Molecular Ecology (2000) **9**, 1783–1792

Phylogeography of colonially nesting seabirds, with special reference to global matrilineal patterns in the sooty tern (*Sterna fuscata*)

JOHN C. AVISE,* WILLIAM S. NELSON,* BRIAN W. BOWEN† and DEETTE WALKER*
**Department of Genetics, University of Georgia, Athens, GA, 30602, ‡Department of Fisheries and Aquatic Sciences, University of Florida, Gainesville, FL, 32653–3071, USA*

Abstract

Sooty tern (*Sterna fuscata*) rookeries are scattered throughout the tropical oceans. When not nesting, individuals wander great distances across open seas, but, like many other seabirds, they tend to be site-faithful to nesting locales in successive years. Here we examine the matrilineal history of sooty terns on a global scale. Assayed colonies within an ocean are poorly differentiated in mitochondrial DNA sequence, a result indicating tight historical ties. However, a shallow genealogical partition distinguishes Atlantic from Indo-Pacific rookeries. Phylogeographic patterns in the sooty tern are compared to those in other colonially nesting seabirds, as well as in the green turtle (*Chelonia mydas*), an analogue of tropical seabirds in some salient aspects of natural history. Phylogeographic structure within an ocean is normally weak in seabirds, unlike the pronounced matrilineal structure in green turtles. However, the phylogeographic partition between Atlantic and Indo-Pacific rookeries in sooty terns mirrors, albeit in shallower evolutionary time, the major matrilineal subdivision in green turtles. Thus, global geology has apparently influenced historical gene movements in these two circumtropical species.

Keywords: dispersal, gene flow, green turtles, mitochondrial DNA, population structure, vicariance

Received 31 March 2000; revision received 14 June 2000; accepted 14 June 2000

Introduction

The sooty tern (*Sterna fuscata*) is among the most abundant and pelagic of seabirds (Tuck & Heinzel 1978). The species nests in large, discrete colonies typically on islands scattered throughout the tropical Atlantic, Pacific and Indian Oceans. Nesting occurs in dense aggregations, either annually or, sometimes, on a 9- to 10-month reproductive cycle (Ashmole 1963). When not nesting, the birds travel vast distances across open sea in search of epipelagic prey.

Several aspects of sooty tern demography and natural history are shared by other seabird species (Ashmole 1971; Wooller *et al*. 1992). These include: a long lifespan (up to 30 years in the sooty tern); delayed breeding (usually not earlier than at five years in this species); low reproductive rate (one offspring per tern nest); colonial nesting; nesting fidelity to natal sites despite long-distance travels at other times in the life cycle (Carr 1967); and dramatic fluctuations in population size often tied to episodic regional factors, such as El Niño (Schreiber & Schreiber 1989), or to rookery-specific events, such as storms or flooding (Wooller *et al*. 1992).

Several key facets of sooty tern natural history are also shared with the green sea turtle (*Chelonia mydas*). Indeed, as phrased by Carr (1967), 'There is a mystic alliance between the two'. Long-lived green turtles are also distributed circumtropically and nest in discrete rookeries, often on the same islands utilized by sooty terns. Furthermore, green turtles migrate great distances in the ocean, to feeding grounds hundreds or even thousands of kilometres from the rookery sites. Green turtle colonies from around the world have been surveyed for mitochondrial DNA (mtDNA; reviews in Bowen & Avise 1996; Bowen & Karl 1997; Karl & Bowen 1999), and two salient phylogeographic findings emerged: (i) pronounced (but shallow) matrilineal population structure within an ocean basin, suggesting strong propensities for natal homing by females (Meylan *et al*.

Correspondence: John C. Avise. Fax: (706) 542 3910; E-mail: avise@arches.uga.edu

1990; Bowen *et al*. 1992; Encalada *et al*. 1996); and (ii) a relatively deep phylogenetic split distinguishing assayed rookeries in the Indo-Pacific basin from those in the Atlantic Ocean and Mediterranean Sea, suggesting a vicariant separation probably associated with the rise of the Isthmus of Panama (Bowen *et al*. 1992).

Here we assay mtDNA restriction sites and control-region sequences in sooty terns from nesting colonies in the Indian, Pacific and Atlantic Oceans. Patterns of phylogeographic population structure will be compared to those of green turtles from nearly the same rookery sites. Have the comparable lifestyles and geographical distributions of these two species translated into similar phylogeographic patterns within and across ocean basins? How do the phylogeographic signatures in sooty terns compare to those described previously for high-latitude species of colonially nesting seabirds?

Materials and methods

A total of 56 samples was obtained from five sooty tern rookeries (Fig. 1). Only the samples from Ascension Island and Johnston Island were included in the mtDNA restriction-site assays. All specimens (except one from Johnston Island) were included in subsequent assays of control-region sequences.

Closed-circular mtDNA was isolated from fresh heart, liver, or muscle by CsCl–ethidium bromide density gradient centrifugation (Lansman *et al*. 1981). In the restriction assays, these molecules were digested using the 19 informative endonucleases listed in Table 1, and the digestion products were run through 1.0–1.6% agarose gels (Lansman *et al*. 1981; Maniatis *et al*. 1982). Data were recorded in a presence–absence matrix of restriction sites, from which sequence divergence estimates were calculated (Nei & Li 1979) and a hand-generated parsimony network was constructed.

In the sequence assays, standard polymerase chain reaction (PCR) techniques (Palumbi *et al*. 1991) were used to amplify ≈ 450-base pair (bp) products, from which sequences 343 bp in length were scored for each of 55 individuals. The PCR primers for sooty terns were those employed previously in other avian species to amplify the one-third of the control region adjacent to the $tRNA^{GLU}$ gene (Desjardins & Morais 1990, 1991; Quinn & Wilson 1993; Wenink *et al*. 1994): TS437R, 5′-GGGTTGCTGATTTCACGTGA-3′; CH16746L, 5′-ACCCCAAGGACTACGGCTTGAA-3′.

Double-stranded amplification products were sequenced using the *fmol* DNA Sequencing System (Promega). Sequences were aligned without ambiguity.

Estimates of sequence divergence (δ) between mtDNA haplotypes were calculated using Kimura's two-parameter model (Kimura 1980). Virtually identical results were obtained using the distance estimators of Jukes & Cantor (1969), Felsenstein (1984) and Tamura & Nei (1993), as calculated in MATRIX 1.5 by Posada *et al*. (2000). The resulting distance matrix was employed to estimate matrilineal relationships by neighbour-joining (Saitou & Nei 1987) and (for comparative purposes) by UPGMA clustering (Sneath & Sokal 1973), using the programs PHYLIP (Felsenstein 1991) and PAUP* (Swofford 1999). Support for nodes was examined

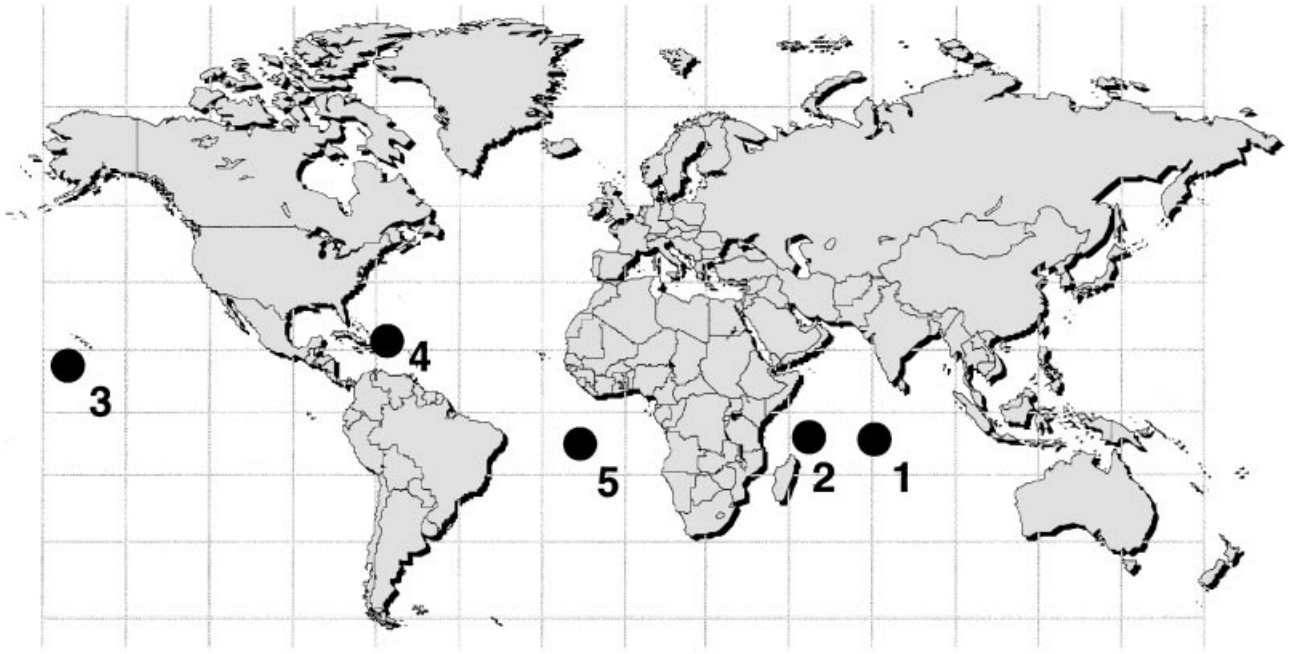

Fig. 1 Sooty tern rookeries genetically analysed: 1, Chagos Archipelago, Indian Ocean (six birds); 2, Seychelles, Indian Ocean (13 birds); 3, Johnston Island, Pacific Ocean (11 birds); 4, Puerto Rico, Caribbean Sea (nine birds); and 5, Ascension Island, Atlantic Ocean (17 birds).

Table 1 The 12 mtDNA haplotypes in sooty terns as revealed in restriction digests of the full-length molecule. Letters, from left to right, refer to multifragment digestion profiles* produced by *Ava*I, *Ava*II, *Bam*HI, *Bcl*I, *Bgl*I, *Bgl*II, *Bst*EII, *Cla*I, *Dra*I, *Eco*RI, *Eco*109, *Hin*dIII, *Msp*I, *Nci*I, *Pst*I, *Pvu*II, *Spe*I, *Sst*II, and *Stu*I

1	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
2	B	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3	D	—	—	B	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
4	D	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5	—	D	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6	—	—	—	—	—	—	—	—	—	—	—	B	—	—	—	—	—	—	—
7	—	B	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8	C′	—	—	D	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9	—	B	—	—	—	—	—	—	D	—	—	—	—	—	—	—	—	—	—
10	—	—	—	D	—	—	—	—	—	—	—	—	—	D	—	—	—	—	—
11	—	—	—	D	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12	—	—	—	D	—	—	—	—	—	—	—	—	—	—	—	—	—	—	D

*Adjacent letters in the alphabet indicate that the digestion profiles differ by one restriction site at the indicated enzyme; nonadjacent letters differ by two restriction sites. The C′ pattern in haplotype 8 differs from C by one restriction site, and from B and D by two each. Dashes indicate identity of the digestion profile to that in the top row (pattern C).

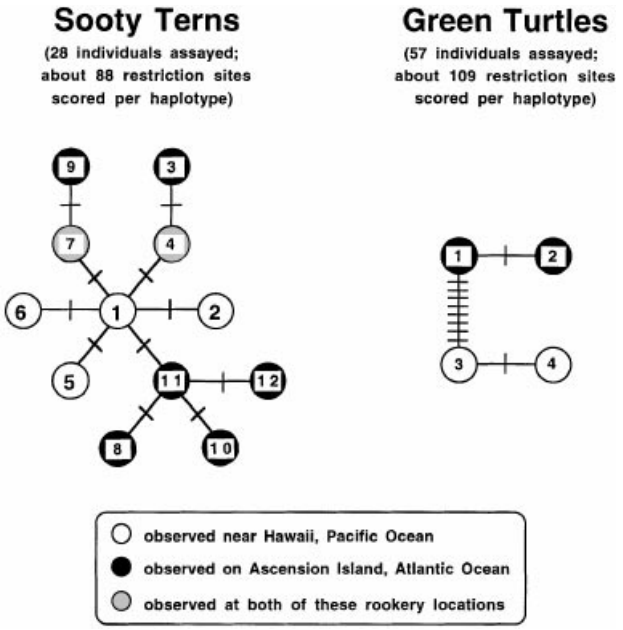

Fig. 2 Parsimony networks for sooty terns (left) and green turtles (right) based on comparable restriction-site surveys of full-length mtDNA from specimens taken at nesting sites near Hawaii (Johnston Island and French Frigate Shoals in the two respective species) and on Ascension Island. Green turtle data are from Bowen *et al*. (1992).

by bootstrapping (1000 replicates). Haplotypic and nucleotide diversities were calculated according to Nei (1987). Molecular variation within and among rookeries from the two major ocean basins was partitioned and statistically evaluated by a nested AMOVA (analysis of molecular variance; Excoffier *et al*. 1992) that considers molecular distances between haplotypes as well as haplotype frequencies.

Dates of evolutionary separation between gene-tree lineages were estimated using conventional mtDNA clock calibrations as described later. Population divergence times were estimated using molecular clocks as applied to net genetic distance values (δ_c) corrected for within-population variation (Avise 1994): $\delta_c = \delta_{AB} - 0.5\ (\delta_A + \delta_B)$, where δ_{AB} is the mean pairwise genetic distance between individuals in populations A and B, and δ_A and δ_B are nucleotide diversities (mean genetic distances between individuals) within the two populations. This procedure assumes that lineage diversity in the ancestral population was similar to the mean values in extant populations.

Results

Restriction sites

Preliminary mtDNA assays involved restriction-site comparisons of birds from Ascension Island (central Atlantic) and Johnston Island (central Pacific). Twelve different mtDNA haplotypes were detected (Table 1) in assays which involved a mean of about 88 scored restriction sites (516 bp of recognition sequence) in each of 28 specimens. All differences among mtDNA digestion profiles could be interpreted in terms of restriction-site changes. Haplotype diversities were 0.82 and 0.84 at Ascension and Johnston Islands, respectively; nucleotide diversity within each rookery was 0.002.

The 12 mtDNA haplotypes could be joined into a parsimony network (Fig. 2) in which all branches were of unit length (one restriction-site change each). Furthermore, no homoplasy need be invoked to account for the structure of this minimum-length network (i.e. the sum of the branch lengths connecting any pair of haplotypes matches exactly the corresponding number of observed restriction-site differences).

In the restriction-site data for sooty terns, there was no indication of a consistent matrilineal partition between the Atlantic and Pacific rookeries. Two of the composite mtDNA haplotypes (numbers 4 and 7) were shared by these two locales, and the various haplotypes confined to Ascension Island were dispersed across two different sections of the parsimony network (Fig. 2).

Control-region sequences

The lack of obvious phylogeographic structure in restriction-site data from sooty tern rookeries on opposite sides of the earth prompted subsequent sequencing assays of the mtDNA control region. In other avian species, this

Table 2 Variability and geographical distribution of the control-region sequences of sooty terns

	Individuals per locality*					Variable sequence position
						1111111111111111111122222222223
						1111111222333455556677889000123444555788999990000001229O
Haplotype	IO(a)	IO(b)	HI	PR	AS	4023456946723681239067904345692146767854645678013567036 22
st 104†	1					CTTTGTAACACTCCTATCCTTTCTATGCTGCTACCCCCCGCACCATTTCTTATAAGG
st 1			1			----------C----------C----------
st 113		1				----------C----------T----T-C-C---------
st 24			2			----------CGC----------T---T-GC----------
st 114		1	1			----------CGC----------T---T--C----------
st 102	1					-C----------CGC----------T---T--C--------G--
st 2			1			----------T---C-CGC----------T---T----------
st 13			1			----------CGC----------T---G---C----------
st 119		1				------G-----T----------CGC----------T----TAC----------
st 106	1					------G-----T----------CGC----------T----TGC----------
st 101	1					---C--------T----------CGC----------T----T-C----------
st 115		1				-----C------T----------CGC----------T----T-C----------
st 103	1					------G-----T----------CGCA-C---------T----TGC----------
st 116		1				-C----------CGC---A--------T----TGC----------
st 41			1			--C--CG---T-T----------CGC----------T----TGC---------A-
st 111		1				--C---G----------CGC---A--------T------C----------
st 40			1			--C---G----------CGC----------T------C----------
st 36			1			--C-A-G----------CGC---A--------T------C---------A-
st 118		1				--CC----T----------CGC----------T------C----------
st 117		1				--C---G-----T----------CGC---------T--T------C--T-------A
st 109		1				---C--------T----------CGC---A--------T------CC-------G--
st 105	1					------GGT----------CTCGC----------T----T-C-------G---
st 17			1			----------C-CGC---------T--T----T-C-------G---
st 120		1				--CC--------T---C------CGC----------T------TGC----------
st 110		1				-----CG-T---T--G--T----CGC---A--------T----T-C----C------
st 112		1				--C--CG-T---T--G--T----CGC---A--------T----T-C----C----AA
st 108		1				-----C----T---C--------CGC---A--GT----TA---T-C----C------
st 85					1	T-C---G-----T----------CGC----------T----T--C----------
st 64				1		T-C--CG---T-T----------CGC-----C------T----T--C----------
st 81					2	T-CC--G---T-T----------CGC-----C------T----T--C----------
st 68				1		T-C--CG---T-T------C---CGC-----C----T-T----T--C----------
st 67				1		T-C--CG---T-T------C---CGC---ATC------T----T--C----------
st 65				1		T-----G---T-T------C---CGC-----C------T----T--C-T--------
st 80					1	T---------T-T----------CGC-----C------T----T--C----------
st 77					1	T---------T---------C--CGC-----C------T----T--C----------
st 76					1	T----C----T---------C--CGC-----C------T----T--C----------
st 75					2	T-C-------T-TT---------CGC-----C------T----T-CC--------A-
st 73					1	T-C---------T-C--------CGC-----C----------T--C--------A-
st 62				1		T-CC------T-T----------C-C-----C------T----T--C-T--G-----
st 66				1		T-C--CG---T-T----------CGC-----C----T-T----T--CC--CG-----
st 78					3	T----CG--GT-T----------CGC---A-C--T---T----T--C-T--------
st 70				1		T-C--CG--GT-T----------CGC---A-C--T---T----T--C--------A-
st 69				1		TC---C----TCT----------CGC-T-A-C------T----T--C----------
st 87					1	T-C---G---T----------C-CGC----------T----T--C--C----G--
st 72					3	T-C---G---T----------C-CGC----------T----T--C--C-------
st 71					1	T-C---G---T----------C-CGC----------T----T--C--C--C----
st 63				1		T-CC------T-TT---------CGC---A-C--------T-TT-CC----------

*IO(a) = Chagos Archipelago; IO(b) = Seychelles; HI = Johnston Island (near Hawaii); PR = Puerto Rico; AS = Ascension Island
†The full 343-bp sequence of this haplotype has been deposited in GenBank (accession no. AF205605).

portion of the molecule often (but not invariably; see Baker *et al*. 1994; Zink *et al*. 1999) has proved to be more variable than typical mitochondrial coding sequences (Quinn 1992; Baker & Marshall 1997).

Sequencing of the control region did reveal additional mtDNA variation in sooty terns. In the 343-bp section surveyed, 47 different mtDNA haplotypes were detected in 55 specimens (Table 2). From these data, haplotype

Table 3 Comparative levels of mtDNA variation in sooty terns (present study) and green turtles* from the same geographical suite of rookery sites

	Restriction assays (whole molecule)				Direct sequencing (control region)			
Rookery site	No. indiv.	No. haplo.	Haplotype diversity	Nucleotide diversity	No. indiv.	No. haplo.	Haplotype diversity	Nucleotide diversity
Sooty terns								
Indian Ocean (IOa)	—	—	—	—	6	6	1.00	0.022
Indian Ocean (IOb)	—	—	—	—	13	13	1.00	0.026
Central Pacific (HI)	11	6	0.84	0.002	10	9	0.98	0.018
Atlantic (PR)	—	—	—	—	9	9	1.00	0.022
Atlantic (AS)	17	8	0.82	0.002	17	11	0.94	0.019
Total, or pooled value	28	12†	0.90	0.002	55	47†	0.99	0.029
Green turtles								
Indian Ocean (IO)	15	1	0.00	0.000	—	—	—	—
Central Pacific (HI)	22	2	0.40	0.001	—	—	—	—
Atlantic (AS)	35	2	0.06	<0.001	20	3	0.35	0.001
Atlantic (FL)	24	2	0.22	0.001	24	3	0.56	0.001
Total, or pooled value	96	6†	0.77	0.007	44	6	0.72	0.006

No. indiv., number of individuals; No. haplo., number of haplotypes.
*Restriction-site data from Bowen *et al*. (1992); control-region sequence data from Encalada *et al*. (1996).
†Total number of haplotypes is less than the sum of the rookery-specific numbers when some haplotypes are shared across locales.

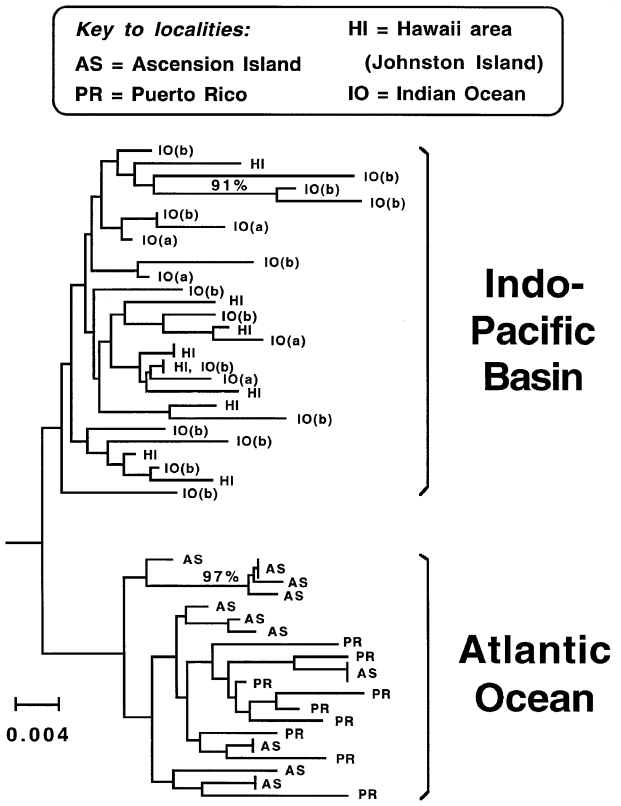

Fig. 3 Neighbour-joining tree for mtDNA haplotypes (control-region sequences) in global collections of the sooty tern. The network is mid-point rooted. With only two exceptions (as noted), no lineages in the tree received bootstrap support at levels greater than 75%. IO(a) and IO(b) refer to the Chagos and Seychelles rookeries, respectively.

diversities within all five rookery sites were greater than 0.94 (close to the maximum possible value of 1.0), and within-colony nucleotide diversities ranged from 0.018 to 0.029 (Table 3), about an order of magnitude higher than those in restriction-site data from the whole mtDNA molecule.

The mtDNA lineages were not strongly grouped geographically within either oceanic basin (Indo-Pacific or Atlantic). In other words, rookery samples from the Pacific and Indian Oceans were interspersed throughout the estimated matrilineal tree, and the same can be said for those from Puerto Rico and Ascension Island in the Atlantic Ocean (Fig. 3). Furthermore, only two minor lineages received strong bootstrap support (Fig. 3). However, all 29 assayed individuals from the Indo-Pacific grouped separately from all 26 specimens from the Atlantic Ocean (Figs 3, 4). This most-basal split in the matrilineal phylogeny was not strongly supported by bootstrapping (Fig. 3), but the distinction was registered by a diagnostic (ocean-specific) nucleotide substitution at control-region sequence position number 4 (in our numbering system), and by near-diagnostic sequence differences at positions 27, 131, 198 and 200 (Table 2).

Discussion

Two primary findings emerge from the sooty tern data. First, assayed colonies within an oceanic basin are at best only weakly differentiated in matrilineal composition, with similar or identical mtDNA haplotypes shared across nesting sites separated by as much as 16 000 km

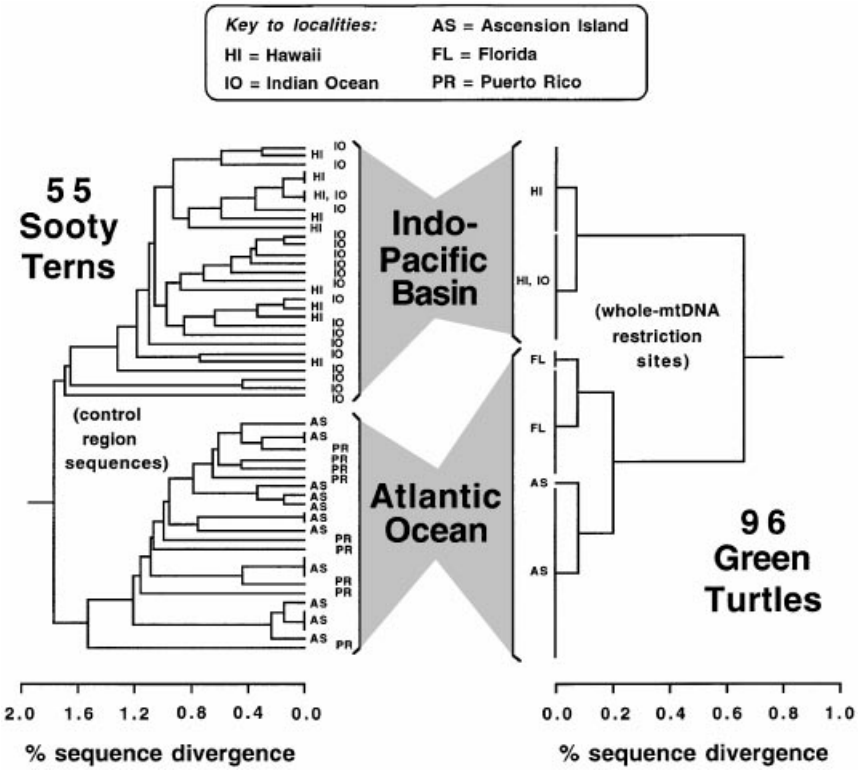

Fig. 4 Phenograms summarizing control-region sequence data in sooty terns (left), and whole-mtDNA restriction site data in green turtles (right). For comparative purposes, the four nesting areas shown for green turtles (data from Bowen *et al*. 1992) in the world's major oceanic basins were matched to those for the sooty tern (see Key).

(Johnston Island and the Seychelles). Second, a shallow phylogenetic gap separates all surveyed sooty terns in the Atlantic from those in the Indo-Pacific. These phylogeographic outcomes can be compared to patterns reported previously in green turtles, as well as to those in other colonially nesting seabirds.

Phylogeographic comparisons with green turtles

A comparative summary of mtDNA variation in the sooty tern and four spatial-counterpart rookeries of green turtles is presented in Table 3. Table 4 reports for these two species how the nested AMOVAs partitioned total genetic variance within and among rookeries from two major ocean basins.

The absence of salient within-ocean phylogeographic structure in sooty terns contrasts with the pronounced matrilineal separation among rookeries often observed in mtDNA surveys of green turtles. Consider, for example, the contrasting outcomes for the two Atlantic rookery sites analysed in both species (Fig. 2). Furthermore, green turtle rookeries on Ascension Island and in Florida show fixed haplotype differences in whole mtDNA restriction sites as well as in control-region sequences (Encalada *et al*. 1996) (Fig. 4). Most other green turtle rookeries likewise show limited within-colony variation, and many (but not all; Fig. 4) rookery pairs display nearly fixed matrilineal differences (Bowen *et al*. 1992; Encalada *et al*. 1996). In contrast, the sooty tern rookeries on Ascension Island and Puerto Rico display high within-colony mtDNA variation (Table 3), but no evident matrilineal distinctions (Figs 3, 4).

Table 4 Comparative results of the nested AMOVA analyses for the five sooty tern colonies and four spatially analogous rookeries in the green turtle*

Variance component	Sooty terns	Green turtles
Within rookeries	58.8%	2.0%
Among rookeries with an oceanic basin	3.1%	9.2%
Between oceanic basins	38.1%	88.8%

*All values except for 'among rookeries within an oceanic basin' in sooty terns are significant at $P < 0.01$.

These differences are reflected further in the fact that only 2% of the total genetic variance in these four green turtle rookeries occurred within nesting sites, whereas 59% of the total genetic variance was distributed within (as opposed to among) globally assayed rookeries of the sooty tern (Table 4). The latter observation also suggests that sooty tern rookeries are probably colonized by many rather than by only one or a few animals.

Ecological differences between sooty terns and green turtles might account in part for this contrast in phylogeographic patterns. Sooty terns presumably are rovers, moving constantly across the pelagic realm. Green turtles, by contrast, are migrators, returning to specific feeding areas and staying there. Thus, sooty terns more so than green turtles may encounter other appropriate rookery habitats in their oceanic movements.

In terms of matrilines, a detectable split appears to characterize the mtDNA phylogeny in both species. In the green turtle, this split is deep and consistent with a historical sundering of an ancestral population into Atlantic–Mediterranean vs. Indo-Pacific units, probably by the rise of the Isthmus of Panama about 3 Ma (assuming a slow mtDNA clock calibration for marine turtles; Avise *et al*. 1992a; Bowen *et al*. 1992, 1993). Does the basal separation in the sooty tern phylogeny also date to this approximate time frame?

We provisionally assume that the pace of control-region sequence divergence in sooty terns falls within the range of evolutionary rates identified in other avian species (Quinn 1992; Wenink *et al*. 1996): 8–20% per Myr, or roughly 4–10 times faster than for typical mtDNA coding sequences. Use of these calibrations indicates that the ocean-specific mtDNA *lineages* in sooty terns separated about 180 000–450 000 years ago. However, lineage separations in a gene tree normally predate population-level splits (Avise 2000), so a correction is needed for within-ocean nucleotide diversity (0.021). The net genetic distance ($\delta_c = 0.015$ in the control region) indicates that any historical sundering of sooty tern populations into Atlantic and Indo-Pacific units probably occurred a mere 7500–187 000 years ago. The lack of a more ancient separation is also consistent with the absence of diagnostic characters in the restriction-site data.

This separation date is far shallower than the comparable estimate for green turtles. Thus, historical connections between these two oceanic basins must have been recent, even if (as seems indicated by the control-region data) appreciable interoceanic gene flow is absent today. The genetic data suggest that the Panamanian Isthmus has been a significant barrier to gene exchange, but also one which has been breached by sooty terns following closure of the natural Panamanian sea channel some 3 Ma.

Phylogeographic comparisons with other colonially nesting seabirds

From field observations and tagging studies, strong fidelity to natal sites has been documented for many species of colonially nesting seabirds including shearwaters (Wooller *et al*. 1990), fairy prions (Harper 1976), murres and guillemots (Southern *et al*. 1965; Gaston *et al*. 1994), brants (Shields 1990), kittiwakes (de Coulson & de Mèvergnies 1992), albatrosses (Furness 1990) and some gulls (Greenwood & Harvey 1982). Several of these species have been investigated for mtDNA phylogeographic patterns and an interesting finding has emerged. Despite documented philopatric tendencies to natal sites by individual birds, seldom have conspecific rookeries within an oceanic basin shown strong differentiation in matrilineal composition (Table 5).

Such observations do not necessarily imply complete spatial genetic homogeneity. First, sample sizes in available surveys generally have been too small to permit robust appraisals of possible frequency differences in closely related haplotypes. Second, an occasional rookery *is* fixed for haplotypes not observed elsewhere (see Kidd & Friesen 1998b). Third, upon close inspection some colonial seabirds display microspatial genetic variation suggestive of kin-groups at a site, even in the absence of genetic differentiation over broader oceanic regions (Friesen *et al*. 1996c). Finally, a few notable exceptions to the absence of deep matrilineal separations do exist within traditionally recognized seabird species (Friesen *et al*. 1996b).

Shallow phylogeographic patterns over great distances also have been reported in some highly mobile fish species, such as pelagic tuna and billfish (Graves 1996). Thus, vagile marine organisms often display phylogeographic signatures that contrast dramatically with the deep matrilineal separations typically observed in terrestrial and freshwater animals over spatial scales often orders-of-magnitude smaller (reviews in Avise 1998, 2000).

How can the direct observational evidence for natal homing in many seabirds be reconciled with genetic data showing tight connections among conspecific rookeries over wide areas? Several factors probably contribute. First, even in species where natal homing predominates, philopatric behaviour may be far from absolute. For example, long-term field studies documented that about 40% of short-tailed shearwaters hatched on a small Australian island later returned there to nest, and that 45% of the breeding population consisted of locally banded natal recruits (Serventy & Curry 1984). These findings were interpreted to indicate remarkable nest-site fidelity (given the species' vast dispersal potential), but they leave considerable room for inter-rookery dispersal by females. Under neutrality theory, the exchange of even a few females per generation can override genetic drift which would otherwise promote differentiation in mtDNA haplotype frequencies (Birky *et al*. 1983).

Second, the *prima facie* observation that seabirds are distributed across multiple rookeries means that natal homing cannot be perfect, a point underscored by the fact that many nesting sites today (particularly in high latitudes) were unavailable as recently as 10 000 years ago. Thus, a paucity of contemporary genetic structure in high-latitude seabirds (Table 5) may be in large part the historical legacy of population mixing attendant with a

Table 5 Intraspecific phylogeographic patterns (primarily in mtDNA) reported in colonial seabirds

Species (reference)	No. individuals	No. rookeries	Assay method	General phylogeographic findings
Thick-billed murre, *Uria lomvia* (Birt-Friesen *et al*. 1992)	219	6	*cytb* sequences	lack of genetic structure across the Atlantic; clean separation of Atlantic from Pacific
Common guillemot, *Uria aalge* (Friesen *et al*. 1996a)	160	10	*cytb* sequences	mild clinal genetic structure across the Atlantic; clean separation of Atlantic from Pacific
Fairy prion, *Pachyptila turtur* (Ovenden *et al*. 1991)	61	3	restriction sites	no appreciable genetic structure around the island of Tasmania
Short-tailed shearwater, *Puffinus tenuirostris* (Austin *et al*. 1994)	335	11	restriction sites	no appreciable genetic structure throughout southern Australia
Black guillemot, *Cepphus grylle* (Kidd & Friesen 1998a,b)	65	7	control-region sequences	only modest genetic structure and no discernible geographical pattern throughout Holarctic region
Pigeon guillemot, *Cepphus columba* (Kidd & Friesen 1998a, b)	54	3	control-region sequences	moderate population genetic structure along the west coast of North America
Marbled murrelet, *Brachyramphus marmoratus* (Friesen *et al*. 1996b)	47	9	*cytb* sequences	no appreciable genetic structure, Alaska to Oregon; highly divergent form (cryptic species) in Russia
Black brant, *Branta bernicla* (Shields 1990)	19	5	restriction sites	no appreciable genetic structure across much of the American Arctic (except for one highly distinct population on Melville Island)
Cory's shearwater, *Calonectris diomedea* (Randi *et al*. 1989; da Silva & Granadeiro 1999)	145	5	allozymes (36 loci)	only modest population-genetic structure and moderately high gene-flow estimates in Mediterranean and eastern Atlantic
	148	8	DNA fingerprinting	only a 'small degree of population structure'

rapid and recent colonization of rookery sites from ancestral refugia. The mtDNA analysis of sooty terns indicates that similar explanations may account for the shallow phylogeographic depths in some tropical colonial seabirds as well.

A related possibility is that inter-rookery gene flow now, and at most times in the past, is low due to natal-homing tendencies, but each species' metapopulation (Hanski & Gilpin 1997) is nonetheless connected tightly in a genealogical sense due to rare or periodic pulses of gene flow. Such pulses might be linked to rookery turnovers via demographic fluctuations, site abandonment, occasional extinction and recolonization (Avise 2000). A case-in-point involving colonially nesting snow geese is detailed in Avise *et al*. (1992b) and Quinn (1992).

As elaborated by Avise *et al*. (1992b) and Templeton & Georgiadis (1996), important object lessons come from contrasts between alternative classes of information on population structure. Direct contemporary observations on individual dispersal and gene flow (e.g. from tag returns) offer an incomplete picture of population structure because they fail to address genealogical aspects of population connectedness. Conversely, geographical distributions of genetic markers can provide a misleading impression of present-day dispersal and gene flow because they retain records of historical demographic parameters and idiosyncratic events of the collective past. Thus, a full appreciation of population structure in any species requires an integration of contemporary and historical views.

Acknowledgements

We thank Andrew DeWoody and Peter Smouse for help with the AMOVA analyses, and Charlie Chase, Sandra Encalada, Steve Karl, Jeanne Mortimer and Peter Symens for providing tissue samples. We also acknowledge with thanks the cooperation of J.J. Beale and the government of Ascension Island. Andrew DeWoody, Anthony Fiumera, Amber Keyser, Mark Mackiewicz, Devon Pearse and Brady Porter provided useful comments. This work was supported by the Pew Foundation, and funds from the University of Georgia.

References

Ashmole NP (1963) The biology of the Wideawake or Sooty Tern *Sterna fuscata* on Ascension Island. *Ibis*, **103b**, 297–364.

Ashmole NP (1971) Sea bird ecology and the marine environment. In: *Avian Biology*, Vol. 1 (eds Farner DS, King JR), pp. 223–286. Academic Press, New York.

Austin JJ, White RWG, Ovenden JR (1994) Population-genetic structure of a philopatric, colonially nesting seabird, the short-tailed shearwater (*Puffinus tenuirostris*). *Auk*, **111**, 70–79.

Avise JC (1994) *Molecular Markers, Natural History and Evolution*. Chapman & Hall, New York.

Avise JC (1998) Conservation genetics in the marine realm. *Journal of Heredity*, **89**, 377–382.

Avise JC (2000) *Phylogeography: the History and Formation of Species*. Harvard University Press, Cambridge, MA.

Avise JC, Alisauskas RT, Nelson WS, Ankney CD (1992b) Matriarchal population genetic structure in an avian species with female natal philopatry. *Evolution*, **46**, 1084–1096.

Avise JC, Bowen BW, Lamb T, Meylan AB, Bermingham E

(1992a) Mitochondrial evolution at a turtle's pace: evidence for low genetic variability and reduced microevolutionary rate in the Testudines. *Molecular Biology and Evolution*, **9**, 457–473.

Baker AJ, Marshall HD (1997) Mitochondrial control region sequences as tools for understanding evolution. In: *Avian Molecular Evolution and Systematics* (ed. Mindell DP), pp. 51–82. Academic Press, New York.

Baker AJ, Piersma T, Rosenmeier L (1994) Unraveling the intraspecific phylogeography of knots *Calidris canutus*: a progress report on the search for genetic markers. *Journal of Ornithology*, **135**, 599–608.

Birky CW Jr, Maruyama T, Fuerst P (1983) An approach to population and evolutionary theory for genes in mitochondria and chloroplasts, and some results. *Genetics*, **103**, 513–527.

Birt-Friesen VL, Montevecchi WA, Gaston AJ, Davidson WS (1992) Genetic structure of thick-billed murre (*Uria lomvia*) populations examined using direct sequence analysis of amplified DNA. *Evolution*, **46**, 267–272.

Bowen BW, Avise JC (1996) Conservation genetics of marine turtles. In: *Conservation Genetics: Case Histories from Nature* (eds Avise JC, Hamrick JL), pp. 190–237. Chapman & Hall, New York.

Bowen BW, Karl SA (1997) Population genetics, phylogeography, and molecular evolution. In: *The Biology of Sea Turtles* (eds Lutz PL, Musick JA), pp. 29–50. CRC Press, Boca Raton, FL.

Bowen BW, Meylan AB, Ross JP, Limpus CJ, Balazs GH, Avise JC (1992) Global population structure and natural history of the green turtle (*Chelonia mydas*) in terms of matriarchal phylogeny. *Evolution*, **46**, 865–881.

Bowen BW, Nelson WS, Avise JC (1993) A molecular phylogeny for marine turtles: trait mapping, rate assessment, and conservation relevance. *Proceedings of the National Academy of Sciences of the USA*, **90**, 5574–5577.

Carr AF (1967) *So Excellent a Fishe*, p. 39. University of Texas Press. Austin TX.

de Coulson JCM, Èvergnies GN (1992) Where do young kittiwakes *Rissa tridactyla* breed, philopatry or dispersal? *Ardea*, **80**, 187–197.

da Silva MC, Granadeiro JP (1999) Genetic variability and isolation of Cory's Shearwater colonies in the Northeast Atlantic. *Condor*, **101**, 174–179.

Desjardins P, Morais R (1990) Sequence and gene organisation of the chicken mitochondrial genome: a novel gene order in higher vertebrates. *Journal of Molecular Biology*, **212**, 599–634.

Desjardins P, Morais R (1991) Nucleotide sequence and evolution of coding and noncoding regions of a quail mitochondrial genome. *Journal of Molecular Evolution*, **32**, 153–161.

Encalada SE, Lahanas PH, Bjorndal KA, Bolten AB, Miyamoto MM, Bowen BW (1996) Phylogeography and population structure of the green turtle (*Chelonia mydas*) in the Atlantic Ocean and Mediterranean Sea: a mitochondrial DNA control region sequence assessment. *Molecular Ecology*, **5**, 473–484.

Excoffier L, Smouse PE, Quattro JM (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics*, **131**, 479–491.

Felsenstein J (1984) Distance methods for inferring phylogenies: a justification. *Evolution*, **38**, 16–24.

Felsenstein J (1991) PHYLIP: *Phylogeny Inference Package*, Version 3.4. Department of Genetics, SK-50, University of Washington, Seattle, WA.

Friesen VL, Montevecchi WA, Baker AJ, Barretts RT, Davidson WS (1996a) Population differentiation and evolution in the common guillemot *Uria aalge*. *Molecular Ecology*, **5**, 793–805.

Friesen VL, Montevecchi WA, Gaston AJ, Barrett RT, Davidson WS (1996c) Molecular evidence for kin groups in the absence of large-scale genetic differentiation in a migratory bird. *Evolution*, **50**, 924–930.

Friesen VL, Piatt JF, Baker AJ (1996b) Evidence from cytochrome *B* sequences and allozymes for a 'new' species of alcid: the long-billed murrelet (*Brachyramphus perdix*). *Condor*, **98**, 681–690.

Furness RW (1990) Easy gliders. *Natural History*, **8**, 62–69.

Gaston AJ, de Forest LN, Donaldson G, Noble DG (1994) Population parameters of thick-billed murres at Coats Island, Northwest Territories, Canada. *Condor*, **96**, 935–948.

Graves JE (1996) Conservation genetics of fishes in the pelagic marine realm. In: *Conservation Genetics: Case Histories from Nature* (eds Avise JC, Hamrick JL), pp. 335–366. Chapman & Hall, New York.

Greenwood PJ, Harvey PH (1982) The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics*, **13**, 1–21.

Hanski IA, Gilpin ME, eds (1997) *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, New York.

Harper PC (1976) Breeding biology of the Fairy Prion (*Pachyptila turtur*) at the Poor Knights Islands, New Zealand. *New Zealand Journal of Zoology*, **3**, 351–371.

Jukes TH, Cantor CR (1969) Evolution of protein molecules. In: *Mammalian Protein Metabolism* (ed. Munro HN), pp. 21–132. Academic Press, New York.

Karl SA, Bowen BW (1999) Evolutionary significant units versus geopolitical taxonomy: molecular systematics of an endangered sea turtle (genus *Chelonia*). *Conservation Biology*, **13**, 990–999.

Kidd MG, Friesen VL (1998a) Sequence variation in the guillemot (Alcidae: *Cepphus*) mitochondrial control region and its nuclear homolog. *Molecular Biology and Evolution*, **15**, 61–70.

Kidd MG, Friesen VL (1998b) Patterns of control region variation in populations of *Cepphus* guillemots: testing microevolutionary hypotheses. *Evolution*, **52**, 1158–1168.

Kimura M (1980) A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, **16**, 111–120.

Lansman RA, Shade RO, Shapira JF, Avise JC (1981) The use of restriction endonucleases to measure mitochondrial DNA sequence relatedness in natural populations. III. Techniques and potential applications. *Journal of Molecular Evolution*, **17**, 214–226.

Maniatis T, Fritsch EF, Sambrook J (1982) *Molecular Cloning*. Cold Spring Harbor Laboratory, Cold Spring Harbor NY.

Meylan AB, Bowen BW, Avise JC (1990) A genetic test of the natal homing versus social facilitation models for green turtle migration. *Science*, **248**, 724–727.

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

Nei M, Li W-H (1979) Mathematical models for studying genetic variation in terms of restriction endonucleases. *Proceedings of the National Academy of Sciences of the USA*, **76**, 5269–5273.

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

Palumbi SR, Martin AP, Romano S, McMillan WO, Stice L, Grabowski G (1991) *The Simple Fool's Guide to PCR*, Version 2. Department of Zoology, University of Hawaii, Honolulu, HI.

Posada D, Crandall KA, Templeton AR (2000) GeoDis: a program for the cladistic nested analysis of the geographical distribution of genetic haplotypes. *Molecular Ecology*, **9**, 487–488.

Quinn TW (1992) The genetic legacy of mother goose — phylogeographic patterns of lesser snow goose *Chen caerulescens caerulescens* maternal lineages. *Molecular Ecology*, **1**, 105–117.

Quinn TW, Wilson AC (1993) Sequence evolution in and around the mitochondrial control region in birds. *Journal of Molecular Evolution*, **37**, 417–425.

Randi E, Spina F, Massa B (1989) Genetic variability in Cory's shearwater (*Calonectris diomedea*). *Auk*, **106**, 411–417.

Saitou N, Nei M (1987) The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution*, **4**, 406–425.

Schreiber EA, Schreiber RW (1989) Insights into seabird ecology from a global 'natural experiment'. *National Geographic Research*, **5**, 64–81.

Serventy DL, Curry PJ (1984) Observations on colony size, breeding success, recruitment and inter-colony dispersal in a Tasmanian colony of Short-tailed Shearwaters *Puffinus tenuirostris* over a 30-year period. *Emu*, **84**, 71–79.

Shields GF (1990) Analysis of mitochondrial DNA of Pacific black brant (*Branta bernicla nigricans*). *Auk*, **107**, 620–623.

Sneath PHA, Sokal RR (1973) *Numerical Taxonomy*. Freeman, San Francisco.

Southern HN, Carrick R, Potter WG (1965) The natural history of a population of guillemots *Uria aalge*. *Journal of Animal Ecology*, **35**, 1–11.

Swofford DL (1999) *PAUP* 4.0: Phylogenetic Analysis Using Parsimony*. Sinauer, Sunderland, MA.

Tamura K, Nei M (1993) Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution*, **10**, 512–526.

Templeton AR, Georgiadis NJ (1996) A landscape approach to conservation genetics: conserving evolutionary processes in the African Bovidae. In: *Conservation Genetics: Case Histories from Nature* (eds Avise JC, Hamrick JL), pp. 398–430. Chapman & Hall, New York.

Tuck G, Heinzel H (1978) *A Field Guide to Seabirds of Britain and the World*. Collins, London.

Wenink PW, Baker AJ, Rösner H-U, Tilanus MGJ (1996) Global mitochondrial DNA phylogeography of holarctic breeding dunlins (*Calidris alpina*). *Evolution*, **50**, 318–330.

Wenink PW, Baker AJ, Tilanus MGJ (1994) Mitochondrial control-region sequences in two shorebird species, the turnstone and the dunlin, and their utility in population genetic studies. *Molecular Biology and Evolution*, **11**, 22–31.

Wooller RD, Bradley JS, Skira IJ, Serventy DL (1990) Reproductive success of Short-tailed Shearwaters *Puffinus tenuirostris* in relation to their age and breeding experience. *Journal of Animal Ecology*, **59**, 161–170.

Wooller RD, Bradley JS, Croxall JP (1992) Long-term population studies of seabirds. *Trends in Ecology and Evolution*, **7**, 111–114.

Zink RM, Dittmann DL, Klicka J, Blackwell-Rago RC (1999) Evolutionary patterns of morphometrics, allozymes, and mitochondrial DNA in thrashers (genus *Toxostoma*). *Auk*, **116**, 1021–1038.

The current paper is a follow-up to earlier global work on marine turtles spearheaded by one of Avise's former graduate students, Brian Bowen. Bill Nelson and DeEtte Walker have been research technicians in the Avise lab.
