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POPULATION GENETIC STRUCTURE OF AMERICAN BLACK BEARS (*URSUS AMERICANUS*) IN NOVA SCOTIA, CANADA

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ABSTRACT

The population genetic structure of American Black Bears (*Ursus americanus*) in the Maritimes Provinces, Canada, with an emphasis on Nova Scotia, was examined. The study used hunter-sourced tooth samples from across Nova Scotia, as well as samples from New Brunswick. Allelic variation was examined for a suite of 15 microsatellite markers. Population structure was assessed using a Bayesian clustering method (STRUCTURE) and by conducting an isolation by distance (IBD) test. Three weakly differentiated genetic subpopulations were found with their general geographic locations being New Brunswick, Northeastern Nova Scotia, and Southwestern Nova Scotia. The New Brunswick subpopulation had higher measures of genetic diversity as well as effective population size relative to both subpopulations in Nova Scotia, but in particular compared to the Southwestern Nova Scotia subpopulation. The Shubenacadie Canal system, primarily comprised of the Shubenacadie River and Shubenacadie Grand Lake, is the geological feature separating the two subpopulations of Black Bears found in Nova Scotia.

Keywords: Black Bears, gene flow, microsatellites, genetic diversity, inbreeding

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INTRODUCTION

Approximately one quarter of all assessed mammalian species are listed by the International Union for the Conservation of Nature as Vulnerable, Endangered or Critically Endangered (IUCN 2025). The principal threat to these species is anthropogenic impacts to landscapes (Baillie *et al.* 2004). These include habitat loss and habitat fragmentation, which often act synergistically (Segan *et al.* 2016). Because of these anthropogenic factors, populations of impacted species may lose allelic diversity, exhibit decreased levels of genetic heterozygosity and experience reduced gene flow and more inbreeding (Turnock *et al.* 2024). This reduction in genetic diversity and associated deleterious effects on population genetic structure has been called "genomic erosion" (e.g., Pinto *et al.* 2024). Large terrestrial carnivores are at particular risk of anthropogenic land impacts due to their extensive area requirements (Shafer *et al.* 2015). American black bears (*Ursus americanus*) are no exception to this trend, having lost nearly half of their range in the last century, largely due to habitat loss and fragmentation, and, to a lesser extent, over-exploitation (Pelton *et al.* 1999). Black bear populations in the more northern portions of their range exist in relatively undisturbed continuous habitats (Pelletier *et al.* 2012, Sawaya *et al.* 2014), whereas populations in the southern part of their range exist in highly fragmented landscapes (Dixon *et al.* 2007, Draper *et al.* 2017).

No large-scale studies have investigated the relative threats to black bears associated with anthropogenic impacts on habitats in Nova Scotia, Canada. Although the province is estimated to have ~75% forest coverage at present, a history of intensive forestry practices has led to heavily altered forest compositions and much of the province is managed for timber (Nova Scotia Department of Natural Resources Renewable Resources Branch 2017). According to Statistics Canada, Nova Scotia has experienced roughly a doubling of its human population in the last century. In addition to these anthropogenic factors acting within the province, the nearly insular nature of Nova Scotia may naturally hamper black bear movement and gene flow over a larger geographic scale. The narrow land bridge, the Isthmus of Chignecto, connecting the province to the rest of North America has been identified as a partial barrier to some mammalian species (e.g. moose, *Alces alces americana*, Scott *et al.* 2023, Scott and Hebda 2004, Beazley

et al. 2006), but not to others (e.g. coyotes, *Canis latrans* var, Power *et al.* 2015). Anthropogenic impacts including construction of highways, railways, wind turbines, communication towers, and agriculture and forestry activity have likely further reduced the ability of various mammals to move through this region (Nussey and Noseworthy 2018, Needham *et al.* 2020). It is not known how this geographic feature affects black bear movement.

Given the threats faced by many species, monitoring local populations to evaluate their viability using population genetic markers is important for wildlife management (Allendorf 2017). Particularly useful is the assessment of population genetic structure of a species in areas of interest (e.g. Pelletier *et al.* 2017, Wang *et al.* 2017). Such assessments involve using information gathered on the regional genetic composition of a species to distinguish patterns of genetic similarity and dissimilarity on a geographical scale. These assessments, consequently, allow the delineation of genetic subpopulation groupings, and with it the ability to identify gene flow patterns, and to estimate measures of genetic diversity. Accordingly, the objective of this study is to conduct a spatial population genetic analysis of black bears in Nova Scotia using tissue samples derived largely from hunter- and trapper-sourced black bears from across the province. Samples from New Brunswick were also obtained for comparative purposes. Ultimately, information gathered from this study will be useful to wildlife agencies to aid in making management decisions, with consideration for this species' regional conservation needs.

METHODS

Sample Collection and Processing

Black bear samples from Nova Scotia were supplied by the Nova Scotia Department of Natural Resources (formerly known as either the Department of Natural Resources and Renewables or the Nova Scotia Department of Lands and Forestry) from material obtained from hunters and trappers in 2017. Samples from New Brunswick, which originated from legally harvested, road killed, or euthanized nuisance black bears from 2017 and 2018, were supplied by the New Brunswick Department of Energy and Resource Development. Nova Scotia (NS) County of origin or New Brunswick (NB) Wildlife Management Zone (NB) included in the metadata for each sample. All samples provided

by these government agencies consisted of teeth. Because samples had already been collected by government agencies for other purposes, an animal care protocol was not required as per Canadian Council on Animal Care policies (Canadian Council on Animal Care 2020).

DNA was isolated from dried epithelial tissue scraped off teeth onto a fresh piece of wax paper using a sterile scalpel. Multiple scalpels were used in rotation; between samples, scalpels were soaked in 10% bleach for a minimum of 60 min, dipped in 100% ethanol, rinsed with distilled water, and sterilized over a flame. Dried tissue transferred to a 1.5 ml microcentrifuge tube and stored at -40°C. DNA was extracted using a DNeasy 96 Blood and Tissue Kit or a standard DNeasy Blood and Tissue Kit (Qiagen) following the manufacturer's recommended protocols, with the exception that samples were incubated in the proteinase K solution for 72 hrs to digest. Samples were vortexed once every 24 hrs, and any tissue samples that were not fully digested had an additional 10 µl of Proteinase K solution added and were incubated at 57°C for an additional 24 hrs.

Polymerase Chain Reactions (PCRs) and microsatellite genotyping were conducted in the Natural Resources Wildlife DNA Profiling and Forensic Centre at Trent University. Primers for a suite of 15 microsatellites (G10C, G1A, G10B, G1D, G10L, MU05, G10H, MU50, G10P, G10U, MU59, G10M, MSUT6, G10J, G10X) were used to amplify DNA in two sets of pooled multiplexed PCRs as per Crompton *et al.* (2008) which also provides original references for these primers. Additionally, primers SE47 and SE48 were used to determine sex (Yamamoto *et al.* 2002). PCR products were genotyped using a 48-capillary ABI 3730 DNA analyzer.

Data Analysis

To identify microsatellite loci with a high frequency of null alleles (i.e., microsatellite alleles that do not PCR-amplify to a detectable level), the data set was visually inspected for loci with a high level of homozygosity as well as low amplification success. Additionally, the program Cervus was used to estimate the frequency of null alleles for each locus (Kalinowski *et al.* 2007). Cervus was also used to estimate polymorphic information content (PIC) for each locus. PIC, which can range from 0 to 1, measures how variable, and therefore how useful, a microsatellite locus is for population genetic studies (Roy *et al.* 2023). Last, Cervus was used to estimate the probability of identity (PID),

which is the average probability a genotype at a given locus is identical between two unrelated individuals, as well as the more conservative PIDsib, which is the average probability that a genotype at a given locus is identical between full siblings.

Several assessments of black bear population structure were conducted. These consisted of testing for Hardy-Weinberg equilibrium (HWE) within the entire data set as well as within Nova Scotia and New Brunswick separately; using a Bayesian clustering method to detect population genetic structure by grouping individuals in a way that maximizes agreement with Hardy-Weinberg expectations; and conducting an isolation by distance (IBD) test to assess the effect of geographic distance on genetic differentiation across Nova Scotia as well as across Nova Scotia and New Brunswick. Details of each of these analyses are provided below.

The Hardy Weinberg Exact Test from Genepop v. 4.2 (Rousset 2008) was used to estimate HWE within the entire data set, as well as within Nova Scotia and New Brunswick, respectively, using the Probability Test sub-option. Default settings were used for the Markov Chain parameters to estimate an unbiased p-value for the HWE test using the Fisher Method (Guo and Thompson 1992).

The Bayesian clustering program STRUCTURE 2.3.4 (Pritchard *et al.* 2000) was used to detect genetic sub-structuring within the microsatellite data set. The STRUCTURE program was run assuming admixture with a Burnin Period Length of 100 000 and 100 000 Markov Chain Monte Carlo (MCMC) repetitions for values of K=1 to 10 with 10 iterations and the Allele Frequencies Correlated Model option was selected as well. Two related methods were used to determine the most likely number (K) of genetic subpopulations within the data set. The first method assessed when Ln P(D), i.e., the log of the posterior probability of the data, began to stabilize for each value of K (Pritchard *et al.* 2010). The second method, which assesses the rate of change in the log of the posterior probability of the data between successive K values (Evanno *et al.* 2005), was implemented through the Structure Harvester web interface (Earl 2012).

Once the most probable K value was determined, the 10 iterations of those runs were uploaded onto the CLUMPAK web interface (Kopelman *et al.* 2015) to create a single standardized result set. This set was then imported into R (R Core Team 2017) in which the final q matrix (where q is the probability of an individual belonging to a given

genetic subpopulation) was constructed using ggplot2 (Wickham 2016). The ggplot2 package was then used to create a plot of county- and WMZ-level proportions of the likelihood of genetic subpopulations on a geographical map of Nova Scotia and New Brunswick. Individuals were assigned to their most probable K population as in Pelletier *et al.* (2012). Following their methodology, various values of q threshold (i.e., the threshold of probability to assign an individual to a K population) were assessed. The ideal q threshold was chosen with the goal of: (1) weighing the number of individuals that were unable to be assigned to any of the K populations because their q values for each K population were below the q threshold, and (2) maintaining accurate assignment likelihoods, such that the general pattern of K assignment does not change from the original pattern. Values for q of 0.9, 0.8, 0.7, and 0.6 were evaluated. The number of individuals unassigned at each assignment threshold was counted. Plots of q values at each threshold were constructed to assess whether there were any major deviations in K patterning at the various threshold values. Additionally, Chi-squared tests were performed to test for significant changes in proportions of K assignment among the different threshold values. When the appropriate threshold was chosen, a geographical plot was created using ggplot2 to depict the genetic subpopulations on an individual level. Upon completion of the ggplot2 analysis, it was determined that Halifax County was a meeting area of two genetic subpopulations. Because of this, in cases for which more detailed geographic information was available, precise coordinates were used to map individual black bears in Halifax County to further clarify genetic patterning in this region.

Finally, the program Adegenet in R was used to investigate Isolation-by-Distance (IBD) using a Mantel test with 999 Monte-Carlo repetitions. The genetic distance matrices were calculated using pairwise Euclidean genetic distance. Geographic matrices consisted of pairwise linear geographic distances. This was performed at the county level for both mainland Nova Scotia, as well as for mainland Nova Scotia and New Brunswick.

The program FSTAT v. 2.3.9 (Goudet 1995) was used to estimate F_{ST} values between pairs of genetic subpopulations as identified by STRUCTURE. Significance of these values was tested by comparing observed values to values obtained by randomizing alleles throughout the data set mimicking panmixia using 1000 permutations. A Bonferroni

correction was then applied to these tests to account for conducting multiple statistical tests.

For each genetic subpopulation as identified by STRUCTURE, the program GenAIEx v. 6.5 (Peakall and Smouse 2012) was used to calculate the observed (H_O) and expected heterozygosity (H_E) under HWE. Whether H_O and H_E differed significantly was tested in GENEPOP with the Hardy Weinberg Exact Test using the same settings as listed above. FSTAT was used to estimate inbreeding coefficients (F_{IS}), allelic diversity (N_A), and allelic richness (A_R) (Peakall and Smouse 2012). One-sample T-tests were used in R to test if F_{IS} values significantly differed from zero, and a one-way ANOVA and Tukey test were implemented to test if F_{IS} values were significantly different between subpopulations.

Another important and commonly used population-level assessment that was carried out for each genetic subpopulation was estimating its effective population size, N_e, which is useful for predicting the rate of loss of genetic variation in a population (e.g. Pinto *et al.* 2024). N_e was estimated using the program NeEstimator v. 2 (Do *et al.* 2014). The Linkage Disequilibrium-Model with random mating was used as this has been found to be the most robust method when detailed demographic data are unknown (Gilbert and Whitlock 2015). The lowest threshold for allele frequency (P_{CRIT}) used was 0.02 to screen out rare alleles, with confidence intervals calculated using the JackKnife 95% option as per Waples and Do (2008).

RESULTS

Overview of Distribution of Samples

A total of 309 individuals was analyzed for this study; 213 from Nova Scotia and 96 from New Brunswick (Table 1). More samples were collected and processed, however, several degraded samples that had no or five or fewer loci successfully amplify were removed from further analysis. Each of the samples included had at least six loci amplify and the majority (83%) of samples were genotyped for all 14 loci. Due to relatively few specimens from Southwestern Nova Scotia, samples from Yarmouth, Digby, and Shelburne counties were pooled together under 'South Shore.' Similarly, samples from Inverness, Cape Breton, and Victoria counties from Cape Breton Island, Nova Scotia, were pooled together under 'Cape Breton'.

Table 1 **The number of individuals (n) analyzed per location from Nova Scotia counties and New Brunswick Wildlife Management Zones (WMZ); total number analyzed=309.**

Region	Total analyzed	Region	Total analyzed
Nova Scotia	**n**	**New Brunswick**	
Annapolis	13	WMZ7	15
Antigonish	4	WMZ8	15
Cape Breton	1	WMZ9	1
Colchester	25	WMZ11	1
Cumberland	30	WMZ12	30
Digby	6	WMZ13	6
Guysborough	17	WMZ14	10
Halifax	24	WMZ16	4
Hants	15	WMZ17	3
Inverness	2	WMZ18	1
Kings	18	WMZ19	5
Lunenburg	7	WMZ23	1
Pictou	31	WMZ25	4
Queens	10		
Shelburne	1		
Victoria	4		
Yarmouth	5		
SUBTOTAL	**213**	**SUBTOTAL**	**96**

Table 2 **Frequency of null alleles (F(Null)) and polymorphic information content (PIC) of each locus as estimated through Cervus.**

Locus	F(Null)	PIC
G10C	0.052	0.741
G10B	0.050	0.585
G10H	0.048	0.840
G10L	0.028	0.827
MU05	0.034	0.653
G1A	0.039	0.644
G1D	0.027	0.761
G10J	0.057	0.755
G10U	0.067	0.635
MSUT6	0.082	0.635
G10M	0.014	0.778
MU59	0.017	0.720
G10P	0.594	0.828
MU50	0.053	0.837
G10X	0.034	0.866

Upon visual inspection of the data set, locus G10P exhibited high rates of homozygosity as well as relatively low genotyping success. G10P had a considerably larger estimated frequency of null alleles compared to the other loci (Table 2). Because of this, G10P was removed from subsequent analyses. All remaining 13 loci had a mean polymorphic information content (PIC) of 0.740 (Table 2). Genotypes between individual samples had a low probability of being identical ($PID=1.442x10^{-17}$; $PIDsib=5.700x10^{-7}$).

Assessment of Hardy-Weinberg Equilibrium

A significant departure from Hardy-Weinberg equilibrium (HWE) expected genotype frequencies was found for the Nova Scotia samples ($p=3.480x10^{-13}$), as well as for the entire data set ($p=4.990x10^{-11}$). No significant departure from HWE expectations was found for the New Brunswick samples alone (p=0.181).

Bayesian Clustering, Isolation by Distance, and Genetic Differentiation as Assessed by F_{ST}

A plot of Ln P(D) values over runs of K=1 to 10 showed leveling out of the curve at K=3 (Fig 1). Additionally, K=3 had the largest delta K value using the Evanno method (Fig 2), consistent with three genetic

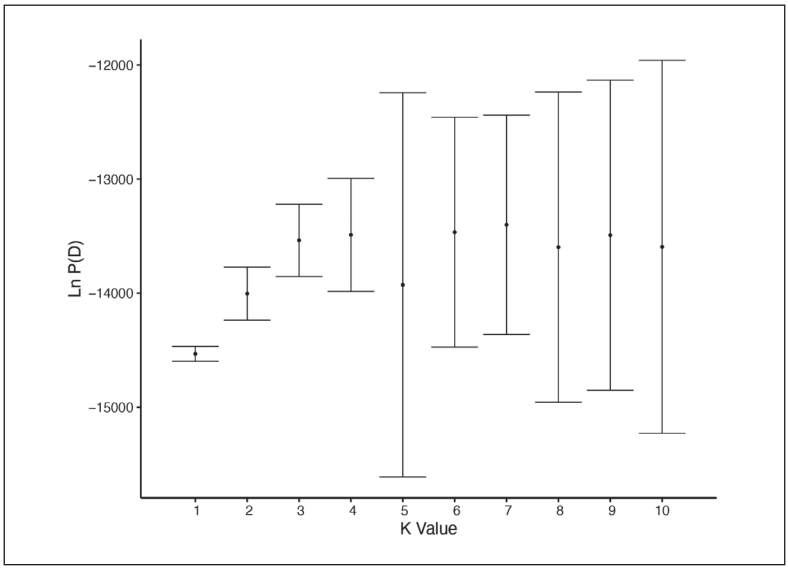


Fig 1 **Average Ln P(D) over values of *K*=1-10. Error bars are variances as calculated through STRUCTURE.**

subpopulations in the data set. When the qplot was examined for the data set at K=3, a large proportion of individuals showed strong assignment likelihoods (Fig 3). The three genetic subpopulations among these samples were New Brunswick, Northeastern Nova Scotia (NENS), and Southwestern Nova Scotia (SWNS) (Fig 4). The haplotype composition of the Cape Breton samples was also seemingly distinct from the adjacent mainland. Unfortunately, only a total of seven samples from across three counties - Inverness, Cape Breton and Victoria – were available for analysis.

When assigning individuals to genetic subpopulations at a threshold of q=0.9, 70 individuals could not be confidently assigned to any genetic subpopulation with this high degree probability. At q=0.8, 42 individuals were excluded. At q=0.7, 26 individuals were excluded, and at q=0.6, 16 individuals were excluded. When q plots for these different thresholds were compared, patterns of K assignment are similar (Fig 5).

No significant changes in K proportions were found among the different thresholds (K1.: X^2=0.098, df=6, p=1; K2: X^2=0.098, df=6, p=1; K3: X^2=0.099, df=6, p=1). Because there were no significant differences in assignment patterning or proportions of each K subpopulation, q=0.6 was chosen to represent this sample set (Fig 6).

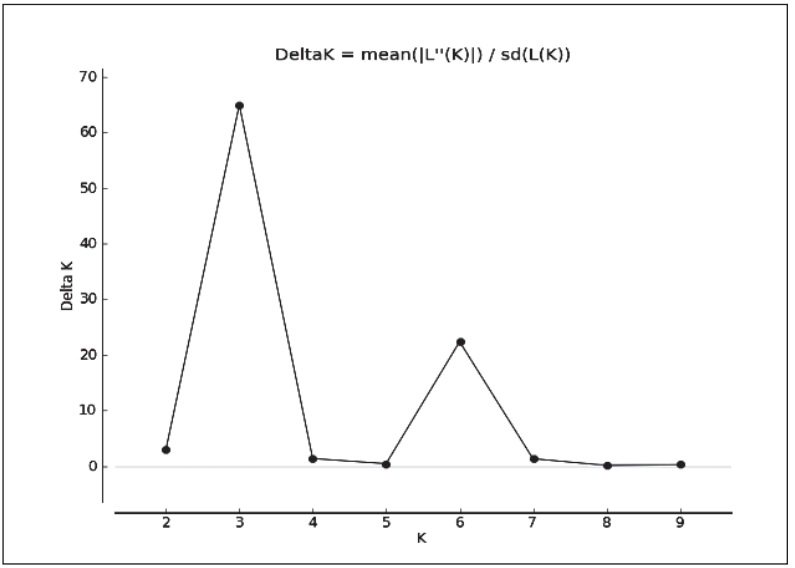


Fig 2 Probability of number of distinct subpopulations (K value) from 1-10 as calculated by the Evanno method with highest delta K at K=3.

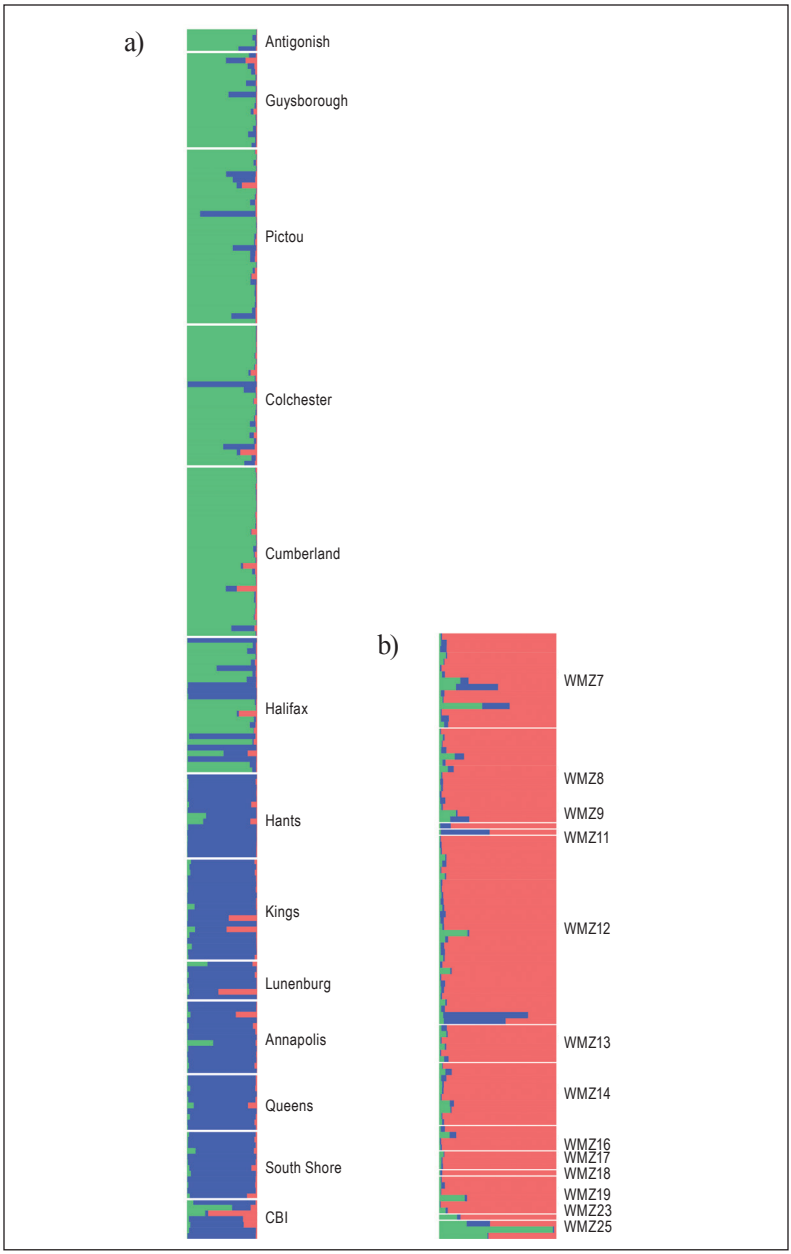


Fig 3 **Final qplot for all 309 samples for *K*=3; each individual is on the inverted x-axis and their relative likelihoods of belonging to each *K* is depicted with red, green, and blue. Pane a) shows results for Nova Scotia. Pane b) shows results for New Brunswick.**

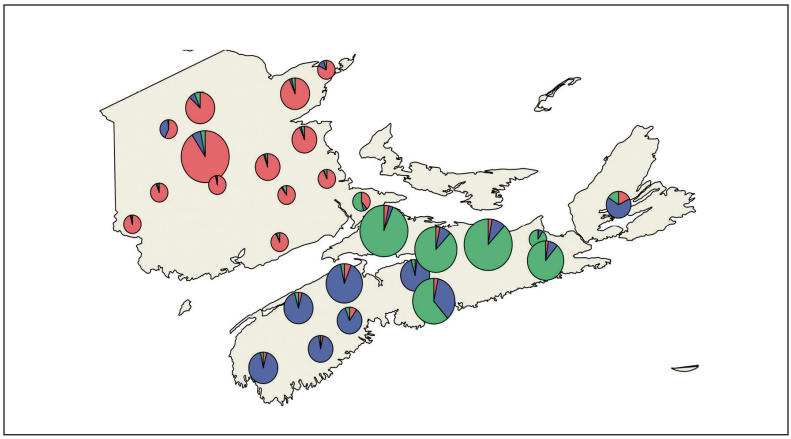


Fig 4 **Geographical map of the Maritimes showing the pie charts of the relative proportion of probable *K* population for individuals within a region (county/WMZ). Pie chart size is proportional to the number of samples from that region.**

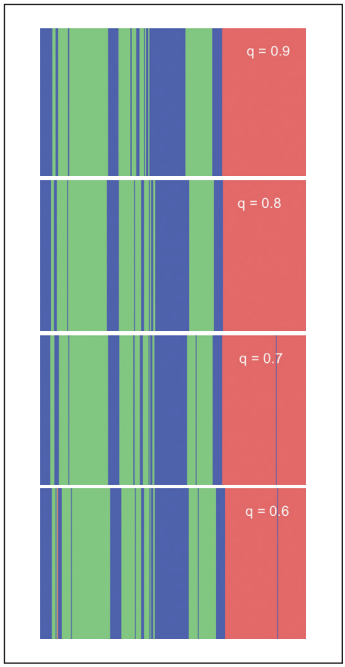


Fig 5 **Pattern of *K* assignment for individuals (x-axis) at various assignment thresholds (q=0.9, 0.8, 0.7, and 0.6). The general pattern of assignments is consistent across all threshold values as well as the proportion of individuals assigned per subpopulation for each *K* value.**

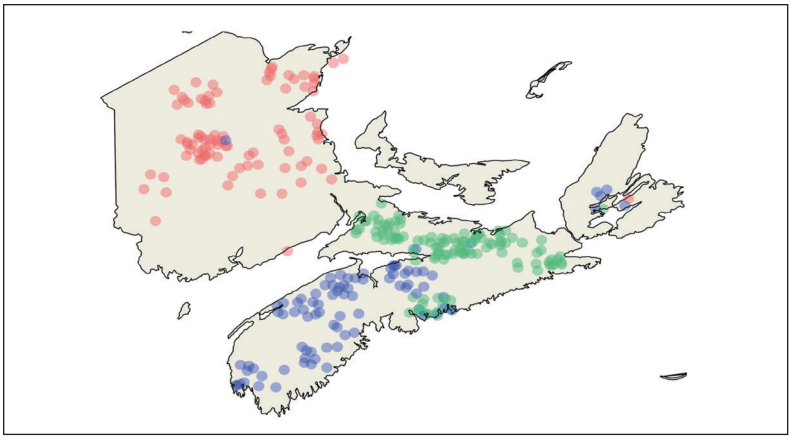


Fig 6 **Individual black bears plotted with their assigned *K* population at a threshold of q=0.6. Overlapping points are jittered slightly so that each can be seen.**

As such, the 16 individuals that were unable to be confidently assigned to a genetic subpopulation were excluded from subsequent subpopulation assessments.

Evidence for a significant positive correlation between genetic distance and geographic distance was found across Nova Scotia and New Brunswick (Fig 7a; r=0.192, p=0.001), as well as across counties of mainland Nova Scotia (Fig 7b; r=0.183, p=0.001).

Pairwise F_{ST} values between each genetic subpopulation were fairly similar, and all above 0.05 (Table 3). All pairwise comparisons were found to be significantly different than if individuals were randomly distributed ($p < 0.05$), and all comparisons were significantly different after Bonferroni corrections.

Genetic Diversity and Effective Population Size (N_e)

The predominantly New Brunswick (NB) genetic subpopulation as identified by STRUCTURE had the largest allelic diversity and richness of all three (Table 4). The NB genetic subpopulation also had the highest observed heterozygosity (Ho=0.77±0.02), which was not found to significantly differ from its expected heterozygosity (He=0.78±0.02; p=0.529). Observed heterozygosities were about 10% lower for both Nova Scotian subpopulations than for New Brunswick (Table 4). For both Nova Scotian subpopulations, Ho and He significantly differed (SWNS: p=0.004; NENS: p=0.045). Both Nova Scotian subpopulations also demonstrated lower allelic diversity and richness compared to

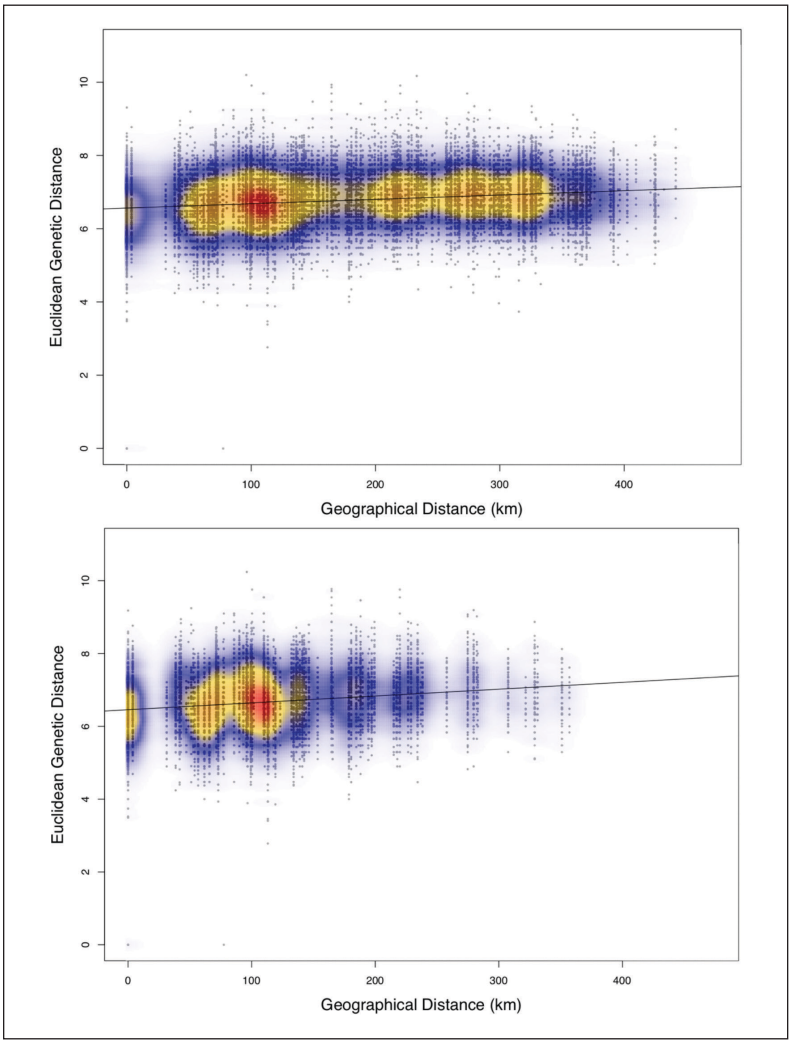


Fig 7 **Euclidean pairwise genetic distance over geographic pairwise distance for individuals in mainland Nova Scotia and New Brunswick (upper panel; r=0.192, p=0.001) and mainland Nova Scotia alone (lower panel; r=0.183, p=0.001). The different colours indicate density of points with red being most dense and blue being least dense.**

the New Brunswick subpopulation. The NB genetic subpopulation had the lowest inbreeding coefficient (FIS) and the SW NS subpopulation had the largest (Table 4). The only subpopulation whose FIS value significantly differed from zero was the SWNS subpopulation (p=0.003).

Table 3 **Pairwise FST values between each pair of genetic subpopulations are found below the diagonal. Above the diagonal, '**' indicates pairs with significant differences after Bonferroni correction.**

	New Brunswick	Northeast Nova Scotia	Southeast Nova Scotia
New Brunswick	-	**	**
Northeast Nova Scotia	0.055	-	**
Southeast Nova Scotia	0.061	0.085	-

** indicates pairs with significant differences after Bonferroni correction.

Table 4 **Number of individuals assigned to each genetic subpopulation (n), observed (Ho) and expected heterozygosity (He), mean number of alleles per locus (NA), allelic richness (A), and inbreeding coefficient (FIS) for each genetic subpopulation with 95% confidence intervals.**

Variable	New Brunswick	N.E. Nova Scotia	S.W. Nova Scotia
n	89	117	87
H_o	0.773±0.021	0.670±0.043	0.687±0.022
H_e	0.781±0.019	0.685±0.044	0.736±0.017
N_A	9.500±1.800	7.143±1.480	6.643±0.910
A_r	9.426±1.741	6.907±1.463	6.616±0.907
F_{IS}	0.015±0.032	0.023±0.023	0.073±0.039

The ANOVA and Tukey tests indicated that the only two subpopulations whose FIS values significantly differed were the NB and SWNS subpopulation (p=0.044).

The New Brunswick subpopulation had the largest effective population size (N_e=551.2 (212.1-infinity)), followed by the Northeastern Nova Scotia subpopulation (N_e=145.4 (101.6-233.8)), and lastly the Southwestern Nova Scotia subpopulation (Ne=76.8 (46.3-152.2)).

Examination of a possible subpopulation divide in Halifax County

Of the 19 hunters and trappers contacted (some had multiple bears), eight supplied detailed GPS information for 10 black bears caught in Halifax County. Two of these bears were unassigned at q=0.6 and thus not included. All samples found north of the City of Halifax belonged to the predominantly NENS genetic subpopulation, whereas samples found south of the city belonged to the predominantly SWNS genetic subpopulation (Fig 8).

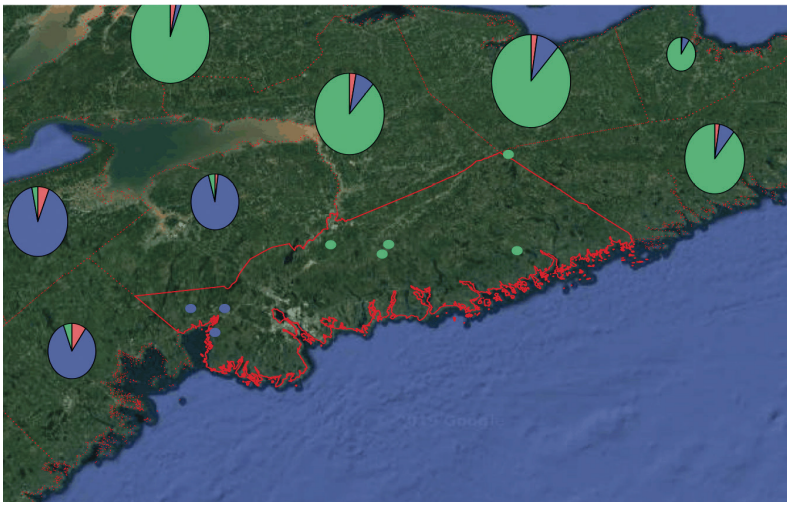


Fig 8 **Individual black bears plotted within Halifax County coloured according to their assigned K population at a threshold of q = 0.6. These points were jittered so that overlapping points could be seen. Surrounding counties have a pie chart of their relative proportions of probabilities for individuals to be assigned to each K population. Pie chart size is proportional to the sample size from that county.**

DISCUSSION

Subpopulations and Patterns of Differentiation

Overview of population structure – This study found evidence of three genetic subpopulations of black bears in the Maritimes with their generalized geographic distributions being (1) New Brunswick, (2) Northeast Nova Scotia, and (3) Southwest Nova Scotia. This finding was supported by STRUCTURE analyses, as well as by Hardy-Weinberg equilibrium assessments that indicated a deviation from HWE across the Maritimes, as well as within Nova Scotia, but not in New Brunswick. With F_{ST} values above 0.05 and below 0.15, these subpopulations exhibited a low to moderate degree of genetic differentiation from one another based on classic interpretations of population genetic structure, as described in Hartl and Clark (1997). These FST values are higher than findings in studies of black bear populations that are connected by mostly continuous habitats (e.g. Northern Ontario, FST=0.0075, Pelletier *et al.* 2012, Newfoundland, FST<0.04, Marshall *et al.* 2011), however they are lower than between some populations separated by anthropogenic barriers (e.g. Florida, FST=0.24, Dixon

et al. 2007, Alabama, F_{ST}=0.20-0.57, Draper *et al.* 2017, Graham 2016, Georgia, F_{ST}=0.14-0.32, Hooker *et al.* 2019), geographical barriers (e.g. Southeast Alaska, F_{ST}>0.12, Peacock 2004, Peacock *et al.* 2007), or a mix of both (e.g. Ontario, F_{ST}=0.14, Pelletier *et al.* 2012). This low degree of differentiation indicates that there is sufficient gene flow to prevent strong differentiation across the Maritimes. Alternatively, the low level of differentiation observed reflect the fact that existing barriers between subpopulations are relatively recent. For example, Proctor *et al.* (2016) found low dispersal rates of black bears across a highway despite little genetic differentiation between black bears on either side. This result is an important consideration in the Maritimes given that the human population of Nova Scotia has doubled in only the last 100 years, bringing with it increased infrastructure (Canada 2013). This situation is especially true within the Halifax Regional Municipality, near where the NENS and SWNS subpopulation meet.

New Brunswick Subpopulation – The New Brunswick subpopulation had a higher allelic diversity than other black bear populations reported to date in the literature. The New Brunswick subpopulation also demonstrated relatively high observed heterozygosity (H_O=0.773±0.021), consistent with populations that exist in continuous forested habitats (Paetkau and Strobeck 1994, Pelletier *et al.* 2012, Sawaya *et al.* 2014). The expected and observed heterozygosities were not found to significantly differ, indicating a stable level of heterozygosity. Additionally, this subpopulation had an inbreeding coefficient that was not found to significantly differ from zero indicating more or less randomized mating within this subpopulation (Keller 2002). The New Brunswick subpopulation had the largest effective population size (N_e) of all three subpopulations in the Maritimes and was the only one of the three within the recommended minimum N_e for a sustainable population (N_e=500-1000, Franklin and Frankham 1998, Lynch and Lande 1998, Ryman *et al.* 2019). The infinite upper limit of its confidence interval is consistent with other large populations that do not appear to be experiencing strong genetic drift. In terms of interpreting the potential "infinite" estimate of numbers for this population, it is important to note that NeEstimator works best for estimating N_e in small populations in which the signal for genetic drift is large (Waples and Do 2010). Collectively, this evidence indicates that the New Brunswick subpopulation of black bears exhibits high genetic variability, an adequate level of connectivity, and that it has a reasonably large (but obviously not infinite) effective

population size. Such a subpopulation is likely at a low risk for extirpation from population-genetic related parameters (e.g. loss of allelic variation, low heterozygosity, inbreeding, etc.).

Northeast Nova Scotia Subpopulation – The Northeast Nova Scotia subpopulation had a fairly high allelic diversity and richness compared to other black bear populations, however, it had approximately 10% lower observed heterozygosity than the New Brunswick subpopulation (H_O=0.670±0.043). The difference between H_E and H_O was found to be significantly different, indicating an excess of homozygosity in this subpopulation, which could be caused by genetic drift or inbreeding. This subpopulation, however, was not found to have an F_{IS} value significantly different from zero. The Northeast Nova Scotia subpopulation had the second largest N_e estimate of the three subpopulations; however, it was almost 75% smaller than that of the New Brunswick subpopulation. The N_e estimate was far below the recommended size for long-term conservation ($N_e \geq 500$), however, it was within an acceptable range for short term conservation ($N_e > 50$, Ryman *et al.* 2019). Populations with N_e values in this range are expected to lose genetic diversity over time through drift, however, at fairly slow rates. The N_e estimate for the Northeast Nova Scotia subpopulation was similar to the one found for black bears in eastern Utah that had fairly low genetic diversity levels (N_e=142-222 calculated using two different methods by Sinclair *et al.* 2003). This result likely indicates that genetic drift has significantly affected genetic diversity of black bears in NENS. In all, these findings indicate the NENS black bear population is viable and likely at a low risk for extirpation; however, the subpopulation should be monitored to prevent further loss of genetic diversity.

Southwest Nova Scotia Subpopulation – The Southwest Nova Scotia subpopulation had the lowest allelic diversity and richness of all three Maritime subpopulations. Although this subpopulation had a similar observed heterozygosity as the Northeast subpopulation, it had a larger significant difference from its expected heterozygosity. This indicates a greater homozygote excess in comparison to the NENS subpopulation. This subpopulation had the largest F_{IS} value, and the only F_{IS} value significantly larger than zero. With an F_{IS} value similar or larger to values found in disjunct black bear populations (Arizona, F_{IS}=0.038-0.110) (Varas-Nelson 2010), it is probable that inbreeding is a contributing factor to reduced heterozygosity in this region. The N_e

estimate for black bears in this subpopulation was about half of that of the Northeast Nova Scotia subpopulation, N_e=76.8 (47.3-152.2). Although not quite as low as severely disjunct black bear populations (e.g. Mobile River Basin, N_e=31 (20.5-47.4) or Northeastern Alabama, N_e=3.4 (2.8-4.8)(Draper *et al.* 2017), this finding indicates strong effects of genetic drift and/or inbreeding in the black bears of SWNS. Together, these findings point to this subpopulation having experiemced a loss of genetic diversity both in allelic variation and heterozygosity. This is particularly interesting as black bear density was estimated to be highest in the southwest portion of the province (Pulsifer *et al.* nd.), indicating the SWNS subpopulation should have a comparatively large census size. Having a large number of individuals should help minimize effects of genetic drift. These findings indicate a need to closely monitor this subpopulation and further investigate drivers of genetic diversity loss.

Drivers of Genetic Differentiation

Nova Scotia vs. New Brunswick – As important as it is to delineate genetic subpopulations in wildlife studies, it is also important to understand what the drivers of genetic differentiation are between them (Pelletier *et al.* 2012). Genetic differentiation across black bear populations in continuous habitats tends to be largely driven by distance, following the isolation by distance (IBD) pattern (e.g., r=0.552, p=0.002). Across the Maritimes, a weak but significant signature of IBD between black bears was detected (r=0.192, p=0.001). This is a similar degree of correlation in IBD as found in the study by Pelletier *et al.* (2012) when the isolated population of black bears on Bruce Peninsula was included in their IBD assessment (r=0.161, p=0.002). This suggests that across the Maritimes, IBD can account for some, but not all, of the observed genetic differentiation among black bears. According to the STRUCTURE analysis, the New Brunswick and NENS subpopulations geographically meet on the western side of the Isthmus of Chignecto. This finding is consistent with the hypothesis that black bear dispersal is compromised between these provinces due to the natural geography and possibly anthropogenic barriers to black bear dispersal associated with the Isthmus of Chignecto. A future study with a more extensive and even-sized sample set from both sides of this divide, as well as samples with known GPS-coordinates would be beneficial to help delineate potential landscape features contributing to this genetic divide.

Northeast vs. Southwest Nova Scotia – IBD seems to play a similar role across the mainland of Nova Scotia compared to between Nova Scotia and New Brunswick (r=0.183, p=0.001). This result suggests that IBD accounts for some but not all of the genetic structure within the province. Additionally, STRUCTURE analysis indicated the two Nova Scotian subpopulations' geographic boundary bisected the province into northeast and southwest regions. To further investigate what may be contributing to this genetic divide, it can be helpful to consider important features found at the subpopulation boundary. Hants and Colchester counties are found along the western portion of this boundary. Black bears in Hants County were found to predominately belong to the SWNS subpopulation, whereas black bears in Colchester County were found to predominately belong to the NENS subpopulation. This fairly clear divide indicated that the black bear subpopulation genetic differentiation roughly follows the political divide between these two counties, which in turn follows the Shubenacadie River, with notably powerful tides and currents (e.g. Rulifson and Tull 1999). Additionally, these counties are divided in part by Highway 102, which is currently one of the busiest roads in the Maritimes (Nova Scotia Department of Public Works 2023). Highways have been shown to act as dispersal barriers for black bear populations (Whittle 2009, Sawaya *et al.* 2014, Proctor *et al.* 2016). Even before Highway 102 was completed, there was a series of high-traffic, secondary highways that similarly intersected this part of the province. One or both these factors (i.e., highways and waterways) are likely contributing to the population structure on the western portion of this genetic boundary.

Along the eastern side of the boundary is Halifax County, which includes the Halifax Regional Municipality, the most urbanized region of the province (Government of Canada, Statistics Canada 2017). The northern portion of this county, however, is largely forested. STRUCTURE analysis indicated that a large proportion of individuals within Halifax County had high assignment likelihoods to either the Northeast Nova Scotia or Southwest Nova Scotia subpopulation, with a couple admixed individuals. This led to the hypothesis that the subpopulation delineations were somewhere within the county. The closer analysis performed using corrected GPS-coordinates in Halifax County revealed that individuals assigned to the Northeast subpopulation were only found north of the city of Halifax, and individuals assigned to the Southwest subpopulation were only found

south of the city. This pattern suggests the city of Halifax is a barrier to black bear dispersal on the eastern portion of this genetic boundary, supported by the fact that black bears have been found to avoid urban zones (Whittle 2009).

It is also possible that the Strait of Canso that separates Cape Breton Island from mainland Nova Scotia was an historic barrier to gene flow in the northeastern region of the province. Analysis of additional samples from Cape Breton is certainly warranted based on apparent haplotype frequency differences in the present samples.

General Implications Regarding the Population Structure of Black Bears in Nova Scotia

There is no recent estimate of black bear densities or population census for Nova Scotia (Airst and Fleming 2024). The New Brunswick Department of Natural Resources Minister estimated the census population for that province at ~16 500 a decade ago (CBC 2014), which corresponds to a density of ~0.22/km. If this value is similar for Nova Scotia, there would be ~12 000 black bears in this province. From data presented in Fudge *et al.* (2007), which included co-authors from the Nova Scotia Department of Natural Resources, the Nova Scotia black bear census population was ~6 000 at that time. Using these two values (6 000 to 12 000) as a general range, black bears in Nova Scotia would have an effective population size/census population size (i.e., N_e/N_c) of 0.019-0.037 (when combining N_e estimates from Northeast and Southwest subpopulations). Most wildlife populations have a ratio of about 0.1 (Frankham 1995). This is a strong indication that genetic drift has had a notable effect on genetic variation in black bears in Nova Scotia. This ratio could also be an indication of an historic bottleneck event (Luikart *et al.* 2010), which could have been caused by the largely unregulated historical harvest of black bears in the region until the late 1990s (Nette 1994), or potentially by the division of a formerly panmictic population into subpopulations through anthropogenic development. Moving forward, it will be important to monitor this relatively low N_e value for black bears in Nova Scotia so that measures can be taken to mitigate loss of genetic variation.

To further investigate the various potential factors contributing to the population genetic structure of black bears in Nova Scotia, it would be informative to examine variation in mtDNA. Because mtDNA is maternally inherited, is nonrecombining and evolves at a generally

predictable rate, analyzing this molecular marker would be useful to help understand how long these subpopulations have existed and to assess whether anthropogenic land conversion has been an important factor in determining their current structure (e.g. Shafer *et al.* 2011). Additionally, obtaining precise GPS coordinates for samples in the future may allow the identification of particular landscape features creating dispersal barriers for black bears (Proctor *et al.* 2016). Detailed GPS data proved useful to a degree in the Halifax County level investigation, however, this analysis only included eight individuals. Finally, it would be beneficial in future to study the black bear population structure on Cape Breton Island. Only seven samples were collected from Cape Breton Island for this study, and thus it is inappropriate to draw conclusions regarding black bear population genetics in that region at present.

Management Implications

Divergence between subpopulations in nuclear-encoded genes can reflect the effects of natural selection and thus may signify distinct, ecologically functional units within a species (Moritz 1994). Thus, the delineation of genetic subpopulations can be useful for wildlife management officials to construct ecologically relevant Management Units (MUs). By constructing MUs of a species using subpopulation boundaries, the specific needs of each subpopulation can be addressed. For example, it could be beneficial for black bears on mainland Nova Scotia to be managed separately in NENS from SWNS if the Shubenacadie Canal system is a partial geographic barrier slowing the rate of gene flow between these regions. It would be particularly beneficial to increase monitoring of black bears in SWNS which are exhibiting lower levels of genetic diversity, and to implement management strategies aimed at ensuring no further loss of genetic diversity occurs in this subpopulation.

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