Available online at www.sciencedirect.com
ScienceDirect
Molecular Phylogenetics and Evolution 43 (2007) 755–773
MOLECULAR PHYLOGENETICS AND EVOLUTION
www.elsevier.com/locate/ympev

Global phylogeography of the band-rumped storm-petrel (*Oceanodroma castro*; Procellariiformes: Hydrobatidae)

Andrea L. Smith [a], Luis Monteiro [b,†], Osamu Hasegawa [c], Vicki L. Friesen [a,*]

[a] *Department of Biology, Queen's University, Kingston, Ont., Canada K7L 3N6*
[b] *Department of Oceanography and Fisheries, University of Azores, 9901-862 Horta, Portugal*
[c] *Section of Integrated Environmental Science, Faculty of Environmental Earth Science, Hokkaido University, North 10, South 8, Kita-ku, Sapporo 060-0810, Japan*

Received 9 May 2006; revised 26 January 2007; accepted 2 February 2007
Available online 23 February 2007

Abstract

Factors shaping population differentiation in low latitude seabirds are not well-understood. In this study, we examined global patterns of DNA sequence variation in the mitochondrial control region of the band-rumped storm-petrel (*Oceanodroma castro*), a highly pelagic seabird distributed across the sub-tropical and tropical Atlantic and Pacific Oceans. Despite previous classification as a single, monotypic species, fixed haplotype differences occurred between Atlantic and Pacific populations, and among all Pacific populations. In addition, Cape Verde and Galapagos birds formed distinct clades, estimated to have diverged from all other populations at least 150,000 years ago. Azores hot season populations were also genetically distinct, lending support to previous phenotypic evidence that they be recognized as a separate species. Seasonal populations in Madeira probably represent separate genetic management units. The phylogeography of the band-rumped storm-petrel appears to have been shaped by both nonphysical barriers to gene flow and Pleistocene oceanographic conditions. Ancestral populations likely expanded through contiguous range expansion and infrequent long-distance colonization into their current breeding range. These findings suggest several possible revisions to the taxonomy of the band-rumped storm-petrel.
© 2007 Elsevier Inc. All rights reserved.

Keywords: Band-rumped storm-petrel; Mitochondrial control region; Phylogeography; Population differentiation; Storm-petrel taxonomy

1. Introduction

1.1. Phylogeographic patterns in Arctic, temperate, and tropical seabirds

Seabirds are predominantly marine organisms, since many spend over half their lives at sea and require land only for breeding (Brown, 1980; Haney and Solow, 1992; Schreiber and Burger, 2002 and chapters therein). Like other marine species, seabirds tend to be highly mobile and broadly distributed over vast areas (Harrison, 1983), suggesting that extensive gene flow and low genetic differentiation should characterize their population genetic structure. Yet many seabirds exhibit strong philopatry (e.g., Ainley et al., 1983; Baillie and Milne, 1989; Noble et al., 1991; Ovenden et al., 1991; although many species do not; reviewed in Coulson, 2002; Gaston, 2004), which presumably should lead to pronounced geographic variation across their ranges.

At higher latitudes, contemporary intraspecific diversity in seabirds has been influenced by Pleistocene glacial episodes (e.g., Friesen et al., 1996; Kidd and Friesen, 1998; Congdon et al., 2000; Moum and Árnason, 2001; reviewed in Friesen et al., 2007). Many species experienced severe range contractions during glacial cycles, with populations restricted to a few small, isolated refugia during glacial maxima. The resulting vicariant subdivision of species likely resulted in much of the population structuring

* Corresponding author. Fax: +1 613 533 6617.
E-mail address: friesenv@biology.queensu.ca (V.L. Friesen).
† Deceased.

1055-7903/$ - see front matter © 2007 Elsevier Inc. All rights reserved.
doi:10.1016/j.ympev.2007.02.012

evident in high latitude seabirds today (Ainley et al., 1983; Friesen et al., 1996; Kidd and Friesen, 1998; Liebers et al., 2004). As glaciers receded approximately 15,000 years ago, these species would have undergone rapid population expansions into newly available habitat (Congdon et al., 2000; Hewitt, 2000; Tiedemann et al., 2004). The relatively recent history of demographic change suggests that many high latitude seabird populations are not yet in genetic equilibrium and therefore carry the signature of past historical associations in their population genetic structure (Friesen et al., 1996, 2007; Congdon et al., 2000; Patirana et al., 2002; Liebers et al., 2004).

The extent to which seabird populations differ genetically in mid to low latitudes has received far less attention. While Pleistocene glaciation influenced the biogeography of the tropics and sub-tropics, its effects were not as dramatic as in temperate and arctic zones (Hewitt, 2000). Compared with contemporary conditions, climate would have been colder and drier during the last Ice Age and sea levels may have been reduced by as much as 120 m in nonglaciated regions (Hewitt, 2000). These environmental differences could have translated into increased nesting habitat (lower sea levels) and increased foraging opportunities (more cold water upwellings) for seabirds in the tropics and sub-tropics (Lea et al., 2000). Following deglaciation, nesting sites may have become limited due to rising sea levels, while foraging ranges may have expanded because of declining ocean productivity (Nunn, 1997). The rapid population expansions typical of high latitude species probably did not occur at lower latitudes. Instead, slower distributional changes are believed to have maintained large effective population sizes and relatively high levels of genetic diversity in many organisms (Hewitt, 2000).

Despite the high vagility of marine birds, recent studies of tropical and sub-tropical species suggest that physical barriers have also played a role in their diversification (Avise et al., 2000; Steeves et al., 2003, 2005a,b; Cagnon et al., 2004; Gómez-Díaz et al., 2006). The Strait of Gibraltar, for example, appears to have severely restricted gene flow between Atlantic and Mediterranean populations of the British storm-petrel (*Hydrobates pelagicus*) during the Pleistocene (Cagnon et al., 2004). Similarly, the Isthmus of Panama likely acts as a significant barrier to genetic exchange between Atlantic and Pacific populations of the masked booby (*Sula dactylatra*) and sooty tern (*Sterna fuscata*) (Steeves et al., 2005a). In contrast, the southern tip of Africa has been a more permeable barrier to these species, allowing dispersal between the Atlantic and Indian Oceans under certain oceanographic conditions (Avise et al., 2000; Steeves et al., 2005a). Information on divergence patterns of other mid to low latitude marine birds is largely lacking, although strong philopatry appears to play an important role in genetic structuring at both micro- and macrogeographic scales in some species (e.g., Rabouam et al., 2000; Dearborn et al., 2003; Steeves et al., 2005b; Gómez-Díaz et al., 2006).

1.2. Differentiation in the band-rumped storm-petrel

The band-rumped storm-petrel (*Oceanodroma castro*, also known as the Madeiran storm-petrel) has been the focus of recent taxonomic investigations because of its unusual breeding phenology (Monteiro and Furness, 1998; Smith and Friesen, 2006). It is an extremely mobile, highly pelagic seabird with a widespread tropical and sub-tropical distribution in both the Atlantic and Pacific Oceans (del Hoyo et al., 1992). Birds breed colonially on isolated oceanic islands, nesting in rock crevices and burrows (del Hoyo et al., 1992). Adults tend to nest at the same colony each year, and at least some return to their natal colony, but the strength of philopatry is unclear at present due to infrequent recovery of birds banded as chicks (Harris, 1969, 1979, 1984; Monteiro and Furness, 1998; Bried and Bolton, 2005).

Band-rumped storm-petrels show considerable geographic variation in several morphological characters (bill and wing morphology, rump colouration), leading some researchers to propose the recognition of several subspecies (Harris, 1969; Cramp and Simmons, 1982). In general, birds breeding in warm surface waters tend to have longer bills and wings, and less white on the rump than birds breeding in cooler waters (Cramp and Simmons, 1982). Only birds from the vicinity of São Tome, however, display significant differences in these features compared with other populations (Harris, 1969). While birds from this region may represent a subspecies of the band-rumped storm-petrel, no breeding colony has yet been found in the Gulf of Guinea (Luis Monteiro, personal observations). Band-rumped storm-petrels thus are currently classified as monotypic (del Hoyo et al., 1992). To date, no study has examined the global phylogeography of band-rumped storm-petrels to determine whether genetic structure supports patterns of morphological variation.

Recent studies have revealed, however, that both genetic and morphological differences exist between sympatric seasonal populations of these birds. At most colonies worldwide, band-rumped storm-petrels have a single, synchronous breeding season, occurring either in the hot or cool season (Monteiro and Furness, 1998). In the Azores, Madeira, and the Galapagos Islands, however, birds have two main reproductive periods approximately four to six months apart (Snow and Snow, 1966; Zino et al., 1994; Monteiro and Furness, 1998). Significant genetic structure has been found between temporally segregated populations in the Galapagos, suggesting that these sympatric breeding populations are partially or entirely reproductively isolated (Smith and Friesen, 2006). Clarification of the global phylogeography of band-rumped storm-petrels is needed to resolve the systematics of sympatric populations and to highlight which populations worldwide may require conservation attention.

In this study we examined global patterns of mtDNA variation within band-rumped storm-petrels, with two objectives:

(i) To determine if the current monotypic status of the species is supported by genetic data, and
(ii) To infer the roles of physical and nonphysical barriers to dispersal, and historical processes in shaping its phylogeography.

We predicted that diversity in band-rumped storm-petrels has been shaped by several factors: their high mobility (resulting in low genetic differentiation within ocean basins), and physical barriers to gene flow (resulting in high genetic differentiation between Atlantic and Pacific populations). In addition, we predicted that band-rumped storm-petrel populations will show evidence of population decline following the last glacial retreat since associated oceanographic changes may have restricted breeding habitat and foraging success for these birds in the sub-tropics and tropics.

2. Materials and methods

2.1. Sample collection

Ten to fifty microliters of blood was obtained from the brachial vein of each of 386 adult band-rumped storm-petrels at colonies throughout their breeding range (Fig. 1 and Table 1). All birds had vascularized brood patches and thus were presumed to be active breeders. Blood was either dried on filter paper and stored at −80 °C or preserved in lysis buffer (100 mM Tris, pH 8.0, 10 mM EDTA, pH 8.0, 100 mM NaCl, 0.5% SDS) or STE buffer (10 mM Tris–HCl, pH 8.0, 1 mM EDTA, pH 8.0, 100 mM NaCl). In addition, feet were collected from three dead adults on Ascension and stored in lysis buffer (total = 389 samples).

2.2. Laboratory analyses

DNA was extracted by protease digestion and either phenol–chloroform purification followed by isopropanol precipitation (Sambrook et al., 1989) or the Puregene® extraction/purification method (Gentra Systems Inc., Minneapolis, Minnesota) for blood stains. Samples were re-suspended in ddH_20 or TE buffer and diluted if necessary.

A 584-base pair (bp) fragment of the 5′ end of the mitochondrial control region was amplified from 120 DNA samples using primers ND6 (Kidd and Friesen, 1998) and H521 (Quinn and Wilson, 1993) following standard protocols (Friesen et al., 1997) with annealing at 60 °C. PCR products were subjected to electrophoresis through 2% agarose gels and purified with QiaQuick® PCR purification kits (Qiagen, Mississauga, Ontario) according to the manufacturer's instructions. DNA was sequenced with AmpliCycle® sequencing kits (Applied Biosystems, Streetsville, Ontario) following the manufacturer's protocol.

The resulting sequences contained a consistent ambiguous region ~150 bp long, beginning 60 bp from the 5′ end of the control region, suggesting the presence of at least

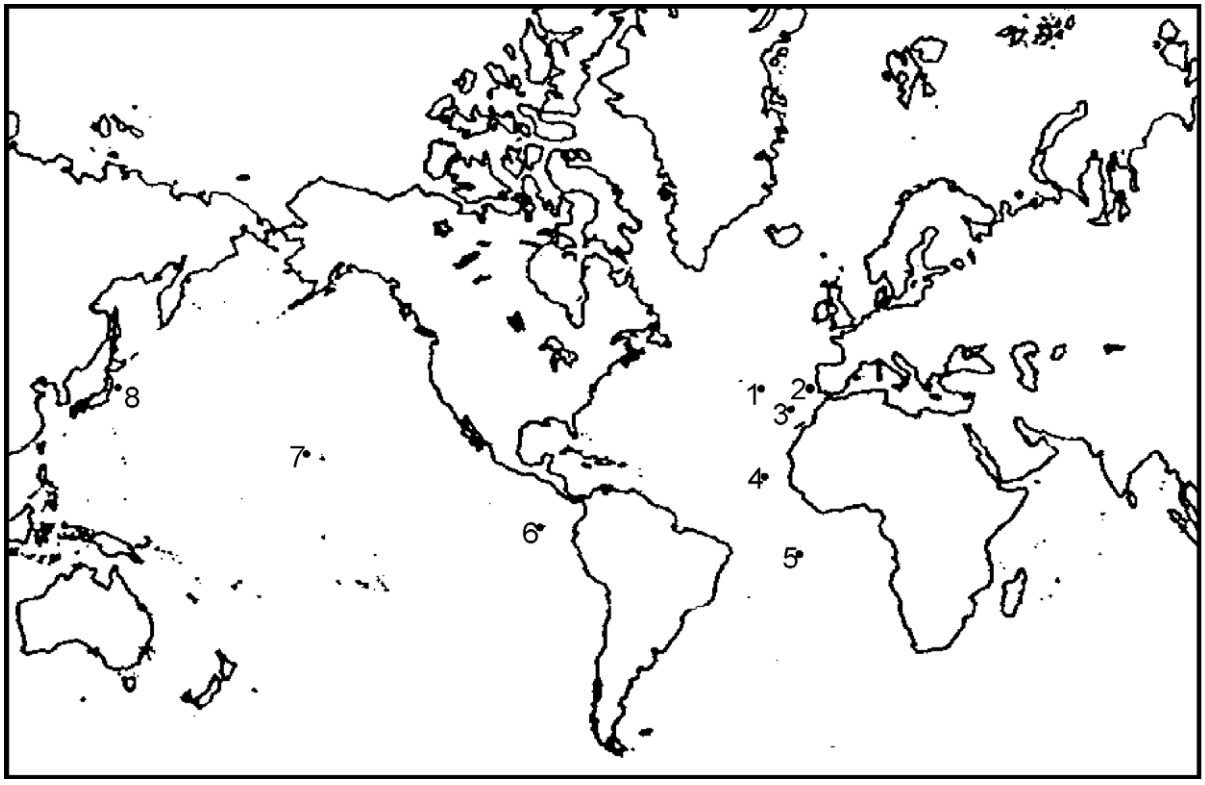

Fig. 1. Distribution of band-rumped storm-petrel colonies sampled in this study (1, Azores; 2, Farilhoes; 3, Madeira; 4, Cape Verde; 5, Ascension; 6, Galapagos; 7, Hawaii; and 8, Japan).

Table 1
Summary of populations sampled across the band-rumped storm-petrel breeding range, and estimates of haplotypic and nucleotide diversity

Colony	Breeding season	Date of collection	Sample size	Haplotype diversity (H_s)	Nucleotide diversity (π)
1. Azores					
Baixo	Hot	June 1994, June 1999	47	0.93 ± 0.02	0.01 ± 0.007
	Cool	September 1996	13	0.85 ± 0.09	0.004 ± 0.003
Praia	Hot	June 2003	31	0.94 ± 0.02	0.01 ± 0.006
	Cool	September 1996	19	0.86 ± 0.05	0.007 ± 0.004
Vila[a]	Cool	September 1996, December 1999	30	0.89 ± 0.03	0.01 ± 0.006
2. Farilhoes[a]	Cool	November 1994	12	0.92 ± 0.06	0.008 ± 0.005
3. Madeira					
Selvagem Grande	Hot	June 1999	32	0.82 ± 0.05	0.004 ± 0.003
	Cool	October 1999	28	0.92 ± 0.03	0.006 ± 0.004
Desertas[b]	Cool	November 1999	27	0.82 ± 0.07	0.006 ± 0.003
4. Cape Verde[c]					
Branco	Cool	June 1999	26	0.96 ± 0.03	0.02 ± 0.008
Raso	Cool	April 1999	25	0.92 ± 0.03	0.006 ± 0.004
5. Ascension[d]	Hot	October 2001	3	1.00 ± 0.18	0.06 ± 0.04
6. Galapagos	Hot	December 2001	30	0.98 ± 0.01	0.01 ± 0.007
	Cool	May 2001	34	0.98 ± 0.01	0.01 ± 0.005
7. Hawaii[d]	Hot	October 2000	2	1.00 ± 0.50	0.01 ± 0.01
8. Japan[d]	Hot	August 2002	30	0.89 ± 0.04	0.02 ± 0.009

[a] Only cool season breeding occurs here.
[b] Both cool and hot season breeding occurs here but only the cool season was sampled.
[c] A single protracted cool season breeding period appears to occur here, extending from December until June (Bannerman and Bannerman, 1968; M. Bolton, personal communication).
[d] Only hot season breeding occurs here.

two distinct sequences. Two heavy-strand PCR primers (OcH200-1: 5′-GGTAGGATAGTGGCCGTRGGTGG-3′; OcH200-2: 5′-GGTAGGATAGTGGCCGTRGGTT C-3′) were designed to amplify these copies separately. Both fragments [arbitrarily designated Copies 1 and 2] were amplified and sequenced for four individuals. Analysis of the resulting sequences confirmed the presence of two copies, and suggested that both may represent functional copies of the mitochondrial control region (see Section 3). A light-strand primer was designed for Copy 1 (OcL61: 5′-C AGTAGCGGGGCGGCTYTATGTAT-3′) and was used in combination with CgH825 (a primer previously designed to anneal within Conserved Sequence Block 1 in alcids; V.L. Friesen unpublished) to derive more complete sequence for one storm-petrel to confirm the presence of various conserved sequence blocks (see Section 3).

OcL61 was subsequently used with H521 to amplify a 448-bp fragment of mtDNA, comprising 266 bp of Domain I and 180 bp of Domain II, from all 389 storm-petrel samples. PCRs were run in 25 μL reaction volumes containing 2.5 mM $MgCl_2$, 10 mM Tris (pH 8.5), 50 mM KCl, 0.2 % gelatin, 62.5 μg/ml bovine serum albumin, 0.2 mM of each of the four dNTPs, 0.32 μM each of the primers OcL61 and H521, and 0.75 units of *Taq* DNA polymerase (Roche Diagnostics, Laval, Quebec). The PCR profile consisted of an initial denaturing step (1.5 min at 96 °C), followed by 31 cycles of 30 s denaturation at 96 °C, 30 s annealing at 60 °C, and 1 min primer extension at 72 °C, ending with a final 3-min primer extension step at 72 °C. Amplified DNA was subjected to electrophoresis through 0.8% or 2% agarose gels and purified with QiaQuik® kits according to the manufacturer's instructions or with filtered pipette tips (Dean and Greenwald, 1995). DNA was sequenced on an ABI 373A automated DNA sequencer (Mobix Labs, McMaster University, Hamilton, Ontario) and sequences were aligned manually in the program BIOEDIT (version 5.0.9; Hall, 1999). Only unambiguous sequences from Copy 1 were included in further analyses.

2.3. Data analyses

Standard population genetic analyses were carried out in the program ARLEQUIN (version 2.0; Schneider et al., 2000) using a significance level of 0.05. Sequential Bonferroni corrections were applied to all pairwise comparisons of populations to control for Type I errors (Rice, 1989). All means are reported as ±SE.

Haplotypic diversity (H_s; Nei, 1987) and nucleotide diversity (π; Tajima, 1983) were calculated as an index of genetic variation within populations. To test whether patterns of genetic variation deviated from selective neutrality, and to examine the historical demography of populations, Ewens–Watterson and Tajima's neutrality tests (Ewens, 1972; Watterson, 1978; Tajima, 1989; Slatkin, 1994, 1996), and Chakraborty's test of population amalgamation (Chakraborty, 1990) were conducted, and mismatch distributions (Rogers and Harpending, 1992) were calculated. However, since pairwise comparisons generated through mismatch analyses may not be ideally suited to control region data (Kuhner et al., 1998; Schneider and Excoffier, 1999), we also employed a maximum likelihood estimate based on coalescent theory using the program FLUCTUATE (Kuhner et al., 1998) to test for evidence of popula-

tion growth or decline. Significant population growth was determined by comparing twice the difference between the log likelihood at the maximum growth estimate and the log likelihood at zero growth with the critical χ^2 value for one degree of freedom. Based on results from AMOVA (see below), we grouped populations as follows for the FLUCTUATE analysis: Azores hot, Azores cool, Farilhoes, Madeira hot and cool, Cape Verde, Galapagos hot, Galapagos cool, and Japan. For populations with unimodal mismatch distributions and significant population growth indicated by FLUCTUATE, and assuming a molecular clock (Wilson et al., 1985), we used the equation $t = \tau/2\mu$ (where τ is the mode of the mismatch distribution, and μ is the mutation rate per year of the mitochondrial fragment, calculated by dividing the divergence rate of Domain I of the control region [21% million years^{-1}; Quinn, 1992] by 2 and multiplying by the length of the sequence, 448 bp) to estimate the approximate time of expansion (Rogers and Harpending, 1992). Due to low sample sizes, Ascension ($n = 3$) and Hawaii ($n = 2$) populations were excluded from tests of neutrality and population growth.

Analyses of molecular variance (AMOVA; Excoffier et al., 1992) were used to index the distribution of sequence variation among populations, using Kimura's two-parameter model of substitution (Kimura, 1980) with a rate parameter (α) of 0.47 (based on estimates for Domain I of the control region in finches, *Fringilla* and *Carduelis* spp., Marshall and Baker, 1997). Exact tests of population differentiation were also used to test for population structure. Statistical significance was determined for both Φ_{st} and exact tests with 10,000 randomizations of the data.

Percent sequence divergence between populations (both uncorrected [π_{xy}] and corrected for sequence variation within populations [δ]; Wilson et al., 1985) was calculated and used to estimate time since divergence for populations that did not share haplotypes using the equation $t = \delta/r$ (where t is divergence time in years and r is the sequence divergence rate, taken as 21% million years^{-1}; Quinn, 1992).

Since populations that share haplotypes may not be in genetic equilibrium, traditional methods for calculating time since divergence (e.g. above) and gene flow (e.g., using analogs of Wright's F_{st}; Wright, 1951) may be inaccurate, reflecting a combination of historical and contemporary conditions. To overcome this problem, a nonequilibrium method based on coalescent theory and Bayesian statistics in the program MDIV (Nielsen and Wakeley, 2001) was used to estimate divergence time ($t = T\theta/2\mu$, where T is population divergence time in N_f generations, θ is $2N_f\mu$ [both estimated from MDIV], and μ is the mutation rate per year of the mitochondrial fragment) and gene flow (M, in number of females per generation) for populations that were not reciprocally monophyletic. The mean generation time of band-rumped storm-petrels was estimated as 12 years (M. Bolton, personal communication). We ran the MDIV program under the finite sites mutation model (Hasegawa et al., 1985) with three chains (length of Markov chain = 5,000,000 cycles; burn-in time = 500,000 cycles) and three different random seeds. M_{max} was set between 1 and 500 (depending on what value approximated a Poisson-shaped posterior probability distribution), and T_{max} was set between 1 and 15 (depending on what value yielded an asymptotic posterior probability distribution). Maximum likelihood tests were used to test whether M or T were significantly different from zero (Nielsen and Wakeley, 2001).

The phylogeny of control region haplotypes was inferred by constructing statistical parsimony networks using the program TCS (version 1.13; Clement et al., 2000). Ambiguous haplotype connections were resolved following Crandall and Templeton (1993). A nested clade analysis (NCA) was performed on the main tree (containing the majority of haplotypes) to reconstruct population histories (Templeton et al., 1987; Templeton and Sing, 1993) using GEODIS (version 2.2; Posada, 2004). NCA organizes the haplotype tree into a hierarchical series of nested clades according to specific nesting rules (see Templeton et al., 1987; Templeton and Sing, 1993; Templeton, 2004). The spatial distribution of genetic variation is then quantified through statistical analyses of clade distance (D_c, the geographic range of a given clade) and nested clade distance (D_n, the geographic distribution of a given clade relative to its closest related clades) to test the null hypothesis of no association between haplotype and geography (Templeton, 1998). The evolutionary causes of any significant phylogeographic associations are subsequently tested with an inference key. For the present study, the statistical significance of the various NCA distance measures was determined with 10,000 randomizations of the data. Templeton's (2004) inference key (updated at http://darwin.uvigo.es/software/geodis.html) was used to identify potential processes leading to the observed spatial association of haplotypes, and supplementary tests, as outlined in Templeton (2001), were performed when appropriate to test for secondary contact.

3. Results

3.1. Sequence variation

A total of 170 haplotypes were found in copy 1 of the mitochondrial control region in the 389 individuals sampled using primers OcL61 and H521 (GenBank Accession Nos. AY600297, AY771004, AY771005, DQ 178703–DQ 178869; Supplementary Fig. 1). Whereas other researchers have reported nuclear copies of the mitochondrial control region in birds (e.g., Kidd and Friesen, 1998), several lines of evidence were consistent with a mitochondrial origin for the sequences that we amplified (both Copies 1 and 2): (1) sequences for the tRNA^{glu} formed a typical cloverleaf secondary structure (Desjardins and Morais, 1990), (2) the tRNA^{glu} sequence was highly conserved, with only one

variable site, which occurred in a loop, (3) sequence at the 5′ end contained several strings of multiple Cs forming a hairpin loop secondary structure, (4) sequence closely matching the highly conserved F-box found in other birds occurred in the appropriate location, (5) sequence variation was concentrated near the 5′ end (corresponding to Domain I), with no variation in the central region (Domain II), and (6) base composition was biased against Gs (27% A, 25% T, 33% C, 15% G) (cf. Baker and Marshall, 1997). Some sites appeared to vary in concert between the two copies, others appeared to represent fixed differences between the copies, while other sites appeared to vary independently between copies. These results are similar to patterns found in functional duplicated control regions of other avian taxa (Eberhard et al., 2001; Abbott et al., 2005).

The 170 haplotypes for Copy 1 were defined by 139 polymorphic sites, 136 of which consisted of substitutions, and three of which involved insertions or deletions (indels). Most variable sites (89) involved transitions, while 19 included both a transition and a transversion, and 28 involved transversions. Haplotypes differed by a mean of 16.4 ± 7.3 substitutions (or 4.0% of their sequence), with a range of one to 47 substitutions. The most common haplotype, Y, was found in 9.2% of individuals and only in northeastern Atlantic colonies. All populations contained unique haplotypes. Haplotypic diversity was similar among populations, averaging 0.92 ± 0.004 while nucleotide diversity averaged 0.01 ± 0.0008 (Table 1).

3.2. Tests for neutrality and demographic history

Estimates of Tajima's D were negative but nonsignificant both for individual populations and for all populations pooled (all $P > 0.07$). No significant deviations from neutrality were detected for populations using the Ewens-Watterson test (all $P > 0.3$). When populations were combined they exhibited higher genetic variability than expected based on the observed haplotype diversity (Chakraborty's test: $k = 170$, expected $= 108$, $P < 0.001$); however, Chakraborty's tests were not significant for any population after Bonferroni correction (all populations $P > 0.03$).

The mismatch distributions, both for individual populations and for all samples combined, did not differ from the patterns expected under a rapid population expansion (all $P > 0.2$; Supplementary Fig. 2). Raggedness indices (which index population stability) also were nonsignificant (all $P \geq 0.2$), suggesting that populations maybe growing. FLUCTUATE results indicated that all populations have undergone significant population growth except Azores cool, Cape Verde and Japan (all significant P were <0.01). Population expansions appear to have occurred within the last 12,000 to 54,000 years (Supplementary Fig. 2). Due to low statistical power, accurate population and growth estimates could not be obtained for the Galapagos hot population using FLUCTUATE.

3.3. Population genetic structure

No haplotypes were shared either between Atlantic and Pacific populations or amongst Pacific colonies except between the Galapagos seasonal populations (Table 2; although only two birds were sampled from Hawaii). Within the Atlantic, haplotypes were shared among northeastern populations (i.e., among Azores, Madeira, and Farilhoes) and between Cape Verde populations (Branco and Raso) (Table 2). Both Cape Verde and Ascension populations were distinct from all other Atlantic populations (although only three birds were sampled from Ascension).

Both AMOVA and the exact test of population differentiation indicated significant population structure in control region sequences (global $\Phi_{st} = 0.74$, $P < 0.001$; exact $P < 0.001$). Significant pairwise Φ_{st} values and significant differentiation in haplotype frequencies were found between (1) Atlantic and Pacific colonies, (2) Cape Verde and all other populations, (3) sympatric seasonal populations in the Azores, and (4) sympatric seasonal populations in Madeira (Table 3). Pairwise Φ_{st} estimates also indicated significant differentiation between Galapagos seasonal populations (Table 3). Hierarchical AMOVAs revealed that variation was best explained (i.e., the proportion of within group variation was minimized while the proportion of among group variation was maximized) when populations were arranged in 10 'groups': (1) Azores hot, (2) Azores cool, (3) Madeira hot, (4) Madeira cool and Farilhoes, (5) Cape Verde, (6) Ascension, (7) Galapagos hot, (8) Galapagos cool, (9) Hawaii, and (10) Japan ($\Phi_{ct} = 0.74$, $P < 0.001$; $\Phi_{sc} = 0.02$, $P < 0.001$).

3.4. Estimates of divergence time and gene flow

Corrected percent sequence divergence values suggested that Cape Verde populations (at least, females) have been separated from all other populations for 200,000 to 340,000 years (Table 3). Galapagos populations appear to have diverged from Atlantic populations within the last 220,000 to 300,000 years, but from other Pacific populations around 150,000 to 190,000 years ago. The Japan population is estimated to have diverged from Atlantic populations as recently as 110,000 years ago.

MDIV results for the northeastern Atlantic revealed a range of estimates for female-mediated gene flow and divergence time (Tables 3 and 4). Gene flow between sympatric seasonal populations in the Azores was estimated as less than one female per generation, and the null hypothesis that $M = 0$ could not be rejected by the likelihood ratio test (likelihood ratio tests, all $P > 0.05$). Gene flow between seasonal populations in Madeira was slightly higher (0.66 to 4.1 females per generation), but also did not differ from zero (both $P > 0.05$; note however that estimates of M are unreliable if T does not differ from 0 [R. Nielsen,

Table 2
Distribution and frequency of haplotypes within 16 global populations of band-rumped storm-petrels, and nested clade structure of haplotypes in the main statistical parsimony tree (Fig. 2)

5-Step clade	4-Step clade	3-Step clade	2-Step clade	1-Step clade	Haplotype	BxH	BxC	PrH	PrC	ViC	FaC	SeH	SeC	DeC	BrC	RaC	AsH	GaH	GaC	HaH	JaH	Total
5-1	4-1	3-2	2-3	1-10	BD																3	3
					KD																1	1
				1-11	WC																9	9
					GD																1	1
			2-4	1-12	YC																2	2
					AD																2	2
				1-13	JD																1	1
			2-5	1-14	ZC																2	2
		3-11	2-6	1-56	XC																4	4
					DD																1	1
	4-2	3-4	2-11	1-15	C4					1												1
			2-12	1-16	D4					1												1
		3-12	2-13	1-17	B4					1												1
	4-5	3-3	2-8	1-36	YD									1								1
			2-9	1-38	M2						2											2
				1-39	RD									2								2
					H2		1				1		2									4
			2-10	1-37	ND									2								2
				1-40	VD									1								1
					XD									1								1
					K2						1											1
		3-9	2-7	1-57	CD																1	1
			2-15	1-35	I1		1															1
					X2					1												1
				1-41	A1		2		4				1	1								8
					Y2					1			1									2
			2-30	1-6	LB								1									1
				1-7	XB								1									1
				1-8	U5							1										1
				1-9	LD									2								2
					R1	1																1
				1-58	Z		1		2													3
				1-59	W	2	5		2		2	1	6	4								22
					B1				1													1
					D1				1													1
					T5							1										1
		3-13	2-14	1-34	Z2					1												1
5-2	4-3	3-5	2-16	1-21	C	2		5														7
					A2	1																1
				1-22	P	2		2														4
					U1	3																3
			2-17	1-25	O1	5																5
				1-26	V1	1																1
		3-6	2-18	1-24	O			1														1
			2-19	1-23	N			1														1
			2-20	1-18	R	1		1	1													3

(*continued on next page*)

Table 2 (*continued*)

5-Step clade	4-Step clade	3-Step clade	2-Step clade	1-Step clade	Haplotype	BxH	BxC	PrH	PrC	ViC	FaC	SeH	SeC	DeC	BrC	RaC	AsH	GaH	GaC	HaH	JaH	Total
			2-21	1-27	B	1		1														2
					D	6		5														11
					K			2														2
	4-4	3-7	2-22	1-19	W4										1							1
				1-20	L			2														2
				1-29	G2	2																2
			2-23	1-28	Z1	1																1
				1-31	F			2														2
					V	6		1														7
		3-8	2-24	1-30	A			1														1
					H	8		3														11
				1-32	Q	1		1														2
			2-25	1-33	E			1														1
					G	2		2														4
5-3	4-6	3-1	2-29	1-50	CB							1										1
				1-52	BB							1										1
					EB							1										1
					QB							13	5									18
					ZB								1									1
			2-32	1-51	HB								1									1
		3-10	2-1	1-1	VC												1					1
			2-2	1-2	RB								1									1
					X1	1																1
				1-55	WB								1									1
			2-26	1-43	O2						1											1
				1-44	R2					5	1											6
					U2					1												1
			2-27	1-46	Z5							1										1
				1-47	AB							1	1									2
			2-31	1-3	DB							1										1
					IB							7	1									8
				1-4	S2					1				1								2
					T2					1												1
				1-5	V2					6												6
					A4					1												1
				1-45	X				2		1											3
				1-48	M1		1															1
				1-49	ID																1	1
				1-60	Y		2		6	7	3	3	4	11								36
					OB								1									1
					FD																1	1
					MD									1								1
					W2					2												2
				1-61	HD																1	1
			2-40	1-62	B5										1							1

AA			1				1
BA			1				1
CA			3	3			6
DA			1				1
EA			1				1
FA			1				1
GA			1				1
HA			1				1
IA			1	1			2
JA			1				1
KA			1				1
LA			2				2
MA			1				1
NA			1				1
OA			3				3
PA			1				1
QA			1	1			2
RA				3			3
SA				2			2
TA				1			1
UA				2			2
VA				1			1
WA				1			1
XA				1			1
LC					1		1
MC					1		1
TC		1					1
UC		1					1
F2	1						1
A3				1			1
B3				1			1
C3				1			1
D3				2			2
E3				1			1
F3			1	2			3
G3				1			1
H3				1			1
I3				1			1
J3				1			1
K3				1			1
L3				1			1
M3				1			1
N3				1			1
O3				1			1
P3				1			1
Q3			1				1
R3			1				1
S3			1				1

(*continued on next page*)

Table 2 (*continued*)

5-Step clade	4-Step clade	3-Step clade	2-Step clade	1-Step clade	Haplotype	BxH	BxC	PrH	PrC	ViC	FaC	SeH	SeC	DeC	BrC	RaC	AsH	GaH	GaC	HaH	JaH	Total
					T3													1				1
					V3													1				1
					W3													1				1
					X3													1				1
					E4											1						1
					F4											1						1
					G4											2						2
					H4										1	3						4
					J4											3						3
					K4											1						1
					L4											1						1
					M4										5	6						11
					N4										2	2						4
					O4											2						2
					P4											1						1
					Q4											1						1
					R4											1						1
					X4										1							1
					Y4										1							1
					Z4										2							2
					A5										1							1
					C5										1							1
					D5										1							1
					F5										1							1
					G5										1							1
					H5										1							1
					J5										1							1
					K5										1							1
					O5										1							1
					P5										2							2
					R5										1							1

Abbreviations refer to the following populations: BxH, Baixo hot season; BxC, Baixo cool season; PrH, Praia hot season; PrC, Praia cool season; ViC, Vila cool season; SeH, Selvagem Grande hot season; SeC, Selvagem Grande cool season; DeC, Desertas cool season; BrH, Branco hot season; RaH, Raso hot season; AsH, Ascension hot season; GaH, Galapagos hot season; GaC, Galapagos cool season; HaH, Hawaii hot season; JaH, Japan hot season. Horizontal broken line indicates end of haplotypes in main network.

Table 3
Estimates of Φ_{st} (upper number above the diagonal), t (lower number above the diagonal) and δ (below the diagonal) for global populations of band-rumped storm-petrels

	BxH	BxC	PrH	PrC	ViC	FaC	SeH	SeC	DeC	BrC	RaC	AsH	GaH	GaC	HaH	JaH
BxH		**0.58***	0.008	**0.56***	**0.58***	**0.55***	**0.65***	**0.61***	**0.62***	**0.75***	**0.83***	**0.53***	**0.77***	**0.81***	0.78*	**0.64***
		113,000	*4000*	*101,000*	*154,000*	*107,000*	*98,000*	*110,000*	*111,000*	218,000	270,000	88,000	240,000	259,000	256,000	125,000
BxC	1.74*		**0.68***	−0.001	**0.10**	0.01	**0.20***	−0.008	0.005	**0.79***	**0.92***	0.35*	**0.80***	**0.85***	0.91	**0.66***
			88,000	*100*	*9000*	*100*	*9000*	*100*	*100*	236,000	287,000	19,000	225,000	240,000	258,000	112,000
PrH	0.01	2.11*		**0.66***	**0.66***	**0.65***	**0.74***	**0.70***	**0.71***	**0.76***	**0.86***	0.59*	**0.79***	**0.83***	0.66*	**0.66***
				70,000	*121,000*	*92,000*	*92,000*	*96,000*	*102,000*	218,000	269,000	104,000	240,000	260,000	251,000	127,000
PrC	1.61*	0.002	1.97*		0.05	0.01	**0.12***	0.007	0.03	**0.79***	**0.90***	0.36*	**0.80***	**0.84***	0.88*	**0.66***
					14,000	*100*	*7000*	*4000*	*5000*	231,000	283,000	18,000	219,000	234,000	259,000	110,000
ViC	1.88*	0.12	2.28*	0.05		0.05	**0.13***	**0.09***	**0.10***	**0.78***	**0.87***	0.38*	**0.79***	**0.83***	0.83	**0.66***
						5000	*11,000*	*11,000*	*17,000*	245,000	298,000	30,000	233,000	248,000	283,000	125,000
FaC	1.71*	0.007	2.09*	0.006	0.07		**0.18***	0.03	0.004	**0.77***	**0.90***	0.31*	0.79*	**0.84***	0.86*	**0.64***
							12,000	*200*	*1000*	233,000	285,000	25,000	226,000	240,000	260,000	114,000
SeH	1.98*	0.11*	2.36*	0.07*	0.12*	0.11*		0.07*	**0.17***	**0.83***	**0.92***	0.55*	**0.84***	**0.88***	0.93	**0.73***
								1000	*10,000*	241,000	293,000	30,000	234,000	249,000	272,000	125,000
SeC	1.81*	−0.005	2.18*	0.004	0.09*	0.02	0.04*		**0.03**	**0.81***	**0.91***	0.45*	**0.82***	**0.86***	0.90*	**0.69***
									8000	239,000	291,000	23,000	227,000	242,000	264,000	116,000
DeC	1.87*	0.005	2.25	0.02	0.10*	−0.004	0.11*	0.02		**0.82***	**0.91***	0.46*	**0.82***	**0.86***	0.90*	**0.70***
										242,000	293,000	25,000	230,000	245,000	264,000	119,000
BrC	4.57*	4.96*	4.57*	4.85*	5.13*	4.89*	5.06*	5.02*	5.09*		0.06	0.71*	**0.78***	**0.82***	0.74*	**0.72***
											300	276,000	269,000	280,000	237,000	202,000
RaC	5.67*	6.03*	5.64*	5.94*	6.25*	5.98*	6.16*	6.11*	6.16*	0.07		0.85*	**0.85***	**0.88***	0.90	**0.82***
												340,000	295,000	305,000	250,000	239,000
AsH	1.84*	0.41*	2.18*	0.37*	0.62*	0.52*	0.63*	0.48*	0.52*	5.80*	7.14*		0.72*	0.78*	0.53	0.54*
													248,000	266,000	311,000	104,000
GaH	5.04*	4.73*	5.05*	4.60*	4.90*	4.74*	4.92*	4.77*	4.84*	5.65*	6.20*	5.21*		0.03	0.72	**0.68***
														3000	180,000	154,000
GaC	5.43*	5.04*	5.45*	4.91*	5.20*	5.04*	5.23*	5.08*	5.15*	5.88*	6.40*	5.58*	0.04		0.80*	**0.74***
															192,000	169,000
HaH	5.38*	5.41*	5.27*	5.45*	5.94	5.46	5.71	5.54*	5.54*	4.97	5.26*	6.54*	3.79*	4.04*		0.68
																158,000
JaH	2.62*	2.35*	2.67*	2.31*	2.63*	2.39*	2.63*	2.43*	2.49*	4.24*	5.02*	2.18*	3.23*	3.55*	3.31	

Values with asterisks were significant at $\alpha = 0.05$ after sequential Bonferroni correction. Values in bold indicate significant differentiation between populations after sequential Bonferroni correction. Pairwise estimates of t for populations that were not reciprocally monophyletic were calculated in MDIV and are indicated in italics. All other values are based on δ estimates. Population abbreviations identical to Table 2.

personal communication]). Sympatric seasonal populations in the Azores were estimated to have diverged at least 80,000 years ago ($P < 0.0001$; Tables 3 and 4), and Desertas and Selvagem Grande populations diverged approximately 8000 to 10,000 years ago ($P < 0.05$). In contrast, gene flow estimates were considerably higher between allopatric populations breeding within the same season in the Azores, ranging from 1.2 to 37.2 females per generation (Table 4), and divergence times for these populations were not significantly greater than zero (likelihood ratio tests, all $P > 0.10$).

The estimate for T between Branco and Raso (Cape Verde) was not significantly greater than zero ($R = 0$, $P = 0.99$). These populations were estimated to exchange 3.6 females per generation (Table 4). In the Galapagos, the estimate of T between sympatric seasonal populations was not significantly different from 0, and suggested that these populations have probably been genetically separated for less than 4000 years (Smith and Friesen, 2006).

3.5. Statistical parsimony and nested clade analyses

The 95% probable connection limit for the statistical parsimony analysis was nine mutational differences. Four haplotype trees were identified (Fig. 2), while three haplotypes (below) remained unconnected because they differed by more than nine mutations from all other haplotypes. The main tree (containing the majority of haplotypes) was comprised of mainly Atlantic haplotypes, and included the two most common haplotypes: 'Y' (the likely root to the tree, and found in 36 individuals from Azores cool, Farilhoes, and Madeira hot and cool populations) and 'W' (found in 22 individuals from Azores hot and cool, Farilhoes, and Madeira hot and cool populations; Fig. 2a). All Japanese haplotypes also occurred in this tree and were most closely related to Azores cool haplotypes (Fig. 2a). Two Cape Verde haplotypes ('W4' and 'B5') were found in the main tree (Fig. 2a), while the rest grouped in a tree separate from all other haplotypes (Fig. 2b). Haplotypes from Branco and Raso islands (Cape Verde) were

Table 4
Estimates of T (population divergence time in N_f generations; upper number above diagonal), θ ($2N_f\mu$; lower number above diagonal), and M (number of females exchanged per generation; lower number below diagonal) calculated in MDIV for populations sharing haplotypes

	BxH	BxC	PrH	PrC	ViC	FaC	SeH	SeC	DeC	BrC	RaC	GaH	GaC
BxH		1.49*	0.05	1.49*	1.56*	1.20*	1.35*	1.37	1.51*				
		9.45	8.92	8.49	12.32	11.18	9.04	10.06	9.22				
BxC	0.42		1.24*	0.004	0.19*	0.004	0.28	0.004	0.004				
			8.92	2.98	6.06	3.93	3.84	4.48	3.02				
PrH	23.7*	0.032		1.08*	1.32*	1.03*	1.34*	1.12*	1.39*				
				8.06	11.50	11.11	8.61	10.75	9.21				
PrC	0.68*	37.2	0.16		0.16*	0.004	0.24*	0.09	0.14				
					11.28	4.19	3.76	5.53	4.15				
ViC	0.19	1.44	0.004	1.20*		0.07	0.22*	0.18*	0.33*				
						8.10	6.48	7.87	6.48				
FaC	0.43*	9.00	0.016	3.20	3.84		0.31*	0.004	0.04				
							4.81	6.04	4.42				
SeH	0.30	1.28	0.004	0.83	0.32	1.04		0.02	0.29*				
								5.18	4.26				
SeC	0.31*	77.0*	0.004	3.45	0.66	16.2	4.12		0.18				
									5.46				
DeC	0.34*	8.40	0.004	2.34	0.96	2.55*	0.66	2.10					
BrC											0.004		
											9.97		
RaC										3.6*			
GaH													0.02
													17.3
GaC												13.8*	

Values of T and M with asterisks indicate estimates that are significantly greater than zero. Shaded areas indicate populations with fixed haplotype differences. Population abbreviations identical to Table 2.

interspersed throughout the Cape Verde tree (Fig. 2b). All Galapagos haplotypes also occurred in their own tree, with hot and cool season haplotypes mixed throughout (Fig. 2c). Two Hawaii haplotypes grouped together in a tree (Fig. 2d). The remaining unconnected haplotypes represented Ascension ('UC'), Baixo hot ('F2'), and Branco ('D5').

Within the main tree (Fig. 2a), several clades across different nested clade levels showed significant geographic associations (Tables 2 and 5; because of the number of clades, nesting is given in Table 2 instead of on the haplotype tree). In particular, northeastern Atlantic populations (Azores, Madeira, Farilhoes) showed an overall pattern of restricted gene flow and isolation by distance (clades 2-30, 3-9, 4-5) with either infrequent long distance colonization and subsequent fragmentation or past fragmentation followed by range expansion (clades 3-10, and 5-1). Supplementary tests applied to these clades indicated that populations from Vila (in the Azores) and Selvagem Grande (in Madeira) were likely isolated from other northeastern Atlantic populations in the past, but have since undergone secondary contact with Azores populations (Table 5 and Supplementary Fig. 3). The distribution of haplotypes in these clades suggests that this more recent admixture mainly involved cool season birds (Fig. 2a and Table 5). Atlantic and Japanese haplotypes also showed evidence of restricted gene flow combined with some long distance dispersal (clades 2-31, 4-6, Table 5). Finally, the distribution of haplotypes across the entire main tree appears to be due to contiguous range expansion (total cladogram, Table 5).

4. Discussion

4.1. Taxonomy of the band-rumped storm-petrel

Many marine species exhibit less phylogeographic structure than terrestrial species, presumably because of their typically large population sizes, their high vagility, and the paucity of spatial barriers to dispersal in marine environments (e.g. Avise, 1998; Stamatis et al., 2004). In seabirds, strong dispersal capabilities should lead to low genetic differentiation among populations, since some species routinely travel over a thousand kilometers during foraging trips, while others have trans-hemispheric or trans-oceanic migratory patterns (Harrison, 1983;

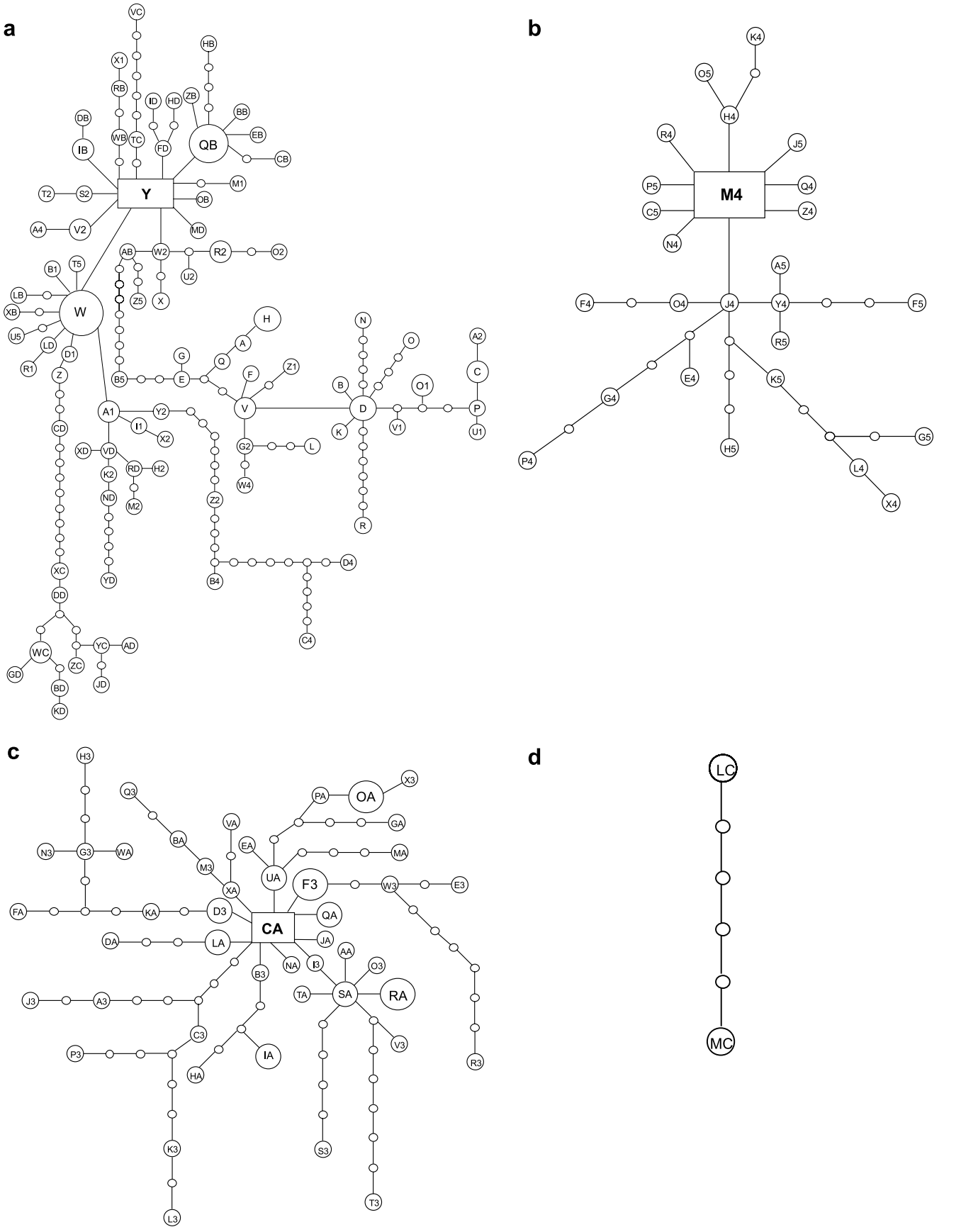

Fig. 2. Statistical parsimony networks for (a) Atlantic and Japan haplotypes, (b) Cape Verde haplotypes, (c) Galapagos haplotypes, and (d) Hawaii haplotypes. Haplotypes in squares represent probable roots to networks (or most ancestral haplotypes). Sizes of haplotype circles or squares are proportional to frequencies in population samples. Clear circles indicate missing haplotypes (either unsampled or extinct).

Table 5
Inferences of population history based on nested clade analysis

Clade	Inference chain	Populations involved	Inferred pattern
2-30	1-2-11-17-4 No	Azores hot and cool, Farilhoes, Madeira hot and cool	Restricted gene flow with isolation by distance
2-31	1-2-3-5-6-7-Yes	Azores cool, Farilhoes, Madeira hot and cool, Japan	Restricted gene flow with some long-distance dispersal
3-9	1-2-11-17-4 No	Azores hot and cool, Madeira hot and cool, Japan	Restricted gene flow with isolation by distance
3-10	1-2-3-5-6-13 Yes + Supplementary tests	Azores hot and cool, Farilhoes, Madeira hot and cool, Cape Verde, Ascension, Japan	Past fragmentation followed by range expansion
4-5	1-2-11-17-4 No	Azores hot and cool, Farilhoes, Madeira hot and cool	Restricted gene flow with isolation by distance
4-6	1-2-3-5-6-7 Yes	Azores hot and cool, Farilhoes, Madeira hot and cool, Cape Verde, Ascension, Japan	Restricted gene flow with some long-distance dispersal
5-1	1-2-11-12-13 Yes + Supplementary tests	Azores hot and cool, Farilhoes, Madeira hot and cool, Japan	Past fragmentation followed by range expansion
Total cladogram	1-2-11-12 No	All	Contiguous range expansion

Weimerskirch, 1998). Yet despite their high vagility, physical (e.g., major landmasses) and nonphysical (e.g., philopatry) barriers to gene flow have promoted diversification in many seabird species (Avise et al., 2000; Friesen et al., 2007). Population differentiation tends to be lower in temperate and polar species than in tropical and subtropical ones (Friesen et al., 2007), perhaps because of the direct influence of Pleistocene glaciers at higher latitudes (e.g., historical associations still may be retained in populations that have undergone recent rapid population expansions following the last glacial retreat).

In the case of band-rumped storm-petrels, global populations display significant differentiation in their mitochondrial control regions despite high vagility. Strong genetic differentiation among populations occurs both spatially and temporally, and is evident at several geographic scales: no haplotypes are shared (1) between Atlantic and Pacific populations, (2) among Japan, Hawaii, and Galapagos populations within the Pacific Ocean (although only two birds were sampled from Hawaii) or (3) between Cape Verde, Ascension, and populations from northeastern Atlantic colonies (i.e., Azores, Farilhoes, and Madeira, although only three birds were sampled from Ascension; Table 2). Significant population genetic structure also occurred between sympatric seasonal populations of band-rumped storm-petrels within the Azores, Madeira and Galapagos, although no fixed haplotype differences existed between seasonally segregated populations (Table 2; Smith and Friesen, 2006).

What constitutes a species, and how species boundaries should be defined, has long been contentious in biology (Goldstein et al., 2000). Although numerous species concepts have been proposed, most definitions recognize that a species is comprised of diagnosable groups of populations that share a common evolutionary fate and are genetically exchangeable (Harrison, 1998; Helbig et al., 2002). According to these criteria, Galapagos and Cape Verde populations may qualify as phylogenetic and biological species: both form clades distinct from all other populations in the statistical parsimony tree (Fig. 2), and populations in both locations appear to have been genetically isolated for at least 150,000 years (Table 3). Furthermore, estimates of δ are significantly greater than zero (3.23 to 6.40% divergence from all other populations for Galapagos populations, and 4.24–7.14% divergence for Cape Verde populations; Table 3), and are high compared with mitochondrial control region values recorded between subspecies of rock ptarmigan (*Lagopus mutus*, average 0.67%; Holder et al., 1999), albatross taxa (*Thalassarche cauta* and *T. steadi*, 0.60%; Abbott and Double, 2003), and species within the herring gull complex (*Larus cachinnans fuscus*, average 0.38%; Liebers et al., 2004). Thus, Galapagos and Cape Verde populations may represent two new species, although the present results need to be confirmed with nuclear data.

Hot season populations of Madeiran storm-petrel breeding in the Azores also appear to represent a separate, cryptic species. Azores hot and cool season populations are diagnosable based on morphometric variation, vocalizations and ecological characteristics (Monteiro and Furness, 1998; Monteiro et al., 1998; Bolton, in press), they exchange few if any female migrants (Table 4), and they exhibit strong genetic differentiation (Table 3). In addition, Azores hot and cool season populations share only two haplotypes (Table 2), and are otherwise separated by a large mutational distance in the gene tree (Fig. 2). Estimates of δ between seasonal populations are significantly greater than zero (1.74% for Baixo and 1.97% for Praia), and are high compared with other species that have been studied (above). In contrast, cool season populations in the Azores differ little from cool season populations elsewhere in the northeastern Atlantic (Tables 3 and 4). Thus, the hot season populations in the Azores appear to qualify as a distinct species, although this possibility also should be confirmed with nuclear data.

Unlike the Azores populations, temporally segregated populations of band-rumped storm-petrels in Madeira are not diagnosable in their mtDNA because no single mutation discriminates between them. Whether these populations are diagnosable by breeding season is unclear since, although estimates of female-mediated gene flow do not different from zero, the gene flow estimates may be unreliable and no recapture data exist for these populations. It is also unknown at present whether they can be distinguished by phenotypic characteristics such as morphometrics or vocalizations. Nevertheless, estimates of δ, Φ_{st} and T indicate that Madeira seasonal populations are genetically differentiated. These results are similar to mtDNA variation in their Galapagos counterparts, for which Smith and Friesen (2006) recommended recognition of distinct management units (*sensu* Moritz, 1994) on the basis of slight differences in morphology, vocalizations and mtDNA variation. Thus, until additional phenotypic and genetic data are available, we recommend that Madeira seasonal populations be classified as separate management units.

4.2. Role of physical and nonphysical barriers to gene flow

Current phylogeographic patterns in band-rumped storm-petrels appear to be shaped predominantly by nonphysical barriers to gene flow. The statistical parsimony trees (Fig. 2) and nested clade analysis (Table 5) suggest that population genetic structuring in global populations is largely due to limited dispersal. Apart from the grouping of haplotypes from Japan and the northeast Atlantic, samples from different regions form independent haplotype trees, indicating that female-mediated gene flow is nonexistent beyond a few thousand kilometers. Within northeastern Atlantic locations, phylogeographic structure is mainly characterized by restricted gene flow due to isolation by distance, although fragmentation and secondary contact are also evident. In contrast, the Japan population appears to be derived from one or more long distance dispersal events from the northeast Atlantic. However, the number of steps between most of the Japan haplotypes and the Atlantic haplotypes is very close to the connection limit, suggesting that the Japan population may, in fact, not belong in the Atlantic tree.

Within the northeastern Atlantic islands, the main tree shows that many rare haplotypes have arisen from a few higher frequency ancestral hubs (Fig. 2), consistent with a pattern of colonization and range expansion. This pattern is further supported by the NCA, which found evidence of contiguous range expansion (Table 5), and results from the mismatch distributions and FLUCTUATE, which indicate population expansions at most colonies. Both Madeira and Vila populations appear to have been fragmented from other northeastern Atlantic colonies in the past, but have since regained contact. Historical isolation from neighbouring colonies may have been influenced by variable climatic conditions during Pleistocene glacial cycles. For example, rising sea levels during interstadial or interglacial periods may have caused population bottlenecks at Madeira or Vila colonies, while altered ocean currents could have changed their dispersal or foraging patterns.

4.3. Phylogeography of the band-rumped storm-petrel

Late Pleistocene glacial activity has been linked to both intra- and interspecific diversification of avian species in temperate zones (Lovette, 2005). The role of recent Ice Ages in shaping phylogeographic divergence of tropical and sub-tropical birds, however, is relatively unknown. In the case of band-rumped storm-petrels, most major phylogeographic subdivisions within and between ocean basins predate the last Ice Age, which extended from approximately 70,000 to 15,000 years before present (ybp; Rahmstorf, 2002). The high genetic heterogeneity observed in contemporary populations of band-rumped storm-petrels worldwide also suggests that genetic diversity was not diminished during recent glacial activity. However, most populations observed in this study have experienced recent demographic expansions, coinciding with either marine isotope stage 3 (approximately 60,000 to 25,000 ybp) or interglacial conditions since the final Pleistocene glacial retreat (between 15,000 and 7000 ybp). A similar evolutionary pattern has been documented in another mid to low latitude seabird, the sooty tern (Peck and Congdon, 2004). Marine isotope stage 3 was characterized by several stadial and interstadial events, causing frequent shifts in worldwide climate, and accompanying fluctuations of global sea levels (Siddall et al., 2003), sea surface temperatures (Sachs and Lehman, 1999; Lea et al., 2000; Thompson, 2000), ocean circulation patterns (Rahmstorf, 2002) and marine eutrophication and stratification (Kameo et al., 2004). Sea levels are estimated to have dropped by as much as 35 m during cool phases (Siddall et al., 2003), potentially providing increased breeding habitat for band-rumped storm-petrels.

Population growth of band-rumped storm-petrels may have been further enhanced by oceanographic conditions in the Atlantic and Pacific during glacial advances. Compared with contemporary conditions, sea surface temperatures were likely 3 °C cooler in the tropical Pacific and as much as 5–6 °C cooler in the tropical Atlantic during stadial periods (Lea et al., 2000; Thompson, 2000). Equatorial Pacific trade winds strengthened at these times, leading to increased cold water upwellings in the eastern Pacific basin, similar to under modern La Niña events (Bigg, 1996; Lea et al., 2000). In the Atlantic, stadial periods generally corresponded with increased oceanic mixing at mid to low latitudes, resulting in higher productivity of surface waters (Crowley, 1981; Rahmstorf, 2002). This combination of climatic factors may have increased foraging opportunities for band-rumped storm-petrels, which are typically associated with regions of upwelling such as eddies and frontal zones (Haney, 1985; Smith and Hyrenbach, 2003).

4.4. Conclusions

Identifying where seabird populations lie on the continuum between panmixis and complete genetic isolation is important for determining conservation priorities for different species. If populations of a species differ genetically, then loss of a population will lead to a decline in the species' genetic diversity, potentially increasing the overall risk of extinction (Soulé, 1980). Moreover, other populations may be slow to recolonize extirpated areas and may lack local adaptations if migration is naturally low. Conversely, while the management of panmictic populations would appear much more straightforward, complications may arise if metapopulation dynamics exist. In this case, loss of individual populations would have different effects on the overall viability of a species, depending on whether they were sources or sinks (Pulliam, 1988).

Band-rumped storm-petrels have traditionally been classified as monotypic, suggesting that gene flow is extensive throughout the breeding range. However, the present study reveals that they exhibit considerable heterogeneity in control region sequences across their breeding range, and several populations show fixed differences, indicating that the species is far from panmictic. Instead, band-rumped storm-petrels appear to represent several distinct cryptic lineages, some of which may warrant recognition as new species. In particular, we recommend that additional genetic and/or phenotypic data be collected to determine whether Cape Verde and Galapagos birds are, in fact, genetically isolated from other populations worldwide.

The phylogeography and population dynamics of band-rumped storm-petrels has apparently been associated with Pleistocene glacial activity, adding to growing evidence that glaciation has had profound effects on taxa beyond polar and temperate regions (e.g., Lessios et al., 2001; Muss et al., 2001). While glacial cycles may not have created allopatric barriers to dispersal in mid to low latitudes, storm-petrels in these regions were likely affected by the corresponding fluctuations in oceanographic conditions. The absence of female-mediated gene flow among regions within ocean basins indicates that nonphysical barriers to gene flow, such as philopatry or local adaptation, also have contributed to diversification of band-rumped storm-petrels.

Like other storm-petrels, band-rumped storm-petrels are extremely sensitive to anthropogenic disturbance. Breeding activity is concentrated in small, relatively isolated colonies throughout the Atlantic and Pacific, making colonies particularly vulnerable to local extinction. Given that gene flow among colonies is apparently low, recolonization of breeding habitat following disturbance may be severely limited. Conservation efforts should recognize the diversity of this species by protecting not only genetically distinct populations, but also the 'natural network of genetic connections' among populations necessary for the maintenance of adaptive diversity and evolutionary potential (Crandall et al., 2000).

Acknowledgments

We thank the following people for assistance with sample collection: Atlantic samples—Mark Bolton, Maria Carvalho, Bob Furness, Luis Monteiro, Veronica Neves, Tammy Steeves, and Richard White; Pacific samples—Yutaka Watanuki and Tom Telfer. We are grateful to Evelyng Astudillo Sánchez, Mark Bolton, Andrew Paterson, and Santiago Torres for help with Galapagos field work. Logistical support was provided by David Anderson, Patricia Robayo, Heidi Snell, the Charles Darwin Research Station, the Galapagos National Park Service, and TAME Airlines. We thank Matthew Atkey, Tim Birt, Theresa Burg, Shawn Garner, Rhonda Kristensen, and Tammy Steeves for help with laboratory work, and Sherry Taylor for use of her laboratory facilities for a portion of this project. We are grateful to Ken Warheit for helpful discussions, and Louis Bernatchez, Laurene Ratcliffe, Sherry Taylor, Virginia Walker and two anonymous reviewers for comments on earlier drafts of this manuscript. Funding was provided by the American Museum of Natural History (Frank M. Chapman Memorial Award to A.L.S.), the American Ornithologists Union (Blake Fund award to A.L.S.), the Cooper Ornithological Society (Joseph Grinnell Student Research Award to A.L.S.), the Natural Sciences and Engineering Research Council of Canada (research grants to V.L.F.), a Premier's Research Excellence Award (to V.L.F.), and Queen's University (Graduate Dean's Doctoral Field Travel Grant and Thesis Completion Bursary to A.L.S.).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2007.02.012.

References

Abbott, C., Double, M.C., 2003. Phylogeography of shy and white-capped albatrosses inferred from mitochondrial DNA sequences: implications for population history and taxonomy. Mol. Ecol. 12, 2747–2758.

Abbott, C.L., Double, M.C., Trueman, J.W.H., Robinson, A., Cockburn, A., 2005. An unusual source of apparent mitochondrial heteroplasmy: duplicate control regions in *Thalassarche* albatrosses. Mol. Ecol. 14, 3605–3613.

Ainley, D.G., Le Reseche, R.E., Sladen, W.J., 1983. Breeding Biology of the Adélie Penguin. University of California Press, Berkeley.

Avise, J.C., 1998. Conservation genetics in the marine realm. J. Hered. 89, 377–382.

Avise, J.C., Nelson, W.S., Bowen, B.W., Walker, D., 2000. Phylogeography of colonially nesting seabirds, with special reference to global matrilineal patterns in the sooty tern (*Sterna fuscata*). Mol. Ecol. 9, 1783–1792.

Baillie, S.R., Milne, H., 1989. Movements of eiders *Somateria mollissima* on the east coast of Britain. IBIS 131, 321–335.

Baker, A.J., Marshall, H.D., 1997. Mitochondrial control region sequences as tools for understanding evolution. In: Mindell, D.P.

(Ed.), Avian Molecular Evolution and Systematics. Academic Press, San Diego, pp. 51–82.
Bannerman, D.A., Bannerman, W.M., 1968. Birds of the Atlantic Islands. Vol. 4. History of the Birds of the Cape Verde Islands. Oliver and Boyd, Edinburgh.
Bigg, G.R., 1996. The Oceans and Climate. Cambridge University Press, New York.
Bolton, M., in press. Playback experiments indicate absence of vocal recognition among temporally and geographically separated populations of Madeiran storm-petrels *Oceanodroma castro*. Ibis.
Bried, J., Bolton, M., 2005. An initial estimate of age at first return and breeding in Madeiran storm-petrels *Oceanodroma castro*. Atlantic Seabirds 7, 71–74.
Brown, R.G.B., 1980. Seabirds as marine animals. In: Burger, J., Olla, B.L., Winn, W.E. (Eds.), Behavior of Marine Mammals, vol. 4. Plenum Press, New York, pp. 1–39.
Cagnon, C., Lauga, B., Hémery, G., Mouchès, C., 2004. Phylogeographic differentiation of storm-petrels (*Hydrobates pelagicus*) based on cytochrome *b* mitochondrial DNA variation. Mar. Biol. 145, 1257–1264.
Chakraborty, R., 1990. Mitochondrial DNA polymorphism reveals hidden heterogeneity within some Asian populations. Am. J. Hum. Genet. 47, 87–94.
Clement, M., Posada, D., Crandall, D., 2000. TCS: a computer program to estimate gene genealogies. Mol. Ecol. 9, 1657.
Congdon, B.C., Piatt, J.F., Martin, K., Friesen, V.L., 2000. Mechanisms of population differentiation in marbled murrelets: historical versus contemporary processes. Evolution 54, 974–986.
Coulson, J.C., 2002. Colonial breeding in seabirds. In: Schreiber, E.A., Burger, J. (Eds.), Biology of Marine Birds. CRC Press, Boca Raton, pp. 87–114.
Cramp, S.K., Simmons, E.L., 1982. Handbook of the Birds of Europe, the Middle East and North Africa: the Birds of the Western Palearctic. Vol. 1. Ostrich–Ducks. Oxford University Press, New York.
Crandall, K.A., Templeton, A.R., 1993. Empirical tests of some predictions from coalescent theory with applications to intraspecific phylogeny reconstruction. Genetics 134, 959–969.
Crandall, K.A., Bininda-Edmonds, O.R.P., Mace, G.M., Wayne, R.K., 2000. Considering evolutionary processes in conservation biology. TREE 15, 290–295.
Crowley, T.J., 1981. Temperature and circulation changes in the eastern North Atlantic during the last 150,000 years: evidence from the planktonic foraminiferal record. Mar. Micropaleo. 6, 97–129.
Dean, A.D., Greenwald, J.E., 1995. Use of filtered pipet tips to elute DNA from agarose gels. Biotechniques 18, 980.
Dearborn, D.C., Anders, A.D., Schreiber, E.A., Adams, R.M.M., Mueller, U.G., 2003. Inter-island movements and population differentiation in a pelagic seabird. Mol. Ecol. 12, 2835–2843.
del Hoyo, J., Elliot, A., Sargatel, J., 1992. Handbook of Birds of the World, Vol. I. Lynx Editions, Barelona.
Desjardins, P., Morais, R., 1990. Sequence and gene organization of the chicken mitochondrial genome: a novel gene order in higher vertebrates. J. Mol. Biol. 212, 599–634.
Eberhard, J.R., Wright, T.F., Bermingham, E., 2001. Duplication and concerted evolution of the mitochondrial control region in the parrot genus *Amazona*. Mol. Biol. Evol. 18, 1330–1342.
Ewens, W.J., 1972. The sampling theory of selectively neutral alleles. Theor. Pop. Biol. 3, 87–112.
Excoffier, L., Smouse, P.E., Quattro, J.M., 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. Genetics 131, 479–491.
Friesen, V.L., Montevecchi, W.A., Baker, A.J., Barrett, R.T., Davidson, W.S., 1996. Population differentiation and evolution in the common guillemont *Uria aalge*. Mol. Ecol. 5, 793–805.
Friesen, V.L., Congdon, B.C., Walsh, H.E., Birt, T.P., 1997. Intron variation in marbled murrelets detected using analyses of single-stranded conformational polymorphisms. Mol. Ecol. 6, 1047–1058.
Friesen, V.L., Burg, T. M, McKoy, K.D., 2007. Mechanisms of population differentiation in seabirds. Mol. Ecol., in press.
Gaston, A.J., 2004. Seabirds: A Natural History. Yale University Press, New Haven.
Goldstein, P.S., Desalle, R., Amato, G., Vogler, A.P., 2000. Conservation genetics at the species boundary. Cons. Biol. 14, 120–131.
Gómez-Díaz, E., González-Solís, J., Peinado, M.A., Page, R.D.M., 2006. Phylogeography of the *Calonectris* shearwaters using molecular and morphometric data. Mol. Phylogen. Evol. 41, 322–332.
Hall, T.A., 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nuc. Ac. Symp. Ser. 41, 95–98.
Haney, J.C., 1985. Band-rumped storm-petrel occurrences in relation to upwelling off the coast of the south-eastern United States. Wilson Bull. 97, 543–547.
Haney, J.C., Solow, A.R., 1992. Analyzing quantitative relationships between seabirds and marine resource patches. Curr. Ornithol. 9, 105–151.
Harris, M.P., 1969. The biology of storm-petrels in the Galapagos Islands. Proc. Calif. Acad. Sci. 37, 95–166.
Harris, M.P., 1979. Survival and ages of first breeding of Galapagos seabirds. Bird Banding 50, 56–61.
Harris, M.P., 1984. The seabirds. In: Perry, R. (Ed.), Key Environments: Galapogas. Pergamon Press, New York, pp. 191–206.
Harrison, P., 1983. Seabirds: an Identification Guide. Houghton Mifflin Co., New York.
Harrison, R.G., 1998. Linking evolutionary pattern and process: the relevance of species concepts for the study of speciation. In: Howard, D.J., Berlocher, S.H. (Eds.), Endless Forms: Species and Speciation. Oxford University Press., New York, pp. 19–31.
Hasegawa, M., Kishino, H., Yano, T., 1985. Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. J. Mol. Evol. 21, 160–174.
Helbig, A.J., Knox, A.G., Parkin, D.T., Sangster, G., Collinson, M., 2002. Guidelines for assigning species rank. IBIS 144, 518–525.
Hewitt, G., 2000. The genetic legacy of the Quaternary ice ages. Nature 405, 907–913.
Holder, K., Montgomerie, R., Friesen, V.L., 1999. A test of the glacial refugium hypothesis using patterns of mitochondrial and nuclear DNA sequence variation in rock ptarmigan (*Lagopus mutus*). Evolution 53, 1936–1950.
Kameo, K., Shearer, M.C., Droxler, A.W., Mita, I., Watanabe, R., Sato, T., 2004. Glacial-interglacial surface water variations in the Caribbean Sea during the last 300 ky based on calcareous nannofossil analysis. Palaeogeog., Palaeoclimatol., Palaeoecol. 212, 65–76.
Kidd, M.G., Friesen, V.L., 1998. Analysis of mechanisms of microevolutionary change in *Cepphus* guillemots using patterns of control region variation. Evolution 52, 1158–1168.
Kimura, M., 1980. A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. J. Mol. Evol. 16, 111–120.
Kuhner, M.K., Yamato, Y., Felsenstein, J., 1998. Maximum likelihood estimation of population growth based on the coalescent. Genetics 149, 429–434.
Lea, D.W., Pak, D.K., Spero, H.J., 2000. Climate impact of Late Quaternary Equatorial Pacific sea surface temperature variations. Science 289, 1719–1724.
Lessios, H.A., Kessing, B.D., Pearse, J.S., 2001. Population structure and speciation in tropical seas: global phylogeography of the sea urchin *Diadema*. Evolution 55, 955–975.
Liebers, D., de Knijff, P., Helbig, A.J., 2004. The herring gull complex is not a ring species. Proc. Roy. Soc. Lond. B. 271, 893–901.
Lovette, I.J., 2005. Glacial cycles and the tempo of avian speciation. TREE 20, 57–59.
Marshall, H.D., Baker, A.J., 1997. Structural conservation and variation in the mitochondrial control region of fringilline finches (*Fringilla* spp.) and the greenfinch (*Carduelis chloris*). Mol. Biol. Evol. 14, 173–184.

Monteiro, L.R., Furness, R.W., 1998. Speciation through temporal segregation of Madeiran storm-petrel (*Oceanodroma castro*) populations in the Azores? Phil. Trans. Roy. Soc. Lond. 353, 945–953.

Monteiro, L.R., Granadeiro, J.P., Furness, R.W., 1998. Relationship between mercury levels and diet in Azores seabirds. Mar. Ecol. Progr. Ser. 166, 259–265.

Moritz, C., 1994. Applications of mitochondrial DNA analysis in conservation: a critical review. Mol. Ecol. 3, 401–411.

Moum, T., Árnason, E., 2001. Genetic diversity and population history of two related seabird species based on mitochondrial DNA control region sequences. Mol. Ecol. 10, 2463–2478.

Muss, A., Robertson, D.R., Stepien, C.A., Wirtz, P., Bowen, B.W., 2001. Phylogeography of *Ophioblennius*: the role of ocean currents and geography in reef fish evolution. Evolution 55, 561–572.

Nei, M., 1987. Molecular Evolutionary Genetics. Columbia University Press, New York.

Nielsen, R., Wakeley, J., 2001. Distinguishing migration from isolation: a Markov chain Monte Carlo approach. Genetics 158, 885–896.

Noble, D.G., Gaston, A.J., Elliot, R.D., 1991. Preliminary estimates of survivorship and recruitment for thick-billed murres at Coats Island. In: Gaston, A.J., Elliot, R.D. (Eds.), Studies of High Arctic Seabirds. (2) Conservation Biology of the Thick-Billed Murre in the Northwest Atlantic. Can. Wildlife Serv. Occas. Paper No. 69, pp. 45–51.

Nunn, P.D., 1997. Late Quaternary environmental changes on Pacific islands: controversy, certainty and conjecture. Quatern. Sci. 12, 443–450.

Ovenden, J.R., Wust-Saucy, A., Bywater, R., 1991. Genetic evidence for philopatry in a colonially nesting seabird, the fairy prion (*Pachyptila turtur*). Auk 108, 688–694.

Patirana, A., Hatch, S.A., Friesen, V.L., 2002. Population differentiation in the red-legged kittiwake (*Rissa brevirostris*) as revealed by mitochondrial DNA. Conserv. Gen. 3, 335–340.

Peck, D.R., Congdon, B.C., 2004. Reconciling historical processes and population structure in the sooty tern *Sterna fuscata*. J. Avian Biol. 35, 327–335.

Posada, D., 2004. Geodis 2.2: Differentiating Population Structure from History. Biology Faculty, University of Vigo, Vigo, Spain.

Pulliam, H.R., 1988. Sources, sinks, and population regulation. Am. Nat. 132, 652–661.

Quinn, T.W., 1992. The genetic legacy of Mother Goose—phylogeographic patterns of lesser snow goose *Chen caerulescens caerulescens* maternal lineages. Mol. Ecol. 1, 105–117.

Quinn, T.W., Wilson, A.C., 1993. Sequence evolution in and around the mitochondrial control region in birds. J. Mol. Evol. 37, 417–425.

Rabouam, C., Bretagnolle, V., Bigot, Y., Periquet, G., 2000. Genetic relationships of Cory's shearwater: parentage, mating assortment, and geographic differentiation revealed by DNA fingerprinting. Auk 117, 651–662.

Rahmstorf, S., 2002. Ocean circulation and climate during the past 120,000 years. Nature 419, 207–214.

Rice, W.R., 1989. Analyzing tables of statistical tests. Evolution 43, 223–225.

Rogers, A.R., Harpending, H., 1992. Population growth makes waves in the distribution of pairwise genetic differences. Mol. Biol. Evol. 9, 552–569.

Sachs, J.P., Lehman, S.J., 1999. Subtropical North Atlantic temperatures 60,000 to 30,000 years ago. Science 286, 756–759.

Sambrook, J., Fritsch, E.F., Maniatis, T., 1989. Molecular Cloning: a Laboratory Manual, 2nd ed. Wiley, New York.

Schneider, S., Excoffier, L., 1999. Estimation of past demographic parameters from the distribution of pairwise differences when the mutation rates vary among sites: application to human mitochondrial DNA. Genetics 152, 1079–1089.

Schneider, S.D., Roessli, D., Excoffier, L., 2000. ARLEQUIN ver 2.000: a software for population genetics data analysis. Genetics and Biometry Laboratory, University of Geneva, Geneva, Switzerland.

Schreiber, E.A., Burger, J., 2002. Biology of Marine Birds. CRC Press, Boca Raton.

Siddall, M., Rohling, E.J., Almogi-Labin, A., Hemleben, Ch., Meischner, D., Schmeizer, I., Smeed, D.A., 2003. Sea-level fluctuations during the last glacial cycle. Nature 423, 853–858.

Slatkin, M., 1994. An exact test for neutrality based on the Ewens sampling distribution. Gen. Res 64, 71–74.

Slatkin, M., 1996. A correction to the exact test based on the Ewens sampling distribution. Gen. Res 68, 259–260.

Smith, A.L., Friesen, V.L., 2006. Differentiation of sympatric populations of the band-rumped storm-petrel in the Galapagos Islands: an examination of genetics, morphology, and vocalizations. Mol. Ecol., in press.

Smith, J.L., Hyrenbach, K.D., 2003. Galápagos Islands to British Columbia: seabird communities along a 9000 km transect from the tropical to the subarctic eastern Pacific Ocean. Mar. Ornithol. 31, 155–166.

Snow, D.W., Snow, B.K., 1966. The breeding season of the Madeiran storm-petrel *Oceanodroma castro* in the Galapagos. IBIS 108, 283–284.

Soulé, M.E., 1980. Thresholds for survival: maintaining fitness and evolutionary potential. In: Soulé, M.E., Wilcox, B.A. (Eds.), Conservation Biology: an Ecological–Evolutionary Perspective. Sinauer Associates, Sunderland, MA, pp. 151–169.

Stamatis, C., Triantafyllidis, A., Moutou, K.A., Mamuris, Z., 2004. Mitochondrial DNA variation in northeast Atlantic and Mediterranean populations of Norway lobster, *Nephrops norvegicus*. Mol. Ecol. 13, 1377–1390.

Steeves, T.E., Anderson, D.J., McNally, H., Kim, M.H., Friesen, V.L., 2003. Phylogeography of *Sula*: the role of physical barriers to gene flow in the diversification of tropical seabirds. J. Avian Biol. 34, 217–223.

Steeves, T.E., Anderson, D.J., Friesen, V.L., 2005a. The Isthmus of Panama: a major physical barrier to gene flow in highly mobile pantropical seabirds. J. Evol. Biol. 18, 1000–1008.

Steeves, T.E., Anderson, D.J., Friesen, V.L., 2005b. A role for nonphysical barriers to gene flow in the diversification of a highly vagile seabird, the masked booby (*Sula dactylatra*). Mol. Ecol. 14, 3877–3887.

Tajima, F., 1983. Evolutionary relationships of DNA sequences in finite populations. Genetics 105, 437–460.

Tajima, F., 1989. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123, 585–595.

Templeton, A.R., 1998. Nested clade analyses of phylogeographic data: testing hypotheses about gene flow and population history. Mol. Ecol. 7, 381–397.

Templeton, A.R., 2001. Using phylogeographic analyses of gene trees to test species status and processes. Mol. Ecol. 10, 779–791.

Templeton, A.R., 2004. Statistical phylogeography: methods of evaluating and minimizing inference errors. Mol. Ecol. 13, 789–809.

Templeton, A.R., Sing, C.F., 1993. A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping. IV. Nested analysis with cladogram uncertainty and recombination. Genetics 134, 659–669.

Templeton, A.R., Boerwinkle, E., Sing, C.F., 1987. A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping. I. Basic theory and analysis of alcohol dehydrogenase activity in *Drosophila*. Genetics 117, 343–351.

Thompson, L.G., 2000. Ice core evidence for climate change in the tropics: implications for our future. Quat. Sci. Rev. 19, 19–35.

Tiedemann, R., Paulus, K.B., Scheer, M., Von Kistowski, K.G., Skírnisson, K., Bloch, D., Dam, M., 2004. Mitochondrial DNA and microsatellite variation in the eider duck (*Somateria mollissima*) indicate stepwise postglacial colonization of Europe and limited current long-distance dispersal. Mol. Ecol. 13, 1481–1494.

Watterson, G., 1978. The homozygosity test of neutrality. Genetics 88, 405–417.

Weimerskirch, H., 1998. How can a pelagic seabird provision its chick when relying on a distant food resource? Cyclic attendance of the

colony, foraging decision and body condition in sooty shearwaters. J. Anim. Ecol. 67, 99–109.

Wilson, A.C., Cann, R.L., Carr, S.M., George, M., Gyllensten, U.B., Helm-Bychowski, K.M., Higuchi, R.G., Palumbi, S.R., Prager, E.M., Sage, R.D., Stoneking, M., 1985. Mitochondrial DNA and two perspectives on evolutionary genetics. Biol. J. Linn. Soc. 26, 375–400.

Wright, S., 1951. The genetical structure of populations. Ann. Eugen. 15, 323–354.

Zino, F., Biscoito, M.J., Zino, P.A., 1994. Madeiran storm-petrel, *Oceanodroma castro*. In: Tucker, G.M., Heath, M.F., Tomialojc, L., Grimmett, R.F.A. (Eds.), Birds in Europe: their Conservation Status. BirdLife Conservation Series 3. BirdLife International, Cambridge, pp. 78–79.