

American black bear population abundance and genetic structure on an island archipelago

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Abstract: American black bears (*Ursus americanus*) occur on numerous islands within the Apostle Islands National Lakeshore in Lake Superior, Wisconsin, USA, and provide an opportunity to better understand patterns in abundance and genetic structure among island populations. In 2002 and 2010, we derived genotypes from DNA obtained from hair samples collected at hair traps to estimate population abundance on Stockton (40.7 km²), Sand (11.9 km²), and Oak (20.6 km²; 2010 only) islands. We used Huggins closed-population mark-recapture models to estimate island-specific abundance and density. We used Program STRUCTURE and parentage analysis to examine inter-island population structure, migration patterns, and relatedness. In 2010, we estimated abundance on Stockton, Sand, and Oak islands to be 13.1 (95% CI = 12.4–13.8), 10.1 (95% CI = 9.3–11.0), and 18.1 (95% CI = 17.3–19.0) bears, with a density of 0.32, 0.85, and 0.88 bears/km², respectively. Whereas abundance on Sand Island increased 60% since 2002 ($N = 6.3$, 95% CI = 4.0–8.6), abundance on Stockton declined 50% ($N = 26.3$, 95% CI = 24.7–27.9), including an 83% decline in detected females. Density on Oak Island was the highest reported in Wisconsin, although we identified 13 individuals as likely mates or offspring of a single male. We identified 4 genetic groups, corresponding to Stockton, Sand, Oak, and Mainland ancestry. No individuals on Stockton or Sand islands were assigned ancestry from another island, whereas one male on Oak Island was assigned Stockton ancestry. We detected individuals of predominately Mainland ancestry on all but Hermit Island, suggesting a high rate of immigration from the mainland. We suggest these islands can support high bear densities, but may undergo rapid shifts in sex-specific abundance. Genetic connectivity appears maintained by male-mediated gene flow, but a small number of wide-ranging females may sustain inter-island population viability.

Key words: American black bear, Apostle Islands National Lakeshore, density, genetic structure, mark-recapture, migration, *Ursus americanus*, Wisconsin

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The spatial distribution of suitable habitat is fundamental to the regulation and persistence of animal populations (Hanski and Gilpin 1991). Populations occupying small isolated habitat patches may be more vulnerable to intrinsic and extrinsic demographic processes. For example, population persistence among discrete patches may depend on inter-patch connectivity, where dispersal of individuals among patches counters local extinctions (Harrison 1991). Connectivity, which is influenced by distance between patches and a species' dispersal

ability, impacts gene flow, colonization rates, and population density across patches (Schmiegelow and Nudds 1987, Lande 1988, Hanski and Gilpin 1991). Additionally, isolated populations may develop or harbor unique genetic characteristics (Hedrick 1995, Chatzimanolis et al. 2010), adding to the list of considerations surrounding conservation of isolated populations.

Large mammals often occur at low densities and require expansive, contiguous landscapes to maintain viable populations (Proctor et al. 2012). Though such species may be highly mobile, natural or anthropogenic fragmentation may create barriers

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to migration, producing metapopulation dynamics and increasing extinction risk among isolated populations (Coulon et al. 2004, Hanski et al. 2013). Moreover, many mammals exhibit male-biased dispersal and female-biased philopatry (Greenwood 1980, Mabry et al. 2013) that may facilitate sex-specific gene flow (Proctor et al. 2012).

Black bears (*Ursus americanus*) are highly adaptable, range widely, have male-biased dispersal, and often occur in fragmented or isolated habitats across their range in North America (Hellgren and Maehr 1992, Pelton et al. 1999, Costello et al. 2008). In such isolated habitat, greater male dispersal distances may facilitate genetic connectivity among patches, whereas female philopatry may limit population growth and long-term viability. Onorato et al. (2007) demonstrated that long-distance male dispersal primarily maintained genetic connectivity in a black bear metapopulation in southwestern North America, and Proctor et al. (2012) hypothesized that restricted female genetic interchange among subpopulations diminished long-term population viability for grizzly bears (*U. arctos*) in western North America. Understanding spatio-temporal limitations to bear population viability in increasingly fragmented landscapes is critical for effective conservation planning throughout their range (Shaffer 1981, Hellgren and Maehr 1992).

Archipelagos offer a unique system for studying spatio-temporal patterns of population demographics in patchy landscapes. Within the Apostle Islands National Lakeshore (AINL) in Lake Superior, USA, biologists have documented black bears on 14 of 21 islands (Van Stappen et al. 2006). Black bear populations at AINL may be functioning as a metapopulation (Hanski and Gilpin 1991), with population persistence among islands supported via immigration from a mainland population or neighboring islands (Belant et al. 2005). Although previous studies suggested some movement among islands (Trauba 1996), research has not addressed island-specific genetic population structure and connectivity throughout the archipelago.

Our primary objective was to estimate population abundance, density, and sex ratios of black bears on Stockton, Sand, and Oak islands, and to compare bear density on Stockton and Sand islands to 2002 estimates (see Belant et al. 2005). We also examined genetic population structure, genetic variability, and each individual's population of origin to explain migration patterns and gene flow at AINL. We predicted that islands would contain genetically

distinct black bear populations and that individuals detected on the same island would be apportioned similar genetic ancestry, with contrasting ancestries less common among females. As hypothesized by Belant et al. (2005), we also predicted that we would observe high levels of genetic variation consistent with a high rate of immigration of mainland-origin individuals to island populations.

Study area

Study area descriptions follow Belant et al. (2005). The Apostle Islands archipelago is located off the northern tip of the Bayfield Peninsula in southwestern Lake Superior (46°42'–47°05'N, 90°24'–91°03'W), Wisconsin, USA (Fig. 1). The archipelago represents the continental northwestern limit of the hemlock (*Tsuga canadensis*)–white pine (*Pinus strobus*)–northern hardwood forest and consists of 22 islands ranging from 0.01 to 40.7 km², with all except 1 island comprising AINL (Kraft et al. 2007). Under their standard regulations, the State of Wisconsin has permitted hunting in the AINL since its designation as a National Lakeshore in 1970 (Van Stappen et al. 2006). Mean maximum and minimum monthly temperatures are 24.7° and 13.4°C in July and –5.4° and –14.4°C in January, respectively (National Climatic Data Center 2011). Annual precipitation is approximately 75 cm, with approximately 200 cm of snow. A maturing second-growth northern hardwood forest dominates the landcover of the archipelago (Kraft et al. 2007, Sanders and Grochowski 2012).

Stockton Island is 7.7 km from the mainland, 40.7 km², and the largest island within AINL. Elevation ranges from 183 m (lake level) to approximately 240 m (Rose 1988, Kraft et al. 2007). Logging during the late 1800s destroyed much of the island's forests. Logging ended in 1955, but there were also extensive fires during the 1950s (Rakestraw 1976). Deciduous forests now cover 87% of Stockton Island (Trauba 1996). Other landcover types include forested wetlands (6% of the island), beaver flowages (3%), and red (*Pinus resinosa*) and white pine-dominated forests (2%). Though the timing and duration of black bear occurrence among islands is unknown, the most recent colonization of Stockton Island likely occurred in the early 1970s or later (Anderson and Trauba 1991). Density on Stockton Island was estimated at 0.52 bears/km² in 1992 (Smith et al. 1994).

Sand Island is 11.9 km² and is located 2 km from the mainland, with elevations rising to 200 m above

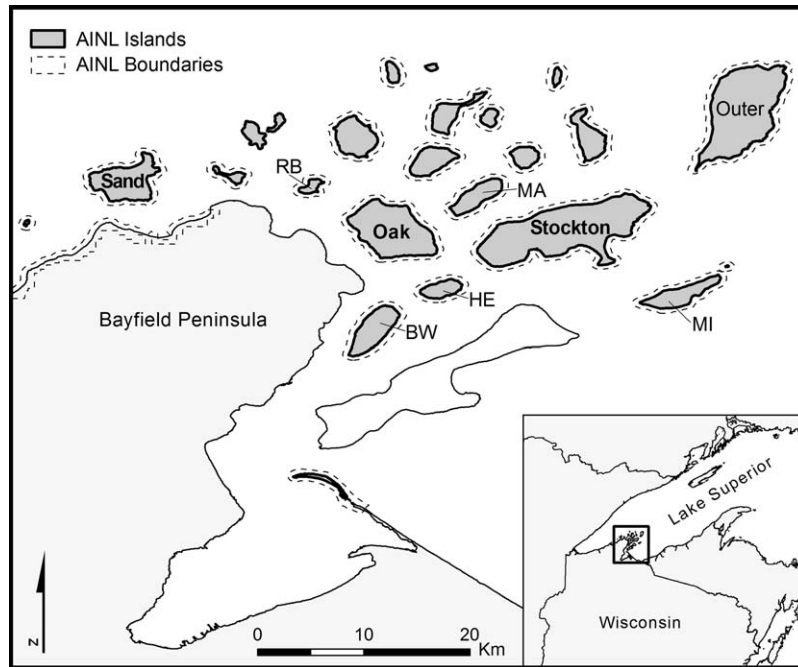


Fig. 1. Location of islands surveyed using hair traps to estimate American black bear abundance and genetic structure during 2002 and 2010. Surveyed islands included Stockton, Sand, Oak, Outer, Basswood (BW), Hermit (HE), Manitou (MA), Michigan (MI), and Raspberry (RB) islands at Apostle Islands National Lakeshore (AINL), Wisconsin, USA.

lake level. Intensive logging continued from the late 1800s until 1975. Currently, mixed hardwood–conifer forests cover approximately 83% of the island; Canada yew (*Taxus canadensis*) and mountain maple (*Acer spicatum*) are common in the understory. Less abundant landcovers include approximately 7% black spruce (*Picea mariana*)–tamarack (*Larix laricina*) swamp, 6% semi-open bog, and 3% white pine–hemlock forest.

We added Oak Island to our survey in 2010 because evidence suggested presence of a viable bear population (Belant et al. 2005; J.F. Van Stappen, AINL, unpublished data). Oak Island is 20.6 km² and is located between Stockton Island (2.6 km distant) and mainland Wisconsin (2.1 km). Maximum elevation is 330 m and high clay bluffs and sandstone cliffs characterize the shoreline, with rugged deep ravines supporting numerous streams (Rose 1988, Kraft et al. 2007). Most ravines were intensively logged from the 1850s to 1929, and approximately 80% of the island burned in 1943 (Judziewicz and Koch 1993, Busch 2008). Selective logging for red oak occurred on much of the island in the 1940s (Beals and Cottam 1960). Currently, Oak

Island contains predominately northern hardwood–hemlock, bigtooth aspen (*Populus grandidentata*)–paper birch (*Betula papyrifera*), and balsam fir (*Abies balsamea*) forests (Sanders and Grochowski 2012).

Islands are separated from each other and the mainland by ≥ 2 km. Although inter-island and island–mainland movements occasionally occurred (Trauba 1996; J.F. Van Stappen, unpublished data), we assumed immigration and emigration were low. Trauba (1996) observed only 4 instances of natural emigration and 1 instance of immigration during a 12-year study on Stockton Island, and Fleming (1997) estimated mean annual subadult and adult mortality on Stockton Island at $<10\%$. Additionally, a mark–recapture analysis by Belant et al. (2005) further suggested population closure on Stockton and Sand Island. Based on these findings, and the short duration of our study, we assumed our study areas to be geographically and demographically closed during the 2002 and 2010 sampling periods.

We also sampled 6 other islands with previous records of bear occurrence, including Outer (32.4 km²), Basswood (8.0 km²), Michigan (6.5 km²), Manitou (5.4 km²), Hermit (3.1 km²), and Raspberry

(1.3 km²) islands. Outer Island is approximately 24 km from the mainland and ≤ 6 km from neighboring islands; Basswood Island is approximately 2 km from the mainland; Michigan Island is approximately 18 km from the mainland and 4 km from Stockton Island; Manitou Island is approximately 2 km from Stockton and Oak islands; Hermit Island is approximately 4 km from the mainland and 2.5 km from Stockton, Oak, and Basswood islands; Raspberry Island is approximately 3 km from the mainland and neighboring islands (Fig. 1).

Methods

Hair-trapping

We overlaid a 1.6-km $\times$ 1.6-km grid on each island and grouped cells composed of $<50\%$ land with adjacent cells (Belant *et al.* 2005). We constructed hair-sampling sites (hair traps) using 4-barbed, 15.5-gauge wire to create an enclosure around ≥ 3 trees (approx. 1.5-m radius) with a single wire approximately 50 cm above ground (Woods *et al.* 1999). We placed one hair trap in each grid cell and set traps in areas believed to maximize black bear detection (e.g., animal trails, near potential food sources). We placed decaying logs in the center of the enclosure and saturated them with 0.5 L of fish oil as an attractant. We applied anise oil to vegetation at or near the perimeter of the trap, approximately 2 m above ground. We reapplied both lures at the beginning of each sampling session.

Traub (1996) estimated black bear home ranges on Stockton Island at 7.2 and 32.9 km² for adult females and males, respectively. Given an average trap density of 1/2.8 km² on Stockton Island, adult female home ranges contained approximately 3 traps and adult males approximately 12 traps. Home range estimates were unavailable for Sand and Oak islands. Trap density was similar to other black bear hair-trap mark-recapture studies (Boersen *et al.* 2003, Settlage *et al.* 2008, Sollmann *et al.* 2012, Wilton *et al.* 2014).

In 2002, we set 15 hair traps on Stockton (1 trap/2.7 km²) and 5 traps on Sand Island (1 trap/2.4 km²). We checked traps for 4 sessions between 26 June and 13 August 2002 and collected hair from traps at approximately 2-week intervals. Similarly, in 2010, we set 14 traps on Stockton Island (1 trap/2.9 km²), 5 traps on Sand Island (1 trap/2.4 km²), and 7 traps on Oak Island (1 trap/2.9 km²) and checked them for 4 sessions at approximately 10-day intervals between 3

June and 9 July 2010. The difference in timing and duration of sampling between years resulted from logistical constraints. During each trap check, we removed all hair from each barb and placed each sample in a separate paper envelope that we labeled and air-dried before processing. We did not move traps among sessions because of our high trap density.

For genetic structure and ancestry analyses, we also set hair traps on the mainland (4 in 2003), Oak (3 in 2003), Basswood (2 in 2004; 4 in 2010), Manitou (1 in 2004 and 2010), Hermit (2 in 2010), Michigan (2 in 2004; 3 in 2010), Outer (2 in 2004), and Raspberry (1 in 2004) islands. We opportunistically collected hair samples from these traps 1–3 times/year.

DNA analyses

We analyzed samples that contained a minimum of 1 visible guard-hair root or 5 underfur, extracting DNA with QIAGEN DNeasy Tissue kits following the manufacturer's instructions (Qiagen Inc., Mississauga, Ontario, Canada). We followed a strict laboratory protocol and quality assurance monitoring to prevent DNA contamination among samples (Paetkau 2003). We omitted from further analyses any results that indicated a mixture of DNA from ≥ 2 individual bears. In 2002, we identified individuals by genotyping samples at 6 microsatellite loci (G1D, G10C, G10H, G10M, G10X, MU59), adding a seventh locus (G10L) for genotyping samples collected in 2010 (Paetkau and Strobeck 1998). We reanalyzed genotypes at individual markers that failed to satisfy a series of strength and pattern criteria for high confidence scoring, after which samples with any low-confidence scores remaining in their 6- or 7-locus genotypes were culled (Paetkau 2003). To ensure accurate individual identifications (Kendall *et al.* 2009) we reanalyzed mismatching markers in similar pairs of genotypes (Paetkau 2003). We estimated genetic diversity by calculating number of alleles (A), expected heterozygosity (H_E), and observed heterozygosity (H_O) for each locus using Program GENEPOP version 4.2 (Raymond and Rousset 1995, Rousset 2008). We determined the sex of the identified bears by analyzing 1 sample/multilocus genotype (i.e., 1 sample/individual) using size polymorphism in the amelogenin gene (Ennis and Gallagher 1994). We also analyzed 1 sample/individual at 8 or 9 additional microsatellite markers (CXX20, CXX110, G1A, G10B, G10J, G10L, G10P, G10U, Mu50; Paetkau *et al.* 1998), for 15 total microsatellites, to aid analyses of population structure and relatedness.

Population abundance estimates

We used Huggins closed-population mark–recapture models in Program MARK (Huggins 1991, White and Burnham 1999) to estimate population abundance for Stockton, Sand, and Oak islands. We pooled capture histories among islands to increase sample size, but derived abundance estimates for each island. We compared 14 a priori candidate models with varying effects on capture and recapture probability. First we developed 7 models, including models with a behavioral response following initial capture (Behavior), a session-specific change in capture probability (Time), island-specific capture probabilities (Island), and all combinations of these effects. Then we duplicated each model (i.e., 14 models) and added sex as an individual covariate on capture probabilities (Sex). We used Akaike Information Criterion corrected for small sample size (AIC_c) to rank model support (Burnham and Anderson 2002), and we derived population abundance estimates by model-averaging all models using AIC_c weights (w_i) to accommodate model uncertainty and minimize the effect of uninformative parameters (Arnold 2010).

Population structure

We used Program STRUCTURE (Pritchard et al. 2000) to identify population genetic structure and estimate the proportion of each individual's ancestry in each genetically identified population to infer potential natal origin (Davies et al. 1999). This analysis used 15-locus genotypes from the 2002 and 2010 population studies, as well as additional samples collected on the mainland and other surveyed islands during 2003 and 2004. We included genotypes from black bear hair samples collected at Pictured Rocks National Lakeshore, Michigan, USA (Sollmann et al. 2012), to increase the mainland sample size ($n = 4$) and to confirm which genetic group in the analysis represented "Mainland" ancestry. We determined the number of genetic groups by varying the putative number of populations (k). We tested values of k from 2 to 7 because these encompassed the value with the highest maximized likelihood and values that exceeded a biologically plausible population structure (see Results). We performed 4 repetitions at each value of k , except for 8 runs at $k = 4$ and $k = 5$, with a 450,000 iteration-step run and 50,000-step burn-in, under the assumptions of correlated allele frequencies and admixture, and without reference to source population. We selected the optimal value of k as the value with the highest maximum likelihood estimate and by assessing the biological plausibility

of the inferred genetic structure at each value of k (Pritchard et al. 2000).

We also examined potential parent–offspring pairs by searching for individuals that shared alleles at all 15 microsatellites (Mendel 1866). We were unable to use programs that attempt to assign probabilities to given relationships by reference to allele frequencies because they are inappropriate in a study system where allele frequencies vary so dramatically (see Results).

Results

Hair-trapping

In 2002, we collected 635 hair samples from Stockton and Sand Island, 372 (59%) of which contained sufficient material for genetic analysis and comprised 324 usable hair samples on Stockton Island and 48 samples on Sand Island (Belant et al. 2005). In 2010, we collected 553 hair samples from Stockton, Sand, and Oak islands, 475 (86%) of which contained sufficient material for genetic analysis and comprised 250 usable hair samples on Stockton Island, 80 samples on Sand Island, and 145 samples on Oak Island. We collected hair samples during each session from an average of 90% ($SD = 15$) of total hair traps set per island and averaged 5.1 ($SD = 2.3$) hair samples per trap per session during 2002 and 2010 (Table 1).

DNA analyses

Of hair samples with sufficient material for genetic analysis, we observed a 69% ($n = 256$) and 85% ($n = 403$) amplification rate in 2002 and 2010, respectively. We did not perform match probability analyses (e.g., P_{ID} , P_{SIB}) because they lack meaning given the severe population structure and local consanguinity in the study system (see Results – Population structure), but we noted that only 1 pair of multilocus genotypes matched at 6 of the 7 markers used for individual identification, suggesting low risk of having sampled 2 individuals with identical 7-locus genotypes (Paetkau 2003). Mean H_E and H_O on Stockton Island in 2002 was 0.77 and 0.84 ($n = 6$ loci) and in 2010 was 0.79 and 0.86 ($n = 7$ loci), respectively (Table 2). Mean H_E and H_O on Oak Island in 2010 was 0.71 and 0.77, respectively. Though sample size was limited for Sand Island, mean H_O in 2010 was 0.87 ($n = 6$ loci), which was an 8% decline from 2002 (Belant et al. 2005).

We identified 67 bears during the 2002 and 2010 surveys, comprising 32 bears in 2002 on Stockton and Sand islands (Belant et al. 2005) and 41 bears in

Table 1. American black bear hair-trapping results from Stockton, Sand, and Oak islands at Apostle Islands National Lakeshore, Wisconsin, USA, during 2002 and 2010.

Island	Year	Session	Traps with hair samples	Hair samples/trap		No. bears	No. new bears	
				$\bar{x}$	SD		M	F
Stockton	2002	1	14	7.8	2.9	17	9	8
		2	15	7.6	4.1	22	3	4
		3	13	4.3	2.5	17	2	0
		4	14	3.2	1.7	15	0	0
Total			56			71	14	12
	2010	1	11	5.4	3.2	10	8	2
		2	14	5.6	2.3	7	2	0
		3	14	5.4	2.4	7	1	0
		4	14	5.0	1.4	6	0	0
Total			53			30	11	2
Sand	2002	1	3	3.3	1.5	4	1	3
		2	4	3.8	2.8	4	0	2
		3	3	1.7	0.6	2	0	0
		4	4	4.5	3.9	3	0	0
Total			14			13	1	5
	2010	1	5	7.0	3.3	7	3	4
		2	5	5.8	1.6	7	0	2
		3	3	3.3	1.7	5	0	1
		4	5	5.2	1.6	5	0	0
Total			18			24	3	7
Oak	2010	1	7	7.4	1.3	13	6	7
		2	7	4.7	1.9	12	3	2
		3	7	6.1	2.3	9	0	0
		4	7	5.6	2.3	9	0	0
Total			28			43	9	9

2010 on Stockton, Sand, and Oak islands. In 2002, we detected 26 bears (14 M, 12 F) on Stockton Island and 6 bears (1 M, 5 F) on Sand Island. In 2010, we detected 13 bears (11 M, 2 F) on Stockton Island, 10 bears (3 M, 7 F) on Sand Island, and 18 bears (9 M, 9 F) on Oak Island. We detected 4 bears (2 M, 2 F) on Stockton Island and 2 female bears on Sand Island in both 2002 and 2010. There were 84 detections in 2002 and 97 detections in 2010

(Table 1). In 2002, we did not detect new individuals on Stockton Island after session 3 or on Sand Island after session 2. In 2010, we did not detect new individuals on Stockton or Sand Island after session 3 or on Oak Island after session 2 (Table 1). Overall, 25 of 32 (78%) bears in 2002 and 30 of 41 (73%) bears in 2010 were detected at >1 hair trap across all sessions. In 2002, we detected 4 bears in 1 session, 11 bears in 2 sessions, 11 bears in 3 sessions, and 6 bears

Table 2. Expected heterozygosity (H_E), observed heterozygosity (H_O), and number of alleles (A) for 7 microsatellite loci used to identify individual American black bears on Stockton Island, Apostle Islands National Lakeshore, Wisconsin, USA, 2002 and 2010.

Marker	2002			2010		
	H_E	H_O	A	H_E	H_O	A
G10C	0.63	0.69	7	0.68	0.69	5
G1D	0.83	0.88	8	0.81	1.00	7
G10H	0.77	0.88	9	0.81	0.85	7
G10M	0.75	0.81	7	0.71	1.00	4
MU59	0.84	0.92	8	0.82	0.62	6
G10X	0.80	0.85	9	0.83	0.92	6
G10L	—	—	—	0.84	0.92	7
Mean	0.77	0.84	8	0.79	0.86	6

Table 3. Model selection results for 2002 and 2010 Huggins closed-population mark–recapture models ranked by Akaike Information Criterion corrected for small sample size (AIC_c) with number of parameters (K), the difference in AIC_c between each model and the top-ranked model (ΔAIC_c), AIC_c weights (w_i), and model deviance to estimate American black bear abundance for Stockton, Sand, and Oak islands at Apostle Islands National Lakeshore, Wisconsin, USA. Models listed include models up to a cumulative w_i of 90%. Post hoc model omitted in 2002 because of poor parameter estimation is denoted with an asterisk (*).

Year	Model	K	AIC_c	ΔAIC_c	w_i	Deviance
2002	Island	2	165.86	0.00	0.24	161.77
	Null	1	166.98	1.11	0.14	164.94
	Time	4	167.27	1.41	0.12	158.95
	Behavior + Island	3	167.48	1.62	0.11	161.29
	*Behavior + Island + Sex	5	168.07	2.21	0.08	157.58
	Time + Behavior + Island	6	168.33	2.47	0.07	155.64
	Behavior	2	168.37	2.51	0.07	164.28
	Null + Sex	2	168.86	3.00	0.05	164.76
	Time + Behavior	5	169.36	3.50	0.04	158.87
2010	Behavior	2	215.84	0.00	0.40	211.77
	Behavior + Sex	4	216.94	1.10	0.23	208.69
	Behavior + Island + Sex	8	217.43	1.59	0.18	200.50
	Behavior + Island	4	219.95	4.11	0.05	211.70
	Null + Sex	2	220.55	4.71	0.04	216.48
	Time	4	221.19	5.34	0.03	212.93

in 4 sessions. In 2010, we detected 14 bears in 1 session, 9 bears in 2 sessions, 7 bears in 3 sessions, and 11 bears in 4 sessions.

Population abundance estimates

For Stockton and Sand islands in 2002, the island group (Island) model had 1.7 times more support than the next-highest-ranked model (Null; Table 3); abundance estimates between the Island and Null models were similar. Model-averaged estimated abundance in 2002 on Stockton Island was 26.3 (95% CI = 24.7–27.9) and on Sand Island was 6.3 (95% CI = 4.0–8.6), with an estimated density of 0.65 and 0.53 bears/km², respectively (Table 4). For Stockton, Sand, and Oak islands in 2010, the behavioral capture response (Behavior) model had 1.7 times more support than the next-highest-ranked model (Behavior + Sex; Table 3). Model-averaged estimated abundance in 2010 on Stockton, Sand, and Oak islands was 13.1 (95% CI = 12.4–13.8),

10.1 (95% CI = 9.3–11.0), and 18.1 (95% CI = 17.3–19.0) individuals, with an estimated density of 0.32, 0.85, and 0.88 bears/km², respectively (Table 4). Mean annual growth rate on Stockton Island was –8.3% and on Sand Island was 6.1%.

For 2002 and 2010 Stockton Island population abundance estimates, model-averaged capture and recapture probability among sessions was ≥ 0.67 and ≥ 0.53 , respectively (Table 4). Capture and recapture probability among sessions for Sand Island was ≥ 0.58 and ≥ 0.53 , respectively. In 2010, model-averaged capture and recapture probability among sessions for Oak Island was 0.74 and 0.52.

Population structure

We used 15-locus microsatellite genotypes from 95 individuals (54 M, 41 F) for the analysis of genetic population structure and individual ancestry (Fig. 2). These comprised 35 bears (23 M, 12 F) detected on

Table 4. Estimated American black bear abundance (N), density (D , bears/km²), initial capture probability (P), and recapture probability (c), including 95% confidence intervals (CI) for Stockton, Sand, and Oak islands at Apostle Islands National Lakeshore, Wisconsin, USA.

Island	Year	N	95% CI	D	95% CI	P	95% CI	c	95% CI
Stockton	2002	26.3	24.7–27.9	0.65	0.61–0.69	0.67	0.35–0.88	0.65	0.47–0.80
	2010	13.1	12.4–13.8	0.32	0.30–0.34	0.75	0.51–0.89	0.53	0.37–0.67
Sand	2002	6.3	4.0–8.6	0.53	0.34–0.72	0.58	0.20–0.89	0.53	0.26–0.79
	2010	10.1	9.3–11.0	0.85	0.78–0.92	0.75	0.51–0.90	0.54	0.37–0.71
Oak	2010	18.1	17.3–19.0	0.88	0.84–0.92	0.74	0.53–0.88	0.52	0.40–0.63

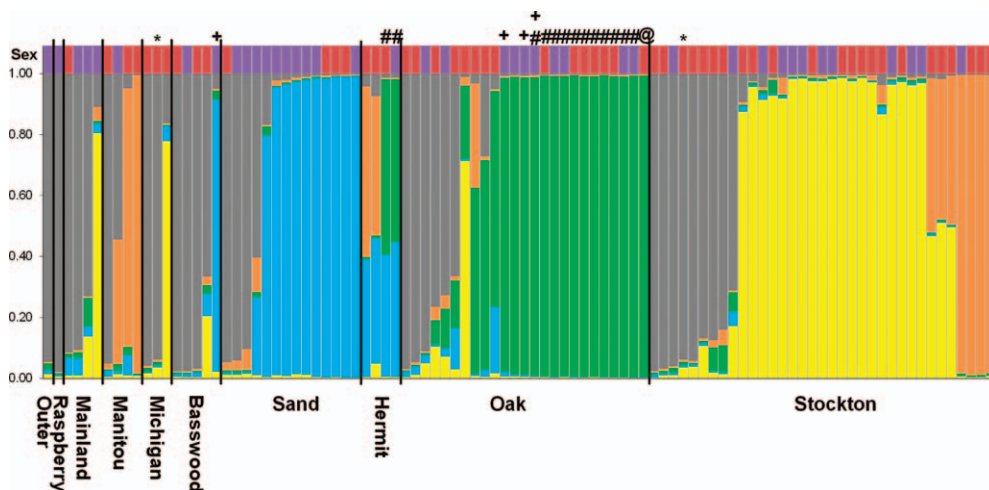


Fig. 2. Individual genetic ancestry results from American black bear hair samples collected during 2002, 2003, 2004, and 2010 at Apostle Islands National Lakeshore (AINL), Wisconsin, USA. Estimates of individual ancestry were derived from the STRUCTURE run that produced the highest likelihood, which occurred when 5 populations were assumed (i.e., $k = 5$). Populations corresponded to Stockton (yellow, orange), Sand (blue), Oak (green), and Mainland (grey). Males and females are coded above ancestry as red and purple, respectively. One individual was detected on 2 islands, so is represented twice in the bar plot (*; it was only included once in the analysis). The putative offspring (#) and mates (+) of a founding male from Oak Island (@) are indicated, including 2 offspring of mixed ancestry on Hermit Island, whose mother was assigned Sand Island genetic ancestry, but was detected on Basswood Island. Note that 1 of the 4 mates to the founding male may also have been his daughter.

Stockton Island, 14 (4 M, 10 F) on Sand Island, 25 (15 M, 10 F) on Oak Island, 5 (3 M, 2 F) on Basswood Island, 4 (3 M, 1 F) on Manitou Island, 4 (3 M, 1 F) on Hermit Island, 2 (M) on Michigan Island, 1 (F) on Outer Island, 1 (F) on Raspberry Island, and 4 (1 M, 3 F) on the mainland unit.

Because of our low number of mainland samples from AINL, inclusion of the Pictured Rocks reference data set was necessary to initially identify which group represented Mainland ancestry. However, enough individuals with Mainland ancestry ($n = 31$ with $>50\%$) were present in the local AINL data set to satisfy sample-size requirements (i.e., 25–30 individuals; Hale *et al.* 2012) and genetic grouping performed better without the reference data. Therefore, our final STRUCTURE analysis excluded the Pictured Rocks reference data set. At each step of k from 2 through 5, a group of individuals assigned common ancestry in the previous step was split comparatively cleanly in two, with a group from Oak Island being distinguished from the rest at $k = 2$, followed by the separation of a Stockton Island group ($k = 3$), a Sand Island group ($k = 4$), and finally a second Stockton group ($k = 5$; Fig. 2). Likelihoods were maximized at

$k = 5$, after which further subdivisions of data were less biologically coherent (i.e., putative populations contained no purebred members).

At $k = 5$, our analysis did not assign any individuals detected on Stockton or Sand islands substantial ancestry from a genetic group associated with another island, but one male bear detected on Oak Island was assigned predominantly Stockton Island ancestry (Fig. 2). However, 7 of 23 males and 2 of 12 females on Stockton Island, 1 of 4 males and 3 of 10 females on Sand Island, and 4 of 15 males and 2 of 10 females on Oak Island were assigned predominately Mainland ancestry. We detected 4 bears on the mainland—3 (1 M, 2 F) with Mainland ancestry and 1 female with predominantly Stockton ancestry. Of 9 males whose first detection was on Stockton Island in 2010, 6 had Stockton and 3 had Mainland ancestry.

Individuals detected on Basswood ($n = 5$), Hermit ($n = 4$), Manitou ($n = 4$), Michigan ($n = 2$), Outer ($n = 1$), and Raspberry ($n = 1$) islands were of mixed (approx. 50:50) or distinct ancestries. Comparing genetic cluster assignments of all individuals to their geographic capture locations, we identified 24 of 54 males and 14 of 41 females as plausible migrants, though we could not verify them as the actual

migrant versus the offspring of a migrant. We also identified one inter-island movement by a male bear that we detected on Stockton Island in 2002 and on Michigan Island in 2004 (Fig. 2).

Our analysis did not place any single bear in the Stockton, Sand, or Mainland genetic groups in >6 potential parent–offspring relationships, with many of those putative relationships probably being sibling relationships rather than parent–offspring. By contrast, we identified a single male of Oak Island genetic ancestry as the likely mate of 3 females, giving rise to 10 offspring (6 M, 4 F), with all 14 members of this family group being detected on Oak Island in 2010, and being assigned >97% Oak Island ancestry (Fig. 2). The genotype of one of these putative mothers was also compatible with her being the offspring of the dominant breeding male. This male also appeared to have sired 2 bears (1 M, 1 F) that we detected on Hermit Island, with a mother whose only detection was on Basswood Island, but whose ancestry was apportioned 85% to Sand Island by STRUCTURE. These 2 Hermit Island offspring were assigned roughly 50:50 Oak:Sand ancestry. Water crossings among these 4 islands and between islands and the mainland were ≤ 4 km (Fig. 1).

Discussion

The density of bears on Oak Island in 2010 (0.88/km²) was the highest reported in Wisconsin (Kohn 1982, Smith et al. 1994, Storlid 1995, Fleming 1997, Belant et al. 2005), surpassing Stockton Island in 2002 by 35.4%, but similar to Sand Island in 2010. Density on Stockton Island decreased 50% in 8 years, whereas density on Sand Island increased 60% during the same period, exceeding that on Stockton Island. Moreover, the density of known females on Sand Island increased 40% from 2002 to 2010 and was also greater than known female density on Stockton Island (0.05/km²) in 2010. We note that with only 2 sampling years, small sample sizes, and absence of age data, the observed abundance trend on Sand Island may be less accurate. However, our high mean capture and recapture probabilities and absence of new bears detected after sampling session 2 or 3 suggest that we detected most, if not all, bears on surveyed islands. The apparent stability of the known female population on Sand Island and loss of known females on Stockton Island lends support for the suggestion by Belant et al. (2005) that greater food abundance on Sand Island, closer proximity to

the mainland bear population, or an interaction of these factors may sustain the greater female density on Sand Island. Belant et al. (2005) also suggested the small size (<12 km²) of Sand Island may limit its capacity to support >1 male bear. Though our data do not reveal home-range characteristics or age of bears, the 3 males detected in 2010 all had Sand Island genetic ancestry and were individuals that we did not detect during our 2002 survey. These findings suggest that either Sand Island's habitat may be able to support additional males, that some or all of these males were yearlings that had not dispersed, or that multiple males may divide their home range between Sand Island and the mainland.

Although our sample sizes precluded sex-specific abundance estimates, the observed decline from 12 to 2 detected females on Stockton Island is interesting given the relatively stable number of males detected during the same years (14 and 11, respectively). We note that changing sex ratio was not due to management removal ($n = 0$) or legal harvest (J.F. Van Stappen, unpublished data). We suggest ≥ 3 possible explanations for this pattern. First, trap-shy behavior by females may have limited trap encounters (Ebert et al. 2010), though this was unlikely given high overall capture probabilities observed in 2002 and 2010. Second, we may not have detected females as frequently because of their smaller average home-range size (Trauba 1996). This is also unlikely given that home ranges of adult females on Stockton Island were 7.2 km² (Trauba 1996), which provided approximately 2.5 traps available per female. In addition, trap density was similar between 2002 and 2010 survey periods (2.7/km² and 2.9/km², respectively). Third, the observed 50% decrease in total abundance from 2002 to 2010 (26.3 to 13.1 bears) may have resulted from an actual decline in number of females on Stockton Island.

Consistent with our prediction, we identified proportionally fewer females (34%) than males (44%) with genetic group assignments that suggested emigration from their genetic natal origin. The rarity of female natal dispersal (Costello et al. 2008) and potential geographic barriers to migration (Paetkau et al. 1998) may have facilitated the decline in female abundance on Stockton Island. Assignment of natal origins suggested 2 plausible female immigration events to Stockton Island from the mainland and 1 plausible female emigration event to the mainland from Stockton Island. We note that although these individuals have natal origins that suggest a migration

event, it is also plausible that they are offspring of the actual migrants. Moreover, of females having a Stockton Island capture location and genetic ancestry ($n = 10$), all had $\geq 86\%$ Stockton assignment, suggesting little admixture among Stockton and other genetic groups. Female philopatry and the distances among islands and between islands and the mainland may limit the rate of successful migration events (Belant *et al.* 2005). Water crossings of 2–4 km inhibited female brown bear (*U. arctos*) dispersal, but male dispersal persisted over water barriers ≤ 7 km (Paetkau *et al.* 1998). Stockton Island is separated from the mainland by 7.7 km and from other islands by > 2 km, potentially limiting female immigration.

Constraints on female migration may not be sufficient to explain the observed decline on Stockton Island. Though reproductive data were unavailable, the only 2 females detected on Stockton Island in 2010 were also present in 2002, suggesting that no or few new females entered the Stockton population by births or immigration, while potentially 10 females died or emigrated since 2002. It is plausible that high density in 2002 caused density-dependent suppression of recruitment by birth (Garshelis 1994). If female recruitment by immigration was negligible, female abundance could decline as a result of infanticidal or aggressive males that suppress recruitment through increased emigration or cub mortality (Lindzey *et al.* 1986, Garshelis 1994). Increasing density on Stockton Island in the 1990s corresponded to increased cub mortality by infanticide and starvation (Anderson and Trauba 1991, Trauba 1996). In 2010, we detected 9 (82% of detected males) previously unidentified males on Stockton Island that we assigned either Stockton or Mainland ancestry, suggesting greater male immigration from the mainland and/or greater male birth rates. A heavily male-biased adult sex ratio may have increased the probability of males encountering and killing cubs that were not their own (Clark 1991, Garshelis 1994). Infanticide by males may strongly regulate populations, and this apparently high male turnover and high male:female ratio on Stockton Island may have increased this occurrence (LeCount 1987, Odden *et al.* 2014) and its consequent effect on female abundance.

However, the apparent low retention of males (14%, $n = 14$) and females (17%, $n = 12$) from 2002 to 2010 on Stockton Island also suggests low food availability as a primary factor influencing population abundance (Lindzey *et al.* 1986). Reproductive

success of female black bears and cub survival is closely associated with food availability (Bunnell and Tait 1981, Rogers 1987, Odden *et al.* 2014). Anecdotal evidence suggested that food availability may have decreased on Stockton Island over the study period. Clear-cuts and selectively logged forests in early seral stages may provide abundant berry forage and support increased bear density (Young and Beecham 1986, Brodeur *et al.* 2008, Peacock *et al.* 2011). Logging on Stockton Island ceased in 1955 and succession of older cut areas may have reduced soft mast production. Lindzey *et al.* (1986) associated decreased berry production following succession of clear-cut areas with a declining black bear population over 10 years on an island. Moreover, they associated reduced food availability with decreased cub production and survival, and increased subadult dispersal and adult emigration.

The apparent low female recruitment from immigration may limit population viability on Stockton Island if cub recruitment is also suppressed. If female migration among islands is limited, demographic rescue from the mainland or other islands may be insufficient to balance local extinctions (Harrison 1991, van Oort *et al.* 2010). However, we identified a female on Basswood Island (having Sand Island ancestry) that mated with a male detected on Oak Island; she then gave birth to 2 offspring (1 M, 1 F) detected on Hermit Island. Though these suggested movements among 4 islands separated by ≤ 4 -km water crossings may have resulted from a combination of familial movements, this demonstrates the strong reproductive influence that individuals may have on inter-island genetic structure. Although our results do not describe how this archipelago functions as a metapopulation, a small number of wide-ranging females may sustain inter-island population viability.

Parentage analysis identified many competing hypotheses in the genetic groups other than Oak Island, and these hypotheses would require field data on age and association to resolve. The identification of a founding male on Oak Island was the key to determining its first-order relatives that comprised most of the Oak Island genetic “population” and illustrates how the boundary between a population-level paradigm and an individual-level paradigm becomes blurred as our understanding of individual origins and relationships increases in detail. For example, genetic drift in a small population can be understood as a mathematical population process, but on Oak Island we see it operating at the

individual level, where we observed 61% mean heterozygosity ($n = 15$ loci) in the 10 offspring of the founding male, compared with 81% for the 31 bears of Mainland ancestry; this was a large decline only a few generations post-colonization.

The Oak Island results also illustrate how allele frequencies can change dramatically in a few generations of close breeding to produce the signature of a unique genetic population in grouping analyses. The Stockton results are even more intriguing from this perspective; they suggest waves of colonization, expansion, and decline by groups with comparatively uniform allele frequencies that may be little more than extended families. One could speculate that the oldest extant genetic group is currently in decline through a process of emigration and interbreeding, because it is disproportionately represented on neighboring islands, particularly in individuals of approximately 50:50 ancestry. Meanwhile, the group that currently dominates the island contains 19 purebred members, exceeding half of Stockton Island's genetic population, but new mainland immigrants may begin to interbreed with or supplant that dominant group, especially as inbreeding limits the duration of a single family's dominance (Hedrick et al. 2014).

A similar pattern has been suggested in another island in Lake Superior, with wolves (*Canis lupus*) on Isle Royale having colonized in approximately 1950, only to experience a near total decline in successful reproduction as inbreeding was thought to have severely limited fitness (Hedrick et al. 2014). The difference is that the Apostle Island archipelago is close enough to the mainland to permit regular recolonization, or intermixing that reduces inbreeding depression and extirpation risk (Tallmon et al. 2004). We detected bears having $\geq 50\%$ Mainland ancestry on all but Hermit Island, and our STRUCTURE analysis assigned 11 females detected on various islands to a Mainland natal origin. Also, despite small population sizes, we observed high genetic variability compatible only with a high level of immigration of Mainland-origin individuals (Paetkau et al. 1998, Belant et al. 2005). Though female philopatry may limit the frequency of movements between genetic groups, the detection of a Mainland-ancestry female on Outer Island (32.4 km²; approx. 24 km from the mainland and 6 km from the nearest island) implies that female-mediated gene flow throughout the archipelago is possible. However, no females were detected on Michigan Island (6.5 km²), which is approximately 4 km from Stockton Island and 18 km

from the mainland (Belant and Van Stappen 2002). Our parentage and grouping analyses were limited by sample size and number of microsatellite markers, but provided direct evidence of male- and female-mediated gene flow and parent-offspring relationships among islands (Waser and Stroheck 1999).

Observed patterns of population change on Stockton and Sand islands indicate the potential for rapid shifts in density and that island genetic groups may be reacting differently to island-specific rates of immigration, emigration, and habitat succession (i.e., food availability; Lindzey et al. 1986). Additionally, female philopatry may limit female migration rates, but the presence of few wide-ranging females may be important for sustaining genetic groups throughout the archipelago (Proctor et al. 2012). Though our data do not reveal extrinsic or intrinsic mechanisms underlying these demographic patterns, they lend evidence to the sensitivity of small, isolated black bear populations to environmental and demographic variability (Lindzey et al. 1986, Hellgren et al. 2005). However, the occurrence of individuals with predominately Mainland ancestry on nearly all islands suggests strong resiliency of these populations through immigration from the mainland bear population (Belant et al. 2005). Our 2002 and 2010 surveys suggest a complex interaction among black bear life history, metapopulation dynamics, and temporal shifts in habitat suitability.

Continued monitoring of total and sex-specific population abundance, growth, and migration rates at AINL is important to better determine how the archipelago is functioning as a metapopulation (Harrison 1991, van Oort et al. 2010). Our results corroborate Belant et al. (2005) and suggest that maintaining a viable mainland population may be key to long-term persistence of AINL bear populations. We recommend further examination of genetic population structure, population fitness, and gene flow among islands and between islands and the mainland population. Estimating these parameters will further our understanding of the interaction among metapopulation theory, genetic structure, and black bear population regulation in archipelagos and fragmented landscapes.

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