



The structure and connectivity of an archipelagic population of black bears

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Abstract

Understanding factors that influence the viability of populations is central to conservation biology. Small and isolated populations have elevated risk of extinction due to demographic and genetic stochasticity. The Apostle Islands National Lakeshore features a genetically unique and culturally important population of archipelagic black bears (*Makwa*; *Ursus americanus*). While dispersal is central to population viability, previous studies of this population did not sample the adjacent mainland black bear population on the Red Cliff Reservation (*Gaa-miskwaabikaang*). Therefore, we lack robust estimates of dispersal, gene flow and overall connectivity among the islands and with the mainland population. In partnership with Red Cliff Band of Lake Superior Chippewa and the National Park Service, we non-invasively collected black bear hair, and used 17 microsatellite markers to genotype 141 black bears. We then estimated genetic diversity, population structure, dispersal, and conducted a pedigree network analysis to identify areas of the archipelago important for connectivity and reproduction. We found evidence of a well-connected archipelagic bear population structured into five clusters and characterized by moderate dispersal between islands and mainland. We found that three of the islands are disproportionately important for genetically connecting the archipelago, but the islands were nevertheless reliant upon the mainland for gene flow and genetic diversity. The high connectivity between islands and the mainland demonstrates a potential metapopulation dynamic, where islands may serve as a reservoir of individuals for the mainland and the mainland supplying individuals likely important for maintaining genetic diversity of island populations. Given the importance of island–mainland connectivity, future tribal and federal collaboration will be important to maintain a genetically and demographically viable population of black bears.

Keywords Island biogeography · Large carnivore · Non-invasive genetics · Population dynamics · Dispersal and connectivity · Genetic structure

Introduction

Understanding factors that influence the viability of wild populations is a fundamental goal for population ecology and conservation biology (Wootton and Pfister 2013). Small and isolated populations are frequently targeted for conservation due to their increased risk of extinction. Indeed, stochastic effects on demographic processes such as reproduction, death, or dispersal have proportionally larger effects on smaller populations (Shaffer 1981). The demographic vulnerability of small and isolated wildlife populations can also interact with genetic factors (Gilpin and Soule 1986) to increase extinction risk as part of the ‘small population paradigm’ (Caughley 1994). Small, isolated populations lose genetic diversity over time, primarily via

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inbreeding and genetic drift, which may compound extinction risk if demographic performance is compromised by declining genetic diversity (Soulé and Mills 1998). Isolated populations, especially those found on islands, often experience increased levels of inbreeding and a greater impact of genetic drift. Consequently, island populations generally have lower levels of genetic diversity and fitness than counterparts found in mainland populations (Frankham 1998).

Dispersal of individuals between populations can demographically or genetically rescue small, isolated populations (Grauer et al. 2019; Lowe and Allendorf 2010; Musmann et al. 2017). Successful migrants can augment small populations and increase vital rates like reproduction or survival (Aiken and Whitlock 2013) and play a key role in maintaining metapopulation persistence (Hanski 1998). Gene flow can introduce genetic diversity back into a population where genetic drift may have eroded it (Peery et al. 2008), increasing population adaptive capacity (Weeks et al. 2011). Indeed, even ostensibly nominal levels of dispersal – as low as a single immigrant per generation can be sufficient to maintain a stable population (Mills and Allendorf 1996).

In the Anthropocene, animal populations are increasingly facing fragmented and patchy environments (Newbold et al. 2015). Indeed, fragmentation poses one of the greatest threats to terrestrial biodiversity (Haddad et al. 2015). A robust understanding of how isolation interacts with demographic and genetic processes in naturally patchy populations can help maintain viable populations. Carnivores (Class Mammalia) have experienced global declines in abundance and distribution in the last century, in part from habitat loss and fragmentation (Estes et al. 2011). Given the disproportionate role that carnivores can have on community-to-ecosystem processes (Ripple et al. 2014), the recovery of these species has become a focus of many conservation efforts. Understanding, then, connectivity of carnivore populations within increasingly fragmented landscapes will be central to recovery (Crooks et al. 2011). While dispersal is central to population viability, it is often challenging to quantify in wild populations, particularly among carnivores (Pauli et al. 2012), which naturally occur at low densities, inhabit broad spatial scales and are increasingly rare due to historical declines in both abundance and distribution (Estes et al. 2011, Crooks et al. 2011).

Non-invasive genetic methods have been transformative in their ability to detect rare and elusive animals, including carnivores (Pauli et al. 2009). Genetic tagging is an effective way to measure demographic and genetic population parameters, including dispersal and gene flow (Lamb et al. 2019). Population genetic approaches (Sundqvist et al. 2016), genetic assignment (Pritchard et al. 2000), kinship or pedigrees (Peery et al. 2010), and network analysis (Dyer and Nason 2004) are frequently used to quantify dispersal.

These methods have been particularly effective for quantifying demogenetic parameters among carnivore populations in patchy or fragmented landscapes (Proctor et al. 2012; Pauli et al. 2009). Bears (Ursidae) have been widely studied using these methods (Woods et al. 1999; Lamb et al. 2020; Laidre et al. 2022). Bears are vagile and capable of dispersing long distances (Rogers 1987). Despite their dispersal capability, highways, mountain ranges, open grasslands, and fjords can structure populations (Proctor et al. 2020; Paetkau et al. 1998; Larson et al. 2018). Notably, bear populations can be structured by water crossings due to water channels limiting gene flow (Paetkau et al. 1998; Lewis et al. 2020; Peacock et al. 2007). For example, grizzly bear dispersal in southeast Alaska was limited by as little as 2 km of water crossings (Paetkau et al. 1998), while black bears in southeast Alaska were structured into 10 distinct genetic populations (Lewis et al. 2020) and gene flow appeared to be limited by a seawater crossing of less than 100 m, and marine fjords 10–18 km wide (Peacock et al. 2007, Lewis et al. 2020).

The Apostle Islands – an archipelago of 22 islands in Lake Superior, USA – is home to a population of American black bears. Twenty-one of the islands are protected as part of the Apostle Island National Lakeshore and managed by the National Park Service. Ten carnivore species occur on the Apostle Islands, but black bears have the highest occupancy of any carnivore (Allen et al. 2018), being detected on 15 of the 22 islands (Wilton et al. 2015). Black bear occurrence is primarily driven by island size and inter-island distance, and to a lesser degree, distance from the mainland (Allen et al. 2018). The islands range in size from 0.08 km² to 40 km² and are separated from each other and the mainland by ≥ 1 km of water. Bear densities on these islands are high; Stockton Island (0.64 bears/km²; Belant et al. 2005) and Oak Island (0.88 bears/km², Wilton et al. 2015) have some of the highest reported bear densities in the United States (southeast Alaska at 1.5 bears/km²; Peacock et al. 2011). Black bears are thought to have most recently colonized Stockton Island in the early 1970s (Anderson and Trauba 1991), though the long-term occupancy and colonization history of other islands is unknown (Wilton et al. 2015). Bears on the islands are genetically structured into five groups, and dispersal has been observed throughout the archipelago (Belant et al. 2005; Wilton et al. 2015). While these observations suggest that connectivity could be high, previous work did not sample the mainland and so a reliable estimation of connectivity was not possible. Thus, we currently lack robust estimates of dispersal among the islands and with the mainland population. Given the role of connectivity in genetic and demographic viability, especially for an archipelagic population (Wilton et al. 2015), quantifying the degree of dispersal is an important a step towards understanding the mechanisms

supporting the persistence of this genetically, ecologically, and culturally important population of black bears. Indeed, much of the adjacent mainland population – of which there has never been a formal population estimate – resides on the Red Cliff Band of Lake Superior Chippewa Reservation.

The Red Cliff Band of Lake Superior Chippewa is one of six Ojibwe (i.e. Chippewa or Anishinaabe) bands that are federally recognized in Wisconsin (Loew 2013). The 58.8 km² Red Cliff Reservation, *Gaa-miskwaabikaang*, was created by the 1854 Treaty of Lapointe, but only 32 km² remained under tribal ownership 150 years later (Red Cliff 2020) due to a series of sovereignty and land-based issues such as the General Allotment Act and forced assimilation policies (Hibbard 2022). In the last decade, Red Cliff band has begun land repatriation efforts, which have included the creation of the first Tribal National Park in the United States, Frog Bay (Red Cliff 2020). The Apostle Islands, *Wenabozho Ominisan*, have long been important to the Anishinaabe. Madeline Island, *Mooniingwanekaaning*, the only island that is not part of the National Park today, was the capital of the Ojibwe Nation (Warren 2009). The islands remain important for practicing treaty rights, traditional practices such as controlled burns, and for being home to culturally significant species. The black bear, *makwa*, is one of the clan or *doodem* animals of Ojibwe traditional governance (Bohaker 2020; Loew 2013). Great Lakes Ojibwe communities maintain clan systems to this day, with each clan represented by an animal relative embodying characteristics, traits, and inherent responsibilities crucial for the community to thrive (Bohaker 2020; Dylan Jennings, personal communication). Thus, it is of interest to the Tribe to quantify *makwa* population dynamics and determine the degree of connectivity across both ceded and unceded territories.

To better understand the overall connectivity of black bears across the archipelago and especially with the mainland, we non-invasively sampled bear populations on four of the Apostle Islands (Sand, Stockton, Oak, and Basswood Islands) as well as on the mainland, including the Red Cliff Reservation. From these efforts, we estimated genetic diversity, population differentiation, population structure, dispersal, and we created a network from a pedigree of black bears to describe patterns of functional connectivity across the region. We hypothesized that the black bear population would exhibit genetic structure dictated by isolation by distance. We predicted that there would be five genetically distinct subpopulations and genetic distance would increase with geographic distance from neighboring subpopulations. We predicted that each island would be genetically related to the mainland, but that genetic connectivity would be highest between nearshore islands and the mainland compared to offshore ones. Finally, we predicted that small islands would

host individual bears with genetic ancestry from other locations, acting as stepping stones for dispersal.

Methods

Genetic analysis

During the summers of 2020, 2021, and 2022 we collected black bear hair non-invasively (Pauli et al. 2010) via hair corrals (Wilton et al. 2014; Woods et al. 1999). Each summer, we deployed 57 hair corrals on the mainland and target islands: Stockton, Oak, Basswood, and Sand. We placed hair corrals in a 1.6 km² grid (Belant et al. 2005; Wilton et al. 2015), with one corral in the center of each grid. We set 17 corrals on Stockton, 8 on Oak, 5 on Sand, 4 on Basswood, and 23 on the mainland (Belant et al. 2005; Wilton et al. 2015). We deployed 1 hair corral per island on non-target islands (Hermit, Manitou, Otter, Bear, Ironwood, Cat, Rocky, and Outer). At target locations, we collected hair every 9–12 days for 6 sessions from May–August 2020–2022. On non-target islands, we collected hair 1–2 times each year. We selected a subset of hair samples for DNA extraction, genotyped them using 17 microsatellite markers, and identified individual black bears (see supporting information for details). We obtained extracted DNA from previous sampling efforts in 2002–2010 (Table S1) and genotyped one sample from each previously identified individual in triplicate at 17 loci where extracted DNA was available (2 samples were depleted). We estimated genetic diversity by calculating expected heterozygosity (H_e), observed heterozygosity (H_o), number of private alleles, Shannon's Information Index, and number of alleles using GenAlEx v6.503 (Peakall and Smouse 2006, 2012). We calculated effective population size (N_e) using NeESTIMATOR v2.1 (Do et al. 2014) with the linkage disequilibrium method and random mating, excluding singleton alleles.

Gene flow and connectivity

We identified genetic differentiation between subpopulations by calculating pairwise G_{ST} (Meirmans and Hedrick 2011; Nei 1987) and Nei's Genetic Distance (Hedrick 2000) using GenAlEx v6.503 (Peakall and Smouse 2006, 2012). We tested for isolation by distance using a Mantel test with 999 permutations comparing genotypic distance (Smouse and Peakall 1999) and geographic distance (Log (1 + distance)) for individuals and populations in GenAlEx v6.503 (Peakall and Smouse 2006, 2012). For individuals, geographic distance was the pairwise distance between the center of each individual's detected locations. For populations, geographic distance was the pairwise distances between center points

of each location. To visualize genetic structure and compare structure across years, we conducted a Discriminant Analysis of Principle Components (DAPC) using adegenet v2.1.10 in R v4.4.0 (Jombart 2008; Jombart et al. 2010; R Core Team 2023). We explored population structure and the number of ancestral genetic groups (STRUCTURE v2.3.4, Pritchard et al. 2000) for bears detected from 2002 to 2022 and for bears detected between 2020 and 2022. Unless otherwise indicated, a significance level of $\alpha=0.05$ was used for all tests.

Pedigree network

We used genotypes and sexes of all bears detected since 2002 to build a pedigree using Colony v2.0.6.8 which jointly infers parentage and sibships with likelihood calculated over the entire pedigree rather than between only pairs of individuals (Wang and Santure 2009; Jones and Wang 2010). When a candidate father or mother is not present among the sampled individuals, a unique ID is created for each inferred parent. In Colony, we ran three high precision, long run-time, full-likelihood analyses with 3 different random seeds. We included inbreeding, polygamy, female and male sibship size of 2.5, genotyping error, allelic dropout, and estimated a 0.4 probability that the true father and mother were present in the dataset. We retained relationships with > 90% probability.

We used a graph-theoretic approach to explore patterns in genetic structure and connectivity, where networks of nodes (i.e., individuals) are connected by edges (i.e., genetic connectivity) to represent network interactions (Dyer and Nason 2004; Urban and Keitt 2001). We used several network metrics to describe aspects of network structure: betweenness centrality measures the number of shortest paths through a node that connects the network (Freeman 1977) and reveals bottlenecks in the network important for maintaining connectivity (Minor and Urban 2008); closeness centrality is the shortest path length between a node and other nodes (Latora and Marchiori 2001), representing individuals whose parents and/or offspring connect multiple locations across the network (McFarlane et al. 2021); eigenvector centrality is a measure of the importance of a node

in the network where a node that is connected to important nodes is given more weight and indicates here individuals that are part of large highly connected family units (Garroway et al. 2008).

We used Cytoscape v3.7.2 (Shannon et al. 2003) to create a directed, unweighted network of parent–offspring relationships for 223 black bears and inferred parents. We created a subnetwork of bears detected in 2020–2022 and their nearest neighbors to include both inferred parents and parents that were detected in previous sampling years. This created continuity across timescale for locations that were asynchronously sampled. We examined how each location-based subnetwork contributed to the full network by comparing the centrality metrics of betweenness, closeness, and eigenvector (McFarlane et al. 2021). We quantified connectivity through multiple approaches; the number of first order relatives that connect different locations, and via a network centrality based approach. We ran Kruskal-Wallis rank sum tests (R Core Team 2023) to determine if there were differences in betweenness and eigenvector centralities between locations, and a Dunn test with Holm correction to test for pairwise differences (Kassambara 2023). We ran a one-way ANOVA to test if closeness centralities differed between locations, a Levine test for heterogeneity of variance, and a post hoc Games Howell test with Holm correction to determine pairwise differences (Fox and Weisberg 2019; Kassambara 2023). We visualized boxplots of pairwise comparisons between location-based centralities using ggstatsplot in R v4.4.0 (Patil 2021; R Core Team 2023).

Results

Genetic analysis

We identified 141 unique individuals during 2020–2022. We recaptured 11 of the 93 unique individuals genotyped from 2002 to 2010 for a total of 223 black bears (Table S1). The mean number of alleles and private alleles was highest on the mainland and then Stockton and lowest on Basswood Island, tracking population and island size (Table 1). Island black bear populations had higher heterozygosity than

Table 1 Genetic diversity of black bears (*Ursus americanus*) on four islands (basswood, Oak, Sand and Stockton) in the Apostle Islands National Lakeshore and the mainland Bayfield Peninsula from 2020–2022. Area of study location (km²), census size (N), effective population size (ne; no singleton alleles), number of alleles (na), private alleles (Pa), observed heterozygosity (Ho), and expected heterozygosity (he). Values in parenthesis indicate standard error

Location	Area	N	Ne	Na	Pa	Ho	He
Basswood	8	7	5.1 (2.5–12)	3.41 (0.2)	0 (0)	0.71 (0.07)	0.57 (0.04)
Oak	20.6	18	10.6 (8.3–13.6)	6.29 (0.71)	0.12 (0.12)	0.70 (0.05)	0.69 (0.03)
Mainland	69.1	76	105.7 (89.6–126.9)	9.71 (1.27)	1.82 (0.62)	0.74 (0.03)	0.78 (0.02)
Sand	11.9	11	4.4 (2.8–7.5)	5.59 (0.45)	0 (0)	0.76 (0.05)	0.70 (0.03)
Stockton	40.7	25	9.8 (8.3–11.5)	6.71 (0.57)	0.06 (0.06)	0.74 (0.04)	0.72 (0.03)

Table 2 Genetic diversity of black bears (*Ursus americanus*) on two islands (sand and Stockton) in the Apostle islands National Lakeshore in 2002, 2010 and 2020. Black bear census size (N), number (standard error) of alleles (na), Shannon's Information Index (I), number of private alleles (Pa), observed heterozygosity (Ho), and expected heterozygosity (he)

Location	Year	N	Na	I	Pa	Ho	He
Sand	2002	6	3.82 (0.21)	1.08 (0.08)	0.35 (0.15)	0.68 (0.06)	0.58 (0.04)
Sand	2010	7	4.12 (0.28)	1.23 (0.07)	0.29 (0.11)	0.71 (0.51)	0.63 (0.03)
Sand	2020	8	4.35 (0.28)	1.26 (0.08)	1 (0.21)	0.79 (0.05)	0.67 (0.03)
Stockton	2002	21	6.59 (0.58)	1.55 (0.09)	1.23 (0.35)	0.75 (0.04)	0.74 (0.02)
Stockton	2010	12	5.41 (0.42)	1.41 (0.08)	0.24 (0.14)	0.83 (0.04)	0.70 (0.02)
Stockton	2020	16	5.77 (0.50)	1.43 (0.09)	0.47 (0.15)	0.78 (0.04)	0.70 (0.03)

Table 3 Pairwise GST (above diagonal), Nei's D (below diagonal) between populations of black bears (*Ursus americanus*) from 2020–2022 in the Apostle Islands National Lakeshore and Bayfield Peninsula, Wisconsin USA. $P < 0.001$ for GST after 999 permutations

	Basswood	Oak	Mainland	Sand	Stockton
Basswood	0.000	0.081	0.062	0.081	0.088
Oak	0.484	0.000	0.021	0.049	0.049
Mainland	0.393	0.170	0.000	0.020	0.032
Sand	0.526	0.400	0.209	0.000	0.038
Stockton	0.564	0.367	0.266	0.331	0.000

expected while mainland black bears had lower heterozygosity than expected. Effective population sizes (N_e) on all islands were smaller than census sizes, but on the mainland, effective population size was larger than census size (Table 1). Genetic diversity decreased between 2002 and 2010 and increased between 2010 and 2020 on Stockton Island while genetic diversity on Sand Island increased from 2002 to 2020; both islands genetic diversity tracked population and island size (Table 2).

Gene flow and connectivity

Black bears on the Apostle Islands and Bayfield Peninsula exhibited low to moderate pairwise genetic differentiation ($G_{ST} = 0.02$ – 0.088 ; Table 3). We found no relationship between linear genotypic and geographic distance between populations ($R^2 = 0.17$, $p = 0.15$) but a weak relationship between individuals and geographic distance ($R^2 = 0.01$, $p = 0.001$). Genetic structure remained similar over a 20-year period between islands, with 67% confidence intervals overlapping across sampling years (Figure S1). We found support for 5 genetic clusters over 20 years across our study area (Figure S2). There were unique genetic groups on four islands and the mainland, and evidence of dispersal throughout the archipelago and mainland (Fig. 1, Figure S3). The smallest islands were home to individuals with genetic ancestry from larger islands or the mainland. Over a shorter timescale (2020–2022), we found evidence for 3–4 genetic populations (Figure S2). The same unique populations existed on Stockton and Oak; however, Sand, Basswood and the Mainland shared one to two genetic groups (Figure S4). While the whole archipelago was connected,

the highest dispersal was between islands and the mainland, not between islands.

We found the highest connectivity in the pedigree network (nodes with edges connecting individuals across locations) between islands and the mainland, with Sand Island and the mainland and Stockton Island and the mainland exhibiting the highest connectivity (Fig. 2; Table 4). The indices of centrality for our network (Fig. 3, Figure S6) revealed differing connectivity across the archipelago; specifically, betweenness, closeness, and eigenvector centralities differed between locations ($U_4 = 22.56$, $p < 0.001$; $F_{4, 215} = 25.6$, $p < 0.001$; $U_4 = 130.32$, $p < 0.001$). Pairwise differences in betweenness centrality only existed between the mainland and Stockton; closeness centrality differed between all locations except Stockton, Oak, and Basswood; and pairwise differences between eigenvector centralities existed between all locations except between Stockton, Oak, and Basswood (Fig. 3, Table S3).

Discussion

We found a genetically structured but well-connected archipelagic population of black bears. Interestingly, isolation by distance only weakly structured the population, and other mechanisms (e.g., resource availability or island size) contributed to population structure. We found that dispersal was high, which suggests that bear populations on the islands are well-connected, and may explain why these populations are distributed across much of the archipelago and have persisted for so long.

Overall, the genetic diversity of black bears – both on the mainland and islands – was similar to what has been observed in other well-connected bear populations (Proctor et al. 2020; Larson et al. 2018), and higher than very isolated island populations (Marshall et al. 2011). Heterozygosity on the mainland was lower than expected, likely due to the Wahlund effect (Waples et al. 2018). Harvest intensity has been shown to limit natal dispersal, alter mate selection, and increase inbreeding in black bears (Moore et al. 2014), and may contribute to the lower heterozygosity observed in the mainland population. Allelic diversity

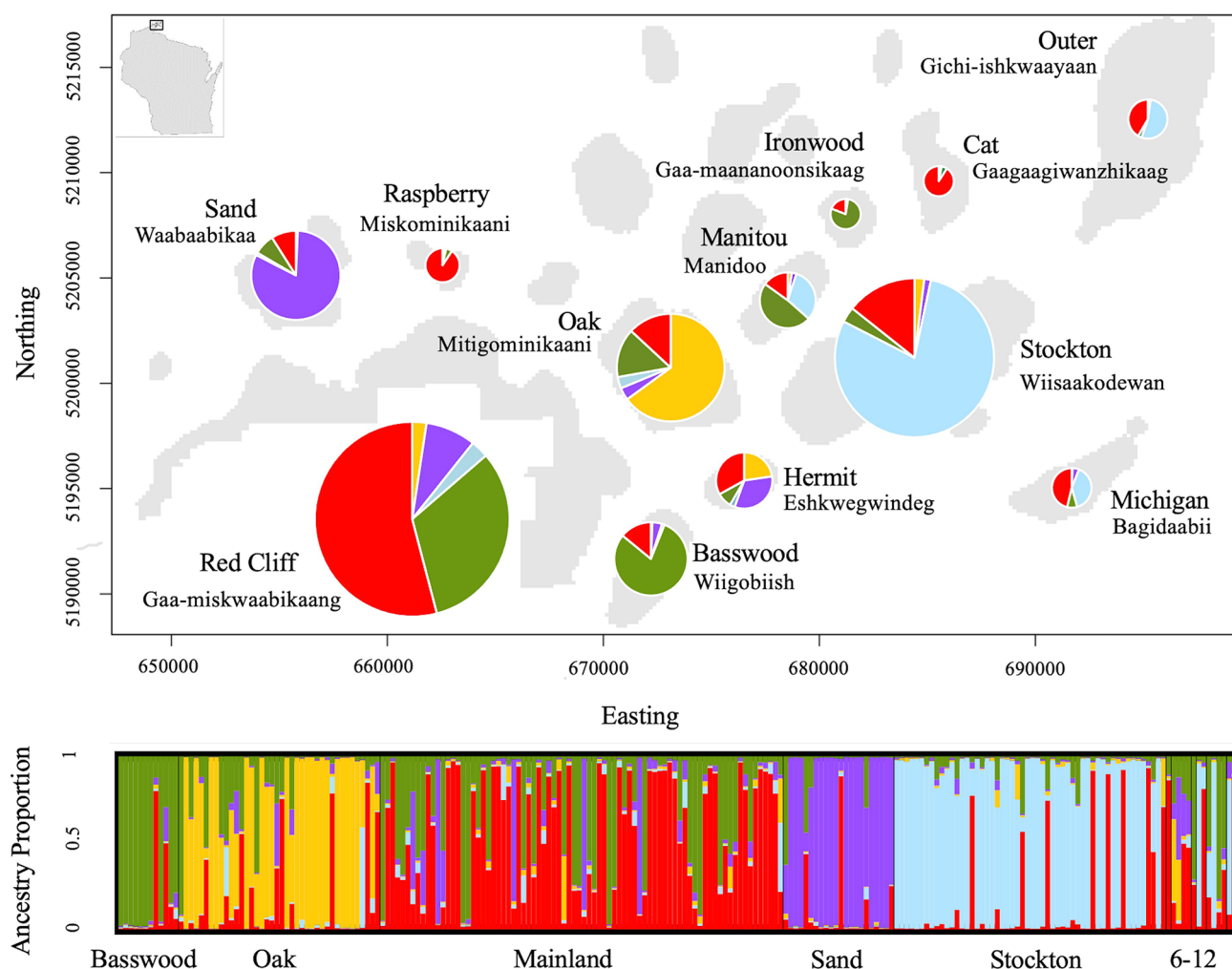


Fig. 1 Admixture proportions for 223 black bears (*Ursus americanus*) detected in 2002–2022 in the Apostle Islands and Bayfield Peninsula. $K = 5$ populations (6–12 = Cat, Hermit, Manitou, Outer, Ironwood, Michigan, Raspberry). Sizes of pies correspond to relative abundance

generally responds more rapidly to population bottlenecks than heterozygosity (Allendorf 1986). Interestingly, the number of alleles and bear abundance, particularly the number of females, declined sharply in 2010 on Stockton Island (Wilton et al. 2015). Yet, we observed that these estimates rebounded by 2020; we suspect that the recovery of this population on Stockton Island is due in part to connectivity with the mainland. The genetic diversity on the islands was relatively stable over 20 years and it appears that large population sizes on these small islands combined with gene flow has been sufficient to maintain genetic diversity thus far in this population.

We observed a frequent exchange of individuals across water barriers from the mainland to the islands, between islands and from islands back to the mainland. Indeed, we observed six dispersal events in only three years of sampling. Nevertheless, this movement less frequently led to actual gene flow; two of the observed dispersers successfully reproduced. Most black bears on the islands maintain

year-round territories, including hibernating on the islands (Fleming 1997; Trauba 1996). Previous research on the Apostle Islands has found frequent temporary movements of bears between islands and suggested that some bears likely have home ranges across multiple islands (Trauba 1996). There is some migration between them, but for the most part, these genetic clusters arise from isolation over multiple generations. We suspect that many of the island bears that migrate to the mainland are harvested by hunters (Fleming 1997), while many of the mainland bears that migrate to the islands may not successfully find territories or mates. These two factors may contribute to higher levels of temporary immigration/emigration than actual gene flow resulting in the genetic structure that exists despite the high levels of dispersing individuals observed. Consequently, we found only weak evidence for isolation by distance but moderate genetic structuring across the archipelago. Populations featuring high dispersal and genetic structure have been observed previously when dispersal is temporary and does

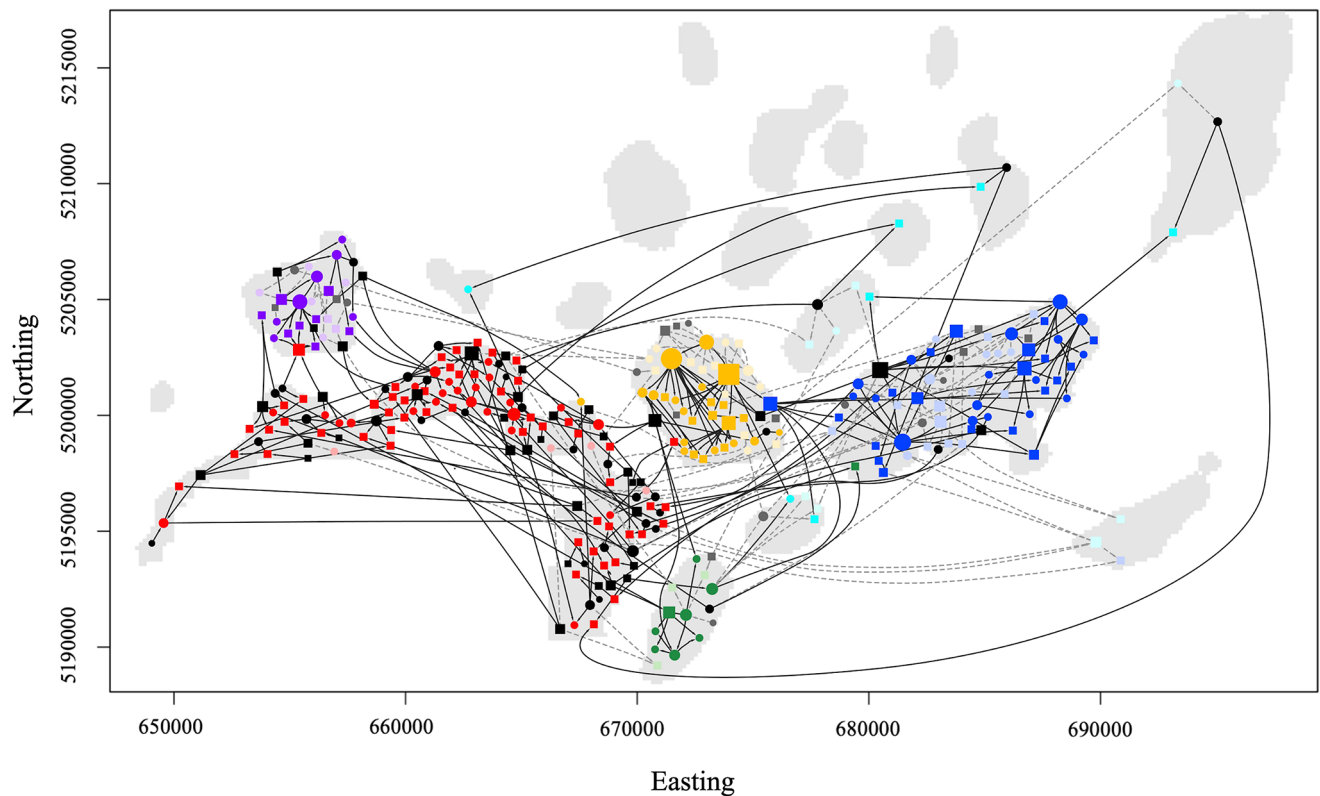


Fig. 2 Pedigree network of 223 black bears (*Ursus americanus*) on islands and the mainland in the Apostle Islands National Lakeshore and Red Cliff Reservation of northern Wisconsin from 2002–2022 and their inferred parents. Nodes represent individual bears (circles = females, squares = males) and edges and arrows connect parents to offspring. Node color and/or location indicates where individuals were detected (green = Basswood, orange = Oak, red = Mainland, purple = Sand, blue = Stockton, teal = all other islands, black = never cap-

tured but kinship inferred). Inferred individuals' locations were visualized and analyzed as the most parsimonious location (where they had the most relatives) or assigned randomly between equal likelihoods. Darkly shaded nodes and solid black edges denote a network of bears detected in 2020–2022 and their parents- used in further analyses. Lightly shaded nodes and dotted grey edges denote 2002–2010 bears and inferred parents that did not sire contemporary bears. Node sizes correspond to relative number of offspring

Table 4 Number of migrants black bears between locations (direction agnostic) above diagonal, and number of parent offspring dyads split between locations (direction agnostic) below diagonal; calculated using pedigree network. Observed migrant individuals were placed in the location where they migrated to for the calculations, and ranges of values depend on where inferred individuals were located

	Basswood	Oak	Mainland	Sand	Stockton
Basswood	NA	1	3	0–1	0–1
Oak	3–4	NA	2–3	0	2
Mainland	4–5	2–4	NA	4–5	3–4
Sand	0–1	0	7–8	NA	0
Stockton	0–2	6–7	4–6	0	NA

not augment the breeding population (Peery et al. 2010). It is likely that the configuration of the archipelago and how close neighboring islands are to one another (average inter-island distance is 2.4 km) creates steppingstones for bears to access far-shore islands up to 23.8 km from the mainland (Allen et al. 2018). Indeed, landscape configuration is known to be an important predictor of individual movement (Poli et al. 2020). In this archipelagic system, water crossings around 2.4 km allow frequent dispersal of individuals,

yet these distances limit dispersal enough to create genetic structure.

Other factors can contribute to some of the genetic structuring that we observed on the islands. When the species–area relationship has been applied to population genetics, it is often found that allelic richness increases with area (Johnson et al. 2000; Exposito-Alonso et al. 2022). We observed that larger islands like Stockton and Oak had the greatest number of alleles, and smaller islands like Basswood and Sand had the fewest. Thus, we suspect that in the Apostle Islands, island size interacts with isolation to structure this black bear population. Furthermore, the size of the island and the amount of suitable habitat may also contribute to genetic structure (Fahrig 2003). Islands larger than 7.7 km² appear to be sufficiently large and possess enough food resources to support reproducing populations at high densities. These larger, resource-rich islands allow for populations to persist long enough for multigenerational family groups to create genetic structure. Outer Island is the exception; it is the second-largest island that we sampled

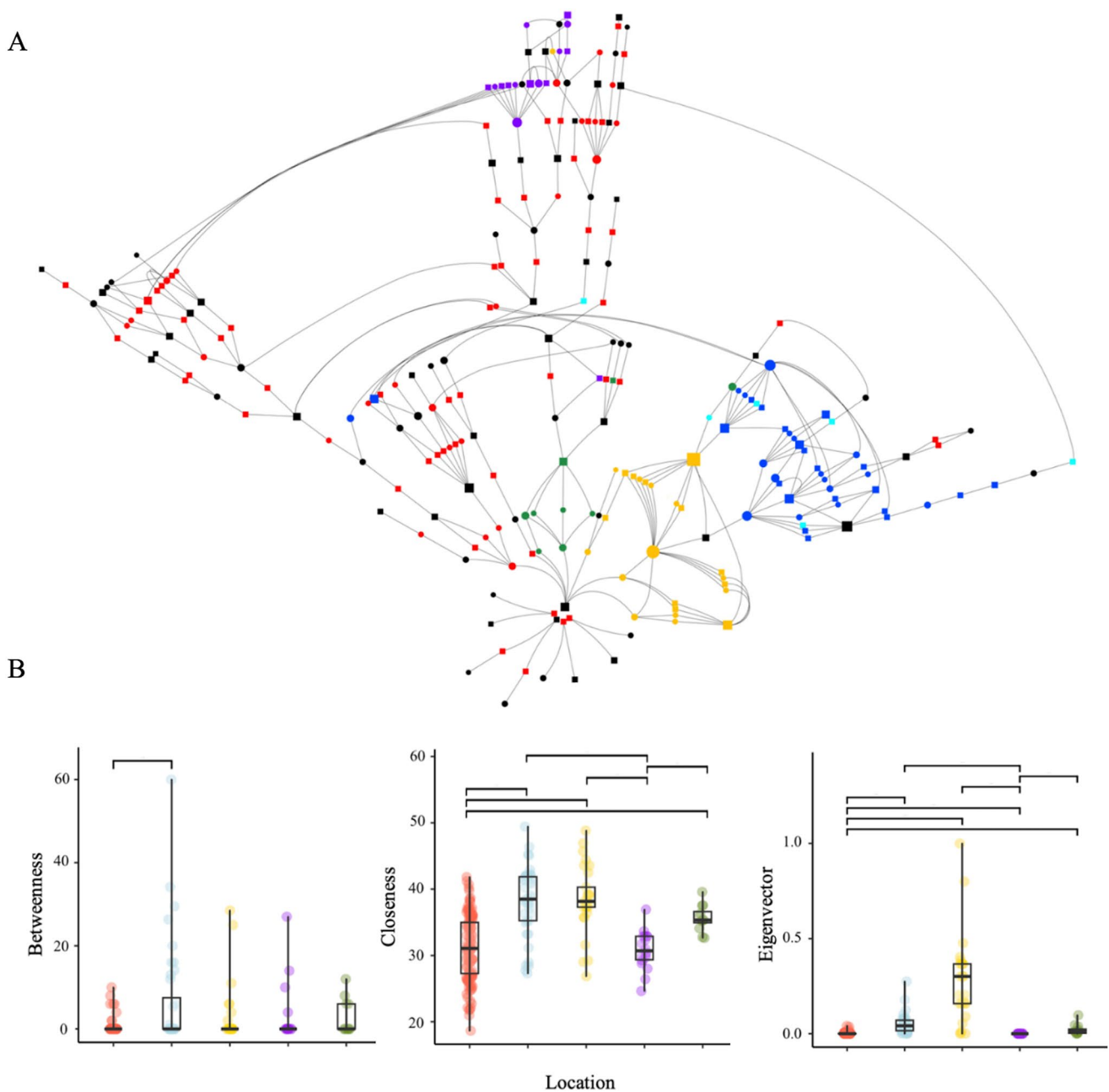


Fig. 3 A) Pedigree network of 141 black bears (*Ursus americanus*) detected in 2020–2022 and their parents (inferred or from previously sampled years 2002–2010) on islands and the mainland in the Apostle Islands National Lakeshore and Red Cliff Reservation of northern Wisconsin from 2002–2022. Nodes represent individual bears (circles=females, squares=males) and edges connect parents to offspring. Node color indicates where individuals were detected (green=Basswood, orange=Oak, red=Mainland, purple=Sand,

blue=Stockton, teal=all other islands, black=never captured but kinship inferred). Node sizes correspond to relative number of offspring. B) Betweenness, closeness and eigenvector centralities of the pedigree network. Bears are grouped by sub-networks of bears detected in each location plus inferred individuals (Mainland=red, Stockton=blue, Oak=orange, Sand=purple, Basswood=green). Bars above boxes indicate significant pairwise differences at $p < 0.05$

but the farthest from the mainland, and we detected only one individual. Overall, the combination of isolation, island configuration, island size, and resource availability form the patterns of connectivity and genetic structure in this archipelagic black bear population.

We found that dispersal between islands and the mainland was higher than dispersal between islands. We suspect that annual fluctuations in resource availability and subsequent local demographic rates could result in bears migrating to where there may be more resources and territories—whether

that is from islands to the mainland, or from mainland to the islands. Growing island populations and saturated territories may lead to surplus individuals seeking territories on the mainland. Fleming (1997) detected five Stockton Island bears emigrating to the mainland during an 11-year period and hypothesized that increasing density encouraged adult bears to leave the island in search of food and breeding grounds. They only detected three bears dispersing to the island during that time, from unknown locations. The phenomenon of island-to-mainland dispersal has been reported in multiple taxa and has led to a paradigm shift toward islands having the potential to function as sources rather than sinks (Bellemain and Ricklefs 2008). This pattern has even been described in other carnivore populations in the Apostle Islands (Shen et al. 2021; Smith et al. 2021). For instance, Smith et al. (2021) detected an asymmetric pattern of dispersal from the Apostle Islands to mainland Wisconsin, identifying the Apostle Islands as important refuge subpopulations for the state endangered American marten (*Martes americana*) recovery network. Since islands are relatively protected from anthropogenic disturbances including land change, hunting pressure, and human conflict, they may also act as a refuge for bear populations (Smith et al. 2021; Fleming 1997). Indeed, hunting pressure has been shown to alter mating patterns and dispersal distance in black bears (Moore et al. 2014). Across the range of grizzly bears in North America, Lamb et al. (2020) found that with increasing human influence on the landscape, more immigrants were required to sustain a stable bear population. High black bear density on the Apostle Islands could lead to islands having potential to act as source populations. Determining whether any metapopulation-like structure exists on these islands would require robust estimates of vital rates and abundance in addition to the dispersal that we documented herein.

Even in this well-connected system, not every island played an equal role in connectivity. Our network analysis revealed that bears on Stockton, Basswood, and particularly Oak Islands are a part of large, closely related family groups. Individuals with many offspring have offspring that are in turn highly reproductive (i.e., eigenvector centrality). In a separate system but using similar network analyses, McFarlane et al. (2021) found that tightly related family groups of caribou occurred more often in isolated patches. While these tightly related family groups certainly result from the effect of isolation, reproductive skew is also common in high-density black bear populations. When the density of reproductive males is high and home ranges overlap, social hierarchies form and dominant males sire most offspring (Costello et al. 2009). While most individuals on Oak, Stockton and Basswoods Islands are only related to other individuals on the same island, some individuals connected

the islands to other islands and the mainland. Indeed, Oak, Stockton, and Basswood Islands also had the highest closeness centrality, indicating that these islands are most important for spreading genetic material throughout the network (Latora and Marchiori 2001). Interestingly, many of the bears inhabiting the smaller islands are related to bears on Stockton, Oak, and Basswood Islands. For example, a male that we detected on Stockton and Oak Islands produced offspring on Stockton, Hermit, and Basswood Islands, while his parents were detected on Oak and Basswood Islands. These findings demonstrate how the islands act as steppingstones; and some lineages importantly connect multiple islands. Like the mating dynamics described by Moore et al. (2015) in Michigan black bears, a few individuals create genetic cohesion, have multiple mates and generations of offspring. One female, who was detected on Stockton Island from 2002 to 2022 and has produced many of the current Stockton Island bears, has the highest betweenness centrality in the network. This sow connects Stockton Island with mainland lineages, demonstrating the importance of dispersing individuals in demographic viability of island populations. Analyzing the pedigree data using a network graph allowed us to uncover unexpected patterns and important areas for reproduction and gene flow amongst bear populations within the archipelago.

The bears on the Apostle Islands appear to be well-connected yet structured into five clusters. We suspect that islands are reliant upon the mainland for continued genetic and demographic viability, yet also augment mainland bear populations. Our work reveals the potential for a metapopulation dynamic and demonstrates the existence of gene flow between small, isolated populations. Our work demonstrates that these black bear populations, which span lands stewarded by the Tribe and National Park, are tightly linked. Altogether these results highlight the overall high connectivity of bear populations across multiple jurisdictions, and the importance of inter-agency co-management between the Apostle Islands National Lakeshore and Red Cliff Band of Lake Superior Chippewa to sustain this population into the future.

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Data availability Data available from lead author upon reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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