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

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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

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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.*

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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 2 Variability and geographical distribution of the control-region sequences of sooty terns[illegible]

*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

Rookery site	Restriction assays (whole molecule)				Direct sequencing (control region)			
	No. indiv.	No. haplo.	Haplotype diversity	Nucleotide diversity	No. indiv.	No. haplo.	Haplotype diversity	Nucleotide diversity
<i>Sooty terns</i>								
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
<i>Green turtles</i>								
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

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	3.1%	9.2%
with an oceanic basin		
Between oceanic basins	38.1%	88.8%

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

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).

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 matrilineal, 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; *Avice 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 (*Avice* 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 *Avice* 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, <i>Uria lomvia</i> (Birt-Friesen <i>et al.</i> 1992)	219	6	<i>cytb</i> sequences	lack of genetic structure across the Atlantic; clean separation of Atlantic from Pacific
Common guillemot, <i>Uria aalge</i> (Friesen <i>et al.</i> 1996a)	160	10	<i>cytb</i> sequences	mild clinal genetic structure across the Atlantic; clean separation of Atlantic from Pacific
Fairy prion, <i>Pachyptila turtur</i> (Ovenden <i>et al.</i> 1991)	61	3	restriction sites	no appreciable genetic structure around the island of Tasmania
Short-tailed shearwater, <i>Puffinus tenuirostris</i> (Austin <i>et al.</i> 1994)	335	11	restriction sites	no appreciable genetic structure throughout southern Australia
Black guillemot, <i>Cephus grylle</i> (Kidd & Friesen 1998a,b)	65	7	control-region sequences	only modest genetic structure and no discernible geographical pattern throughout Holarctic region
Pigeon guillemot, <i>Cephus columba</i> (Kidd & Friesen 1998a, b)	54	3	control-region sequences	moderate population genetic structure along the west coast of North America
Marbled murrelet, <i>Brachyramphus marmoratus</i> (Friesen <i>et al.</i> 1996b)	47	9	<i>cytb</i> sequences	no appreciable genetic structure, Alaska to Oregon; highly divergent form (cryptic species) in Russia
Black brant, <i>Branta bernicla</i> (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, <i>Calonectris diomedea</i> (Randi <i>et al.</i> 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 turn-overs via demographic fluctuations, site abandonment, occasional extinction and recolonization (Avisé 2000). A case-in-point involving colonially nesting snow geese is detailed in Avisé *et al.* (1992b) and Quinn (1992).

As elaborated by Avisé *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.

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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.