



Research Article

Integrating Genetic Data and Demographic Modeling to Facilitate Conservation of Small, Isolated Mountain Goat Populations

KEVIN S. WHITE,¹ Division of Wildlife Conservation, Alaska Department of Fish and Game, Juneau, AK 99811, USA

TAAL LEVI, Department of Fish and Wildlife, Oregon State University, Corvallis, OR 97331, USA

JESSICA BREEN, Forensics Program, Trent University, Peterborough, ON K9J 7B8, Canada

MEGHAN BRITT, Forensics Program, Trent University, Peterborough, ON K9J 7B8, Canada

JUSTIN MERÖNDUN, Environmental and Life Sciences Graduate Program, Trent University, Peterborough, ON K9J 7B8, Canada

DARIA MARTCHENKO, Environmental and Life Sciences Graduate Program, Trent University, Peterborough, ON K9J 7B8, Canada

YASAMAN N. SHAKERI, Division of Wildlife Conservation, Alaska Department of Fish and Game, Juneau, AK 99811, USA

BOYD PORTER, Division of Wildlife Conservation, Alaska Department of Fish and Game, Ketchikan, AK 99901, USA

AARON B. A. SHAFER, Forensic Science Program and Environmental and Life Sciences Graduate Program, Trent University, Peterborough, ON K9J 7B8, Canada

ABSTRACT Acquisition of field data and analytical methods needed for conservation and management of wildlife populations represent significant challenges, particularly for species that inhabit landscapes that are difficult to access or species that persist in small, isolated populations. In such instances, integrating diverse and complementary data streams, such as genetic and non-genetic data, can advance our understanding of population dynamics and associated management implications. We examined how genetic and morphologic data can be used to articulate population structure of a low-density, peninsular population of mountain goats (*Oreamnos americanus*) on the Cleveland Peninsula, Alaska, USA, and surrounding areas, 2005–2018. We then use a population demographic modeling approach to examine how the use of population structure information influences sustainable harvest quotas, as compared to a panmictic, null model. Specifically, we conducted extensive field sampling of genetic ($n = 446$) and morphologic (i.e., horn length, $n = 371$) data to characterize population structure. We conducted demographic analyses and examined harvest modeling scenarios using a sex- and age-specific matrix population modeling approach. Genetic and morphologic data analyses suggested peninsular subpopulations were demographically isolated, relative to surrounding mainland populations. Specifically, genetic structuring was evident and followed an isolation-by-distance, stepping-stone pattern indicating limited interchange, low effective population sizes, and reduced genetic diversity along a peninsular extremity to mainland gradient. Harvest modeling indicated that overharvest would likely occur if the panmictic, null model was used to guide harvest because the smallest genetically defined population at the peninsular extremity was too small to permit any level of sustainable harvest. Our analyses illustrate the importance of using genetic and morphologic data, in combination with demographic modeling, to quantitatively delineate population boundaries and dynamics for ensuring viability of small, isolated populations. © 2020 The Wildlife Society.

KEY WORDS Alaska, demographic modeling, horn size, mountain goat, non-invasive sampling, *Oreamnos americanus*, population genetics.

Conservation and management of large mammals is a broad-ranging endeavour that seeks to balance human use and sustainability of wildlife populations. The regulated hunting of free-ranging wildlife populations in North America has a long tradition and generates substantial financial resources that directly and indirectly benefit society, wildlife management, and conservation efforts (i.e.,

the North American Model; Organ et al. 2012). For example, hunting generates approximately 1 billion dollars annually through license and excise tax fees in the United States (U.S. Fish And Wildlife Service 2017), and a significant fraction of this money is used to support wildlife population monitoring, research, and management programs. Even still, acquisition of field data and analytical methods needed to determine sustainable harvest of wildlife populations represent significant challenges, particularly for species that inhabit landscapes that are difficult to access or species that persist in small, isolated populations.

Received: 3 March 2020; Accepted: 17 October 2020

¹E-mail: kevin.white@alaska.gov

To ensure population viability (or sustainability, in the case of harvested populations), significant field data collection and analytical efforts are required, particularly for low-density populations characterized by low population growth rates and high societal value. At the most basic level, population size projection, or harvest simulation, from one year to the next, or across longer time horizons, requires knowledge about population size, recruitment, survival, and the extent to which populations are freely interbreeding. Conventional field techniques involving radio-marking, and subsequent observations, can enable estimation of population size, recruitment, and survival but are not well suited or are impractical for assessing demographic boundaries and dispersal between populations because of large and often unattainable sample size requirements. In this regard, population genetic methods represent a cost-effective and powerful tool for parameterizing this important component of applied demographic models. For example, estimating the number of migrants per generation between 2 adjacent populations can provide key insight about whether perturbations in one population are likely to affect the other or, alternatively, the extent to which one population might be able to demographically rescue another from unintended anthropogenic effects such as overharvest.

Mountain goats (*Oreamnos americanus*) are an iconic species of northern mountain ecosystems and are widely valued and used by a diverse public. For example, mountain goat viewing is a popular tourism activity among the >1,000,000 annual visitors to coastal Alaska, USA. The species is also a highly coveted subsistence and sport hunting resource with approximately 500 mountain goats harvested each year throughout the state. Mountain goat wool, horns, and hooves have been used in culturally significant ways (Ravenstail and Chilkat blankets, spoons, rattles) by indigenous groups for centuries (Rofkar 2014). As such, the sustained persistence of healthy mountain goat populations entails societal gain and enduring cultural significance.

Mountain goats are habitat specialists that are uniquely adapted to extreme mountain environments, characteristics that result in restricted distribution and low density relative to other northern ungulates. The species has a slow life-history strategy (slow growth rates, late age of maturity, high costs of reproduction, reproductive pauses) and consequently low reproductive rates leading to relatively low population growth and rates of sustainable harvest (Hamel et al. 2006, Festa-Bianchet and Côté 2008, Rice and Gay 2010, White et al. 2018). Mountain goats are also particularly sensitive to indirect anthropogenic disturbance (Festa-Bianchet and Côté 2008, Northern Wild Sheep and Goat Council 2020) and extreme weather and climatic variability (Poole et al. 2009; White et al. 2011, 2018; Richard et al. 2014). These factors pose a significant conservation challenge for mountain goats, relative to other species in terms of population monitoring, management, and conservation (Poole 2007, Festa-Bianchet and Côté 2008, Rice et al. 2009).

A combination of observational, radio-telemetry, and genetic data have been used to fill knowledge gaps regarding

population patterns and processes (Festa-Bianchet and Côté 2008, Mainguy et al. 2009, Shafer et al. 2012). Genetic tools, in particular, allow for delineating populations boundaries and estimating parameters such as migration rates (i.e., gene flow), heterozygosity, and effective population size (N_e), all of which can assist with management decisions (Wolf et al. 2020). This is relevant to mountain goats because they are often managed at relatively small hunt-unit scales that are typically delineated based on expert opinion assessments of local geography, hunter access, aerial survey abundance, distributional data, and historical harvest patterns. Although practical in some respects, such an approach involves subjective determination of demographic boundaries and, in some contexts, can be difficult to justify and implement consistently across large areas. Spatial characterization of population genetic structure offers an objective and explicitly data-based method for delineating management or conservation units.

Across their North American distribution, mountain goats often persist in small, isolated populations that are particularly vulnerable to stochastic events and direct or indirect human disturbance (Hamel et al. 2006, White et al. 2018). In this regard, the study of peninsular populations can offer a unique opportunity to understand the inter-relationships between geography, population genetics, and demography. The Cleveland Peninsula (Fig. 1), a somewhat unique peninsular geography composed of several small and potentially isolated populations located in coastal Alaska, represents a compelling case study to explore such dynamics in a conservation and management-relevant context. In this area, putative subpopulations are separated by extensive (≤ 32 km) low-elevation terrain that is generally deemed unsuitable for the species (Smith and Raedeke 1982, White et al. 2010). The consequent geographical juxtaposition suggests that populations may be significantly isolated from each other. Notably, mountain goats in this area tend to have disproportionately large horns, with 4 of the top 10 Boone and Crockett records coming from the lower peninsula despite a very low historical harvest rate (1–3 animals/yr; Buckner et al. 2009; B. Porter, Alaska Department of Fish and Game, unpublished data), an ecotypic observation that further suggests population isolation. Based on the strict habitat requirements of mountain goats and their apparent geographic isolation, it is currently unclear whether there is any mountain goat movement between the putative geographical subpopulations on the peninsula and those inhabiting the mainland coastal mountain source population, a factor that has key implications for management and conservation of the most isolated subpopulation on the peninsular extremity.

In the 1980s there were an estimated 50–70 individuals across 8 suitable habitat patches found on the lower part of the Cleveland Peninsula (Smith and Raedeke 1982). In 2004, high harvests and an apparent population decline led managers to close the area to hunting because of population viability concerns. In 2013–2014, only 4 patches were occupied with an estimated 36 individuals, suggesting further population decline. Consequently, acquisition of knowledge

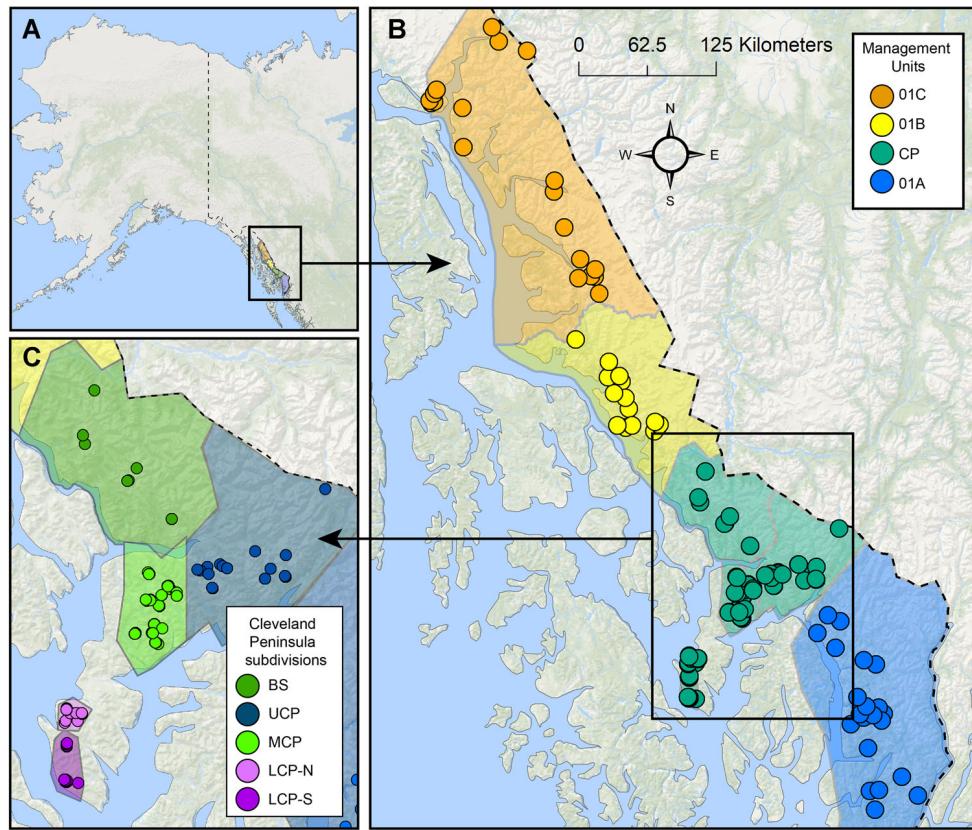


Figure 1. The location and distribution of mountain goat genetic samples ($n=446$) collected and successfully genotyped in southeastern Alaska, USA, 2005–2018. Separate panels illustrate increasing level of spatial detail including A) the location of the study area in Alaska, B) the major Game Management Units (GMUs) sampled, and C) juxtaposition of the 5 focal subdivisions in the Cleveland Peninsula and adjacent areas: Lower Cleveland Peninsula North (LCP-N), Lower Cleveland Peninsula South (LCP-S), Middle Cleveland Peninsula (MCP), Upper Cleveland Peninsula (UCP) and Bradfield-Stikine (BS).

about the degree to which the populations are isolated and how much genetic interchange is occurring offers an important opportunity to assess the resilience of the population to stochastic events and the extent to which genetic rescue could aid the population in the event of natural or anthropogenic mediated declines. It also advances our understanding of how biogeographic structure influences gene flow and demography in a conservation context.

In this study, our objective was to characterize population structure on the Cleveland Peninsula and surrounding areas in southeastern Alaska using genetic and morphologic data collected during a multi-year field effort that involved extensive sampling. We then examined how the use of genetic and morphologic population structure information influenced sustainable harvest quotas, as compared to a panmictic, null model by using a population demographic modeling approach. Ultimately, our goal was to assess the management implications of using population structure information and how such information can be used to ensure viability and sustainable harvest of small, isolated populations.

STUDY AREA

We studied mountain goats in a mainland coastal mountain region of southeastern Alaska (55.0–58.5N, 130.5–134.5W; Fig. 1) during 2009–2018. Within this broad region, we conducted extensive sampling in a focal sub-study area

located on the Cleveland Peninsula area (Smith and Raedeke 1982). The maritime climate in this area is characterized by cool, wet summers and relatively warm, snowy winters. Total annual precipitation at sea-level averaged 143–368 cm including 223–122 cm of snowfall deposited during November–March (for Juneau Airport and Beaver Falls—Ketchikan, respectively; National Weather Service 2019). Elevations at 800 m typically received approximately 650 cm of snowfall, annually (Eaglecrest Ski Area Juneau, AK; National Weather Service 2019). Winter (Nov–Mar) temperatures at sea-level averaged $-1.2\text{--}2.1^{\circ}\text{C}$ (and were rarely less than -20°C), whereas summer (Jun–Aug) temperatures averaged $12.8\text{--}14.1^{\circ}\text{C}$ (and rarely exceeded 27°C ; Juneau Airport and Beaver Falls—Ketchikan, respectively; National Weather Service 2019). Predominant vegetative communities occurring at low to moderate elevations (<500 m) included Sitka spruce (*Picea sitchensis*)—western hemlock (*Tsuga heterophylla*)-dominated coniferous forest, mixed-conifer muskeg, and deciduous riparian forests. Mountain hemlock (*Tsuga mertensiana*)-dominated krummholz forest comprised a subalpine, timberline band occupying elevations between 500–750 m. Alpine plant communities (750–1,400 m) were composed of a mosaic of relatively dry ericaceous heathlands, moist meadows dominated by grasses and forbs, and wet fens. Avalanche chutes were common in the study area, bisected all plant community types, and often terminated at sea-level. Mountain goat habitats

within this region are largely unaltered by human activity; however, in localized areas land use activities involving industrial-scale timber harvest, road construction, mining, and hydroelectric development occur. Mountain goats were generally allopatric with other potential interspecific competitors such as moose (*Alces alces*) and Sitka black-tailed (*Odocoileus hemionus sitkensis*) deer, but some overlap occurred. Documented predators of mountain goats included wolves (*Canis lupus*), brown bears (*Ursus arctos*), and black bears (*Ursus americanus*). Wolverines (*Gulo gulo*) and coyotes (*Canis latrans*) were also present.

METHODS

Data Collection

We captured mountain goats on the Lower Cleveland Peninsula (LCP) during September 2009–2010, and other areas of southeastern Alaska during 2005–2017, using standard helicopter darting techniques and immobilized them by injecting 2.4–3.0 mg of carfentanil citrate, depending on sex and time of year (Taylor 2000, White et al. 2010), via projectile syringe fired from a Palmer dart gun (Cap-Chur, Douglasville, GA, USA). During handling, we carefully examined and monitored all animals following standard veterinary procedures (Taylor 2000) and collected routine biological samples and morphological data. All animals were equipped with red or orange global positioning system (GPS; Telonics TGW-3590; Telonics, Mesa, AZ) or very high frequency (VHF)-radio collars (Telonics MOD-500, MOD-410) and ear tags (Allflex, Dallas, TX, USA). Following handling procedures, we reversed the effects of the immobilizing agent with 100 mg of naltrexone hydrochloride/1 mg of carfentanil citrate (Taylor 2000). We captured and radio-collared mountain goats to acquire genetic (ear tissue) samples, estimate morphological characteristics, and estimate population size (via follow-up aerial surveys and subsequent mark-resight population estimation). All capture procedures were approved by the State of Alaska Animal Care and Use Committee (protocol 09–24).

We collated horn measurements from mountain goats captured in southeastern Alaska between 2005 and 2017 (K. S. White, Alaska Department of Fish and Game, unpublished data) and compared measurements to those captured on the LCP. We evaluated horn growth for male and female mountain goats in southeast Alaska by first generating length-by-age regression curves. We fit a polynomial regression with horn length as the response variable, location (LCP or southeast Alaska), sex, and age as explanatory variables, and sampling year as a random effect, with a quadratic function applied to the age variable. We compared the annuli length at years 1, 2, and 3 using a Student's *t*-test.

We employed multiple sample collection methods to efficiently attain a robust and geographically representative sample of genetic material. Specifically, we collected tissue samples from live captured mountain goats, harvested mountain goats, and non-invasively collected fecal pellet samples during 2005–2018. We used a sterilized hole punch

to collect a small piece of ear tissue (4-mm diameter) during live capture events. Regional biologists also collected tissue samples from hunters by during post-hunt horn inspections. We preserved all tissue samples using 95% ethanol in 2-ml vials. Although the combination of live capture and hunter harvest allowed for extensive sampling across a broad geographic distribution, a few sampling gaps remained. To supplement genetic samples using the methods described above, we conducted non-invasive sampling of fecal pellets in inadequately sampled areas. Specifically, during June–August 2014, 2016–2018, we used a helicopter to visually locate mountain goats on the Cleveland Peninsula and the adjacent Stikine-Bradfield (S-B) area. Once we located animals, we conducted a ground-based search to find and sample fecal pellets. When we found a fresh (i.e., mucous sheen evident) fecal pellet group, we rubbed a sampling swab on multiple individual pellets so fecal mucosa (and presumably genetic material from sloughed intestinal cells) would adhere to the swab. We then placed swabs in a 2-ml vial filled with Longmire's solution (100 mM Tris, 100 mM EDTA, 10 mM NaCl, 0.5% SDS, 0.2% sodium azide). Preliminary testing indicated that fecal pellet sample genotyping success was improved when using Longmire's solution, as compared to 95% ethanol or dry storage (A. B. A. Shafer, Trent University, unpublished data). We divided samples from the Cleveland Peninsula into 4 sampling regions based on the geographic location of major alpine complexes including the Lower Cleveland Peninsula-North (LCP-N), Lower Cleveland Peninsula-South (LCP-S), Middle Cleveland Peninsula (MCP), and Upper Cleveland Peninsula (UCP). We also sampled 4 mainland areas including B-S, game management unit (GMU) 1A, GMU 1B, and GMU 1C; the former 2 regions were adjacent to the Cleveland Peninsula but separated by putative barriers to mountain goat movement such as marine fiords and large river systems, whereas the remaining areas were geographically disjunct and located north of the B-S area (Fig. 1).

Genetic Analysis

We extracted genomic DNA from the tissue and the non-invasive fecal samples with QIAGEN DNeasy blood and tissue kits (Qiagen, Valencia, CA, USA). We swabbed fecal samples with a cotton swab that had been wetted with deionized water. We placed ear punches and swabs that we collected in the field into 1.5-ml tubes. We digested all samples overnight (~24 hrs) in 180 μ L of Qiagen's Buffer ATL and 20 μ L of Pro-K before we extracted them following standard Qiagen protocol. We quantified extractions using a Qubit 3.0 Fluorometer (Thermo Fisher Scientific, Waltham, MA, USA) and stored extractions at -20°C .

We amplified 18 polymorphic microsatellite loci in 3 polymerase chain reaction pools (Table S1, available online in Supporting Information); Mainguy et al. (2005) and Poissant et al. (2009) provide detailed locus information. Each polymerase chain reaction followed the approach of Shafer et al. (2011a); we genotyped samples on an ABI 3730 DNA analyzer (Applied Biosystems, Foster City, CA,

USA) and scored them using the program Geneious R10 (Kearse et al. 2012). We amplified all non-invasive samples in triplicate; we compared genotype calls for each locus across the 3 replicates and if there were disagreements (i.e., alleles were not the same), we compared the peaks visually and removed the weak ones (relative fluorescent units < 250). If >1 replicate at a locus had discrepancy between heterozygosity or homozygosity after 3 replicates, we considered the locus to be missing (scored 0). We screened the resulting data set with the R package Allelomatch 2.03 (Galpern et al. 2012) to remove potential duplicate individuals. We removed from analysis individual samples and microsatellite loci with >50% missing data.

We determined the number of alleles, heterozygosity, and inbreeding and differentiation indices using the program GenAIEx version 6.5 (Peakall and Smouse 2006). We estimated the effective number of migrants (N_m) per generation between the sampled populations. We compared diversity statistics between the tissue and non-invasive samples from the LCP-S to determine whether sample quality influenced the results. We collected all of our samples within 13 years (1–3 generations), thereby reflecting a snapshot of population history; as such we estimated the effective population size (N_e) using a single point in time and linkage disequilibrium method available in NeEstimator V2.1 (Do et al. 2014). We conducted isolation-by-distance by taking the natural logarithm of the Euclidean distance between sampling area centroids and comparing this to the genetic differentiation with the metric F_{ST} . We assessed significance using a Mantel test and 1,000 permutations (Mantel 1967). We used BOTTLENECK V1.2.02 to test for bottlenecks under a stepwise mutation model (Cornuet and Luikart 1996).

We then used the Bayesian clustering program STRUCTURE (version 2.3.4) to identify the number of genetic clusters (K) or subpopulations (Pritchard et al. 2000). We parallelized admixture models within STRUCTURE with StrAuto for $K=1$ –10 with a burn-in of 5×10^5 followed by 1×10^6 Monte Carlo Markov chains with 20 replicate runs for each K ; we selected this value of K because it far exceeds that detected in adjacent populations (Wolf et al. 2020). We sorted and averaged the results of the runs for each K with CLUMPP 1.1.2 (Jakobsson and Rosenberg 2007). We completed this process once with the PopFlag parameter set to 1, which defines *a priori* population assignments for known groups, and once with the PopFlag parameter set to 0. The assignment results were comparable with and without the PopFlag parameter, so we used our results without pre-defined reference groups to allow the software to find its own population divisions. We also used a principal component analysis (PCA) and discriminant analysis of principal components (DAPC) in the R package adegenet (Jombart 2008) to visualize population genetic structure and confirm the STRUCTURE results.

We sequenced all samples from the LCP at the mitochondrial DNA d-loop to confirm species identity because the population is sympatric with Sitka black-tailed deer (*Odocoileus hemionus sitkensis*). We sequenced a subset of MCP, UCP, and B-S samples to include in the analysis. We

amplified samples following the approach and primers in Shafer et al. (2011a) and sequenced in both directions with negative controls. We ran the polymerase chain reaction product on a gel to ensure sufficient DNA, and then cleaned it via ExoSAP-IT protocol and ethanol precipitation prior to submission. We sequenced samples on an ABI 3730 DNA Analyzer, and edited and aligned them with the program BioEdit (Hall 1999). We generated consensus sequences and resolved any discrepancies by visual inspection of the chromatogram. For mtDNA analysis, we obtained 38 additional mountain goat d-loop sequences from southeast Alaska from GenBank to create a spatial outgroup. We estimated the genetic p-distance, the number of nucleotide differences divided by the fragment length, between sampling areas using MEGA7 (Kumar et al. 2016) and quantified the number of unique haplotypes on the Cleveland Peninsula.

Population Modeling Simulations

We conducted population modeling simulations to examine management implications associated with using population genetic data to delineate demographic populations. Specifically, we contrasted a pair of conservative static harvest treatments (i.e., 1 mountain goat harvested or 1 female mountain goat harvested annually) for a null model (i.e., that defined the entire Cleveland Peninsula as a single, large panmictic population) with scenarios that incorporated genetic information (i.e., and recognized the LCP, MCP, and UCP as genetically distinct, relatively small and demographically independent populations). We conducted simulations using an existing sex- and age-structured population model (White et al. 2018), modified to simulate harvest (T. Levi, Oregon State University, unpublished data; Supplemental Text S1, available online in Supporting Information). Briefly, the population model projects population size through time based on sex-, age-, and climate-specific reproduction and survival estimates based on relationships derived from a spatially and temporally extensive, 37-year known-fates data set collected from mountain goats throughout coastal Alaska, including the Cleveland Peninsula ($n=10$ study sites, 447 individuals, 1,179 mountain goat yrs; White et al. 2011, 2018). We derived initial population sizes for each modeling scenario (i.e., null model plus different geographic population delineations) by averaging population estimates calculated over multiple surveys per area (Supplemental Text S2, Tables S2–S4, available online in Supporting Information). This approach was intended to provide generalized but realistic initial population size estimates for each area using the best available data, recognizing that certain assumptions apply (i.e., constant aerial survey sighting probabilities across space and time).

Harvest simulations.—We considered 2 harvest treatments for each area-specific modeling scenario. The first treatment simulated the annual harvest of 1 adult female mountain goat randomly selected from all age classes excluding kids and yearlings. This treatment represented a historically realistic but worst-case scenario. The second treatment (i.e., constant harvest) involved harvest of 1 adult male or female mountain goat annually. For this treatment, the model randomly selected an individual for harvest based on the

sex-specific selection patterns of hunters in Alaska (based on historical harvest data; Alaska Department of Fish and Game, unpublished data) combined with the proportion of males versus females in the population by age class (excluding kids and yearlings; S1). For example, in a given initial harvest simulation, males are roughly twice as likely to be selected relative to females. The harvest simulation approach, however, adjusts sex-specific harvest based on the relative proportion of individuals in the population. When males are abundant in the population, harvest occurs mostly on males. If the proportion of males in the population declines, however, then more females are harvested because of the relative scarcity of males in the population. The functional relationship for how the ratio of males to females in the harvest varies with respect to their ratio in the population is based on empirical harvest data and associated predicted population sex ratios. This approach is less conservative than earlier mountain goat population modeling efforts (Hamel et al. 2006, which assumes 50% chance of harvesting females) but is explicitly based on actual mountain goat harvest data collected in Alaska, including our study area (GMU 1A).

Evaluating sustainable harvest.—We evaluated sustainable harvest in 2 complementary ways. First, based on the initial population size, we determined the maximum number of mountain goats that could be harvested while maintaining a rate of population growth (λ) ≥ 1 over a 50-year time span. Second, we determined whether a single mountain goat could be harvested under each given scenario by examining whether $\lambda \geq 1$ for a majority of simulations over a 50-year time span (i.e., an outcome that would denote harvest would be sustainable).

RESULTS

Horn Analysis

We collected 371 horn measurements for analyses. Results of regression analysis revealed that horn length of

mountain goats on the LCP was significantly longer, on average, relative to the remainder of southeastern Alaska (LCP, $\bar{x} \pm SE = 24.0 \pm 3.9$ cm; southeastern Alaska = 21.7 ± 2.6 cm, $F = 14.26$, $P \leq 0.01$; Fig. 2); the polynomial model cumulatively explained a moderate amount of the variation in horn length (conditional $R^2 = 0.34$; Fig. 2). The random effect of sampling year added no variance ($\sigma^2 < 0.01$) and we dropped it from the final model. Growth during the first year was higher on the LCP compared to the mainland (LCP = 17.2 ± 2.1 cm; southeastern Alaska = 15.7 ± 2.1 cm; $t = 2.46$, $P = 0.03$). We observed a similar trend in the second annuli (LCP = 4.2 ± 1.2 cm; southeastern Alaska = 3.5 ± 1.1 cm; $t = 1.95$, $P = 0.08$; Fig. S1).

Population Genetic Analysis

Overall, we spent 9 days sampling mountain goat fecal pellets throughout the entire Cleveland Peninsula and adjacent B-S areas during June–August 2014–2018. We collected 639 pellet groups and used 214 tissue samples from our regional mountain goat tissue repository (i.e., collected via live-capture and hunter harvest). After data filtering (i.e., missing data, duplicates) we genotyped 468 samples; 201 from the mainland (tissue), 15 from the B-S transition zone (pellet), and 252 from the Cleveland Peninsula (239 pellet, 13 tissue; Table 1). All 18 loci had <50% missing data; therefore, we used all loci. The overall genotyping data set was 84% complete. Comparing fecal samples to the tissue samples revealed near identical relatedness distributions (Fig. S2) and similar estimates of observed heterozygosity (Table S5).

Estimates of F_{ST} between our samples from the mainland (GMU 1A, 1B, 1C) and the Cleveland Peninsula, excluding B-S, ranged from 0.02–0.12 with N_m at approximately 3 migrants/generation (Table S6). Between the 4 grouped populations on the Cleveland Peninsula and B-S, pairwise F_{ST} ranged from 0.02–0.11 (Table S7), with B-S being the

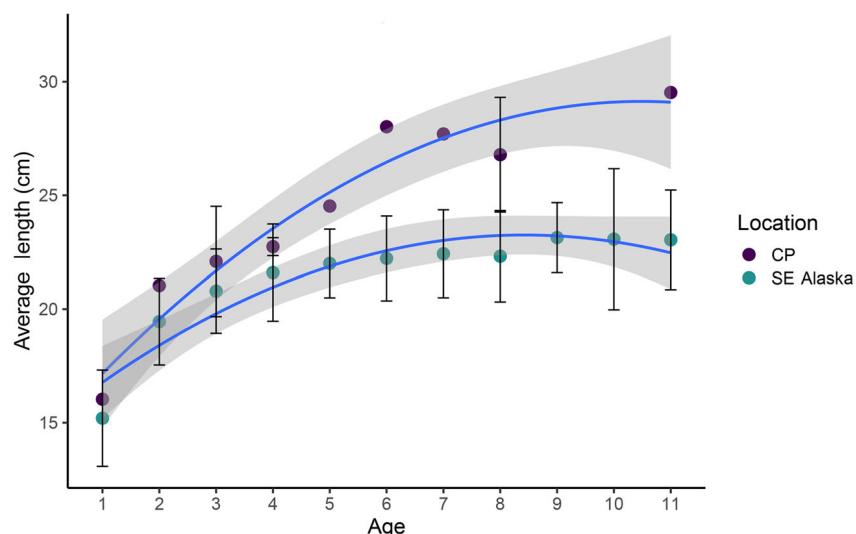


Figure 2. Relationship between mountain goat horn length and age (yr) for the Lower Cleveland Peninsula (CP) and the remainder of southeastern Alaska (SE Alaska), USA, 2005–2018, based on 371 samples. We estimated the curvilinear relationship using a polynomial model accounting for fixed (age, sex, area [CP vs. SE Alaska]) and random effects. Age-specific ($\pm SE$) values are summarized.

Table 1. Number of mountain goat genetic samples collected in relation to geographic area and sample type in southeastern Alaska, USA, 2005–2018.

Region	Area ^a	Number of samples		
		Tissue	Fecal pellets	Total
Mainland	GMU 1A	60	0	60
	GMU 1B	50	0	50
	GMU 1C	91	0	91
Transition	Bradfield—Stikine	0	15	15
Cleveland Peninsula	Upper	0	36	36
	Middle	0	102	102
	Lower—North	6	22	28
	Lower—South	7	57	64

^a GMU = Game Management Unit.

most differentiated. Observed heterozygosity (H_O) for 1A, 1B, and 1C ranged from 0.41 to 0.48 (Table 2). Within the groupings on the Cleveland Peninsula, H_O ranged from 0.23 to 0.34, with B-S at 0.40; thus, genetic diversity decreased the farther mountain goat populations occurred down the peninsula, with inbreeding coefficients also becoming elevated (Table 2). This was further supported via evidence for a series of bottlenecks on the peninsula (Table 2). Thus, there was a clear pattern of isolation-by-distance (Mantel $r=0.60$; $P\leq 0.01$; Fig. S3). Our estimates of N_e ranged from 5–15 individuals (Table 2) for the LCP using the lowest allele frequency. Estimates of N_e for the total mainland metapopulation ranged from 36–120 (Table 2). There was no relationship between sample size and estimate of N_e ($\beta=0.28$; $P=0.28$; Fig. S4).

We used the algorithm developed by Evanno et al. (2005) to identify mountain goat group clusters (K). Choice of appropriate number of clusters was informed by $\Delta(K)$, which identified $K=2$ as the optimal number of clusters in the genotypic data (Fig. S5), which largely divided the Cleveland Peninsula from the mainland (Fig. 3; K of 2–5 are also shown). Notably, a K of 5 is consistent with the isolation-by-distance pattern, which is also seen in the PCA and DAPC (Figs. S6 and S7).

We sequenced the mitochondrial DNA of 94 samples from the Cleveland Peninsula (GenBank accession numbers

MK279742–MK279839) and an additional 38 samples from southeastern Alaska that were also available on GenBank. From our 94 mtDNA sequences from the Cleveland Peninsula, we identified 25 unique haplotypes, with the highest frequencies of unique haplotypes found on the LCP (Fig. 4).

Population Modeling Simulations

Population modeling simulations indicated that the sex composition of harvest had a strong effect on population growth and sustainable harvest. Harvest of 1 female mountain goat annually resulted in projected population declines for all scenarios, except the null model scenario that assumed the entire Cleveland Peninsula was panmictic and composed of an intermixing population of 184 mountain goats (Table 3; Fig. 5). In contrast, harvest of 1 mountain goat, based on the less conservative constant harvest simulation approach, would maintain a positive population growth rate for populations with >74 mountain goats (Table 4; Fig. 5). Overall, harvest modeling simulations indicate that genetically defined delineation of Cleveland Peninsula mountain goat populations would not permit sustainable harvest (i.e., $\lambda\leq 1$ for a majority of simulations over a 50-year time span) of the smallest and most isolated LCP population ($n=36$) but would allow for sustainable harvest of the larger MCP ($n=74$) and UCP ($n=84$) Cleveland Peninsula populations, provided harvest was not exclusively composed of females and instead emulated the constant harvest pattern.

DISCUSSION

The results of our analysis suggest that the mountain goat subpopulations on the Cleveland Peninsula are morphologically and genetically differentiated from the larger, more geographically interconnected mainland areas. Metrics of diversity suggest the Cleveland Peninsula is genetically differentiated with reduced gene flow and is thus at risk of inbreeding depression and increased extinction risk (Caballero et al. 2017). Populations on the peninsula appear to be interconnected, constituting a meta-population, with a pattern consistent with a stepping-stone model with

Table 2. Summary of genetic diversity statistics for mountain goats sampled in southeastern Alaska, USA, 2005–2018. We report the mean (\pm SE) for number of alleles, observed heterozygosity (H_O), and fixation index. The effective population size estimates (N_e) reflect the upper and lower estimates. We assessed bottleneck estimates using a stepwise mutation model and evaluated heterozygosity excess using a sign test (in parentheses).

Population and subdivision ^a	Number of alleles		H_O		Fixation index		N_e	Bottleneck	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE		Estimate	P
Mainland									
GMU 1A	4.8	0.61	0.41	0.05	0.1	0.04	36.0–58.1	10.41	0.16
GMU 1B	5.4	0.58	0.46	0.04	0.17	0.04	81.4–119.4	10.45	0.31
GMU 1C	5.6	0.54	0.48	0.04	0.1	0.03	64.3–95.7	10.53	0.51
Transition zone									
Bradfield-Stikine	3.1	0.3	0.4	0.05	0.08	0.08	2.0–2.4	10.29	0.01
Cleveland Peninsula									
Upper	3.9	0.56	0.34	0.04	0.3	0.06	14.7–17.5	10.33	0.02
Middle	4.8	0.64	0.31	0.04	0.37	0.05	27.3–47.7	10.38	0.20
Lower-North	4.4	0.46	0.23	0.04	0.5	0.07	7.3–14.9	10.11	0.49
Lower-South	4.3	0.44	0.28	0.04	0.38	0.05	4.8–7.9	10.44	0.02

^a GMU = Game Management Unit.

Table 3. Mountain goat demographic responses to a simulated harvest of 1 adult female for different genetically distinguished sub-populations on the Cleveland Peninsula, Alaska, USA. Initial population size estimates are based on aerial surveys conducted during 2014–2016. The null model scenario simulates the response for the entire Cleveland Peninsula (all areas combined) and assumes no population substructure. Sustainable harvest denotes the number of adult females that can be harvested where rate of population growth (λ) ≥ 1 for a majority of simulations over a 50-year time span.

Area	Harvest = 1 female			
	Population size	λ	Simulations declining (proportion)	Sustainable harvest
Lower Cleveland Peninsula—North	13	0.846	1.00	0
Lower Cleveland Peninsula—South	23	0.853	1.00	0
Lower Cleveland Peninsula—both	36	0.879	1.00	0
Middle Cleveland Peninsula	74	0.963	0.99	0
Upper Cleveland Peninsula	84	0.979	0.98	0
Null model; all areas combined	194	1.004	0.27	1

Table 4. Mountain goat demographic responses to a simulated harvest of 1 adult (constant harvest) for different genetically distinguished sub-populations on the Cleveland Peninsula, Alaska, USA. Initial population size estimates are based on aerial surveys conducted during 2014–2016. The null model scenario simulates the response for the entire Cleveland Peninsula (all areas combined) and assumes no population substructure. Sustainable harvest denotes the number of animals harvested under the constant harvest treatment where rate of population growth (λ) ≥ 1 for a majority of simulations over a 50-year time span.

Area	Harvest = 1 mountain goat			
	Population size	λ	Simulations declining (proportion)	Sustainable harvest
Lower Cleveland Peninsula—North	13	0.980	0.99	0
Lower Cleveland Peninsula—South	23	0.983	0.95	0
Lower Cleveland Peninsula—both	36	0.996	0.64	0
Middle Cleveland Peninsula	74	1.006	0.18	1
Upper Cleveland Peninsula	84	1.008	0.15	1–2
Null model; all areas combined	194	1.011	0.05	4–5

decreasing diversity as you move down the peninsula due to reduced migration (i.e., gene flow). How these data and patterns can assist with actual management, however, is more nuanced.

A gap has emerged between genetic research studies and on-the-ground conservation and management needs

(Shafer et al. 2015, Taylor et al. 2017). Although there are a plethora of reasons for this gap (Taylor et al. 2017, Britt et al. 2018, Mair et al. 2018), part of the problem stems from the abstract and relative nature of many genetic parameters, which makes them difficult to interpret and act upon in ways that are relevant to management. General

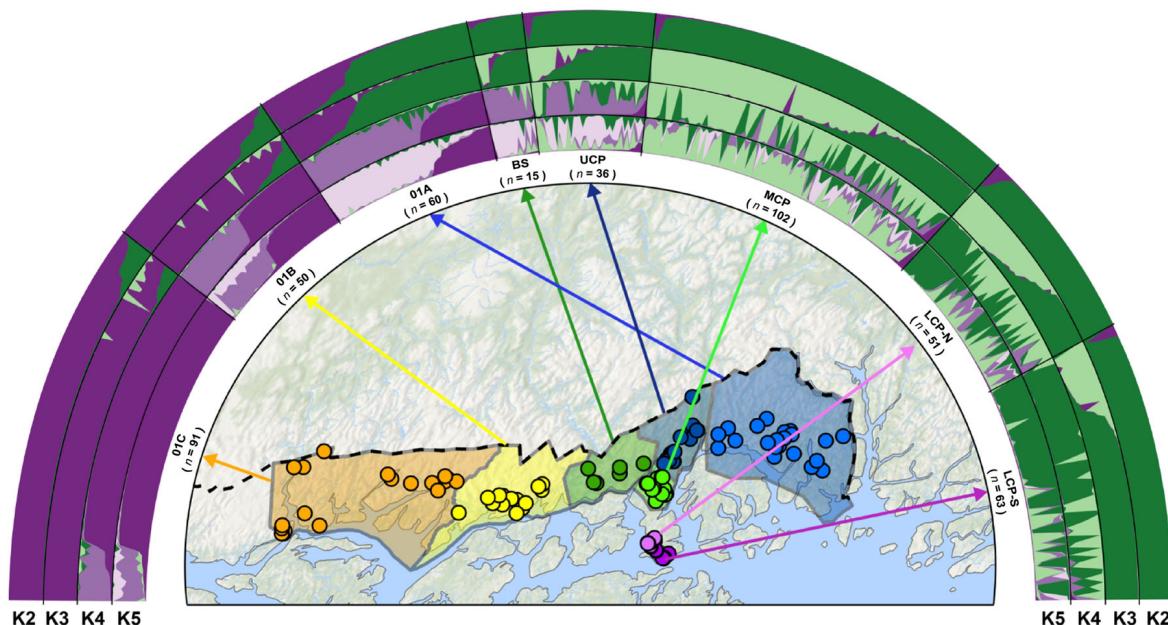


Figure 3. Results of STRUCTURE analysis showing mountain goat genetic subdivision at $K=2$ through 5, based on samples collected in southeastern Alaska, USA, 2005–2018. The map of population assignments denotes the geographic subdivisions considered, which include Lower Cleveland Peninsula North (LCP-N), Lower Cleveland Peninsula South (LCP-S), Middle Cleveland Peninsula (MCP), Upper Cleveland Peninsula (UCP), Bradfield-Stikine (BS), and Game Management Units (GMU; 01A, 01B 01C).

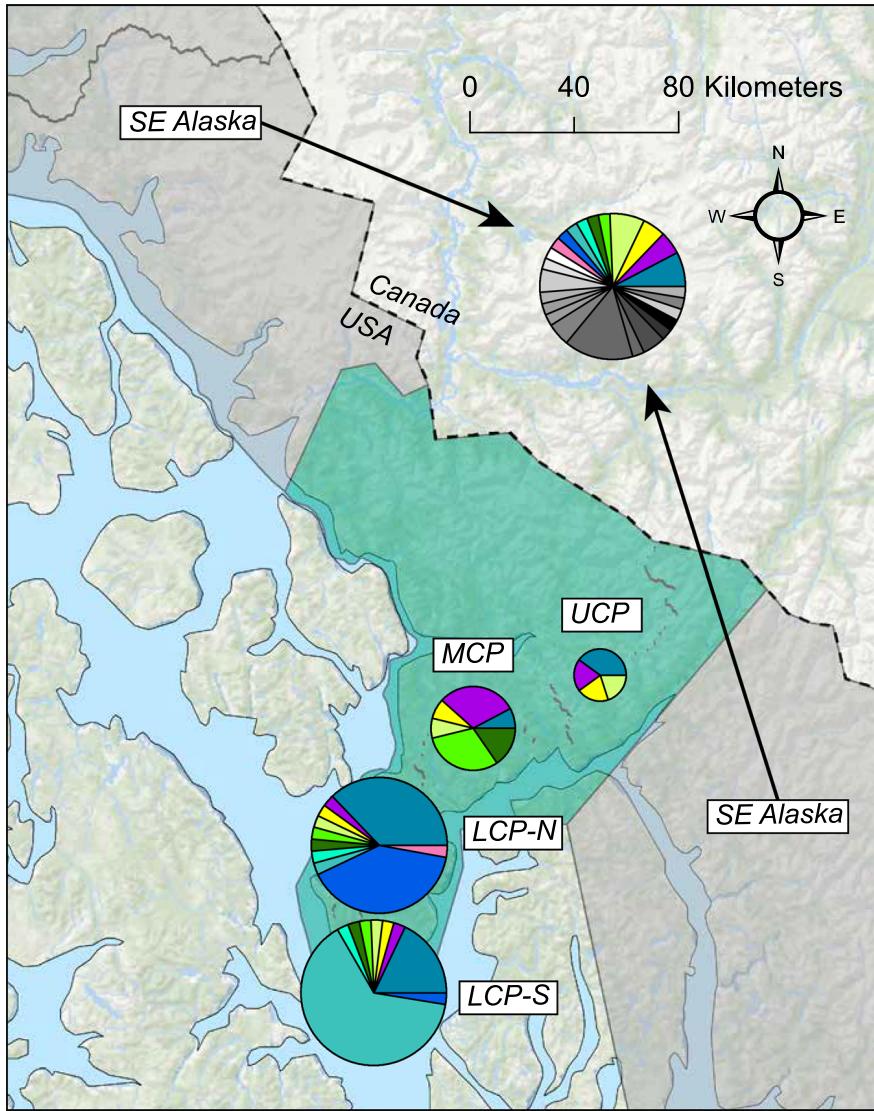


Figure 4. Haplotype distribution diagram for mountain goats in southeastern Alaska, USA, 2005–2018, illustrating the proportion of different mitochondrial haplotypes (i.e., color-coded pie charts) between the Cleveland Peninsula ($n=95$) and mainland areas ($n=38$). Haplotype pie charts are provided for geographic subdivisions on and near the Cleveland Peninsula including Lower Cleveland Peninsula North (LCP-N), Lower Cleveland Peninsula South (LCP-S), Middle Cleveland Peninsula (MCP), Upper Cleveland Peninsula (UCP), and the remainder of southeastern Alaska (SE Alaska).

convention describes that $F_{ST} < 0.05$ constitutes little genetic difference, $F_{ST} = 0.05\text{--}0.15$ as moderate genetic difference, $F_{ST} = 0.15\text{--}0.25$ as large genetic differentiation, and $F_{ST} > 0.25$ as significant genetic difference (Hartl and Clark 1997). Thus, the Cleveland Peninsula population can be considered moderately differentiated from the mainland, recognizing that F_{ST} is a relative measure of differentiation. We cannot, however, distinguish whether the population is recently isolated with no current gene flow (i.e., meaning signatures of N_m simply stem from recent common ancestry) or if the mountain goats on the Cleveland Peninsula have been isolated for a long time with periodic genetic interchange. The large proportion of individuals containing the unique Cleveland Peninsula mtDNA haplotypes combined with the propensity for both sexes to disperse (Shafer et al. 2011b), would support the latter, further supporting the demographic uniqueness of this population.

The N_e is a key population genetic parameter and can be defined as the theoretical number of individuals in an ideal population that would lose genetic variation at the same rate as the observed population (i.e., the census size [N_C]; Wright 1931). Interpreting this parameter, however, can be difficult because the approach used herein reflects the parental generation's N_e but can be influenced by changes further in the past (Waples 2005). Moreover, N_e estimates across a diverse suite of species typically fall into a narrow range (Gillespie 2004). Knowing this, linking N_e to N_C is desirable because it allows converting a genetic parameter to the number of individuals on the landscape; however, N_e/N_C ratios often span multiple orders of magnitude, leading to high uncertainty (Palstra and Fraser 2012). Ortego et al. (2011) reported the ratio of N_e/N_C between 0.4 and 0.6 in the mountain goat population found on Caw Ridge, Alberta, Canada. This seems reasonable for the lower Cleveland Peninsula given the N_e of <15 and recent

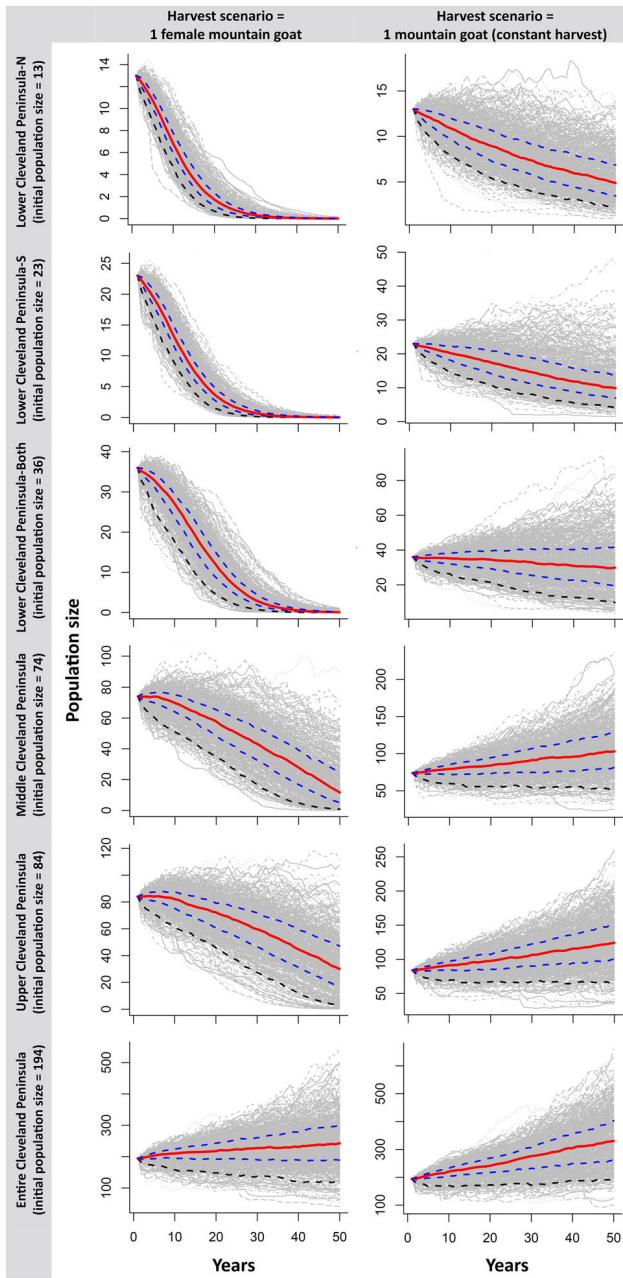


Figure 5. Mountain goat demographic responses to a simulated harvest of 1 female adult (left frames) or 1 mountain goat under the constant harvest treatment (right frames) for different genetically distinguished subpopulations on the Cleveland Peninsula, Alaska, USA, based on data collected 2005–2018. The grey lines denote the outcome of all simulations, and the red line denotes the mean response. The bottom set of panels (Entire Cleveland Peninsula) illustrates the simulated response for the entire Cleveland Peninsula, a null model scenario that assumes no population substructure. The set of panels labeled Lower Cleveland Peninsula-Both illustrate the simulated response if the Lower Cleveland Peninsula-North and Lower Cleveland Peninsula-South are combined, a scenario that assumes no substructure among that pair of subpopulations.

aerial survey estimates of 36 individuals. The N_e estimates for the mainland are clearly elevated, (Table 2), but direct conversions do not align with current N_C , likely because of a species-wide bottleneck (Marchenko et al. 2019) and lack of isolation (unlike the Cleveland Peninsula and Caw Ridge). In sum, these results clearly indicate reduced

diversity on the lower and upper Cleveland Peninsula, relative to the mainland, and likely result from a more recent bottleneck on the Cleveland Peninsula (Gillespie 2004).

The small effective population size and high inbreeding coefficient on the LCP is an indication of a lack of genetic variability and could lead to reduced fitness of individuals, an increased risk of inbreeding depression, and further reduction in population size if not managed accordingly (Armbuster and Reed 2005). Mountain goat habitat on the LCP is atypical (i.e., primarily subalpine), patchily distributed, and spatially limited (Smith and Raedeke 1982). Although current densities do not suggest strong nutritional limitation, it is unlikely that sufficient habitat and resources exist to accommodate substantially more individuals, especially given expected negative effects of recent clearcut logging of important low-elevation, forested winter range habitats (Smith and Raedeke 1982, Porter 2014). Previous research in this location indicated that habitat alteration and human disturbance associated with clearcut logging is likely to reduce inter-ridge movement of males and increase mortality leading to reproductive isolation and demographic instability of remaining groups (Smith and Raedeke 1982). Without gene flow from the mainland, it is reasonable to predict genetic diversity will continue to decrease if population numbers do not change. A low N_e combined with minimal interchange with the mainland likely equates to reduced adaptive potential, making the population more susceptible to environmental and demographic perturbations than their mainland counterparts.

Our population modeling simulations underscore the sensitivity of mountain goat populations to female harvest, a finding similar to previous analyses of the species (Hamel et al. 2006, Rice and Gay 2011). In contrast to the constant harvest treatment, female only harvest simulations resulted in substantially lower levels of sustainable harvest even though constant harvest simulations includes a modest proportion of female harvest. Such findings highlight the slow reproductive characteristics of mountain goat populations (late age of reproductive maturity, small litter size, occurrence of reproductive pauses; Festa-Bianchet and Cote 2008) and consequent relative importance of adult females for sustaining mountain goat population growth and viability, in comparison to other ungulate species. Because mountain goat sex is difficult to determine in field settings, in contrast to most cervids, hunting regulations typically permit either sex harvest; a situation that requires careful monitoring and assessment in light of our simulations, especially when considering small, isolated populations.

MANAGEMENT IMPLICATIONS

The small population size ($N_C=36$) of mountain goats on the LCP combined with evidence for geographic isolation, morphological differences, and genetic distinctiveness suggests continued harvest moratoria on the LCP is warranted. This conclusion is further supported by our harvest modeling simulations that explicitly indicate the LCP is unlikely to sustain harvest under either the conservative female only

or more liberal constant harvest scenarios. Further, only under the constant harvest scenario are populations >74 mountain goats able to be sustainably harvested. More broadly, our harvest modeling scenarios provide a critical real-world illustration of the importance of using population genetic data for delineating populations in the context of sustainable harvest. For example, if population genetic data were not considered and the entire Cleveland Peninsula was treated as 1 freely intermixing, panmictic population of an estimated N_C of 184 mountain goats, a harvest quota of 4–5 mountain goats could be implemented. Such an approach would ignore the discrete population structure of the 3 genetically differentiated populations (i.e., supported by the pattern of isolation by distance) and likely result in unsustainable harvest of the most accessible LCP population, which would lead to overharvest and subsequent population decline, especially if a high proportion of females were harvested. Because of the slow life-history strategy and relatively low reproduction, survival, and sustainable harvest rates of mountain goats, the consequences of overharvest can be significant and result in extended recovery times and long-term management challenges. Population genetic data can represent a key resource for delineating populations and, when integrated in a rigorous and quantitative harvest modeling framework, can significantly advance our ability to sustainably manage populations.

ACKNOWLEDGMENTS

We thank S. E. Haworth and J. F. Wolf for help with sequencing and the bottleneck analysis. R. R. Dorendorf and S. Woodruff provided useful feedback on this manuscript. J. Breen was supported by an EcoCanada Internship. M. Britt was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) undergraduate student research award. D. Martchenko was supported by an Ontario Graduate Scholarship. The project was supported by NSERC Discovery Grant, Canada Foundation for Innovation John R. Evans Leaders Fund, and Compute Canada grants to A. B. A. Shafer. Funding was also provided by the Alaska Department of Fish and Game through the Federal Aid in Wildlife Restoration Program (AKW-19-P6.0).

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Associate Editor: Zach Olson.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Supporting Information

02 November 2020

White, K. S., T. Levi, J. Breen, M. Britt, J. Meröndun, D. Martchenko, Y. N. Shakeri, B. Porter and A. B. A. Shafer. Integrating Genetic and Demographic Approaches to Facilitate Conservation of Small, Isolated Mountain Goat Populations. *Journal of Wildlife Management.*

Supplemental Text Document, S1. Simulating Constant Harvest

The intent of simulating constant harvest is to emulate change in sex-specific harvest as it relates to change in sex ratio, or availability of a given sex in the population. This can be an important way to simulate a real-world scenario that occurs when the availability of males in the population decreases (potentially because of higher initial harvest rates) and leads to higher harvest of females.

To simulate constant harvest, we first determined the proportion of the current harvestable population (not including kids or yearlings) that was male. Next, we used the proportion of males to determine the probability that a male is harvested using a selection parameter that indicates how much males are preferentially harvested over females.

The probability of male harvest (*phi.used*) as a function of proportion male (*Pm.used*) depends on selection coefficient (*Sm*) such that,

$$\textit{phi.used} = \textit{Pm.used} \times \textit{Sm} / (\textit{Pm.used} \times \textit{Sm} + (1 - \textit{Pm.used}) \times (1 - \textit{Sm}))$$

For example, if *Sm* = 1, then *phi.used* = 1 and constant harvest will always be male. If *Sm* = 0.5, then *phi.used* = *Pm*, meaning that the probability that a male is harvested equals the probability of encountering a male (proportion of males in the population). And, if *Sm* = 0, there is no chance a male is harvested regardless of proportion male.

We calibrated Sm based on empirical harvest data indicating that 72% of the harvest is male when 45.7% of the population is male.

$$phi_cal = 0.72 \text{ #proportion males in harvest for calibration (find } Sm)$$

$$Pm_cal = 0.457 \text{ #proportion males in population for calibration (find } Sm)$$

$$Sm = phi_cal \times (Pm_cal - 1) / (2 \times phi_cal \times Pm_cal - phi_cal - Pm_cal)$$

The probability of harvesting a male is then used to randomly harvest either a male or female. For example, 1 individual is randomly harvested out of an age class, where the probability of that age class being chosen is equal to the proportion of individuals in the age class.

Supplemental Text Document, S2. Estimating Initial Population Size

Aerial surveys.— We conducted population abundance and composition surveys using fixed-wing aircraft (Piper PA-18 Super Cub, Piper Aircraft, Vero Beach, FL, USA; Cessna 180, Cessna, Wichita, KS, USA) during August–October 2012–2016. We conducted aerial surveys when conditions met the following requirements: flight ceiling >1,524 m above sea level, wind speed <37 km/hour, and sea level temperature <18.8° C. We flew surveys at speeds 110–130 km/hour along established flight paths between 760 m and 1,060 m above sea level (i.e., alpine mountain goat summer range habitat) and followed a single geographic contour. We typically observed mountain goats from 500 m to 1,500 m away. The pilot and experienced observers enumerated and classified all mountain goats seen as either adults (includes adults and sub-adults) or kids. In addition, observers checked each mountain goat group to determine whether radio-collared animals were present.

Population estimation.—For the Lower Cleveland Peninsula (the only area with radio-collared mountain goats), we estimated population size by enumerating the number of radio-collared animals seen during surveys and comparing this value to the number of radio-collared animals present in the area surveyed. This approach enabled derivation of mark-resight population estimates using the Chapman (1954) estimator, a modified Lincoln-Peterson estimator with reduced bias for low sample sizes (Williams et al. 2001). For areas without radio-collared mountain goats, such as Middle and Upper Cleveland Peninsula, we combined aerial survey minimum counts with the average sighting probability derived from Lower Cleveland Peninsula mark-resight surveys to derive population estimates. The intent of these analyses was to derive biologically realistic initial population size estimates for use in subsequent population and harvest modeling simulations (Table S5–S7).

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Table S1. Microsatellite loci and pools used to genotype mountain goat samples collected during 2005–2018 in southeastern Alaska, USA. We used loci based on previous analyses described in Mainguy et al. (2005) and Poissant et al. (2009).

	Locus
Pool 1	MAF36
	TGLA122
	OARJMP58
	TGLA10
	ILSTS058
	RT9
Pool 2	BR3510
	MCM152
	ARO28
	OARCP26
	BM1225
	OARJMP29
Pool 3	OARHH62
	MAF64
	HUJ1177
	OARHH35
	RT27
	HUH616

Table S2. Mountain goat aerial survey minimum count and mark-resight population estimates, Lower Cleveland Peninsula, Alaska, USA, 2012–2014. We report the total number of animals seen during surveys (Minimum count), the proportion of radio-marked mountain goats seen (Prop. seen), associated population estimates, and 95% confidence intervals.

Year	Date	Minimum count			Mark-resight population estimate				
		Adults	Kids	Total seen	Number marked	Number resighted	Prop. seen	Estimate	CI
2012	25 Sep 2012	14	3	17	8	2	0.25	53	39
2012	2 Oct 2012	10	3	13	8	1	0.13	62	58
2013	2 Oct 2013	12	5	17	7	3	0.43	35	20
2013	8 Oct 2013	10	5	15	7	4	0.57	25	10
2013	17 Oct 2013	9	3	12	7	3	0.43	25	13
2014	4 Aug 2014	14	3	17	5	2	0.40	35	23

Table S3. Mountain goat aerial survey minimum count and estimated population sizes (with 95% CIs), Cleveland Peninsula, Alaska, USA, 2012–2016. We derived estimates based on the number of animals seen and the associated aerial survey sighting probability (p).

Area	Year	Date	Adult	Kids	Total	p	Estimate	CI
Lower Clev. Pen. - North ^a	2012	9/25/12	4	1	5	0.25	16	--
Lower Clev. Pen. - North ^a	2012	10/2/12	5	1	6	0.13	29	
Lower Clev. Pen. - North ^a	2013	10/2/13	4	5	9	0.43	18	
Lower Clev. Pen. - North ^a	2013	10/8/13	3	4	7	0.57	12	
Lower Clev. Pen. - North ^a	2013	10/17/13	0	0	0	0.43	0	
Lower Clev. Pen. - North ^a	2014	8/4/14	3	0	3	0.40	7	
\bar{x} ^a			3	2	5	0.36	13	
Lower Clev. Pen. - South ^a	2012	9/25/12	10	2	12	0.25	37	
Lower Clev. Pen. - South ^a	2012	10/2/12	5	2	7	0.13	33	
Lower Clev. Pen. - South ^a	2013	10/2/13	8	0	8	0.43	17	
Lower Clev. Pen. - South ^a	2013	10/8/13	7	1	8	0.57	13	
Lower Clev. Pen. - South ^a	2013	10/17/13	9	3	12	0.43	25	
Lower Clev. Pen. - South ^a	2014	8/4/14	11	3	14	0.40	28	
\bar{x} ^a			8	2	10	0.36	23	
Lower Clev. Pen. - Both ^b	2012	9/25/12	14	3	17	0.25	53	39
Lower Clev. Pen. - Both ^b	2012	10/2/12	10	3	13	0.13	62	58
Lower Clev. Pen. - Both ^b	2013	10/2/13	12	5	17	0.43	35	20
Lower Clev. Pen. - Both ^b	2013	10/8/13	10	5	15	0.57	25	10
Lower Clev. Pen. - Both ^b	2013	10/17/13	9	3	12	0.43	25	13
Lower Clev. Pen. - Both ^b	2014	8/4/14	14	3	17	0.40	35	23
\bar{x} ^a			12	4	15	0.36	36	23
Middle Clev. Pen. ^c	2014	8/5/14	18	7	25	0.36	58	
Middle Clev. Pen. ^c	2016	8/5/16	33	6	39	0.36	90	
\bar{x} ^a			26	7	32	0.36	74	
Upper Clev. Pen. ^c	2016	8/5/16	29	7	36	0.36	84	

^aEstimates for Lower Cleveland Peninsula North and South are based on mark-resight sighting probabilities for the combined area.

^bEstimates based on actual survey-specific mark-resight estimates.

^cEstimates based on average mark-resight sighting probability for the Lower Cleveland Peninsula.

Table S4. Multi-year average mountain goat aerial survey minimum count, estimated population sizes (with 95% CIs), and aerial survey sighting probability (p), Cleveland Peninsula, Alaska, USA, 2012–2016. We used these estimates to determine initial population sizes and simulate the effects of harvest using a population projection modeling approach and evaluate the effects of explicitly using genetic structure data to spatially define populations. Populations are Lower Cleveland Peninsula North (Lower Clev. Pen. - North), Lower Cleveland Peninsula South (Lower Clev. Pen. - South), Middle Cleveland Peninsula (Middle Clev. Pen.), Upper Cleveland Peninsula (Upper Clev. Pen.).

Area	Year	Adults	Kids	Total	p	Estimate	CI
Lower Clev. Pen. - North	2012–2014	3	2	5	0.36	13	
Lower Clev. Pen. - South	2012–2014	8	2	10	0.36	23	
Lower Clev. Pen. - Both	2012–2014	12	4	15	0.36	36	23
Middle Clev. Pen.	2014–2016	26	7	32	0.36	74	
Upper Clev. Pen.	2016	29	7	36	0.36	84	

Table S5. Diversity statistics between mountain goat tissue and non-invasive samples collected on the Lower Cleveland Peninsula, Alaska, USA, during 2005–2018. Average number of alleles per locus (\pm SE) and observed heterozygosity (\pm SE) is provided.

Population	Number of samples	Number of alleles	Observed heterozygosity
Tissue	13	2.444 ± 0.271	0.286 ± 0.065
Non-invasive	101	4.778 ± 0.461	0.245 ± 0.034

Table S6. Microsatellite (Microsats) pairwise genetic differentiation (F_{ST} ; lower matrix) and migration rate per generation (upper matrix) based on samples collected from mountain goats in southeastern Alaska, USA, during 2015–2018. Populations are Lower Cleveland Peninsula North (LCP-N), Lower Cleveland Peninsula South (LCP-S), Middle Cleveland Peninsula (MCP), Upper Cleveland Peninsula (UCP), Bradfield-Stikine (BS), and Game Management Units (GMUs) 01A, 01B, and 01C. Significant F_{ST} values are in bold. Mitochondrial genetic distances (p-distance) are shown in the lower panel and compared sequences from southeastern Alaska (SE-A).

Microsats	01A	01B	01C	B-S	LCP-N	LCP-S	MCP	UCP
01A	-	4.0	3.7	4.5	3.3	3.7	5.3	7.7
01B	0.059	-	8.5	3.6	2.3	2.4	3.2	3.6
01C	0.064	0.028	-	3.1	2.0	1.9	3.0	3.5
B-S	0.052	0.064	0.076	-	2.1	2.9	3.8	5.2
LCP-N	0.071	0.096	0.113	0.107	-	9.0	5.5	4.3
LCP-S	0.063	0.095	0.116	0.080	0.027	-	4.2	4.4
MCP	0.045	0.072	0.077	0.062	0.043	0.056	-	11.2
UCP	0.031	0.064	0.067	0.046	0.055	0.054	0.022	-

MtDNA	SE-A	LCP-S	LCP-N	MCP	UCP-
SE-A	-				
LCP-S	0.02	-			
LCP-N	0.02	0.005	-		
MCP	0.03	0.03	0.03	-	
UCP	0.03	0.03	0.009	0.03	-

Table S7. Pairwise genetic differentiation (F_{ST} ; lower matrix) and migration rate per generation (upper matrix) based on samples collected from mountain goats in southeastern Alaska, USA, during 20015–2018. Values are reported for subpopulations on the Cleveland Peninsula: Lower Cleveland Peninsula North (LCP-N), Lower Cleveland Peninsula South (LCP-S), Middle Cleveland Peninsula (MCP), Upper Cleveland Peninsula (UCP), and Bradfield-Stikine (B-S).

Area	B-S	UCP	MCP	LCP-N	LCP-S
B-S	-	5.2	3.8	2.1	2.9
UCP	0.046	-	11.2	4.3	4.4
MCP	0.062	0.022	-	5.5	4.2
LCP-N	0.107	0.055	0.043	-	9.0
LCP-S	0.080	0.054	0.056	0.027	-

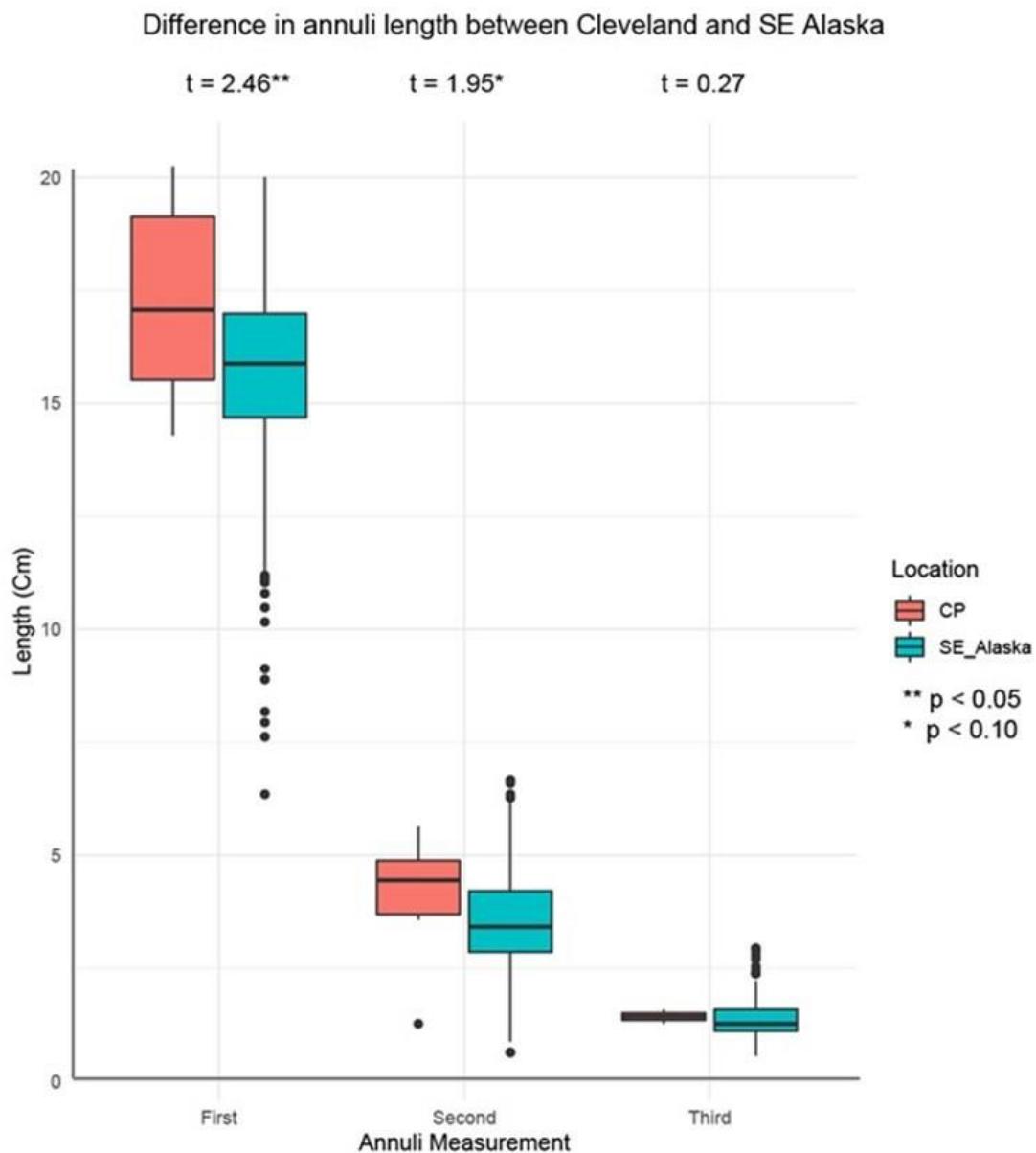


Figure S1. Comparison of horn annuli length between mountain goats inhabiting the Lower Cleveland Peninsula (CP) and the remainder of southeastern Alaska, USA (SE Alaska) based on measurements collected during 2005–2018. We performed Student's t -tests on each annuli length to assess differentiation; asterisks denote statistical significance.

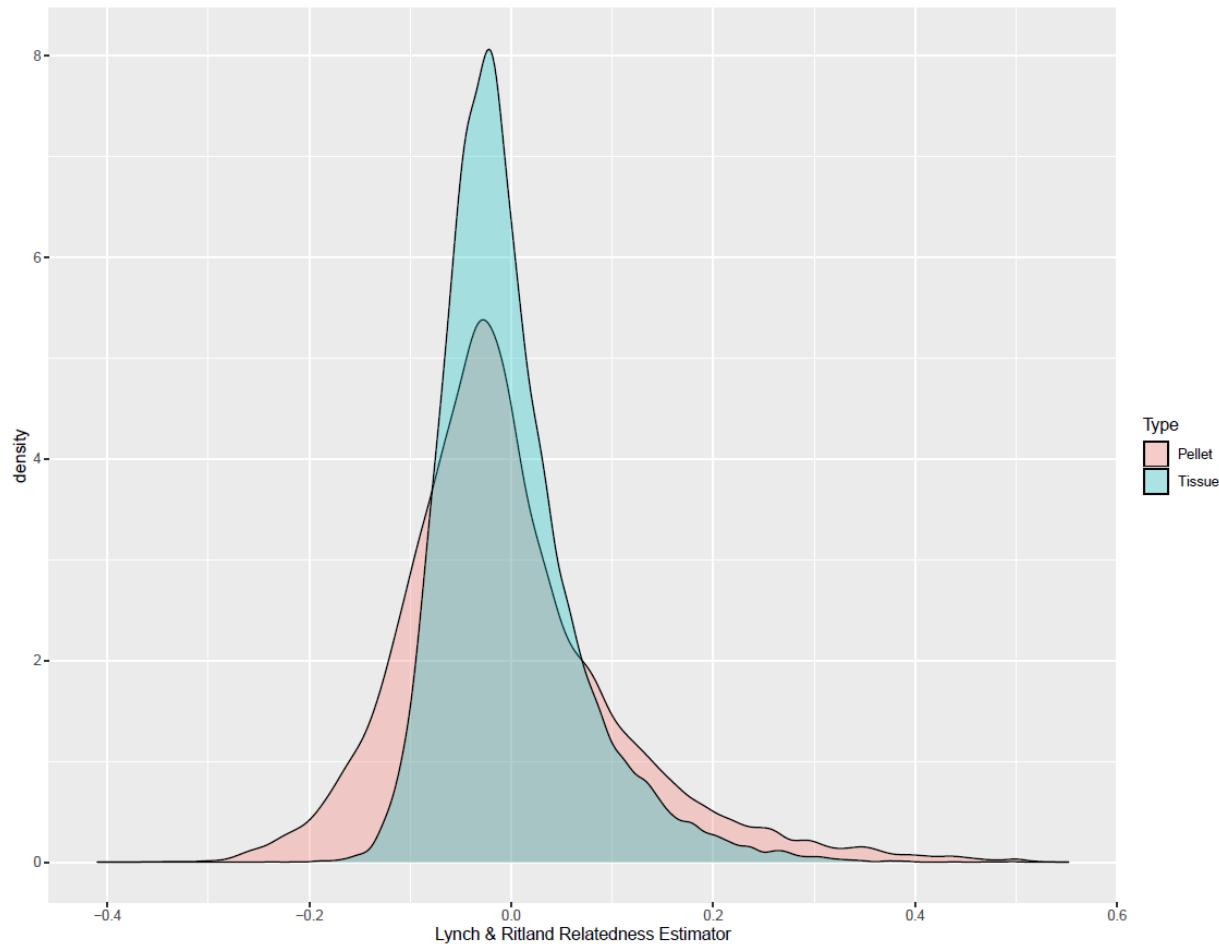
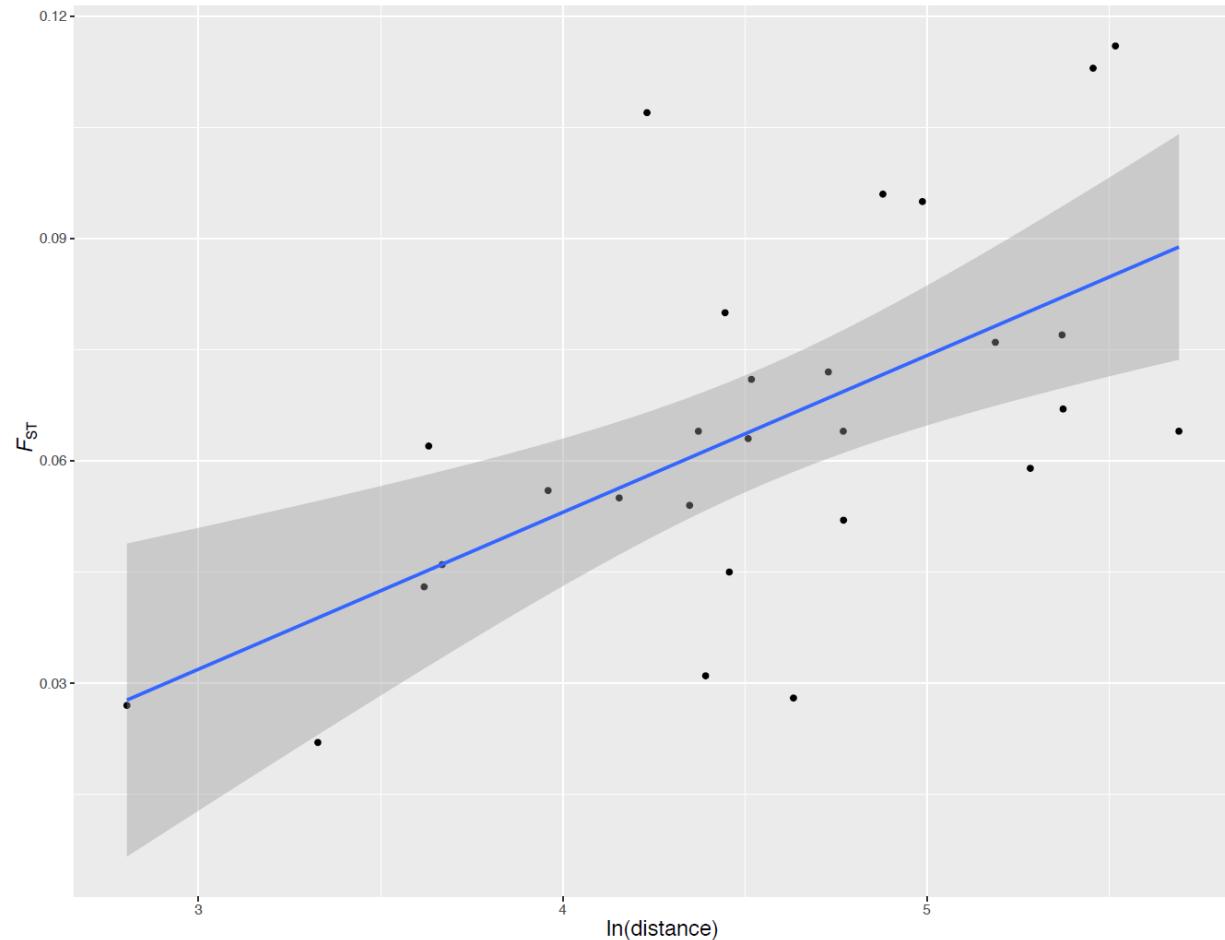


Figure S2. Comparison of the distribution of relatedness values (Lynch and Ritland relatedness estimator) between tissue and fecal pellet samples collected from mountain goats during 2005–2018 on the Cleveland Peninsula and surrounding areas in southeastern Alaska, USA.



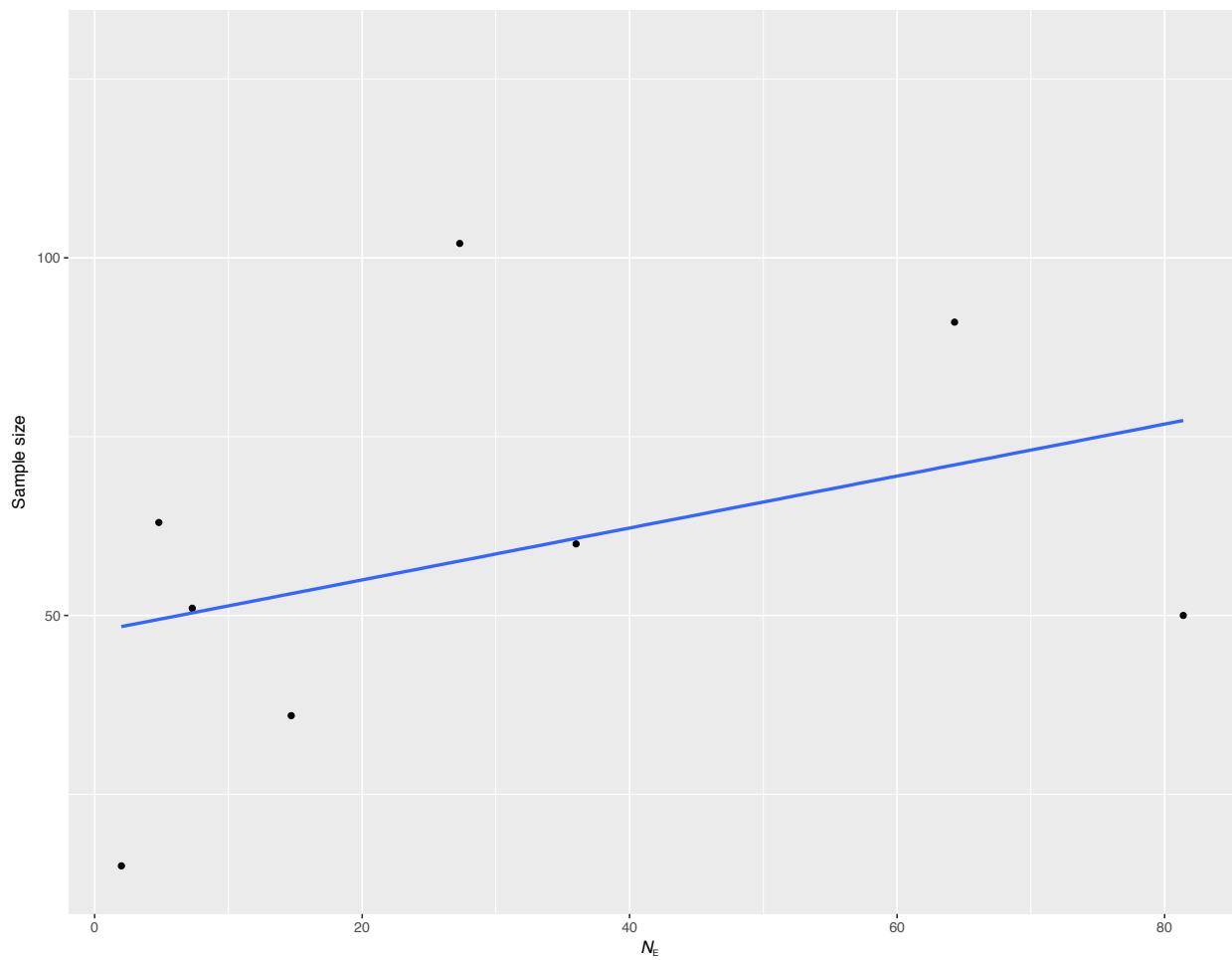


Figure S4. Relationship between sample size and the lowest N_E estimate (effective population size) for mountain goat subpopulations sampled in southeastern Alaska, USA, during 2005–2018.

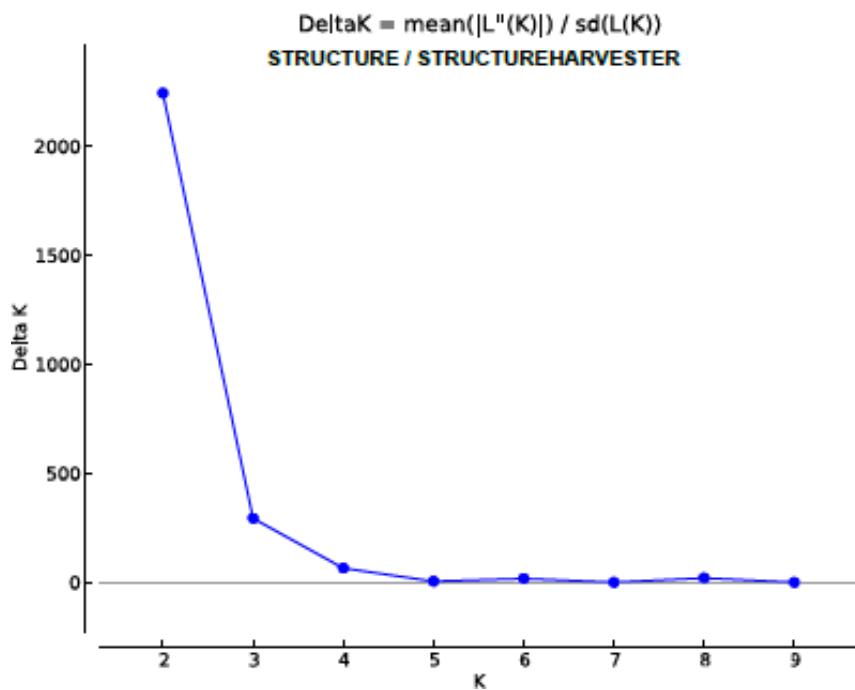
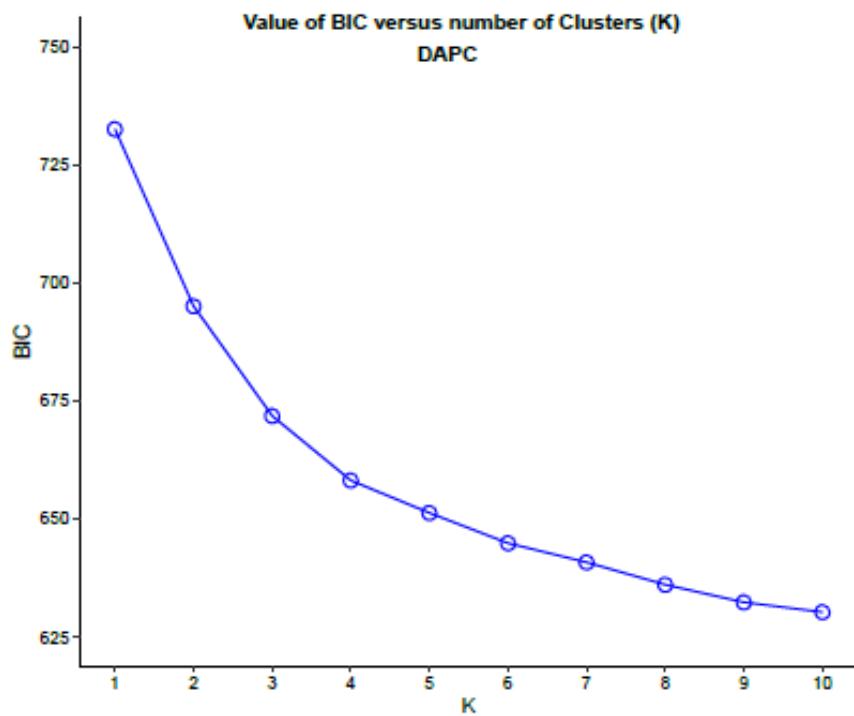


Figure S5. Relationship between BIC (Bayesian Information Criterion) values for different K values (the number of genetic clusters) determined by DAPC (Discriminat Analysis of Principal Components; top), and delta K values from the STRUCTURE analysis (bottom). We evaluated K values to characterize population structure of mountain goats in southeastern Alaska, USA, during 2005–2018.

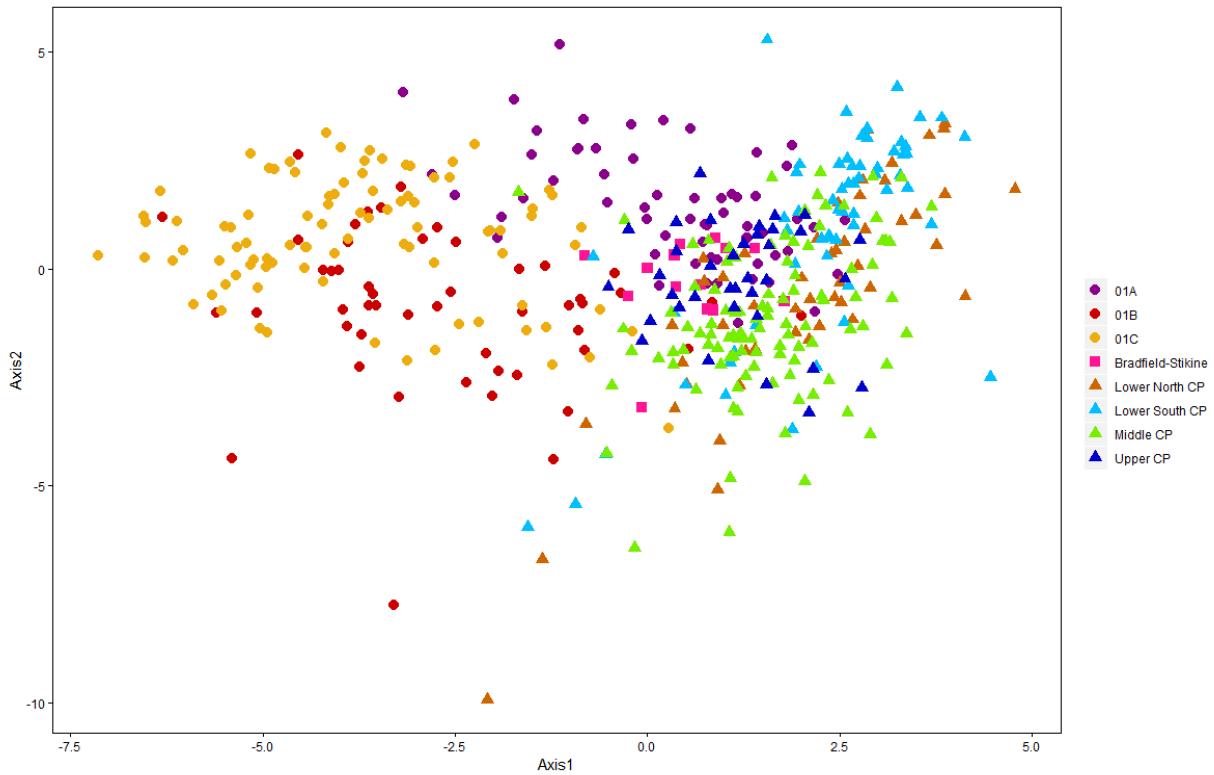


Figure S6. Principal Components Analysis plot illustrating structure of mountain goat subpopulations based on data collected in southeastern Alaska, USA, during 2005–2018. Population assignments denote the geographic subdivisions considered, which include Lower Cleveland Peninsula North (Lower North CP), Lower Cleveland Peninsula South (Lower South CP), Middle Cleveland Peninsula (Middle CP), Upper Cleveland Peninsula (Upper CP), Bradfield-Stikine, and Game Management Units (GMU; 01A, 01B 01C).

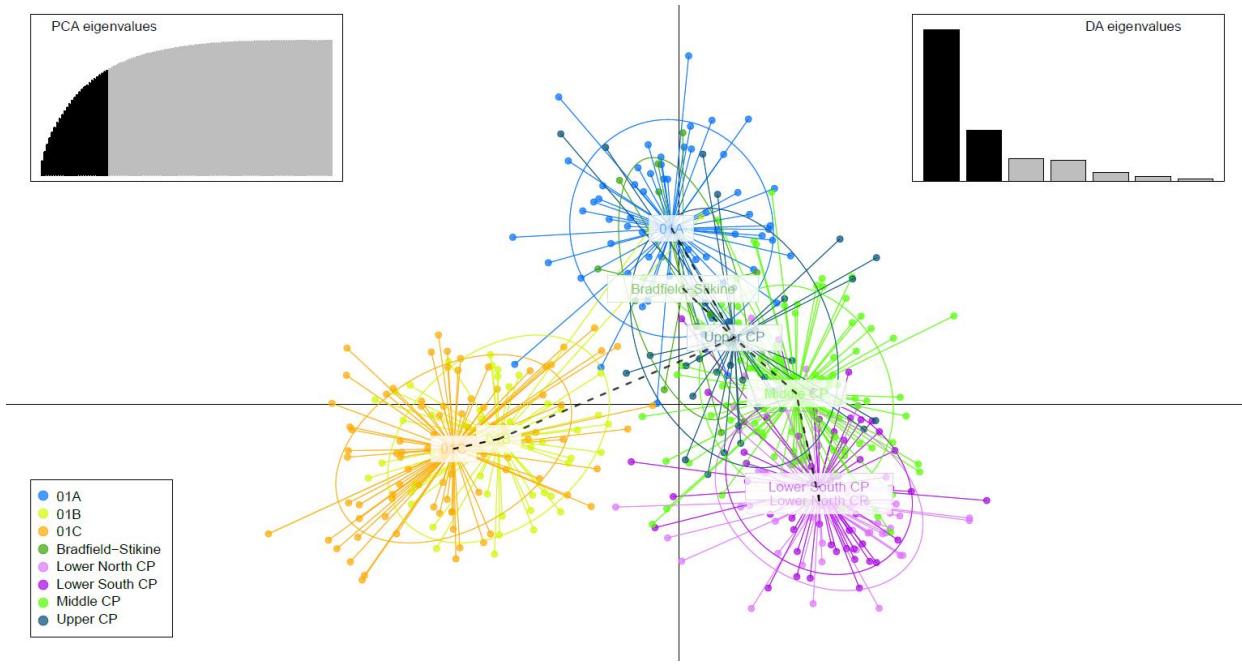


Figure S7. DAPC (Discriminant Analysis of Principal Components), PCA (Principal Components Analysis) and DA (Discriminant Analysis) eigenvalue plots illustrating structure of mountain goat subpopulations based on data collected in southeastern Alaska, USA, during 2005–2018. Population assignments denote the geographic subdivisions considered, which include Lower Cleveland Peninsula North (Lower North CP), Lower Cleveland Peninsula South (Lower South CP), Middle Cleveland Peninsula (Middle CP), Upper Cleveland Peninsula (Upper CP), Bradfield-Stikine, and Game Management Units (GMU; 01A, 01B 01C).