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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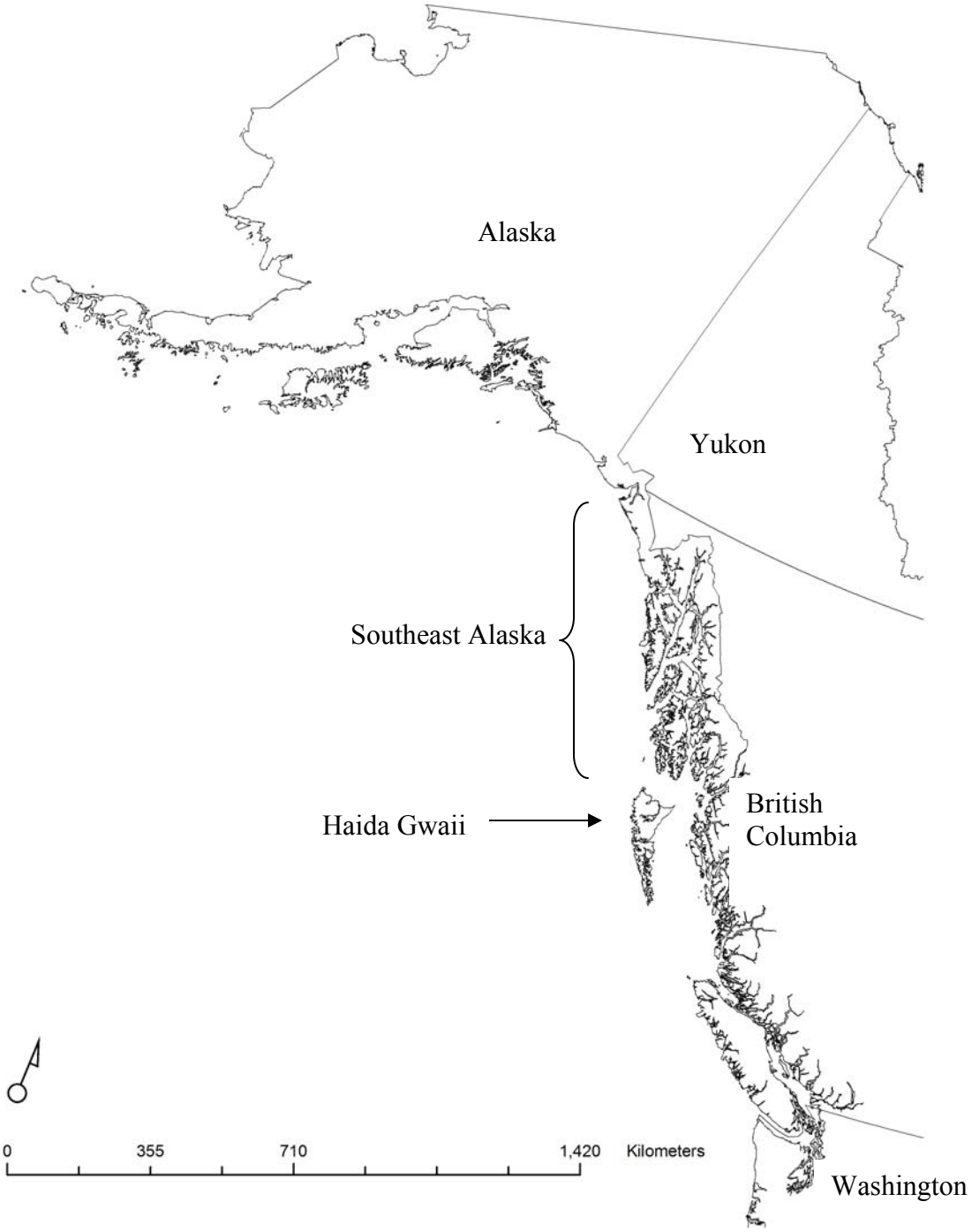

Figure 1. The North Pacific coast of North America.

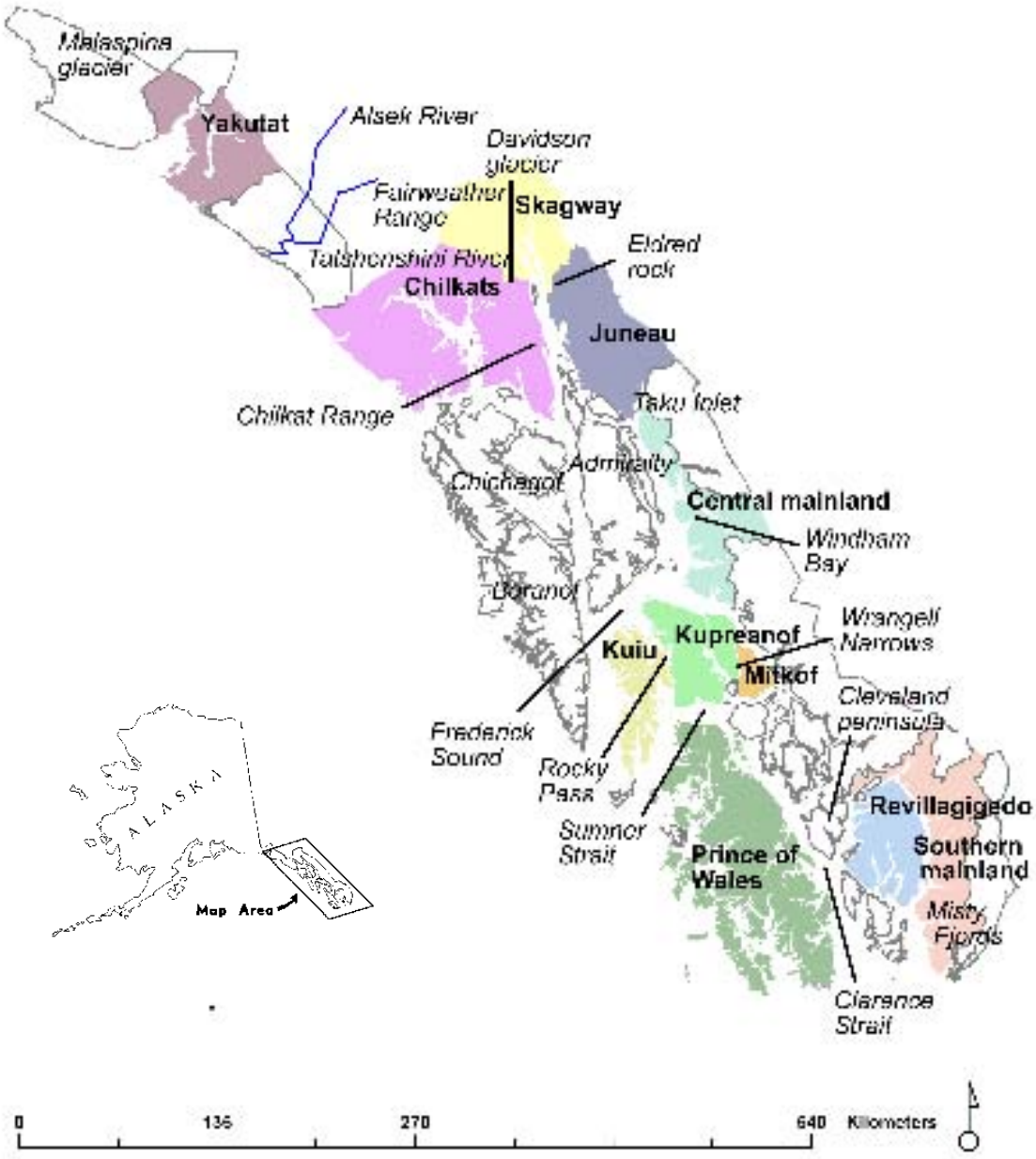

Figure 2. Black bear sampling regions (bold) and place names in Southeast Alaska.

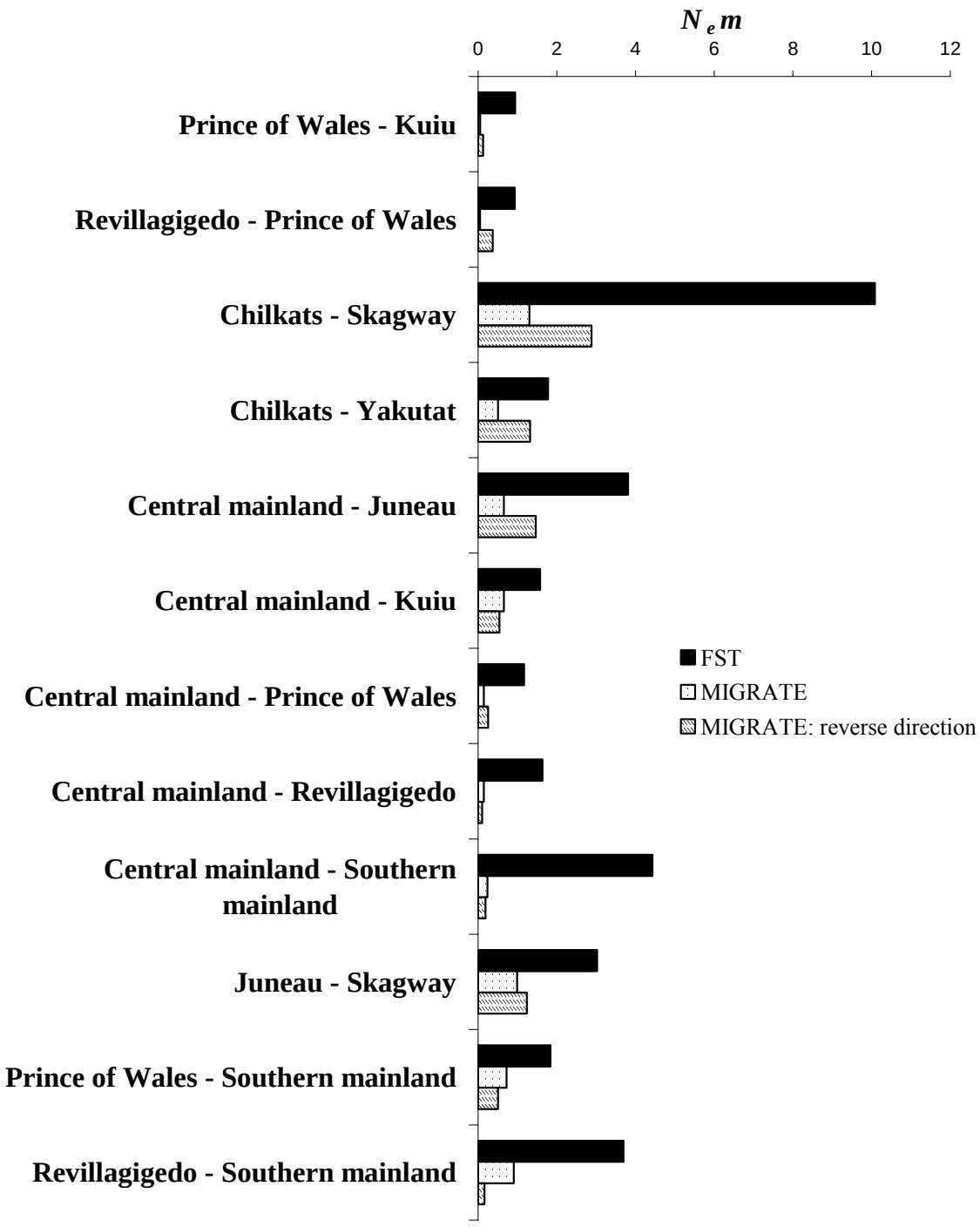

Figure 3. Comparison of F_{ST}-derived and maximum-likelihood coalescence-derived (MIGRATE) estimates of the effective number of migrants/generation (N_em) between a subset of the sampling regions. The gene flow estimate derived from F_{ST} is a pair-wise value; the estimates derived from MIGRATE are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

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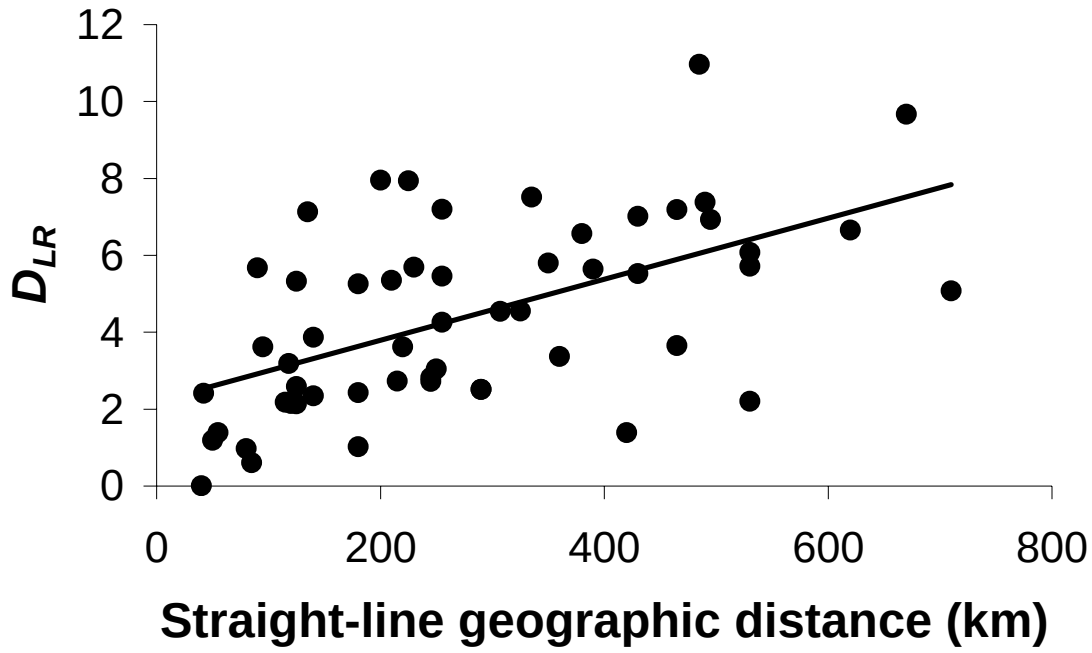


Figure 4. Genetic distance (D_{LR}) regressed on straight-line geographic distance between the geographic centers of sampling regions: y = 0.008x + 2.2; R^2 = 0.31, p = 0.000.

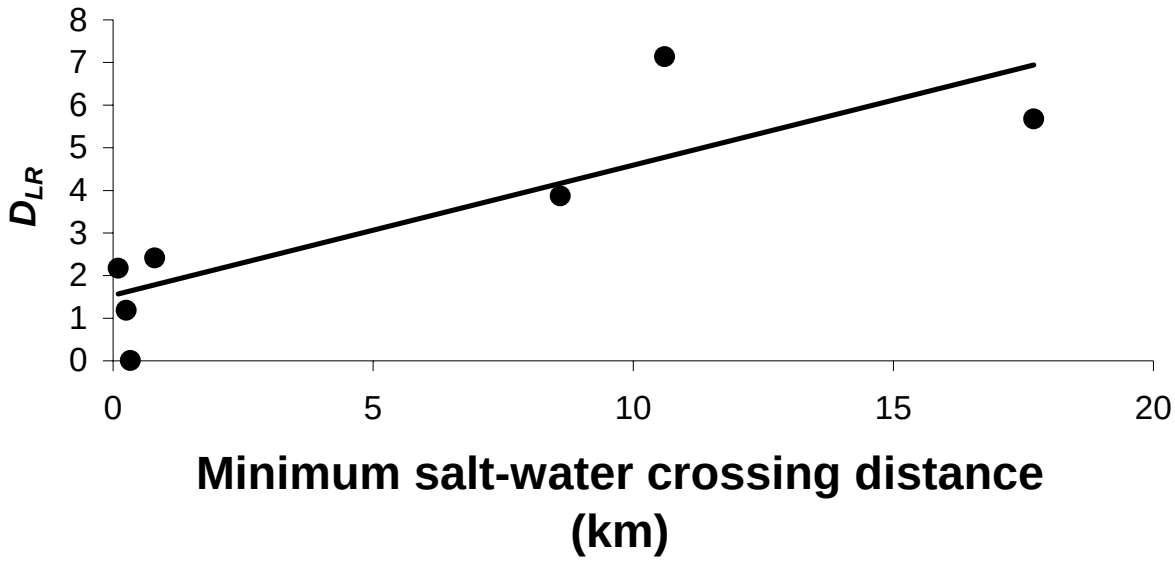


Figure 5. Genetic distance (D_{LR}) regressed on the minimum salt water crossing distance between pairs of sampling regions, separated by one crossing: y = 0.31x + 1.5; R^2 = 0.71, p = 0.017.

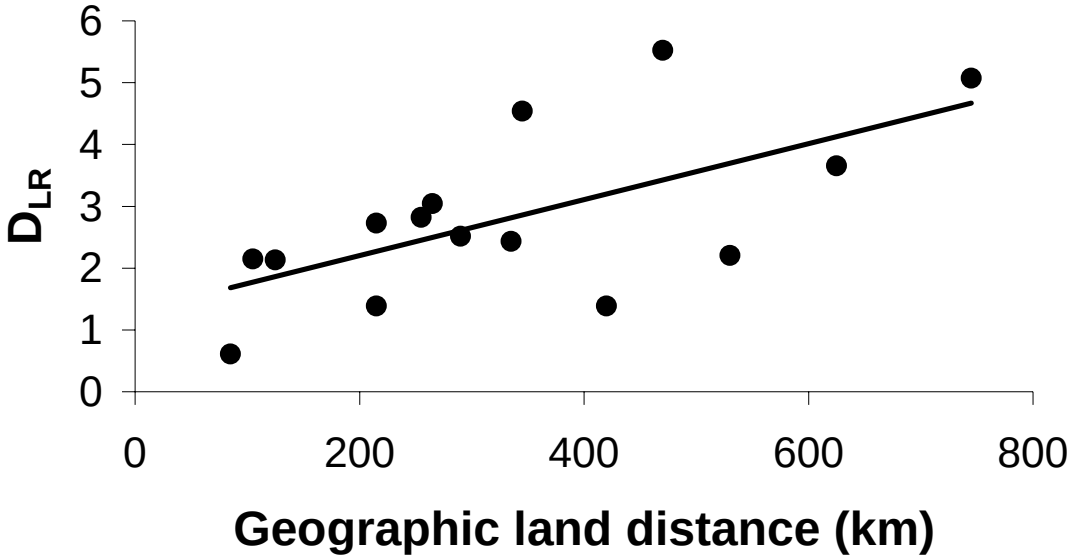


Figure 6. Genetic distance (D_{LR}) regressed on geographic land (not straight-line) distance between centers of mainland sampling regions. y = 0.0045x + 1.30; R^2 = 0.4.

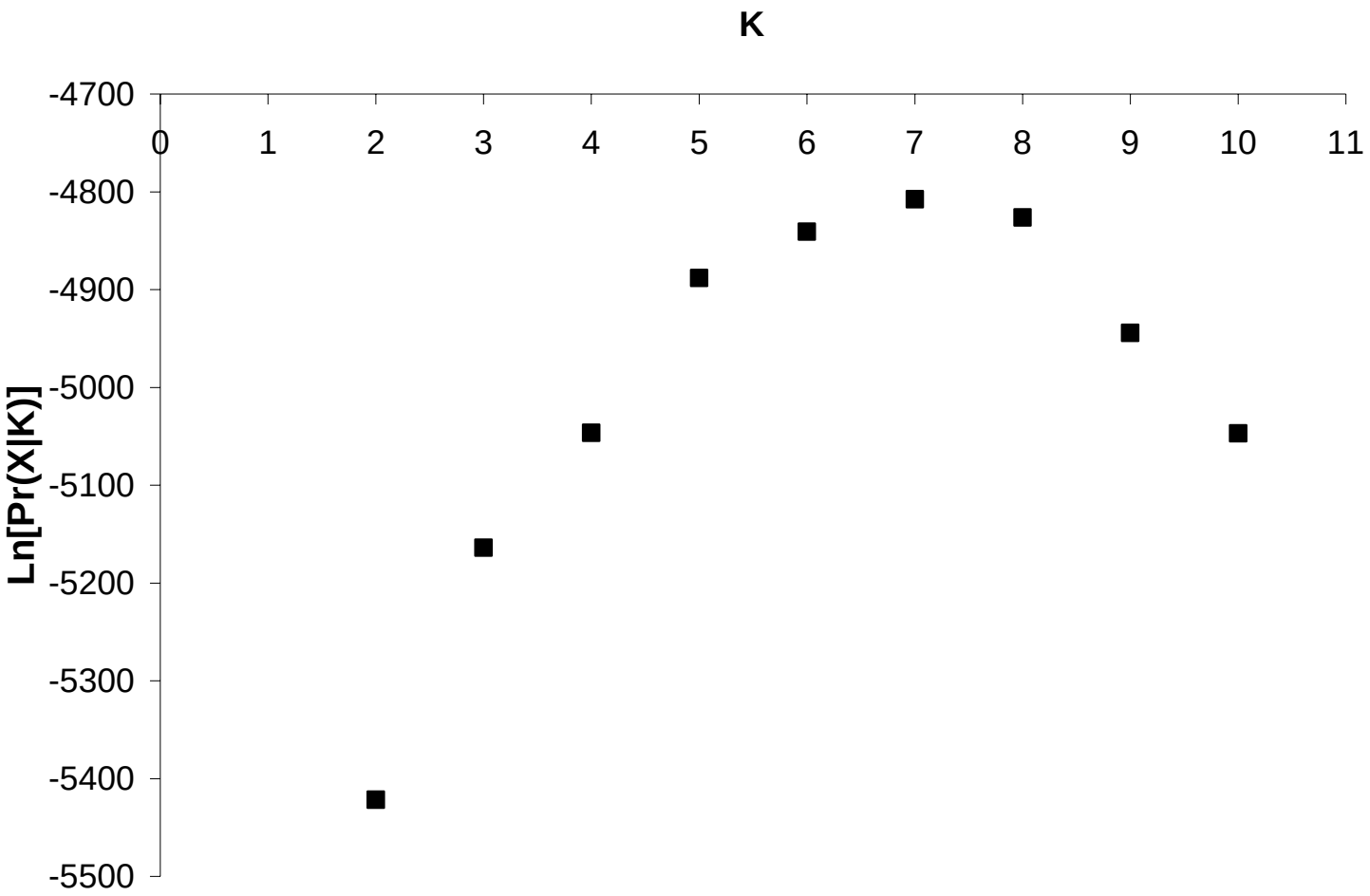
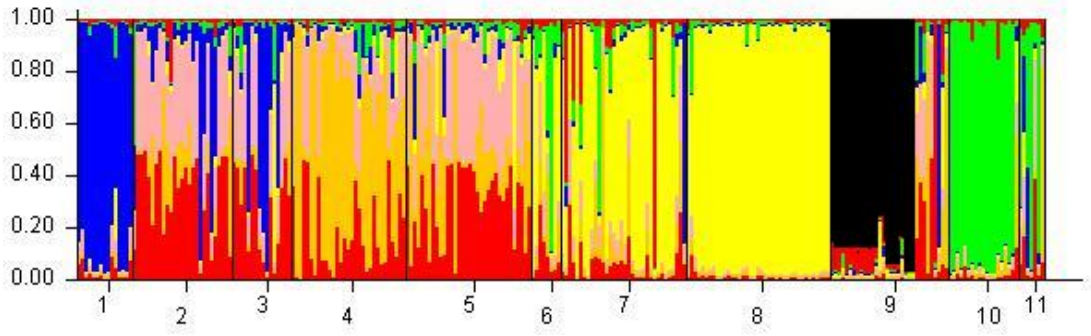
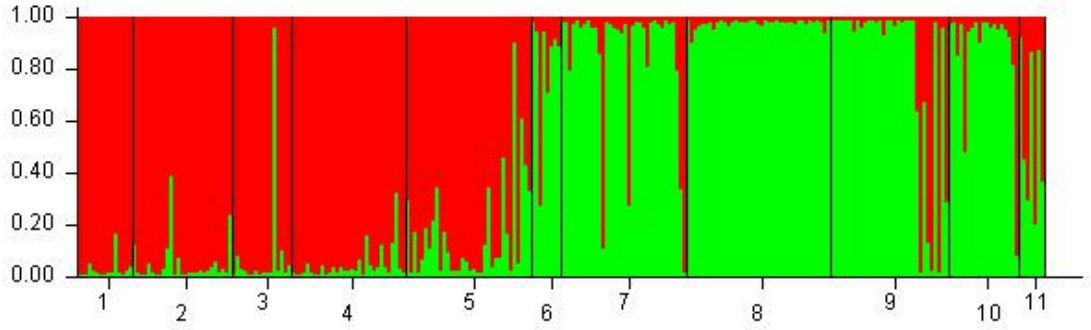


Figure 7. The negative natural log of the probability of the data, given the number of population clusters (K) chosen for Southeast Alaskan black bears.



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*.

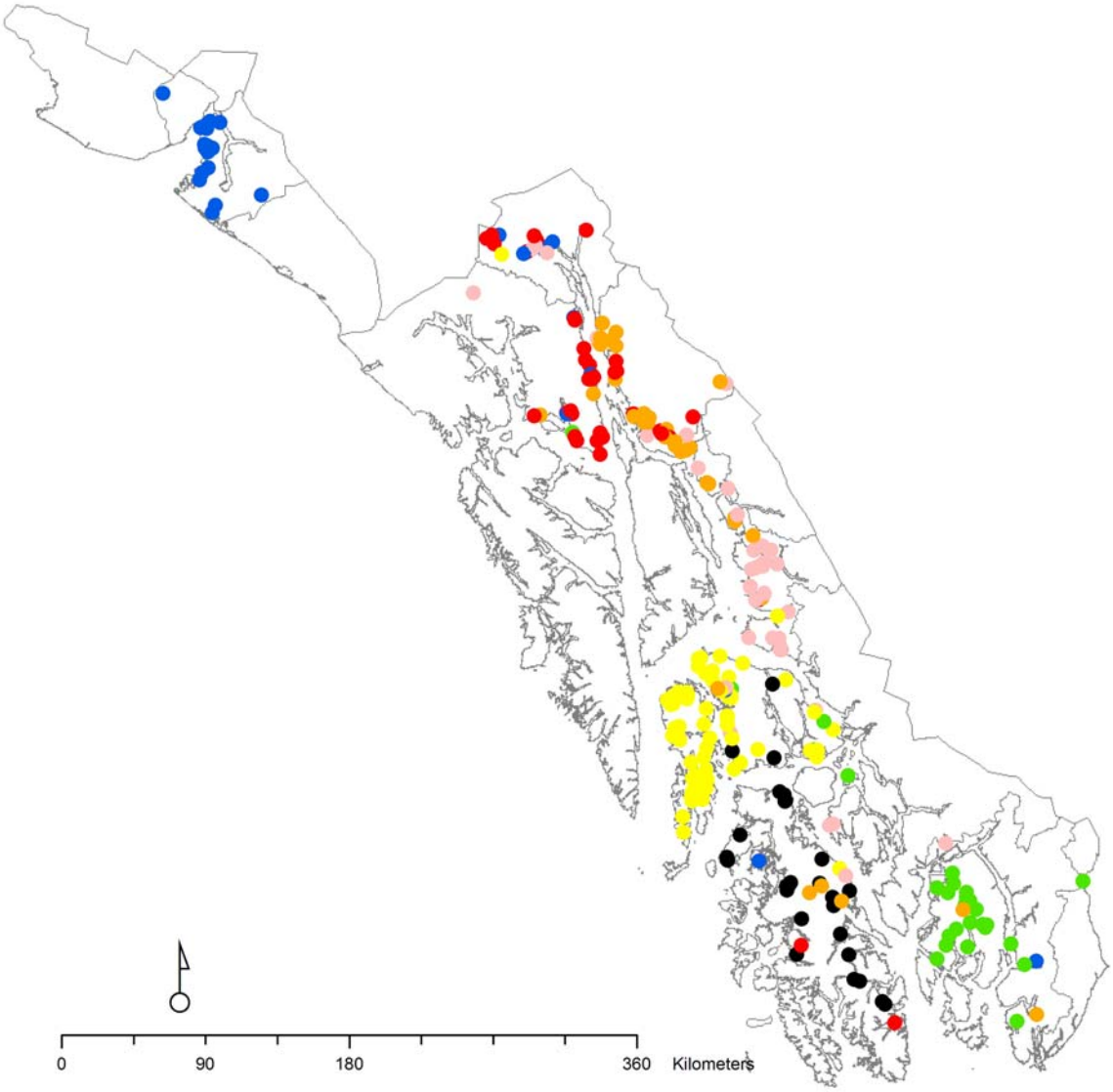


Figure 9. Assignment of individual black bears to the seven genetic clusters in Southeast Alaska, identified by STRUCTURE. Clusters are represented by different colors; dots indicate where the bears were sampled. Colors represent: blue, *Yakutat Cluster*; orange, *Juneau Cluster*; pink, *Central Southeast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

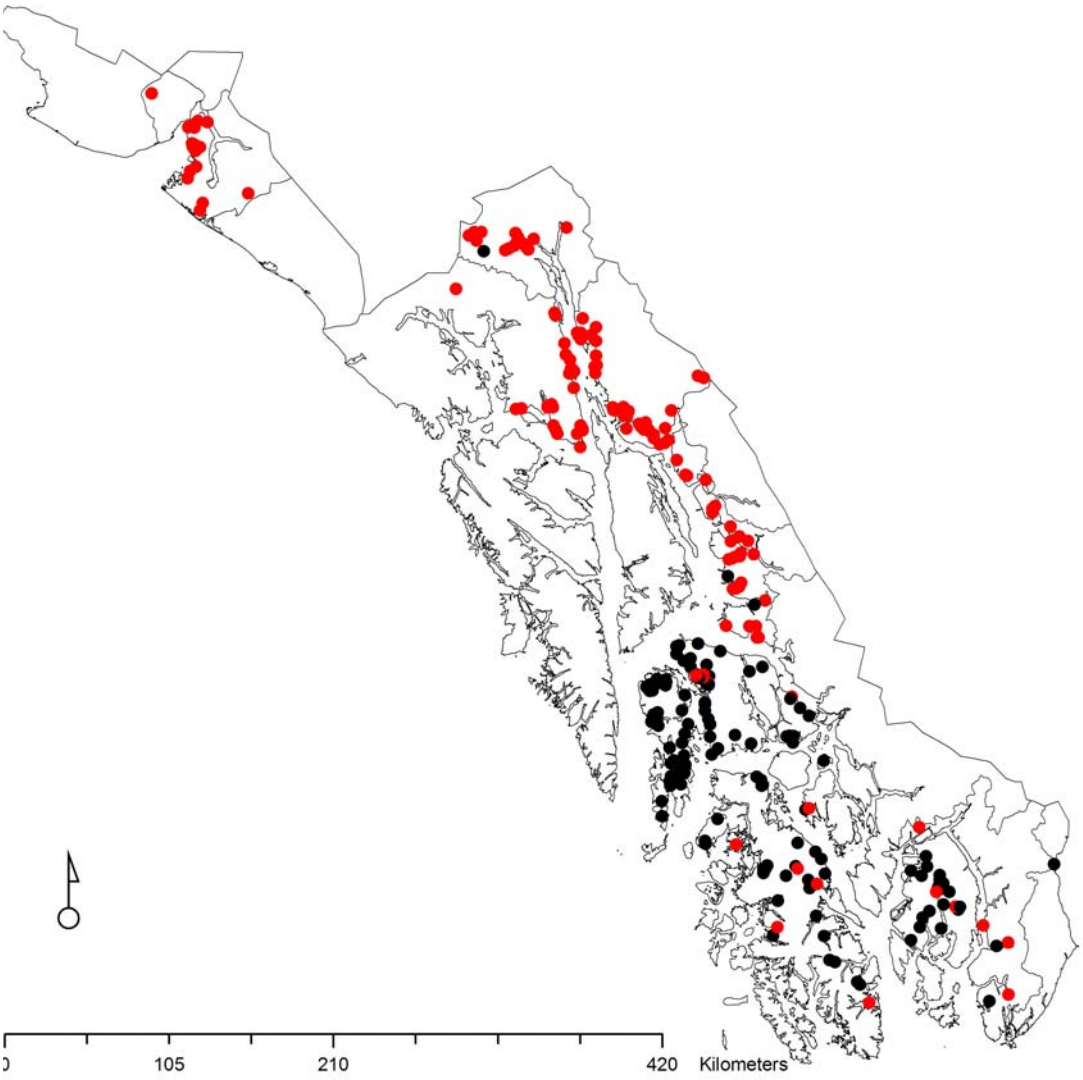


Figure 10. Assignment of individual black bears to the *Island* (black dots) and *Mainland* (red dots) *Clusters* in Southeast Alaska, identified by STRUCTURE.

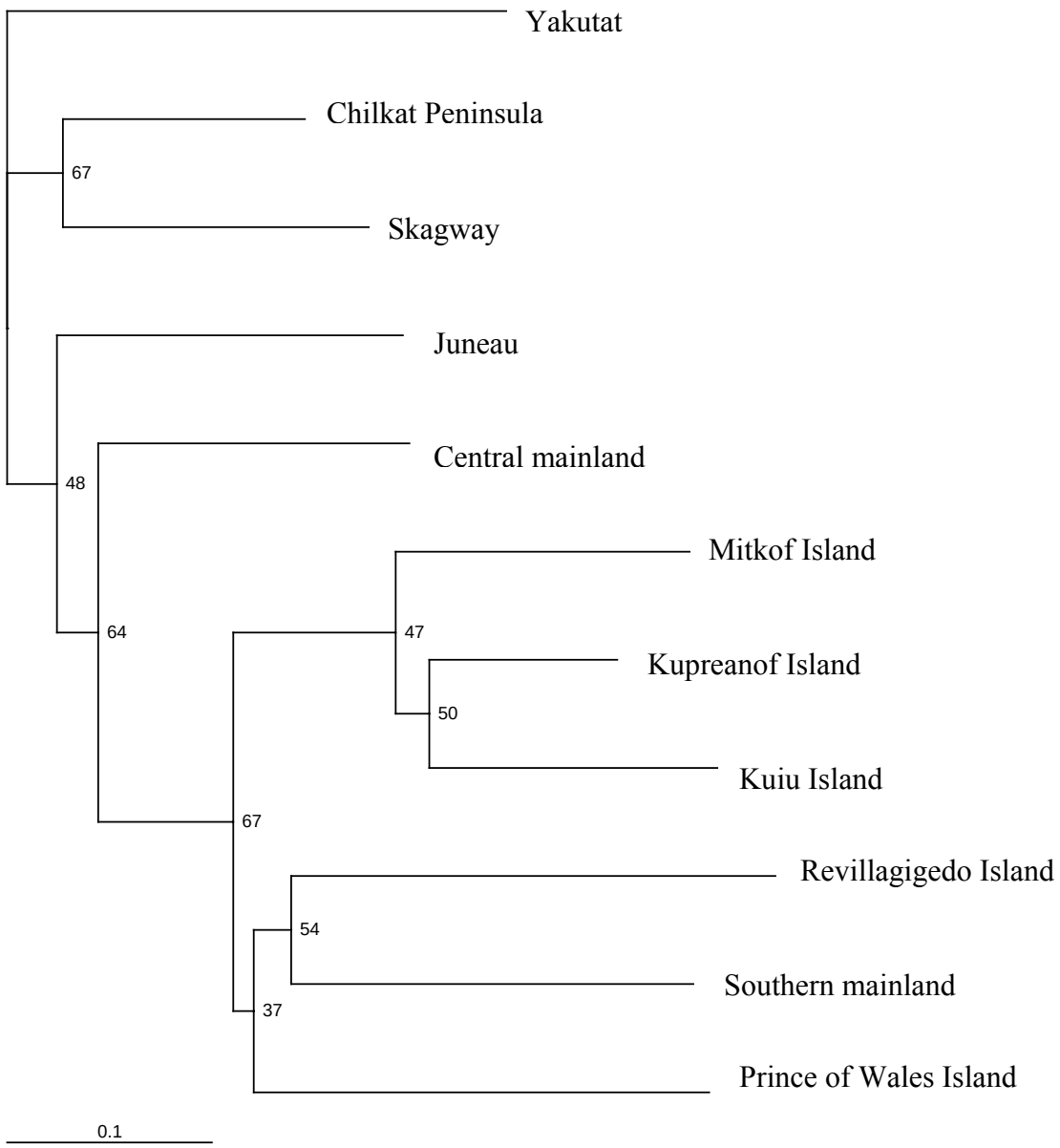


Figure 11. Rooted (Yakutat) neighbor-joining tree of Southeast Alaskan black bear sampling regions based on Cavalli-Sforza distance (scale bar shown). Bootstrap values are given at the node (5,000 replicates).

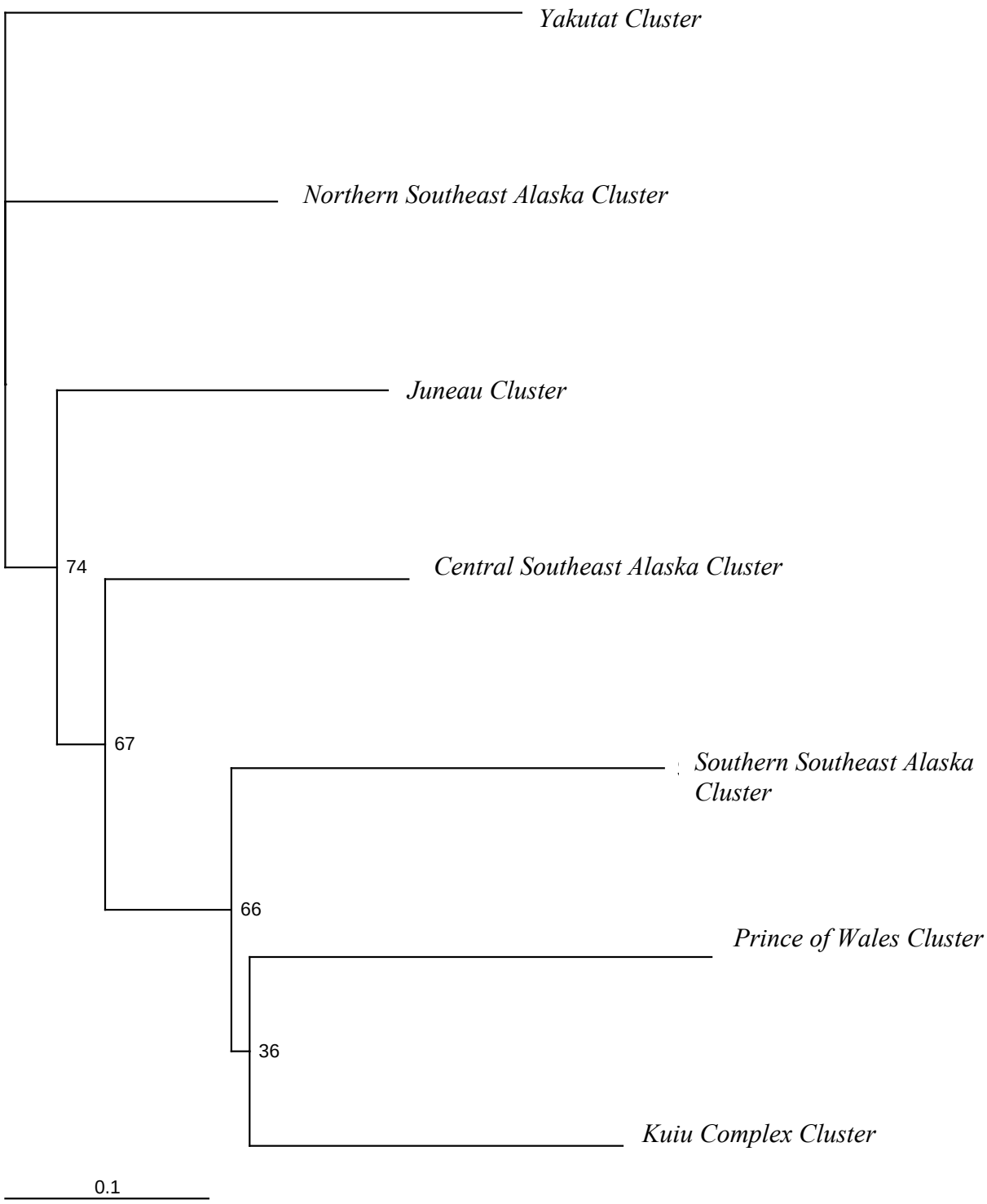


Figure 12. Rooted (Yakutat) neighbor-joining tree based on Cavalli-Sforza distance (scale bar shown) of genetic clusters of Southeast Alaska. Bootstrap values are given at the node (5,000 replicates).

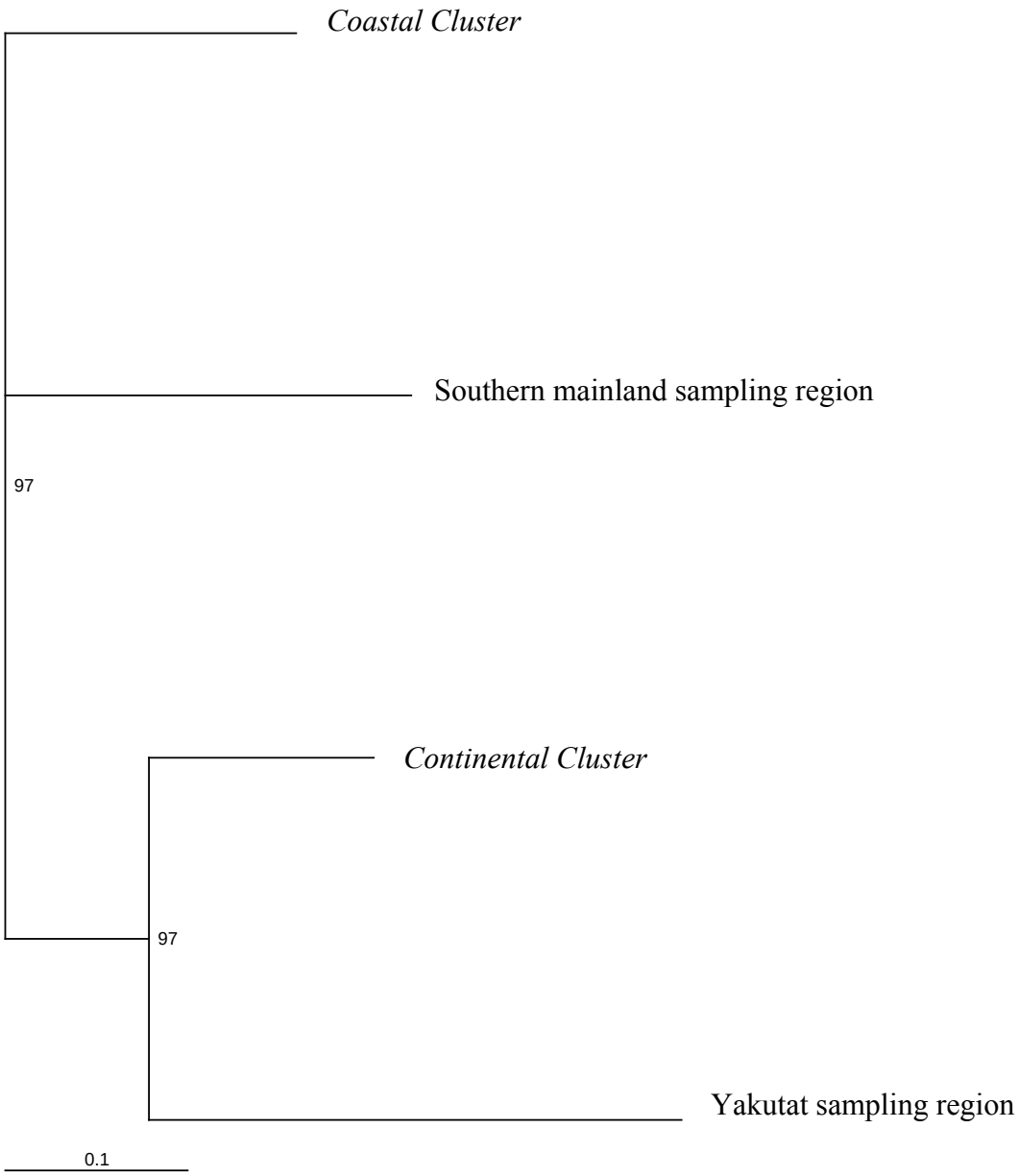


Figure 13. Rooted (Yakutat) neighbor-joining tree based on Cavalli-Sforza distance of four groupings of individuals of Southeast Alaska. Bootstrap values are given at the node (5,000 replicates).

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

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