineNumB, Identfld)
        End If
        End If
        End If
        Next LineNumB
        If B(LineNumA, Identfld) = "" Then
                B(LineNumA, Identfld) = Str(Ct)
                Ct = Ct + 1
         End If
Next LineNumA

Open SaveFile For Output As #2
For lp = 0 To NumSamp
        LineStr = B(lp, 0) + ","
For lp2 = NumLoci + 1 To NumLoci + 3
        LineStr = LineStr + B(lp, lp2) + ","
Next lp2
Print #2, LineStr
Next lp
```

```
Close #2
End If
End Sub

Private Sub CmdOpen_Click()
With CommonDialog1
        .Filter = "text files (*.txt)|*TXT"
        .CancelError = False
        .DefaultExt = "txt"
        .InitDir = "c:\"
        .DialogTitle = "Open"
        .ShowOpen
End With 'closes statement
        FileName = CommonDialog1.FileName
        filetmp = Split(FileName, ".txt")
End Sub

Private Sub CmdSave_Click()
With CommonDialog1
        .Filter = "comma delimited (*.csv)|*CSV"
        .CancelError = False
        .DefaultExt = "csv"
        .InitDir = "c:\"
        .DialogTitle = "Save as"
        .FileName = filetmp(0) + "res"
        .ShowSave
End With
SaveFile = CommonDialog1.FileName
End Sub

Private Sub NumLociBox_Change()
If Val(NumLociBox.Text) = 0 And NumLociBox.Text <> "" And NumLociBox.Text <>
"0" Then
   MsgBox "Value must be a number", 16,
   NumLociBox.Text = "0"
End If

End Sub
```

APPENDIX II

SUPPLEMENTAL TABLE FROM CHAPTER 1

Table AII – 1. Probabilistic expectations of bears recovered in a Brownie recovery model (Brownie *et al.* 1987) for bears marked with tetracycline on Kuiu Island in 2000. f is the estimated recovery rate; S is the estimated survival rate.

Year marked	Number marked	Year of recovery		
		2000	2001	2002
2000	N_1	N_1f_1	$N_1f_1S_1$	$N_1f_1S_1S_2$
2001	0	0	0	0
2002	N_2			N_3f_3

APPENDIX III

SUPPLEMENTAL DESCRIPTIONS OF GENETIC METHODS

G-STATISTIC

I tested for significance of the differentiation with the log likelihood G-statistic (Goudet *et al.* 1996):

$$G = -2\sum_{l-1}^{nl}\sum_{k-1}^{np}\sum_{i-1}^{ni} n_{ikl} \ln\left(\frac{n_{ikl}}{n_k \overline{p}_i}\right)$$

where l was the number of loci, k was the number of populations, and p_i was the frequency of the i^{th} allele. Multilocus genotypes were randomized between the two populations in a pairwise comparison, and a G-statistic was calculated for this randomization. The proportion of G-statistics from randomized data sets that were larger than that for the observed data set provided the probability that the null hypothesis was true, *i.e.*, the two populations were not differentiated (Goudet *et al.* 1996). Due to multiple comparisons, the α value was corrected using the standard Bonferroni procedure, and used as the significance criterion.

POPULATION BOTTLENECKS

The M-ratio is the average across all microsatellite loci of the ratio of the number of alleles (k) to the range of allele (r, in base pairs). The authors hypothesized that k decreased faster than r when the population was severely and quickly reduced in census size, as rare alleles, which did not generally define the extent of the range of alleles, were eliminated first. Garza and Williamson (2001) suggested that an M-ratio of 0.68 would

signify that a significant bottleneck had occurred in a population. M-ratios may be >0.68 yet still significant, depending on the amount of time since the bottleneck occurred or if there is immigration from other populations. For example using this hypothesis, bottlenecks were identified populations considered endangered (*e.g.*, the Koala and northern elephant seal), and were not found in known thriving populations (*e.g.,* coyotes, harbor seal, Garza and Williamson (2001).

In Garza and Williamson's (2001) program, randomizations were used to create equilibrium distributions for the M-ratio from the microsatellite allelic data sets from each black bear island*,* and the observed M-ratio was compared with the distribution to determine the probability of the observed value. Garza and Williamson's (2001) program assumed a two-phase mutation model, and that 88% of mutations involved the addition or deletion of one repeat unit. The mean size of larger mutations was set to 1.2 microsatellite-repeat units. These parameters were found to best describe empirical data on mutational patterns of microsatellite loci (Garza and Williamson 2001).

STRUCTURE

In a given system, individuals could be grouped into *K* clusters. Each allele from an individual's genotype was treated as a random sample from a cluster's allele frequency distribution. Random draws of alleles from a frequency distribution, *P*, of an unknown population of origin, *Z*, described the probability distribution $Pr(X|Z,P,Q)$, where *X* represented the data (genotypes) and *Q* was the individual's proportional membership (assignment) in *Z*. The prior distributions, $Pr(Z)$ and $Pr(P)$, reflected the Hardy-Weinberg and linkage equilibrium models. The posterior distribution was: $Pr(Z,$

$P|X) \propto Pr(Z)\ Pr(P)\ Pr(X|Z,P)$. To ultimately infer K from the posterior distribution, $Pr(K|X) \propto Pr(X|K)Pr(K)$, a harmonic mean estimator was used estimate the prior, $Pr(X|K)$ (Pritchard *et al.* 2000). The posterior distribution used to infer Q is $Pr(Z,P,Q|X)$, which uses the priors $Pr(P,Q|X,Z)$ and $Pr\ (Z|X,P,Q)$. Arithmetic solutions of posterior distributions were not possible, and sampling from the priors was approximated using Markov chain Monte Carlo (MCMC), using Gibb's sampling to construct the chain (Pritchard *et al.* 2000). MCMC was used as a sampling tool that enables us to explore the posterior distributions (Sorensen and Gianola 2002). Markov chains of the parameters $((Z^{(1)}, P^{(1)}\ Q^{(1)}), (Z^{(2)},P^{(2)},Q^{(2)})\ldots(Z^{(m)},P^{(m)}\ Q^{(m)}))$ are generated until the posterior distributions were stable, which was dependent on the number of chains, m (Pritchard *et al.* 2000). In STRUCTURE, m was the burn-in period, which was the number of iterations required to stabilize the posterior distributions. The value of m was determined by evaluating whether the inferred values of the parameters (*e.g.*, $ln\ Pr(X|K)$) from the posterior distributions had converged. I chose 10^6 iterations for m, and used 10^6 iterations of the chain to approximate the posterior distributions. STRUCTURE determined the natural log of the probability of the data given a certain number of clusters ($ln\ Pr(X|K)$) for each value of K. I chose the value of K, that maximized this log likelihood. The probability of the data, given K (posterior probability of K) was determined by:

$$\Pr(X \mid K) = \frac{e^{\ln \Pr(X|K_{best})}}{\sum_{1}^{K} e^{\ln \Pr(X|K)}}$$

where K_{best} was the most likely value for K, and K was the maximum number of clusters which were evaluated in the scheme (Pritchard and Wen 2003).

APPENDIX IV

SUPPLEMENTAL GRAPHS FOR CHAPTER 2

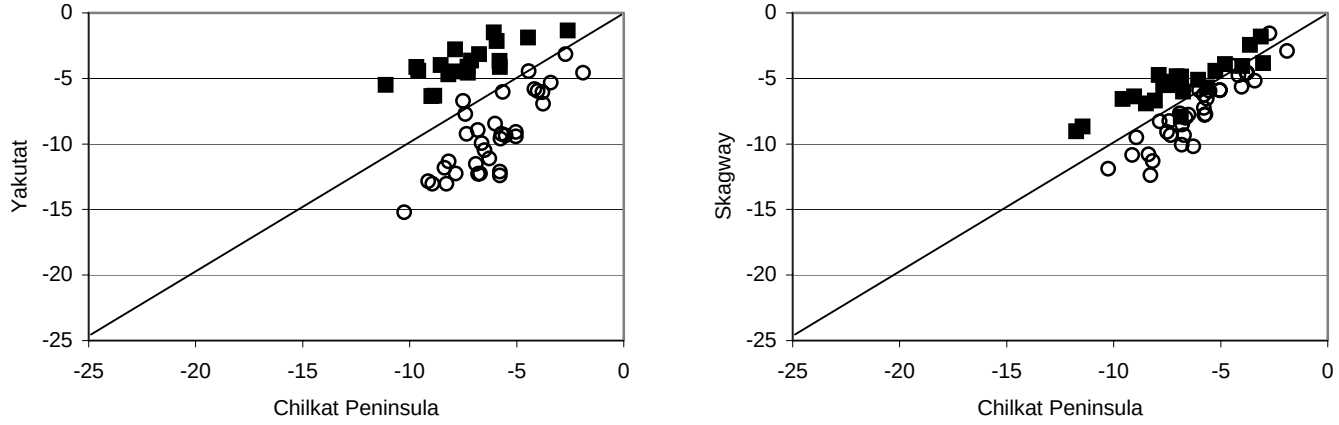
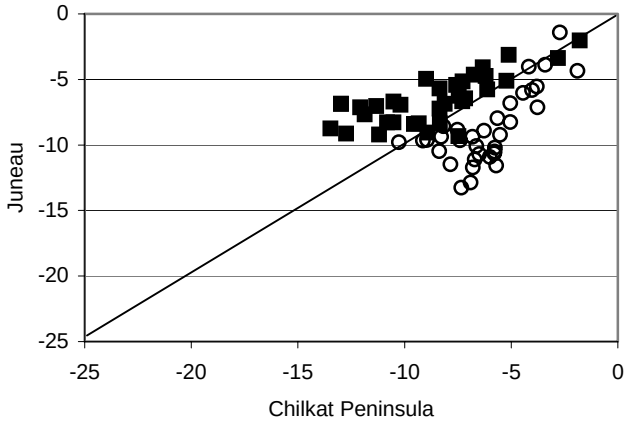


Figure A4 – 1. Assignment plots for all pair-wise comparisons (n = 55) of sampling regions in Southeast Alaska. X-axis the negative log likelihood of an individual being from the sampling region on the X axis relative to the negative log likelihood of an individual being from the sampling region on the Y-axis. Y-axis, vice versa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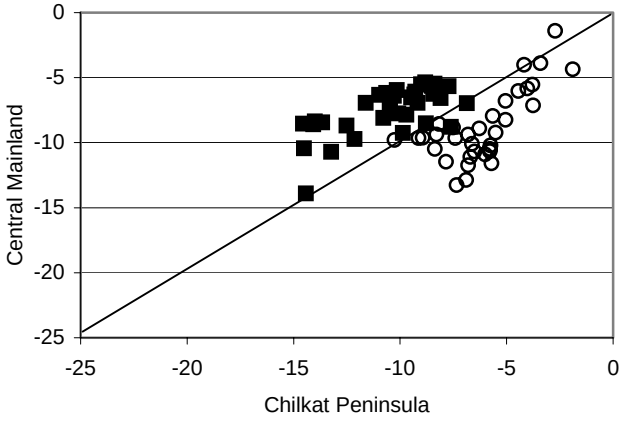
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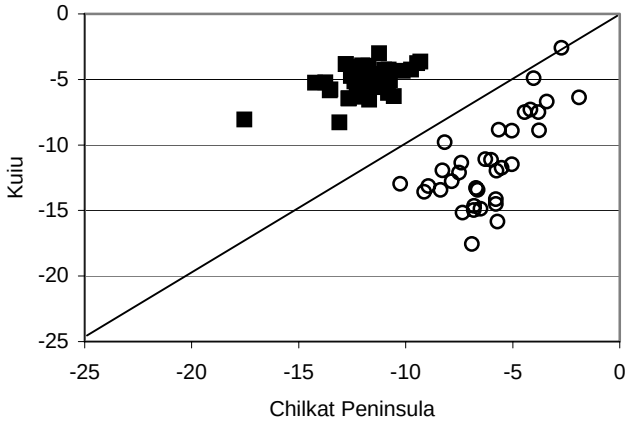
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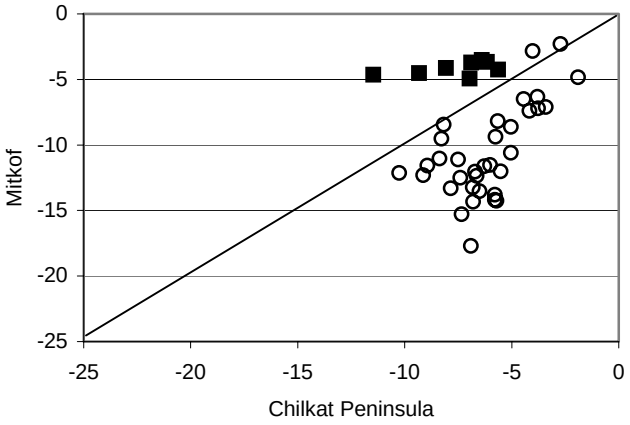
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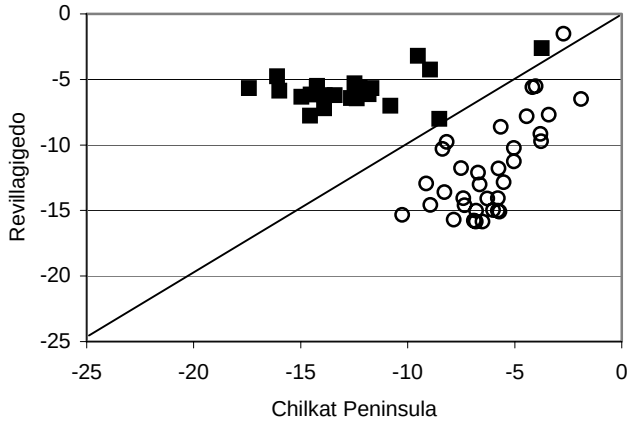
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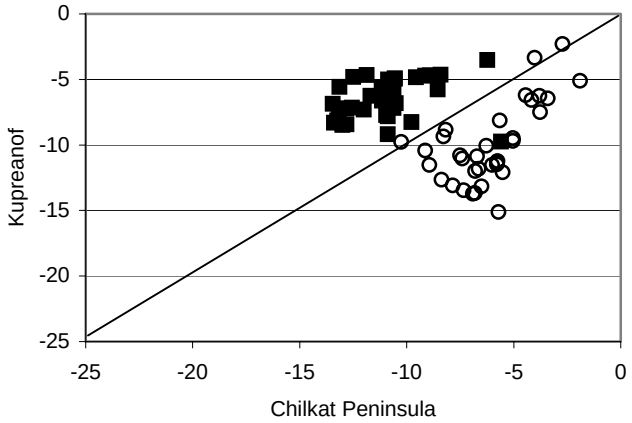
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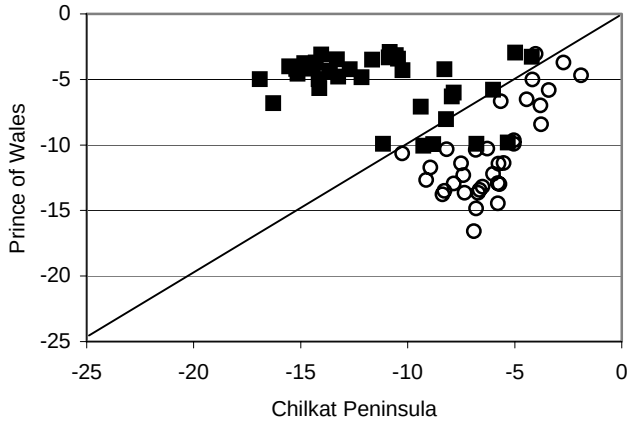
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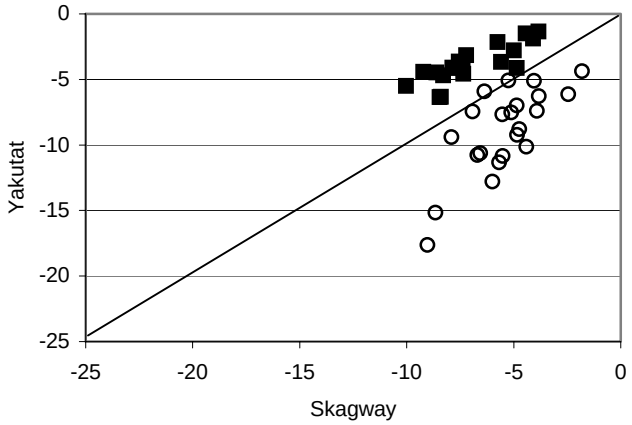
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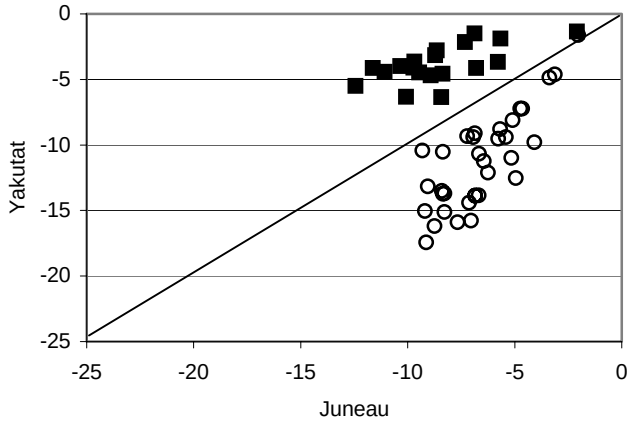
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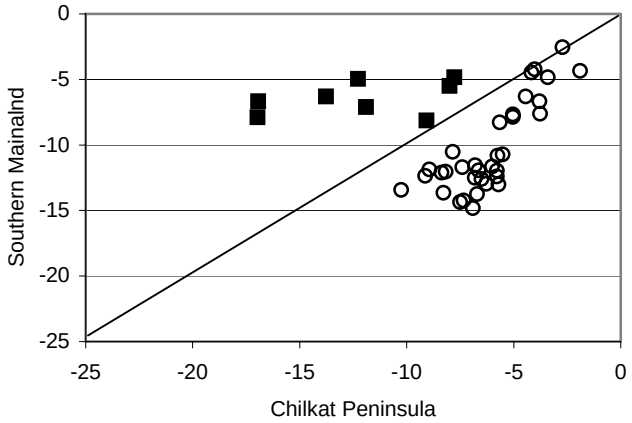
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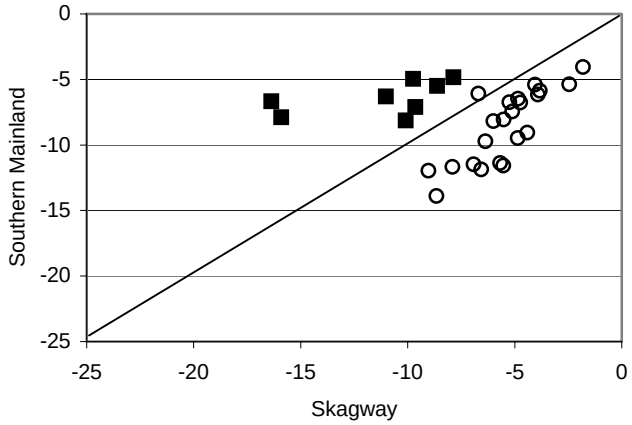
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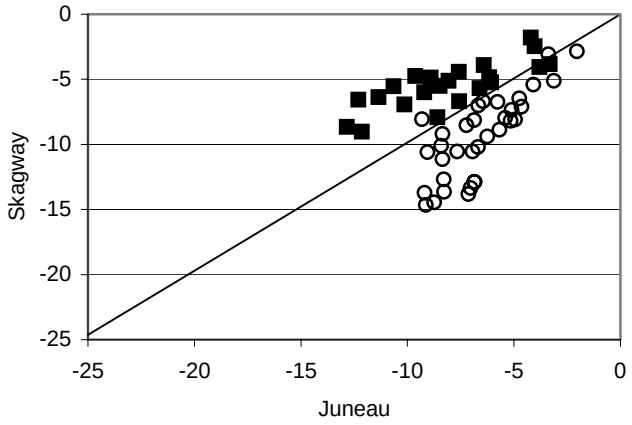
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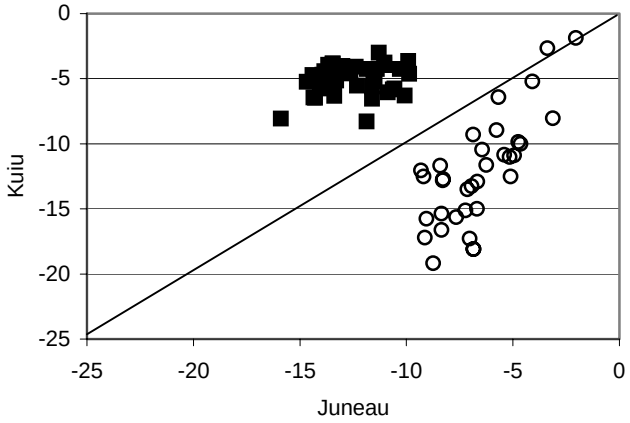
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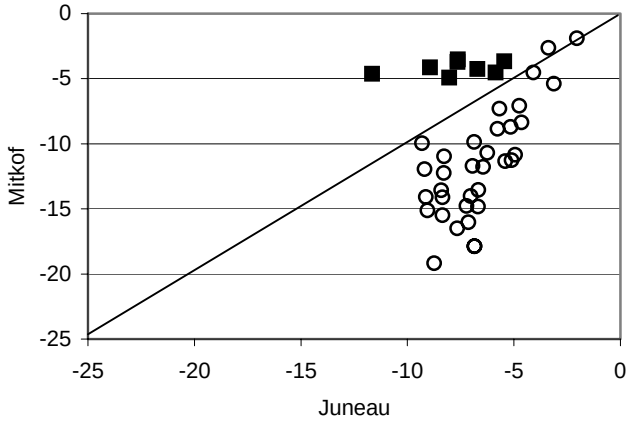
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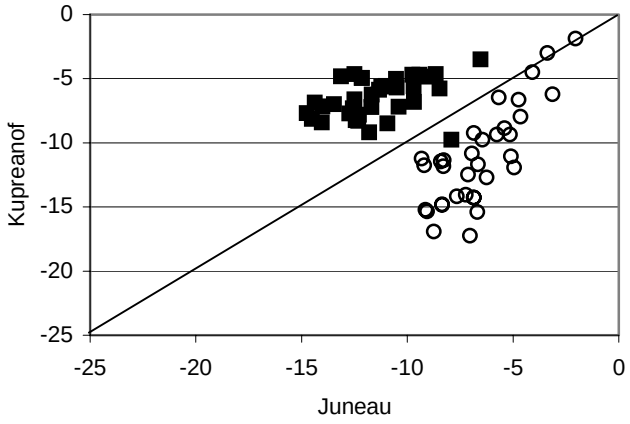
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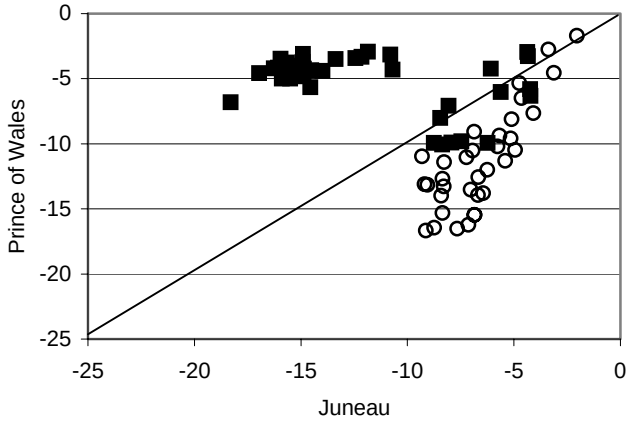
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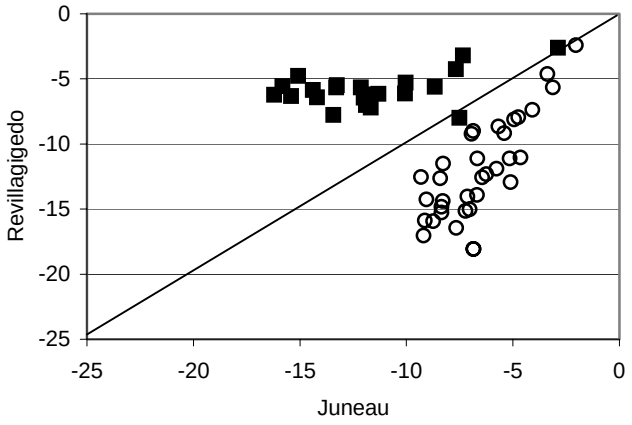
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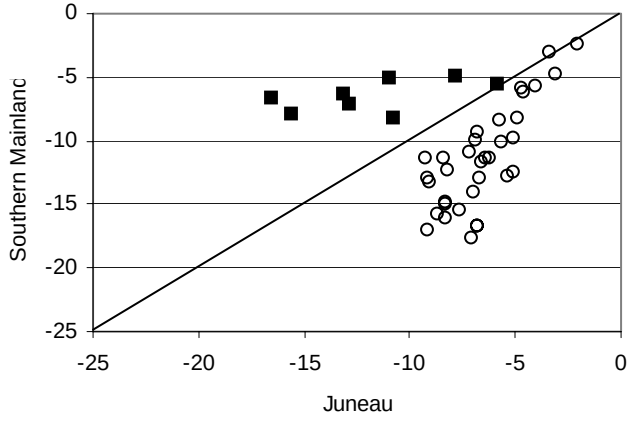
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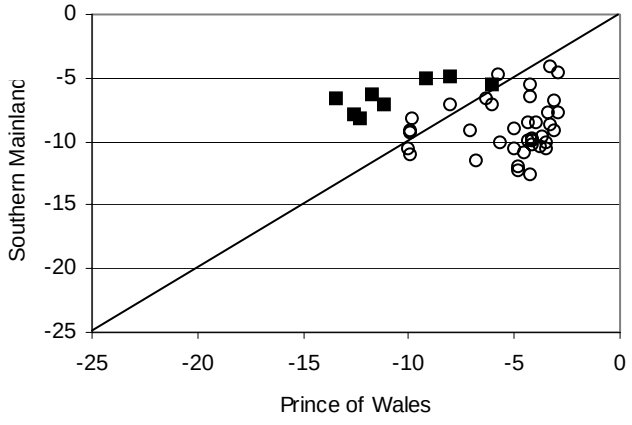
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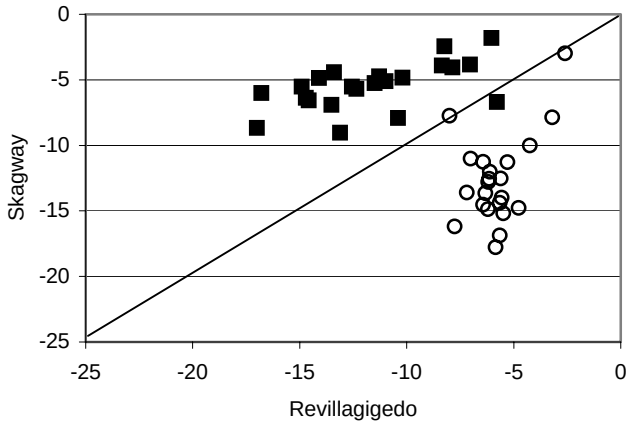
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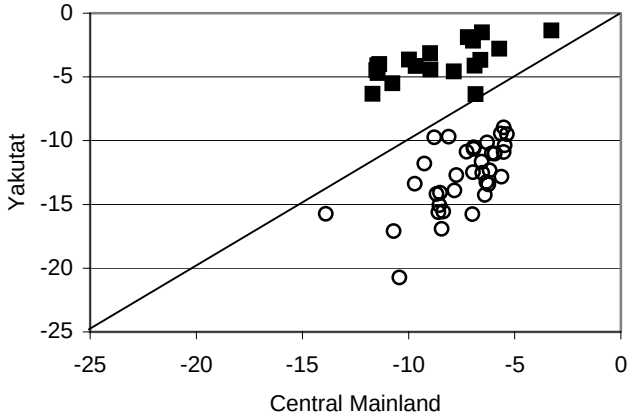
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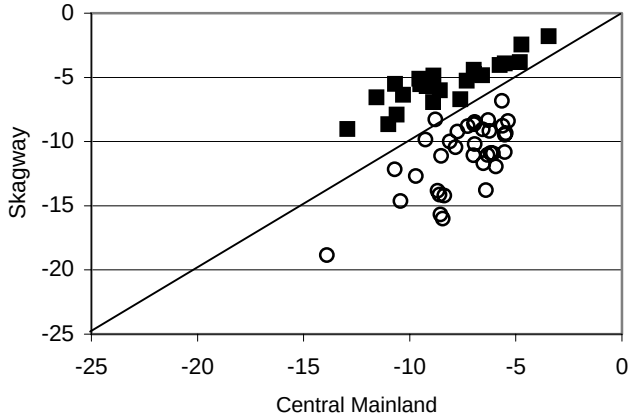
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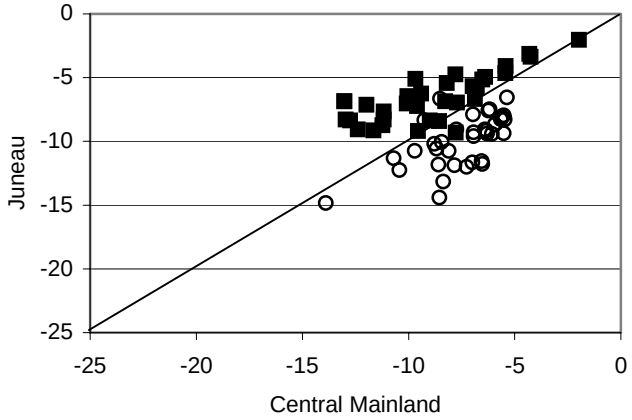
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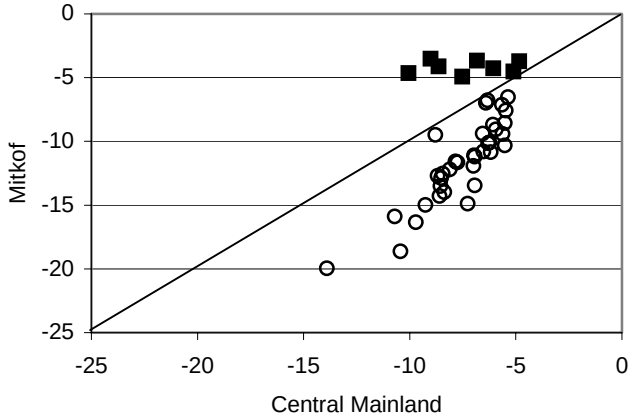
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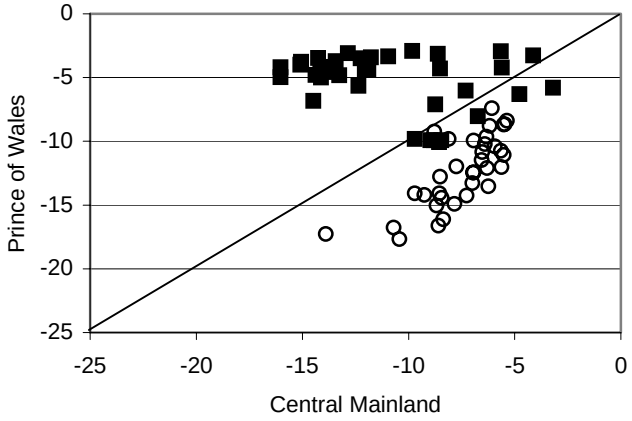
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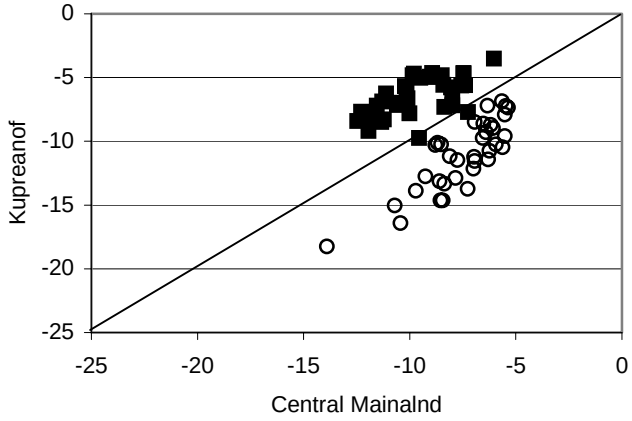
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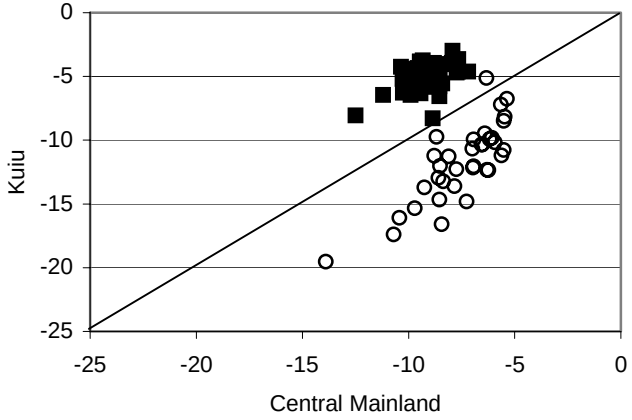
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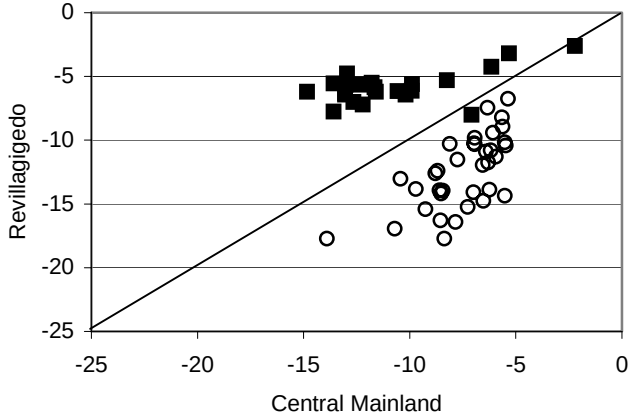
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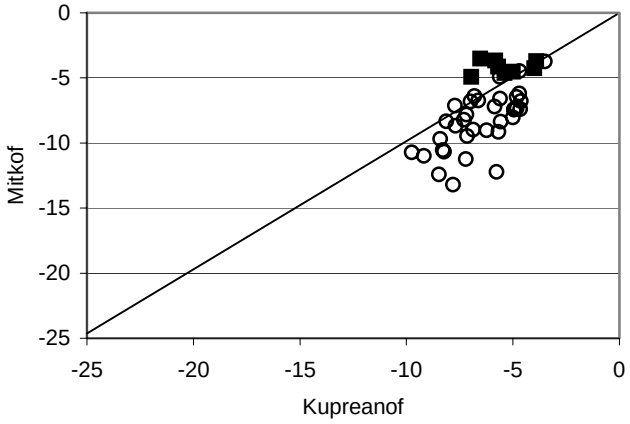
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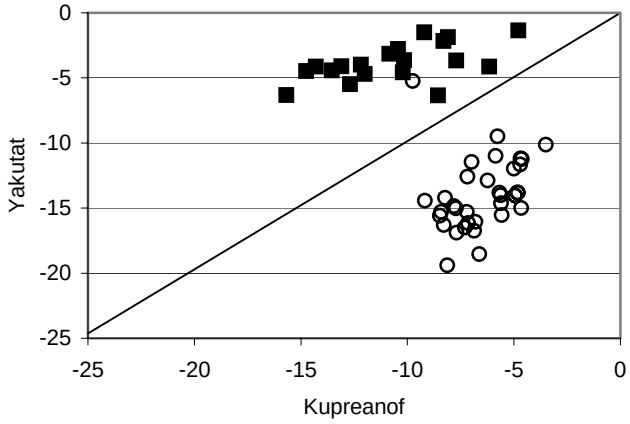
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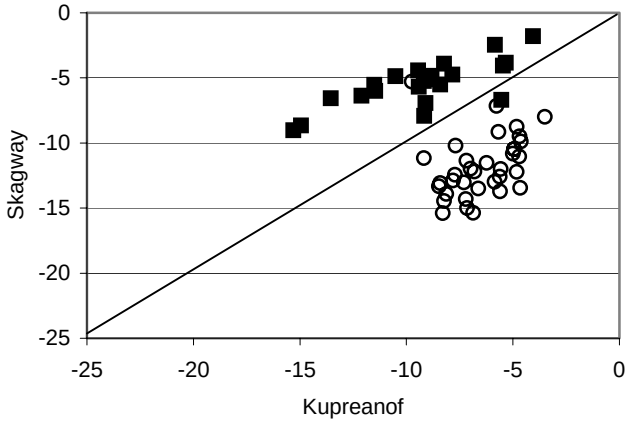
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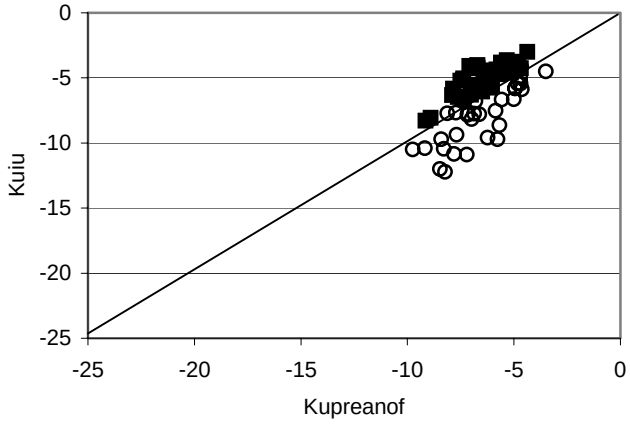
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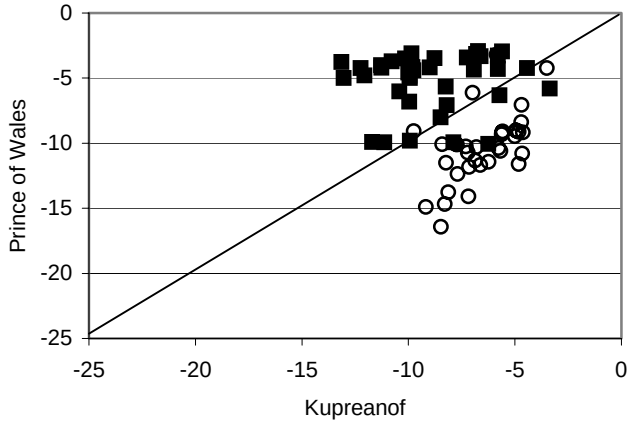
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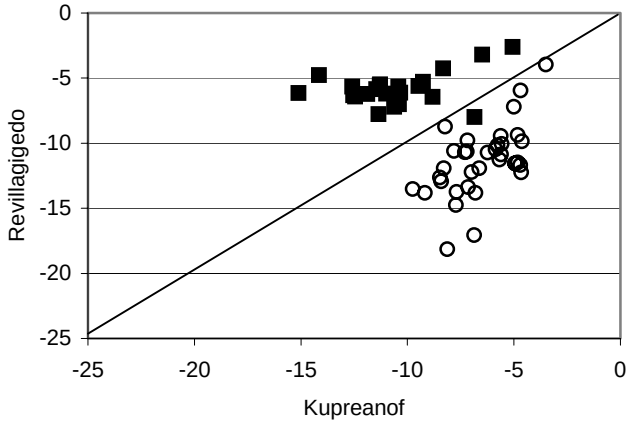
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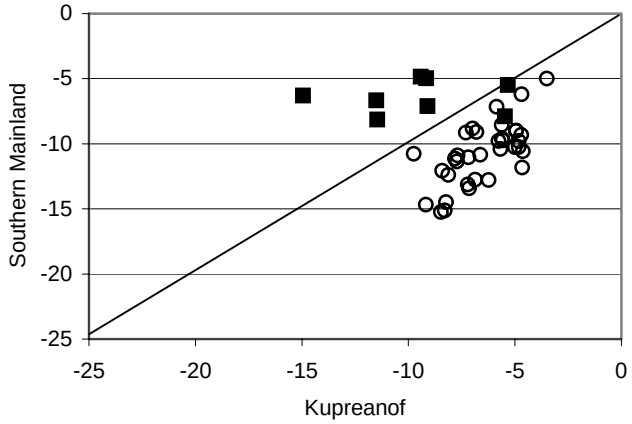
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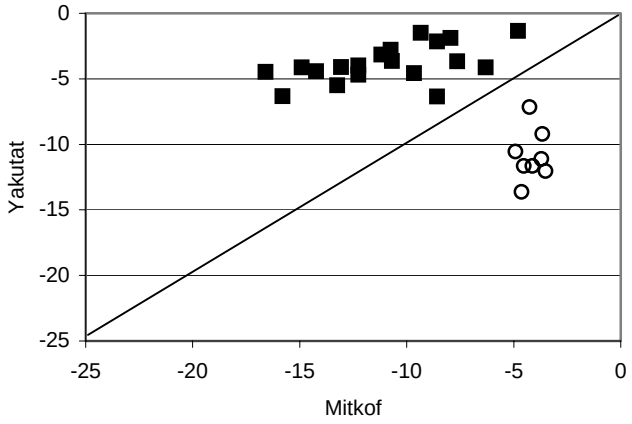
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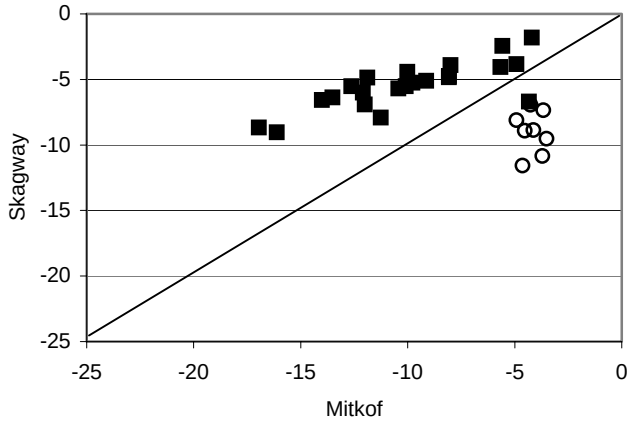
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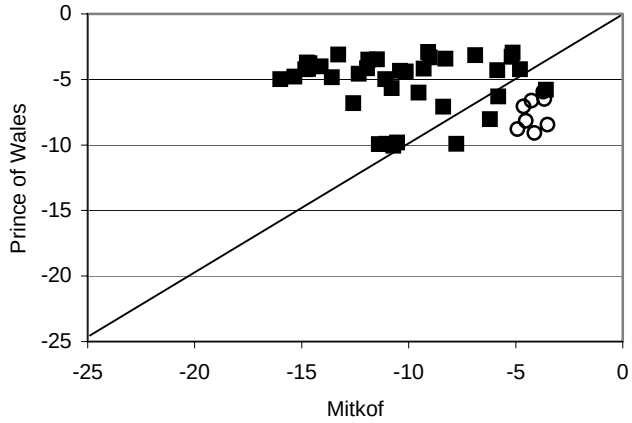
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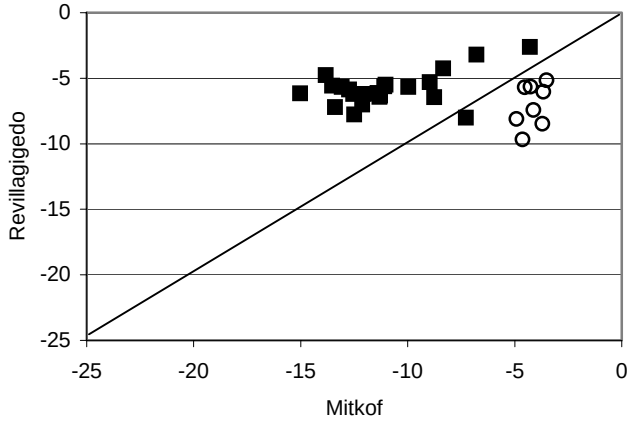
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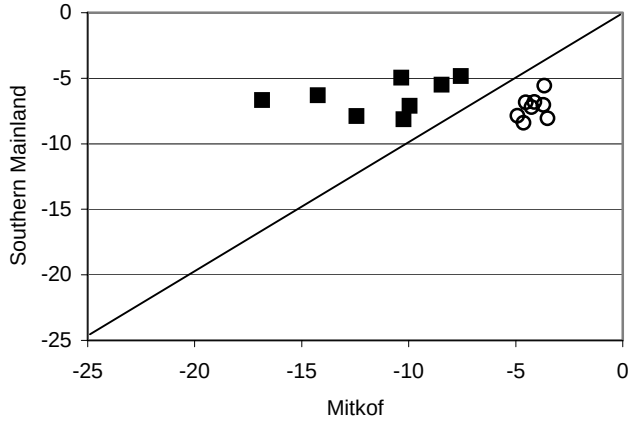
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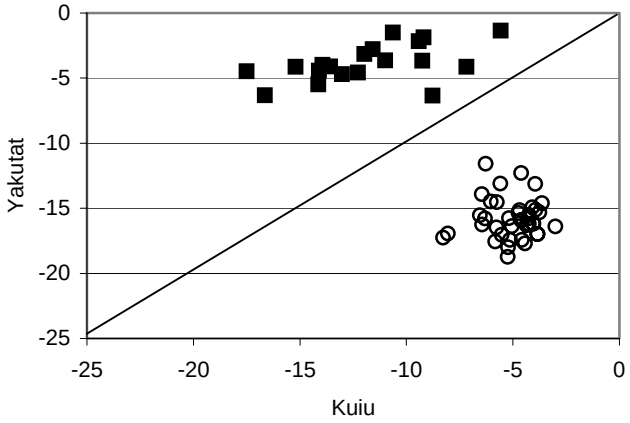
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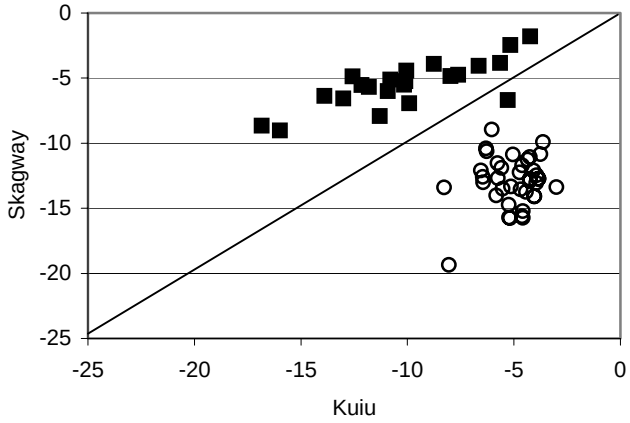
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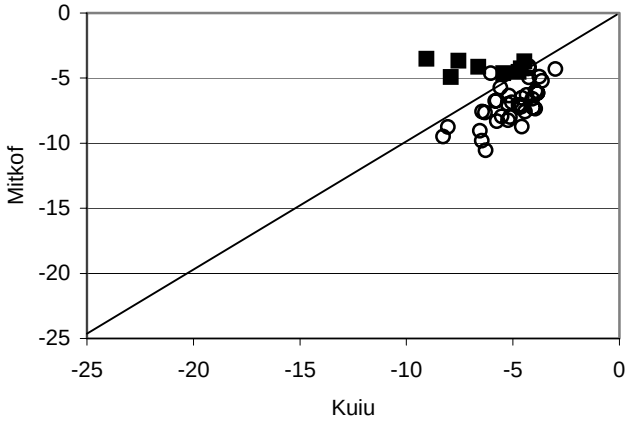
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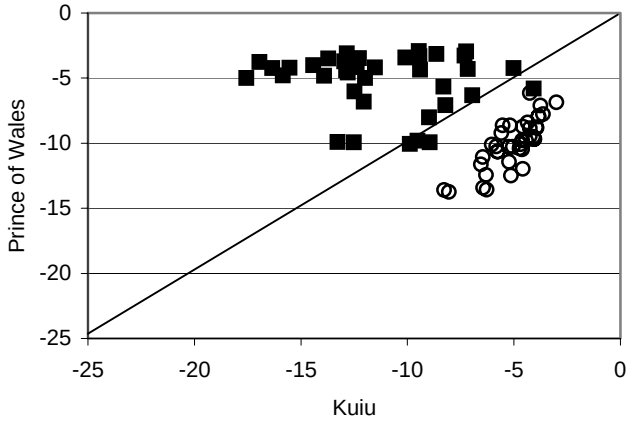
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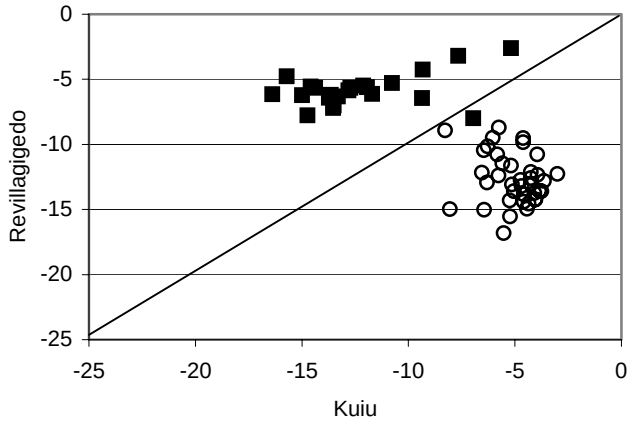
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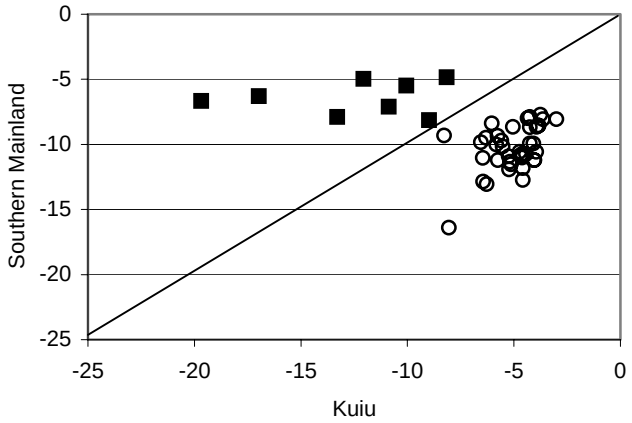
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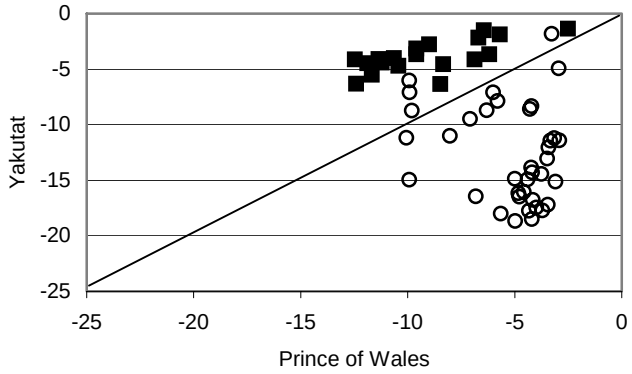
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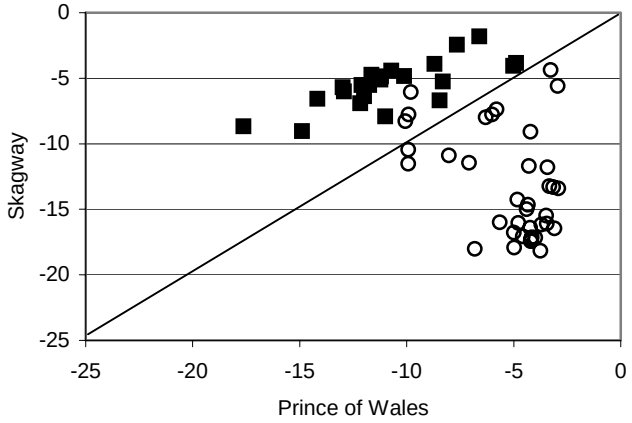
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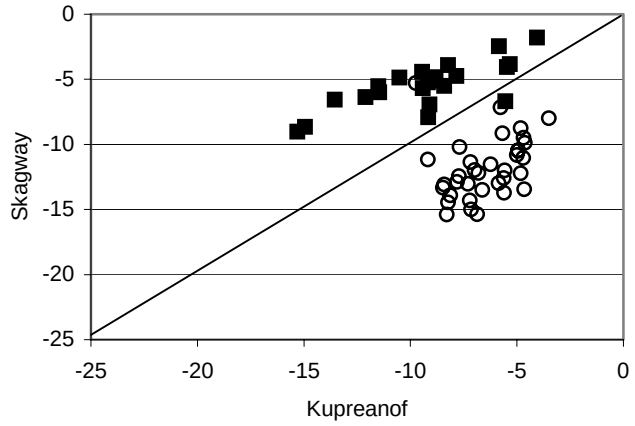
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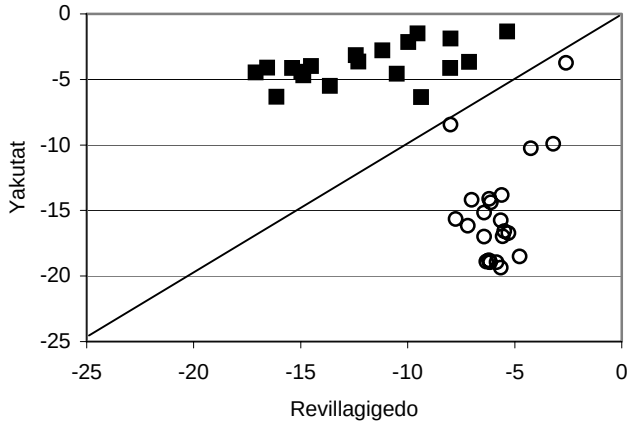
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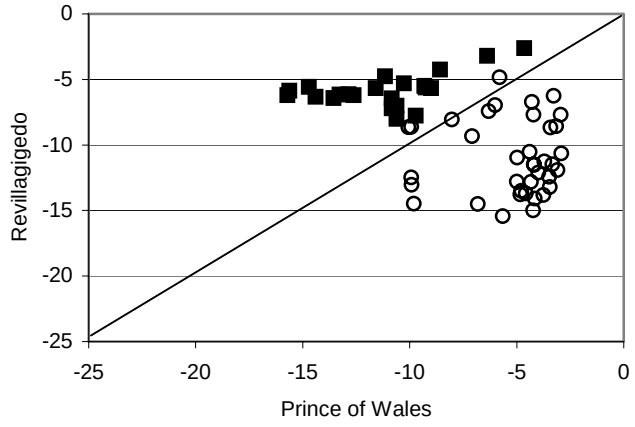
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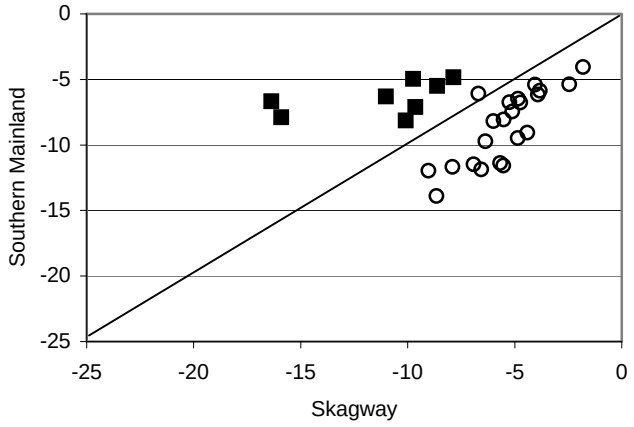
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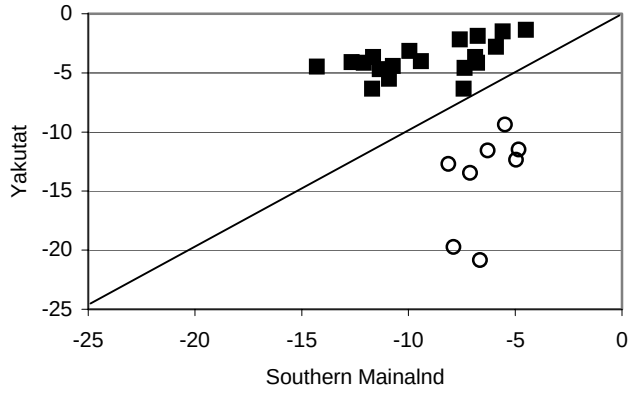
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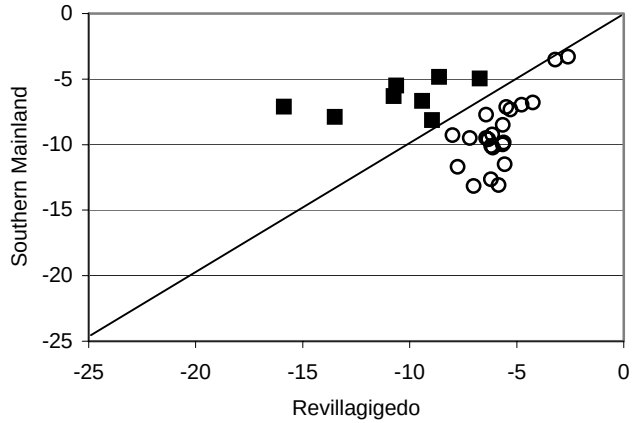
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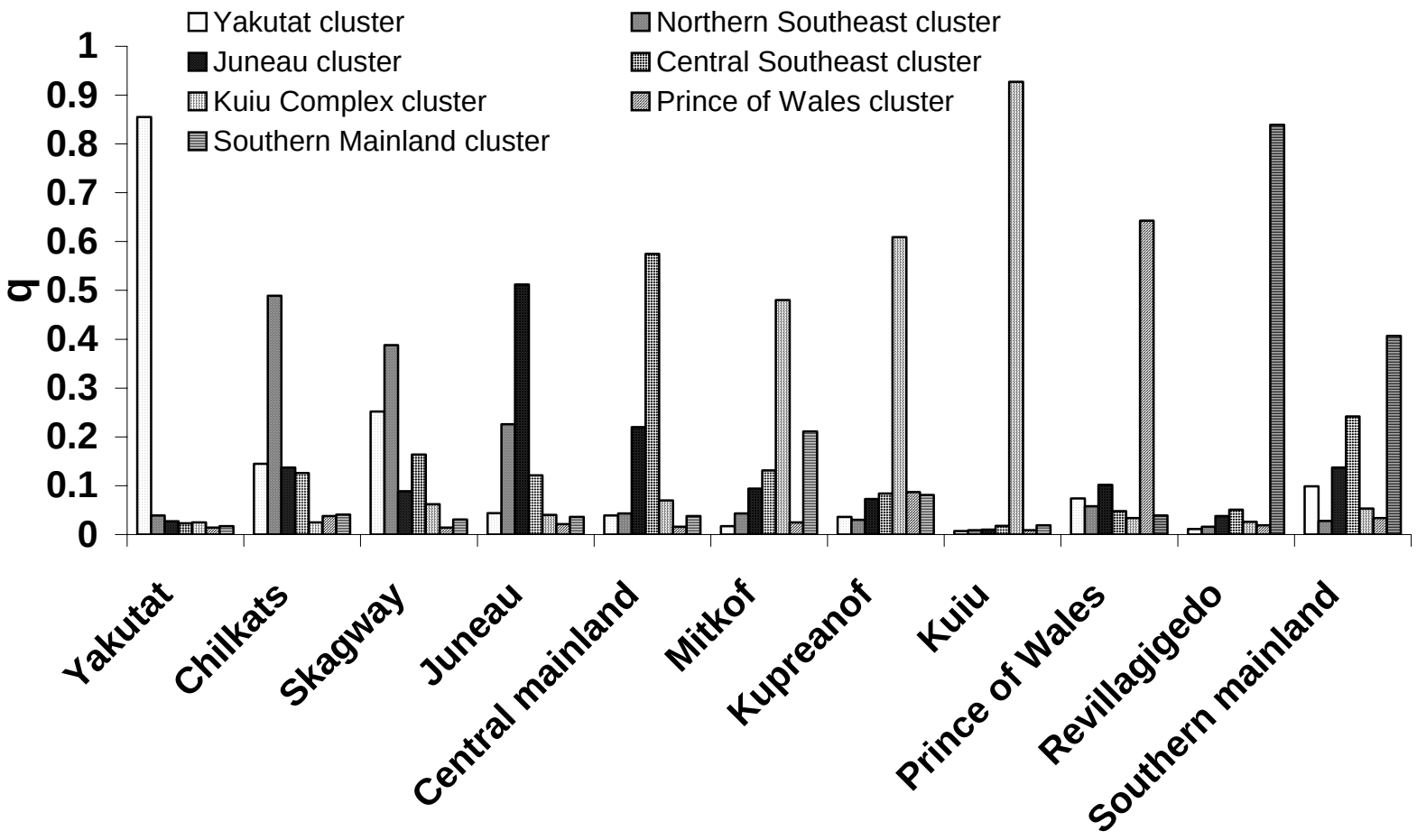

Figure A4 – 2.Average proportional membership (q) of individuals from sampling regions to the seven clusters identified by STRUCTURE.

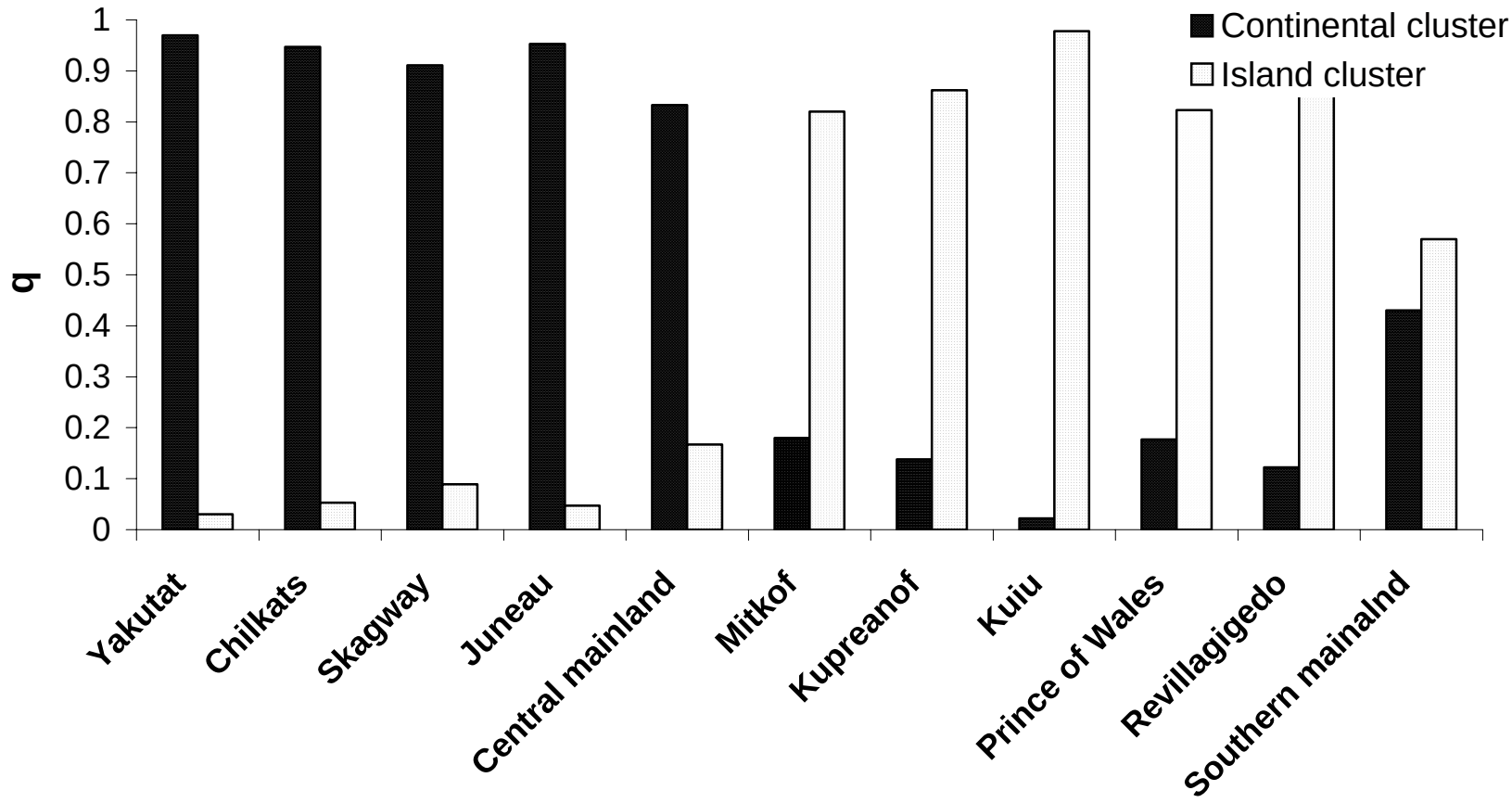

Figure A4 – 3. Average proportional membership (q) of individuals from sampling regions to two clusters identified by STRUCTURE.

APPENDIX V

Capture histories for each stream-year. 1 indicates capture, and 0 indicates not captured. The number following the series of 1's and 0's is the number of individuals with the particular capture history.

Saginaw Creek 2000

00000001 8 ;
00000010 7 ;
00000100 9 ;
00000110 1 ;
00000111 1 ;
00001000 8 ;
00001011 1 ;
00001100 2 ;
00001110 1 ;
00010000 14 ;
00011000 1 ;
00011011 1 ;
00011100 3 ;
00100000 13 ;
00100100 1 ;
00100101 1 ;
00101000 1 ;
00110100 1 ;
01000000 11 ;
01001000 1 ;
01011000 1 ;
01101010 1 ;
10000000 13 ;
10000010 1 ;
10010000 1 ;
11000000 1 ;
11010000 1 ;
11100000 1 ;
11111000 1 ;

Saginaw Creek, July 1st – July 26th 2000

0001 17 ;
0010 19 ;
0011 3 ;
0100 1 ;
1011 1 ;

Saginaw Creek, July 12th – Aug 1st 2000

0001 15 ;
0010 16 ;
0011 1 ;
0100 18 ;
0101 1 ;
0110 2 ;
0111 2 ;
1000 1 ;

Saginaw Creek, July 20th – Aug 6th 2000

0001 19 ;
0010 16 ;
0011 1 ;
0100 12 ;
0101 1 ;
0110 1 ;
1000 14 ;
1001 1 ;
1100 1 ;
1101 1 ;
1110 1 ;
1111 1 ;

Saginaw Creek, July 26th – Aug 13th 2000

1000 12 ;
1000 15 ;
1100 5 ;
1000 15 ;
1010 1 ;
1100 1 ;
1000 12 ;
1001 1 ;
1010 1 ;
1011 1 ;
1100 1 ;
1101 1 ;
1111 1 ;

Saginaw Creek, August 1st – August 20th 2000

0001 11 ;
0010 10 ;
0011 3 ;
0100 16 ;
0110 3 ;
0111 3 ;
1000 14 ;
1001 2 ;
1010 2 ;
1101 1 ;
1110 1 ;

Saginaw Creek, August 7th – August 26th 2000

0001 8 ;
0010 11 ;
0011 2 ;
0100 10 ;
0101 2 ;
0110 2 ;
0111 1 ;
1000 16 ;
1010 1 ;
1100 3 ;
1101 1 ;
1110 3 ;

Saginaw Creek, August 13th – September 1st 2000

0001 7 ;
0010 8 ;
0100 11 ;
0101 1 ;
0110 1 ;
0111 1 ;
1000 13 ;
1010 1 ;
1011 2 ;
1100 5 ;
1110 1 ;

Security Creek

0000000010 8 ;
0000000100 6 ;

0000001000 4 ;
0000010000 11 ;
0000010100 1 ;
0000100000 9 ;
0000101000 1 ;
0000110000 1 ;
0001000000 7 ;
0010000000 5 ;
0011000000 1 ;
0100000000 2 ;
1000000000 3 ;
1000100000 1 ;
1010000000 1 ;

Cabin Creek 2000

0001 5 ;
0010 8 ;
0011 2 ;
0100 2 ;
1000 3 ;
1001 2 ;
1011 1 ;
1111 1 ;

Portage Creek 2000

000001 8 ;
000010 2 ;
000100 5 ;
000101 1 ;
001000 4 ;
010000 2 ;
010010 1 ;
100000 5 ;

Upper Kadake Creek 2000

000001 8 ;
000010 6 ;
000100 3 ;
000101 2 ;
001000 3 ;
001001 2 ;
010000 1 ;

100000 9 ;
101000 2 ;

Lower Kadake Creek 2000
000001 8 ;
000010 6 ;
000100 3 ;
000101 2 ;
001000 3 ;
001001 2 ;
010000 1 ;
100000 9 ;
101000 2 ;

Saginaw Creek 2002

000000001 5 ;
000000010 6 ;
000000100 2 ;
000001000 8 ;
000001100 2 ;
000010000 7 ;
000010010 1 ;
000010110 1 ;
000011000 1 ;
000100000 12 ;
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001100000 1 ;
010000000 8 ;
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010100000 1 ;
011000000 1 ;
011100000 1 ;
100000000 8 ;
100000010 1 ;
100000110 1 ;
101000000 2 ;

Skinny Rowan Creek 2002

000000010 2 ;
000000100 3 ;

000000110 1 ;
000001000 2 ;
000010000 1 ;
000100000 3 ;
001000000 2 ;
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Cabin Creek 2002

00000001 3 ;
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00001000 3 ;
00010000 1 ;
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10000010 2 ;
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Portage Creek 2002

00000001 1 ;
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10000000 1 ;

Rowan Creek 2002

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10010000 1 ;
10110000 1 ;
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11100000 1 ;

APPENDIX VI

SUPPLEMENTAL TABLES AND FIGURES FOR CHAPTER 3.

Table A6 – 1. CJS models for black bears on Cabin Creek 2000. All tested models with ΔAICc ≤ 5.0 and φ(t)p(t) are presented. **Bold** indicates the constant ***φ*(.)*p*(.)** and saturated ***φ*(t)*p*(t)** models. φ(t)p(t) was the most saturated model run as cohorts were pooled. (.) indicates that the parameter is constant over all time intervals. (T) indicates a trend in the parameter over time, where (2T) refers to two groupings into which intervals were collapsed. (t) refers to a time-specific (non-linear) effect on the parameter, where (3t) refers to three groupings of intervals. φ represents apparent survival, or the likelihood of a bear remaining on the stream from one interval to the next, and p represents recapture probability.

Model	AICc	ΔAICc	AICc weight	Model likelihood	# Parameters	Deviance
***φ*(.)*p*(.)**	42.103	0.00	0.49324	1.0000	1	12.017
φ(.)p(T)	43.608	1.50	0.23248	0.4713	2	11.090
φ(.)p(2T)	43.773	1.67	0.21405	0.4340	2	11.255
φ(.)p(3t)	46.309	4.21	0.06024	0.1221	3	11.089
***φ*(t)*p*(t)§**	49.281	7.18	0.01344	0.0276	4	11.050

§ Information on relative fit of φ(t)p(t) if it were to be included in the set of models, however since many time-specific parameters were inestimable, this model was removed from the group, and therefore AICc weights presented for all other models do not incorporate the influence of the φ(t)p(t) model.

Table A6 – 2. CJS models for black bears on Cabin Creek 2002. Only models with ΔAICc ≤ 3.0 are presented. **Bold** indicates the constant ***φ*(.)*p*(.)** and saturated ***φ*(t)*p*(t)** models. $\varphi(t)p(t)$ was the most saturated model run as cohorts were pooled. (.) indicates that the parameter is constant over all time intervals. (t) refers to a time-specific (non-linear) effect on the parameter. (T) indicates a trend in the parameter over time, where (XT) refers to the number of groupings into which intervals were collapsed. φ represents apparent survival, or the likelihood of a bear remaining on the stream from one interval to the next, and p represents recapture probability.

Model	AICc	ΔAICc	AICc weight	Model likelihood	# Parameters	Deviance
***φ*(t)*p*(t)§**	94.805	0.00	0.47398	1.0000	7	47.994
***φ*(.)*p*(.)**	97.063	0.00	0.29127	1.0000	2	63.331
$\varphi(.)p(4T)$	97.895	0.83	0.19212	0.6596	3	61.831
$\varphi(.)p(2T)$	98.238	1.17	0.16190	0.5558	3	62.173
$\varphi(.)p(6T)$	98.558	1.5.0	0.13792	0.4735	3	62.493
$\varphi(.)p(5T)$	98.905	1.84	0.11597	0.3982	3	62.840
$\varphi(.)p(3T)$	99.185	2.12	0.10081	0.3461	3	63.120

§ Information on relative fit of $\varphi(t)p(t)$ if it were to be included in the set of models, however since many time-specific parameters were inestimable, this model was removed from the group, and therefore AICc weights presented for all other models do not incorporate the influence of the $\varphi(t)p(t)$ model.

Table A6 – 3. CJS models for black bears on Portage Creek 2000. Only one model had an ΔAICc ≤ 3.0; φ (t)p(t) is also presented. **Bold** indicates the constant $\boldsymbol{\varphi}$**(.)**$\boldsymbol{p}$**(.)** and saturated $\boldsymbol{\varphi}$**(t)**$\boldsymbol{p}$**(t)** models. φ(t)p(t) was the most saturated model run as cohorts were pooled. (.) indicates that the parameter is constant over all time intervals. (t) refers to a time-specific (non-linear) effect on the parameter. φ represents apparent survival, or the likelihood of a bear remaining on the stream from one interval to the next, and p represents recapture probability.

Model	AICc	ΔAICc	AICc weight	Model likelihood	# Parameters	Deviance
φ (.)p(.)	19.946	0.00	0.8751	1.0000	1	8.51
φ (t)p(t)§	19.065	0.00	0.5766	1.0000	3	5.17

§ Information on relative fit of φ(t)p(t) if it were to be included in the set of models, however since many time-specific parameters were inestimable, this model was removed from the group, and therefore AICc weights presented for all other models do not incorporate the influence of the φ(t)p(t) model.

Table A6 – 4. CJS models for black bears on Portage Creek 2002. Only models with ΔAICc ≤ 3.0 are presented. **Bold** indicates the constant ***φ*(.)*p*(.)** and saturated ***φ*(t)*p*(t)** models. *φ*(t)*p*(t) was the most saturated model run as cohorts were pooled. (.) indicates that the parameter is constant over all time intervals. (T) indicates a trend in the parameter over time, where (XT) refers to the number of groupings into which intervals were collapsed. (t) refers to a time-specific (non-linear) effect on the parameter, where (2t) refers to two groupings of intervals. *φ* represents apparent survival, or the likelihood of a bear remaining on the stream from one interval to the next, and *p* represents recapture probability.

Model	AICc	ΔAICc	AICc weight	Model likelihood	# Parameters	Deviance
***φ*(.)*p*(.)**	39.652	0.00	0.11585	1.0000	2	21.979
φ(T)*p*(.)	40.088	0.44	0.09316	0.8042	3	19.425
φ(6T)*p*(.)	40.101	0.45	0.09257	0.7991	3	19.438
φ(.)*p*(2T)	40.106	0.45	0.09233	0.7970	3	19.443
φ(4T)*p*(.)	40.206	0.55	0.08782	0.7581	3	19.544
φ(3T)*p*(.)	40.232	0.58	0.08671	0.7485	3	19.569
φ(5T)*p*(.)	40.297	0.64	0.08394	0.7246	3	19.634
φ(.)*p*(4T)	41.071	1.42	0.05698	0.4919	3	20.409
φ(.)*p*(T)	41.101	1.45	0.05614	0.4846	3	20.438
φ(.)*p*(5T)	41.239	1.59	0.05240	0.4523	3	20.576
***φ*(t)*p*(t)§**	41.257	1.60	0.04937	0.4483	5	12.986
φ(.)*p*(3T)	41.855	2.20	0.03851	0.3324	3	21.192
φ(.)*p*(2t)	42.067	2.41	0.03464	0.2990	3	21.404

§ Information on relative fit of *φ*(t)*p*(t) if it were to be included in the set of models, however since many time-specific parameters were inestimable, this model was removed from the group, and therefore AICc weights presented for all other models do not incorporate the influence of the *φ*(t)*p*(t) model.

Table A6 – 5. CJS models for black bears on Saginaw Creek 2000. Only models with ΔAICc ≤ 3.0 and φ(t)p(t) are presented. **Bold** indicates the constant $\boldsymbol{\varphi}$**(.)**$\boldsymbol{p}$**(.)** and saturated $\boldsymbol{\varphi}$**(t)**$\boldsymbol{p}$**(t)** models. φ(t)p(t) was the most saturated model run as cohorts were pooled. (.) indicates that the parameter is constant over all time intervals. (T) indicates a trend in the parameter over time, where (XT) refers to the number of groupings into which intervals were collapsed. (t) refers to a time-specific (non-linear) effect on the parameter, where (Xt) refers to three groupings of intervals. φ represents apparent survival, or the likelihood of a bear remaining on the stream from one interval to the next, and p represents recapture probability.

Model	AICc	ΔAICc	AICc weight	Model likelihood	# Parameters	Deviance
φ(.)p(.)	248.702	0.00	0.08107	1.0000	2	80.431
φ(3T)p(3T)	249.510	0.81	0.05413	0.6677	4	77.025
φ(4T)p(3T)	250.113	1.41	0.04004	0.4939	4	77.628
φ(.)p(5T)	250.146	1.44	0.03938	0.4858	3	79.784
φ(3T)p(5T)	250.231	1.53	0.03774	0.4655	4	77.746
φ(.)p(3T)	250.235	1.53	0.03767	0.4647	3	79.873
φ(4T)p(5T)	250.245	1.54	0.03747	0.4622	4	77.761
φ(2T)p(2T)	250.287	1.58	0.03670	0.4527	4	77.802
φ(.)p(3t)	250.300	1.60	0.03647	0.4499	4	77.815
φ(.)p(6T)	250.336	1.63	0.03581	0.4417	3	79.974
φ(T)p(3T)	250.354	1.65	0.03549	0.4378	4	77.870
φ(T)p(5T)	250.484	1.78	0.03326	0.4103	4	77.999
φ(5T)p(3T)	250.487	1.78	0.03321	0.4097	4	78.002
φ(.)p(2T)	250.609	1.91	0.03124	0.3854	3	80.247
φ(.)p(2t)	250.609	1.91	0.03124	0.3854	3	80.247
φ(.)p(4T)	250.610	1.91	0.03123	0.3852	3	80.248
φ(2T)p(.)	250.728	2.03	0.02944	0.3631	3	80.366
φ(.)p(4t)	250.751	2.05	0.02909	0.3588	3	80.389
φ(2T)p(5T)	251.096	2.39	0.02449	0.3021	4	78.612
φ(2T)p(3T)	251.218	2.52	0.02304	0.2842	4	78.733
φ(T)p(6T)	251.268	2.57	0.02247	0.2772	4	78.784
φ(4T)p(4T)	251.324	2.62	0.02185	0.2695	4	78.839
φ(.)p(3t)	251.435	2.73	0.02067	0.2550	4	78.951
φ(T)p(T)	251.494	2.79	0.02008	0.2477	4	79.009
φ(3T)p(4T)	251.498	2.80	0.02004	0.2472	4	79.013
φ(T)p(4T)	251.740	3.04	0.01775	0.2189	4	79.255
φ(t)p(t)	267.101	18.4	0.00001	0.0001	13	73.960

§ Information on relative fit of φ(t)p(t) if it were to be included in the set of models, however since many time-specific parameters were inestimable, this model was removed from the group, and therefore AICc weights presented for all other models do not incorporate the influence of the φ(t)p(t) model.

Table A6 – 6. CJS models for black bears on Saginaw Creek 2002. Only models with ΔAICc ≤ 3.0 are presented. **Bold** indicates the constant ***φ*(.)*p*(.)** and saturated ***φ*(t)*p*(t)** models. *φ*(t) *p*(t) was the most saturated model run as cohorts were pooled. (.) indicates that the parameter is constant over all time intervals. (t) refers to a time-specific (non-linear) effect on the parameter. (T) indicates a trend in the parameter over time, where (XT) refers to the number of groupings into which intervals were collapsed. *φ* represents apparent survival, or the likelihood of a bear remaining on the stream from one interval to the next, and *p* represents recapture probability.

Model	AICc	Δ AICc	AICc weight	Model likelihood	#Parameters	Deviance
***φ*(t)*p*(t)§**	**153.525**	**0.00**	**0.45811**	**1.0000**	**8**	**29.972**
***φ*(.)*p*(.)**	**158.219**	**0.00**	**0.08088**	**1.0000**	**2**	**48.175**
φ(3T)*p*(.)	158.751	0.53	0.06200	0.7665	3	46.576
φ(5T)*p*(6T)	158.935	0.72	0.05653	0.6989	4	44.584
φ(7T)*p*(.)	159.034	0.81	0.05383	0.6655	3	46.859
φ(6T)*p*(.)	159.063	0.84	0.05305	0.6559	3	46.888
φ(5T)*p*(4T)	159.205	0.99	0.04941	0.6109	4	44.854
φ(.)*p*(5T)	159.409	1.19	0.04462	0.5517	3	47.234
φ(4T)*p*(.)	159.411	1.19	0.04456	0.5509	3	47.237
φ(.)*p*(3T)	159.632	1.41	0.03991	0.4934	3	47.458
φ(5T)*p*(2T)	159.714	1.49	0.03831	0.4736	4	45.363
φ(5T)*p*(T)	159.813	1.59	0.03645	0.4507	4	45.462
φ(5T)*p*(7T)	160.064	1.84	0.03215	0.3975	4	45.713
φ(.)*p*(T)	160.085	1.87	0.03182	0.3934	3	47.91
φ(.)*p*(6T)	160.093	1.87	0.03170	0.3919	3	47.918
φ(3T)*p*(6T)	160.112	1.89	0.03139	0.3881	4	45.761
φ(2T)*p*(.)	160.129	1.91	0.03113	0.3849	3	47.954
φ(3T)*p*(2T)	160.211	1.99	0.02988	0.3694	4	45.86
φ(.)*p*(4T)	160.229	2.01	0.02961	0.3661	3	48.054
φ(5T)*p*(5T)	160.293	2.07	0.02868	0.3546	4	45.942
φ(.)*p*(2T)	160.344	2.12	0.02796	0.3457	3	48.17
φ(5T)*p*(3T)	160.441	2.22	0.02663	0.3292	4	46.09
φ(3T)*p*(T)	160.483	2.26	0.02608	0.3224	4	46.131
φ(T)*p*(T)	160.764	2.54	0.02266	0.2802	4	46.413
φ(7T)*p*(T)	160.783	2.56	0.02245	0.2776	4	46.432
φ(6T)*p*(T)	160.877	2.66	0.02141	0.2647	4	46.526
φ(4T)*p*(2T)	161.012	2.79	0.02002	0.2475	4	46.66

§ Information on relative fit of *φ*(t)*p*(t) if it were to be included in the set of models, however since many time-specific parameters were inestimable, this model was removed from the group, and therefore AICc weights presented for all other models do not incorporate the influence of the *φ*(t)*p*(t) model.

Table A6 – 7. CJS models for black bears on Lower Kadake Creek 2000. Only models with ΔAICc ≤ 3.0 are presented. **Bold** indicates the constant ***φ*(.)*p*(.)** and saturated ***φ*(t)*p*(t)** models. φ(t)*p*(t) was the most saturated model run as cohorts were pooled. (.) indicates that the parameter is constant over all time intervals. (T) indicates a trend in the parameter over time, where (3T) refers to the three groupings into which intervals were collapsed. (t) refers to a time-specific (non-linear) effect on the parameter, where (2t) refers to two groupings of intervals. φ represents apparent survival, or the likelihood of a bear remaining on the stream from one interval to the next, and *p* represents recapture probability.

Model	AICc	ΔAICc	AICc weight	Model likelihood	# Parameters	Deviance
***φ*(t)*p*(t)§**	34.327	0.00	0.99633	1.0000	2	5.9916
***φ*(.)*p*(.)**	48.500	0.00	0.22704	1.0000	2	20.164
φ(T)*p*(.)	49.577	1.08	0.13247	0.5835	3	18.763
φ(.)*p*(T)	49.708	1.21	0.12409	0.5466	3	18.893
φ(3T)*p*(.)	49.720	1.22	0.12331	0.5431	3	18.906
φ(.)*p*(3T)	49.927	1.43	0.11122	0.4899	3	19.112
φ(.)*p*(2t)	50.536	2.04	0.08202	0.3613	3	19.722

§ Information on relative fit of φ(t)*p*(t) if it were to be included in the set of models, however since many time-specific parameters were inestimable, this model was removed from the group, and therefore AICc weights presented for all other models do not incorporate the influence of the φ(t)*p*(t) model.

Table A6 – 8. CJS models for black bears on Security Creek 2000. Only models with ΔAICc ≤ 3.0 are presented. **Bold** indicates the constant ***φ*(.)*p*(.)** and saturated ***φ*(t)*p*(t)** models. *φ*(t)*p*(t) was the most saturated model run as cohorts were pooled. (.) indicates that the parameter is constant over all time intervals. (T) indicates a trend in the parameter over time, where (XT) refers to the number of groupings into which intervals were collapsed. (t) refers to a time-specific effect on the parameter. *φ* represents apparent survival, or the likelihood of a bear remaining on the stream from one interval to the next, and *p* represents recapture probability.

Model	AICc	ΔAICc	AICc weight	Model likelihood	# Parameters	Deviance
φ(3T)*p*(.)	56.641	0.00	0.09409	1.0000	3	15.207
φ(4T)*p*(.)	57.089	0.45	0.07522	0.7994	3	15.655
φ(5T)*p*(.)	57.336	0.70	0.06647	0.7064	3	15.902
***φ*(.)*p*(.)**	57.348	0.71	0.06607	0.7022	2	18.137
φ(.)*p*(5T)	57.705	1.06	0.05526	0.5873	3	16.272
φ(.)*p*(T)	57.729	1.09	0.05460	0.5803	3	16.296
φ(2T)*p*(.)	57.805	1.16	0.05258	0.5588	3	16.371
φ(.)*p*(4T)	57.822	1.18	0.05213	0.5540	3	16.388
φ(.)*p*(3T)	57.823	1.18	0.05210	0.5537	3	16.390
φ(.)*p*(2T)	58.127	1.49	0.04475	0.4756	3	16.694
***φ*(t)*p*(t)§**	58.174	1.53	0.04228	0.4644	6	9.5622
φ(3T)*p*(2T)	58.855	2.21	0.03110	0.3305	4	15.117
φ(3T)*p*(3T)	58.931	2.29	0.02993	0.3181	4	15.193
φ(3T)*p*(5T)	58.935	2.29	0.02988	0.3176	4	15.197
φ(3T)*p*(T)	58.937	2.30	0.02985	0.3172	4	15.199
φ(3T)*p*(4T)	58.941	2.30	0.02979	0.3166	4	15.203
φ(T)*p*(T)	59.087	2.45	0.02770	0.2944	4	15.349
φ(4T)*p*(2T)	59.312	2.67	0.02474	0.2629	4	15.574
φ(4T)*p*(T)	59.346	2.70	0.02433	0.2586	4	15.608
φ(4T)*p*(3T)	59.361	2.72	0.02414	0.2566	4	15.623
φ(5T)*p*(2T)	59.484	2.84	0.02271	0.2414	4	15.746
φ(5T)*p*(T)	59.534	2.89	0.02214	0.2353	4	15.796
φ(5T)*p*(3T)	59.553	2.91	0.02194	0.2332	4	15.815
φ(5T)*p*(5T)	59.566	2.92	0.02180	0.2317	4	15.828

§ Information on relative fit of *φ*(t)*p*(t) if it were to be included in the set of models, however since many time-specific parameters were inestimable, this model was removed from the group, and therefore AICc weights presented for all other models do not incorporate the influence of the *φ*(t)*p*(t) model.

Table A6 – 9. CJS models for black bears on Rowan Creek 2002. Only models with ΔAICc ≤ 3.0 and φ(t)p(t) are presented. **Bold** indicates the constant $\boldsymbol{\varphi}$**(.)**$\boldsymbol{p}$**(.)** and saturated $\boldsymbol{\varphi}$**(t)**$\boldsymbol{p}$**(t)** models. φ(t)p(t) was the most saturated model run as cohorts were pooled. (.) indicates that the parameter is constant over all time intervals. (T) indicates a trend in the parameter over time, where (XT) refers to the number of groupings into which intervals were collapsed. (t) refers to a time-specific (non-linear) effect on the parameter, where (Xt) refers to two groupings of intervals. φ represents apparent survival, or the likelihood of a bear remaining on the stream from one interval to the next, and p represents recapture probability.

Model	AICc	ΔAICc	AICc weight	Model likelihood	# Parameters	Deviance
φ(.)p(.)	207.641	0.00	0.12543	1.0000	2	71.148
φ(3t)p(.)	208.225	0.58	0.09369	0.7470	3	69.607
φ(.)p(3t)	209.251	1.61	0.05609	0.4472	4	68.463
φ(.)p(T)	209.264	1.62	0.05573	0.4443	3	70.645
φ(T)p(.)	209.299	1.66	0.05476	0.4366	3	70.681
φ(.)p(3T)	209.328	1.69	0.05396	0.4302	3	70.710
φ(.)p(6T)	209.361	1.72	0.05310	0.4234	3	70.742
φ(.)p(4T)	209.458	1.82	0.05056	0.4031	3	70.840
φ(.)p(2T)	209.495	1.85	0.04964	0.3958	3	70.877
φ(.)p(2t)	209.495	1.85	0.04964	0.3958	3	70.877
φ(3T)p(.)	209.526	1.88	0.04889	0.3898	3	70.907
φ(.)p(5T)	209.723	2.08	0.04430	0.3532	3	71.104
φ(.)p(2t)	209.734	2.09	0.04405	0.3512	3	71.116
φ(t)p(t)§	227.172	19.5	0.00001	0.0001	13	64.617

§ Information on relative fit of φ(t)p(t) if it were to be included in the set of models, however since many time-specific parameters were inestimable, this model was removed from the group, and therefore AICc weights presented for all other models do not incorporate the influence of the φ(t)p(t) model.

Table A6 – 10. CJS models for black bears on Skinny Rowan Creek 2002. Only models with ΔAICc ≤ 3.0 and $\varphi(.)p(.)$ are presented. **Bold** indicates the constant $\boldsymbol{\varphi(.)p(.)}$ and saturated $\boldsymbol{\varphi(t)p(t)}$ models. $\varphi(t)p(t)$ was the most saturated model run as cohorts were pooled. (.) indicates that the parameter is constant over all time intervals. (t) refers to a time-specific (non-linear) effect on the parameter. (T) indicates a trend in the parameter over time, where (XT) refers to the number of groupings into which intervals were collapsed. φ represents apparent survival, or the likelihood of a bear remaining on the stream from one interval to the next, and p represents recapture probability.

Model	AICc	ΔAICc	AICc weight	Model likelihood	# Parameters	Deviance
$\varphi(3T)p(.)$	102.584	0.00	0.07618	1.0000	3	64.257
$\varphi(5T)p(.)$	103.059	0.48	0.06006	0.7884	3	64.733
$\varphi(T)p(.)$	103.238	0.65	0.05493	0.7210	3	64.911
$\varphi(3T)p(6T)$	103.530	0.95	0.04746	0.6230	4	62.789
$\varphi(4T)p(.)$	103.898	1.31	0.03948	0.5182	3	65.572
$\varphi(6T)p(.)$	103.979	1.40	0.03791	0.4976	3	65.652
$\varphi(6T)p(T)$	104.185	1.60	0.03421	0.4490	4	63.443
$\varphi(3T)p(T)$	104.323	1.74	0.03193	0.4191	4	63.582
$\varphi(6T)p(6T)$	104.391	1.81	0.03086	0.4051	4	63.650
$\varphi(3T)p(4T)$	104.477	1.89	0.02956	0.3880	4	63.735
$\varphi(6T)p(4T)$	104.512	1.93	0.02905	0.3813	4	63.771
$\varphi(6T)p(2T)$	104.515	1.93	0.02901	0.3808	4	63.773
$\varphi(3T)p(2T)$	104.529	1.95	0.02880	0.3780	4	63.788
$\varphi(6T)p(5T)$	104.572	1.99	0.02820	0.3702	4	63.830
$\varphi(3T)p(5T)$	104.672	2.09	0.02681	0.3519	4	63.931
$\varphi(4T)p(6T)$	104.864	2.28	0.02436	0.3198	4	64.122
$\varphi(5T)p(T)$	104.901	2.32	0.02392	0.3140	4	64.159
$\varphi(6T)p(3T)$	104.947	2.36	0.02338	0.3069	4	64.205
$\varphi(T)p(T)$	104.983	2.40	0.02295	0.3012	4	64.242
$\varphi(3T)p(3T)$	104.996	2.41	0.02280	0.2993	4	64.255
$\varphi(5T)p(2T)$	105.006	2.42	0.02269	0.2978	4	64.265
$\boldsymbol{\varphi(t)p(t)}$§	**105.257**	**2.67**	**0.01962**	**0.2627**	**8**	**53.515**
$\varphi(5T)p(5T)$	105.109	2.53	0.02155	0.2829	4	64.367
$\varphi(5T)p(4T)$	105.120	2.54	0.02143	0.2813	4	64.379
$\varphi(T)p(2T)$	105.136	2.55	0.02126	0.2791	4	64.395
$\varphi(T)p(4T)$	105.183	2.60	0.02077	0.2726	4	64.442
$\varphi(T)p(6T)$	105.255	2.67	0.02003	0.2629	4	64.514
$\varphi(T)p(5T)$	105.358	2.77	0.01903	0.2498	4	64.616
$\varphi(5T)p(3T)$	105.407	2.82	0.01857	0.2438	4	64.665
$\varphi(T)p(3T)$	105.603	3.02	0.01683	0.2209	4	64.862
$\boldsymbol{\varphi(.)p(.)}$	**107.094**	**4.51**	**0.00799**	**0.1049**	**2**	**71.066**

§ Information on relative fit of $\varphi(t)p(t)$ if it were to be included in the set of models, however since many time-specific parameters were inestimable, this model was removed from the group, and therefore AICc weights presented for all other models do not incorporate the influence of the $\varphi(t)p(t)$ model.

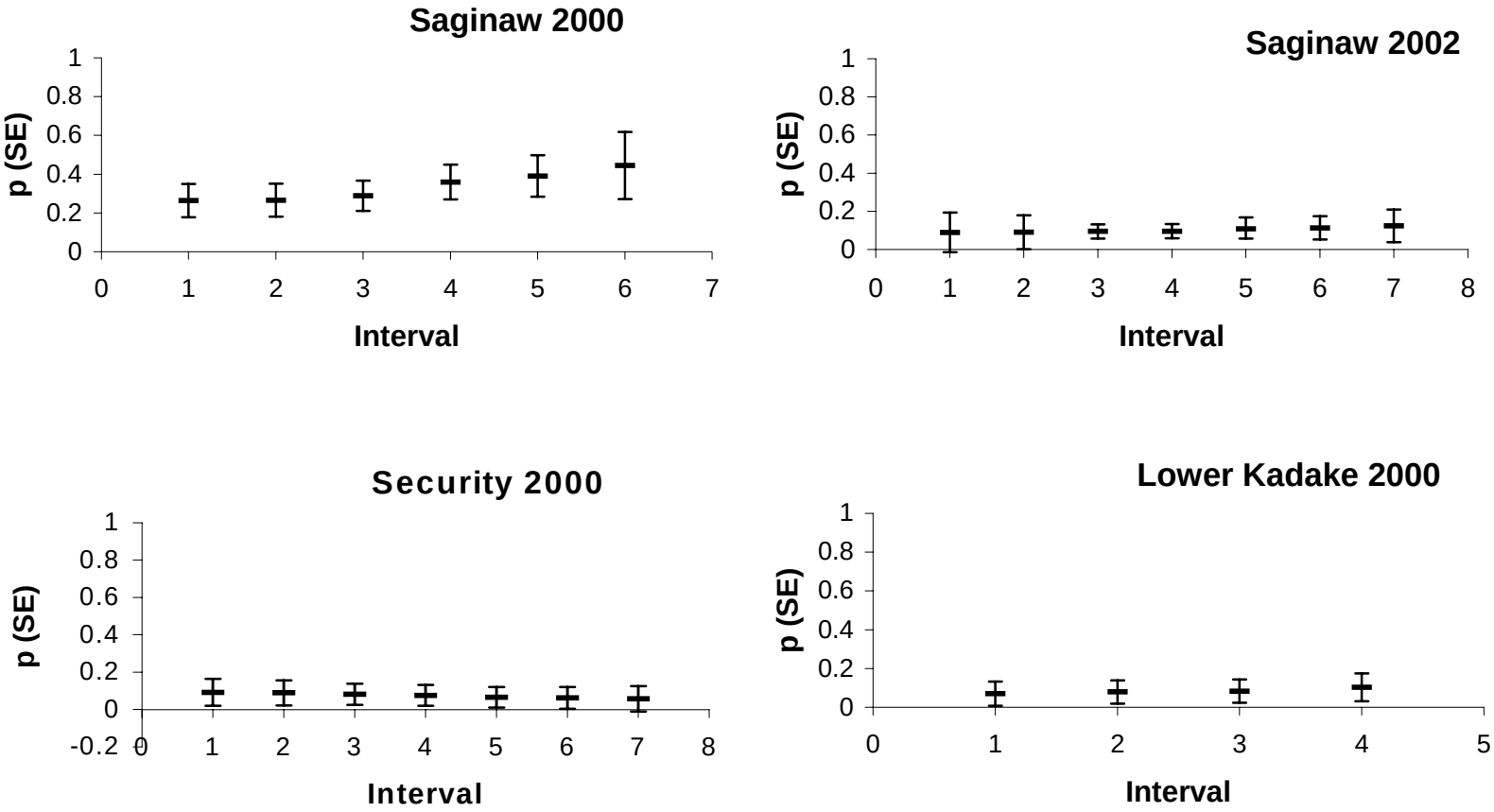
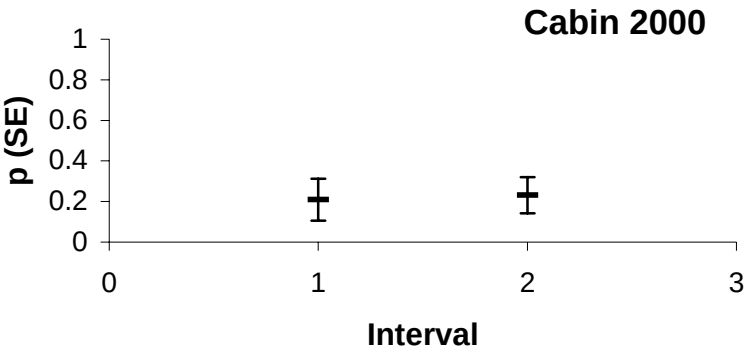


Figure A6 – 1. Recapture probabilities (*p*) for black bears in ten salmon stream-year data sets over week-long intervals, as estimated in CJS. All estimates are model-averaged. Error bars are ± SE.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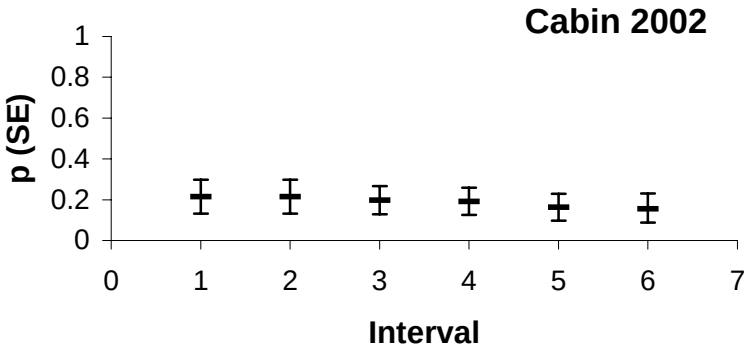
0.6
0.4
0.2
0
0
1
2
3
Interval


Cabin 2002
p (SE)
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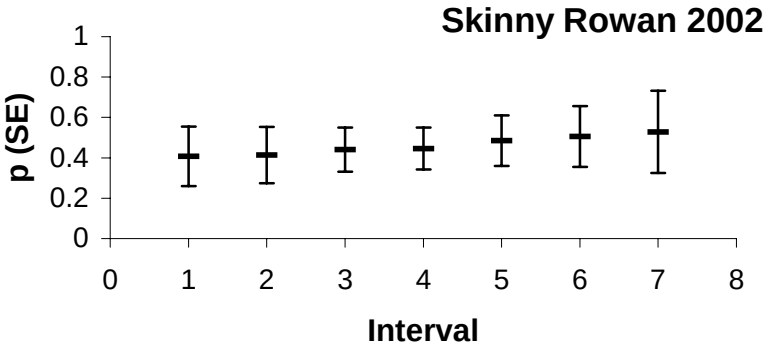
0.6
0.4
0.2
0
0
1
2
3
4
5
6
7
Interval


Skinny Rowan 2002
p (SE)
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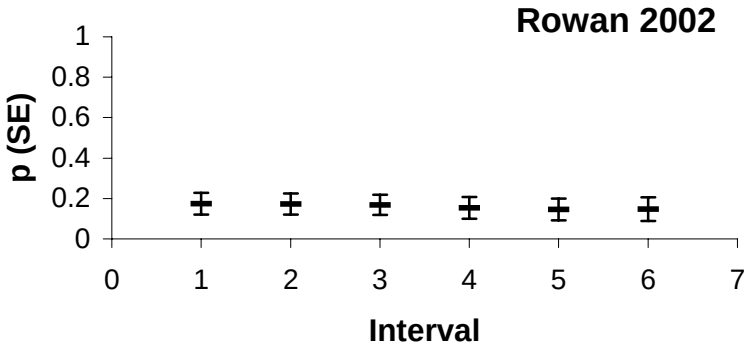
0.4
0.2
0
0
1
2
3
4
5
6
7
8
Interval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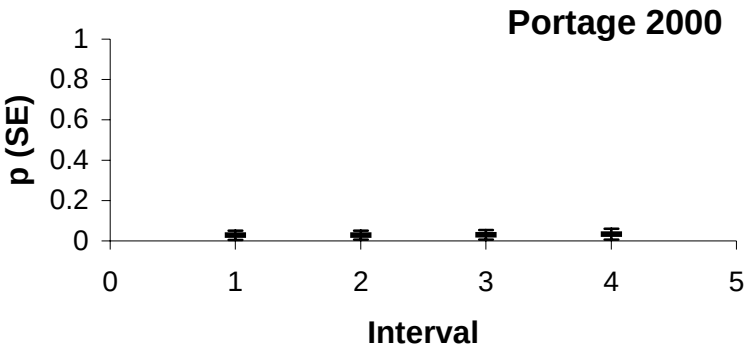
0.4
0.2
0
0
1
2
3
4
5
6
7
Interval


Portage 2000
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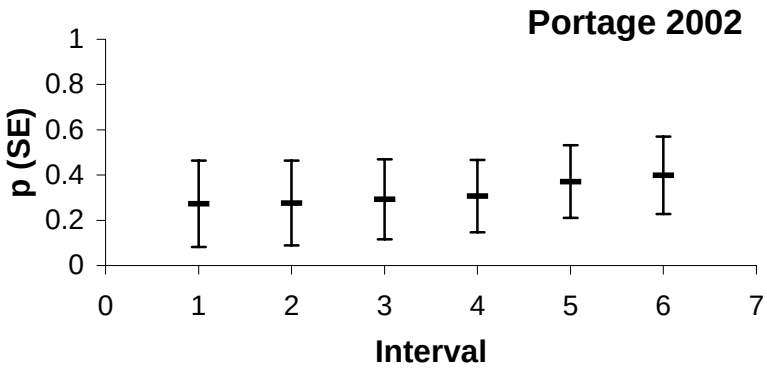
0.8
0.6
0.4
0.2
0
0
1
2
3
4
5
Interval


Portage 2002
p (SE)
1
0.8
0.6
0.4
0.2
0
0
1
2
3
4
5
6
7
Interval

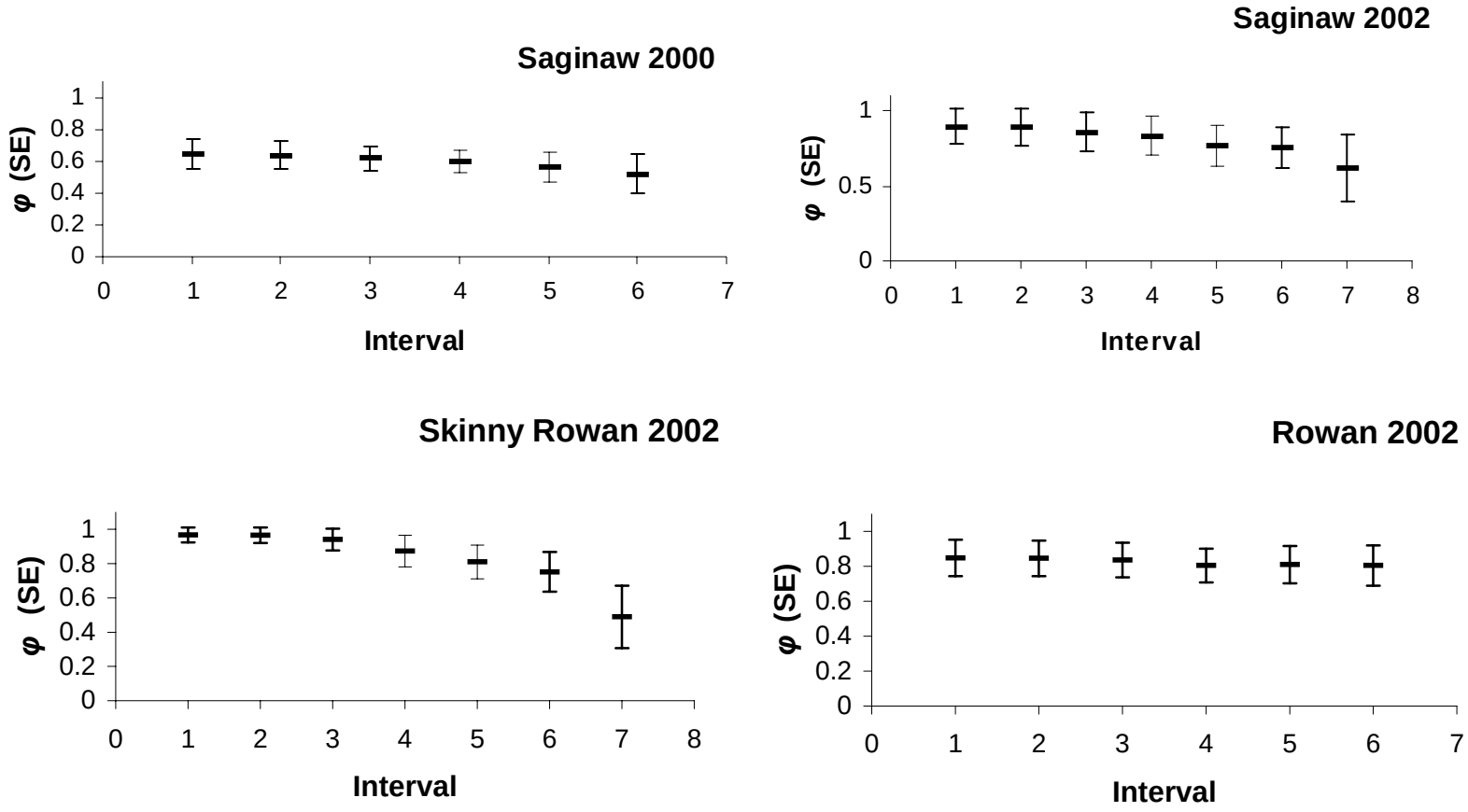
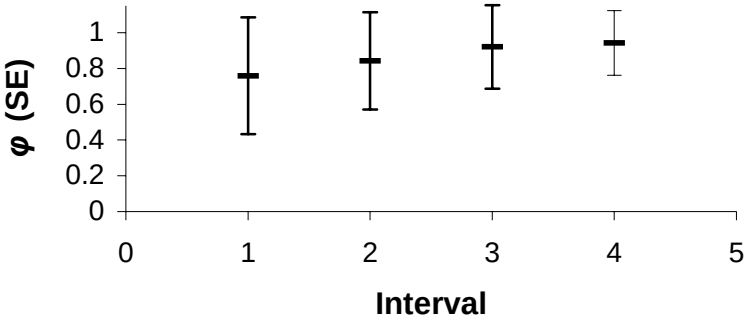
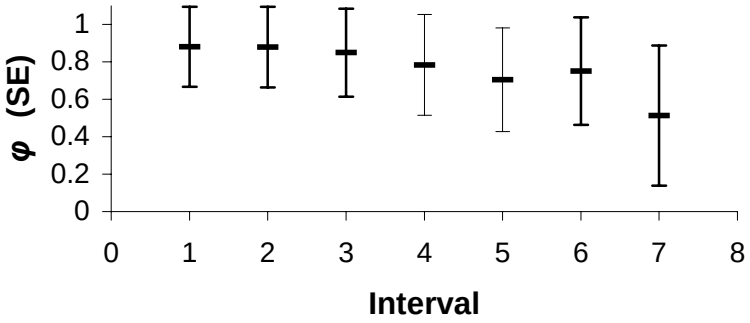


Figure A6 – 2. Apparent survival (φ), for black bears for eight salmon stream-year data sets over week-long intervals, as estimated in CJS. All φ are model-averaged estimates. Error bars are ± SE.

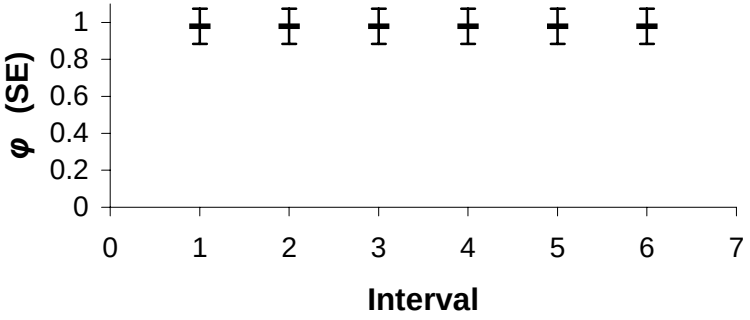
Lower Kadake 2000



Security 2000



Cabin 2002



Portage 2002