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RESEARCH

Population genetic structure of the American oystercatcher in Northwestern Mexico

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Abstract

Assessments of genetic diversity and population structure are essential for defining management units to prioritize conservation and management efforts. A susbspecies of the American oystercatcher (*Haematopus palliatus frazari*) breeds in northwestern Mexico and is endangered due to its small population size, restricted distribution, and high vulnerability to anthropogenic activities. This study analyzed the genetic diversity and population structure of the American oystercatcher in six areas in northwestern Mexico. We used two molecular markers, the mtDNA control region and single nucleotide polymorphisms (SNPs), to calculate genetic diversity, population structure, the kinship coefficient, and migration rates among these geographic areas. Genetic diversity was high when calculated using mtDNA (h = 0.689) and relatively high for SNPs (h = 0.222). We identified genetic structure across geographic areas based on 1,889 SNPs. Individuals from the Baja California peninsula were genetically differentiated from those of the Sonora and Sinaloa populations. Indeed, the population of the Baja California peninsula can be considered a distinct demographic unit. This may be explained by high philopatry (low dispersal and recruitment of breeders) and regional habitat discontinuity (Sonora and Sinaloa were similar but different from the Baja California peninsula). Of note, the Bahia Santa María (Sinaloa) population serves as a source of individuals to other populations in the region. We recommend that conservation efforts prioritize major concentration sites, such as Bahia Santa María (Sinaloa), while also protecting smaller, isolated demographic units, such as the populations of Bahia de la Paz (Baja California Sur) and Bahia de Ceuta (Sinaloa).

Keywords American oystercatcher · Genetic divergence · Molecular markers · MtDNA · Shorebirds · SNPs · Source population

Introduction

Shorebirds utilize various habitats during their life cycles and are important indicators of ecological integrity (Piersma and Lindström 2004). Concerningly, shorebird populations in North America have declined by 37% since 1970 (Rosenberg et al. 2019) due to numerous threats, particularly habitat loss and degradation (Newbold et al. 2015; Wang et al. 2022). Given this notable decline, information on shorebird breeding populations in tropical and subtropical regions is critical for their conservation, yet this information is scarce (Clay et al. 2014). Thus, assessing the structure of shorebird populations is essential for understanding their natural history and developing informed conservation strategies (Howe et al. 1989; Clay et al. 2014).

Genetic diversity is essential for the evolutionary potential and long-term survival of species (Ellegren and Galtier

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2016; Scott et al. 2020). Despite their ability to travel long distances, bird populations, such as those of the Hawaiian petrel (*Pterodroma sandwichensis*) (Lombal et al. 2020), are often geographically close but genetically distinct (Friesen et al. 2007). This suggests that ecological factors, such as environmental discontinuity, play important roles in species dispersal and population structure. In addition, historical processes, such as the colonization of new breeding and nesting sites or the utilization of glacial refuges during the Pleistocene (Sonsthagen et al. 2012; Sternkopf et al. 2014), may have strengthened the genetic structure of various populations (Lombal et al. 2020). Assessments of genetic diversity and population structure are essential for identifying and defining management units for threatened species to prioritize conservation efforts and specific actions (Moritz 1994; Palsbøll et al. 2007; Almaki et al., 2016; Laikre et al. 2020).

The molecular techniques used to evaluate the genetic structure of populations have different resolution capacities and costs. Traditionally, studies focused on the mitochondrial genome or nuclear segments; however, more recently, reduced-representation sequencing methods, such as RAD-Seq (restriction-site associated DNA Sequencing; Baird et al. 2008) have provided a better means to evaluate gene flow and connectivity among populations (Davey and Blaxter 2010). These methods employ thousands of molecular markers, such as single nucleotide polymorphisms (SNPs), and offer high-resolution information on the entire genome. The resulting broad genome coverage and the use of SNPs provide a better way to identify and demographically evaluate populations than traditional methods (Friesen 2015; Younger et al. 2017; Taylor et al. 2018; Rexer-Huber et al. 2019). For the purposes of management, each genetically distinct group can be treated as a management unit (Seddon et al. 2005; Younger et al. 2017; Zimmerman et al. 2020; D'Urban-Jackson et al. 2020).

The American oystercatcher (*Haematopus palliatus*) utilizes coastal habitats year-round (Clay et al. 2014). Although the taxonomic classification of this species remains controversial (Jehl 1985; American Oystercatcher Working Group et al. 2020), the subspecies *Haematopus palliatus frazari* resides on both coasts of the Baja California peninsula and along the shores of mainland Mexico (American Oystercatcher Working Group et al. 2020; Clay et al. 2014). A zone of hybridization between American (*H. palliatus frazari*) and black (*Haematopus bachmani*) oystercatchers has been reported on the west coast of the Baja California peninsula (Jehl 1985), which could impact the genetic diversity of both species. Based on extrapolations from existing data, the size of the *H. palliatus frazari* population has been estimated to be ~3000 individuals (Clay et al. 2014). Due to its small population size, restricted distribution, and high vulnerability to anthropogenic activities, *H. palliatus frazari* is classified as endangered by the Mexican government (Secretaría de Medio Ambiente y Recursos Naturales 2018).

The American oystercatcher is a long-lived species that does not breed until reaching three years of age (American Oystercatcher Working Group et al. 2020). Breeding pairs defend their territories and tend to nest in the same ones for several consecutive years (American Oystercatcher Working Group et al. 2020). A study in El Rancho Island, located in Bahia Santa María-La Reforma, Sinaloa, Mexico, has confirmed that banded birds retain the same breeding territories (G. Fernández and J. A. Castillo-Guerrero, unpubl. data), which has also been reported for the American oystercatcher in locations on the Atlantic coast (American Oystercatcher Working Group et al. 2020). Natal philopatry in this species is relatively high, with birds banded as chicks being resighted between 0.5 and 69.0 km from their natal territories in different breeding sites along the Atlantic coast (American Oystercatcher Working Group et al. 2020). In El Rancho Island, 131 chicks have been banded since 2018; of these, 8 chicks (6.1%) were resighted as breeders within Bahía Santa María and Bahía Navachiste, at distances of 0.3 to 51.2 km (13.7 ± 20.5 SD) from their natal territories (G. Fernández and J. A. Castillo-Guerrero, unpubl. data). Thus, genetic structure may be present in the populations of the American oystercatcher breeding in northwestern Mexico due to its high philopatry and, consequently, potentially limited gene flow.

Prior to this study, no information on the genetic diversity or population structure of the American oystercatcher in northwestern Mexico was available. To address this lack of information, we conducted the first extensive study to assess the genetic diversity and population structure of *H. palliatus frazari* in this region. We also evaluated the kinship coefficient and migration rates across its reproductive distribution range. By determining the genetic structure and diversity of *H. palliatus frazari*, management units that support and inform conservation strategies for this endangered shorebird may be established.

Methods

Study area

The region of northwestern Mexico includes the states of Sonora, Sinaloa, Nayarit, Baja California, and Baja California Sur, as well as the Gulf of California and islands of the Pacific Ocean (Fig. 1). The climate of the region is primarily desert-like, with extremely few periods of high-intensity rainfall, which occur in late-summer, and low-intensity storms during winter (García 2004). In particular, the

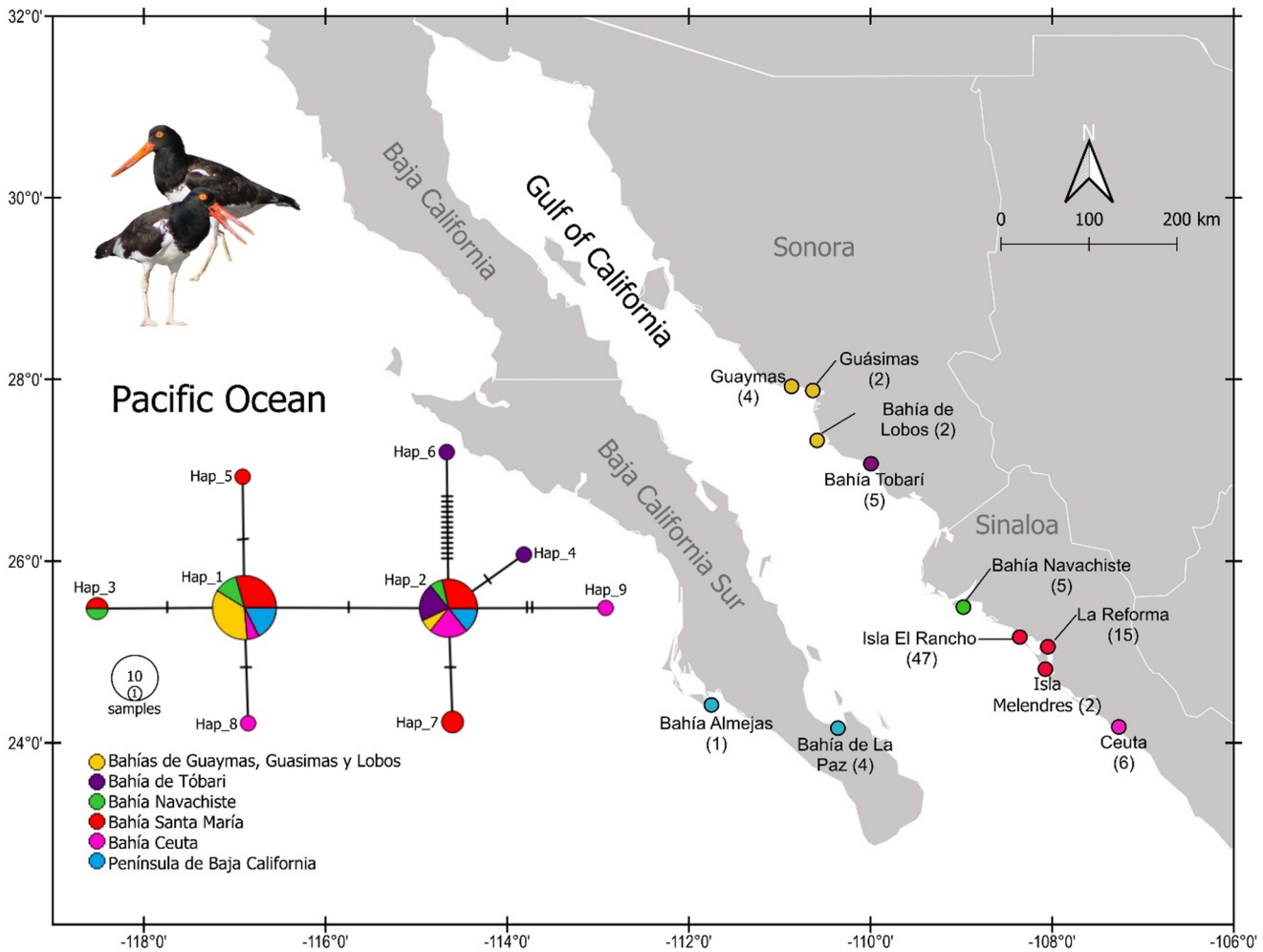

Fig. 1 Sampling locations during the reproductive season in northwestern Mexico and American oystercatcher (*Haematopus palliatus frazari*) haplotype network (mitochondrial control region). The color indicates the area of origin. The black lines perpendicular to the connecting line indicate the number of mutations between haplotypes. The number of samples per site is shown in parentheses

climate of most of the Baja California peninsula and western Sonora is arid, with these areas usually receiving less than 250 mm of rain annually. In contrast, Sinaloa exhibits a tropical wet-and-dry climate with a dry season; the dry winter months typically receive less than 40 mm of rain, while over 150 mm of rain falls during each summer month.

Our study included 11 breeding sites (2 sites in Baja California Sur and 9 sites in mainland Mexico; Fig. 1): Bahía Almejas (24°25′3.78″ N, 111°44′54.13″ W; 1 sample), Bahía de La Paz (24°9′44.67″ N, 110°21′21.12″ W; 4 samples), Guaymas (27°55′22.50″, 110°52′0.30″ W; 4 samples), Guasimas (27°52′38.61″ N, 110°37′56.17″ W; 2 samples), Salina de Lobos (27°19′41.40″ N, 110°35′7.26″ W; 2 samples), Bahía Tobari (27°4′16.14″ N, 109°59′32.18″ W; 5 samples), Los Anegados-Bahía Navachiste (25°29′41.00″ N, 108°58′28.07″ W; 5 samples), Isla El Rancho (25°9′54.58″ N, 108°21′14.44″ W; 47 samples), La Reforma (25°3′31.21″ N, 108° 2′39.28″ W; 15 samples), Melendres (24°48′41.22″ N, 108°4′18.84″ W; 2 samples), and Playa Ceuta (24°10′31.36″ N, 107°15′47.87″ W; 6 samples). The 11 sites were grouped into six areas, considering discrete coastal wetlands. However, when the sample size was very small (<5), they were grouped into areas with the nearest site as follows: PEN (Peninsula de Baja California, 5 samples), GUA (Bahía de Guaymas-Lobos, 8 samples), TOB (Bahía Tobarí, 5 samples), NAV (Bahía Navachiste, 5 samples), BSM (Bahía Santa María, 64 samples), and CEU (Bahía de Ceuta, 6 samples; Fig. 1).

Sampling and DNA extraction

We captured oystercatchers from February to July during the breeding season when adults defended their territories. Adult individuals were captured using decoy and noose mats. Territorial birds attacked the decoy and became trapped in the

knots of the mat. The chicks were captured when they were between 4 and 6 weeks old. Once captured, the adults and chicks were measured, weighed, and marked with colored alphanumeric bands. A blood sample from each individual was collected from the brachial vein using a disposable 25G syringe. Briefly, the puncture area was cleaned with alcohol, and 500 µL of blood was extracted and preserved with 450 µL of lysis buffer (100mM EDTA, 100mM Tris, 10mM NaCl, and 10% SDS). DNA was extracted following a proteinase K protocol (Gemmel and Akiyama, 1996) and quantified by fluorometry with a Qubit 2.0 instrument (Life Technologies; Carlsbad, CA).

mtDNA markers

We selected 40 representative samples from the six areas considered in this study, retaining most of the samples from PEN (5), GUA (7), TOB (5), NAV (4), and CEU (6), as well as 13 of the 64 samples from BSM. Thus, we covered the whole geographic distribution of *H. palliatus frazari*. We amplified the mitochondrial DNA control region (mtDNA CR) using the primers RC_NCBI_F (5'-AACGCATATCT CCCACACGG-3') and RC_NCBI_R (5'-GAGCAAGTT GTGCTAGGGGT-3'), which were designed based on the mitogenome of the Eurasian oystercatcher (*Haematopus ostralegus*) and blackish oystercatcher (*Haematopus ater*). The PCR reaction conditions consisted of cycling at 95 °C for 5 min followed by 35 cycles of 30 s at 95 °C, 1 min at 53 °C, and 1 min at 72 °C. The PCR products were sent for sequencing to Macrogen, Inc. (Seoul, South Korea). We evaluated the quality of the sequences with Codon Code Aligner v. 9.0.2 (CodonCode Corporation, Dedham, MA), and sequences were aligned in MEGA-X v. 11.0.9 (Kumar et al. 2018).

SNP analysis

Genomic DNA (20 ng) from 93 individuals was used to prepare the NextRAD sequencing genotyping libraries used by SNPsaurus, LLC (Eugene, USA), following the methodology described by Rusello et al. (2015); gDNA was fragmented and adapter-linked by tagmentation using a Nextera DNA Flex (Illumina Inc., San Diego, USA). Subsequently, the fragmented DNA was amplified for 27 cycles using restrictive-sequence primers with an additional fragment at the 3' end (GTGTAGAGCC) to systematically reduce the diversity of the library fragments. In this way, only fragments starting with this sequence could be hybridized and efficiently amplified. NextRAD libraries were sequenced with a Novaseq 6000 SP sequencing system (Illumina) with 122-bp single-end reads.

A quality analysis of reads was performed with FastQC v. 0.11.9 (Babraham Bioinformatics, Cambridge, UK; https://www.bioinformatics.babraham.ac.uk/projects/fastqc/). The adapter sequence (CTGTCTCTCTTATA) was trimmed with Cutadapt v. 2.8 (Marcel 2011). A reference assembly was generated with 'denovo.pl' from the 'Stacks' pipeline (Catchen et al. 2013) using ten samples that were randomly selected across the entire geographic distribution. In the 'Stacks' pipeline ('pstacks' -> 'cstacks' -> 'sstacks' -> 'sstacks' -> 'cstacks' -> 'sstacks' -> 'populations'), the parameters were set to -*M*=3 (number of mismatches allowed between stacked reads within an individual), -*n*=3 (number of mismatches permitted between stacked reads between individuals), -R=0.85 (percent representativeness needed for a locus to be processed), --*max-obs-het*=0.7, and --*min-maf*=0.01 (minimum minor allele frequency required to process a locus). In addition, with VCFTOOLS v. 0.1.13 (Danecek et al. 2011), we filtered the data with --*max-alleles*=3 (each locus had a maximum of three alleles) and --*hwe*=0.01; sites with *p*-values lower than the threshold defined by this option were considered out of Hardy-Weinberg equilibrium and excluded. Finally, after applying these filters, the samples were checked to ensure they contained<30% missing data; otherwise, they were discarded.

Genetic diversity, structure, and genetic differentiation

For mitochondrial DNA analysis, we identified haplotypes, constructed haplotype networks, estimated diversity (h and π), and calculated paired F_{ST} between populations using DNAsp v. 6 (Rozas et al. 2017). For the SNP dataset, we calculated observed heterozygosity (Ho) and expected heterozygosity (He) (total and per area) using GenAlEx v. 6.5 (Peakall and Smouse 2012). F-statistics were calculated for the mtDNA control region and SNPs to analyze population structure with Arlequin (Excoffier and Lischer 2010) and to assess genetic differentiation with the R package 'hierfstat' v. 0.04-22 (Goudet and Jombart 2015). We applied a Benjamini-Hochberg FDR (false discovery rate) correction to p-values. This method is flexible and maintains sensitivity when handling a high number of comparisons. To visualize the haplotype distribution across the sampling sites, a mid-joining haplotype network map was created with the mtDNA control region sequences using PopArt (Leigh et al. 2015).

Additionally, we analyzed population structure using a discriminant analysis of principal components (DAPC) of

the individuals when they were grouped by areas, which was based on genetic distances and conducted with the 'adegenet' package in R Studio (R Core Team 2016). Finally, individuals were grouped using the Bayesian clustering algorithm in Structure v. 2.3.4 (Pritchard et al. 2000), which calculates the proportion of ancestry each individual shares with ancestral population clusters (*K*) and assigns a probability to each cluster. *K* values from 1 to 10 were tested with 5 independent Markov Chain Monte Carlo (MCMC) runs, each with a burn-in period of 50,000 iterations, which were followed by 200,000 iterations. We provided sampling areas (i.e., site as prior information) to help detect subtle structure. Finally, the ad-hoc Δ*K* method (Evanno et al. 2005) was implemented in StructureSelector (Li and Liu 2018) to select the best *K* value. The independent runs of the optimal *K* value were merged with the 'Clumpak' pipeline (Kopelman et al. 2015), and bar graphs were generated.

Kinship analysis

An analysis of kinship among areas using SNP data was conducted with SEEKIN (Dou et al. 2017) using an approach based on a genetic relationship matrix, which was calculated as the covariance between genotypes adjusted for allele frequencies. The kinship coefficient, φij, which was proposed by Manichaikul et al. (2010), was used to assign the following relationships: unrelated (0), third-degree related (0.06), second-degree related (0.125), siblings/parents-offspring (0.25), and monozygotic twins (0.5).

Migration analysis

Using the SNP data, we estimated recent migration with BayesAss v. 3 (Wilson and Rannala 2003), which allowed for many SNP markers to be analyzed. Based on the results, each individual was assigned to a population, and the probability that the individual was a recent immigrant from another population was calculated based on the differences in allele frequencies between populations. After testing different combinations, we used 5,000,000 MCMC steps with 2,000 sampling intervals and 1,000,000 burn-in iterations. The migration rate represented the fraction of immigrants from another population.

Results

A total of 40 sequences (240 bp) were obtained for the mtDNA control region; 398.59 million reads were obtained for the 93 samples with the SNPs. On average, each sample contained 4.15 (± 1.36) million reads. After applying quality and cleaning filters, 1889 SNP markers were retained in 85 samples. The raw read files can be accessed through NCBI-SRA under the Bioproject PRJNA1109518.

Genetic diversity

Nine haplotypes were identified in the mtDNA control region sequences. High haplotype diversity was observed in five areas (> 0.600), except for GUA, which had a diversity of 0.286 (Table 1). The highest numbers of haplotypes were detected in BSM (5) and CEU (4), whereas GUA and PEN had only two haplotypes (Table 1). The haplotype network showed that two haplotypes were present in all areas, and unique haplotypes were found at all sites except PEN (Fig. 1). These haplotypes originated from the common haplotypes shared across all localities and were mainly connected by a few mutations, with the exception of Hap_9 (Fig. 1). Additionally, private haplotypes exhibited low frequencies across the overall population (Fig. 1). Based on the SNP markers, all areas demonstrated similar heterozygosity (Ho) values (average: 0.219 ± 0.002). The area with the highest heterozygosity value was CEU (0.273 ± 0.007), while NAV and SON had the lowest values (0.203 ± 0.005 and 0.203 ± 0.004, respectively) (Table 1).

Table 1 Genetic diversity of the American oystercatcher (*Haematopus palliatus frazari*) during the breeding season in Northwestern Mexico estimated using the mitochondrial DNA control region and single-nucleotide polymorphisms (SNPs) for each area (Bahía Santa María [BSM], Bahía Navachiste [NAV], Bahía de Ceuta [CEU], Bahía Tobari [TOB], Bahía Guaymas-Lobos [GUA], and the Baja California Peninsula [PEN]) and all areas combined (total). Sample size (n), number of haplotypes (H), haplotype diversity index (h), and nucleotide diversity index (π). Na = number of alleles, ho = observed heterozygosity, and he = expected heterozygosity (standard error in parentheses)

	mitochondrial control region				single nucleotide polymorphisms (SNPs)			
Area	*n*	H	h	π	*n*	Na	Ho	He
PEN	5	2	0.600	0.00259	5	1.642 (0.11)	0.230 (0.006)	0.249 (0.005)
GUA	7	2	0.286	0.00124	8	1.698 (0.09)	0.199 (0.004)	0.240 (0.005)
TOB	5	3	0.700	0.02881	5	1.987 (0.005)	0.212 (0.004)	0.246 (0.004)
NAV	4	3	0.833	0.00426	5	1.602 (0.009)	0.208 (0.004)	0.239 (0.004)
BSM	13	5	0.782	0.00486	64	1.621 (0.011)	0.206 (0.005)	0.241 (0.004)
CEU	6	4	0.800	0.00652	6	1.587 (0.10)	0.224 (0.007)	0.254 (0.004)
TOTAL	40	9	0.706	0.00705	93	1.894 (0.192)	0.219(0.002)	0.243 (0.002)

Population structure

The mtDNA control region AMOVA showed a global F_{ST} value of 0.061 ($p = 0.149$). Meanwhile, the pair comparisons among areas revealed a significant difference between TOB and GUA ($F_{ST} = 0.490$, $p = 0.009 \pm 0.0091$; Table 2). On the other hand, SNP markers showed a global F_{ST} of 0.046 ($p = 0.055$), and most p-values in the F_{ST} matrix were significant. The highest F_{ST} values occurred between PEN and CEU (0.119, $p = 0.031$) and PEN and TOB (0.091, $p = 0.023$). In contrast, BSM had the lowest yet significant values when compared with GUA ($F_{ST} = 0.017$, $p = 0.026$) and NAV ($F_{ST} = 0.025$, $p = 0.026$; Table 3). The DAPC analysis retained 25 principal components and identified

Table 2 Analysis of genetic differentiation with the haplotype frequencies of mitochondrial markers in the American oystercatcher (*Haematopus palliatus frazari*) during the breeding season in Northwestern mexico. The F_{ST} values are shown below the diagonal, and p-values are shown above the diagonal (* = $P < 0.05$). Bahía Santa María (BSM), Bahía Navachiste (NAV), Bahía de Ceuta (CEU), Bahía Tobari (TOB), Bahía Guaymas-Lobos (GUA), and the Baja California Peninsula (PEN)

	BSM	NAV	TOB	GUA	CEU	PEN
BSM	-	0.991 ± 0.003	0.108 ± 0.023	0.126 ± 0.036	0.387 ± 0.051	0.711 ± 0.045
NAV	−0.130	-	0.225 ± 0.024	0.496 ± 0.062	0.432 ± 0.029	0.991 ± 0.003
TOB	0.083	0.103	-	0.009 ± 0.009 *	0.991 ± 0.003	0.315 ± 0.077
GUA	0.108	0.018	0.490	-	0.108 ± 0.026	0.567 ± 0.045
CEU	−0.010	−0.029	−0.073	0.324	-	0.315 ± 0.041
PEN	−0.083	−0.186	0.144	−0.010	−0.005	-

Table 3 Paired F_{ST} matrix of American oystercatcher (*Haematopus palliatus frazari*) samples calculated with single-nucleotide polymorphisms (SNPs). Above the diagonal: P values adjusted by FDR-BH (* = $P < 0.05$; ** = $P < 0.01$); below the diagonal: F_{ST} values. Bahia Santa María (BSM), Bahía Navachiste (NAV), Bahía de Ceuta (CEU), Bahía Tobari (TOB), Bahía Guaymas-Lobos (GUA), and the Baja California Peninsula (PEN)

	BSM	NAV	TOB	GUA	CEU	PEN
BSM	-	0.026 *	0.022 *	0.026 *	0.043 *	0.000 **
NAV	0.025	-	0.031 *	0.022 *	0.004 **	0.022 *
TOB	0.043	0.076	-	0.022 *	0.004 **	0.023 *
GUA	0.017	0.033	0.047	-	0.052	0.071
CEU	0.035	0.089	0.084	0.039	-	0.031 *
PEN	0.074	0.071	0.091	0.076	0.119	-

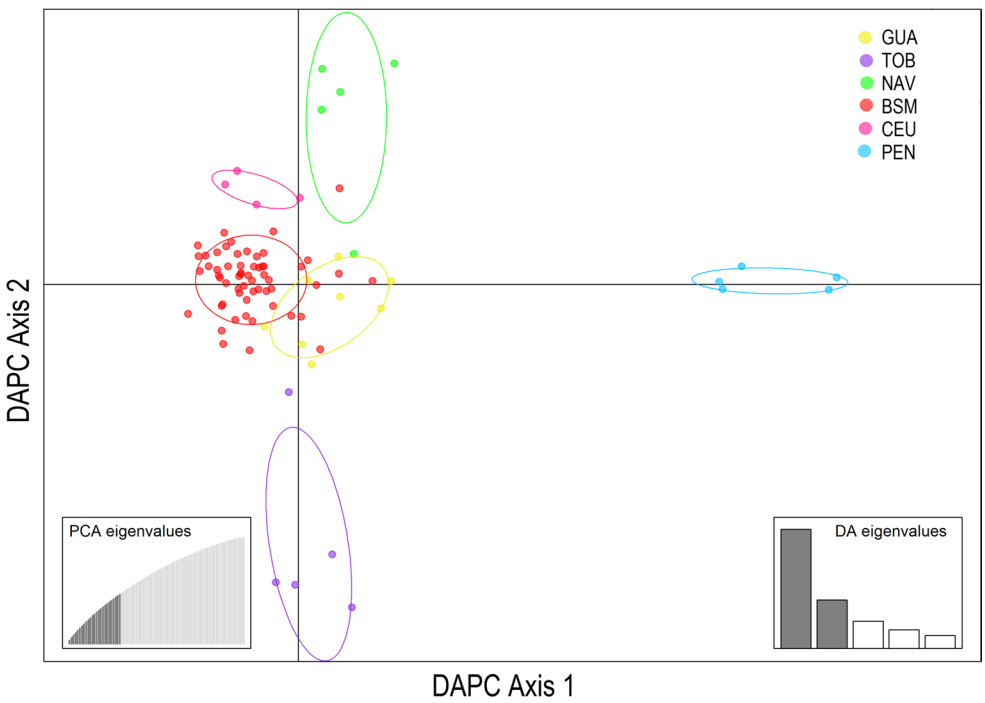

Fig. 2 Discriminant analysis of principal components (DAPC) based on 1889 neutral single nucleotide polymorphisms (SNPs) of the American oystercatcher (*Haematopus palliatus frazari*) during the breeding season in northwestern Mexico. DAPC scatterplot: all DAPCs include a 95% inertia ellipsis for each population, with each dot representing a single individual. Bahía Guaymas-Lobos (GUA), Bahía Tobari (TOB), Bahía Navachiste (NAV), Bahía Santa María (BSM), Bahía de Ceuta, and the Baja California peninsula (PEN)

six genetic clusters, one for each area (non-overlapping ellipses; Fig. 2). The group with the most differentiation was PEN, although TOB, NAV, and CEU also formed separate groups; BSM and GUA were the most similar groups (Fig. 2). These results indicate that the peninsula harbors a differentiated population, as well as substructure across various areas of the mainland (Sonora and Sinaloa). Finally, the Bayesian cluster analysis in Structure identified three genetic clusters ($K=3$) based on the ΔK of Evanno et al. (2005). Almost all areas, except for PEN, were dominated by a widely distributed cluster (Fig. 3). A visual inspection of Structure admixture plots for $K=4$ (Fig. 3) revealed a new cluster with considerable influence on CEU and TOB, which was consistent with the results of the DAPC and F_{ST} analyses.

Kinship analysis

The degree of kinship among individuals within each area varied considerably. The mean kinship coefficient value in PEN and CEU showed a second-degree relationship between the individuals in the sample, indicating close kinship. In TOB, the individuals exhibited a third-degree relationship, whereas in BSM, GUA, and NAV, the low index values indicated that there was no kinship relationship between the individuals sampled (Fig. 4).

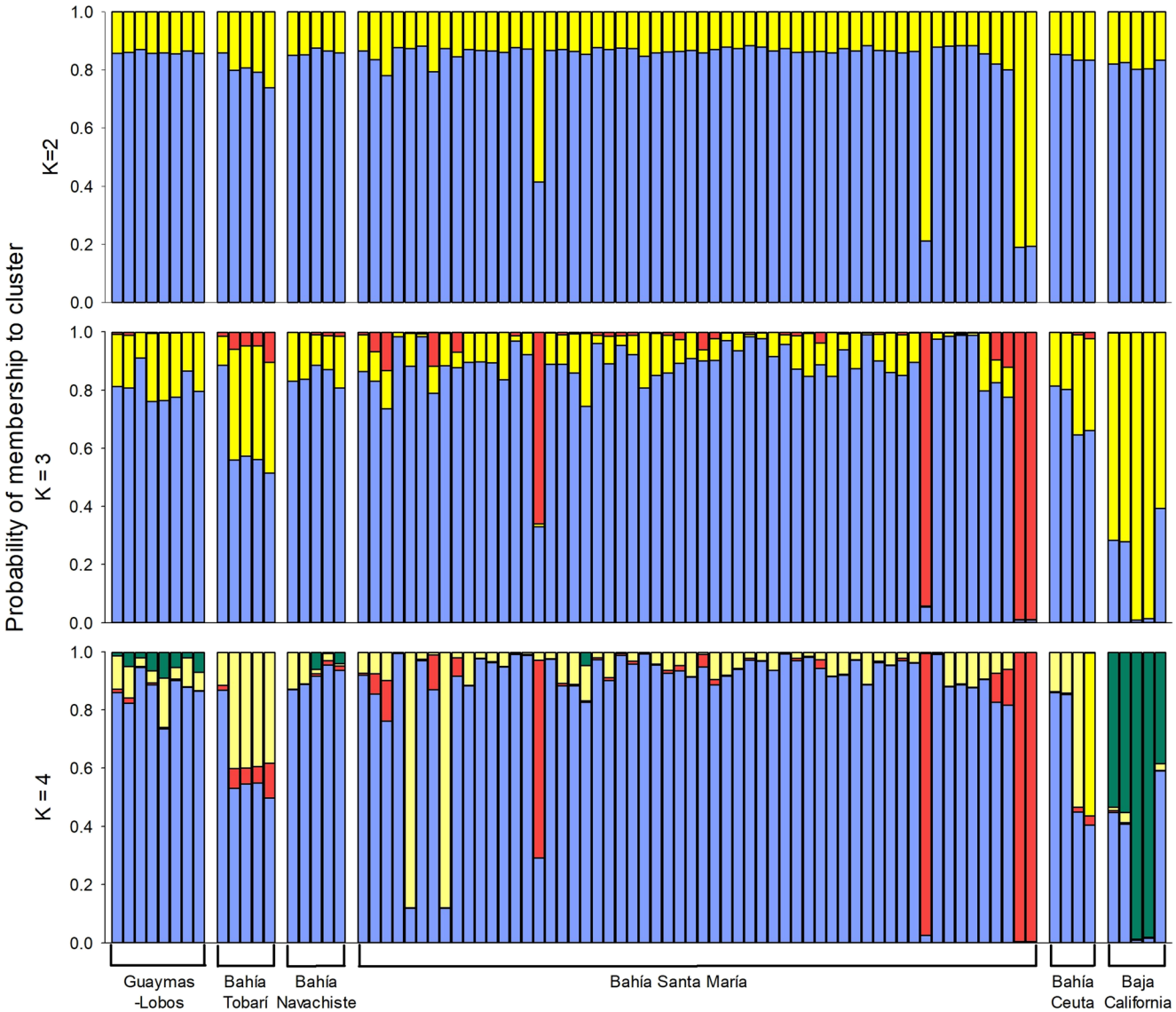

Fig. 3 Structure results displaying population structure for the American oystercatcher (*Haematopus palliatus frazari*) from $K=2$ to $K=4$. The membership threshold proportions (q) for assigning individuals to specific clusters were $K2=0.66$, $K3=0.64$, and $K4=0.74$. Each individual is shown as a vertical bar, with colors representing the proportion of ancestry assigned to each cluster. The samples range from northern Sonora to southern Sinaloa, concluding with individuals from the Baja California peninsula

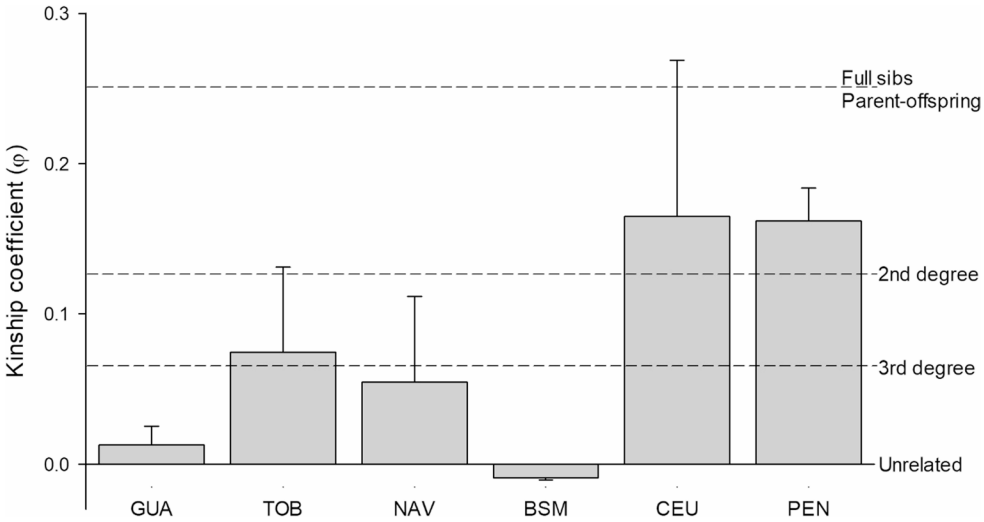

Fig. 4 Mean Kinship coefficient across breeding areas of the American oystercatcher (*Haematopus palliatus frazari*). Horizontal lines indicate kinship thresholds: unrelated individuals, third-degree relatives, second-degree relatives, and full siblings/parent-offspring (dash-dotted line). Standard errors are present on bars. Bahía Guaymas-Lobos (GUA), Bahía Tobari (TOB), Bahía Navachiste (NAV), Bahía Santa María (BSM), Bahía de Ceuta, and the Baja California peninsula (PEN)

Migration analysis

The migration rates varied among sites (Table 4). We found that BSM received the lowest proportion of immigrants while contributing the largest proportion to other areas, indicating that it acts as a source population, especially for GUA and TOB. Migration to and from the different areas was relatively low (Table 4).

Discussion

The genetic analyses using a reduced-representation SNP set presented here are the first for the American oystercatcher and have implications for the management and conservation of its subspecies *H. palliatus frazari*. The results offer compelling evidence of genetic population structuring. Based on the three analyses (DAPC, F_{ST}, and Structure), individuals from PEN showed notably greater differentiation from those of the remaining mainland locations. Limited gene flow was present among populations despite the relatively short distances between them, with migration detected primarily from BSM to other areas.

Genetic diversity

The mitochondrial markers revealed high haplotype diversity (>0.6) in most areas; nucleotide diversity was similar to that reported in other Charadriiformes species with wide distributions (Liebers et al. 2001; Küpper et al. 2009; Dantas et al. 2012). In contrast, the SNP markers indicated moderate-to-high heterozygosity (H_o = 0.222), which is similar to the values reported for other Charadriiformes such as *Calidris canutus* (0.183; Conklin et al. 2022) and *Larus bulleri* (0.263; Mischler et al. 2018). Low genetic diversity is expected in small populations or those that tend to decrease in size (Bazin et al. 2006). Considering that the diversity values (based on both mtDNA and SNP markers) of the population of the American oystercatcher in northwestern Mexico are similar to those of some species with broader distributions and larger populations, it is reasonable to conclude that the *frazari* subspecies is genetically "healthy," despite its restricted distribution and small size. High diversity values in small or fragmented populations can be maintained by several mechanisms, including the increased relative fitness of more outcrossed individuals and the retention of variation at genes important for adaptation (Mable

Table 4 Matrix of migration rates (proportion of individuals per generation; mean ± SD) between breeding areas of the American oystercatcher (*Haematopus palliatus frazari*). Bahia Santa María (BSM), Bahía Navachiste (NAV), Bahía de Ceuta (CEU), Bahía Tobari (TOB), Bahía Guaymas-Lobos (GUA), and the Baja California Peninsula (PEN). The direction of migration is shown, with the area of origin indicated in the first row and the area of destination in the column

		Migration from					
		BSM	NAV	PEN	CEU	TOB	GUA
Migration to	BSM		0.0053 ± 0.00	0.0053 ± 0.00	0.0051 ± 0.00	0.0052 ± 0.00	0.0053 ± 0.00
	NAV	0.1487 ± 0.04		0.0293 ± 0.03	0.0297 ± 0.03	0.0301 ± 0.03	0.0302 ± 0.03
	PEN	0.1446 ± 0.05	0.0312 ± 0.03		0.0307 ± 0.03	0.0299 ± 0.03	0.0296 ± 0.03
	CEU	0.1674 ± 0.05	0.0330 ± 0.03	0.0331 ± 0.03		0.0327 ± 0.03	0.0322 ± 0.03
	TOB	0.1810 ± 0.04	0.0302 ± 0.03	0.0301 ± 0.03	0.0316 ± 0.03		0.0295 ± 0.03
	GUA	0.2149 ± 0.04	0.0240 ± 0.02	0.0241 ± 0.02	0.0244 ± 0.02	0.0234 ± 0.02	

2019). High values could also be explained by a constant population size or even a demographic expansion without significant declines over long periods (Ballard and Whitlock 2004; Toews and Brelsford 2012).

There are differences between the nature of SNPs and mtDNA markers, which can affect estimates of genetic diversity. Mitochondrial markers reflect matrilineal history (Bazin et al. 2006; Zink and Barrowclough 2008) and are consequently biased, whereas SNP markers can represent both parents, as well as demographic and functional processes (Zimmerman et al. 2020). Furthermore, mitochondrial markers represent a single locus and provide only a tiny glimpse into the evolutionary history of species, whereas SNP markers span thousands of loci (Zhang and Hewitt 2003). In addition, SNP markers provide information that represents the entire genome, including alleles under the influence of natural selection (Zimmerman et al. 2020). Finally, due to its uniparental inheritance, mtDNA loses ancestral polymorphisms faster than nuclear DNA (Mischler et al. 2018).

Population structure

The pairwise F_{ST} analyses based on the haplotype frequencies of the mitochondrial control region revealed one significant differentiation between TOB and GUA (F_{ST} = 0.49, $p = 0.009 \pm 0.009$) despite small sample sizes (BSM $n = 13$; CEU $n = 6$; TOB $n = 5$; NAV $n = 4$; GUA $n = 7$; PEN $n = 5$). TOB exhibited a unique and highly divergent haplotype (Hap_6) and a high internal kinship coefficient, which could reflect a mixture of historical local drift, philopatry, or a sampling effect, as small N values inflate F_{ST} (Willing et al. 2012; Weir and Cockerham 1984). Several studies have shown that mitochondrial markers cannot always adequately differentiate among groups when compared to the ability of other nuclear molecular markers (García-De León et al. 2023; D'Urban-Jackson et al. 2020; Mischler et al. 2018; Dantas et al. 2012). As mentioned above (Genetic diversity subsection), this may be because the information obtained with mitochondrial markers reflects maternal inheritance; polymorphic sites are lost more quickly with mitochondrial markers than with nuclear markers (García-De León et al. 2023; Mischler et al. 2018).

Based on our SNP results, PEN was differentiated from the other areas. Although the sample size from PEN was small (5), the power of the SNP markers allowed us to draw these conclusions. The observed structure was likely mainly shaped by the strong philopatry and limited dispersal of the American oystercatcher (American Oystercatcher Working Group et al. 2020; Vega-Ruiz et al. 2021), as well as the geographic isolation created by the Gulf of California, which separates the peninsula from Sonora and Sinaloa. Although there are no obvious geographic barriers between the other areas, the F_{ST} and DAPC analyses also revealed differences among GUA, TOB, NAV, BSM, and CEU. Therefore, philopatry and low individual dispersal likely contributed to this differentiation.

The observed maximum natal dispersal for the American oystercatcher in BSM is approximately 50 km (G. Fernández and J. A. Castillo-Guerrero, unpubl. data), which is similar to distances reported for populations along the east coast of the United States (American Oystercatcher Working Group et al. 2020). This study revealed genetic structure; individuals from PEN were significantly different from those of the mainland. Additionally, we observed a possible substructuring among BSM, TOB, CEU, and NAV, likely due to limited gene flow, despite some areas having low sample sizes. Small populations with low genetic diversity and restricted gene flow are more vulnerable to extinction, thus particular attention should be given to PEN and CEU. In addition, these locations showed the highest kinship values, making them more prone to issues such as inbreeding, stochastic events, and genetic erosion caused by genetic drift or allele fixation (Fischer and Lindenmayer 2007).

Furthermore, breeding adults are known to exhibit high site fidelity in BSM (Vega-Ruiz et al. 2021). In this area, individuals banded as chicks in El Rancho Island (Fig. 1) have been found to remain in BSM or in nearby bays (NAV) as juveniles (G. Fernández and J. A. Castillo-Guerrero, unpubl. data), indicating that individuals move between nearby locations outside the reproductive season. However, these movements of younger birds do not imply that these individuals do not return to reproduce in natal sites. Finally, these observations could be biased by the sampling effort in BSM, which was the greatest among the areas in this study. The movements of individuals in other areas could include travelling to distant sites or reproducing in areas other than their natal sites.

Shorebirds exhibit a particular population dynamic that combines philopatry, which promotes structured populations, with a high dispersal capacity, which supports panmixia (Bray and Hockey 2015). The dispersal of the American oystercatcher outside the breeding season is known to be low and varies within members of the same family (American Oystercatcher Working Group et al. 2020). Thus, the low degree of movement between sites may be related to the availability of suitable habitats, as individuals will remain close to their breeding sites if resource availability is sufficient to cover their essential needs and to avoid competition, despite their dispersal capability (Ronce 2007). As such, low dispersal and high philopatric behavior can promote genetic structure (Friesen 2015; Lombal et al. 2020).

The migration analysis revealed restricted flow among sites. Nevertheless, BSM appeared to be a source population for the others, especially GUA and TOB. The BSM population also received fewer individuals from the other areas. Excluding BSM, the flow of individuals among PEN, CEU, GUA, TOB, and NAV was low. In addition, CEU and PEN had small populations and received only a few individuals due to migration; these populations also showed a higher degree of relatedness compared to those of the other areas, making them vulnerable to genetic drift and inbreeding. These results highlight the importance of understanding the genetic diversity and population structure of the American oystercatcher in northwestern Mexico. As such, conservation efforts should be redirected to the BSM population, as it directly affects the populations in the other areas.

Implications for the conservation of the American oystercatcher in Northwestern Mexico

Future studies must include unrepresented sites to clarify the connectivity of the American oystercatcher across its geographical breeding range and assess population viability through new genomic and demographic information. Given that the genetic differentiation results are based only on a few organisms from PEN, more samples from this area are needed to conduct finer population analyses and confirm the results of this study. Indeed, some sites in PEN host the American oystercatcher in notable numbers during the breeding season, such as Guerrero Negro and Laguna San Ignacio (Palacios et al. 2017), and should be included in future studies. Notably, the SNP markers generated in this work can serve as a basis for future studies. For example, a panel of SNP markers in array format with adequate representation from all sites would allow potential differences to be identified cost-effectively. This information can further define management units and inform and support conservation strategies for *H. palliatus frazari*.

The American oystercatcher is endangered in Mexico (Secretaría de Medio Ambiente y Recursos Naturales 2018) and faces multiple anthropogenic threats (Schulte and Simons 2015; Vega-Ruiz et al. 2021). Identifying management units is essential to conserving this species, given that these units allow managers and policy makers to understand the natural boundaries of the population (Funk et al. 2012). Once identified, the conservation units can be used to accomplish short-term management goals, such as habitat and population monitoring (Funk et al. 2012). In the long-term, maintaining these conservation units will maximize the evolutionary potential of the American oystercatcher in the face of environmental change. Based on connectivity between areas, migration rates, and genetic divergence, we recommend establishing three management units for the American oystercatcher in northwestern Mexico: (1) the southern portion of the Baja California peninsula, which was the most differentiated area in all population structure analyses; (2) the region of southern Sonora-northern Sinaloa (GUA, TOB, NAV, and BSM), which exhibited greater ecological continuity (a wetland continuum) and less genetic distance despite some differentiation between areas, according to the structure and DAPC analyses; and (3) Ceuta Bay, which was well differentiated from other areas and exhibited a high degree of kinship and little genetic flow to other sites. Understanding the differentiation patterns of the American oystercatcher in northwestern Mexico is essential for making wise management decisions.

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Data availability The raw read files were deposited into the National Center of Biotechnology Information (NCBI-SRA) under the Bioproject PRJNA1109518 (https://www.ncbi.nlm.nih.gov/bioproject/1109518).

Declarations

Competing interests The authors declare no competing interests.

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