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Research Article

Diverging Genetic Structure of Coexisting Populations of the Black Storm-Petrel and the Least Storm-Petrel in the Gulf of California

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Abstract

Estimations on the influence of evolutionary and ecological forces as drivers of population gene diversity and genetic structure have been performed on a growing number of colonial seabirds, but many remain poorly studied. In particular, the population genetic structure of storm-petrels (Hydrobatidae) has been evaluated in only a few of the 24 recognized species. We assessed the genetic diversity and population structure of the Black Storm-Petrel (*Hydrobates melania*) and the Least Storm-Petrel (*Hydrobates microsoma*) in the Gulf of California. The two species were selected because they are pelagic seabirds with comparable ecological traits and breeding grounds. Recent threats such as introduced species of predators and human disturbance have resulted in a decline of many insular vertebrate populations in this region and affected many different aspects of their life histories (ranging from reproductive success to mate selection), with a concomitant loss of genetic diversity. To elucidate to what extent the population genetic structure occurs in *H. melania* and *H. microsoma*, we used 719 base pairs from the mitochondrial cytochrome oxidase c subunit I gene. The evaluation of their molecular diversity, genetic structure, and gene flow were performed through diversity indices, analyses of molecular and spatial variance, and isolation by distance (IBD) across sampling sites, respectively. The population genetic structure (via AMOVA and SAMOVA) and isolation by distance (pairwise *p*-distances and $F_{ST}/1–F_{ST}$ (using Φ_{ST}) were inferred for *H. microsoma*. However, for *H. melania* evidence was inconclusive. We discuss explanations leading to divergent population genetic structure signatures in these species, and the consequences for their conservation.

Keywords

Black Storm-Petrel, Least Storm-Petrel, genetic structure, mtDNA COI, Gulf of California

In most mammals and birds, environmental change, population density, mating systems, resource defense, and inbreeding avoidance are some of the factors affecting the genetic diversity, gene flow, and population genetic structure (Berg et al., 2009; Chesser, 1991; Steiner & Gaston, 2005). Specifically, vagility and mating systems are factors that can determine the magnitude of gene flow (Lowe et al., 2004), determine philopatry (Ribeiro et al., 2012), and lead to genetic structuring (Zan et al., 2008). For example, if philopatry is present, then genetic differentiation may occur at small or large scales (Cristofari et al., 2015; Ibarguchi et al., 2011). The genetic structure may be strong

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between large and geographically distant populations if there is low or no exchange of individuals inducing genetic flow (Milot et al., 2008). Consequently, dispersion patterns result in a genetic structure at different scales (fine or coarse), at the level of social groups, and across territories (Beck et al., 2008; Finnegan et al., 2013; Van Dijk et al., 2015). Therefore, when genetics and behavioral patterns are linked, they can have a strong evolutionary effect even in relatively small areas (Bertrand et al., 2014; Sausner et al., 2016), and philopatry and local adaptation can lead to speciation processes, influence divergence between populations, and determine the degree of genetic subdivision (Abbott & Double, 2003; Dearborn et al., 2003).

Mitochondrial and nuclear DNA markers have been widely used for estimating philopatry and the genetic structure of colonial seabirds (Levin & Parker, 2012; Rayner et al., 2010). Among them, certain types of markers may be useful for different genetic analyses that can reveal different evolutionary scales (Avise, 2004; Rubinoff & Holland, 2005). mtDNA markers are subject to fewer recombination events than nuclear ones (Rokas et al., 2003). Moreover, it has been shown that at equilibrium, mtDNA markers could be sensitive to population structure (Zink & Barrowclough, 2008), and are sensitive for detecting population subdivision, improving spatial resolution (Ibarguchi et al., 2011). Different seabird species inhabiting the same geographical areas may not show genetic differentiation despite records of strong philopatry (Friesen, 2015). For example, Levin & Parker (2012) used microsatellites, NADH dehydrogenase subunit 2 (ND2), cytochrome *b* (Cyt-*b*), and cytochrome oxidase I (COI) genes to study the Galapagos Nazca Booby (*Sula granti*) and the Great Frigatebird (*Fregata minor*) from the Galapagos archipelago. Despite the short distances between nesting sites, they found evidence of genetic differentiation in the Nazca Booby, a pattern attributed to natal and breeding philopatry, while Great Frigatebirds showed no evidence at all.

Overall, gene diversity and genetic structure of many groups of seabirds are still poorly studied, as is the case of the storm-petrel species. This is a group of almost exclusively pelagic seabirds with global distribution and populations sizes ranging from thousands to millions of individuals (Spear & Ainley, 2007; International Union for Conservation of Nature, IUCN; http://www.iucnredlist.org). In only a few instances the genetic structure of the storm-petrel species has been evaluated using mitochondrial, nuclear, or both markers. For example, Cagnon et al. (2004) found low genetic differentiation using cytochrome b data within the Mediterranean basin compared to the North Atlantic, with strong differences among populations. Smith et al. (2007) used mitochondrial control region and found significant population structure and differentiation among several colonies (Atlantic and Pacific, Cape Verde and all other populations, sympatric seasonal populations in the Azores, and sympatric seasonal populations in Madeira). Bicknell et al. (2012) found significant global population structure using mitochondrial control region in the Atlantic and Pacific populations of the Leach's storm-petrel (*Oceanodroma leucorhoa leucorhoa*). Silva et al. (2016) found evidence of genetic differentiation also using mitochondrial control region. The most recent study by Antaky et al. (2020) (which used high-throughput sequencing) reported high levels of genetic diversity, with little differentiation between breeding colonies of the Hawaiian Band-rumped Storm-Petrel (*Oceanodroma castro*). Most of these examples found either strong and moderate evidence of genetic structure at large scales and regional scales, respectively (Antaky et al., 2020; Bicknell et al., 2012; Cagnon et al., 2004; Silva et al., 2016; Smith et al., 2007). Although studies such as the one by Silva et al. (2016) considered populations in the eastern Pacific near tropical American continent, none has been performed close to the coasts in this area.

The Black Storm-Petrel (*H. melania*) and the Least Storm-Petrel (*H. microsoma*) are pelagic seabirds showing similar ecological characteristics and distribution ranges. For example, they nest only on very isolated rocky islands with no natural predators (Everett, 1991). Historically, the largest breeding populations of these seabirds are found in Isla Partida Norte, Gulf of California (Figure 1) (Everett & Anderson, 1991; Spear & Ainley, 2007) and Islas San Benito, in the Pacific Ocean off the west coast of the Baja California peninsula (Velarde-González, 2008a, 2008b). However, other breeding populations included small islands in both the Gulf of California and the Pacific Ocean. For *H. melania*, this includes Los Coronados and San Benito in the Pacific and San Luis, Partida Norte and Roca Consag in the Gulf of California. For *H. microsoma*, they are the same islands (American Ornithologists' Union, 1998; Bent, 1922); however, a small breeding site, islote La Lobera (close to Espíritu Santo Island) has also been reported (Carmona et al., 2020). After the breeding season, both species migrate long distances to the north off the coast of northern California and to the south to off the coast of Ecuador (American Ornithologists' Union, 1998; Crossin, 1974). However, in recent times, threats such as introduced species of predators and human disturbance have caused the decline of many insular vertebrate populations (Bedolla-Guzmán et al., 2017). Particularly, islands with important nesting colonies of this species have been invaded by introduced predators, making Isla Partida Norte the most important predator-free colony (Everett & Anderson, 1991; Velarde-González, 2000). Although, the IUCN red list considers the conservation

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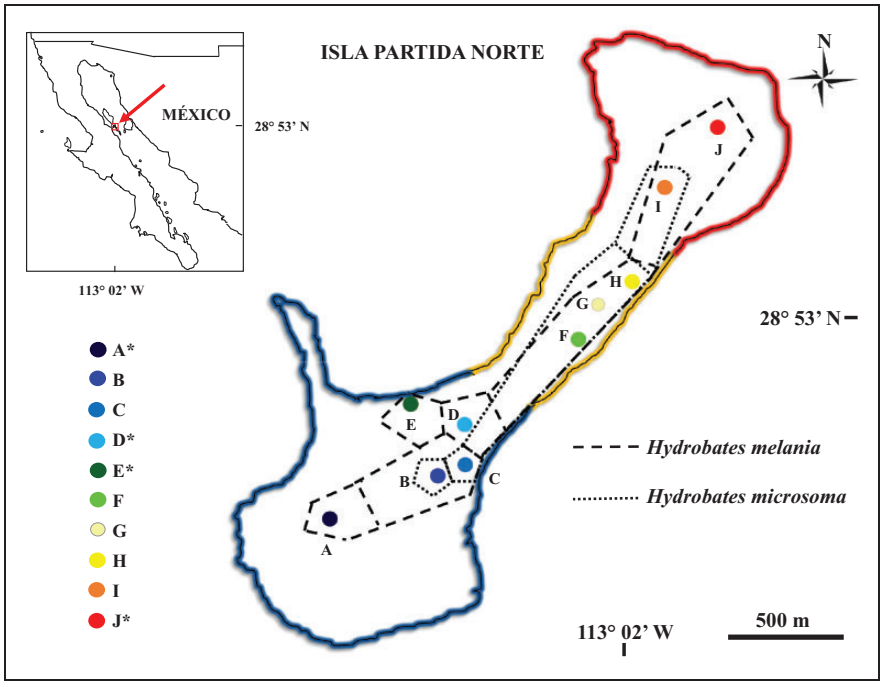


Figure 1. Study Area in Isla Partida Norte, Gulf of California. The map highlights the locations where *H. melania* and *H. microsoma* were sampled (A–J letters). Asterisks represent sites were only *H. melania* individuals were found. In all other sites both species were sampled. The AMOVA groups of geographical zones used in the genetic analyses are identified by colored lines: blue (southwest hill, SW), yellow (land bridge, LB), and red (northeast hill, NE), as depicted in the text (see Methods section). Grouping of sampling localities maximally differentiated found using SAMOVA: Tessellation of *H. melania* groupings ({A} {I, J} {B, C} {D} {F, G, H} {E}), dashed lines; tessellation of *H. microsoma* groupings ({B} {C} {F, G, H} {I}), dotted lines.

status of both *H. melania* and *H. microsoma* as "least concern" (BirdLife International, 2018a, 2018b), under Mexican environmental law (SEMARNAT-NOM-059–2010) they are considered "Amenazadas" (Threatened, in English). Here, we evaluated the genetic diversity and population structure of the Black Storm-Petrel (*H. melania*) and the Least Storm-Petrel (*H. microsoma*), and discuss explanations leading to divergent population genetic structure and potential consequences for their conservation. Different signatures of genetic structure and genetic differentiation may occur because of differences in the range and frequency of migration among colonies (Spear & Ainley, 2007). Despite of some overlap, distribution ranges are different southward because *H. melania* tends to visit the Galapagos Islands and even hundreds of kilometers in open sea, while *H. microsoma* distribution is mostly close to the coasts.

Materials and Methods

Study Site

Isla Partida Norte (28.891667°N, 113040278°W) is a small island within the Gulf of California, Mexico. It is located ~19 km off the eastern coast of Baja California Peninsula. The island is 2 km long, 200–500 m wide, and 105 m high. It consists of two rocky elevations of volcanic origin, joined through a narrow and reduced land bridge, and it is covered with volcanic boulders, mainly basalts. The island climate has not been directly described; however, the nearby Rasa Island (8.5 km southeast of Partida Norte Island) has been characterized with a mid-latitude winter, a subtropical summer, and scant and unpredictable precipitation (Velarde et al., 2014). Vegetation consists of desert scrubs (Flores-Martínez et al., 2015). Among the most common plants are Barclay's saltbush (*Atriplex barclayana*), Alkali weed (*Cressa truxillensis*), Baja California cholla (*Cylindropuntia alcahes*), jumping cholla (*Cylindropuntia fulgida*), and Mexican giant cardon (*Pachycereus pringlei*). *Hydrobates melania* and *H. microsoma* have their nests within rock crevices in specific areas of the island.

Sampling, DNA Amplification, Purification, and Sequencing

For *H. melania*, 113 individuals from 10 breeding sites were sampled, and for *H. microsoma*, 70 individuals from 6 breeding sites. We were certain that all of them were breeding because they visit the islands only for that purpose (Everett & Anderson, 1991) and, as we were

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there early in the breeding season, no chicks were yet observed. Only adult, breeding individuals, recognized as such by comparing them to illustrations in field guides (Kaufman, 2005; Sibley, 2003) regarding color, size, and weight were sampled (research and sample collection permit: SGPA/DGVS/03074/14). From them, we collected ~60 µL of blood samples from each individual's brachial vein (Figure 1) in 7–16 April 2014 and stored them in microtubes with Longmire buffer (2 M Tris-HCl, pH 8.0; 0.5 M EDTA, pH 8.0; 5 M NaCl; 20% SDS; double-distilled water) (Longmire et al., 1997). The samples were kept at –20°C in the Department of Zoology, Escuela Nacional de Ciencias Biológicas until DNA extraction, which in turn was performed using the DNeasy Blood & Tissue Kit (QIAGEN, Hilden, Germany). Each PCR reaction contained 20 ng of genomic DNA, 10 mg mL^{-1} bovine serum albumin (BSA), dimethyl sulfoxide (DMSO) 0.2%, 0.25 mM of each dNTP, and 2× Kapa Taq ReadyMix (Kapa Biosystems, Massachusetts). Amplification of the mitochondrial DNA cytochrome oxidase c subunit I (mtDNA COI) gene (≈770 bp) was performed using the primers COIBirdF1 (5'-TTC TCC AAC CAC AAA GAC ATT GGC AC-3') and COIBirdR1 (5'-ACG TGG GAG ATA ATT CCA AAT CCT G-3') (Hebert et al., 2004; Johnsen et al., 2010) using a T100 Thermal Cycler (BIO-RAD, Singapore). Cycling parameters were as follows: initial denaturalization, 2 min at 94°C, 5 cycles of 30 s at 94°C, 30 s at 45°C, and 30 s at 72°C, followed by 35 cycles of 45 s at 94°C, 45 s at 55°C, and 45 s at 72°C and a final extension of 5 min at 72°C. Amplified products were purified using the GeneJET Gel Extraction Kit (Thermo Fisher Scientific, Massachusetts,), and outsourced for sequencing to Macrogen Inc. (Seoul, Korea). Chromatogram files were edited manually using Chromas Lite ver. 2.1 (2012) and aligned with Seaview ver. 4.5.4 (Gouy et al., 2010).

Molecular Diversity, Genetic Structure, Isolation by Distance, and Haplotype Network

We estimated haplotype richness (*h*), number of segregating sites (*S*), the average number of nucleotide differences (*k*), haplotype diversity (*Hd*), and nucleotide diversity (π) of mtDNA COI gene sequences using DnaSP ver. 6.10.04 (Rozas et al., 2017). To show the nature of variation and identify the evolutionary relationships amongst haplotypes within both *H. melania* and *H. microsoma*, we used the Minimum Spanning Network method and generated a haplotype network using hatch marks to show mutations (Bandelt et al., 1999) using the software PopART ver. 1.7 (Leigh & Bryant, 2015). To identify groups of sample localities with maximum differentiation (for each species), two approaches were followed: 1) *a priori* definition, with an analysis of molecular variance (AMOVA), and 2) *a posteriori* definition, with a spatial analysis of molecular variance (SAMOVA). The AMOVA analysis (Excoffier et al., 1992) was used to examine the statistical significance of the genetic partition using sample localities within three groups of geographical zones: northeast hill (NH), land bridge (LB), and southwest hill (SH) (Figure 1). The *a priori* analysis was designed given that both *H. melania* and *H. microsoma* depend largely on the availability of appropriate crevices below rocks to nest, and the sample localities where they were found are distributed in those sites, separated by several meters of non-rocky, sandy terrain, unsuitable for nesting. We specifically explored the partition of mtDNA COI gene molecular variance into hierarchical levels estimating Φ-statistics from haplotypic data (Weir & Cockerham, 1984), using the program Arlequin ver. 3.5.2.2 (Excoffier & Lischer, 2010). On the other hand, the SAMOVA (Dupanloup et al., 2002) was used to detect the genetic discontinuity between the sampling localities on the island, with no previous assumptions on number and type of ecological or geographical gaps. This method indirectly detects genetic barriers and explicitly defines maximally differentiated groups from each other and considers both geographically homogeneous groups and non-constrained (by geography) groups (Dupanloup, 2020). To identify the number of groups with the highest and significant F_{CT} value, we tested *K* groups from 2 to 9 (total number of localities minus 1). Significance tests were performed with 10,000 iterations. The default value constant A with *P* value was defined as equal to 1% if the difference between F_{CT} and F_{CT}* (the new partition) at the 10,000th iteration was equal to 0.001. All SAMOVA analyses were ran using SAMOVA ver. 2.0 (Dupanloup, 2020). To ensure that the final configuration of the *K* groups was not influenced by a determined initial configuration, the simulated annealing process was repeated 1,000 times. In this way, the configuration with the largest associated F_{CT} and significant *P* values after the process was considered as the best grouping. Finally, we analyzed whether geographic distances are associated with mtDNA COI genetic differences to determine if there was a pattern of isolation by distance (IBD) in both species. The geographical distances (*i.e.*, between localities) and pairwise *p*-distances (*i.e.*, between-group mean distance) were obtained with MEGA v. 6.0 (Tamura et al., 2013) and used to plot a linear regression of least squares, which in turn were evaluated by non-parametric Mantel test (Mantel, 1967). The Mantel test consisted of 1,000 random permutations and was performed using NTSYSpc ver. 2.02j (Jamshidi & Jamshidi, 2011). Likewise, the geographical distances and $F_{ST}/1–F_{ST}$

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(using Φ_{ST}) based distances (Rousset, 1997) were also evaluated for each species.

Results

The mtDNA COI gene sequence length was 719 bp for both species, after alignment and editing. We recovered 113 and 70 sequences of *H. melania* and *H. microsoma*, respectively, each of them with 46 haplotypes (Table 1). Sequences were deposited in GenBank (accession numbers MH510865- MH510977 and MH510978-MH511047 for *H. melania* and *H. microsoma*, respectively). High and similar variability was found across sequences of both species; the number of segregating sites in *H. melania* was 26, while in *H. microsoma* was 28. The analyses of haplotype (*Hd*) and nucleotide (π) diversities showed to be extensive for both species; for *H. melania Hd* was 0.70 (SD = 0.05) and π was 0.00291 (SD = 0.0004), while for *H. microsoma Hd* was 0.95 (SD = 0.02) and π was 0.00559 (SD = 0.0006). However, *H. microsoma* showed higher values than *H. melania*. The Minimum Spanning Network was not fully resolved for *H. melania*, as many alternative connections between haplotypes were observed (Figure 2). Haplotype H4 was the most common and it was shared by 61 individuals, while only very few others were observed in only two individuals (H2, H5, H11, H15, and H27). All other haplotypes were unique and observed in only one individual. Most of the haplotypes that were connected to the most common haplotype H4 do so with one to three mutations, a condition observed in almost all other haplotypes. No clear relationship between the network and the sites defined for the AMOVA analyses was found (Figure 2). For example, haplotype H4 was found in all ten sampled localities. This was also the case between the network and the groupings inferred by SAMOVA results (data not shown). Conversely, the Minimum Spanning Network was better resolved for *H. microsoma*, with fewer alternative connections between haplotypes (Figure 3). The most common haplotypes were H11 and H3 (shared by 14 and 6 individuals, respectively), and four other haplotypes (H9, H10, H16 and H39) were observed in two individuals. All other haplotypes were unique and observed in only one individual. The network showed that very few haplotypes were connected to the most common, and many showed up to five mutations among them. As mentioned for *H. melania*, there was no relationship between the network and the sample localities defined for the AMOVA analyses or the groupings inferred by SAMOVA results. The networks show high frequency of single haplotypes in both species, especially in *H. microsoma*. The results of the AMOVA analysis, including both species Φ-statistics and *P*-values are summarized in Table 1. We found genetic differentiation for *H. melania* and *H microsoma*, although at different sources of variation. In the first case, no genetic differentiation was observed among groups ($\Phi_{CT} = -0.00657$, $P > 0.05$) or within localities ($\Phi_{ST} = 0.0179$, $P > 0.05$) for *H. melania*. However, genetic differentiation was detected among localities within groups ($\Phi_{SC} = 0.02431$, $P < 0.01$). On the other hand, genetic differentiation was detected among groups ($\Phi_{CT} = 0.03456$, $P < 0.05$) for *H. microsoma*, but not when other sources of variation were considered ($\Phi_{SC} = -0.02343$, $P > 0.05$; $\Phi_{ST} = 0.01195$, $P > 0.05$). The results of the SAMOVA analysis using both the geographically homogeneous groups (maximally differentiated from each other) (Figure 1; Table 2) and the maximally differentiated groups (non-constrained (by geography) groups) were almost identical. Therefore, only the results of the geographically homogeneous groups approach were included. The statistically significant and maximally differentiated number of groups identified (*K*) for *H. melania* was six ($F_{CT} = 0.045$, $P < 0.001$; tessellation: {A} {I, J} {B, C} {D} {F, G, H} {E}). A similar pattern was found for *H. microsoma*, as the corresponding maximally differentiated number of groups was four ($F_{CT} = 0.073$, $P = 0.05$; tessellation: {B} {C} {F, G, H} {I}) (Figure 1; Table 2). Finally, when geographical distances *vs* pairwise *p*-distances were plotted, an IBD pattern was observed only for *H. microsoma* (rM = 0.464; $P = 0.033$; $y = 1E\text{-}06x + 0.0043$). This was not the case for *H. melania* (rM = -0.139 $P = 0.033$; $y = 1E\text{-}06x + 0.0043$) (Table 3). Similarly, the plot of geographic distances *vs* $\Phi_{ST}/1-\Phi_{ST}$ distances showed an IBD pattern for *H. microsoma* (rM = 0.497 $P = 0.032$ y = 9E-05x−0.053), while for *H. melania* this pattern resulted

Table 1. Genetic Diversity Estimates and Analysis of Molecular Variance (AMOVA) for *H. melania* and *H. microsoma* From Mitochondrial Sequences of Cytochrome Oxidase Subunit I (COI).

	H. melania	*H. microsoma*
Genetic Diversity		
n	113	70
h	46	46
S	26	28
k	2.095	4.021
Hd (SD)	0.70 (0.05)	0.95 (0.02)
π (SD)	0.00291 (0.0004)	0.00559 (0.0006)
AMOVA		
Φ_{CT}	−0.00657	**0.03456***
Φ_{SC}	**0.02431****	−0.02343
Φ_{ST}	0.0179	0.01195

n, sample size; *h,* haplotype richness; *S,* number of segregating sites; *k,* average number of nucleotide differences; *Hd,* haplotype diversity; π, nucleotide diversity; SD, standard deviation. AMOVA source of variation: among groups (Φ_{CT}), among localities within groups (Φ_{SC}), and within localities (Φ_{ST}); * = $P < 0.05$, ** = $P < 0.01$. Statistically significant values are shown in bold.

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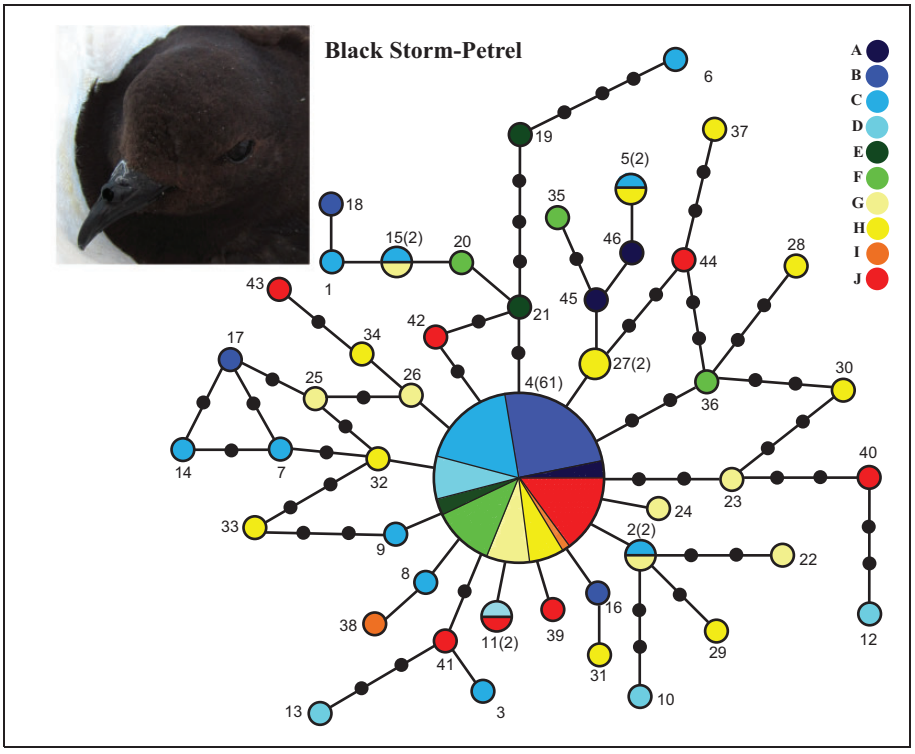


Figure 2. Minimum Spanning Network Showing the Relationship Among Cytochrome Oxidase Subunit I (COI) Haplotypes From *H. melania*. Circles' sizes are proportional to haplotype frequencies. Numbers in parentheses (when provided) are individuals sharing the same haplotype; otherwise, only one individual was found with that haplotype. Hatch marks represent the number of inferred mutations between haplotypes. Colors within the haplotypes represent the sample localities where the samples were taken.

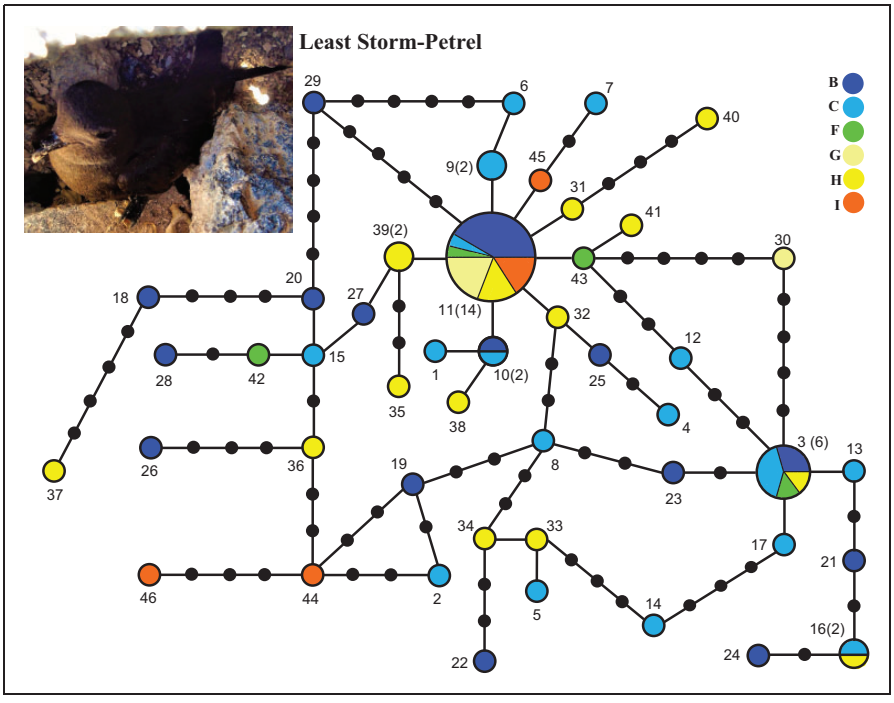


Figure 3. Minimum Spanning Network Showing the Relationship Among Cytochrome Oxidase Subunit I (COI) Haplotypes From *H. microsoma*. Circles' sizes are proportional to haplotype frequencies. Numbers in parentheses (when provided) are individuals sharing the same haplotype; otherwise, only one individual was found with that haplotype. Hatch marks represent the number of inferred mutations between haplotypes. Colors within the haplotypes represent the sample localities where the samples were taken.

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Table 2. Fixation Indices Corresponding to the Groups Geographically Homogeneous and Maximally Differentiated Inferred by Spatial Analysis of Molecular Variance (SAMOVA) for *H. melania* and *H. microsoma*, Tested for Cytochrome Oxidase Subunit I (COI) Mitochondrial Sequences.

K	F_{CT}	*P*	F_{ST}	*P*	F_{SC}	*P*	Grouping of sample localities
H. melania							
2	0.150	0.10	0.156	0.11	0.006	0.25	{E} {A, B, C, D, F, G, H, I, J}
3	0.029	**0.04**	0.031	0.11	0.002	0.50	{D, F, G, H, I, J} {A, B, C} {E}
4	0.045	**0.02**	0.036	0.09	−0.009	0.90	{D, F, G, H, I, J} {A} {B, C} {E}
5	0.045	**0.01**	0.029	0.10	−0.020	0.95	{B, C} {D} {F, G, H, I, J} {E} {A}
6	0.045	**0.00**	0.027	0.09	−0.019	0.83	{**A**} {**I, J**} {**B, C**} {**D**} {**F, G, H**} {**E**}
7	0.042	**0.02**	0.022	0.11	−0.020	0.88	{F, H} {A} {B} {C} {G} {D, I, J} {E}
8	0.047	**0.03**	0.021	0.11	−0.027	0.86	{J} {A} {B} {C} {E} {G, I} {F, H} {D}
9	0.048	0.12	0.020	0.11	−0.029	0.53	{G, I} {A} {B} {C} {D} {E} {J} {F} {H}
H. microsoma							
2	0.053	0.17	0.046	0.45	−0.008	0.65	{B, C, F, G, H} {I}
3	0.048	0.07	0.019	0.41	−0.031	0.89	{B, F, G, H} {I} {C}
4	0.073	**0.05**	0.008	0.40	−0.070	0.90	{**B**} {**C**} {**F, G, H**} {**I**}
5	0.160	0.06	0.003	0.44	−0.186	0.83	{B} {C} {F, G} {I} {H}

K, number of groups maximally differentiated. Source of variation: among groups, F_{CT}; among localities within groups, F_{SC}; and within localities, F_{ST}. The grouping of sample localities maximally differentiated (corresponding to tessellation showed in Figure 1) are showed in bold. Statistically significant *P* values are showed in bold.

Table 3. Isolation by Distance (IBD) Estimates and Mantel's Test for *H. melania* and *H. microsoma* From Mitochondrial Sequences of Cytochrome Oxidase Subunit I (COI).

	m *vs* *p*–distances			m *vs* Φ_{ST} / (1−Φ_{ST})		
	*r*M	*P*	*equation*	*r*M	*P*	*equation*
H. melania	−0.139	0.731	$y = -3E\text{-}07x + 0.003$	−0.007	**0.05**	$y = -2E\text{-}06x + 0.058$
H. microsoma	0.464	**0.033**	$y = 1E\text{-}06x + 0.004$	0.497	**0.032**	$y = 9E\text{-}05x - 0.053$

m *vs* *p*–distances, distance (in meters) vs pairwise sequence differences; m *vs* $\Phi_{ST}/(1\text{-}\Phi_{ST})$, distance (in meters) vs Φ_{ST} based distances (Rousset, 1997); *r*M, a correlation coefficient of Mantel's test. Significant *P* values are shown in bold.

in a negative correlation ($rM = -0.007$ $P = 0.05$ $y = -2E\text{-}06x$ - 0.058) (Table 3). Therefore, only the plots of linear regressions regarding pairwise *p*-distances and $\Phi_{ST}/1–\Phi_{ST}$ distances showed a consistent IBD pattern for *H. microsoma*.

Discussion

In some species of the Procellariiformes group, the patterns of genetic diversity have been explained as the consequence of either ecological (current) and/or evolutionary (historical) events (Antaky et al., 2020; Silva et al., 2016). In the first case, low diversity was associated with intense predation pressure observed in the Atlantic populations of *Oceanodroma leucorhoa* (Leach's Storm-Petrel), while high diversity was observed in the Pacific populations, which in turn were subject to less intense predation pressure (Bicknell et al., 2012). In the second case, low but fixed nucleotide differences between groups of *Hydrobates pelagicus* (British Storm-Petrel) within Atlantic and Mediterranean basins were consistent with long-term geographic isolation, possible because of the existence of some barrier to gene flow or recent changes in demography and ecology (Cagnon et al., 2004). Conversely, high divergence has been linked with low potential for dispersal and intrinsic reproductive barriers, such as high philopatry and local adaptation (Silva et al., 2016). High diversity patterns are consistent with high diversity values found in this study for *H. melania* and *H. microsoma*, as there are no reports of intense predation pressure (at least until recent times) and their potential of dispersal is high in the eastern Pacific. However, the two species clearly showed different haplotype and nucleotide diversity values (both estimates were smaller in *H. melania*), with no overlap. The higher diversity values for *H. microsoma* may account for its much larger population size, which is possibly one order of magnitude greater than that of *H. melania* (Brooke, 2004). A possible explanation for this pattern is that *H. microsoma* may be

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experiencing population expansion, while for *H. melania* this may not be the case. If so, appropriate hypotheses testing of potential bottlenecks (*i.e.* sudden population reduction followed by rapid expansion), along with additional genetic markers, should be considered in any further studies. Moreover, the molecular diversity observed in our focal species was higher or similar to that found in other Procellariiformes. For example, the molecular diversity found in *H. microsoma* was higher than that reported for the *O. leucorhoa* control region (mean $Hd = 0.729$, ± 0.14; mean $\pi = 0.0054 \pm 0.00073$) (Bicknell et al., 2012) and *H. pelagicus* cytochrome *b* ($Hd = 0.7$, ± 0.037; $\pi = 0.00396 \pm 0.00028$) (Cagnon et al., 2004), but similar to that for *O. castro* control region ($Hd = 0.965$, ± 0.007; $\pi = 0.0408 \pm 0.0017$) (Silva et al., 2016).

Although most studies on the population genetic structure of seabirds have focused on large geographical scales, there are some instances where it has been uncovered at microscales. For example, using mtDNA and microsatellites Ibarguchi et al. (2011) evaluated the genetic structure of *Uria lomvia* (Thick-billed Murre) in a colony from Coats Island, Nunavut, Canada. They found no genetic structuring either among ledges or among the subareas level, regardless of grouping. However, in male individuals located in different ledges of the same cliff (less than 205 m long), evidence of low but significant genetic structuring was found, as well as on the east *vs* the west side of the colony. Similar findings have been reported integrating behavior and genetic information (Ibarguchi et al., 2011; Lecomte et al., 2009; Ribeiro et al., 2012). If the population genetic structure at fine-scale level is assessed with molecular markers, two possible scenarios are expected. On one hand, genetic variation can be distributed heterogeneously between groups; that is, genetic structure occurs because of philopatry and reduced gene flow (Ovenden et al., 1991; Rayner et al., 2011; Welch et al., 2012). Alternatively, genetic variation can be homogeneously distributed (*i.e.* panmixia) with reduced molecular diversity; that is, no genetic structure and absence of philopatry due to high gene flow (Austin et al., 1994; Bicknell et al., 2012; Milot et al., 2008). Despite the impossibility of considering differences between sexes due to the selected marker (mtDNA markers are only female inherited), our results agree with the first described scenario for *H. microsoma*, although evidence for *H. melania* was inconclusive. First, for *H. microsoma* the AMOVA analysis identified that variation among the *a priori* grouping of sites (northeast hill, land bridge, and southwest hill, Figure 1) was statistically significant. However, that was not the case for *H. melania*, as variation among groups of sites was lower although non-significant (Table 1). In this case, only variation among sample localities within groups was statistically significant. Second, we found significant differentiation in both species for the number of groups maximally differentiated (*K*) in the *a posteriori* grouping SAMOVA analyses. For *H. melania*, *K* was six (groups of sampling localities: {A} {I, J} {B, C} {D} {F, G, H} {E}), while for *H. microsoma K* was four (groups of sampling localities: {B} {C} {F, G, H} {I}). These values suggest that genetic population structuring is higher in *H. microsoma*, and that its maximally differentiated groups are akin to the sites defined *a priori* for the AMOVA analyses (Table 2; Figure 1). Further, an isolation by distance (IBD) pattern was clearly identified for *H. microsoma*, using both the paired genetic distances (*p*–distances) and genetic differentiation ($\Phi_{ST}/(1 - \Phi_{ST})$); however, this was not the case for *H. melania*, as none of these estimators were significant (Table 3). Given that both species have common evolutionary origins (*i.e.* they are closely related due to phylogenetic relationships; Wallace et al., 2017) and present analogous ecological constraints (e.g., nesting sites are quite similar), it was expected that their population genetic structure was similar. A possible explanation for the contrasting genetic structure in our focal species is that they behave differently enough (*e.g.* in range and frequency of migration among colonies) as to develop subtle but distinct responses to their environment (*e.g.* differentiated foraging due to geographic partition of food availability), leading to divergent population structure signatures. Alternatively, although some evidence for genetic structuring was found, it is important to note that some bias may be caused by sex differences. This may be the case if such genetic structuring is driven mainly by philopatry. For example, previous observations in other seabird studies claim that males are more prone to show philopatry, while a greater dispersion capacity and less fidelity site has been observed in females (Greenwood, 1980; Ibarguchi et al., 2011; Ribeiro et al., 2012). If so, it would be necessary to test for male-biased dispersal (although different genetic markers are required to detect this). However, it is important to note that seemingly inconsistent results do not necessary mean absence of philopatry, because processes of divergence and differentiation can occur despite gene flow (Taylor et al., 2013), as well as panmixia may be inferred despite barriers to gene flow (Oomen et al., 2011). Finally, we acknowledge that mtDNA markers have a number of limitations and shortcomings, such as the nature of its matrilineal inheritance, a lower discrimination power at population level, the occurrence of discrepancies between nuclear and mtDNA inheritance patterns, and artifacts derived from pseudo-genes, among others (Rokas et al., 2003; Rubinoff & Holland, 2005; Zink & Barrowclough, 2008). However, it allowed us to rapidly describe genetic diversity and to test whether genetic

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structure could be observed in two species from one single island in a small spatial scale in the context of the Gulf of California. Further work should consider the exploration and adequate sample collection on other islands such as San Benito Island, off the coast of Baja California (which is where other major breeding sites for both species are located) will allow to test different hypothesis on genetic structure in a broader geographical and ecological context. Other nuclear markers (microsatellites, SNPs, NGS, etc.), as well as sex identification to test for sex-bias, should also need to be considered.

Implications for Conservation

We restricted our study to explore the genetic diversity and fine-scale genetic structure, disregarding other components such as population sink-source dynamics and multiple ecological and evolutionary factors. These components should be included in future conservation studies to describe more extensively the influence of philopatry at the population level within each species, as well as the consideration of the role of alloparenting, kin group selection, and the evolution of helping behavior, among others. Moreover, for both species the maintenance of their genetic diversity is an important factor for conservation management in future generations. Given their restricted breeding ranges, it may be necessary to elucidate which populations require major attention and protection. Our study provides baseline information for comparison with other breeding islands of the same two species, either experiencing similar demographic or ecological scenarios within the Midriff region of the Gulf of California. Although the present study focused on two seabird species of limited and restricted breeding area, it is important because it may be useful as a reference for other, similar studies, both in the same area with other seabird species or in any other areas worldwide with similar or equivalent ecological contexts. In the light of predicted adverse climate change for this region, changes in the demography and other ecological and evolutionary dynamics are expected. Despite the high genetic variation found in the two storm-petrel species, increasing human-induced factors (such as climate change, overfishing, and water and air pollution) threatens their conservation. We raise attention to the urgency to establish conservation programs for these and other seabird species in the region.

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