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Comparative landscape genetics and dynamics in demography within sympatric Ursids in Southeast Alaska

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COMPARATIVE LANDSCAPE GENETICS AND DYNAMICS IN DEMOGRAPHY
WITHIN SYMPATRIC URSIDS IN SOUTHEAST ALASKA

by

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Finally, I would like to thank friends and family. Without their love and support I would not have been successful.

ABSTRACT

The landscape along the northwest coast of North America structures species populations in and around Southeast Alaska. Brown bears (*Ursus arctos*) and American black bears (*U. americanus*) are sympatric in this region. They are similarly sized omnivores and interspecific competition directly affects the resources available to each species as brown bears are larger, more aggressive, and can competitively exclude; however, black bears can better utilize dispersed food sources. Within this system I asked two questions about brown and black bears in Southeast Alaska. The first question had two parts; how has the environment structured gene flow in both species, and are the observed patterns different. I sequenced the DNA from tissue samples for both species from 2017 to 2021 to answer our questions. I analyzed population structure and found support for seven populations of brown bears and six populations of black bears. I used landscape genetics to address gene flow by regressing genetic distance with nine environmental variables. I found that landcover both facilitated and impeded gene flow the most in both species. The categories that contributed the most to gene flow were different for each species and water served as a barrier to both species. The second question was driven by reports from hunters, guides, and management personnel that brown bears are increasingly seen where black bears had previously been found in greater frequency. I analyzed hunter harvest records from 1995 to 2022 to address the question and restricted our analysis to Game Management Units 1C and 1D where these shifts in species density have predominantly been reported. I estimated population size over time, performed a spatial statistical analysis of harvest patterns, and assessed hunter effort and success. From these analyses I found empirical evidence in support of increased brown bear density in areas of 1C but

did not find support in 1D. I demonstrated that gene flow patterns differed between two species with a similar ecological niche across a heterogenous environment. I also illustrated the utility of mortality data in detecting distribution changes within sympatric species.

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The biotic and abiotic interactions of every organism are fundamentally shaped by landscape structure (Zarnetske et al. 2017). The landscape influences species assemblages as well as the biological and behavioral changes that affect the interactions between species (Fischer and Lindenmayer 2007). Patterns of distribution and interaction can change through time and leave genetic signatures of past structure (Landguth et al. 2010). Southeast Alaska is an area with high landscape heterogeneity and a complex geologic and biogeographic history that makes it an ideal place to study how the landscape influences the biotic and abiotic interactions of the species located in this unique part of the world.

Southeast Alaska is an area on the northwestern coast of North America that exhibits complex biogeographical patterns due to its island geography and cycles of glaciation. The 600 km long Alexander Archipelago, one of the largest archipelagos in the world, lies off of the mainland coast and contains over 2,000 named islands (Cook et al. 2006). The high latitude and coastal location of the archipelago means that it has been subject to environmental patterns dominated by advancing and receding glaciers during the Pleistocene. The last glacial maximum (LGM), or the furthest southern glacial extent during the Wisconsin Glacial Episode occurred 22,000 to 17,000 years ago (Pielou 2008). There has been considerable debate on the locations of the glacial refugia in Southeast Alaska; however, evidence suggests that refugia were located off the western coast of Baranof and Prince of Wales Islands during the LGM (Figure 1.1; Sawyer et al. 2019; Carrara et al. 2007; Cook et al. 2006). The Cordilleran Ice Sheet that covered much of
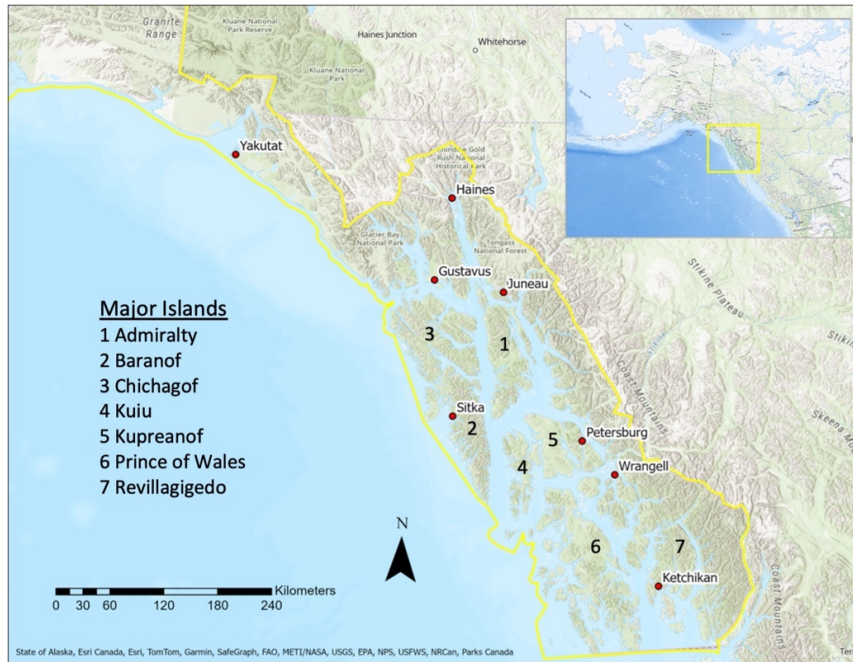
Figure 1.1: Southeast Alaska is outlined in yellow. The numbers correspond to the islands in the legend.

Southeast Alaska began receding around 12,000 years ago and colonization by plants and animals occurred, driving the biogeographical patterns seen today (Colella et al. 2021; Carrara et al. 2007; Cook et al. 2006; Mann and Hamilton 1995; Mann 1986).

The Alexander Archipelago displays a pattern of island biogeography (MacArthur and Wilson 1963). Larger islands that are in closer proximity to the mainland in Southeast Alaska have a higher species richness (Cook et al. 2006; Conroy et al. 1999). Concordant distribution patterns that follow total species richness occur in multiple taxa. The island makeup and larger channels separating Kuiu and Kupreanof Islands from the islands to the north and south may help create the different species assemblages on the Admiralty, Baranof, and Chichagof (ABC) Islands and the Prince of Wales Island complex. In genetic studies, three ermine (*Mustela* erminea) clades group separately with one located on Baranof and Chichagof Islands as well as the mainland, one on Admiralty

Island and the last located on Prince of Wales Island; the three populations originated from Beringia, coastal, and continental clades (Cook et al. 2006; Cook et al. 2001). The pattern was also observed in long-tailed voles (*Microtus longicaudus*), northwestern deermice (*Peromyscus keeni*), dusky shrews (*Sorex monticola*), and martens (*Martes spp.*) in which there are continental and coastal clades (Sawyer et al. 2019; Dawson et al. 2017; Cook et al. 2006; Cook et al. 2001). This pattern of endemism and clade contact holds for the larger brown (*Ursus arctos*) and American black bears (*U. americanus*) in the region as well. Both species are sympatric on the mainland; however, brown bears are the only bear found on the ABC Islands while black bears are the only bear found on Prince of Wales, Kuiu, and Kupreanof Islands. There is a distinct clade of brown bears found on the ABC Islands and sex-biased dispersal is thought to have maintained the genetic signature of that clade (de Jong et al. 2023). Two lineages of black bear, one western and one eastern, have been identified and there appears to be a contact point in Southeast Alaska (Puckett et al. 2015; Cook et al. 2001). The complex patterns of population history in brown and black bears arise from deep biogeographical patterns that are currently maintained by the structured landscape of Southeast Alaska.

Brown and black bears have similar ecology in Southeast Alaska where they are sympatric. The two species diverged an estimated 3.4 million years ago (CI: 2.0–4.7; Kumar et al. 2017). Brown bears have since become adapted to open areas while black bears have adapted to forested habitat (Miller et al. 1997; Herrero 1978). These characteristics are exemplified by the ability of black bears to climb trees in retreat from larger brown bears in areas where they are sympatric.

Both species follow similar seasonal patterns. Broadly, both species hibernate during the winter in dens. They emerge in the spring from March to May and mate in June and July. After the mating season both species enter a period of hyperphagia in the late summer and fall. During this time, they attempt to gain as much fat as possible prior to the onset of hibernation.

Both species are polygamous and mate situationally (Lawson Handley and Perrin 2007). Brown and black bears are both able to delay implantation of a fertilized egg for four to five months at which time implantation occurs if the female has obtained enough resources and her body condition is healthy enough to support cubs (Friebe et al. 2014). If the female was able to gain enough mass and implantation did occur, cubs are born in the den and stay with the female until weaning (Eide et al. 1994). There is no paternal care in either species. Natal dispersal takes place after two to four years in brown bears and one to two years in black bears (Schwartz and Franzmann 1992; Miller 1990). Dispersal in brown and black bears shows inverse density dependence which means that the dispersal distance is shorter when density is higher than it is when density is lower (Kristensen et al. 2018; Costello et al. 2008; Støen et al. 2006).

Brown and black bears display different response patterns to interspecific competition due to their physiology and behavior. Both species are omnivorous and have large dietary overlaps. Brown bears are larger than black bears with male and female brown bears each weighing roughly 100 kg more than male and female black bears. Brown bears are more aggressive than black bears and proactively and successfully defend areas with concentrated resources (Crupi et al. 2014; Flynn 2012; Belant et al. 2006; Aune 1994; McLellan 1993). The interspecific competitive advantage of brown

bears causes black bears to avoid brown bears at a population level (Belant et al. 2010).

In Alaska, brown and black bears use different resources. Male brown bears have the highest proportion of salmon in their diet and use salmon resources more often (Fortin et al. 2007; Rode et al. 2006). In coastal areas where there are only black bears, a high proportion of the black bear diet is salmon which indicates that interspecific competition could be a main driver of salmon use by bears (Jacoby et al. 1999). Where brown bears are present on the same landscape as black bears making salmon unavailable, black bear diet becomes more herbivorous and frugivorous (Fortin et al. 2013). The smaller size of black bears allows them to survive off of lower quality habitat on which brown bears cannot survive (Belant et al. 2010; Mattson et al. 2005). The higher density of black bears in Southeast Alaska may accentuate this effect. In addition, black bears are pushed into higher elevations and closer to human settlement in search of resources while lower elevations are utilized primarily by brown bears (Sawaya et al. 2014; Belant et al. 2010).

It is on this complex background of biogeography and interspecies competition that we chose to ask two main questions. In Chapter 2 we asked whether gene flow in brown and black bears has occurred in response to similar environmental variables. We hypothesized that the patterns of movement would be different based on the interspecific competition dynamics that each species experiences, and that would cause differences in gene flow. To answer this question, we first analyzed population structure in both species by sequencing tissue samples collected from 2017–2021 from across Southeast Alaska. We then compared our results to previous work done in the system. We also analyzed genetic differentiation between subpopulations to determine how genetically similar the populations were to each other across Southeast Alaska. To directly address the question,

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we used landscape genetics to find which environmental variables have been driving gene flow in both species (Dyer 2015; Manel and Holderegger 2013; Manel et al. 2003). In landscape genetics, the genetic distances between individuals are used as the response variable in a linear regression with models of environmental resistance to organism movement as the explanatory variables (Beninde et al. 2023). We compared these models in both species along with straight-line distance to determine which variables best explain the patterns of genetic differences between individuals. We explored nine landscape variables that we thought would have the highest impact on gene flow based on previous literature; the nine layers were: elevation, topographic position index, vector ruggedness measure, landcover, permanent ice and snow, waterbodies, roads, temperature, and precipitation. We then qualitatively compared the results for each species to determine if the patterns of gene flow were different.

In Chapter 3, we asked whether brown and black bear demographics in areas of hunter harvest had changed. For the past fifteen years hunters, guides, and Alaska Department of Fish and Game (ADF&G) personnel have reported that brown bears are being seen more in areas where black bears were primarily seen in the past (Churchwell 2020; Lewis 2012; Scott 2009). Human-bear conflict has also increased in the past four years. To answer whether interspecies demographics are changing we reduced our analysis for this chapter to management areas around the city of Juneau and the towns of Gustavus and Haines in Southeast Alaska (Figure 1.1). We used the demographic information on both species from hunter harvest records from 1995–2022 as input into a Bayesian age-at-harvest state-space model (Allen et al. 2018). The model used the sex, age, and location along with auxiliary demographic information to estimate population

size in the study areas. We then used spatial statistics to determine the spatial pattern of the data and the underlying management areas to which the data was assigned. After determining the spatial patterns in the data, we analyzed trends in hunter effort and success. The population estimation, spatial, and hunter effort and success analyses allowed us to determine whether there was empirical evidence for a shift in the demographics of brown and black bears through time.

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Chapter 2: Comparative landscape genetics of brown (*Ursus arctos*) and American

black bears (*U. americanus*)

INTRODUCTION

Connectivity is an essential characteristic for populations to persist at any scale on landscapes around the world. Connectivity can determine how individuals are distributed and refers to the degree to which a landscape impedes or facilitates movement between populations within a species (Palm et al. 2023; Taylor et al. 1993). Environmental heterogeneity creates different patterns of movement within the same species based on the habitat types that either facilitate or impede those movements (Haddad 1999; Taylor et al. 1993). The patterns of movement shape the ecology of species and we would expect similar species to move across the landscape in similar ways (Palm et al. 2023; Baguette et al. 2013; Nathan et al. 2008; Morales and Ellner 2002). The patterns of connection through time contribute to genetic structure in a species based on the aggregated movements that lead to successful mating events (Zeller et al. 2012).

The field of landscape genetics builds on the methods from population genetics, landscape ecology and spatial statistics to quantify how the environment has shaped gene flow across a species' range (Dyer 2015; Manel and Holderegger 2013; Manel et al. 2003). To do this, landscape genetics correlates landscape variables (explanatory variables) and the genetic distances (response variables) between individuals. The null model for landscape genetics is isolation-by-distance (IBD) in which the only factor that determines genetic similarity is straight-line distance (Wright 1943). In this model, individuals that are closer together will be more genetically similar than individuals that are farther apart. The opposing model is isolation-by-resistance (IBR) in which genetic

populations are structured by population-level movement across the landscape (McRae 2006). In this model, the landscape becomes a surface that facilitates or resists the movement of individuals based on the landscape type and ability of the organism to cross it (Meirmans 2012).

The majority of landscape genetic studies have focused on individual species in a single habitat; however, comparative studies provide further insight into one species across its range or multiple species in the same habitat (Engler et al. 2014). Many of the single species studies focus on the impact of anthropogenic habitat fragmentation. Indeed a considerable number of mammals in North America display genetic structuring from these factors including badger (Kierepka and Latch 2016), puma (Ernest et al. 2014), roe deer (Coulon et al. 2006), and bighorn sheep (Epps et al. 2005). These studies are informative for the specific habitats in which the species was studied; however, comparative studies from across a species' range are important for identifying how they are interacting with differing combinations of environmental variables (Bull et al. 2011). This can be insightful for conservation and ecology questions. For instance, differing effects of the landscape were found in wolves with landcover and mountains dividing populations in Italy (Milanesi et al. 2018) and vegetation types in eastern Europe and North America (Pilot et al. 2006; Geffen et al. 2004). Conclusions in these studies can be location and spatial scale dependent. One study on bobcats found that herbaceous rangeland at a fine scale and mixed rangeland and agriculture at a broad scale were shaping gene flow in Texas (Cancellare et al. 2021). A second study on the same species found that impervious surfaces impact gene flow in southern California (Kozakiewicz et al. 2019). These studies highlight that the conclusions drawn for a single species can be

supported over a continent level in the case of wolves and not supported for different environments in bobcats. Care must be taken to consider the scale and location in landscape genetics results.

The dependence on spatial context in landscape genetics means that if species are compared, they should be analyzed in the same environment. A study in southern California investigated gene flow pattern differences between bobcats and coyotes and found that the highway in the study area acted as a barrier to both species while secondary roads had a greater effect on bobcats (Riley et al. 2006). In a comparative study on jungle cats, leopards, sloth bears, and tigers in central India, landcover was the most important environmental variable structuring gene flow in leopards, sloth bears, and tigers but not jungle cats (Thatte et al. 2020). The study of similar species in the same habitat and how the species cope with similar landscape and environmental factors can be important in conservation and management.

The focus for this study is a landscape genetic analysis between brown (*Ursus arctos*) and American black bears (*U. americanus*) in a portion of their range in North America, specifically Southeast Alaska and an adjacent portion of the Canadian provinces of British Columbia (BC) and the Yukon Territories. This study takes advantage of the unique opportunity to study how two similarly sized sympatric species move across the landscape in a complex and unique environment. Both species of bears are generalist omnivores and compete for similar resources across their range. They are sympatric in the Pacific Northwest of North America including Alaska. Brown and black bears have been extensively studied using landscape genetics in North America (Brown bears; Palm et al. 2023; Henson et al. 2021; Lewis et al. 2015; Proctor et al. 2012; Graves

et al. 2012; Paetkau et al. 1998; black bears; Draheim et al. 2021; Lewis et al. 2020; Draheim et al. 2018; Bull et al. 2011; Cushman and Lewis 2010; Peacock et al. 2007; Cushman et al. 2006). Here, we expand the comparative landscape genetics of bears by conducting the first analysis in Southeast Alaska, in which we compare patterns of IBR between the two sympatric bear species.

The phylogeography of each bear species shows unique complexity across Southeast Alaska (Figure 2.1). North American populations of brown bears represent a major lineage within the species, although populations in western and central Alaska contain increased proportions of east Asian ancestry (de Jong et al. 2023). While all global populations of brown bears contain some introgression from polar bears, the total genomic proportion is highest in brown bears from Admiralty, Baranof, and Chichagof (ABC) Islands in Southeast Alaska (Cahill 2016; Cahill et al. 2015). On Admiralty
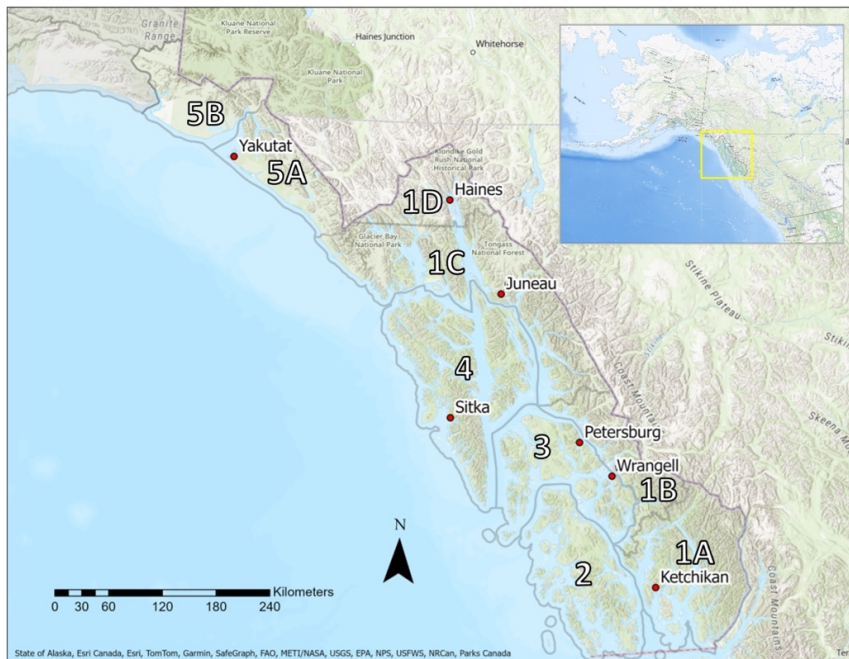
Figure 2.1: The geographic location for each GMU is outlined in gray. GMUs 1A through 1D and 5A and 5B are located along the mainland. GMU 2 encompasses Prince of Wales Island and GMU 4 encompasses the Admiralty, Baranof, and Chichagof Islands.

Island brown bears have 5.9% introgression in the autosomes and 7.5% in the X chromosome (Cahill et al. 2015). Baranof and Chichagof Islands are west of Admiralty Island and they have 8.8% introgression in the autosomes and 9.7% in the X chromosome (Cahill et al. 2015). While mainland Southeast Alaskan brown bears also have polar bear ancestry, the highest proportions have been found on the Alexander Archipelago.

The phylogeography of black bears varies significantly along the north-south axis of Southeast Alaska. Broadly, populations in Southeast Alaska as well as the Kenai Peninsula in Southcentral Alaska are more closely related to black bear populations in eastern North America (Puckett et al. 2015). However, samples from the most southern portion of the Alexander Archipelago were more closely related to the geographically proximate western lineage of black bears (Puckett et al 2015). This suggests that the two lineages have come into contemporary contact in Southeast Alaska and are contributing to the genetic structuring of black bears in Southeast Alaska.

Analysis of aDNA from C^{14} calibrated bone samples collected across the Alexander Archipelago shows an absence of brown and black bears from 28–14kya (da Silva Coelho et al. 2023). These results are similar to a spatially broader study across western and eastern Beringia that shows extirpation of brown bears ~ 33kya (Salis et al. 2021). These authors hypothesized the presence of the short-faced bear (*Arctodus simus*) out-competed brown bears for resources, and only after its extinction were brown bears able to recolonize across Alaska. Thus, brown and black bears have likely occupied Southeast Alaska for a similar amount of time. Previous analyses of brown bear population structure identified eight subpopulation clusters with six of the clusters located along the coastal mainland, one cluster on Admiralty Island and the last cluster on

Baranof and Chichagof Islands (Flynn 2012). In a different study, an additional cluster was identified in Glacier Bay National Park (Lewis et al. 2015). Studies of population structure in black bears identified patterns very similar to brown bears with respect to the spatial locations of genetic clustering (Lewis et al. 2020; Peacock et al. 2007). The corroborated population genetic results between the species suggest that the landscape exerts similar barriers on brown and black bears despite their unique histories within the region.

In this study, we compare patterns of both population structure and barriers to gene flow from landscape genetic analyses between brown and black bears. We generated datasets of single nucleotide polymorphisms (SNPs) from low coverage whole genome sequencing (lcWGS) to identify fine-grained spatial structure patterns across Southeast Alaska. We hypothesized that the movement patterns across the environment would differ based on the capitalization of concentrated resources by brown bears and the population level avoidance of brown bears by black bears. Based on the variables from previous literature from Southeast Alaska, we tested whether landcover, elevation, topographic position index, landscape ruggedness, hydrological features, temperature, and precipitation has had an impact on gene flow in both species (Proctor et al. 2012; Lewis 2012; Cushman and Lewis 2010; Peacock et al. 2007; Paetkau et al. 1998).

METHODS

DNA extraction, genomic library preparation, and sequencing

Tissue samples were collected between 2017–2021 and consisted of either ear plugs or muscle tissue respectively from research animals or hunter harvested brown and black bears across Southeast Alaska. Samples were stored in Longmire's blood buffer

solution until DNA extraction (Longmire et al. 1988). The Fish and Wildlife Branch of the Yukon Department of Environment provided 23 dried muscle tissue samples from the Yukon Territories, Canada. These samples were rehydrated and stored in Longmire's blood buffer solution. We extracted DNA from all samples using the DNeasy Blood & Tissue Kit (Qiagen, Valencia, CA, USA) under the standard extraction protocol without the use of RnaseA. DNA concentration was quantified using the Qubit dsDNA BR Assay Kit on the Qubit 3 fluorometer (Invitrogen by Thermo Fisher Scientific, Waltham, MA, USA).

We prepared libraries for lcWGS individually using the Illumina DNA Prep Kit and protocol (Illumina, San Diego, CA, USA) modified using one-fifth reagent reaction volume for each sample. We used 20 ng of DNA per sample standardized to 3.33 ng/μl. We quantified each library using Qubit, then pooled individual libraries into groups of 48. We analyzed the DNA fragment size using the Agilent High Sensitivity DNA Kit for the Agilent 2100 Bioanalyzer (Agilent Technologies, Santa Clara, CA, USA) to confirm that the fragments were in the target range between 450 and 500 base pairs. Nine pooled libraries were sequenced on an Illumina Novoseq 6000 platform using separate lanes for each pool. We also sent three samples from each species for high coverage sequencing. The libraries were created without the dilution protocol and were sequenced on one lane each.

Reference panel construction and low coverage WGS imputation

We utilized reference panels from existing high coverage genomes sampled across each species range to impute missing sites in our lcWGS data. We downloaded 26 and 32 samples of *U. arctos* and *U. americanus*, respectively, for species-specific

reference panels (Tables S2.2, S2.3). We mapped reads to either the *U. arctos* (Taylor et al., 2018) or *U. americanus* (Srivastava et al., 2019) reference genome using BWA-MEM v0.7.17 (Li & Durbin, 2010) with default parameters. We marked duplicates, then called variants for each sample using the HaplotypeCaller function in GATK v4.1.8.0 (McKenna et al., 2010) where we set the heterozygosity parameter to 5.0×10^{-4}. For each species, we combined the samples using CombineGVCFs before joint genotyping using GenotypeGVCFs in GATK. We hard filtered the dataset using BCFTOOLS v1.9 (Heng Li, 2011) with parameters FS<40.0 && SOR<3 && MQ>40.0 && MQRankSum>-5.0 && MQRankSum<5 && QD>2.0 && ReadPosRankSum>-4.0 && INFO/DP<2500. We set genotypes to unknown if sample depth was less than 4 (FMT/DP<4) or genotype quality was less than 20 (FMT/GQ<20). Next, we removed monomorphic and polymorphic sites, retaining only biallelic SNPs; and finally, removed sites with greater than 10% missing data or a minor allele frequency less than 5%. We phased each reference panel using BEAGLE v5.1 (B. L. Browning, Zhou, & Browning, 2018; S. R. Browning & Browning, 2007). For each species, data was processed on the 36 longest scaffolds representing the autosomes. After filtering, there were 15,105,630 SNPs for *U. arctos*, and 8,753,063 for *U. americanus*.

We imputed missing data from the lcWGS samples using GLIMPSE v1 (Rubinacci et al. 2021). For samples sequenced at low coverage, raw data was mapped to its respective reference genome with bwa as detailed above. However, instead of calling sites with GATK, we followed the best practices provided with GLIMPSE and used the mpileup and consensus call functions within BCFTOOLS to estimate the genotype likelihoods. Samples were individually called before being merged, as imputation

accuracy increases with joint imputation. GLIMPSE imputes at predefined SNPs within the genome. We broke each scaffold into "chunks" for imputation and used a window size of 2Mb with a 200kb slide. Following running the GLIMPSE_phase function on each chunk, the pieces were ligated together.

Data filtering and preparation

Filtering for neutral markers was necessary for this analysis as loci that are under selection can bias gene flow results. First, we masked from 50kb upstream to 50kb downstream of each gene annotated in the genome feature file using VCFtools v0.1.19 (Danecek et al. 2011). We performed a linkage disequilibrium (LD) analysis to filter out highly linked loci. We filtered based on the LD value of 0.5 using the command BCFtools +prune -m 0.5 -w 50kb. We filtered out loci with a minor allele frequency (MAF) less than or equal to 0.05. Following LD and MAF filtering, the *U. arctos* dataset contained 277,446 SNPs, while *U. americanus* had 471,329 SNPs.

To keep relatedness from biasing population assignment in the population genetic analysis, we estimated kinship coefficients between dyads for each species using the --genome flag in PLINK. We first removed individuals related to more than one other individual. We then removed siblings and parent-offspring dyads resulting in retained individuals with a kinship coefficient of less than 0.2.

Population structure and gene flow

To describe population structure, and allow us to compare and contrast our results with previous analyses based on microsatellites, we ran ADMIXTURE v1.3.0 (Alexander et al. 2009). We ran cluster (K) values from one through 20 for each species independently with a cross validation of 20 for each K value. We plotted the cross-

validation error for each K and the lowest CV values for each species were chosen as a guide to select the most supported number of populations.

To quantify gene flow into and out of the management units within Southeast Alaska, we estimated bidirectional gene flow between GMUs using BayesAss3-SNPs (Mussmann et al. 2019; Wilson and Rannala 2003). We used GMUs in this analysis because they are the spatial areas relevant for the management of bears across this landscape. Given the large number of SNPs in the analysis and computational considerations with the mixing model in the software, we first thinned each dataset to 2,000 SNPs using the --thin-count flag in PLINK. Due to sampling variability among the GMUs, we removed GMUs with fewer than 10 samples (except Yukon Territories for black bears with nine samples), and randomly thinned samples down to 20 if a GMU had greater than that number. We then converted from PLINK ped format to immac format using PGDspider (Lischer & Excoffier, 2012). Initial runs of BayesAss3-SNPs were performed to identify appropriate mixing parameters for the allele frequencies (-a), inbreeding coefficients (-f), and migration rate (-m) parameters. These parameters were respectively set to 0.2, 0.5, and 0.15 for brown bears, and 0.1, 0.5, and 0.05 for black bears. All acceptance rates for final models fell between 20–60% for each parameter (Wilson & Rannala, 2003). We ran three independent chains of the MCMC for each species, with 2.5×10^7 iterations, sampling every 10^4 iterations, with 20% burn-in discarded. We estimated pairwise F_{ST} among the GMUs using VCFtools with the same sample subset utilized for the geneflow analysis, although all imputed SNPs were included.

To visualize gene flow, we used estimated effective migration surfaces (EEMS)

(Petkova et al. 2016). This analysis was independent of the GMUs. We ran one chain

three times for each species. We used 20,000,000 iterations with a burn in of 5,000,000

and a thinning rate of 9,999. We ran the brown bear analyses with qEffctProposalS2,

mEffctProposalS2, qVoronoiPr, and negBiProb equal to 0.01, 0.8, 0.3, and 0.5

respectively. For black bears the variables qSeedsProposalS2, mEffctProposalS2,

qVoronoiPr, and negBiProb variables were 0.03, 0.7, 0.4, and 0.9 respectively. The

chains were visually inspected for convergence. We plotted results using the rEEMSplots

v0.0.1 package in R v4.2.2 (R Core Team 2022; Petkova et al. 2016).

Landscape genetics analysis

To create the individual-based genetic distances that served as the response

variable in the landscape genetics analysis, we used the R program popkin (Ochoa and

Storey 2021). We first read in PLINK binary files into R using the BEDMatrix function.

We then utilized the popkin and pwfst functions to create the individual-level pairwise

F_{ST} matrix for input into the landscape genetics analysis.

To assess the effects of the environment on gene flow, we created a model using

landscape level variables across Southeast Alaska. We downloaded nine landscape layers

into ArcGIS Pro v2.9 (ESRI Inc 2021) and utilized the NAD83 datum with the Alaska

state plane coordinate system zone 1 projection. We incorporated four categorical

variables: MODIS land cover (Friedl and Sulla-Menashe 2019), towns and roads (Alaska

DOT&PF 2022), and hydrologic layers. These layers included water as well as permanent

snow and ice (U.S. Geological Survey 2022). Three continuous surfaces included: the

digital elevation model (DEM) (U.S. Geological Survey 2019), temperature (SNAP

2015), and precipitation (SNAP 2022). We created two more continuous layers from the

DEM using the terra package (Hijmans et al. 2023): topographic position index (TPI) and vector ruggedness measurement layers. All layer cell sizes were standardized to the MODIS landcover data size of 463 m^2.

We used the program ResistanceGA v4.2.8 (Peterman 2018) in conjunction with the program Circuitscape v5.12.3 (Hall et al. 2021) written in the Julia language (Bezanson et al. 2017) to perform the landscape genetic analysis. ResistanceGA utilizes a genetic algorithm to optimize the input genetic distances as the response variable to modified landscape layers. The maximum likelihood population effects parameter is built into the regression analysis within ResistanceGA to control for spatial effects. The layers were imported into R and combined into a raster stack object in the raster package v3.6.20 (Hijmans 2020) in R. A spatial points object of the sample coordinates as well as an individual-based genetic distance matrix was imported into R and the GA.prep and jl.prep functions from ResistanceGA were used to prepare the data for analysis. We performed single surface analyses followed by multi-surface analysis. We used the SS_optim function to perform the single surface optimization for each layer in the analysis. We compared the corrected Aikake information criterion (AICc) value with a distance model output by the SS_optim function. Any layer in which the AICc value was not higher than the distance model was not retained in the multi-surface analysis. We analyzed nine single layers for each species. The optimized landcover rasters were input into the Run_CD.jl function within ResistanceGA to create a raster in which each pixel was a measure of the probability of gene flow.

We performed the multi-surface analysis using the MS_optim function and then created a map of the estimated gene flow across the landscape. All layers were stacked in

R for analysis. The output of the analysis included an optimized resistance surface raster as well as a coefficient table and the percent contribution of each layer to the optimized resistance surface. The analyses were repeated three times to test concordance and the models with the lowest AICc values were chosen. The optimized multi-surface raster was input into the Run_CD.jl function like the single surface landcover. We used the output rasters to create maps in ArcGIS Pro.

We compared the relative probability between brown and black bears for each cell in the estimated gene flow raster by creating a map in which each cell value corresponded to the difference in gene flow between the two species. This was done by standardizing the values of the estimated gene flow rasters for each species to values between zero and one by dividing each raster by the highest value on that surface. The brown bear raster was then subtracted from the black bear raster which produced a raster with values between negative and positive one. Pixels with a negative value have a higher probability of gene flow from brown bears across the landscape, while positive values indicated black bears had a higher probability to disperse through that area.

RESULTS

DNA extraction, genomic library preparation, and sequencing

In total, we extracted the DNA from 240 brown bear and 421 black bear samples. Seven brown and 19 black bear samples yielded no DNA due to poor sample quality. We created libraries for 192 brown and 248 black bears, respectively. Of the sequenced libraries, four brown and three black bears were removed from the analysis due to minimal read pairs sequenced. We added 11 brown and 83 black bear lcWGS from a previous sequencing effort to this dataset (Puckett et al. 2023). We added the three high

A)

B)

K = 7

YT   5   4   3   1D   1C   1B 1A
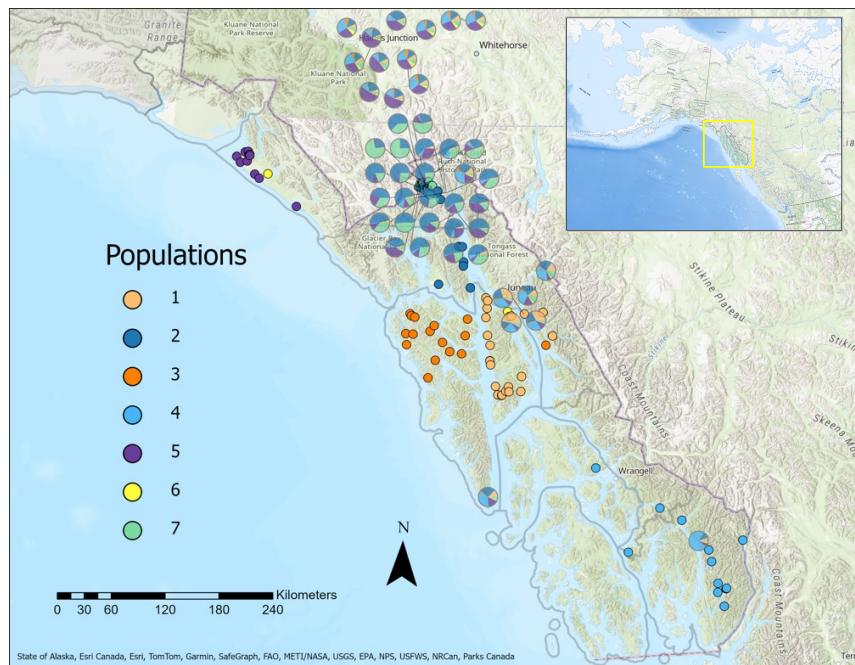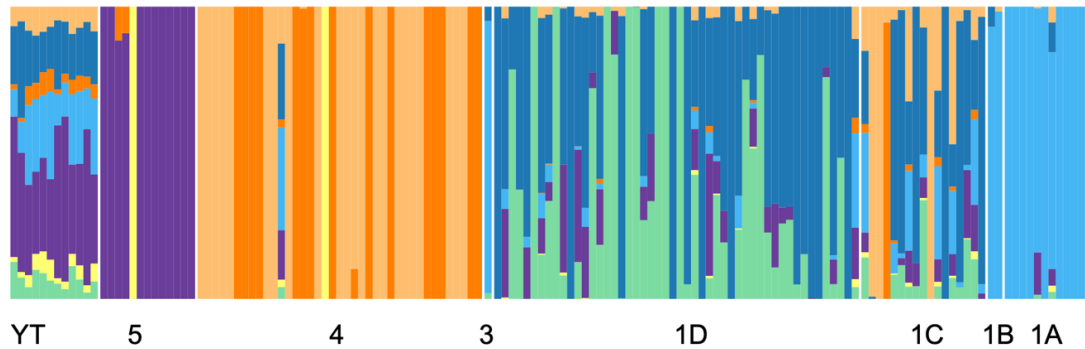
Figure 2.2: (A) The geographic location for each brown bear (*Ursus arctos*) across Southeast Alaska and southwestern Yukon with the GMUs outlined in gray. Sampling locations were colored by the assignment to the seven genetic clusters. The pie charts represent individuals with less than 75% of the genome assigned to a single population. The population numbers in the legend show the order in which the populations split. (B) The best supported ADMIXTURE plot with a K-value of seven for brown bears.

coverage samples for each species to the dataset. Thus, sample sizes prior to filtering for

relatedness were 200 brown bears and 324 black bears. After removing related

individuals from the dataset, we were left with 146 brown and 243 black bears.

Population structure and gene flow

Brown bears- The best supported number of evolutionary clusters was seven (Figure 2.2, S2.1A). At two evolutionary clusters, there was a marked distinction between brown bears on the ABC Islands and mainland, where adding a third cluster separated Admiralty Island from Baranof and Chichagof Islands (Figure S2.2). The southern portion of the study area encompassing GMUs 1A and 1B clustered at K=4. The highest F_{ST} value for brown bears was 0.133 and occurred between 1A and GMU 4 which includes the ABC Islands (Table 2.1). GMU 5 which was primarily sampled around Yakutat, AK clustered at K=5. The second and third highest F_{ST} values for brown bears of 0.131 and 0.115 occurred between GMU 1A in the south and GMUs 5A and 1D in the north of the study area (Table 2.1). The sixth and seventh clusters did not have distinct geographic components. Both clusters show up as individuals with all ancestry assigned to the cluster and as a mixture with other geographically distinct groups (Figure 2.2). There was broad but imperfect concordance between patterns of genetic clustering and the state designated GMUs. GMU 1C, located on the mainland surrounding Juneau, is notable for high

Table 2.1: The FST values between populations of brown bears (*Ursus arctos*) are in the cells above the diagonal while FST values for black bears (*U. americanus*) are below the diagonal. The GMUs are listed in the top row and first column of the table. Brown bears are not found in GMUs 2 and 3 and black bears are not found in GMU 4, so NA values were used for these GMUs.

	GMU 1A	GMU 1C	GMU 1D	GMU 2	GMU 3	GMU 4	GMU 5A	Yukon Territories
GMU 1A	-	0.095	0.115	NA	NA	0.133	0.131	0.088
GMU 1C	0.128	-	0.018	NA	NA	0.035	0.051	0.024
GMU 1D	0.177	0.030	-	NA	NA	0.076	0.058	0.036
GMU 2	0.197	0.259	0.333	-	NA	NA	NA	NA
GMU 3	0.122	0.141	0.191	0.258	-	NA	NA	NA
GMU 4	NA	NA	NA	NA	NA	-	0.079	0.060
GMU 5A	0.122	0.068	0.050	0.397	0.238	NA	-	0.036
Yukon Territories	0.180	0.037	0.052	0.382	0.203	NA	0.079	-

Table 2.2: Gene flow between GMUs in brown bears (*Ursus arctos*) with the cell value representing gene flow from the row GMU to the column GMU. Higher numbers indicate more gene flow.

	GMU 1A	GMU 1C	GMU 1D	GMU 4	GMU 5A	Yukon Territories
GMU 1A	0.890	0.037	0.018	0.017	0.018	0.020
GMU 1C	0.015	0.681	0.188	0.072	0.030	0.014
GMU 1D	0.013	0.026	0.910	0.012	0.013	0.026
GMU 4	0.013	0.026	0.012	0.870	0.065	0.013
GMU 5A	0.018	0.018	0.210	0.018	0.720	0.017
Yukon Territories	0.018	0.020	0.241	0.019	0.018	0.685

variability in ancestry components among animals sampled in that region (Figure 2.2).

The lowest F_{ST} value of 0.018 occurred between GMUs 1C and 1D (Table 2.1).

Ancestry patterns clearly identified recent migrants among the GMUs (Figure 2.2A). To further explore rates of gene flow, we thinned our dataset to 2,000 SNPs and between 10–20 bears per GMU. We observed high gene flow into GMU 1D from three different regions: GMU 1C (18.8%), 5A (21.0%), and SW Yukon (24.1%; Table 2.2). GMU 4 which encompasses the ABC Islands received 7.2% of migrants from GMU 1C which is across the Stephens Passage waterway. Finally, we observed elevated gene flow from GMU 4 into 5A at 6.5% (Table 2.2).

Black bears- Six evolutionary clusters were best supported in the analysis of population structure in black bears (Figure S2.1B). At two clusters, the deepest split was observed between the southern region (GMUs 1A, 2, and 3) and all other regions of the study area (GMUs 1B, 1C, 1D, 5A, and the Yukon Territories; Figures 2.3, S2.3). This initial split that separates GMU 2 from the rest of the study area more broadly coincides with the highest F_{ST} values. GMU 2 has F_{ST} values of 0.397, 0.382, 0.333, and 0.258 with GMUs 5A, the Yukon Territories, 1D and 3, respectively (Table 2.1). At three evolutionary

A)

B)
K = 6

YT 5   3   2   1D   1C   1B   1A
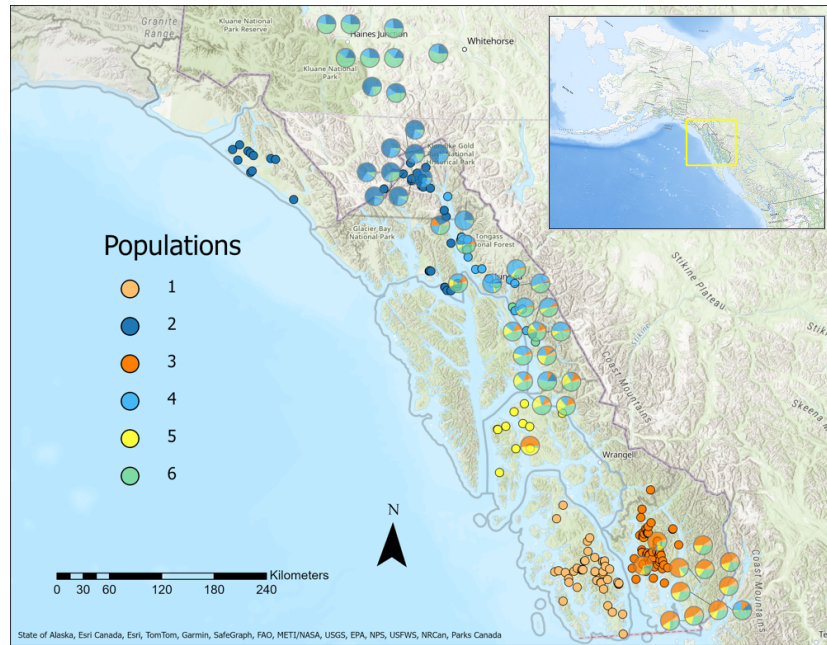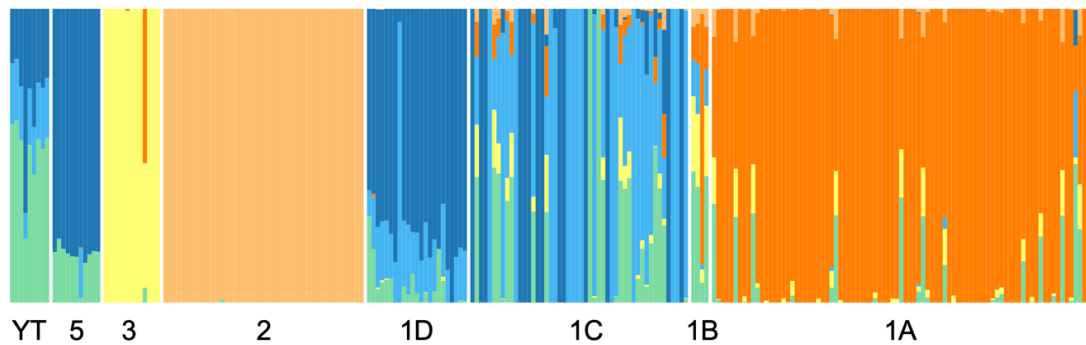
Figure 2.3: The geographic location for each black bear (*Ursus americanus*) across Southeast Alaska and southwestern Yukon with the GMUs outlined in gray. Sampling locations were colored by the assignment to the six genetic clusters. The pie charts represent individuals with less than 75% of the genome assigned to a single population. The population numbers in the legend show the order in which the populations split. (B) The best supported ADMIXTURE plot with a K-values of six for black bears.

clusters, GMU 1A clustered uniquely from GMUs 2 and 3. The fourth cluster was found throughout the central and northern portions of the study area, yet predominated in the central area around GMU 1C. At K=5, black bears from GMU 3 clustered uniquely. The sixth cluster was found throughout the study area but made up the largest proportion of

Table 2.3: Gene flow between GMUs in black bears (*Ursus americanus*) with the cell value representing gene flow from the row GMU to the column GMU. Higher numbers indicate more gene flow.

	GMU 1A	GMU 1C	GMU 1D	GMU 2	GMU 3	GMU 5A	Yukon Territories
GMU 1A	0.914	0.012	0.012	0.013	0.012	0.019	0.025
GMU 1C	0.036	0.804	0.099	0.012	0.012	0.012	0.025
GMU 1D	0.013	0.024	0.889	0.013	0.012	0.037	0.012
GMU 2	0.012	0.013	0.012	0.926	0.013	0.012	0.012
GMU 3	0.033	0.017	0.017	0.016	0.884	0.017	0.017
GMU 5A	0.019	0.019	0.056	0.018	0.018	0.851	0.019
Yukon Territories	0.020	0.021	0.069	0.022	0.022	0.020	0.827

ancestry in bears from either SW Yukon or GMU 1C (Figure 2.3). The lowest and highest F_{ST} values in black bears were 0.030 and 0.397 (Table 2.2).

Our analyses of gene flow among the GMUs identified a single sink population with gene flow elevated over the background level. The sink was found in GMU 1D where GMUs 1C (9.9%), 5A (5.6%), and SW Yukon (6.9%) were sources of elevated gene flow (Table 2.3).

Effective migration surfaces- To complement our analyses of bidirectional gene flow, we estimated effective migration surfaces using our full SNP dataset for each species. In brown bears, the migration surface was characterized by 100-fold less gene flow surrounding GMU 4 (e.g., ABC Islands) and the mainland (Figure 2.4A). Decreased gene flow was also observed on the mainland, primarily between GMUs 1C and populations to the south. Elevated gene flow was found within the geographic regions associated with evolutionary clusters, including: 5A, 4, 1D, 1C, and 1A. Notably the samples from the Yukon Territories were found in an area of elevated gene flow that extended into unsampled British Columbia.

For black bears, a band of low migration ran along both the mainland and the
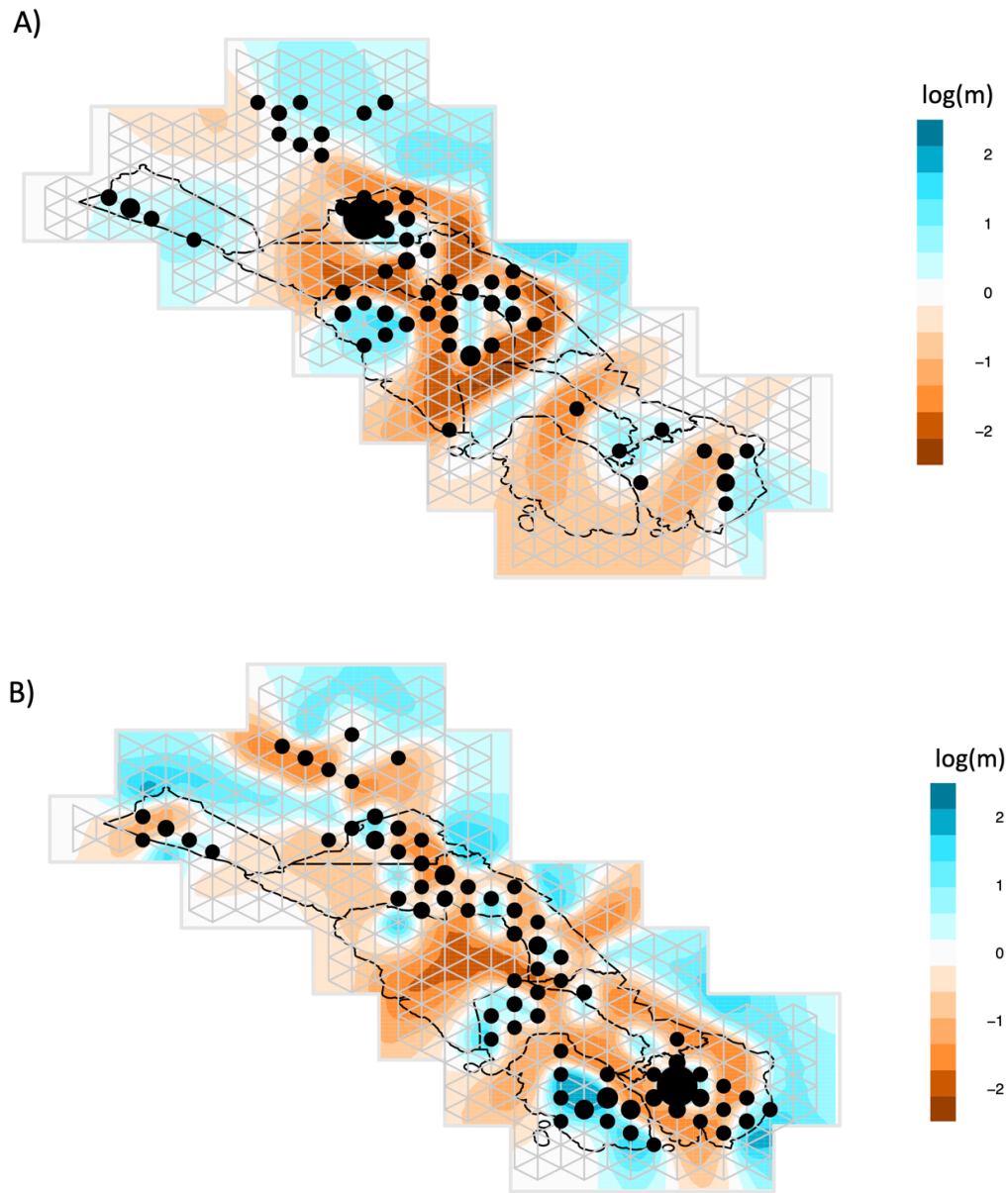
Figure 2.4: Migration rates for brown bears (*Ursus arctos*) are displayed in (A) and black bears (*U. americanus*) in (B) with the log migration values. The points on the maps represent the sampling locations. Areas in light blue indicate higher migration rates while the areas in brown show areas with low effective migration. In brown bears (A) decreased gene flow was observed on the mainland in GMUs 1C. Areas of elevated gene flow correspond to evolutionary clusters including 5A, 4, 1D, 1C, and 1A. For black bears (B) low migration was observed between the mainland and the islands. Gene flow was higher in the GMUs except for 5A and SW Yukon.

was higher within GMUs with the exceptions of 5A and SW Yukon which showed

greater limits of movement within those areas (Figure 2.4B).

Landscape genetics analysis

The brown bear landscape genetics analysis included all continuous and categorical landscape layers as they all explained more genetic variation than the IBD model alone (Table S2.3). For black bears, all single surfaces performed better than IBD except for the roads layer which was not retained in the full model (Table S2.6).

The single layer with the highest AICc value in both species was landcover. The categorical results for the single surface landcover analysis ranked each category from least to most resistant. The patterns for brown and black bears were largely similar, with differences that have plausible biological explanations. We found a large disparity between the most and least supported single layer models for brown bears with a corresponding ΔAIC range difference of 4,747 (Table S2.3). Of the thirteen landcover layers (Table S2.5) there were seven that had a resistance less than 100 indicating a high probability for gene flow. The categories included barren areas, open forests, evergreen needleleaf forests, snow and ice, shrub and grassland mosaic, deciduous broadleaf, and dense herbaceous (Table 2.3). In the resistance surface for brown bears, high gene flow was estimated around Haines and on Admiralty Island. Further, concentrated areas of gene flow occurred on the Chilkat Peninsula, south of Juneau in GMU 1C, and Baranof and Chichagof Islands (Figure 2.5A).

In black bears the ΔAIC was 52,288 between the most and least supported models. There were five categories less than 100 in black bears and they were open deciduous broadleaf, and dense herbaceous (Table 2.4). In the resistance surface for brown bears, high gene flow was estimated around Haines and within Admiralty Island. Further, concentrated areas of gene flow occurred on the Chilkat Peninsula and south of

Table 2.4: The resistance values for the single landcover layer for brown bears (*Ursus arctos*) ranked from the least resistant to the most resistant landcover category.

Landcover Type	Resistance
Barren	1.00
Open Forests	1.37
Evergreen Needleleaf	3.61
Snow/Ice	5.05
Shrubland/Grassland Mosaic	8.29
Deciduous Broadleaf	22.79
Dense Herbaceous	77.64
Mixed Broadleaf/Needleleaf	340.75
Sparse Herbaceous	409.09
Sparse Forests	545.65
Sparse Shrublands	638.87
Dense Shrublands	816.02
Water	1000.00

Table 2.5: The resistance values for the single landcover layer for black bears (*Ursus americanus*) ranked from the least resistant to the most resistant landcover category.

Landcover Type	Resistance
Open Forests	1.00
Barren	1.86
Dense Herbaceous	2.16
Evergreen Needleleaf	3.58
Snow/Ice	17.35
Deciduous Broadleaf	257.27
Mixed Broadleaf/Needleleaf	397.22
Shrubland/Grassland Mosaic	503.30
Dense Shrublands	517.35
Sparse Herbaceous	612.78
Sparse Shrublands	800.18
Water	877.27
Sparse Forests	1000.00

Juneau in GMU 1C (Figure 2.5A).

In black bears the ΔAIC was 52,288 between the most and least supported models. There were five categories less than 100 in black bears, and they were open forests, barren areas, dense herbaceous, evergreen needleleaf forests, and snow and ice. Shrublands were some of the most resistant categories for black bears as well with water and sparse forest the most resistant (Table 2.5). The resistance surface for black bears
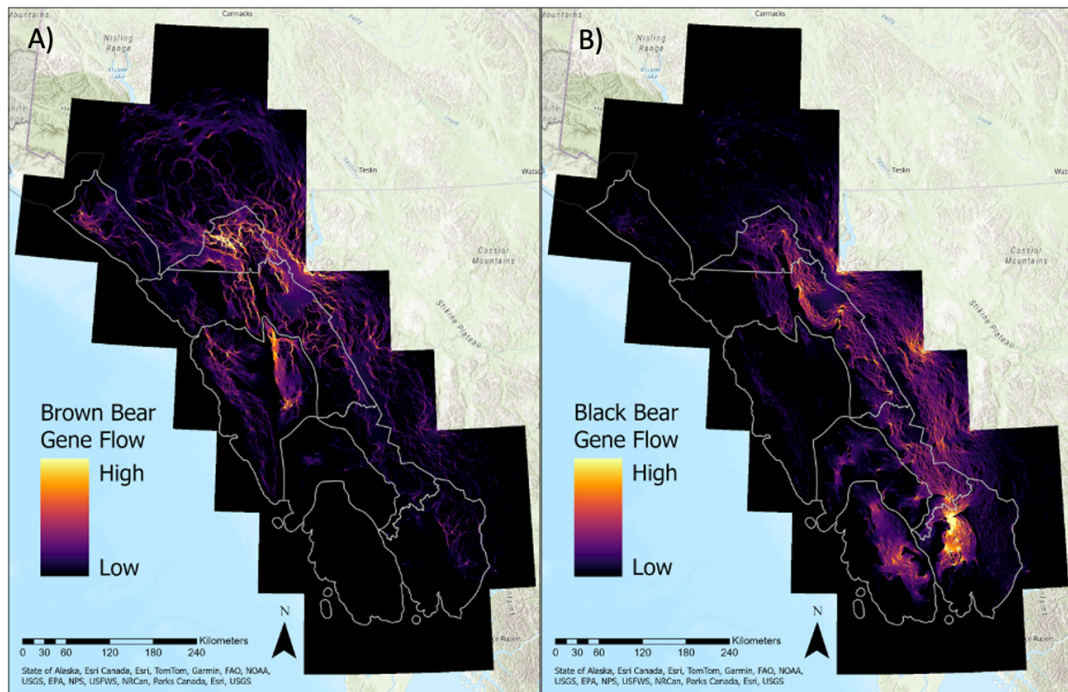
Figure 2.5: These maps show the resistance values for the landcover layers for brown (*Ursus arctos*) (A) and black bears (*U. americanus*) (B). Areas with a higher estimated gene flow are shown with warmer colors. The estimated gene flow is based on the optimized resistance surface output from ResistanceGA. Landcover was the best supported model in both species.

shows general gene flow from the Chilkat Peninsula near Haines and along the southern extent of the mainland coast (Figure 2.5B). There was a band of projected gene flow through the Juneau area that continued down the mainland coast to GMU 1A. There are distinct points across the landscape at which the estimated gene flow is more constrained shown by the yellow and white areas on the gene flow map (Figure 2.5B).

The multi-surface results from ResistanceGA gave us the percentage contribution for each of the layers that were put into the MS_optim function. For brown bears, the three layers with the highest percent contribution to the genetic distances were landcover (61%), water (13%), and permanent ice and snow (6%; Table S2.4). For black bears, landcover (55%), TPI (24%), and water (11%) made up the top three highest contributing

layers (Table S2.7). Except for the top three layers in both models, the contribution by the remaining layers was less than five percent.

We compared patterns of gene flow between brown and black bears across Southeast Alaska to contrast geographic variation. The estimated gene flow was higher for brown bears in the northern portion of the study area specifically around Haines in GMU 1D. The estimated gene flow in black bears can primarily be seen on the southern portion of the study area in GMUs 1A and 2 along with the areas along the mainland. Both bear species have estimated gene flow over areas of ice with the amount of gene flow higher in black bears. Both species display lower gene flow probabilities across waterbodies in most of the study area as compared to the majority of the land masses.

DISCUSSION

Comparative landscape genetics

The main purpose of this study was to quantify and compare how the environment has structured gene flow for brown and black bears. We found that not only was the single landcover layer the best supported model of those tested, but it was also by far the largest contributor to gene flow in the multi-layer analyses (Table S2.5, S2.6). Open forests, barren areas, and snow and ice all displayed low resistance, or high movement, in both species. Open forests, defined as areas with 30–60% tree cover, are patchily distributed in GMUs 2, 3 and 4. The area in which open forests are most prevalent within the study area is Canada. Open forests are the primary habitat there and contribute largely to gene flow in the Yukon Territory bears. The shrubland and grassland habitat type as well as barren areas are also primarily found in Canada. Barren areas and the edges of snow and ice are areas with little vegetation and could provide corridors that are easier to

move across for both species, especially in the spring, and we know that bears travel across areas of least resistance (Carnahan et al. 2021). This transit pattern may contribute to the patterns of gene flow observed on the mainland (Paetkau et al. 1998). A previous radio-collar study shows that brown bears move around the perimeter of glaciers and snow pack and this could explain why permanent snow and ice also show lower resistance (Crupi et al. 2014). Water served as a high resistance barrier which was consistent with results from other studies (Lewis et al. 2020; Lewis et al. 2015; Proctor et al. 2012; Peacock et al. 2007; Paetkau et al. 1998). The high resistance of sparse forests also matches black bear ecology as the species is more adapted to and prioritize moving in areas with forest cover (Belant et al. 2010; Herrero 1978).

Evergreen needleleaf forests and dense herbaceous areas are the two most common landcover types in the study area and the brown and black bear usage patterns reflect their behavioral ecology. The evergreen needleleaf forests in Southeast Alaska are primarily found at the edge of bodies of water. These are areas that contain vegetation in the spring and the streams from which bears catch salmon during the late summer and fall. In Southcentral Alaska, brown bears descend from denning areas in the spring and use vegetation as the primary food source (Belant et al. 2010). We also know that brown bears establish home ranges that encompass areas near the shore (Crupi et al. 2014). Brown bears can exclude black bears from these areas and potentially utilize needleleaf forests more than black bears during natal dispersal and mating movements in the spring (McLellan 1993). Dense herbaceous habitat provided less resistance to black bears. Contributing factors to this pattern could include that black bears can utilize less dense resources than brown bears due to their smaller body size and black bears also may be

forced into higher elevations by brown bears (Belant et al. 2010; Mattson et al. 2005). The higher probability of gene flow along the mainland in black bears could be driven primarily by the higher predicted gene flow in dense herbaceous habitat.

The patchy distribution of resource types drives the differences between areas of low and high gene flow in both species. We see one of two patterns; the first pattern is displayed in brown bears around Haines in GMU 1D (Figure 2.5). In this area gene flow is restricted to specific areas of the environment; however, we know gene flow is high in this region from the population genetics results. The many constrained paths provide diverse avenues for gene flow in the area and connectivity is still high. We see a contrasting pattern in black bears along the mainland. Black bear gene flow in this area shows several points where the probability is high and there is only one path, especially around Juneau. This pattern represents constricted areas within the environment with gene flow few paths. This pattern could be representative of the environment limiting dispersal and structuring black bear populations.

Brown bear landscape genetics

Many studies have investigated areas where anthropogenic impact is high; however, this is not the case in most of Southeast Alaska and one of the strengths of our study is that we analyzed brown bear gene flow without strong anthropogenic effects. The impact of roads and settlement on brown bear connectivity and gene flow can be high in parts of North America and Europe (Palm et al. 2023; Fedorca et al. 2019; Mateo-Sánchez et al. 2014; Proctor et al. 2012). These studies were in interior BC, Canada and the northwestern United States as well as Spain and Romania where anthropogenic impacts are high. When we look at landscape genetics studies from Southeast Alaska

where anthropogenic impact is low in most areas, we see that environmental factors are not anthropogenic in nature such as ruggedness, ice, and water (Lewis et al. 2015; Paetkau et al. 1998). In our study, we found that all single layers described the genetic data better than distance alone and our full model was the second most supported in brown bears. Within the full model, landcover as well as ice and snow made up 74% of the model contribution. Landcover, water, as well as ice and snow were important factors for gene flow in brown bears and that finding agrees with previous work in Southeast Alaska.

Brown bear population structure

In this study we found support for seven subpopulations of brown bears which corresponds to previous population clusters identified across Southeast Alaska as well as within two specific areas, Glacier Bay National Park, and the ABC islands. The overall range of F_{ST} values indicate differentiation in brown bears is not as high as black bears in the study area. We found that the first population split in the admixture analysis was between GMU 4 with four individuals from 1C from the rest of Southeast Alaska (Figure S2.2). The next split was between Admiralty Island and Baranof and Chichagof Islands. Considerable work has been done on these populations since it was discovered that the brown bears on the ABC Islands shared mitochondrial DNA with polar bears (Talbot and Shields 1996). Recent phylogeographic evidence supports the hypothesis that introgression into brown bears by female polar bears occurred around 155 kya on the ABC islands (Wang et al. 2022; Hassanin 2015; Liu et al. 2014). After the introgression event, bears were isolated in a glacial refugia on the western edge of the ABC islands during the LGM (Sawyer et al. 2019). After the LGM, when the ice was receding, the

size of the water channels only allowed the male movement of brown bears into the ABC islands (Paetkau et al. 1998). The male-mediated gene flow maintained the differences in autosomal, X chromosome, and mitochondrial DNA (de Jong et al. 2023; Cahill et al. 2015; Hassanin 2015; Cahill et al. 2013). This supports the genetic differences between the ABC bears and explains why they cluster strongly. The next two groups to split out are the populations on the southern (GMUs 1A, 1B, and 3) and northern (GMU 5A) portions of the study. The two individuals that split at a K of six are anomalous as very little of the cluster can be seen in other individuals. This study does not include any samples from Glacier Bay National Park as there is no legal hunting allowed there. Lewis et al. (2015) found a population cluster within the park and the two outlying individuals in our results could potentially be from that population; however, if that cluster did originate from the park, we would still expect to see more of a genetic signature across individuals in our study. The last cluster highlights the subpopulation mixture in GMU 1C. These subpopulations are concordant with the population structure in Flynn et al. (2012) in which there was a southern population, two populations in GMU 1C along the mainland, one population each in GMUs 1D and 5A, and two populations in GMU 4, one on Admiralty Island and the other on Baranof and Chichagof Islands. The concordance between these studies suggests that the population structure is representative of the true population structures within brown bears. Our EEMS results, which highlight older divergence, were concordant with these findings (Figure 2.4A). We see higher concordance between the Baranof and Chichagof islands, Admiralty Island, and the mainland around Haines which indicate that these are deeper differences through time and not a recent pattern.

Black bear landscape genetics

In the black bears landscape genetics analysis, we found that our results supporting landcover were similar to previous work done in the system. Black bears have been shown to be less affected by anthropogenic factors than brown bears and have been found closer to roads and developed areas (Sawaya et al. 2014; Mattson et al. 2005). For this reason, environmental variables not related to anthropogenic factors are more likely to affect gene flow in areas with higher human impact. Rivers in Michigan as well as glaciers and non-forested regions in Southeast Alaska and the Rocky Mountains have been shown to prevent gene flow in black bears (Draheim et al. 2021; Lewis et al. 2020; Bull et al. 2011). Middle elevations ranging from 1000 to 1500 meters as well as forest cover facilitated black bear gene flow in the Rocky Mountains (Bull et al. 2011). This study corroborates those findings as landcover was the best supported model with open forests, dense herbaceous areas and evergreen needleleaf forests serving as some of the least resistant landcover types.

Black bear population structure

We found support for six subpopulations of black bears. The initial split at a K of two is on a north-south axis with the southern GMUs (1A, 2, 3) separating from the more northern GMUs (1C, 1D, 5A, and the Yukon Territories). This is indicative of the deep lineage in American black bears across North America. There is an eastern and western lineage of black bear with a zone of contact in Southeast Alaska (Puckett et al. 2015). The two lineages were separated for 169 ka (Puckett et al. 2015), and genetic drift increased the allelic divergence between both lineages prior to contact after the LGM. Black bears have not formed a panmictic population across Southeast Alaska, so the

signature of the lineages has not disappeared. The two deep linages explain why the F_{ST}

values in black bears are so much higher than brown bears. This also helps to explain

why the differentiation occurs along the north-south axis. We see the split between

GMUs 1B and 3 in the south and 1C in the north. The structure at a K of three splits

between GMUs 1A and 2 which could reflect the higher gene flow along the mainland.

At a K of five, GMU 3 separates out indicating that the isolation could be enough

for drift to have affected the population. The F_{ST} values of 0.122, 0.141, and 0.191

between GMUs 3 and 1A, 1C, and 1D respectively reflect this later split. The clustering

at K values of four and six reflect degrees of mixture between the eastern and western

lineages centered around GMUs 1C and 1D on the mainland. This gradient of lineage

mixing can be seen in the F_{ST} values between GMU 2 and the mainland. The value

between GMUs 2 and 1A is 0.197. F_{ST} increases as we move north into 1C to 0.259 and

again in 1D at 0.333 with the highest value occurring between GMU 2 and 5A at 0.397.

This is a strong and definitive gradient. When we look in the opposite direction, we see

that the same pattern exists but there are smaller differences between GMU 5A and the

mainland. Interestingly, the F_{ST} value between GMU 1C and the Yukon Territories is less

than the value between 1D and the Yukon Territories. Coastal river systems make the

mountain ranges on the edge of Southeast Alaska permeable to gene flow and there may

be an inland route for gene exchange that reduces the genetic differences between the

Yukon Territories and more southerly GMU 1C (Lewis et al. 2020; Dawson et al. 2007).

Several studies have analyzed the population structure of black bears in Southeast

Alaska (Lewis et al. 2020; Peacock et al. 2007). Lewis et al. (2020) found support for ten

populations from GMU 3 to GMU 5B. The study included samples from Glacier Bay

National Park (GBNP) and GMU 5B, neither of which were included in our study. Our results were broadly concordant with one population cluster in GMU 3, two clusters along the mainland in 1C, one population near Haines in 1D, and one population in 5A. We did not find support for a separate population cluster in the Chilkat Range on the western side of GMU 1C. In our study those individuals grouped with the population in 1D. We also could not compare the GBNP populations to our study. The spatial extent of our study matched that of Peacock et al. (2007) and the results were again, broadly similar; however, we did not find support for nine subpopulations. In GMU 1C and 1D, we found evidence for only three subpopulations in this region, whereas Peacock et al. (2007) found evidence for four. We also did not find two subpopulations in GMU 3. GMU 2 grouped strongly together in our results, unlike Peacock et al. (2007) in which six of their nine clusters were represented in the GMU. The results from these two studies as well as our results show different population structuring; however, the differences appear to be related to assignments within populations rather than completely discordant population structuring. All three studies show subpopulations grouping on islands and different portions of the mainland suggesting, like with brown bears, that these patterns are not spurious. Our EEMS results for black bears support the results at a deeper time scale as we identified barriers to gene flow throughout GMUs 1A, 2, 3, 1D, 5A, and two along the eastern mainland in 1C. These highly resistant surfaces are concordant with the subpopulation delineation that we found in the genomic data.

Caveats and future directions

 A major obstacle that we encountered in this study was that of computational time. We are in the process of searching for new ways to optimize performance and

minimize the computational challenges that were prohibitively large for desktop

computers and took a month or more to run on the high-performance computing cluster.

Reducing the computational load would allow for further development of competing gene

flow models and lead to greater insight into the drivers of gene flow in Southeast Alaska.

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Supplemental Figures

A)

B)
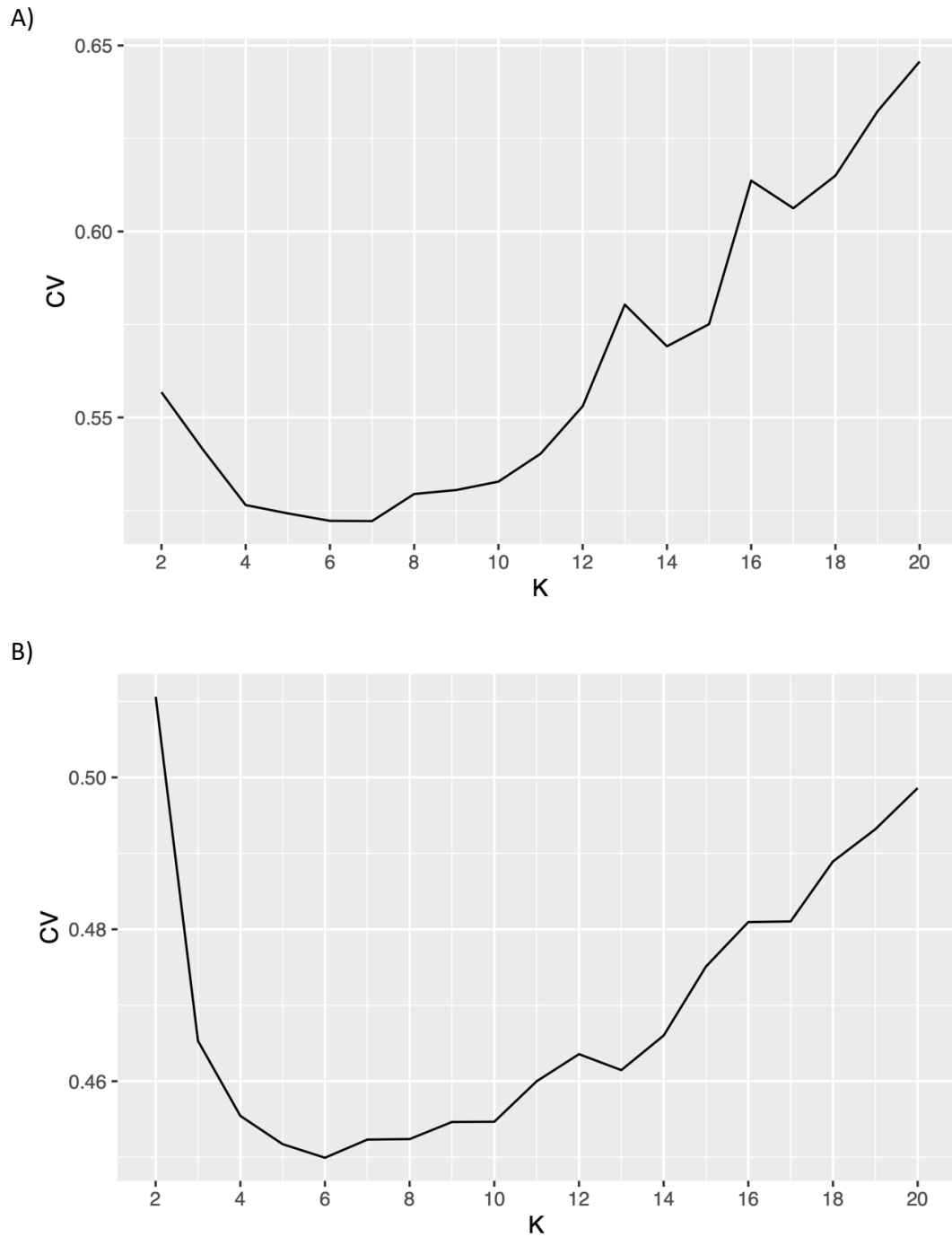
Figure S2.1: Cross validation error (CV) plots from ADMIXTURE for brown bear (*Ursus arctos*) (A) and black bear (*U. americanus*) (B). Clustering was run from 1 to 20 for 20 repetitions of the program to estimate the CV error. The lowest CV values found at K=7 for brown bears and K=6 for black bears.
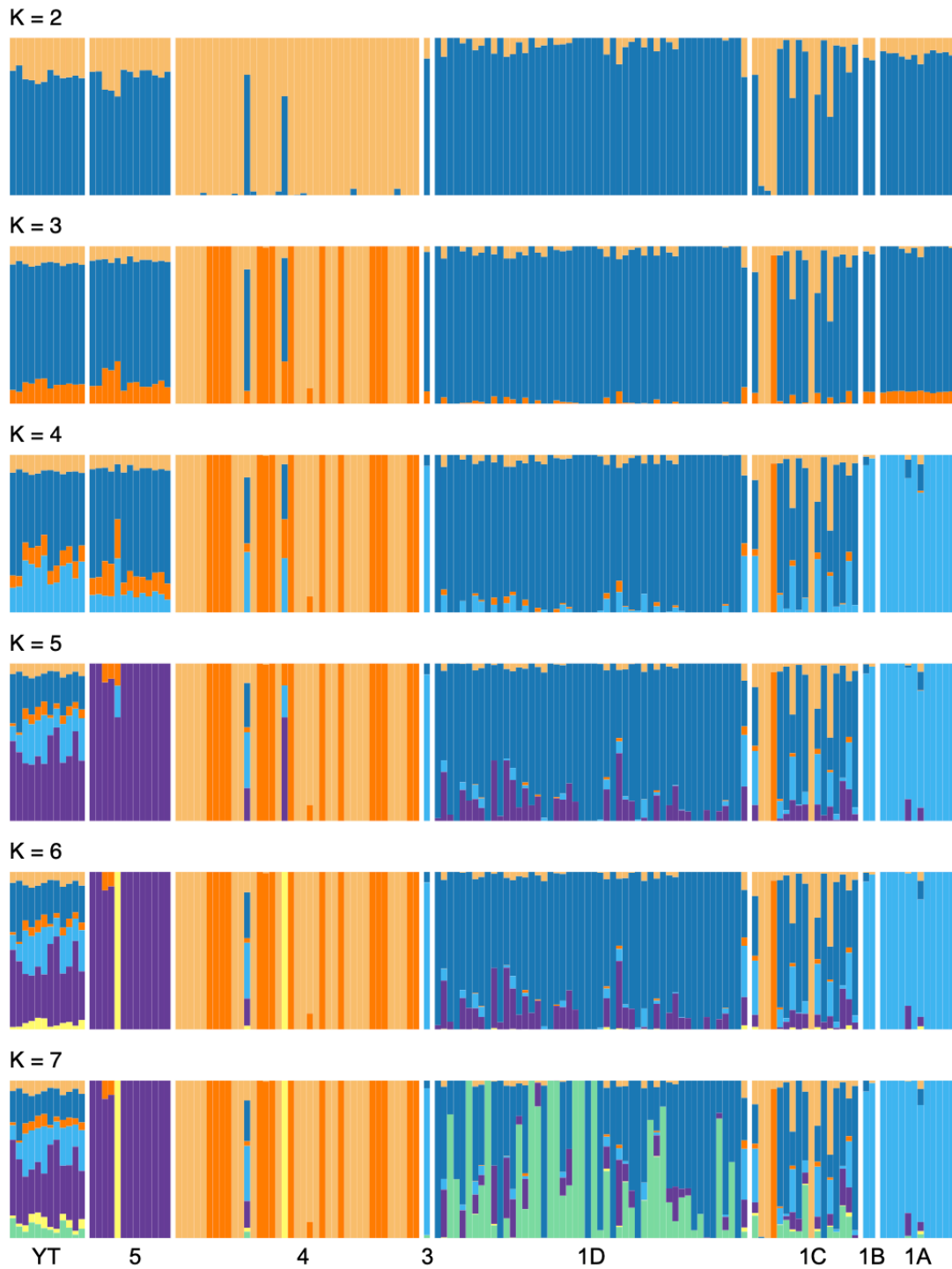
Figure S2.2: Ancestry proportions estimated from ADMIXTURE for brown bear (*Ursus arctos*) samples (n = 146). Samples have been organized based on their Game Management Units (GMUs) designated by ADF&G, except for samples from the Yukon Territories (YT). Support for varying levels of clustering can be seen in Figure S2.1A.
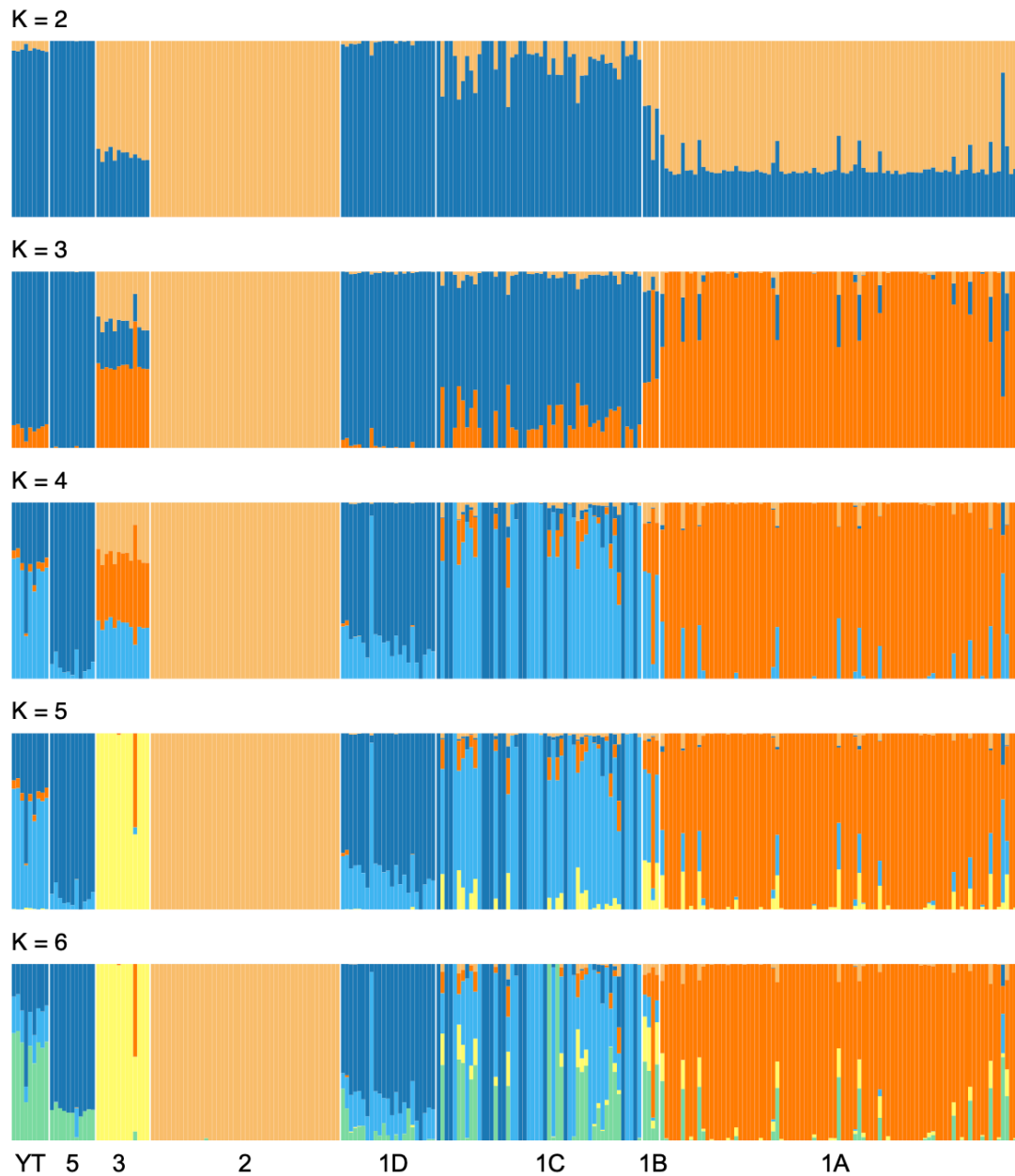
Figure S2.3: Ancestry proportions estimated from ADMIXTURE for black bear (*Ursus americanus*) samples (n = 244). Samples have been organized based on their Game Management Units (GMUs) designated by ADF&G, except for samples from the Yukon Territories (YT). Support for varying levels of clustering can be seen in Figure S2.1B.

Supplemental Tables

Table S2.1: The reference genomes for brown bears (*Ursus arctos*).

Species	Sample ID	SRA Accession	Sex	Reference
U. arctos	GYE906	SAMN30214195	F	Puckett et al 2023
U. arctos	GYE922	SAMN30214196	U	Puckett et al 2023
U. arctos	GYE953	SAMN30214197	U	Puckett et al 2023
U. arctos	AK17500	SAMN30214198	F	Puckett et al 2023
U. arctos	AK17512	SAMN30214199	M	Puckett et al 2023
U. arctos	AK17578	SAMN30214200	F	Puckett et al 2023
U. arctos	RF01	SAMN02256315	F	Liu et al 2014
U. arctos	SJS01	SAMN02256314	F	Liu et al 2014
U. arctos	OFS01	SAMN02256313	F	Liu et al 2014
U. arctos	ALP1	SAMN07422272	F	Benazzo et al 2017
U. arctos	AKAdmiralty2	SAMN02256321	F	Miller et al 2012
U. arctos	AKAdmiralty3	SAMN02045560	F	Cahill et al 2013
U. arctos	AKBaranof1	SAMN01057689	M	Miller et al 2012
U. arctos	AKBaranof2	SAMN02256317	U	Liu et al 2014
U. arctos	AKChichagof1	SAMN02256316	U	Liu et al 2014
U. arctos	AKChichagof2	SAMN02256318	U	Liu et al 2014
U. arctos	AKChichagof3	SAMN02256319	U	Liu et al 2014
U. arctos	AKChichagof4	SAMN02256320	U	Liu et al 2014
U. arctos	AKChichagof5	SAMN03247209	F	Cahill et al 2015
U. arctos	AKDenali1	SAMN02045559	F	Cahill et al 2013
U. arctos	AKKenai	SAMN01057690	F	Miller et al 2012
U. arctos	APN2	SAMN07422262	M	Benazzo et al 2017
U. arctos	GRE2	SAMN07422268	M	Benazzo et al 2017
U. arctos	JPHc1	SAMD00282813	F	Endo et al 2021
U. arctos	JPHc2	SAMD00282814	M	Endo et al 2021
U. arctos	JPHe1	SAMD00282815	F	Endo et al 2021
U. arctos	JPHe2	SAMD00282816	M	Endo et al 2021
U. arctos	JPHs1	SAMD00282811	F	Endo et al 2021
U. arctos	JPHs2	SAMD00282812	M	Endo et al 2021
U. arctos	MTgnp	SAMN02256322	U	Liu et al 2014

Table S2.2: The reference genomes for black bears (*Ursus americanus*).

Species	Sample ID	SRA Accession	Sex	Reference
U. americanus	AK17023	SAMN30214201	M	Puckett et al 2023
U. americanus	AK17047	SAMN30214202	M	Puckett et al 2023
U. americanus	AK17117	SAMN30214203	F	Puckett et al 2023
U. americanus	AZ12	SAMN30214204	U	Puckett et al 2023
U. americanus	ID10	SAMN30214205	M	Puckett et al 2023
U. americanus	MI334	SAMN30214206	M	Puckett et al 2023
U. americanus	MI335	SAMN30214207	F	Puckett et al 2023
U. americanus	MN6083	SAMN30214208	F	Puckett et al 2023
U. americanus	MS3783	SAMN30214209	U	Puckett et al 2023
U. americanus	NC00417	SAMN30214210	F	Puckett et al 2023
U. americanus	NC056	SAMN30214211	F	Puckett et al 2023
U. americanus	NVb83	SAMN30214212	F	Puckett et al 2023
U. americanus	NVb99	SAMN30214213	F	Puckett et al 2023
U. americanus	NVg5	SAMN30214214	M	Puckett et al 2023
U. americanus	WV1701	SAMN30214215	M	Puckett et al 2023
U. americanus	HA1	SAMN30214216	M	Puckett et al 2023
U. americanus	HA2	SAMN30214217	F	Puckett et al 2023
U. americanus	HA3	SAMN30214218	M	Puckett et al 2023
U. americanus	HA4	SAMN30214219	F	Puckett et al 2023
U. americanus	HA5	SAMN30214220	M	Puckett et al 2023
U. americanus	HA6	SAMN30214221	M	Puckett et al 2023
U. americanus	HA7	SAMN30214222	F	Puckett et al 2023
U. americanus	HA8	SAMN30214223	F	Puckett et al 2023
U. americanus	HA9	SAMN30214224	M	Puckett et al 2023
U. americanus	AK18242	TBD	F	Puckett (In Prep)
U. americanus	OR05	TBD	M	Puckett (In Prep)
U. americanus	YT48293	TBD	M	Puckett (In Prep)
U. americanus	AK20340	TBD	M	Puckett (In Prep)
U. americanus	AK20440	TBD	F	Puckett (In Prep)
U. americanus	LA366	TBD	M	Puckett (In Prep)
U. americanus	LA371	TBD	M	Puckett (In Prep)
U. americanus	LAT593	TBD	F	Puckett (In Prep)

Table S2.3: The AICc values for each of the brown bear (*Ursus arctos*) models by individual layer are displayed in the second column with the name of the layer in the first column. AICc for distance is in column three. The full model AICc is in the second to last row and was not compared to the distance model.

Surface	Layer AICc	Distance AICc
TPI	-36503	-36499
VRM	-36589	-36494
Precip	-36608	-36458
Ice	-37226	-37202
Roads	-37231	-37202
Temp	-37564	-36458
DEM	-37722	-36503
Water	-37995	-37202
Full Model	-40133	
Landcover	-41250	-36503

Table S2.4: The percent contribution for each of the layers in the full model in brown bears (*Ursus arctos*) ranked from most contribution to least contribution.

Layer	Percent Contribution
Landcover	0.61
Water Bodies	0.13
Ice and Snow	0.06
TPI	0.04
Roads	0.03
DEM	0.03
Precipitation	0.03
Temp	0.03
VRM	0.03

Table S2.5: The definitions for each landcover type adapted from the metadata of the MODIS landcover MCD12Q1 product. The categories are from the FAO-Land Cover Classification System land cover class definitions.

Landcover Type	Resistance
Barren	At least 60% of area is non-vegetated barren (sand, rock, soil) or permanent snow/ice with less than 10% vegetation.
Permanent Ice and Snow	At least 60% of area is covered by snow and ice for at least 10 months of the year.
Water Bodies	At least 60% of area is covered by permanent water bodies.
Evergreen Needleleaf Forests	Dominated by evergreen conifer trees (>2m). Tree cover >60%.
Deciduous Broadleaf Forests	Dominated by deciduous broadleaf trees (>2m). Tree cover >60%.
Mixed Broadleaf/Needleleaf Forests	Co-dominated (40–60%) by broadleaf deciduous and evergreen needleleaf tree (>2m) types. Tree cover >60%.
Open Forests	Tree cover 30–60% (canopy >2m).
Sparse Forests	Tree cover 10–30% (canopy >2m).
Dense Herbaceous	Dominated by herbaceous annuals (<2m) at least 60% cover.
Sparse Herbaceous	Dominated by herbaceous annuals (<2m) 10–60% cover.
Dense Shrublands	Dominated by woody perennials (1–2m) >60% cover.
Shrubland/Grassland Mosaic	Dominated by woody perennials (1–2m) 10–60% cover with dense herbaceous annual understory.
Sparse Shrublands	Dominated by woody perennials (1–2m) 10–60% cover with minimal herbaceous understory.

Table S2.6: The AICc values for each of the black bear (*Ursus americanus*) models by individual layer are displayed in the second column with the name of the layer in the first column. AICc for distance is in column three. The full model AICc is in the third to last row and was not compared to distance.

Surface	Layer AICc	Distance AICc
TPI	-58430	-58212
Roads	-58860	-59051
Precip	-60459	-59655
Ice	-61554	-59051
VRM	-65329	-58199
Water	-73733	-59051
DEM	-73746	-58226
Full Model	-76046	
Temp	-81262	-59655
Landcover	-110718	-58225

Table S2.7: The percent contribution for each of the layers in the full model in black bears (*Ursus americanus*) ranked from most contribution to least contribution.

Layer	Percent Contribution
Landcover	0.55
TPI	0.24
Water Bodies	0.11
VRM	0.04
Ice and Snow	0.03
DEM	0.01
Precip	0.01
Temp	0.01

60

Chapter 3: Demographic shifts inferred from harvest data between sympatric brown bears (*Ursus arctos*) and American black bears (*U. americanus*) in Southeast Alaska

INTRODUCTION

The ecosystems around us today must be preserved in the face of anthropogenic threat and climate change. Much of the function within ecosystems is provided by the biodiversity found in that location (Mace et al. 2010). To ensure that biodiversity and therefore diverse ecosystem function persists into the future, we must study and protect the processes that support it (Moritz 2002). The worlds large carnivores are disappearing, and humans cannot replicate the effects of carnivores on the landscape such as trophic stability (McLellan et al. 2021; Ripple et al. 2014). The age structure within these species can influence the level of recruitment into future generations which can affect the persistence of a species. These demographic effects may not be reflected in overall census size, which can create challenges to monitoring (Holmes and York 2003). Knowing the age structure can help with survival modeling to determine the resilience of species to perturbation. This knowledge is more necessary for populations that are open for harvest as there is more anthropogenic pressure on the species (McLellan et al. 2017). While hunting can be detrimental to species if it is poorly regulated, state and federal governments have a high incentive to maintain the species populations; this can cause an increase in data collection on harvested species. Some of the data collected by management agencies includes tissue samples, locations of harvest, effort data, as well as demographic data such as age and sex. These metrics can provide information over a long

enough time period to estimate the underlying population demography in harvested
species (Riecke et al. 2019).

Brown (*Ursus arctos*) and American black bears (*U. americanus*; hereafter black
bears) are sympatric in portions of their range across Southeast Alaska. The state of
Alaska has divided the state into a series of 26 geographically based game management
units (GMUs), of which five occur in Southeast Alaska. Both bear species co-occur on
the mainland (GMUs 1 and 5) and several islands within the Alexander Archipelago of
the coast; however, there are also islands on which the brown and black bears do not
coexist. Admiralty, Baranof, and Chichagof Islands (ABC Islands; GMU 4) do not have
black bears. Prince of Wales Island and the surrounding islands of GMUs 2 and 3 do not
have brown bears. Both species are open for harvest in Southeast Alaska, and fecundity
and recruitment have been investigated to aid in setting harvest quotas (Melletti and
Penteriani 2020). In this study, we restricted our analyses to GMUs 1C and 1D to
investigate reports of demographic shifts in these areas. Brown and black bear density
varies across this landscape. Brown bears have been estimated at a density of 90.2 and
98.8 bears per 1000 square kilometers in GMUs 1C and 1D respectively (Crupi et al.
2017; Flynn 2012; Miller 1993). Estimates for black bears in GMUs 1C and 1D were
estimated at 64.7 and 114.2 bears per 1000 square kilometers (Stetz et al. 2014; Flynn
2012; Mowat et al. 2005). Previous black bear density estimates for GMU 1C and 1D
were based on estimates from other areas of the Pacific northwest in the US and Canada.
A factor influencing the lower density of brown bears is their larger body size which
requires a higher caloric intake than black bears which causes them to preferentially
utilize areas of concentrated resources such as salmon streams (Belant et al. 2006). The

smaller size of black bears coupled with their ability to utilize dispersed resources better than brown bears allows them to reach a higher density (Fortin et al. 2013).

Fecundity and recruitment is driven by nutritional status in brown and black bears (Bunnell and Tait 1981). Brown bears reach sexual maturity between four to eight years of age in Alaska and generally have between one to three cubs per litter. Cubs are dependent on their mother for two or more years which makes the reproductive interval average between three to five years for brown bears (Keay et al. 2018; Miller 1994). Brown bear cub survival ranges between 34 to 87 percent in Alaska with causes of mortality including avalanches, starvation, and predation by other bears (Keay et al. 2018; Miller et al. 2003; Miller 1994). Black bears reach sexual maturity between four to six years of age, and they have between one to three cubs like brown bears. Cubs stay with the mother for one to two years, thus the reproductive interval for black bears is shorter at two to three years (Schwartz and Franzmann 1991). Black bear cub survival ranged from 54 to 97 percent on the Kenai peninsula in Alaska (Schwartz and Franzmann 1992; 1991). Cub production is not limited to mating events and inter-birth interval as female nutritional status can affect fecundity. Bears evolved delayed implantation, where blastocysts produced during summer mating will not attach to the uterine wall until a female gains sufficient fat stores during fall hyperphagia to ensure sufficient energy for fetal growth and milk production through the winter hibernation period (Farley and Robbins 1995; Bunnell and Tait 1981).

Scientific inferences and management decisions can be made using data collected from harvested species. The state of Alaska monitors the populations of both brown and black bears using hunter harvest data. Specifically, hunters are required to bring the hide

and the skull of all harvested bears to designated locations where state personnel record the sex, take skull measurements, and extract a premolar tooth for age analysis. The state also records effort data in the form of the number of days that the hunter spent hunting as well as the location of harvest (given as the minor subunit within a GMU). Data collection for brown bears began in 1990. In 2009, hunters were required to have a harvest ticket for black bears and state data collection on hunter effort began.

Annual harvest regulations have changed over time and independently for each bear species. In Alaska the harvest regulatory year for brown bears begins on July 1 and ends June 30, with designated fall (Sept 15-Dec 31) and spring (March 15-May 31) seasons. Within these hunting seasons one brown bear may be harvested by the same hunter every four regulatory years and the hunter must have a hunting registration permit. Hunters are not allowed to harvest a female with cubs. Our study utilized mortality data from 1995–2022. During this period, the Board of Game changed harvest regulations with the intent of maintaining sustainable harvest. The regulations limiting brown bear harvest to one animal every four years was implemented in 1990 along with the requirement that non-resident hunters are accompanied by a guide. In 2003 and 2004, permits for GMU 1D were issued through a lottery system instead of by registration; however, this policy was reverted in 2005 due to the difficulty guides had booking clients because of the unpredictability (Churchwell 2021). In 2013, additional harvest of brown bears in Berner's Bay (GMU 1C) was opened such that hunters could harvest one animal each regulatory year.

As black bears are managed independently, hunting season, harvest quotas, and regulatory changes differ from brown bears. The hunting season is not split into spring

and fall harvest, instead running from September 1 to June 30. Each resident may harvest

two black bears if they possess harvest tickets; however, only one can have the rare

glacier coat color (Lewis et al. 2020). A nonresident hunter may only harvest one bear

per regulatory year with a harvest ticket. These regulations were implemented in 1990.

This was meant to reduce the increase in nonresident harvest and it has successfully done

that since (Churchwell 2020). Black bear baiting is allowed in both GMUs 1C and 1D.

There has been some concern, especially in GMU 1D that baiting attracts brown bears,

and there were some restrictions implemented on where black bear bait stations could be

placed as a result. In 2004, harvest of the white color morph of black bears was

prohibited (Crupi 2011). Since 2010 in GMU 1C and 2012 in GMU 1D, nonresident

hunters not using a registered guide are required to draw for a hunting permit. In 2020,

that requirement for nonresident hunters was lifted for all areas except an area south of

the Taku River in GMU 1C. In 2019, bear baiting stations were allowed outside of

Juneau in GMU 1C; and in 2023, the black bear baiting season was extended in GMU

1D. Similar to brown bears, these policy changes were meant to affect overall harvest

numbers.

Beyond mortalities from harvest, the state also tracks non-harvest mortalities.

Notably, during our study period there was a large increase in "defense of life and

property" (DLP) mortalities of brown bears in GMU 1D in 2020. A similar pattern was

not observed for black bears at the same time. This type of permit is issued when a bear is

deemed to be threatening or harming people, pets, and/or livestock. These mortalities

primarily occurred around the town of Haines (population 2,614; Howell and Sandberg

2022) which is located on the peninsula between the Chilkat and Chilkoot Inlets. The

higher mortality numbers led the state to implement a management plan (Koch 2022) in Spring 2021. The state also closed the fall hunting season in GMU 1D in 2021, 2022, and 2023 after guideline harvest levels were reached to maintain a sustainable population. At a broader scale, these events raised the question if brown bears were displacing black bears at a fine-grained spatial scale in GMU 1D. There has also been anecdotal evidence from hunters in GMU 1C that they are no longer seeing black bears in several areas traditionally dominated by black bears and instead are observing brown bears at a greater frequency (Churchwell 2020; Lewis 2012; Scott 2009).

Here, we sought to answer the question of whether brown bears are displacing black bears in areas of their range within Southeast Alaska. We used spatial statistics to analyze the minor subunit areas and centroids to account for spatial autocorrelation before evaluating three lines of evidence to determine if there were underlying demographic shifts. The three lines of evidence consisted of a Bayesian state-space population estimation, hunter effort and success, and an average harvest location centroid analysis. The state-space model utilized harvest data and gave us an idea of the underlying population sizes for both species during the study period. We used the hunter effort and success as a proxy for density and determined the overall temporal trend of harvest locations using the geographic centroid analysis.

METHODS

Mortality and geographic data

We obtained the mortality records for brown and black bears from Alaska Department of Fish and Game (ADF&G) and retained records from GMUs 1C and 1D between the years 1995–2021 (ADF&G Winfonet 2022). The mortality records included

both harvest and non-harvest mortalities. Categories of non-harvest mortality included: ADF&G agency caused mortality, illegal hunter harvests, vehicle collisions, defense of life and property, research mortality, natural causes, or unknown manner of death. We divided the data for each species into non-overlapping temporal bins of five years, except for the last bin from 2015 to 2021 which contained seven years. Age was estimated from an extracted premolar tooth using cementum annuli layers (Matson et al. 1993). Each GMU within Southeast Alaska is subdivided into minor subunits which is the unit by which the records were organized. Thus, each mortality record does not contain the latitude and longitude of the event, but instead the centroid of the minor subunit. We removed individual records that did not have a recorded minor subunit resulting in the loss of six of 686 brown bear records and 91 of 3,677 black bear records. We plotted harvest and non-harvest mortality using R v4.2.2 and found the means and standard deviations of the data using the stats package in R (R Core Team 2022).

We downloaded the shapefile for the subunits from the ArcGIS ADF&G online database (Alaska Department of Fish & Game 2023). To minimize geographic error in the data, we transformed the coordinates into Alaska state plane coordinate system zone 1 using the NAD83 datum and projected the data using the sf package (Bivand and Pebesma 2023; Pebesma 2018) in R v4.2.2. We removed one subunit each from GMUs 1C and 1D, that contain Glacier Bay National Park, as legal harvest is not allowed within the national park boundary. We visualized the shapefiles using ArcGIS Pro v3.2 (ESRI Inc 2021). We also created an sf object in R using the latitude and longitude for all points using the same projection as the shapefiles.

Temporal population size estimation

We utilized a Bayesian state-space model that used harvest records along with auxiliary

data such as survival and reproduction metrics to estimate change in population
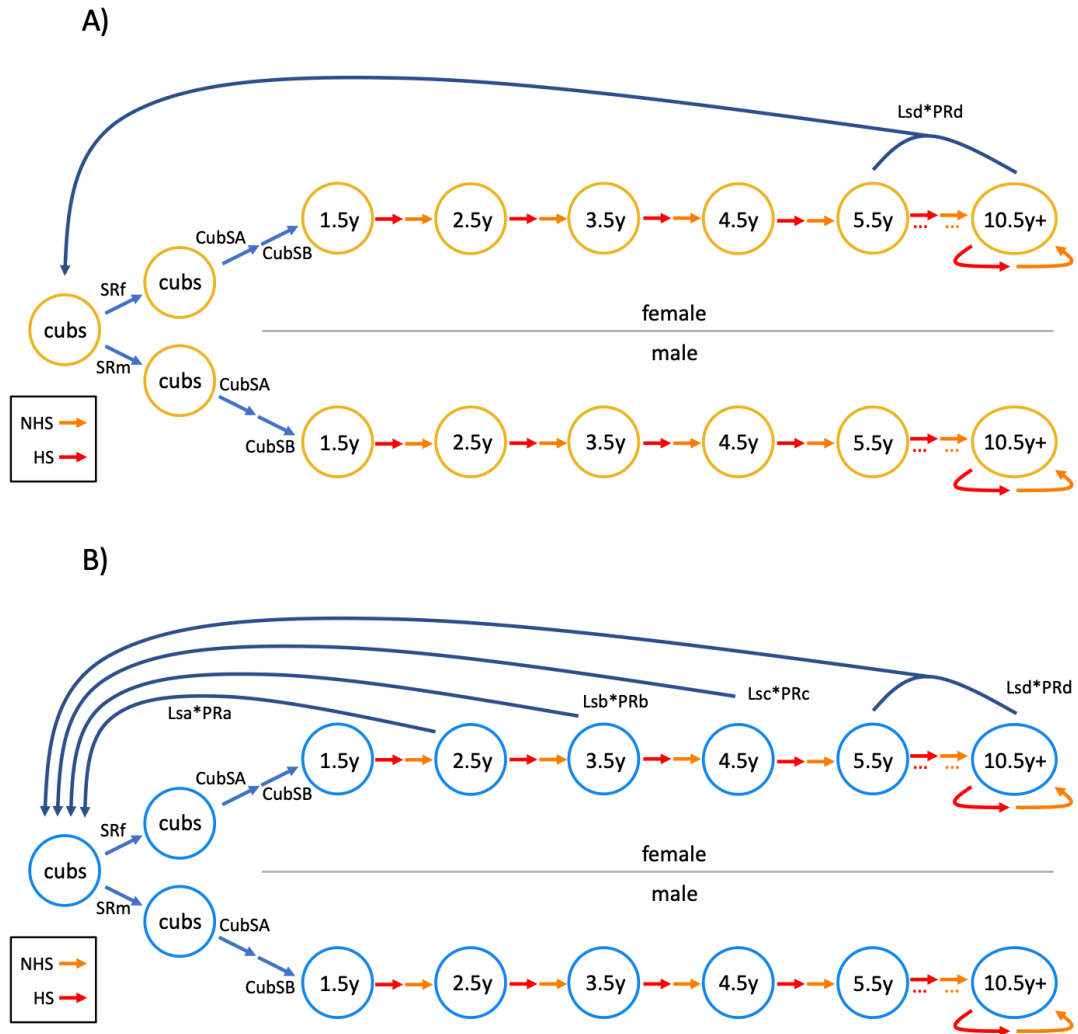
Figure 3.1: The state-space model adapted from Allen et al. (2018). The brown bear model (*Ursus arctos*) (A) is displayed in gold and the black bear model (*U. americanus*) (B) is displayed in blue. Above the dividing line are the females and below are the males. In the model the initial pool of cubs is divided into female and male based on the sex ratios displayed by the first arrow (SRf and SRm). The horizontal circles represent the age classes from 1.5 to 10.5 years with age classes 6.5 through 9.5 abbreviated by the ellipses in the figure. Cub survival was simulated with the values for cub survival a (CubSA) and cub survival b (CubSB) for each sex. To move from one age-class to the next the harvest survival (HS) and non-harvest survival (NHS) was simulated. The arrows above the circles represent the fecundity which was the litter size (Ls) multiplied by the pregnancy rate (PR). The blue lines at the top of each figure show the number of cubs from each age class that enter into the model each year.

size (N) across the study period. To do this we adapted the analysis from Allen et al. (2018) for both brown and black bears in Southeast Alaska. The original code used a Markov Chain Monte Carlo (MCMC) based model to estimate the population size of black bears in Wisconsin. The model iteratively simulates the population size of each age class every year and uses those estimates as the starting values for the next year. We used ten age-classes in the brown bear and black bear models. The first age-class represented all bears between one and two years old. The second age-class represented bears between the age of two and three and so on up to age-class ten with the age classes 6.5 to 9.5 abbreviated by ellipses in Figure 3.1. The last bin groups all individuals together that are older than ten years. The number of cubs was calculated as a group as well; however, they are not explicitly accounted for in the starting populations as it is illegal to harvest cubs in both species. This means that they are unrepresented in the harvest data during that period, but are present in other non-hunting mortalities, such as vehicle collisions. For each age class in every year, the number of individuals that advanced to the next age class in the following year was calculated by multiplying the total by the harvest and non-harvest survival. For the number of cubs entering the model each year, fecundity was calculated by multiplying the litter size by the pregnancy rate for each age class capable of having cubs. The number of cubs was multiplied by the sex ratio to determine the number of males and female cubs. Cub survival into the first age-class was calculated by multiplying cub survival by the total number of cubs. Bears that were ten and older would cycle within the last age class. We adjusted the initial brown bear parameters for our study based on an understanding of their ecology in our study system. We analyzed GMUs 1C and 1D separately for both species based on our analyses of population

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structure and limited gene flow (Chapter 2). We filtered the mortality data to include only

harvest records where the sex of the animal was known, then created two separate

datasets; the first with all individuals regardless of the presence or absence of age data

(*O*), and the second containing only aged individuals (*C*) (Allen et al. 2018). An

assumption of this state-space model using harvest data is that all harvest is reported.

Given the sealing requirements for harvested bears in Southeast Alaska, we believe that

these data meet that assumption.

To initialize the model, we input estimates for the initial population size and

number of bears in each age class for both species based on estimates of density and

usable habitat for brown and black bears (Table 3.1). The estimates for brown and black

bears were based on previous density estimates in GMU 1C (brown bear: Flynn 2012,

black bear: Pinjuv 2013; Flynn 2012) and 1D (brown bear: Crupi et al. 2017; Miller

1993, black bear: Stetz et al. 2014; Mowat et al. 2005) (Tables S3.1 and S3.2). The

density estimates were combined with results from a previous assessment that found the

usable habitat from 265,000 GPS locations of 34 radio-collared brown bears between

Table 3.1: Initial Bayesian state-space model parameters for brown (*Ursus arctos*) and black (*U. americanus*) bear models for each of two game management units (GMUs) in Southeast Alaska. Usable habitat area was estimated to remove portions of the landscape inaccessible to bears (e.g., ice fields) which if included would overestimate initial population size (N) based on literature-based estimates of density (per $1,000 km^2$).

Species	GMU	Initial N	Bear habitat area (km^2)	Density/$1000 km^2$	Source
Brown Bear	1C	484	5361.9	90.2	Flynn et al. 2012
	1D	257	2600.0	98.8	Miller et al. 1993, Crupi et al. 2017
Black Bear	1C	1,400	5361.9	261.1	Flynn et al. 2012, Pinjiv 2013
	1D	297	2600.0	114.2	Mowat et al. 2005, Stetz et al. 2014

2018 and 2020 (Crupi 2020). To determine the starting population size for each species, we multiplied the density by the usable habitat (Table 3.1). We parameterized the sex ratio as 50:50 F:M for year one bears older than 0.5 years, 56:44 in year two, and 60:40 for all subsequent years for brown bears, and a 50:50 F:M ratio for all black bear age classes (Clark et al. 2020; Crupi et al 2017; Beston 2011).

Recruitment parameters- We used five recruitment variables to model the increases in N over time: age-specific litter size (LS_a), age-specific pregnancy rate (PR_a), male:female sex ratio (SP), cub survival from birth to the start of the hunting season (CubSa), and cub survival between the first and second harvest seasons (CubSb; Table 3.2). For brown

Table 3.2: The recruitment and survival priors for brown bears (*Ursus arctos*) are displayed in the table. The shape and rate for the gamma distribution as well as the alpha and beta values for the beta distribution are inside the parentheses. The recovery rate in brown bears differed between the sexes and was split accordingly.

Survival Parameters				
Variable	Parameter	Mean	Long-Term Precision	Annual Precision
HSm	Male Harvest Survival	0.75	3	Gamma (1,2)
HSf	Female Harvest Survival	0.84	3	Gamma (1,1)
NS	Non-harvest Survival	0.81	4	Gamma (3,0.5)
CubSa	Cub Survival years 0.0-0.5	0.5	n/a	n/a
CubSb	Cub Survival years 0.5-1.5	0.6	n/a	n/a
Repf	Recovery Rate	0.9	n/a	n/a
Repm	Recovery Rate	0.85	n/a	n/a
Recruitment Parameters				
Variable	Parameter	Mean	Distribution	
LS-d	Litter Size 5.5-year-olds	2.25	Gamma (450,200)	
PR-d	Pregnancy Rate 5.5-year-olds	0.44	Beta (40,50)	
SP	Sex Proportion (female)	0.46	Beta (45,52)	

Table 3.3: The recruitment and survival priors for black bears (*Ursus americanus*) are displayed in the table. The mean the shape and ratee for the gamma distribution and the alpha and beta values for the beta distribution are inside the parentheses. The litter size and pregnancy rate have two fecundity groups.

Survival Parameters				
Variable	Parameter	Mean	Long-Term Precision	Annual Precision
HSm	Male Harvest Survival	0.75	3	Gamma (20,20)
HSf	Female Harvest Survival	0.85	3	Gamma (0.5,0.5)
NS	Non-harvest Survival	0.91	4	Gamma (20,0.5)
CubSa	Cub Survival years 0.0-0.5	0.83	4	n/a
CubSb	Cub Survival years 0.5-1.5	0.76	4	n/a
Rep	Recovery Rate	0.90	2	n/a
Recruitment Parameters				
Variable	Parameter	Mean	Distribution	
LS-a	Litter Size 5.5-year-olds	2.00	Gamma (20,10)	
LS-b	Litter Size 5.5-year-olds	2.00	Gamma (20,10)	
LS-c	Litter Size 5.5-year-olds	2.00	Gamma (20,10)	
LS-d	Litter Size 5.5-year-olds	2.74	Gamma (16.4,6)	
PR-a	Pregnancy Rate 5.5-year-olds	0.003	Beta (2.61,1000)	
PR-b	Pregnancy Rate 5.5-year-olds	0.25	Beta (34,100)	
PR-c	Pregnancy Rate 5.5-year-olds	0.53	Beta (54,48)	
PR-d	Pregnancy Rate 5.5-year-olds	0.48	Beta (47,50)	
SP	Sex Proportion (female)	0.46	Beta (426,500)	

bears, the age-at-first litter is five years old in Southeast Alaska (Miller 1994), so the first

three litter size, pregnancy rate, and fecundity variables were removed from the analysis

(Figure 3.1A). We used one fecundity group in the model for brown bears to reflect the higher age-at-first litter. For black bears, we used the four fecundity groups from the original model (Allen et al. 2018). We reviewed the literature for brown and black bears from in and around Southeast Alaska and adjusted priors and hyperparameters as necessary for our study system (Peacock 2004; Miller et al. 2003; Miller 1994; Schwartz and Franzmann 1992; Tables 3.2–3.3).

Survival parameters- The model incorporated five variables to describe annual survival (Allen et al. 2018). We used two variables that were age-, sex-, and year-specific; respectively, harvest survival ($HS_{a,s,y}$) and harvest rate ($HR_{a,s,y}$). Within the model the age-, sex-, and year-specific harvest rate was calculated for every year as one minus the harvest survival multiplied by the reporting rate. Two variables were age- and sex-specific: the recovery rate during harvest season ($Rep_{s,a}$) and the survival outside harvest season ($NS_{a,s}$). For brown bears, we divided the recovery rate into male and female values. However, for black bears we used a single value for both sexes. Survival was calculated for every year by multiplying the harvest survival by non-harvest survival. The last variable was the age-specific complementary log-log survival offset term (LHR_a).

Modeling framework- For each of the four models (GMU by species), we implemented the model in R using the JAGS (Plummer 2003) software and rjags (Plummer et al. 2016) package. We ran 220,000 iterations (discarding the first 20,000 as burn-in) with three chains and a thinning rate of four for the MCMC settings in the model. We assessed convergence using visual inspection of the chains as well as the Gelman-Rubin statistics (Gelman and Rubin 1992) calculated using the stableGR package (Knudson 2022) in R. We considered values less than 1.1 indicative of convergence.

Sensitivity analysis- We performed a sensitivity analysis to assess potential bias in our parameters. We followed the sensitivity analysis of Allen et al. (2018) and used a 10% over- and under-estimate for eight of the variables to test if we obtained the same results from the model with higher and lower estimates. The hyperparameters and distribution parameters are shown in Tables S3.1 through S3.4 We used the same MCMC settings for each sensitivity analysis as we did in the main analysis. We also used the same convergence criteria for the sensitivity analysis. We calculated the percent relative change (PRC) and coefficient of variation (CV) based on the equations from Allen et al (2018). By changing the parameters and finding the PRC and CV we were able to estimate how robust the model was to changes in a single starting value within the model. The equations quantified the degree of change between the estimates.

Temporal patterns of bear mortality and hunter effort

To analyze hunter effort and success we filtered out the harvest records where no hunting attempt was made. The filtering step left successful and unsuccessful hunter records in the data set. Each of these records contained the hunter effort measured in days. To visualize the data for both species we plotted hunter effort, hunter success, as well as the number of successful and unsuccessful hunts in R v4.2.2. We also found means and standard deviations for the data using the stats package in R.

Spatial analyses to assess distributional shifts

We performed spatial statistical analyses to assess the autocorrelation and clustering patterns of harvest for the two bear species, then quantified species-specific temporal shifts across the landscape. We used the same mortality dataset but included all records regardless of the presence of sex or age information. As described above, the unit

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of reporting is the subunit. Before we could assess clustering patterns from the data, we had to determine the amount of spatial autocorrelation of the minor subunits. If the arrangement of the subunits was random, then any clustered or dispersed patterns from the data would indicate that respective spatial process on the landscape. However, if the subunits (specifically the centroid of the polygons) were a clustered, then our spatial analyses of the mortality data must show a more extreme pattern than the background to be considered significant.

Minor subunit spatial analysis- To assess the spatial autocorrelation present in the areas of the minor subunits, we calculated the Moran's I statistic (Moran 1950). Spatial autocorrelation is a measure of how similar objects near each other are compared to objects further away (O'Sullivan and Unwin 2003). Moran's I statistics generally fall within the range of -1 to + 1, where 0 represents a random point process which is also the null model. Positive values indicate a clustered process; whereas negative values indicate a dispersed pattern often characterized by a highly regular spacing of points on a landscape (O'Sullivan and Unwin 2003). Geographic objects generally display positive spatial autocorrelation. Determining the spatial autocorrelation of the minor subunit area allowed us to account for the underlying spatial clustering pattern. To calculate Moran's I, we created an object of minor subunit centroid nearest neighbors using rook movements with the poly2nb function in the spdep (Bivand et al. 2013) package within R. We then created the spatial weights object using the areas of each minor subunit using the nb2listw function from the spdep package to account for the spatial structure of the minor subunits. We ran the Moran's I analysis using the moran.test function, also from the spdep package, with the weights object and minor subunit areas as input.

To assess spatial autocorrelation between the minor subunit centroids, we analyzed Ripley's K. We performed this analysis to determine if the spatial pattern of the minor subunits would have an impact on our mortality record results as the records are aggregated to the minor subunit centroids. Ripley's K can identify spatial scales where clustering or dispersion takes place by comparing a point process to a random distribution that's used as a null model. The function takes the number of points within a given radius of all other points, records the number, and repeats that process for expanding radii (O'Sullivan and Unwin 2003). Plotting the function with the random Poisson process curve shows whether there is a higher or lower density of points within certain radii than would be expected given the overall point density across the study area. The Poisson distribution is used within the K function because random counts within a given spatial area follow a Poisson distribution. All values of the function below the Poisson process curve indicate a more dispersed pattern than would be expected while values higher than the Poisson curve represent radii for which the process was more clustered than the random process. The iso correction was used to account for edge effects. We created the centroids from the minor subunit shapefile using the centroids function from the terra package (Hijmans et al. 2023) in R. We then created a point pattern object using the ppp function from the spatstat.geom package (Baddeley et al. 2015) for input into the Kest function within the spatstat.exlpore package (Baddeley et al. 2015). This process produced a K function curve for the centroids. Determining the spatial clustering or dispersion of the centroids was necessary for our analysis because we needed to create a null model for our study area that accounted for any underlying spatial pattern of the centroids.

Cross-K Analyses- Anthropogenic caused mortality such as harvest is not a random processes. People are not present in high density in all or even most of the minor subunits. This pattern should result in variation in harvest and non-harvest mortalities among minor subunits that are not associated or are weakly associated with the distribution of bears on the landscape. To measure the effect of that spatial pattern, we found it necessary to simulate point patterns that represented a random distribution of the mortality data so that we could assess the clustering of the data itself to randomly distributed harvest locations. We created the random pattern across the minor subunit shapefile using the st_sample function from the sf package. This function allowed us to simulate points within the extent of the study area that we defined as the outside perimeter of the aggregated minor subunits. For this analysis, data was grouped into five-year, non-overlapping bins. We added the overall number of harvest and non-harvest mortality events together for each species and input that number into the random point process for each temporal bin so that the number of random points would match the number in the empirical data. After simulating the points, we found the total number within each of the subunits by running the st_intersect function, also from the sf package. This gave us a raw count of the number of points within each of the minor subunits. To create a null distribution, we repeated this process 1,000 times and recorded the number of random points within each subunit.

Once the counts for each minor subunit were tallied from each of the 1,000 simulations, we ran the cross-K analyses on the random point pattern to determine the spatial autocorrelation and amount of clustering within the random data. We used the point patterns from each species as input. This analysis must be performed on a point

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process which is why we used the random point patterns simulated from the data rather than the aggregated number of harvests in each subunit. The method of creating a point process from aerial data for use in a point process analysis has been done previously (Self et al. 2022; Lee et al. 2018). The cross-K function used the same value of Ripley's K; however, instead of using a single group of points in the analysis, the cross-K function determined the clustering between two different categories of points, in our case the brown and black bear mortality data. We created the same plot as the K function, but the cross-K measure shows whether one category of points is more likely to be found within the vicinity of the other category at different radii (O'Sullivan and Unwin 2003). Anywhere the cross-K function is greater than our null model would indicate that there are more brown bear locations close to black bear locations than we would expect under a random process. Lower numbers would indicate that there are less. If the values are positive, we can infer that both species are occurring in similar areas on the landscape. If the values are negative, we could infer that both species occur in different areas on the landscape. We created a point process object using the ppp function from the package sf and then ran the cross-K analysis using the Kcross function in the spatstat.explore package. A cross-K value higher than the random process would indicate that there are more points of one category next to the other than would be expected under a random pattern. A lower value would indicate that there are less brown bear points near black bear points than would be expected.

We performed the cross-K analysis using the mortality data for each species, but we had to simulate the harvest locations prior to analysis since all points were assigned to the centroid location. To simulate the point process, we used the st_sample function in a

custom R script to loop over each of the minor subunits and simulate the locations of the

number of mortality events 100 times for each temporal bin. We then performed the

cross-K analysis on the mortality data using the K-cross function across the full study

area. We added the cross-K data functions to the plot of the cross-K functions for the

random point process to determine if the data displayed a similar clustering pattern to the

random process.

Mortality centroid analysis- To assess spatial trends of harvest across the study period,

we performed a sliding average analysis on the centroid locations of both brown and

black bears. Taking the weighted average of the harvest and mortality subunit centroids

for a given year, or group of years, gives the average centroid location for that year. By

comparing the average points across years, we can see if certain geographic areas with

more mortality events may be pulling the average in a cardinal direction through time. To

find the geographic average of the harvest and non-harvest mortality data we averaged

the latitudes and longitudes of each point within five-year temporal bins with a one-year

slide. We mapped the geographic average locations in R. Minor subunit 101 in both

GMU 1C and 1D, which encompassed Glacier Bay National Park, were omitted because

there were no legal harvests in those minor subunits. We assessed the overall pattern of

average locations in both species across the study period for all mortalities, and

separately for both harvest and non-harvest mortality counts.

RESULTS

Mortality and geographic data

*Brown bears-*The harvest patterns for brown bears differed between GMUs 1C and 1D

throughout the study period (Figure 3.2A,C). Across both GMUs, there were 680
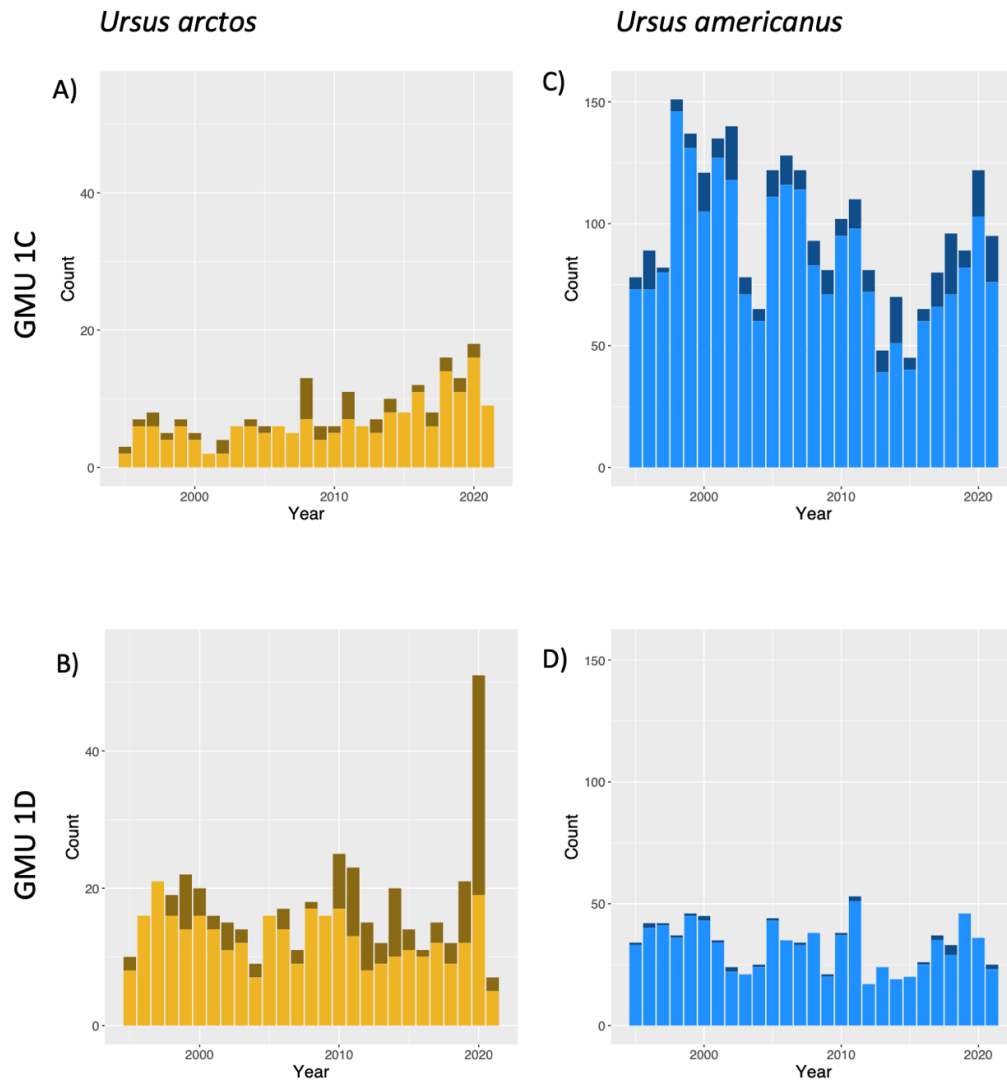
Figure 3.2: Total mortality counts for brown (*Ursus arctos*; A-B) and black (*U. americanus*; C-D) bears in GMUs 1C (A, C) and 1D (B, D). The lighter colors represent harvest mortalities while the darker colors display non-hunting mortalities (including defense of life and property and vehicle strikes). The year 2020 for brown bears highlights a year with unprecedented defense of life and property kills. The scale differs between species. The higher mortalities for black bears reflects the higher number of allowable harvests for that species. There were 680 total brown bear mortality records in GMUs 1C and 1D.

mortalities, where 519 were the result of harvest and the remaining 161 (31%) were non-

harvest mortalities. Of the 107 minor subunits with recorded harvest in GMU 1C, 43

minor subunits have brown bear harvest (Figure S3.1). Most of the mortality events in 1C

occurred on the mainland south of Juneau, and along the Chilkat Peninsula south of

Haines (Figure S3.2). The subunit has a mean of 7.93 mortalities per year with a median of 7.00 and a standard deviation of 3.80. Two years, 2018 and 2020, lie two standard deviations outside of the mean (Figure 3.2A). Of the 27 minor subunits with harvest in 1D, 21 of them recorded brown bear harvest during the study period (Figure S3.3). Most of the mortalities in 1D occurred in the area northwest of Haines (Figure S3.4). The subunit had a mean of 17.26 mortalities per year with a median of 16 and a standard deviation of 8.09. In 2020 there were unprecedented numbers of defense of life and property mortalities on top of a large harvest (Figure 3.2B). The mortalities in that year (n = 51) were over two times as high as any other year and was the only year that was more than two standard deviations from the mean.

Black bears- GMUs 1C and 1D show similar constant numbers of mortalities across the study period punctuated by regulatory changes. In both GMUs there were a total of 3,522 black bear records, where 3,202 were the result of harvest and 320 (10%) were non-hunting mortalities. Of the 107 minor subunits in 1C and 27 in 1D, only one minor subunit in each GMU did not record any black bear mortalities during the study period (Figure S3.1 and S3.2). The areas with the highest mortalities generally occurred around the cities of Juneau, Gustavus, and Haines as well as the southern end of 1C (Figure S3.4). Black bear mean annual mortality in GMU 1C was 97.22 with a median of 93.00 (SD ± 28.55). The mortalities in 1D had a mean of 33.22 with a median of 35.00 (SD ± 9.83). The only year outside of two standard deviations was 2011 in 1D (Figure 3.2D).

Temporal population size estimation

We used the annual mortality records to estimate population size for each species via a Bayesian state-space model. In GMU 1C, the estimated population for brown bears

A)

GMU 1C

B)

GMU 1D
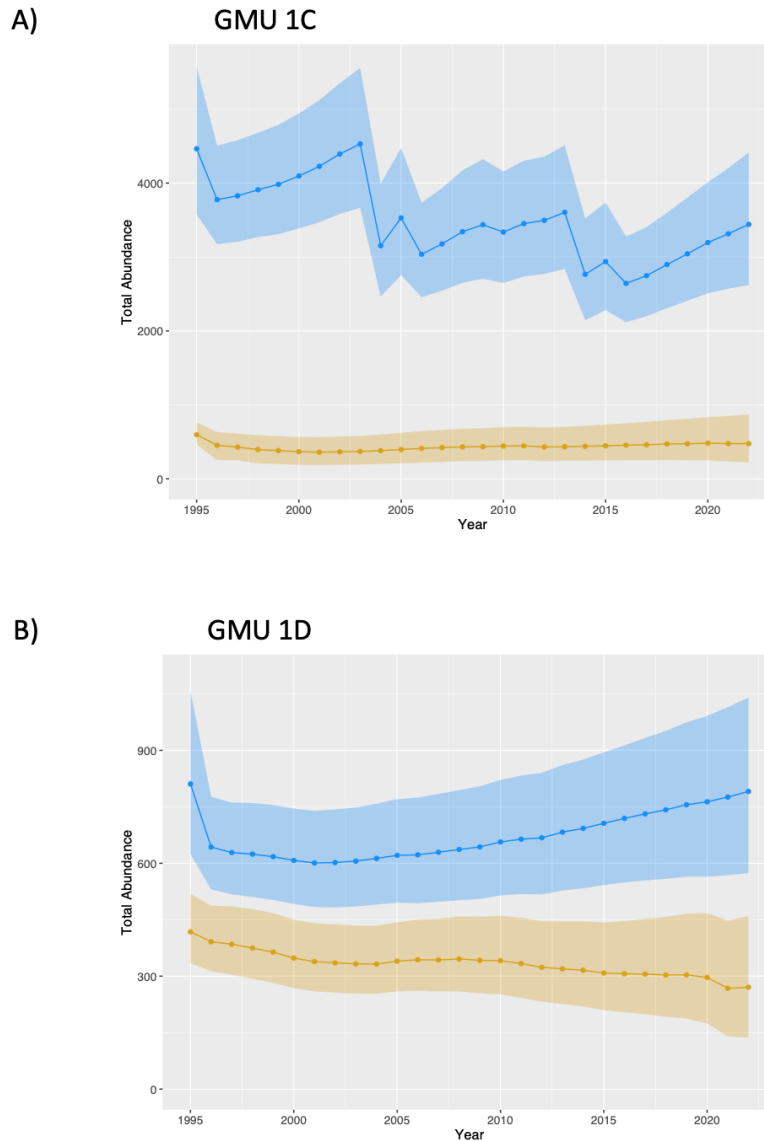
Figure 3.3: These panels show the estimated population size of brown (*Ursus arctos*; gold) and black (*U. americanus*; blue) bears through time in GMUs 1C and 1D between 1995–2022. The estimates for 1C are in panel (A) while estimates for 1D are in panel (B). Point estimates from the model are displayed as dots, and the 95% confidence interval is the shaded area with the color corresponding to the species.

had a mean of 433 (95% CI: 239–688). The population was steady around the mean

across the study period (Figure 3.3A). In contrast to 1C, brown bear population size in

GMU 1D declined over the study period (Figure 3.3B). The mean in 1D was 333 (CI:

240–457). There was an estimated decline in the population of 201.21 bears which was

48% of the estimated starting population (Figure 3.3B). The population estimation in 1C

and 1D was higher for females at every point in the study period and the patterns between the sexes were concordant (Figure S3.5). There was a noticeable drop in 2020 within the model for males and females (Figure S3.5B). That drop corresponds to the higher mortality in 2020 in 1D.

The black bear model estimated two separate patterns for GMUs 1C and 1D. The population mean in 1C for black bears was 3,491 (CI: 2,799–4,321). However, there was a notable cyclic pattern with a 10-year periodicity and a declining trend (Figure 3.3A). In contrast to the estimated decline in 1C, the black bear population estimation increased over the study period for 1D (Figure 3.3B). The mean was 673 (CI: 525–827). Starting in 2000, the population estimation increased steadily (Figure 3.3B). Unlike the pattern observed for brown bears, the estimate for female black bears in 1C was lower than the estimate for males from 1995 to 2009 when the number of females matches the number of males (Figure S3.6). There was a larger group of individuals that moved through the model illustrated by the larger successive age classes that eventually cause the large drop in the estimates when they reach age class 10. The age cohort plots for 1D do not display that same cyclic 10-year pattern. The model estimated that the number of female black bears in 1D was initially lower than the males; however, the number of females surpassed the number of males around the year 2000 and steadily increased.

Temporal patterns of bear mortality and hunter effort

Brown bears-To contextualize variability within the harvest data, we analyzed hunter effort and success. Average individual hunt time was 3.62 and 5.35 days in GMUs 1C and 1D, respectively (Figure 3.4A, D). In GMU 1C, we observed a qualitative decrease in the trend after 2010 but no change over time in 1D. The average hunter was more

successful in 1D than 1C with averages of 23.89% and 13.71% respectively. There was an increasing trend toward success in 1C with 2018 the only year outside of two standard deviations from the mean (Figure 3.4B). The percent of successful hunters fluctuated around the mean in 1D with 2022 the only year outside of two standard deviations from the mean (Figure 3.4E). The total number of registration permits (Figure 3.4C, F) averaged 48.92 per year in 1C and 52.89 in 1D. The number of successes in 1C increased in the latter half of the study period despite fewer permits issued. The number of permits remained relatively constant in 1D until regulatory years 2022 and 2023 (Figure 3.4F). The decrease in permits for those years reflects the fall hunting seasons that were closed by emergency order due to the unprecedented mortality in 2020.

Black bears- We analyzed hunter effort and success in black bears; however, effort data collection began in 2009 for both subunits so there were fewer data points than there were for brown bears. The hunter effort in 1C had a mean of 1.01 days and gradually decreased over time (Figure 3.5A) The only exception to this was an increase in hunter effort to its highest level of 1.67 days on average after the regulatory changes in 2012. In GMU 1D the hunter effort had an average of 4.01 days and displayed an increasing trend (Figure 3.5D). The average for successful hunters during the study period was 34.14% and 28.93% for GMU 1C and 1D respectively. Only one year, 2011 in 1D, was outside two standard deviations from the mean (Figure 3.5E). Both GMUs show high percentages of successful hunts above 40% around 2010 and declining after that (Figure 3.5B, E). Between 2009 and 2022 the average number of harvest tickets issued was 182.71 for 1C and 83.21 for 1D. The number of tickets remained relatively constant during the study period with no years in either GMU falling outside of two standard deviations of the
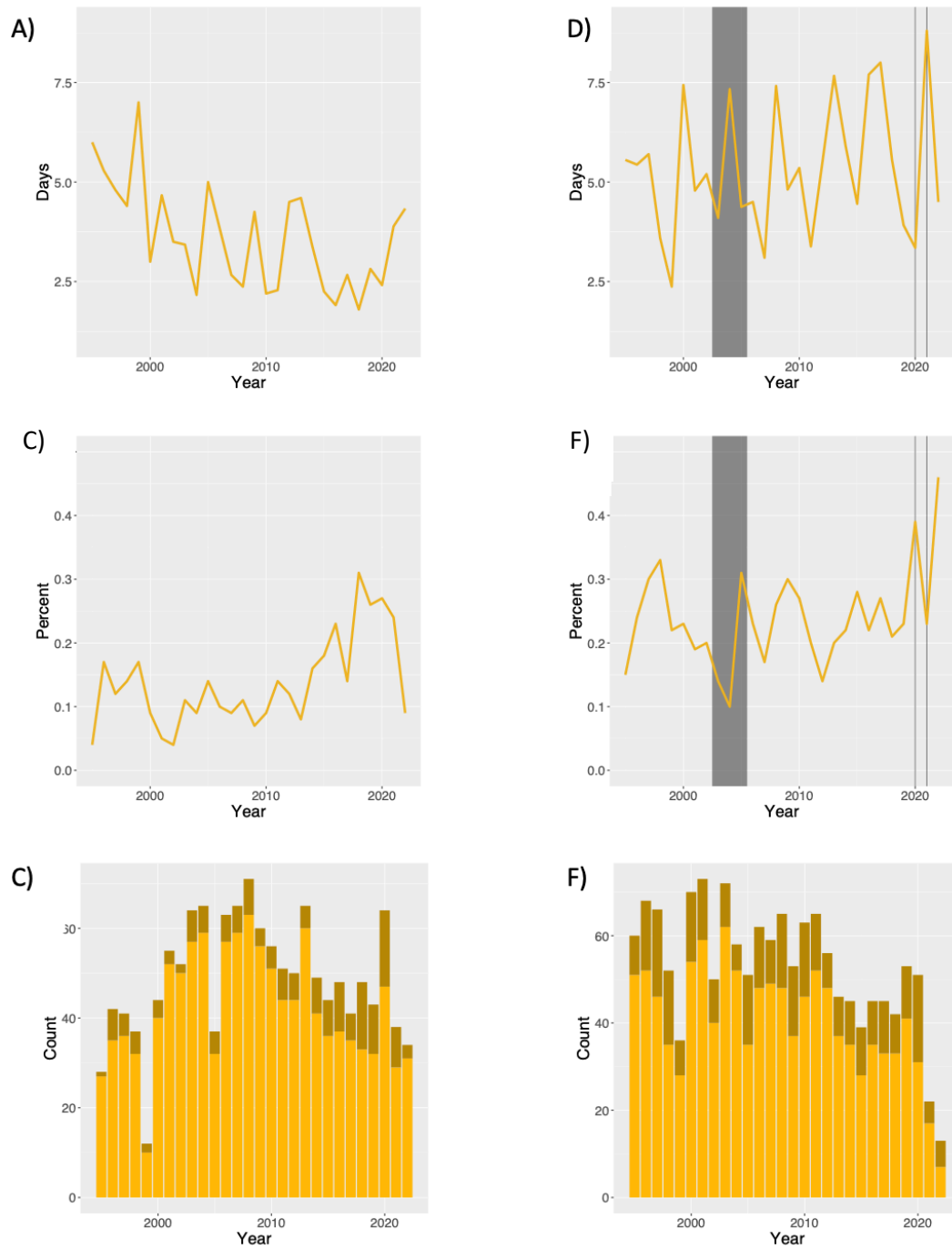
Figure 3.4: This figure displays hunter effort, success, and the ratio of successful to unsuccessful hunts for brown bears (*Ursus arctos*) in GMUs 1C and 1D. The gray lines represent changes in the harvest policy with potential impacts on harvest numbers. Panels (A) through (C) show trends in GMU 1C while panels (D) through (F) show trends in GMU 1D. Panels (A) and (D) display the average number of days spent for a successful hunt. Panels (B) and (E) display the percent of successful hunters that hunted each year. Panels (C) and (F) display the number of successful hunts in dark yellow and unsuccessful hunts in gold with the total height of the bar representing the total count of hunted registration permits.
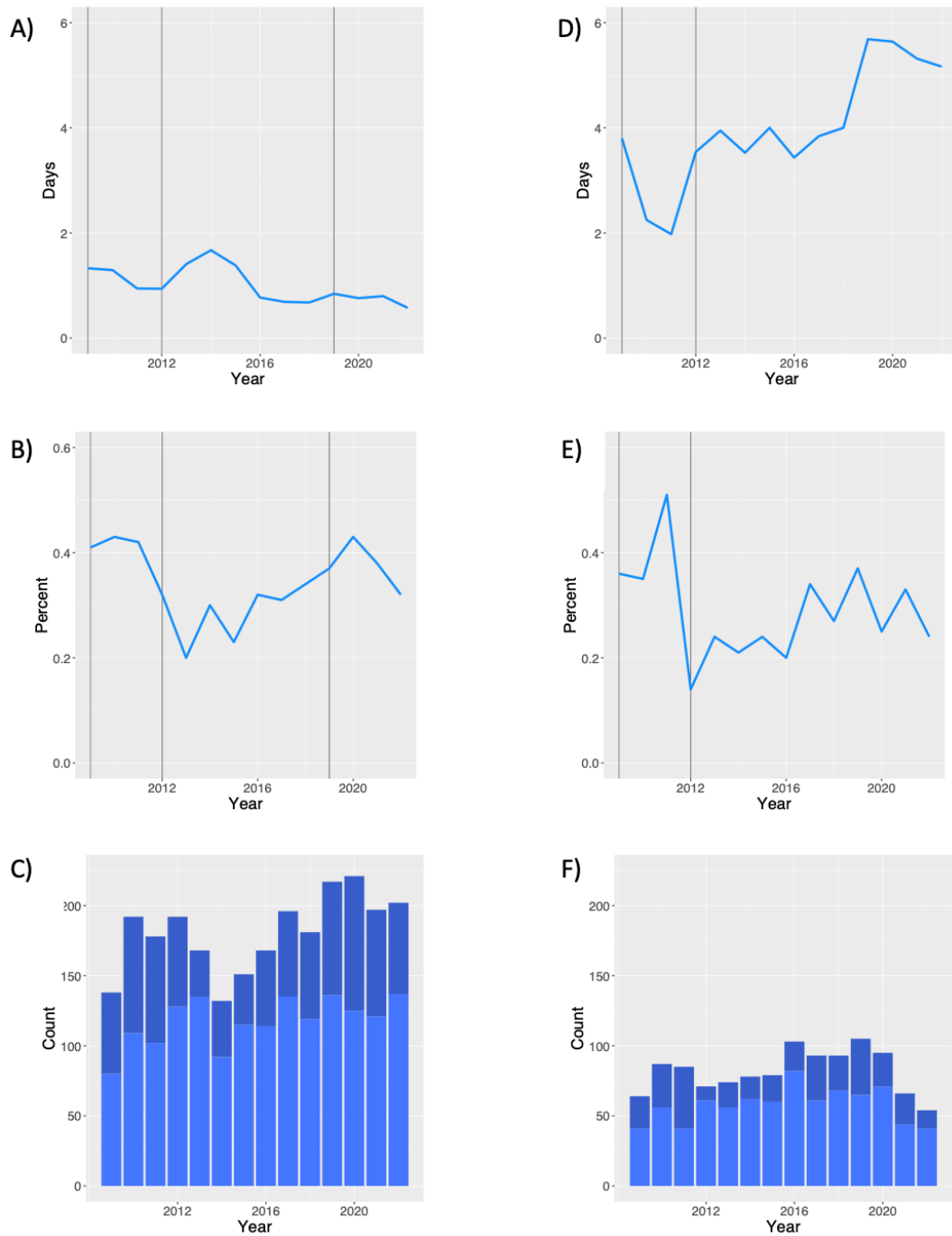
Figure 3.5: This figure displays hunter effort, success, and the ratio of successful to unsuccessful hunts for black bears (Ursus americanus) in GMUs 1C and 1D. The gray lines represent changes in the harvest policy with potential impacts on harvest numbers. Panels (A) through (C) show trends in GMU 1C while panels (D) through (F) show trends in GMU 1D. Panels (A) and (D) display the average number of days spent for a successful hunt. Panels (B) and (E) display the percent of successful hunters that hunted in a given year. Panels (C) and (F) display the number of successful hunts in dark blue and unsuccessful hunts in blue with the total height of the bar representing the number of hunted harvest tickets.

mean (Figure 3.5C and F).

Spatial analyses to assess distributional shifts

Minor subunit spatial analysis- To assess whether our spatial analyses could be confounded by the layout of the minor subunits, we first tested for a random, clustered, or dispersed pattern within the subunits. The Moran's I analysis on the minor subunit areas revealed that the size distribution for minor subunits was random (Moran's I = -0.00048, P = 0.38). In the Ripley's K analysis, the K values matched the random Poisson process for the first 11 km indicating that the point process was random at those distances. The K values were more positive than the random process at distances greater than 11 km which indicates that the points are more clustered than would be expected at greater radii. With these results we determined that the areas of each minor subunit in the study were randomly distributed, and similar sized minor subunits do not cluster together. This was important information because the minor subunits fundamentally constrain the spatial distribution and characteristics of the empirical data and we needed to account for underlying spatial pattern.

Cross-K analyses- We performed the cross-K analysis to determine if brown and black bear mortality events were occurring in similar areas on the landscape or not. All of our values for the random simulations as well as the empirical data were higher than the Poisson point process indicating that they were clustered. For the 1995–1999, 2010–2014, and 2015–2021 temporal bins (Figure 3.6A, D, E) the empirical data simulations were all higher than the values for the random process at all radii. This indicates that there were more brown bear mortality locations within proximity to black bear mortalities than would be expected for a random process. For the 2000–2004 temporal bin the

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empirical data simulations begin to overlap with the random simulations at a radius of 33.39 km. For the 2005–2009 temporal bin the empirical data simulations show a similar pattern of overlap; however, the overlap begins at a radius of 55.65 km. This pattern shows that at smaller radii brown bears mortalities were clustered compared to black bears, but the pattern was random at larger radii within these two time bins.

Mortality centroid analysis- To assess if brown bears were displacing black bears on the landscape while utilizing the spatial information from mortality records, we conducted a centroid analysis. Using 5-year binning of the mortality counts, with a one-year step (Figure S3.7), we calculated a mean longitude and latitude from the weighted minor subunit centroids. This analysis was conducted separately for brown and black bears, so we could then compare if distributions were shifting across time. Notably the estimated centroids fall on a northwest to southeast axis which reflects the orientation of GMUs 1C and 1D (Figure 3.7). Brown bears show a directional shift towards the southeast during the study period. Black bears also shifted in a southeast-ward direction during the middle of the study period; however, the most recent centroid estimates were similar to those from the late 1990s creating a similar start and endpoint during the study period (Figures 3.7, S3.8). The overall spatial-temporal patterns were driven by harvest mortalities. When the centroid analysis was broken into harvest and non-harvest (Figures S3.9-S3.10), the harvest mortality showed a similar pattern for each species to the overall pattern. In contrast, there was limited spatial pattern from the non-harvest mortalities.

DISCUSSION

Our spatial and temporal analyses of bear harvest data support the anecdotal observation that brown bears (*U. arctos*) are displacing American black bears (*U. americanus*)
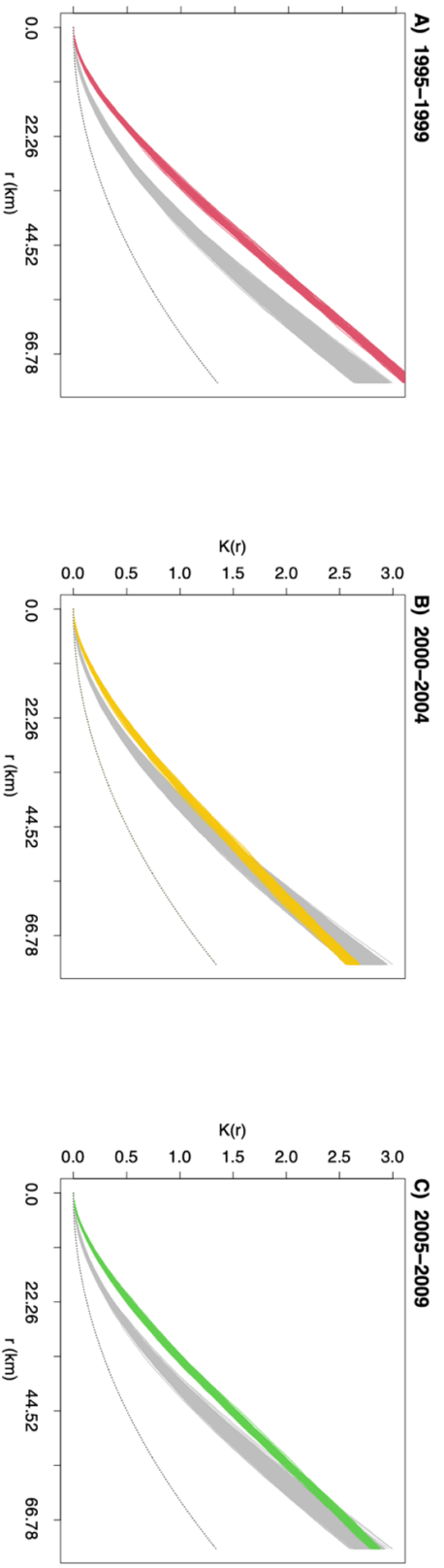
Figure 3.6: The temporal bins of brown and black bear mortalities are displayed in each plot. Plots (A) through (E) correspond to the years 1995–1999, 2000–2004, 2005–2009, 2010–2014, and 2015–2021 respectively. The radius in kilometers is displayed on the x-axis. The K-function values are displayed on the y-axis. The values for a random Poisson point process are represented by the dotted black line. The 1,000 simulations of the random point process are displayed in gray on the plots. Each simulation is represented by a single line. The 100 empirical data simulations are displayed in color according to the year. Each simulation is represented by a single line.

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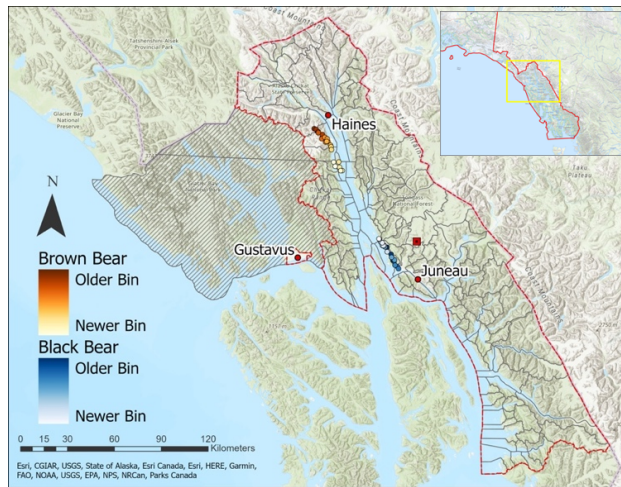
A)   B)
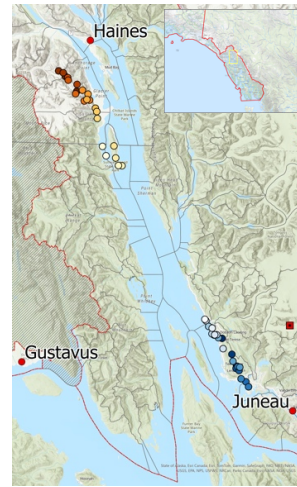
Figure 3.7: The average centroid location for each temporal bin is displayed for both brown (*Ursus arctos*) and black bears (*U. americanus*). The temporal bins show a darker shade if they were further back in time. This figure contains both harvest and non-harvest mortality. The centroid for the study area is displayed with the red and black square. GMUs 1C and 1D are displayed in (A). A closer view of the patterns is displayed in (B).

in Southeast Alaska in GMU 1C, but they do not support black bear displacement in

GMU 1D. Here we detail the predictions that would support or contradict the anecdotal

evidence in 1C and 1D and how our data compares. Before we interpreted the evidence

for and against, we used the cross-K analysis to find if brown and black bears were in the

same locations on the landscape. The pattern in the cross-K analysis is greater than the

random process for most of the spatial and temporal extent of the study (Figure 3.6).

These patterns were driven by clustering in the brown bear data. If the values were

positive, the clustering of brown bears would have occurred near the black bear point

patterns. We interpret that this is partially driven by a clustered pattern of harvest from

successful hunters going to similar harvest locations and/or subunits. This was also

reflected in the localized areas of brown bear harvest that we see across the GMUs

(Figure S3.2). The dispersed and random spatial autocorrelation that we see in black

bears could be a result of the higher distribution of overall harvest throughout the GMUs (Figure S3.4). This pattern could also be the result of the higher harvest rates in black bears, two black bears every regulatory year compared to one brown bear every four regulatory years.

To determine if brown bears were replacing black bears across the landscape, we evaluated three lines of evidence. The first line of evidence was the overall population estimations. Support for the anecdotal evidence would show increasing brown bear abundance relative to black bear population size. Two combinations of factors could produce this pattern; the first being an increase in the brown bear population combined with a steady or decreasing black bear population. The second combination would be a steady brown bear population with a decreasing black bear population. Our state-space models for GMU 1D did not meet those expectations since the brown bear population has decreased while the black bear population increased (Figure 3.3B).

The second line of evidence was hunter effort data in which we again propose if brown bears were replacing black bears, we would anticipate that there were more brown bears in those locations on the landscape and that hunters would encounter them more frequently as a result. This would result in decreased hunter effort over time with either stable or increasing percentage of successful hunts. We did not see this pattern for hunter effort in 1D (Figure 3.4A). We instead observed that the hunter effort was generally steady around the mean of 5.35 days per hunt. The percentage of successful hunters also varied near the mean. It is worth noting that the percent success increased in the last several years of the study period. This was due to the unprecedented mortalities around Haines in GMU 1D in 2020. There is currently not enough data to determine a trend from

the most recent years. Supporting the effort and success results we see that the overall

mortalities remained constant, again apart from 2020 (Figure 3.2). We also observed that

the total number of registration permits has also generally fluctuated around the mean of

52.89. These data for brown bears display that there was not the pattern of decreasing

effort and increasing success that we would expect if there were more brown bears. In

black bears we observed an increase in effort with a general fluctuation around the

average success rate. The number of harvest tickets generally didn't change along with

the overall mortalities. The brown and black bear patterns together did not support large

changes in either species in 1D and so did not support the anecdotal reports.

The third line of evidence that we utilized was the average geographic centroid

analysis. For this part of the analysis, we analyzed GMUs 1D and 1C together. The

brown bear centroid was further north than the black bear centroid reflecting the higher

number of brown bear mortalities in GMU 1D compared to 1C (Figure 3.2A, B; 3.7).

Along this same line of reasoning, the black bear data was closer to the true minor

subunit centroid because there were more mortalities and a higher density in GMU 1C

(Figure 3.2C, D; 3.7). If these data supported the anecdotal evidence, we would anticipate

seeing the brown bear mortality centroid either stay in the same location with the black

bear centroid moving away from Haines, or the brown bear centroid move toward Haines

with the black bear centroid moving away. The brown bear centroid could stay in the

same place if the number of mortalities in both 1D and 1C were increasing at the same

rate. We did not see either of these patterns. The brown bear centroid traveled away from

Haines while the black bear centroid stayed in the same general area. This pattern was

apparent when the harvest and non-harvest mortality were analyzed together compared to

just the harvest mortalities (Figure 3.7; S3.9). The non-harvest mortality centroid

displayed a different pattern in which the later temporal bins were pulled more toward

Haines in brown bears; however, this opposite trend did not affect our overall conclusions

as the number of non-harvest mortalities makes up a small portion of the overall mortality

(Figure 3.2).

Evidence in 1D

The overall evidence for GMU 1D does not match the anecdotal evidence of

displacement; however, there was still an unprecedented level of brown bear mortality in

2020 (Figure 3.2B). This resulted from several factors that led brown bears and people to

both be more present in and around Haines, causing increased conflict and a greater shift

to nocturnal activity in response to increased human activity (Burton et al. 2024). The

first factor had to do with changing resource availability for brown bears. The first half of

2020 was influenced by an El Niño episode which resulted in record snowfall and heavy

snowpack throughout GMU 1D that persisted later into the summer than typical

(ADF&G 2021; Crupi and Sell 2020). These conditions were followed by a La Niña

event consisting of the wettest and cloudiest summer recorded in the area. This was

believed to be the primary factor in the failure of alpine berry production which resulted

in brown bears concentrating their activity at lower elevations (Crupi and Sell 2020). As

a result of the unusual weather patterns, the berry crops began late, senesced early and

impacted biomass yield. The escapement of pink and sockeye salmon was relatively

normal in the Chilkoot River; however, the Chilkat River experienced a large decline in

the number of returning salmon which likely forced bears to search for other food sources

and unsecured attractants in and around the townsite of Haines (ADF&G 2021; Crupi and

Sell 2020). There were 14 DLP bear mortalities in the town of Haines and 16 outside of the townsite (ADF&G 2021). ADF&G (2021) attributes higher number of brown bears in Haines partially due to "unsecured attractants" such as garbage outside of residences and businesses, compost, fruit trees and animal feed. The search for food by bears and their movement into Haines was compounded by the second factor, which was the COVID-19 pandemic. With lockdowns occurring in areas throughout Southeast Alaska, more people isolated at their homes. Brown bears generally avoid people; however, with reduced anthropogenic activity within the town and the drive to find food, brown bears had fewer barriers to moving closer to people's homes. This naturally led to higher vigilance by people and a subsequent increase in brown bear mortalities as people removed bears that were deemed a nuisance under State defense of life and property regulations. Our findings did not support the anecdotal evidence that brown bears have displaced black bears in GMU 1D. It is our interpretation that the higher brown bear conflict in 2020 was driven by unique biotic and abiotic factors that compressed brown bear density to lower elevations near Haines and the places where residents recreate. Subsequently, people were isolated at home due to the COVID-19 pandemic and it became more common to observe bears and become fearful from the media generated narrative that bears were destroying property in search of food.

Evidence in 1C

We saw support for the anecdotal evidence that brown bears have been replacing black bears in GMU 1C. In 2009 ADF&G started publishing that hunters, guides and ADF&G staff had started to see brown bears in areas where they previously only observed black bears; those reports have continued into recent management reports (Churchwell 2020;

Lewis 2012; Scott 2009). The reported areas included sections of the eastern edge of the

Chilkat Mountain Range on the Chilkat Peninsula as well as the area between Tracy and

Endicott Arms and Port Houghton south of Juneau. When we analyzed the data from 1D

we stated that if brown bears were replacing black bears, harvest and effort data would

show three lines of evidence in support of the trend. While we did not observe these

patterns in 1D, all three of these elements supported the anecdotal evidence in 1C. First,

we estimated a stable population size from the state-space model (Figure 3.3A) with an

increase in the overall mortalities in 1C in brown bears (Figure 3.2A). We estimated a

decrease in the population size of black bears which further supported these findings

(Figure 3.3A). Second, we observed a decrease in hunter effort with an increase in the

percent of successful hunts. This showed that hunters were having greater success with

less effort which could indicate that they were encountering more brown bears (Figure

3.4A,B). This pattern was reinforced by a reduction in the number of issued registration

permits (Figure 3.4C). Hunters were more successful across a lower number of permits.

We observed hunter effort centered around the mean in black bears (Figure 3.5A). The

percent success for black bear hunters displayed a decrease and increase concordant with

registration changes (Figure 3.5B). There were no major changes in the number of

harvest tickets issued for black bears (Figure 3.5C). Third, our centroid analysis

demonstrated a temporal shift towards the southeast over time (Figure 3.7). This could

indicate that there were more brown bears harvested in 1C in recent years than there were

at the beginning of the study period (Figure 3.7). The black bear centroid pattern did not

have a temporal pattern (Figure 3.7). These three lines of evidence show support for a

possible increase in the number of brown bears found in areas of GMU 1C. The black

bear pattern when compared to the brown bear data reinforced the conclusions in GMU 1C.

Cyclic harvest and demographic changes

The black bear mortality data in GMUs 1C and 1D showed a cyclic pattern that could be driven by a combination of interspecific competition and changes in available resources. The mortality data in black bears showed three distinct peaks of higher mortality since 1995 with the pattern more apparent in 1C (Figure 3.2C, D). This pattern appeared to be independent of harvest size suggesting that it was caused by an underlying increase in the population size from which higher number of bears were hunted. In the population estimation for 1C there appeared to be larger age-cohorts that progressed through the simulations (Figure S3.6A). Interestingly, the pattern did not show up in the estimated age classes in GMU 1D (Figure S3.6B). The pattern could be a result of a group of older more dominant black bears that were able to better utilize available resources. As the condition of a female bear can have a large effect on initial implantation and subsequent health and success of her cubs, these older more dominant bears with better access to resources could have produced healthier offspring creating the beginning of the next large population pulse (Bunnell and Tait 1981). The competition for resources could have accentuated this pattern rather than reduce it. Interestingly, there is evidence of a five to seven year increase in nuisance bears in Juneau which helps to validate the cyclic nature of a larger age-cohort across the landscape (Churchwell 2020; Barten 2002).

There has been logging in the southern Port Houghton region of GMU 1C where there is anecdotal evidence of demographic change. Logging in this region continued into the 1990s and it has been proposed that the clear-cut forests initially increase the

availability of early successional resources such as berries, which then become

unavailable in 10–20 years as the canopy cover increases and the berry crops decrease in

productivity (Pastick et al. 2018). As the forests grow back in these logged regions the

availability of berry crops to black bears should be reduced. Without the dispersed

resource of berries and with concentrated resources dominated by brown bears, black

bears are relegated to less productive areas of the landscape in search of resources, which

may be at higher elevation and further from the coastline where hunters in GMU 1C tend

to harvest the majority of black bears. Our study covers the time-period in which this

landscape-level process would occur.

In this chapter we sought to determine if brown bears were replacing black bears

in certain areas across the landscape. We did not find support for this in GMU 1D;

however, we did find support in GMU 1C. We also identified a broader population cycle

within black bears in GMU 1C.

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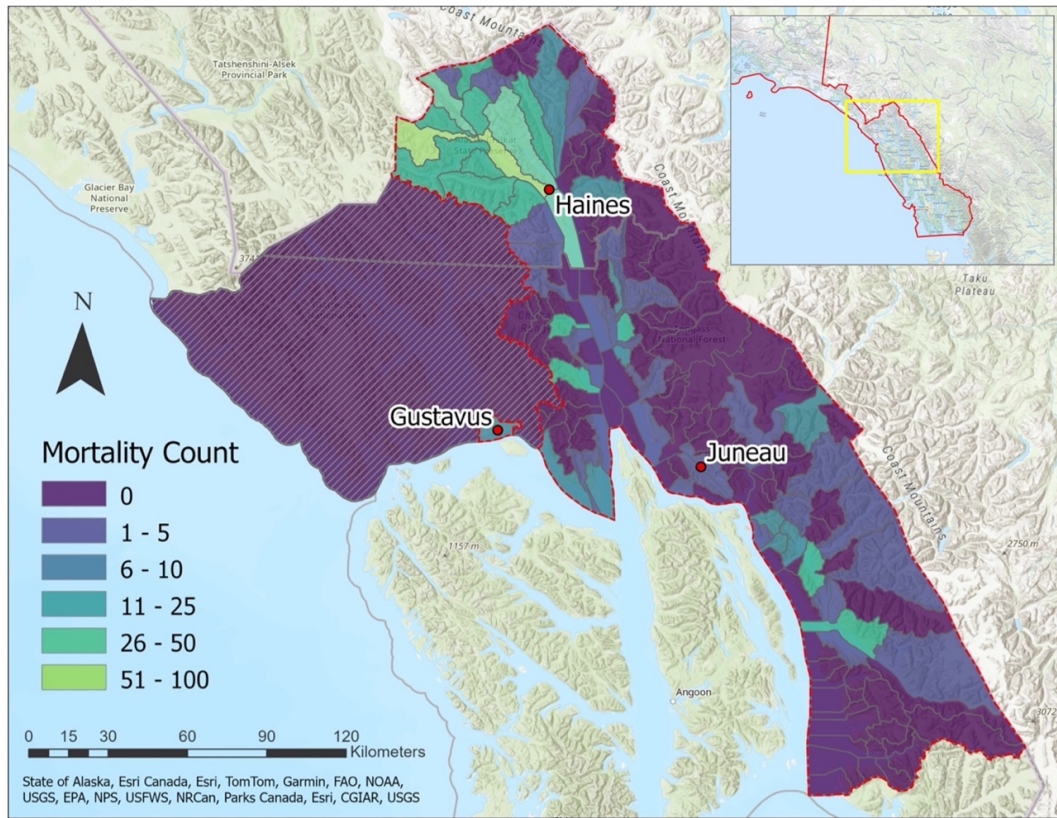
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Figure S3.1: The number of total mortalities for brown (Ursus arctos; gold) and black bears (U. americanus; blue) over time in each minor subunit of GMU 1C. The number of the minor subunit is displayed above each faceted graph.

Figure S3.2: Counts of brown bear (*Ursus arctos*) mortalities in each minor subunit in GMUs 1C and 1D from 1995 to 2021. The state of Alaska is outlined in gray along with the minor subunits. GMUs 1C and 1D, the extent of the spatial analysis, are outlined in dashed red lines with the largest population centers in the region marked with a red dot and labeled. The colors within each minor subunit display the mortality counts within that minor subunit. The legal harvest for brown bears is one bear every four regulatory years. The hatched subunit in the west was removed from analysis as it encompassed the federally owned Glacier Bay National Park where harvest was not permitted.
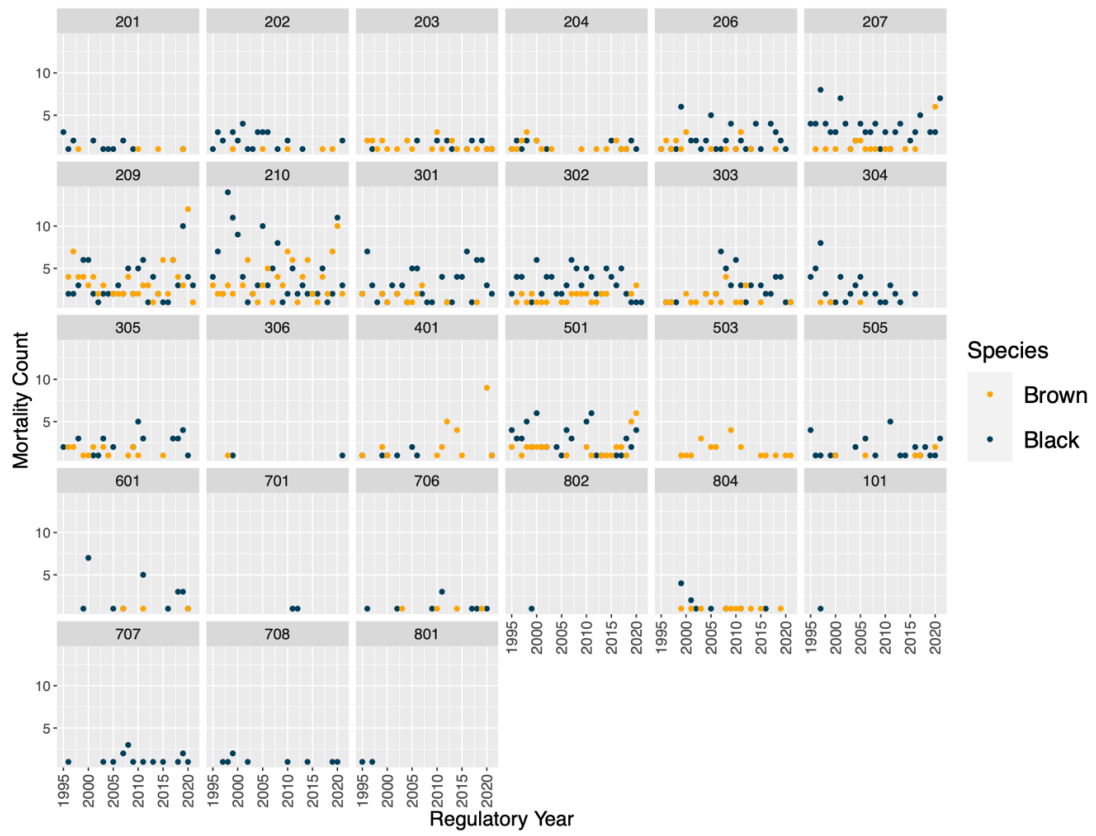
Figure S3.3: The number of total mortalities for brown (*Ursus arctos*; gold) and black bears (*U. americanus;* blue) over time in each minor subunit of GMU 1D. The number of the minor subunit is displayed above each faceted graph.
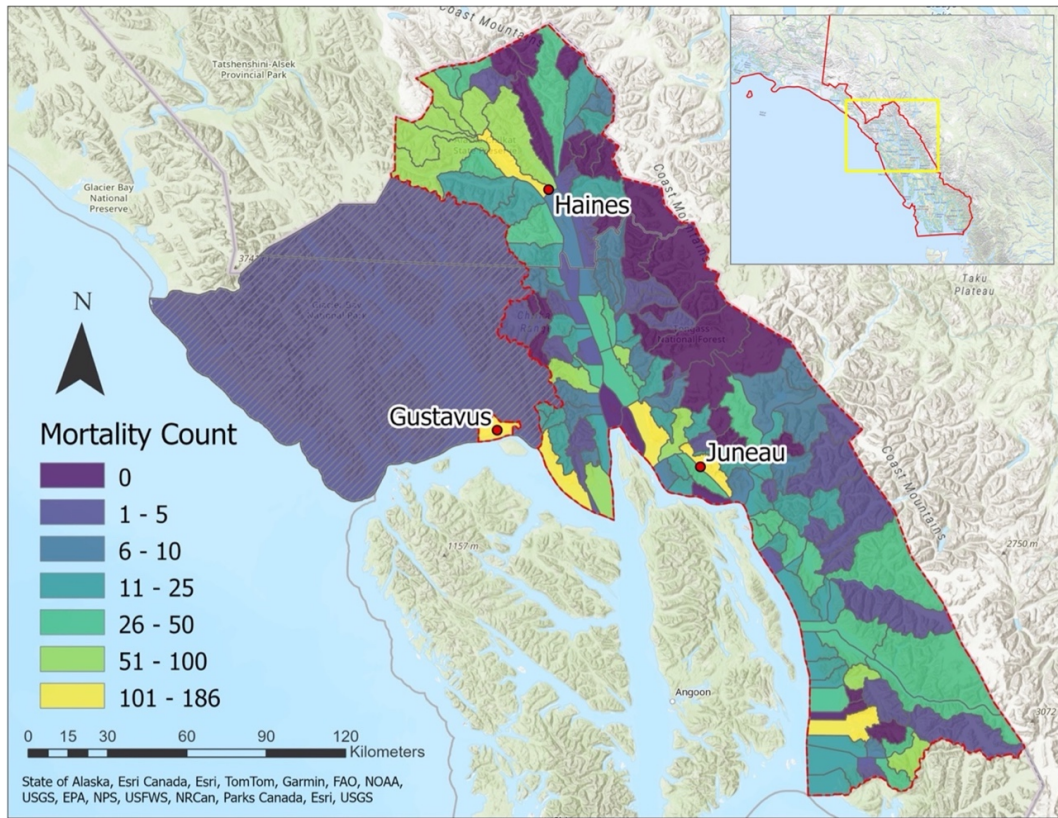
Figure S3.4: Counts of black bear (Ursus americanus) mortalities in each minor subunit in GMUs 1C and 1D from 1995 to 2021. The state of Alaska is outlined in gray along with the minor subunits. GMUs 1C and 1D, the extent of the spatial analysis, are outlined in dashed red lines with the largest population centers in the region marked with a red dot and labeled. The colors within each minor subunit display the mortality counts within that minor subunit. The legal harvest for black bears is two bears every regulatory year. The hatched subunit in the west was removed from analysis as it encompassed the federally owned Glacier Bay National Park where harvest was not permitted.
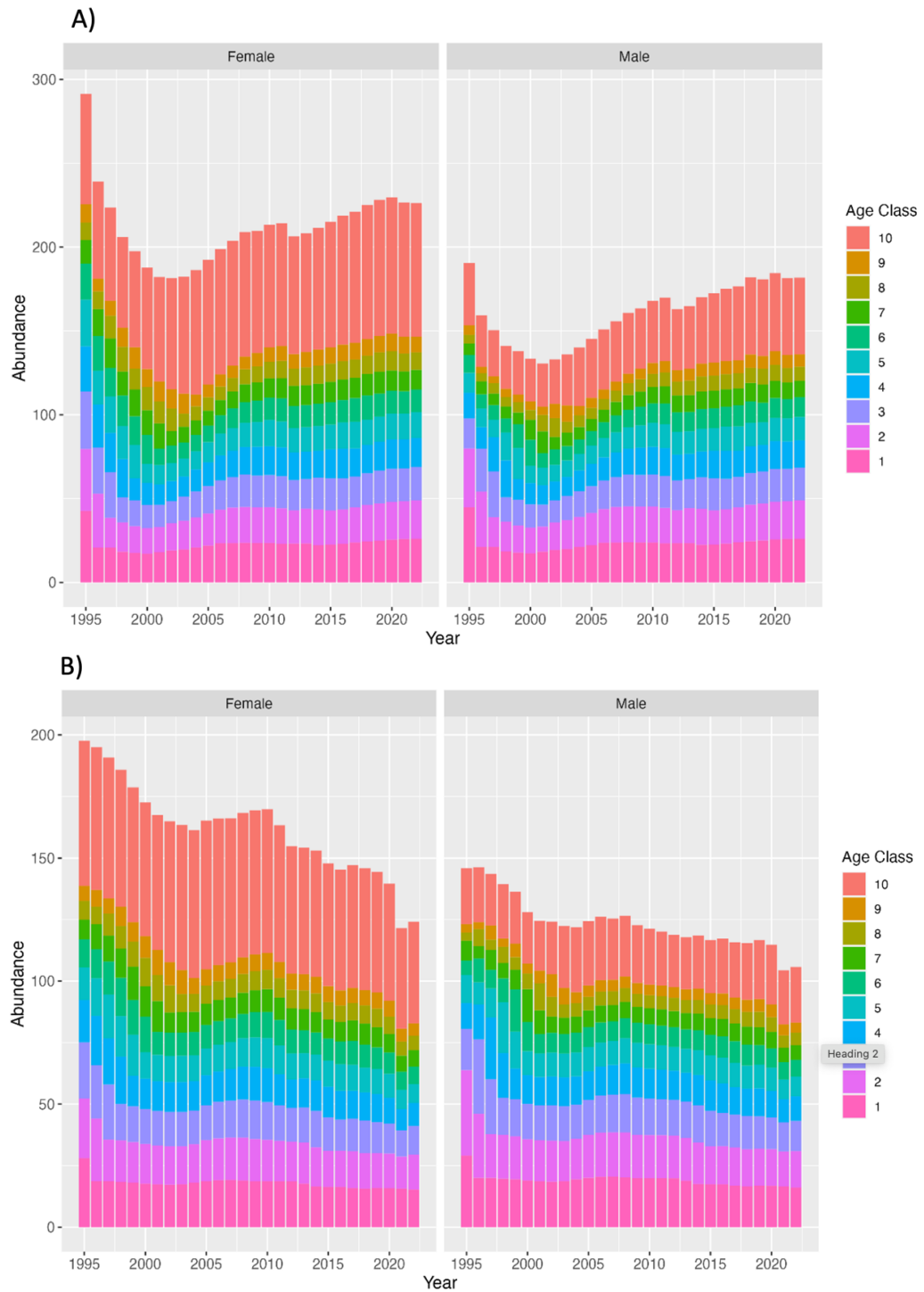
Figure S3.5: Models of brown bear (*Ursus arctos*) abundance in (A) GMU 1C and (B) 1D split by sex (left panels: female; right panels: male) and by age classes.
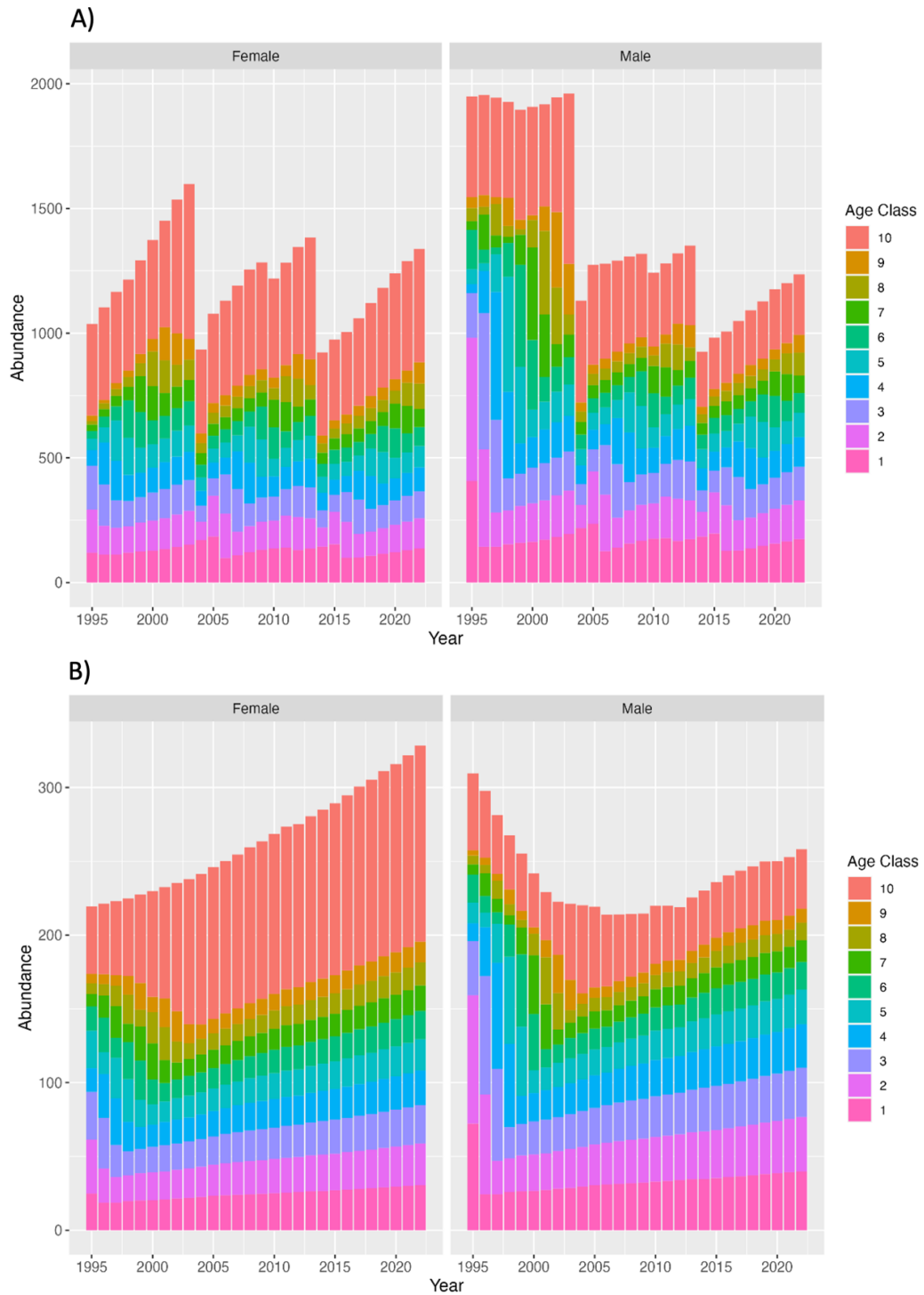
Figure S3.6: Models of black bear (*Ursus americanus*) abundance in (A) GMU 1C and (B) 1D split by sex (left panels: female; right panels: male) and by age classes.
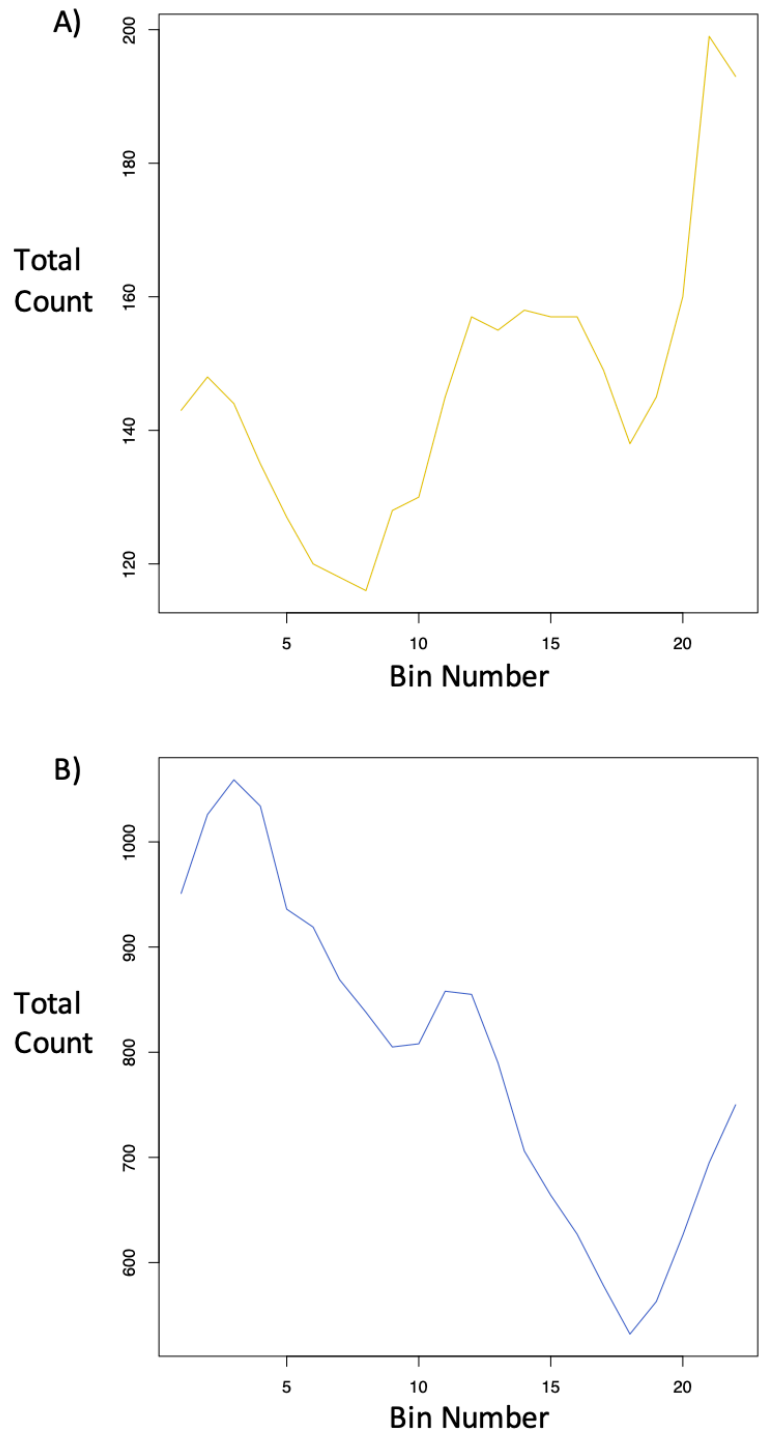
Figure S3.7: Total number of mortality records (A- brown bears, *Ursus arctos*; B- black bears, *U. americanus*) included in each 5-year temporal bin used for the 1-year sliding centroid analysis. The count for the first bin is equal to the total mortality counts for the regulatory years 1995–1999, the second bin is the count for the regulatory years 1996–2000, etc. The span of years increments sequentially by one for each bin.
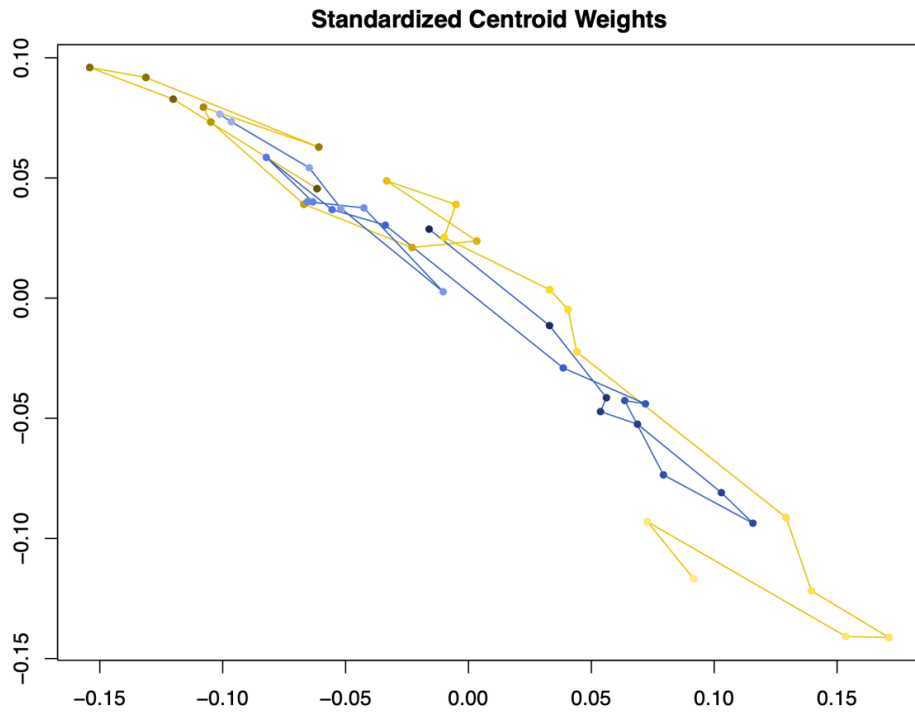
Figure S3.8: Overlay of the average centroid locations for each temporal bin for brown bears (*Ursus arctos*; gold) and black bears (*U. americanus*; blue). The axes display decimal degrees. The same temporal bins were used for the standardized centroid pattern. The darker points for each species are further back in time with the points becoming lighter for each subsequent temporal bin.
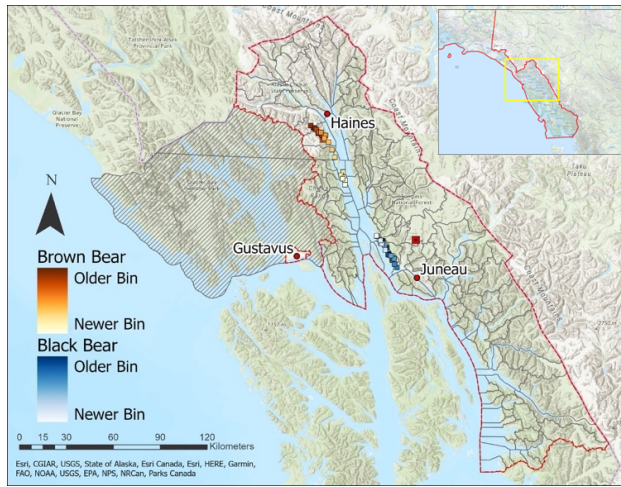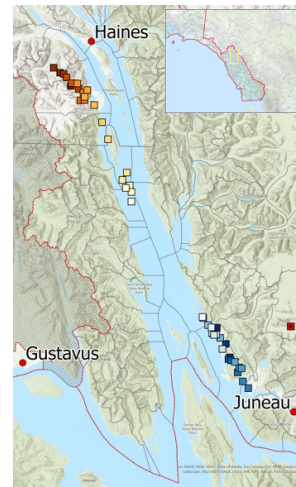
Figure S3.9: The average centroid location for each temporal bin is displayed for both brown (*Ursus arctos*) and black bears (*U. americanus*). The temporal bins are displayed in order of dark to light from past to present. This figure contains only harvest mortalities, and each average centroid is represented by a square. The centroid for the study area is displayed with the red and black square. Glacier Bay National Park is marked with the hatch marks as it was not included in the weighted centroid analysis.
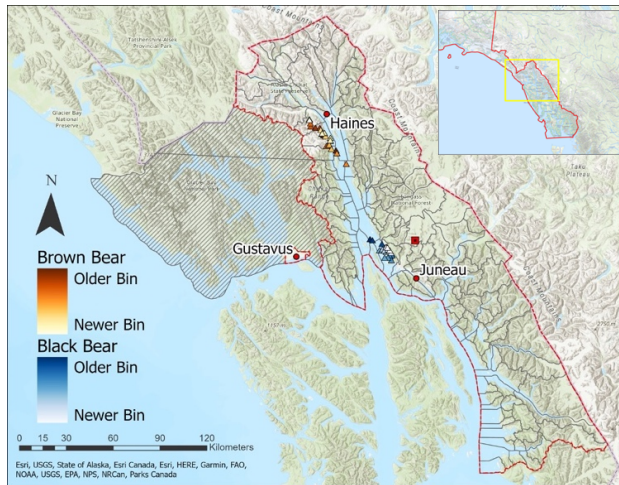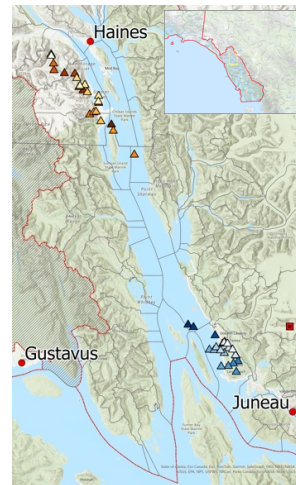
Figure S3.10: The average centroid location for each temporal bin is displayed for both brown (*Ursus arctos*) and black bears (*U. americanus*). The temporal bins are displayed in order of dark to light from past to present. This figure contains only non-harvest mortalities, and each average centroid is represented by a triangle. The centroid for the study area is displayed with the red and black square. Glacier Bay National Park is marked with the hatch marks as it was not included in the weighted centroid analysis.

Supplemental Tables

Table S3.1: Age class is in the first column. The initial starting populations for female brown bears (*Ursus arctos*) in GMUs 1C and 1DS are shown in columns two through seven. The data for male brown bears are shown in columns eight through thirteen. Columns two through four and eight through ten represent GMU 1C. Columns five through seven and eleven through thirteen represent GMU 1D. The ten percent over and under estimations are shown in the two columns after the variable. The values are the number of bears in each class and category.

Age Class	1C female	+ 10%	- 10%	1D female	+ 10%	- 10%	1C male	+ 10%	- 10%	1D male	+ 10%	- 10%
1	48	53	44	26	28	23	48	53	44	26	28	23
2	44	48	39	23	25	21	34	37	30	18	20	16
3	39	43	35	21	23	19	24	27	22	13	14	12
4	34	37	30	18	20	16	19	21	17	10	11	9
5	29	32	26	15	17	14	15	16	13	8	8	7
6	24	27	22	13	14	12	10	11	9	5	6	5
7	15	16	13	8	8	7	7	8	7	4	4	3
8	10	11	9	5	6	5	5	5	4	3	3	2
9	10	11	9	5	6	5	5	5	4	3	3	2
10	39	43	35	21	23	19	27	29	24	14	16	13
Total	290	319	261	154	170	139	194	213	174	103	113	93

Table S3.2: Age class is in the first column. The initial starting populations for female black bears (*Ursus americanus*) in GMUs 1C and 1D are shown in columns two through seven. The data for male brown bears are shown in columns eight through thirteen. Columns two through four and eight through ten represent GMU 1C. Columns five through seven and eleven through thirteen represent GMU 1D. The ten percent over and under estimations are shown in the two columns after the variable. The values are the number of bears in each class and category.

Age Class	1C female	+ 10%	- 10%	1D female	+ 10%	- 10%	1C male	+ 10%	- 10%	1D male	+ 10%	- 10%
1	98	108	88	30	33	27	98	108	88	30	33	27
2	182	200	164	27	29	24	196	216	176	21	23	19
3	98	108	88	24	26	21	84	92	76	15	16	13
4	56	62	50	21	23	19	56	62	50	12	13	11
5	56	62	50	18	20	16	42	46	38	9	10	8
6	42	46	38	15	16	13	56	62	50	6	7	5
7	28	31	25	9	10	8	21	23	19	4	5	4
8	14	15	13	6	7	5	14	15	13	3	3	3
9	14	15	13	6	7	5	14	15	13	3	3	3
10	112	123	101	24	26	21	119	131	107	16	18	15
Total	700	770	630	178	196	160	700	770	630	119	131	107

Table S3.3: This table shows the starting parameters in brown bears (*Ursus arctos*) that were used as input into the state-space model as well as the ten percent increase and decrease in the starting values for the sensitivity analysis. The ten percent over- and under-estimations for each of the variables in the brown bear model. The original mean value is in column three.

Survival Parameters								
Variable	Parameter	Mean	Mean +10%	Long-Term Precision	Annual Precision	Mean - 10%	Long-Term Precision	Annual Precision
HSm	Male Harvest Survival	0.75	0.83	3.00	Gamma (1,2)	0.68	3.00	Gamma (1,2)
HSf	Female Harvest Survival	0.84	0.92	3.00	Gamma (1,1)	0.76	3.00	Gamma (1,1)
NS	Non-harvest Survival	0.81	0.89	4.00	Gamma (3,0.5)	0.73	4.00	Gamma (3,0.5)
CubSa	Cub Survival years 0.0-0.5	0.50	0.55	n/a	n/a	0.45	n/a	n/a
CubSb	Cub Survival years 0.5-1.5	0.60	0.66	n/a	n/a	0.54	n/a	n/a
Repf	Recovery Rate	0.90	0.99	n/a	n/a	0.81	n/a	n/a
Repm	Recovery Rate	0.85	0.94	n/a	n/a	0.77	n/a	n/a
Recruitment Parameters								
Variable	Parameter	Mean	Mean +10%	Distribution		Mean - 10%	Distribution	
LS-d	Litter Size 5.5-y	2.25	2.475	Gamma (495,200)		2.025	Gamma (405,200)	
PR-d	Pregnancy Rate 5.5-y	0.44	0.484	Beta (47,50)		0.396	Beta (33.2,50)	

Table S3.4: This table shows the starting parameters in black bears (*Ursus americanus*) that were used as input into the state-space model as well as the ten percent increase and decrease in the starting values for the sensitivity analysis. The ten percent over- and under-estimations for each of the variables in the brown bear model. The original mean value is in column three.

Survival Parameters								
Variable	Parameter	Mean	Mean +10%	Long-Term Precision	Annual Precision	Mean -10%	Long-Term Precision	Annual Precision
HSm	Male Harvest Survival	0.75	0.825	3.00	Gamma (1,2)	0.675	3.00	Gamma (1,2)
HSf	Female Harvest Survival	0.85	0.935	3.00	Gamma (1,1)	0.765	3.00	Gamma (1,1)
NS	Non-harvest Survival	0.91	0.999	4.00	Gamma (3,0.5)	0.819	4.00	Gamma (3,0.5)
CubSa	Cub Survival years 0.0-0.5	0.83	0.913	4.00	n/a	0.747	4.00	n/a
CubSb	Cub Survival years 0.5-1.5	0.76	0.0.836	4.00	n/a	0.684	4.00	n/a
Rep	Recovery Rate	0.9	0.999	2.00	n/a	0.882	2.00	n/a
Recruitment Parameters								
Variable	Parameter	Mean	Mean +10%	Distribution		Mean -10%	Distribution	
LS-a	Litter Size 5.5-y	2.00	2.20	Gamma (22,10)		1.80	Gamma (18,10)	
LS-b	Litter Size 5.5-y	2.00	2.20	Gamma (22,10)		1.80	Gamma (18,10)	
LS-c	Litter Size 5.5-y	2.00	2.20	Gamma (22,10)		1.80	Gamma (18,10)	
LS-d	Litter Size 5.5-y	2.73	3.00	Gamma (18,6)		2.47	Gamma (14.8,6)	
PR-a	Pregnancy Rate 5.5-y	0.003	0.0033	Beta (1.1,100)		0.0027	Beta (1.1,100)	
PR-b	Pregnancy Rate 5.5-y	0.25	0.28	Beta (32.5,83.5)		0.23	Beta (25,83.5)	
PR-c	Pregnancy Rate 5.5-y	0.53	0.58	Beta (66.8,48)		0.48	Beta (44,48)	
PR-d	Pregnancy Rate 5.5-y	0.48	0.53	Beta (56,50)		0.43	Beta (38.3,50)	

Chapter 4: Conclusion

The broad goal of this master's thesis was to explore the dynamics of biotic and abiotic factors on the interactions of two organisms that compete for the same resources in a spatially structured environment. Southeast Alaska is an ideal place to study how landscape impacts species interactions due to the degree of environmental influence on interspecific interactions. Within this context, brown and black bears are excellent organisms to study in this context since they have considerable dietary overlap and compete directly for resources.

In Chapter 2 we sought to quantify the effect of the environment on brown and black bear gene flow and to compare the patterns between the species. Our results agreed with previous work done in this system and supported the deep lineages found in Southeast Alaska in both brown and black bears. Our finding that brown bears on the ABC Islands split from the mainland populations first was not surprising given the genetic history of polar bear introgression and male-mediated gene flow across these islands. We also found evidence of deep lineages in black bears. The initial split of populations along a north-south axis was also not surprising given the eastern and western lineages of black bears in Southeast Alaska. The assignment of black bear populations to individual island groups matched our expectations; however, there was a stronger-than-expected level of genetic differentiation across such a short distance along the north-south axis starting in GMU 2. We attributed this differentiation to the deep lineages.

Our finding that the resistance values in both species reflect the environmental niches to which they are adapted is not entirely surprising as the species may be more

likely to move across habitat areas that contain the resources on which they depend; however, these categorical variables found in the model may be a proxy for other environmental factors such as elevation and we plan to continue exploring models to tease this apart.

In Chapter 3 we explored whether brown bears are displacing black bears in areas where hunters frequently hunt. Our data did not support displacement in GMU 1D and we attribute the increase in conflict there to the lack of resources due to the harsh winter and wet summer which caused brown bears to move into Haines to find resources.

While we didn't see any evidence of range changes in GMU 1D, we did find evidence in 1C. We hypothesize that the decrease in hunter effort with increasing successes for brown bears, coupled with the projected increase in brown bear population and higher mortality indicate that hunters, guides, and ADF&G staff are seeing more brown bears in places formerly occupied by black bears. Our data from chapter two demonstrated that GMU 1C is a location with high subpopulation mixing in both species suggesting that this may be a region with higher movement and dispersal. If both species of bears are more likely to move in that region, that may make them better able to respond to large-scale changes in available resources. We know from our cross-K analysis that the spatial patterns of both bears cluster together. This indicates that both species are found in the same places and competitive exclusion could be affecting the distribution of black bears.

While we do not have enough information from this study to determine the causes of demographic shifts in GMU 1C, we do see complementary supporting patterns emerge from both chapters. In GMU 1C we see an area of high gene flow probability along the

eastern edge of the Chilkat Peninsula (Figure 2.5). The landcover types in this area facilitate gene flow which may suggest that brown bear movement is more likely. An increase in brown bears on the Chilkat Peninsula could be seen more readily in areas where projected gene flow and subsequently movement is also high. Interestingly, we don't observe a high likelihood for gene flow on the Chilkat Peninsula in black bears (Figure 2.5). The lack of favorable landcover types for black bears in that area could indicate that there is not a high degree of movement for the species. Our population estimation predicted a decline for black bears (Figure 3.3A). If the decline has occurred in areas without predicted gene flow that could mean less movement in black bears and an increased likelihood that brown bears are able to push the remaining black bears further off preferred habitat. Hunters could also be contributing to the demographic changes if they are reducing the number of black bears faster than they are replaced resulting in more available resources for dominant brown bears.

The area around Port Houghton is the other location in GMU 1C from which demographic changes have been reported. Our gene flow analysis does not indicate high probability through this area for brown bears which does not match the reports; however, in our population structure analysis the individuals closest to this area grouped with subpopulations from the ABC islands (Figure 2.2). The lack of gene flow in this area along with the subpopulation assignment suggest that if there is an increase in brown bears in this area the influx may be primarily from the ABC islands. More sampling would create an opportunity to better analyze the population structure in this area.

This thesis explored interspecies competition and how the environment structures movements across the landscape. We found similar genetic patterns and gene flow to

other studies in the area and provided novel insight into the study system. Our results allow us to begin understanding the complex interactions between brown and black bears in Southeast Alaska and lay the foundation for future research.