Ostrich 2007, 78(2): 423–434
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OSTRICH
ISSN 0030–6525
doi: 10.2989/OSTRICH.2007.78.2.49.129

An inventory of Sooty Terns (*Sterna fuscata*) in the western Indian Ocean with special reference to threats and trends

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The western Indian Ocean supports over 6 200 000 pairs of Sooty Terns, some in very large colonies. During the past two centuries colonies have exhibited increase, stability, decline and extinction. The main drivers of these trends have been habitat change and unregulated human exploitation, especially of adults; introduced predators appear to have little effect at the population level but may have prevented re-colonisation following habitat restoration. Regulated harvesting of eggs, based on increasing knowledge of Sooty Tern demography, appears to be sustainable. Some colonies now receive protection but it will be logistically difficult to extend this to all colonies. The main future threats are likely to be climate change and over-exploitation of tuna, on which Sooty Terns depend to feed. Sooty Terns should be monitored to provide insights into these and other perturbations of the marine ecosystem.

Introduction

Sooty Terns (*Sterna fuscata*) nest typically in colonies on oceanic islands but they also nest on some offshore islands. Colonies commonly contain hundreds of thousands of pairs but sometimes house over one million pairs.

Most Indian Ocean Sooty Terns (*Sterna fuscata*), and the largest colonies of this species, occur west of longitude 76°E, i.e. west of India and Sri Lanka (Figure 1, Table 1). Western Indian Ocean colonies are perhaps the best-surveyed Sooty Tern colonies in the world. Most of the largest colonies have been recently censused, permitting revision of data provided by Feare (1984a) and Schreiber *et al.* (2002). The histories of some Seychelles colonies are reasonably well known through records of the local egg harvesting industry, together with research associated with that industry (Ridley and Percy 1958, Feare 1976a, 1976b, 1984b). This paper examines historical changes in population, and factors that have driven population change. Potential drivers of future change are also identified.

Extant Sooty Tern colonies of the western Indian Ocean

Recent estimates of colony size have generally been obtained by measuring nest density and colony area, and multiplying an average of the former by the latter. Nest density has been measured in randomly selected sampling areas (Bowler *et al.* 2002, Feare 1979a, 1999a, 2003, Feare and Gill 1995, 1996, Feare in Rocamora *et al.* 2003, Le Corre and Jaquemet 2005). In addition to these estimates that provide a degree of precision, the literature contains vaguer references to colonies containing 'tens', 'hundreds', 'thousands' or 'tens of thousands' of pairs. These data show that over 6 200 000 pairs currently nest in 35 colonies in the western Indian Ocean (Table 1), most of these nesting in Seychelles and Mozambique Channel colonies.

Extinctions and historical population changes

Fourteen colonies are known to have become extinct within the last century (Table 2), with another colony on islands off Mahebourg, Mauritius, having probably disappeared long before that time (A Cheke, Oxford, UK, pers. comm.). Most were small but those on Ile Pierrot and Ile Combrani (Rodrigues), Diego Garcia (Chagos) and Agalega, were reputedly large, as may have been those on Ile Platte (Seychelles) and Tromelin (Brooke 1981). These colonies became extinct before good records were available but we estimate that a minimum of 600 000 pairs would have nested in them.

Eight extant colonies are known to have been larger in the past (Table 2). Over 1.5 million pairs have been lost from these colonies, mainly in the Seychelles and Mascarenes areas (Table 2).

There is little information on population changes in the Mozambique Channel. However, the population on Europa is probably the most stable since it suffers very little human disturbance; Glorieuses colony may suffer poaching from Mayotte and Madagascar and the Juan de Nova colony may have increased following the cessation of guano exploitation in the 1970s, but there are no data.

The known colony reductions and extinctions suggest that perhaps over two million additional pairs of sooty terns may have bred in the western Indian Ocean a century or more ago, most of these nesting in the Mascarenes and on Bird Island, Seychelles.

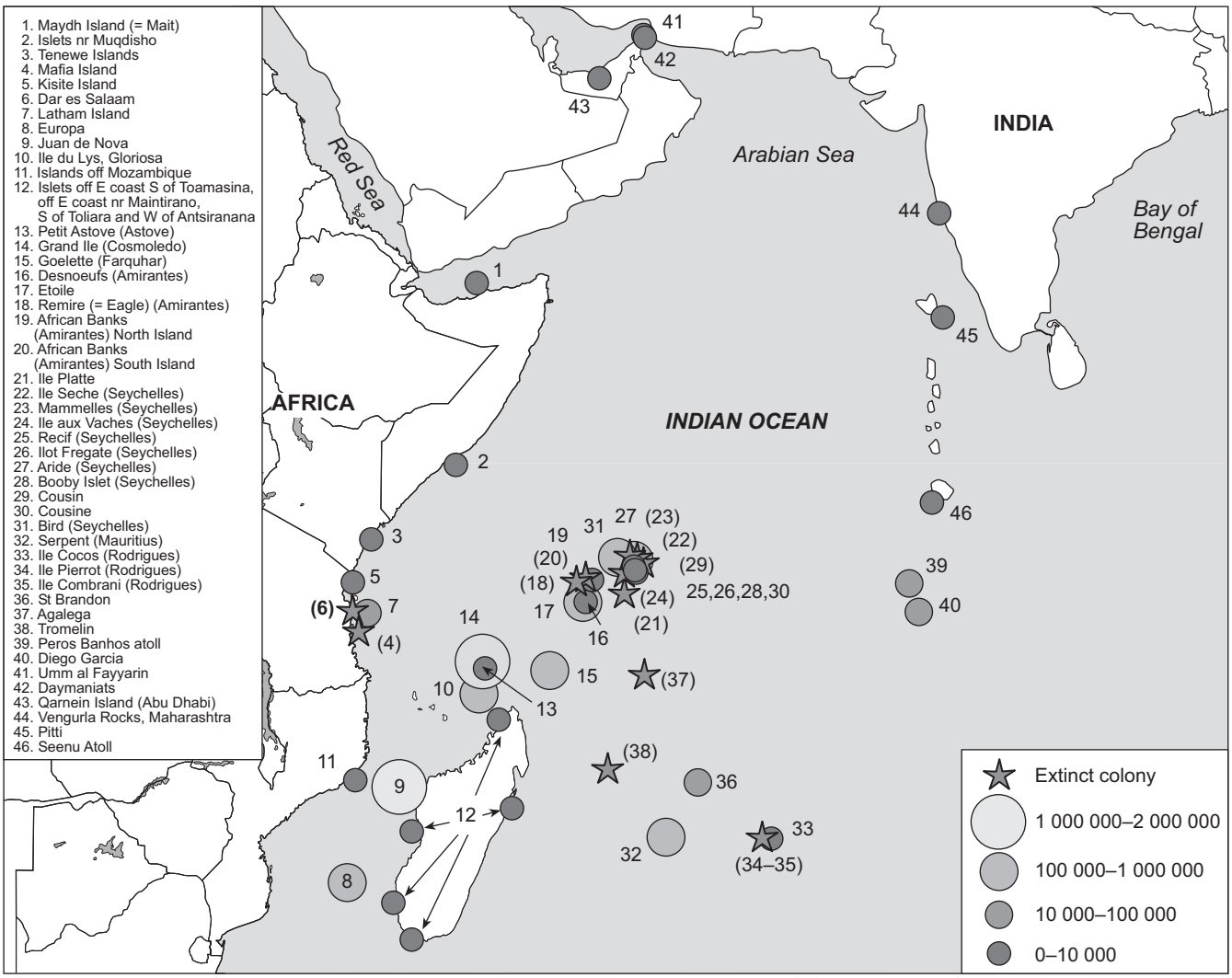

Figure 1: Sooty Tern colonies in the western Indian Ocean: numbers on the map refer to the localities listed in the text box. More details on these localities are given in Table 1. Active colonies are indicated with a proportional plot according to the number of breeding pairs and the number of colonies per size category are indicated in the legend. Extinct colonies are mapped with stars and their numbers are in brackets

It is encouraging to note that there appear to have been some re-colonisations in recent years, notably on Diego Garcia's islets (Symens 1999), Ile Coco (Rodrigues) in the 1990s (J Hume, University of Portsmouth, UK, pers. comm.) and Cousine (Seychelles) in the early 2000s (Q Hagens, Cousine Island, Seychelles, pers. comm.).

Factors underlying population change and extinction

Many factors, that have differed between island groups, have driven population changes and extinctions. Some of the changes pre-dated written records and so we do not know their timing but some descriptions are available of changes in progress during early expeditions and from these the likely impacts can be inferred.

Habitat change

In Seychelles, the most widespread anthropogenic factor that led to declines in Sooty Tern colonies has been habitat modification associated with agriculture, especially the planting of coconuts. The best-documented example is Bird Island, where the planting of coconuts almost excluded Sooty Terns, but numbers increased substantially following partial clearance of the trees (Feare 1976a).

During the late 19th and early 20th centuries coconuts were planted on most islands in the Seychelles (Procter 1984, Stoddart and Fosberg 1984). On sand cays they replaced littoral vegetation, as on Bird Island, but on some of the larger cays they may have replaced littoral woodland. On at least some of the smaller central granitic islands of Seychelles all native woodland vegetation was removed to make way for coconuts (Sauer 1967, Procter 1984). On the sand cays, ground-nesting seabirds probably had a role in maintaining the structure and composition of the open herb and bush communities attractive to Sooty Terns (Stoddart and Fosberg 1984) but in plantations these communities were replaced with understorey of either well-maintained mats of short, dense introduced herbs, such as grasses, or

Table 1: Sooty Tern (*Sterna fuscata nubilosa*) populations in the western Indian Ocean. Numbers in the left hand column refer to locations on Figure 1

No.	Island	Population size (pairs)	Trends E = extinct	Threats (eggs laid)	Breeding season	Source
	Somalia					
1	Maydh Island (= Mait)	Large numbers	?	Rats present 1940s	June	Ash & Miskell (1998), North (1946), Jennings (1995)
2	Islets nr Muqdisho	14–19	?		June	Ash & Miskell (1998)
	Kenya/Tanzania					
3	Tenewe Islands	Thousands	?		August	Britton (1980)
4	Mafia Island	100	E			Britton (1980)
5	Kisite Island	c. 50	?	Egg harvest		Zimmerman *et al.* (1996)
6	Dar es Salaam	?	E			Britton 1980
7	Latham Island	Tens of thousands	?	Rats present	November	Gwynne *et al.* (1970), Britton (1980)
	Mozambique Channel					
8	Europa	760 000	? stable	Rats present	July–August, annual	Le Corre (2001), Le Corre & Jaquemet (in press)
9	Juan de Nova	2 000 000	Possible increase	Former guano exploitation, feral cats	Austral summer, annual	Le Corre & Jaquemet (in press)
10	Ile du Lys, Gloriosa	270 000	?	Rats recently eradicated, possible illegal harvest	Mostly March–April but variable	Le Corre & Jaquemet (in press), Benson *et al.* (1975)
11	Islands off Mozambique	Thousands	?	Harvested illegally		Kromer (1998)
	Madagascar					
12	Islets off E coast S of Toamasina, off E coast nr Maintirano, S of Toliara and W of Antsiranana	Thousands	Decreasing	Unregulated harvest	Variable	Langrand (1990) ZICOMA Project (2001)
	Seychelles					
13	Petit Astove (Astove)	Small (possibly this species)	?		?March or June	Bayne *et al.* (1970)
14	Grand Ile (Cosmoledo)	1 140 000	? stable	Rats, cats, possibly poaching	Late May–June, annual	Rocamora *et al.* (2003)
15	Goelette (Farquhar)	260 000	? stable		Late May–June, annual	CJF unpublished data
16	Desnoeufs (Amirantes)	c. 500 000	? reduced due to vegetation growth; time scale unknown	Excessive growth of *Stachytarpheta jamaicensis*; legal egg harvest on half of colony	Late May–June, annual	Feare & Gill (1995), Feare *et al.* (1997)
17	Etoile		Status uncertain	Island erosion		CJF unpublished data
18	Remire (= Eagle) (Amirantes)		E	Formerly harvested, habitat now unsuitable, + cats		Ridley & Percy (1958), CJF unpublished data
19	African Banks (Amirantes) North Island	<5 000	Much reduced from 20 000+ in 1970s	Intense poaching annually	Late May–June, annual	Feare (1979a), Feare & Gill (1997)
20	African Banks (Amirantes) South Island		E	Island has eroded away		
21	Ile Platte	? large numbers	E			G Savy (Bird Island, Seychelles, pers. comm.)

Table 1: (cont.)

No.	Island	Population size (pairs)	Trends E = extinct	Threats (eggs laid)	Breeding season	Source
22	Ile Seche (Seychelles)	Small numbers	E			Ridley & Percy (1958), CJF unpublished data
23	Mammelles (Seychelles)	Small numbers	E			Ridley & Percy (1958), CJF unpublished data
24	Ile aux Vaches (Seychelles)	Small numbers	E			Ridley & Percy (1958), CJF unpublished data
25	Recif (Seychelles)	c. 47 000	Probably now stable	Periodic illegal harvest, probably now reduced	Late May–June, annual	Feare (2002a)
26	Ilot Fregate (Seychelles)	Few	?	Periodic harvest	Late May–June, annual	CJF unpublished data
27	Aride (Seychelles)	c. 300 000	Stable	Periodic illegal harvest, now reduced	Late May–June, annual	Bowler *et al*. (2002)
28	Booby Islet (Seychelles)	Small numbers	?	Regularly poached	Late May–June, annual	CJF unpublished data, M Betts, (Aride Island, Seychelles, pers. comm.)
29	Cousin	?	E	Formerly harvested, habitat now unsuitable	Late May–June, annual	Ridley & Percy (1958), CJF unpublished data
30	Cousine	?	E	Formerly harvested, limited habitat now	Late May–June, annual	Ridley & Percy (1958), CJF unpublished data
		200	Recent limited re-colonisation			Q Hagens (pers. comm.)
31	Bird (Seychelles)	c. 700 000	Severe decrease to 1960s, since when big increase	Rats eradicated, crazy ants under control in colony area; now periodic legal harvest	Late May–June, annual	Feare & Gill (1996), Feare (1999a)
Mascarenes						
32	Serpent (Mauritius)	200 000–300 000	? stable		Prolonged	Safford (1993); C Jones (pers. comm.) Bell *et al*. (1993)
33	Ile Cocos (Rodrigues)	1 500–2 000	? increasing	Minor human disturbance	Irregular	C Jones (pers. comm.)
34	Ile Pierrot (Rodrigues)	Large numbers	E	Unregulated harvest, now restricted habitat and human disturbance		Cheke (1987), Bell *et al*. (1993)
35	Ile Combrani (Rodrigues)	Large numbers	E	Unregulated harvest, now restricted habitat and human disturbance		Cheke (1987), Bell *et al*. (1993)
36	St Brandon	20 000	Big decline from hundreds of thousands in 1970s	Unregulated harvest of adults and eggs. Rats on some islands	Most months	Newlands (1976), Williams & Rowlands (1980), Swinnerton *et al*. (1996)
37	Agalega	Huge colony	E	Eggs of all seabirds formerly collected; extirpated 1943 by island owner who set fire to nesting area		Cheke & Lawley (1983), who quote Newton (1883) on egg harvest
38	Tromelin	Possibly large	E	*Rattus norvegicus* present		Le Corre (1996)

Table 1: (cont.)

No.	Island	Population size (pairs)	Trends E = extinct	Threats (eggs laid)	Breeding season	Source
Chagos						
39	Peros Banhos atoll (Petit & Grand Coquillage, Yeye, Longue islands)	Colonies of unknown size	Probably much reduced	Unregulated harvest during residence of islanders	May–Aug & Nov–Feb, Sept	Lousteau-Lalanne (1962), P Carr (pers. comm.)
	Peros Banhos atoll (Parasol, Longue, Petite Coquillage islands)	55 800		Fishermen, tourists? Rats?	Laying Feb–Mar	Symens (1999)
40	Diego Garcia	c. 100 000	E	Unregulated harvest during residence of islanders	July, Sept. Data deficient, but possibly all year	Bourne (1886), Finsch (1887), P Carr (pers. comm.)
	Sea Cow, Middle Brother, South Brother	17 200	Re-colonisation?	? rats	Laying Feb–Mar	Symens (1999)
Oman						
41	Umm al Fayyarin	c. 10	?	Egg harvest	June	M Gallagher (Selsey, UK, pers. comm.)
42	Daymaniats	Probable, small nos	?	Egg harvest	June	M Gallagher (pers. comm.)
	United Arab Emirates					
43	Qarnein Island (Abu Dhabi)	Scarce visitor			Does not breed	Aspinall (1996), Richardson (1990)
India						
44	Vengurla Rocks, Maharashtra	?	?	?	?	Ali & Ripley (1969)
Lakshadweep						
45	Pitti	Thousands	?	Some collecting of eggs and adults	Most months	Hume (1876), Betts (1939), Mathew *et al.* (1996)
Maldives						
46	Seenu Atoll	?	?	?	?	Ash & Shafeeg (1994)
		?			March–April	Phillips (1963)
Total (extant only)		> 6 290 000				

Table 2: Principle factors involved in the extinction or reduction of Sooty Tern colonies in the western Indian Ocean. For locations of islands see Table 1 and Figure 1

Extinctions Island	Habitat change	Introduction of predators	Human exploitation	Other factors or unknown (?)
Mafia				?
Dar es Salaam				?
Remire	✓	[1]		
African Banks (S)	✓			
Ile Platte				?
Ile Seche			✓[2]	
Ile aux Vaches (Grand Anse)			✓[2]	
Mammelles			✓[2]	
Cousin	✓		✓[3]	
Mahebourg islands (Mauritius)			✓	
Ile Pierrot			✓	
Ile Combrani			✓	
Agalega			✓	Deliberate removal[4]
Tromelin				?
Diego Garcia			✓	
Reduction				Extent of reduction[5]
Madagascar islets			✓	?
Desnoeufs	✓			?
African Banks (N)			✓	20 000 to 5 000[6]
Cousine	✓		[3]	Now c. 200[7]
Bird	✓			2 000 000 to 18 000 in 1950s, now 700 000[8]
Ile Cocos, Rodrigues			✓?	Formerly many thousands[9]. Recent re-colonisation[10], now to c. 2 000[11]
St Brandon			✓	100s of thousands to 30 000[12]
Chagos islands		[2]	[2]	?

[1] Introduced predators were not implicated in the extinction of the Remire colony but may have deterred recolonisation along with deteriorating habitat.

[2] Human exploitation is assumed to have been involved but there is no direct evidence. Symens (1999) regarded rat infestation as a major factor limiting present seabird numbers.

[3] Eggs were harvested from Cousin and Cousine but changing habitat is likely to have been the main cause of colony decline, with this view now reinforced by limited recolonisation of Cousine following appropriate habitat creation.

[4] The island manager burned the colony area in 1943 — see text.

[5] Sources: [6]Feare 1979b, [7]Q Hagens pers. comm., [8]Feare and Gill 1997, [8]Ridley and Percy 1958, [9]Cheke 1987, [10]Showler 2002, [11]C Jones, Mauritius Wildlife Foundation, pers. comm., J Hume pers. comm., [12]Newlands 1976, [12]Swinnerton *et al.* 1996

dense low trees (Stoddart and Fosberg 1984), both of which would be inimical to Sooty Terns. These habitat changes are most likely to have underlain the extinction of the small (judged from egg harvest data in Ridley and Percy 1958) colonies on Remire (Amirantes), and Cousin and Cousine (Seychelles). Subsequent dereliction of the coconut plantations at these localities led to a dense understory that prevented recolonisation, but a small area that has been cleared on Cousine has recently been recolonised (Q Hagens pers. comm.).

On Desnoeufs, in most years the birds' nesting area is restricted by a dense growth of introduced *Stachytarpheta jamaicensis* (Feare *et al.* 1997). On Aride, the nesting area is restricted in years when introduced *Asystasia gangetica* grows densely (Feare *at al.* 1997).

Geomorphological changes

Sand cays are to varying extents unstable and susceptible to changes in sea level, storm surges and changes in currents. In 1976 South Island of African Banks (Amirantes) was observed to be eroded and was visible only at low tide as a small rocky protrusion above the water (Feare 1979a); this situation still prevailed in 1997 (CJF pers. obs.). In 1976 Etoile had also largely eroded away, leaving a large sea-swept sand bank with a small, c. 0.3ha, vegetated area, supporting some nesting Common Noddies (*Anous stolidus*) but with no evidence of recently-nesting Sooty Terns (CJF pers. obs). In these two cases erosion had deprived Sooty Terns of former nesting areas. Conversely, in the late 1990s and early 2000s accretion of sand on the northern and north-eastern beaches of Bird Island led to the development of early and later successional beach vegetation, which has now (2003 and 2004) been colonised by Sooty Terns, adding c. 2ha to the colony area. Juan de Nova, which is also a sand cay, may also experience similar changes that could affect the Sooty Tern colony.

Introduced mammals and other animals

Most islands have populations of introduced mammals, including commensals, especially Black and Norway Rats *Rattus rattus* and *R. norvegicus*, mice *Mus domesticus*, and

cats *Felis catus.* Some have domestic animals such as pigs, goats, chickens and others, while a few have herbivores, including rabbits *Oryctolagus cuniculus* and hares *Lepus capensis*. There is no evidence that any of these have been responsible for the extinction of Sooty Tern colonies from western Indian Ocean islands. From 1967 to 1995, when Black Rats were introduced and eradicated respectively on Bird Island, Seychelles, the rats took few Sooty Terns (Feare 1976a) and the colony increased greatly despite the dense rat infestation.

On Grand Ile, Cosmoledo, Sooty Terns coexist with both rats and cats but there are no data on the extent of predation or on Sooty Tern population trends. Ridley and Percy (1958) reported abundant rats on Remire but did not mention cats. In 1976 cats were abundant and killing large numbers of Bridled Terns *Sterna anaethetus* and Lesser Noddies *Anous tenuirostris*: many corpses were found over the island during a brief visit (CJF pers. obs.); cat predation here might prevent recolonisation by Sooty Terns if suitable habitat were made available for them. Cats, but not rats, formerly occurred on Cousine, where their presence may, along with lack of suitable habitat, have contributed to the failure to recolonise. Elsewhere in the western Indian Ocean rats have been reported as common on Latham (Gwynne *et al.* 1970, species uncertain), Mait (North 1946), Europa (Le Corre and Jouventin 1997, *R. rattus*), Tromelin (Le Corre 1996, *R. norvegicus*, but some recent control attempts), and on some of the St Brandon islands (Newlands 1976, *R. norvegicus*). On Europa, rats prey on eggs and chicks (SJ pers. obs.) and goats may sometimes trample eggs and chicks. On Juan de Nova, feral cats take huge (but unquantified) numbers of both adults and chicks. On some of these islands Sooty Terns remain numerous, again suggesting the Sooty Tern colonies are relatively unaffected by rat infestations, as seen also on Ascension Island (Atlantic, Ashmole 1963, Hughes 2002) and Raoul Island (Kermadecs, Pacific, Taylor 1979).

On Desnoeufs Island, Sooty Terns have co-existed with rabbits for at least 60 years and did so on Bird Island for a few years until the rabbits were eradicated along with the rats. Rabbits may help to retain herb vegetation in a condition attractive to Sooty Terns between breeding seasons, when seasonal rains promote vegetation growth. Rabbits have been recorded taking tern eggs on a Pacific island but this appears to have been an exceptional incident (Brown 1974)

Sooty Tern eggs and chicks are sometimes taken by both introduced and native birds. Introduced Common Mynas *Acridotheres tristis* and migrant Turnstones *Arenaria interpres* occasionally take deserted eggs around colony edges (Feare 1976a). The endemic Seychelles Fody *Foudia seychellarum* takes seabird eggs when incubating adults are absent on Cousin and Cousine Islands. Seychelles Fodies have recently been introduced (re-introduced?) to Aride Island, where many Sooty Terns nest at low density under the tree canopy. Here, Sooty Terns are much more wary than in more traditional high-density colonies in open areas (CJF pers. obs.), leaving their eggs readily when disturbed, potentially rendering these eggs susceptible to predation by fodies and skinks, *Mabuya wrightii*, the latter of which tend to prey on Sooty Tern eggs after disturbance. Cattle Egrets *Bubulcus ibis* take both eggs and chicks, and also kleptoparasitise chicks by chasing them and forcing them to regurgitate (Feare 1977); the effect of this is probably minimal. Cattle Egrets also attempt to drive incubating adults from their nests, usually without success. During a year with a heavy infestation of *Amblyomma loculosum* ticks on Bird Island, however, incubating adults with engorged ticks on their feet stood over their nests resting on one wing, with the infested foot raised. These birds were more wary of intruders than non-infested birds and left the nest at a Cattle Egret's approach, leading to egg loss (CJF pers. obs.). These predation events are nevertheless comparatively rare. Feare and Gill (1995) found that Cattle Egrets on Desnoeufs spent most time foraging for insects around the colony periphery, rather than in the colony searching for available eggs or chicks. In Seychelles, frigatebirds *Fregate* spp. do not prey on Sooty Tern chicks, but on Europa, frigatebirds, especially juveniles and males, prey on chicks (Weimerskirch *et al.* 2004) as already observed at Ascension (Ashmole 1963). At Europa, Sooty Tern chicks are also preyed on by Barn Owls (*Tyto alba*), as shown by the frequency of bones found in pellets (MLC pers. obs.). Pied crows also wander in the colony, usually scavenging but also occasionally preying on unattended chicks or eggs.

Land crabs (*Ocypode* sp.) take deserted eggs and weak or dying chicks and also scavenge dead adults, while on Europa a hermit crab takes eggs even when adults are incubating. Heavy tick infestation can lead to desertion of parts of nesting colonies (Feare 1976c on Bird Island, SJ pers. obs. on Europa and, to a lesser extent, on Juan de Nova). In 1998–99, an infeatation of introduced Crazy Ants *Anoplolepis longipes* led Bird Island Sooty Terns to avoid c. 2ha of their nesting area, most likely due to irritation by the ants, although the ants were suspected of killing some young chicks (Feare 1999a).

It seems unlikely that predation alone by these mammals, birds or invertebrates has played a part in population declines or extinctions but their presence may have contributed to the terns' failure to recolonise after earlier extirpation.

Guano exploitation

Guano was taken from western Indian Ocean islands from the late 19th century until the 1970s and had ecologically catastrophic effects on the most seriously affected islands, i.e. Assumption (Stoddart *et al.* 1970) and St Pierre (CJF pers. obs.), where entire seabird communities were eliminated. Small quantities were taken from Bird and Desnoeufs islands. Although extraction affected the islands' topography, the effect on Sooty Terns was probably minimal since they nest densely on such areas on Desnoeufs. Guano exploitation occurred on Juan de Nova and Ile du Lys until the 1970s, but its impact on Sooty Terns is unknown.

Human exploitation

In the Seychelles, Sooty Tern eggs have been commercially exploited since at least the beginning of the 20th century (Fryer 1910, Ridley and Percy 1958). In addition, eggs and juveniles are harvested illegally from some islands.

Eggs have generally been collected for local consumption in Seychelles but in the 1930s yolks were separated and barrelled for export. Ridley and Percy (1958) provided data, from Seychelles government records, on the number of eggs collected annually since 1928. The islands from which eggs were collected are open to debate and some of the estimates of eggs harvested from some of the islands, and of the Sooty Tern populations claimed for some islands, are impossibly high (Feare 1976b). Feare concluded that the evidence for a major decline in Sooty Tern numbers was unconvincing, and although some colonies had decreased or become extinct, factors other than over-exploitation (see above) were most likely to have been responsible. Both Bradley (1940) and Ridley and Percy (1958) remarked on the decline in yield apparent during the 1930s export of barrelled yolk and during this period exploitation may have been so great as to reduce populations. Nevertheless, recommendations made by Ridley and Percy (1958, 1966), Feare (1976b) and Feare and Gill (1997) on the management of the industry to ensure sustainability have been largely accepted by the Seychelles government and implemented. Regulations now in operation are (1) the annual harvest should be restricted to no more than 20% of the area of Seychelles and Amirantes colonies, (2) vegetation within colonies should be managed to maximise the area available for nesting, (3) no more than half of any island should be cropped, and the non-cropped part should be strictly protected, (4) 15% of income from the eggs should be returned to the Division of Environment as a levy to fund monitoring, policing and research. Since 1976 the data available indicate that the populations of the major colonies have remained stable or increased, suggesting that the harvest as now undertaken is sustainable.

Despite the existence of a managed industry, illegal harvests continue and have been made easier by improved boats and navigation equipment. Poaching of eggs and adults is generally limited to more remote islets that are difficult to access and difficult to police, such as Booby Islet (Seychelles) and African Banks (Amirantes). However, attempts are made annually to poach from the large (200 000–300 000 pairs) colony on Aride, a strict nature reserve. The quantity of adults taken from Aride is, due to the diligence of the island's managers and staff, small in relation to the population of the island and limited to sections of the colony most distant from the settlement. The extent of poaching from Booby Islet and African Banks, however, is such that it is remarkable that Sooty Terns continue to attempt to nest there; it is doubtful whether any chicks ever leave these islands. The Seychelles islands from which Sooty Tern colonies have disappeared — Ile aux Vaches (Grand Anse), Mammelles and Ile Seche — are close to the main islands and colony loss was probably due to egg collection and disturbance, although there is no direct evidence to support this contention.

Colonies on offshore islands of Madagascar appear to survive despite unregulated harvesting of their eggs but the sizes of most colonies and the extent of harvesting are unknown; some colonies may be declining (MLC pers. obs.).

Sooty Terns formerly nested on islets off Mahebourg, south-east Mauritius (Cheke 1987). These islets are very close to the main island and very accessible, and human disturbance and unregulated egg collecting doubtless led to very early extinction, possibly before 1750 (A Cheke pers. comm.). Serpent Island houses Mauritius's only surviving colony and its survival may be attributed to the rarity of visits due to its hazardous landing (Newton 1956, Safford 1993).

Pierrot/Chat (37.5ha) and Gombrani/Combrani (34.5ha), and at least at certain times Ile Coco, all of which are lagoon islands of Rodrigues, formerly supported large colonies that were extensively exploited (Staub 1973, Cheke 1987). Ease of access doubtless contributed to their demise. The developement of lush introduced vegetation (A Cheke pers. comm.) may prevent recolonisation. The only extant Rodrigues colony is small, on Cocos, a sandy island with open areas that provide suitable habitat, but this colony is the result of recent colonisation, the island having been devoid of Sooty Terns from around 1900 to 1980.

St Brandon (Cardagos Carajos Shoals), among the most isolated of the western Indian Ocean islands, formerly supported huge Sooty Tern colonies (Newlands 1976), reduced in the 1990s to only 30 000 pairs (Swinnerton *et al.* (1996). The decline is likely to have been due to extensive harvesting of adults and eggs by employees of a fishing centre based there, with a significant human presence throughout the year. However, comparison between visits is not straightforward on these islands as Sooty Terns appear to breed all year, with birds at different stages of development being simultaneously present on different islands, and even sections of the same island differing in the stage of the breeding season of its birds (Newton 1956, Newlands 1976).

There is little information about colonies on islands close to the East African coast and the causes of extinction of those that have disappeared are unknown; human disturbance and egg cropping can only be suspected (Kromer 1998). In the Lakshadweep, the colony on Pitti appears to survive unregulated egg harvesting, possibly due to the prolonged breeding season and the inaccessibility of the island for parts of the year.

Colonies for which the reason for reduction/extinction is unclear

Sooty Terns bred in large numbers on Agalega until 1943, when the island manager set fire to the colony and for reasons unknown the birds have not returned since then (Cheke and Lawley 1983); the vegetation is now unsuitable (A Cheke pers. comm.). Prior to that eggs were harvested in large numbers, officially for export to Mauritius but also illegally by labourers on the island.

The extinction of the Sooty Tern colonies on Tromelin and Chagos are surprising in view of their remoteness and distance from centres of human population. Fishermen, however, regularly visit them. Tromelin has a small resident human population and Le Corre (1996) considered human disturbance to be currently low. Whether human predation was involved in the extinction of Sooty Terns is unknown. On Chagos the large colony found by Finsch (1887) and Bourne (1886) on Diego Garcia was being 'severely persecuted' and disappeared within the next 20 years (Bourne 1971), but whether human exploitation alone was

responsible for the demise of this colony is unknown. In the 1960s smaller colonies were found elsewhere in the Chagos Group (Lousteau-Lalanne 1962) but their former status is unknown. In 1996, Symens (1999) found c. 73 000 pairs in colonies on six of the islands, including some on islets of Diego Garcia, which may represent recolonisation. P Carr (Royal Marines, Bicester, UK, pers. comm.) speculates that, with the departure of the 'native' human population following the decline of the copra industry and the construction of a military base on Diego Garcia in the 1970s, Sooty Terns might have been able to return to islands from which they had disappeared; more detailed surveys, covering all months, are needed to test this hypothesis.

Changes in food supply

Ridley and Percy (1958) quoted hearsay evidence that in some years when numbers of birds appeared lower than usual in Seychelles and Amirantes colonies, more birds were claimed to occur in the southern colonies of Cosmoledo and Farquhar. Ridley and Percy thought that this could be related to changes in food supply. In 2000, several birds that had been ringed as breeding adults on Aride and Recif islands nested on Bird Island (Feare and Lesperance 2002). In that year, the Aride colony contained c. 100 000 pairs fewer than the usual c. 300 000 pairs (J Bowler, Aride Island, Seychelles pers. comm.). Aride and Recif are both to the south-east of Bird Island and these movements of breeding birds might indicate a redistribution of food within the Seychelles in 2000. There have been no previous or subsequent appearances of numbers of ringed birds from these two islands on Bird Island (CJF pers. obs.). Fluctuations in food supply might therefore temporarily influence local distributions of Sooty Terns, but there is no evidence that changes in food supply have been responsible for population declines or extinctions on particular islands.

Conclusions

The main causes of extinction and decline in western Indian Ocean Sooty Tern colonies have been habitat loss and human exploitation and disturbance (Table 2), with introduced predators being insignificant with respect to Sooty Terns (but they have of course been of prime importance with regard to other seabird species). Diamond and Feare (1980) found that island size and isolation did not predict the number of breeding seabird species in the Seychelles and that the approximate human population was a better predictor. For Sooty Terns, however, extinction does appear to have been associated with small islands close to human populations. Elsewhere in the western Indian Ocean, however, some large colonies close to human habitation (e.g. Rodrigues) have been lost, but some large comparatively-isolated colonies have also been lost (e.g. St Brandon, Diego Garcia). In all of the cases where human harvest and disturbance are implicated as the main factors underlying extinction, the harvesting has been illegal and unregulated. Under these circumstances, adults are taken along with eggs.

The taking of large numbers of adults may be the critical factor in determining population decline and extinction. Sooty Terns are long-lived seabirds with low fecundity, deferred maturity and high annual survival (Harrington 1974, Feare and Doherty 2004). Population growth in species with these characteristics is considered to be most sensitive to changes in adult survival (Cairns 1992, Pfister 1998) and least sensitive to changes in productivity. Temporary reductions in productivity appear to be a natural feature in the demography of tropical oceanic birds and arise through unpredictable food shortages, adverse weather conditions, parasitic infestations, and cyclic climatic phenomena such as El Niño events (Feare 1976a, 1976c, White *et al.* 1976, Schreiber and Schreiber 1984). Whereas regulated harvests of eggs may act as a surrogate for these unpredictable or periodic natural occurrences, to which the Sooty Tern's demography is adapted, the harvest of adults could depress average annual survival below the threshold required for population stability. Habitat restriction, on the other hand, imposes a density independent ceiling on the number of adults that can breed, irrespective of adult survival, and additionally constrains fecundity below that which could be achieved in the presence of naturally-occurring limiting factors.

There may also be a relationship between extinction probability due to unregulated egg harvest and seasonality of breeding. In the Seychelles and Amirantes, colonies that have become extinct, purportedly through over-exploitation, have generally been small (Table 1) and here nesting is strictly seasonal, allowing an approximate 6–8 week window during which exploitation is possible. Colonies to the south and east of Seychelles that appear to have become extinct through unregulated harvesting have been much larger (Combrani and Pierrot in Rodrigues, St Brandon, Diego Garcia) and the St Brandon and Diego Garcia colonies appear to have had more prolonged, if not all-year, breeding seasons. All-year breeding could have led to all-year human disturbance, allowing disturbance during the pre-laying period — not normally experienced by colonies on an annual cycle — to deter affected birds from breeding.

Current and future threats, and information requirements

Some current threats to Sooty Terns have been or are being removed. In Seychelles, Aride and Cousine are now managed as strict nature reserves, Bird Island is managed as a nature reserve but with periodic managed egg harvest, Recif receives some government protection during the breeding season, as does Desnoeufs as part of the procedure associated with egg harvest (Feare 2003). Eradication of exotic predators has been undertaken on Bird and long-term research is continuing there to assure the sustainability of regulated harvests (Feare 2002b, Feare and Lesperance 2002, Feare and Doherty 2004). Discussions are proceeding to find ways to confer protection on Cosmoledo (Rocamora *et al.* 2003). Rats were recently eradicated from Ile du Lys (Glorieuses) and future monitoring will provide new information on the potential impact of such introduced predators on Sooty Tern population dynamics.

Current threats are likely to remain on other islands and may even be exacerbated by the greater mobility of seafarers. While difficulty of access helps to protect some colonies, others are vulnerable and increasing remoteness

poses great difficulties of enforcing protection measures, especially on islands where the maintenance of a human presence is extremely difficult. Recent surveys of Seychelles and French-administered islands (Feare 1999b, 2000, 2002a, Feare and Gill 1997, Bowler *et al.* 2002, Rocamora *et al.* 2003, Le Corre and Jaquemet in press) however, have brought concerns out into the open and it is hoped that these and further surveys will provide suggestions on the protection of these islands, involving restriction of access, removal of exotics, and maintenance of habitats for Sooty Terns and other seabirds. The search for funding for these schemes will then be a priority.

The past 20 years have seen the development of extensive industrial fishing in the western Indian Ocean. This is commercially important but the prospect of short-term gain, for island states that otherwise have few prospects for earning foreign exchange (EMPS 2000), brings the likelihood of over-exploitation of the fish stocks. This is of particular concern with respect to mid- and shallow-water predatory fish such as tuna, since many tropical seabird species are dependent on schools of these fish to drive small fish to the surface, where they become available to seabirds (Ashmole and Ashmole 1967, Au and Pitman 1988). A decline in these commercial fish populations could have serious impacts on the seabirds. Detecting the onset of such an impact will require regular monitoring of seabird populations over a wide area of the western Indian Ocean. As a widely distributed obligate commensal of tuna shoals, with large colonies available for investigation of nestling growth, adult body condition, colony size etc., the Sooty Tern is the ideal species to study in this respect.

With long-lived species like Sooty Terns, investigations aimed at detecting the effects of marine variables, that are themselves likely to occur over long time-periods, must be designed to be long-term. Such studies will also be invaluable in researching the effects of climate change on marine top predators (Ramos *et al.* 2002). Climate change is likely to have both acute and more insidious effects on tropical marine environments. For example, increasing atmospheric concentrations of carbon dioxide may increase the acidity of surface waters with unknown effects on surface, and sub-surface, dwelling fish and their food. More direct effects are likely to be seen through the predicted rise in sea levels, to which Sooty Tern colonies on sand cays will be especially vulnerable. As nesting habitats for them already seem to be limiting, it seems unlikely that they will be able to find alternative breeding places.

Acknowledgements — CJF thanks the Royal Society, Percy Sladen Memorial Fund, and the Seabird Group for funding that initiated the current Seychelles research, and Bird Island Lodge, Islands Develoment Company and the Division of Environment for essential but willingly-given logistic support. MLC and SJ thank the University of Réunion and Western Indian Ocean Marine Science Association (WIOMSA) for funding.

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