Population genetic relationships in the roseate tern: globally, regionally and locally

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Abstract

The roseate tern, *Sterna dougallii*, is a colonially nesting seabird which breeds on tropical and temperate islands in the Atlantic, Indian and Pacific Oceans. The roseate tern is considered threatened in a number of regions, including the United States, Europe and South Africa. There are currently four or five recognised subspecies of roseate tern: one in the Atlantic Ocean; and three or four in the Indo-Pacific, with many authors questioning the validity of currently circumscribed subspecies.

In this study, two kinds of genetic marker, ND2 and ND6 mitochondrial DNA sequences and microsatellite genotyping, were used to investigate the historical and contemporary relationships among roseate tern breeding colonies. I used samples from breeding colonies in Australia, Japan, Seychelles, South Africa, Azores, Ireland and the United States to investigate population structure in the roseate tern at a global scale, a regional scale and at a local scale within Australia. In addition, samples obtained from the non-breeding aggregations in Australia were included to determine whether mitochondrial DNA or microsatellite markers can be used to determine the origins of individuals in non-breeding aggregations.

Sequencing of a combined total of 1381 base pairs of the ND2 and ND6 genes, and genotyping with five polymorphic microsatellite markers, revealed two distinct lineages of roseate tern: an Atlantic lineage; and an Indo-Pacific lineage. The genetic divergence between the two lineages (3.9% corrected mitochondrial DNA sequence divergence) represents a significant historic separation, with continental Africa implicated as the major long term barrier to gene flow between the two oceanic basins. The star-shaped phylogeny observed for both lineages suggests a recent range expansion from a

common source in each oceanic basin, which is likely to have coincided with the stabilising of sea level following the last glacial period, approximately 20 000 years ago. The lack of population structure in mitochondrial DNA haplotypes within each oceanic basin suggests that cycles of range expansion and contraction to a glacial refuge have occurred during interglacial and glacial periods, respectively. This periodic range contraction, to a common glacial refuge within each oceanic basin, has allowed regular gene flow to occur among individuals within each oceanic basin, ameliorating any genetic divergence that may develop during interglacial periods. The most recent range expansion has resulted in secondary contact and introgression of the two lineages, identified in the breeding colony sampled in South Africa.

The Atlantic subspecies, *S. d. dougallii*, is well supported by this study, but the currently recognised subspecies in the Indo-Pacific are not warranted based on genetic data. I recommend a formal revision of the subspecies designations, merging the three or four currently recognised subspecies in the Indo-Pacific.

Microsatellite markers reveal that population structuring has developed among some breeding regions since the last range expansion. In the Atlantic Ocean, microsatellite analyses suggest that breeding colonies in Ireland and the United States have diverged from the Azores ($R_{ST} = 0.28 – 0.36$, $P < 0.05$); however, due to the potential influence of population declines on the genetic variation in these colonies, I cannot reject the alternate hypothesis that individuals from the north Atlantic breeding colonies are regularly interbreeding.

In the Indo-Pacific, the breeding colony in the Seychelles is divergent from the colonies in Australia and Japan ($R_{ST} = 0.14 – 0.22$, $P < 0.05$), suggesting that the Indian Ocean serves as a current barrier to gene flow. There is no evidence for genetic divergence among colonies in Australia and Japan ($R_{ST} = 0.03$, $P = 0.22$), indicating that gene flow between the two regions, and among colonies in Australia, is occurring regularly. This may be facilitated via the mixing of individuals from different breeding colonies in the non-breeding aggregations. Due to the lack of genetic structure among breeding colonies in Australia and Japan, neither mitochondrial DNA or microsatellites could be used to determine the origins of individuals in non-breeding aggregations in Australia.

During this study, I obtained evidence of hybridisation between roseate and black-naped terns. Further investigation of this revealed that paternal leakage, the transfer of paternal mitochondrial DNA along with the usual maternal transfer, had occurred as a result of the hybridisation event. This is the first evidence of hybridisation between the roseate and black-naped tern, and one of only a handful of instances of paternal leakage of mitochondrial DNA in animals.

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Signature Date