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Plumage polymorphism of red-footed boobies (*Sula sula*) in the western Indian Ocean: an indicator of biogeographic isolation

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Abstract

The pantropical red-footed booby *Sula sula* is one of the most polymorphic seabirds. In the Indian Ocean most extant colonies hold white morph adults except on Europa Island (southern Mozambique Channel), where adults are of the white-tailed brown morph and on Tromelin Island (western Indian Ocean), where one-third of the birds are of the white-tailed brown morph and two-thirds are of the white morph. On Tromelin, the morph ratio has remained constant over the last 40 years. An extinct colony (Glorieuses Islands, northern Mozambique Channel) once supported a white-tailed brown morph population. These results suggest that the colonies of the western Indian ocean do not constitute one great gene pool where exchanges occur, but are isolated at various degree from each other. Particularly, the population of Europa is the only current population of the Indian Ocean constituted almost entirely of white-tailed brown morph, suggesting that it is isolated from other nearby colonies. Possible causes of isolation are discussed in the light of oceanic features of the Mozambique Channel. Although further studies are needed to understand the adaptive significance of plumage coloration in red-footed boobies, I suggest that white-tailed brown morph at Europa may act as a defensive camouflage against kleptoparasitism by great frigatebirds *Fregata minor* and brown skuas *Catharacta antarctica*.

Key words: polymorphism, red-footed booby, *Sula sula*, seabird, kleptoparasitism, isolation

INTRODUCTION

Plumage polymorphism, the occurrence of distinct plumage morphs in adults of a given population, has appeared independently several times among three seabird families: Procellariidae (seven polymorphic species out of 70; del Hoyo *et al*., 1992), Hydrobatidae (two polymorphic species out of 20; del Hoyo *et al*., 1992) and Stercorariidae (four polymorphic species out of seven; Furness, 1996). Although the red-footed booby *Sula sula* is the only polymorphic species of the Sulidae, this species is one of the most polymorphic seabirds. Nelson (1978) has listed three main morphs (from mainly white to all brown) and at least three intermediate morphs. Although this species is highly polymorphic at the scale of its whole pantropical distribution, most regions possess only or almost entirely one morph (Nelson, 1978). The main adaptive advantages evoked to explain polymorphism are an increased adaptability to environmental changes (Mayr, 1963), sexual selection (O'Donald, 1983), and apostatic selection for prey (Clarke, 1962), predators (Paulson, 1973) or kleptoparasites (Paulson, 1973; Arnason, 1978; Caldow & Furness, 1991). The adaptive significance of polymorphism among red-footed boobies is still obscure, although Nelson (1978) suggested that it may be an intra-specific form of adaptive radiation, helping to exploit food more efficiently in various habitats.

The aim of this paper is to interpret new data on plumage polymorphism of red-footed boobies on Europa and Tromelin Islands, two remote and poorly known islands of the western Indian Ocean (Fig. 1). Results are compared with published data from other colonies of the Indian Ocean. The roles of geographical isolation, oceanic environment and other factors are discussed to explain the distribution of the different plumage morphs in the western Indian Ocean.

STUDY AREAS AND METHODS

Europa Island (22°20′S, 40°22′E, Fig. 1) is one of the most important breeding places for seabirds in the

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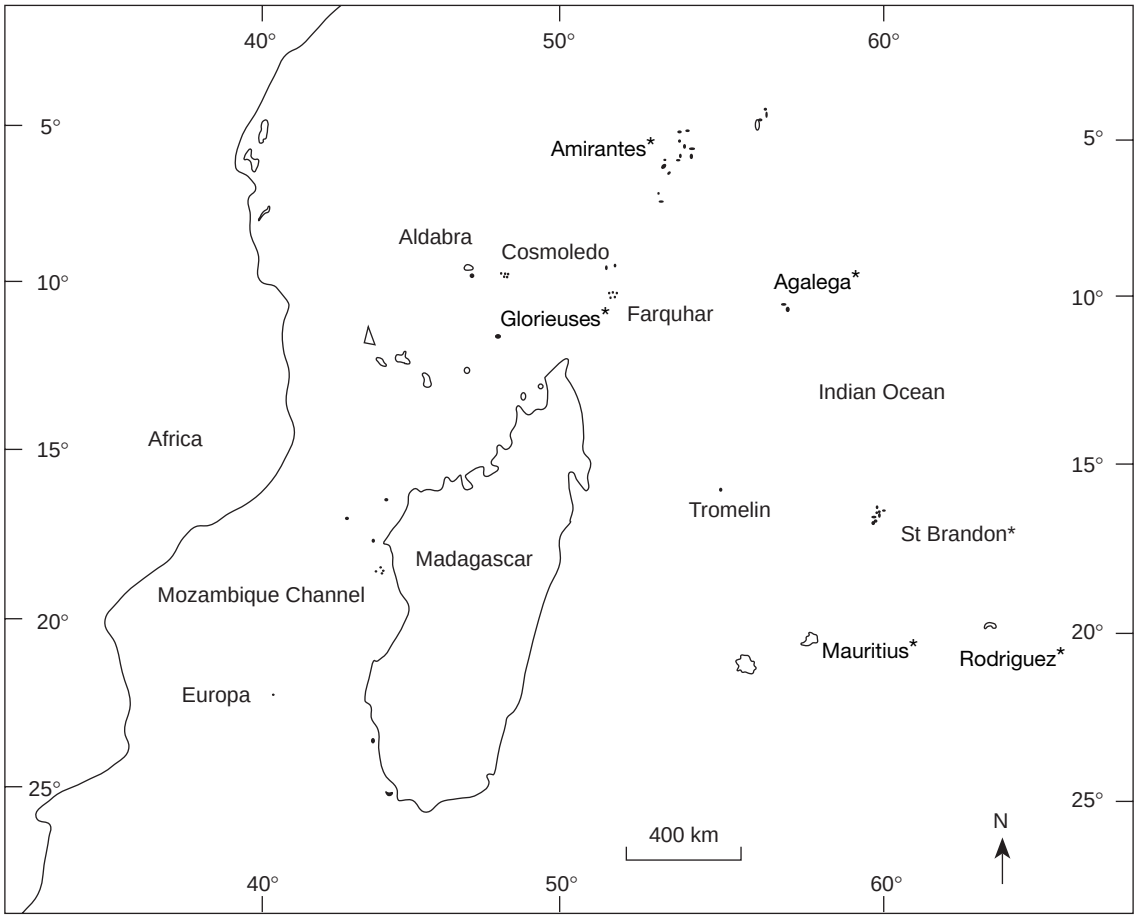

Fig. 1. Localities of all extant and extinct colonies of red-footed boobies of the western Indian Ocean. * Extinct colonies.

Indian Ocean (Le Corre & Jouventin, 1997*a*). The breeding population of red-footed boobies is 2800–3800 pairs and the overall population 8000–10 000 birds (Le Corre & Jouventin, 1997*a*). A small population of 130–180 pairs of red-footed boobies breeds on Tromelin Island (15°33′S, 54°31′E, Fig. 1; Le Corre, 1996).

Field work on plumage polymorphism was conducted during the breeding periods of red-footed boobies, from 8 to 28 June 1994 on Tromelin Island and from 9 September to 28 October 1995 on Europa Island. One study area was defined on each island (30 ha at Europa Island, where 500–570 pairs bred, and 5 ha at Tromelin, where 90 pairs bred). Red-footed boobies are monogamous and both parents share parental care equally during incubation and chick-rearing (Nelson 1978; pers. obs.). Each occupied nest was numbered, marked in the field with a plastic band, and positioned on a map. The plumage morph of breeding adults was checked during subsequent visits to the nests. Breeding adults were classified into one of the following categories: 'white morph', 'white-tailed brown morph' and 'white-tailed brown morph with white scapulars' (see Nelson, 1978: 655–656 for detailed descriptions). To check the colour morph of both partners of a given pair, one was colour marked on the breast. The nest was then checked daily until the unmarked mate was observed.

RESULTS

Plumage polymorphism at Europa and Tromelin islands

On Europa, the plumage morph of 650 breeding adults from 562 breeding pairs was described (Table 1). Most were of the white-tailed brown morph and the other two morphs were rare (Table 1). On Tromelin Island, around two-thirds of the birds were white morph and the other white-tailed brown morph (Table 1). The difference in plumage morph proportions between the two islands was highly significant (Table 1). Although the population size of red-footed booby has decreased during the last 40 years at Tromelin Island (Le Corre, 1996), the proportion of the two morphs did not change during that period (Table 1), suggesting that both morphs were equally sensitive to the factor(s) that caused the decline of the population.

I determined the colour morphs of both partners of a given pair for 128 pairs at Europa and 35 pairs at Tromelin. At Europa, 95.3% of those pairs were constituted of two birds of the white-tailed brown morph and 4.7% of a white morph and a white-tailed brown morph. No pair was composed of two white morphs. At Tromelin, 45.7% of the pairs were composed of two birds of the white morph, 28.6% of a white and a white-tailed brown, and 25.7% of two white-tailed brown

Table 1. Plumage morph proportions of red-footed boobies at Europa and Tromelin Islands

	Europa	Tromelin		
	1995 ($n = 650$)	1954[b] ($n = 106$)	1968[c] (estimate)	1994[d] ($n = 121$)
White morph	1.5%	64.1%	Two-thirds	69.4%
White-tailed brown morph	98.5%[a]	35.8%	One-third	30.6%
Breeding population (pairs)	2800–3800[e]	? > 200	500	130–180[a]

[a] Including 7.2% of white-tailed brown with white scapulars.
Data from: [b] Brygoo, 1955; [c] Staub, 1971; [d] Le Corre, 1996; [e] Le Corre & Jouventin, 1997*a*.
Comparison of proportions of 1954 *vs* 1994 at Tromelin: $\chi^2 = 0.491$, ddl = 1, NS; comparison of proportions at Europa (1995) *vs* Tromelin (1994): $\chi^2 = 440.2$, ddl = 2, $P < 0.001$.

morphs. In the two islands, those proportions were similar to those calculated using the frequency of each morph in each island ($\chi^2 = 0.104$, d.f. = 1, $P > 0.05$, $\chi = 4.030$, d.f. = 2, $P > 0.05$, respectively for Europa and Tromelin Islands). These results suggest that there is no assortative mating related to colour morph in the two populations, and that the two morphs are likely to occur in the two sexes.

DISCUSSION

Polymorphism in the Indian Ocean

The white morph is or was dominant in most of the eight extant and nine extinct breeding colonies of the Indian Ocean (7/8 and 8/9 colonies, respectively: Table 2), as already mentioned by Diamond (1974) and Nelson (1978). The only exceptions are for Europa and the Glorieuses Islands, where most adults are (or were) of the white-tailed brown morph. This latter population was formerly large but has been extinct since the early 20th century (Benson *et al*., 1975). Although Diamond (1974) doubted that white-tailed brown morphs may have bred on the Glorieuses, the descriptions and collection of specimen of Abbott (in Ridgway, 1896) and Nicoll (1906) clearly showed that white-tailed brown morph birds were largely dominant in this archipelago (90% of the population according to Nicoll, 1906).

Isolation of populations in the western Indian Ocean

According to the pattern of polymorphism, red-footed booby colonies of the western Indian Ocean can be classified into three categories: the white morph dominant colonies (most colonies of the Seychelles, Aldabra and Cosmoledo, and the extinct colonies of Saint Brandon and the Mascarenes), the white-tailed brown morph dominant colonies (Europa and the extinct colony of the Glorieuses) and a mixed colony of white and white-tailed brown morphs (Tromelin).

As shown in Table 2, this pattern of polymorphism at the scale of the Indian Ocean is not related to the latitude of the islands. This suggest that there are few exchanges of individuals between these three groups or alternatively, that birds of these groups live in different environments so that the selective value of a given morph varies in different habitats.

The previous existence of a colony of white-tailed brown morph (Glorieuses), very close (and so probably living in a comparable environment) to the group of white dominant colonies, is surprising and may suggest that, at least in the Indian Ocean, there is strong isolating mechanisms between nearby colonies in red-footed boobies.

Considering existing colonies only, it is of particular interest to notice that the population of Europa is the only one in the Indian Ocean to be composed almost entirely of white-tailed brown morph birds. This suggests that this population is probably strongly isolated from other current colonies. The same biogeographic pattern has been described recently for white-tailed tropicbirds *Phaethon lepturus* which are widespread in the western

Table 2. Frequency[a] of the two main morphs of red-footed booby in the Indian Ocean

Latitude	Locality[b]	White-tailed brown morph	White morph
5°S	Amirantes (E)		+++
7°S	Chagos Group		+++
9°S	Assumption (E)		+++
9°S	Aldabra	–	+++
9°S	Cosmoledo		+++
9°S	Providence (E)		+++
10°S	Astove (E)		+++
10°S	Farquhar		+++
10°S	Agalega (E)		+++
11°S	Christmas		+++
11°S	Glorieuses (E)	+++	–
12°S	Cocos–Keeling		+++
15°S	Saint Brandon (E)	–	+++
15°S	Tromelin	+	++
20°S	Rodrigues (E)		+++
21°S	Mauritius (E)		+++
22°S	Europa	+++	–

[a] Frequency: –, < 10%; +, 10–40%; ++, 40–80%; +++, > 80%.
[b] E, extinct population.
Sources: Newton, 1958; Bourne, 1968, 1971; Diamond, 1974; Benson *et al*., 1975; Hutson, 1975; Staub, 1976; Feare, 1978; Nelson, 1978; Williams & Rowlands, 1980; Prys-Jones, Prys-Jones & Lawton, 1981; Cheke & Lawley, 1983; Le Corre, 1996, and this study.

Indian Ocean but with a distinctive subspecies *P. l. europae* restricted to Europa (Le Corre & Jouventin, 1999). We argued for this species that geographic isolation and the specific marine environment of the central Mozambique Channel (high sea-surface temperature) may have contributed to the isolation of the population of Europa Island (Le Corre & Jouventin, 1999).

The same biogeographic hypothesis may be invoked to explain the current distribution of the morphs of red-footed boobies in the western Indian ocean. However, the fact that (1) the Glorieuses once supported a white-tailed brown morph population, and (2) Tromelin is composed of two morphs (with a stable morph ratio during the last 40 years), suggest that isolating mechanisms may act at a smaller scale for red-footed boobies than for white-tailed tropicbirds.

Substantial inter-island movements of both adults and immatures are known to occur in the central Pacific Ocean (Harrington 1977; Woodward in Nelson, 1978) and Nelson (1978: 717) suggested that there are vast areas within which the population is essentially one great gene pool. The distribution of plumage morphs in the Pacific Ocean is consistent with this hypothesis (Nelson, 1978). By contrast, in the western Indian Ocean, the distribution of plumage morphs indicates that this is not the case. Further studies on dispersal and inter-island movements of birds of each colony coupled with DNA analysis, would be of great interest to measure the degree of genetic isolation between the different colonies of the western Indian Ocean, including the apparently isolated Europa population.

Adaptive significance of plumage coloration in the red-footed booby

Another important point when analysing plumage polymorphism in red-footed boobies of the western Indian Ocean is to understand why the white-tailed brown morph is so common in Europa's population and so rare in all other colonies. What is the adaptive significance of plumage coloration in this species?

Several studies have been conducted on the adaptive significance of plumage coloration (see Baker & Parker, 1979 for a review). Among seabirds, the main adaptive processes evoked to explain plumage coloration are aggressive camouflage (Craik, 1944; Cowan, 1972; Simmons, 1972), social stimulation for feeding (Armstrong, 1971; Nelson, 1978; Schreiber & Clapp, 1987), conspicuousness for depolarizing prey schools (Wilson *et al*., 1988), defensive camouflage against predation (Bretagnolle, 1993) or kleptoparasitism (Nelson, 1978), and aggressive or defensive Batesian mimicry (Spear & Ainley, 1993). However, no experimental or comparative study has been conducted on the adaptive significance of plumage coloration in the red-footed booby.

Because white morphs are more conspicuous than dark ones, Nelson (1978) speculated that dark morphs would be favoured at places where the kleptoparasitism risk by frigatebirds is high, inconspicuous dark plumage acting as defensive camouflage. At Europa, red-footed boobies are sympatric with a large population of great frigatebirds *Fregata minor* and kleptoparasitic attempts are very frequent (Le Corre & Jouventin, 1997*b*). The island is also in the wintering range of subantarctic brown skuas *Catharacta antarctica*, which are very efficient kleptoparasites of red-footed boobies (Le Corre & Probst, 1997). Both great frigatebirds and brown skuas represent an important risk of losing food through kleptoparasitism and Le Corre & Jouventin (1997*b*) suggested that high gregariousness and nocturnality in this population of red-footed boobies may have been selected to avoid kleptoparasitism.

The brown plumage of adult red-footed boobies of Europa may act as defensive camouflage against kleptoparasitism. However, at Aldabra (where most red-footed boobies are white), great and lesser frigatebirds largely outnumber boobies. Although no detailed behavioural study has been conducted on the kleptoparasitism interactions in that island, frigatebirds are known to kleptoparasite boobies extensively (Diamond, 1974). Thus one would expect the Aldabra population to be white-tailed brown, instead of white. It would be of interest to quantify the risk of being chased in a mixed population of white and white-tailed brown morphs (like Tromelin Island) and to see if both morphs are equally chased by kleptoparasites.

However, other causes related to feeding ecology, social interactions or temperature regulation may have important effects on plumage coloration adaptivness. Furthermore, colour morphs could have been acquired in a given population by chance or as a result of a 'founding effect', with no selection, if coloration has no impact on the survival of the birds.

Clearly, further comparative and experimental studies are needed to understand adaptive significance of plumage coloration and polymorphism among red-footed boobies. Because the western Indian Ocean holds several breeding colonies with three polymorphism patterns (white, mixed and white-tailed brown), this region provides interesting opportunities for such studies.

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