J. Zool., Lond. (*A*) (1986) **210**, 527-549

The biology of terns nesting at Aldabra Atoll, Indian Ocean, with particular reference to breeding seasonality

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(*Accepted 21 January 1986*)

(With 8 figures in the text)

Five species of tern breed on Aldabra Atoll (09° 24′ S; 46° 20′ E). The Caspian tern *Sterna caspia* and Crested tern *S. bergii* feed exclusively in very shallow reef/lagoon water, the Fairy tern *Gygis alba* and Brown noddy *Anous stolidus* feed out at sea, and the Black-naped tern *Sterna sumatrana* is intermediate in its foraging. Both of the shallow-water species lay during the south-east monsoon season, the Caspian tern from April to August and the Crested tern from June to August, but the Crested tern also lays in December and January. The remaining three species have extended laying periods largely circumscribed by the north-west monsoon season from November to March. Breeding population size of the Caspian tern is in the low tens and of the Brown noddy in the low thousands, with the other species each numbering in the hundreds. The distribution and abundance of the nine species of tern breeding within the Seychelles (*sensu lato*) vary on the different island groups in a manner interpretable in terms of depth of the surrounding waters. Systematic differences between the central Seychelles and Aldabra groups in timing of breeding by terns which feed out at sea may be associated with seasonal latitudinal movement of the divergence zone between the South Equatorial Current and the Equatorial Counter-current, acting *via* correlated latitudinal shifts of prey species and game-fish abundance.

Contents

0022-5460/86/012527+23 $03·00

Introduction

Eleven species of seabird breed at Aldabra (09° 24′ S; 46° 20′ E): one shearwater, two tropicbirds, one booby, two frigatebirds and five terns (Diamond, 1971*a*). The biology of the tropicbirds (Diamond, 1975*a*; Prŷs-Jones & Peet, 1980), booby (Diamond, 1974) and frigatebirds (Diamond, 1975*b*; Reville, 1980, 1983) has already been described in some detail. In this paper we document the biology of the breeding tern species, *i.e.* Caspian *Sterna caspia*, Crested *S. bergii*, Black-naped *S. sumatrana*, Fairy or White *Gygis alba* and Brown noddy *Anous stolidus*, based mainly on work we carried out in the late 1960s and mid 1970s. We compare our results with those available for terns breeding in the rest of the Seychelles, and interpret variation in distribution, abundance and breeding seasonality throughout the region in relation to the marine environment. Five non-breeding species of tern recorded at Aldabra have been discussed elsewhere (Prŷs-Jones, 1984).

Study area and methods

Aldabra is a large atoll of raised coral limestone, lying *c.* 640 km off the east coast of Africa and 240 km north-west of Madagascar. Most of its land area comprises 4 major islands around the atoll rim, which encircle a shallow, mangrove-fringed lagoon connected to the Indian Ocean *via* narrow channels (Stoddart & Wright, 1967; Stoddart, Taylor, Fosberg & Farrow, 1971). Within the lagoon are 5 further islands, and numerous small islets on which most breeding terns nest (Fig. 1). The islets have been grouped into several structural types by Diamond (1971*a*, 1975*a*), whose classification is followed here (Fig. 2). Islets mentioned in the text are summarized in Appendix I.

Despite its proximity to the equator, Aldabra has a markedly seasonal climate (Stoddart & Mole, 1977). More than 75 % of average annual precipitation occurs between December and April, after which rainfall decreases progressively to nearly zero in September and October (Prŷs-Jones & Peet, 1980). Mean monthly temperatures vary between *c.* 28 °C in February and *c.* 25 °C in August. The south-east monsoon blows from April through October; for the rest of the year the winds of the north-west monsoon are lighter and more variable. Occasional heavy storms occur, but the area is outside the normal cyclone zone. Aldabra experiences an unusually high tidal range (2·7 m) for an oceanic atoll, and the lagoon itself is strongly tidal with a variable lag time which in places exceeds 4 hours relative to the seaward reef flats (Farrow & Brander, 1971).

A.W.D. worked at Aldabra from September 1967–March 1968 and March–September 1969; R.P.P-J. did so from July 1974–June 1975 and November 1975–February 1977. A.W.D. studied the comparative ecology of the seabirds (Diamond, 1971*b*), and visited their nesting areas at frequent, irregular intervals. R.P.P-J. worked predominantly on the landbirds, obtaining most of his seabird data in the course of islet censuses conducted during most months of his second visit (see Appendix I). On each visit to a colony or nest site, we counted nests, eggs and chicks. A.W.D. also caught adults at colonies and roosts, which he ringed and scored for primary moult following Ashmole (1962), collected food samples, and timed incubation shifts and intervals between chick-feeds to assess the potential foraging range of breeding adults.

Results

Caspian tern

Distribution and numbers

We found nine breeding pairs in 1969 and at least seven in 1976; a record of 30 adults at Îles Moustique in May 1972 (C. Frith, *in litt.*) is the maximum count on record. Most pairs nested

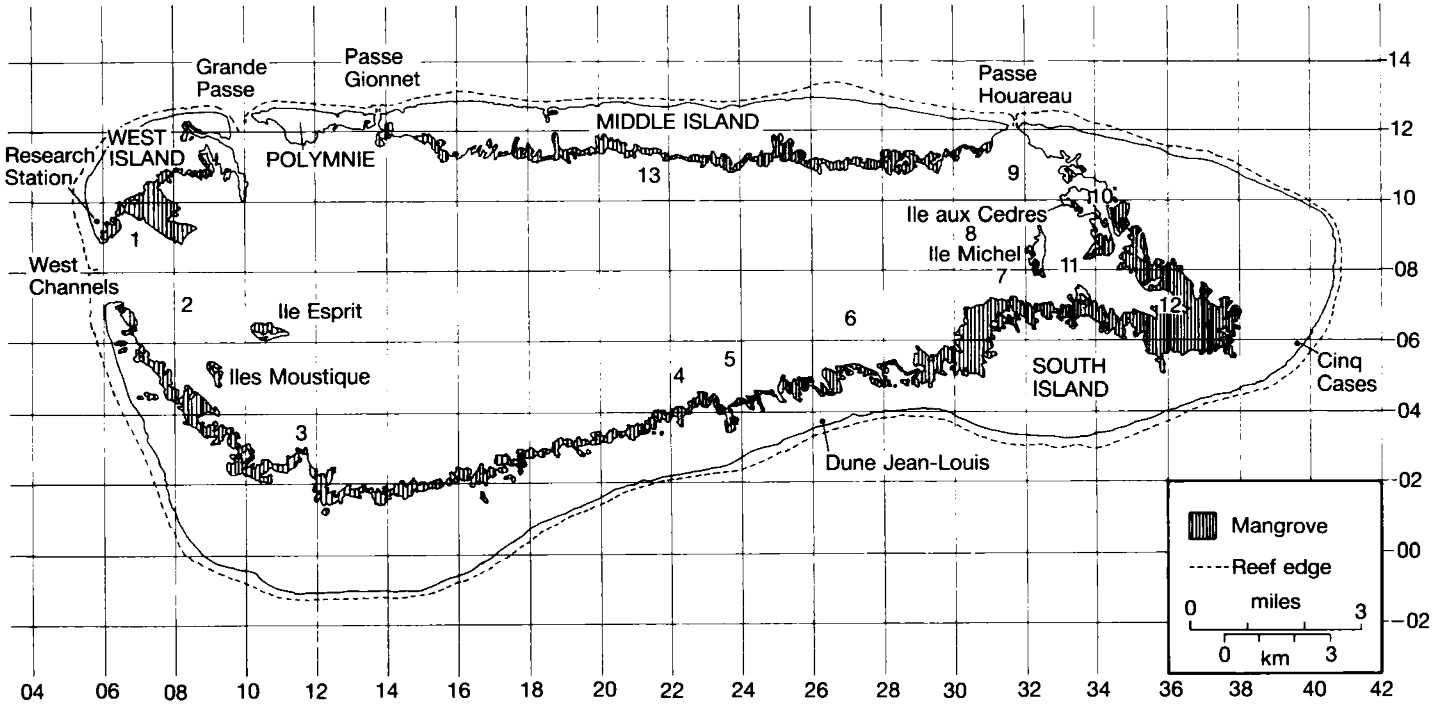

FIG. 1. Map of Aldabra Atoll, with a 2 km grid superimposed. Numbers in lagoon indicate positions of main islets/islet groups censused (see Appendix I for names). For a comprehensive map of all named localities on Aldabra, see Stoddart & Westoll (1979: 264).

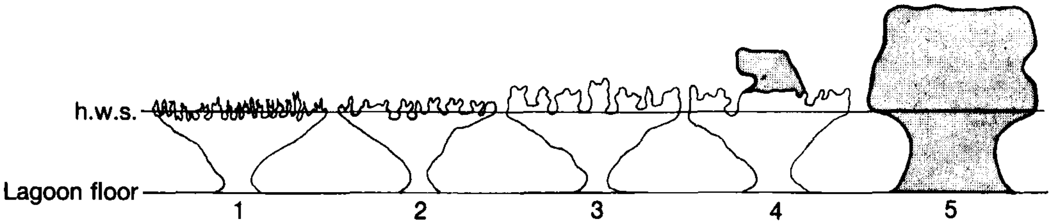

FIG. 2. Main structural types of lagoon islet. Unshaded = Takamaka limestone, shaded = Aldabra limestone (for definition and description of rock types, see Braithwaite *et al.*, 1973); h.w.s. = high-water spring tide level (*c.* 2·5 m). Type 3 is subdivided into 3a and 3b in text discussion; the latter tend to rise higher above sea-level. Distribution of different islet types within the Aldabra lagoon is given by Diamond (1971*a*, 1975*a*).

on Îles Moustique, but a single pair nested on Île Esprit in 1968 (J. Frazier & R. N. Hughes, pers. comm.), 1969 and 1976, and a further pair probably bred on Île Michel in 1969 and 1976. The species is apparently resident.

Breeding cycle

Twenty-five clutches and broods found over five years show a clearly defined laying season from April to August (Fig. 3), with no marked differences between years. The later laying attempts probably consisted largely of replacement clutches (see below). All nests were either unlined scrapes in the sand, or hollows containing debris in the lagoon strand line. The nests on Îles Moustique, a low sand island, were placed on the edges of tidal sand flats surrounded by mangroves. No nest was far above the high-spring tide mark, and several were below it; nests were frequently destroyed by flooding. One strand line nest successfully fledged young despite being washed up the shore by a high tide during the incubation stage. Minimum inter-nest distance was *c.* 10 metres.

Of 21 clutches found, 14 contained two eggs and the rest one. This observed average of 1·7 eggs equals that recorded in northern Madagascar (Milon, 1950), the nearest breeding site to Aldabra. During 1969, when the Îles Moustique breeding population was studied most closely, most pairs lost one or more clutches of eggs, and several lost chicks. Of seven clutches documented lost, four were apparently replaced; the pair in one location lost and replaced two clutches. High tides caused most losses, but predators, in particular Black rats *Rattus rattus*, which occur throughout Aldabra except on the small islets, may also have contributed.

Incubation shifts were measured in 1969 during two dawn-to-dusk watches from a hide overlooking two nests, the members of each pair being distinguished by differences in the amount and pattern of white in the crown. Since the non-incubating bird often remained near the nest, time out of sight (absence interval) was also measured to give an estimate of the maximum time available for feeding. Nine complete incubation shifts averaged 66 minutes (range 23–118), and 21 absence intervals averaged 27 minutes (range 1–80); the off-duty bird thus spent only 40 % of its time away from the nest. Chicks older than about one week were difficult to find as they hid under mangrove bushes or in tide-line debris. The only two chicks known to have fledged in 1969 were first seen flying aged 47 and 49 days. This apparently low breeding success was repeated in 1976, when only one juvenile could be found accompanying four pairs of adults present at Îles Moustique in late September.

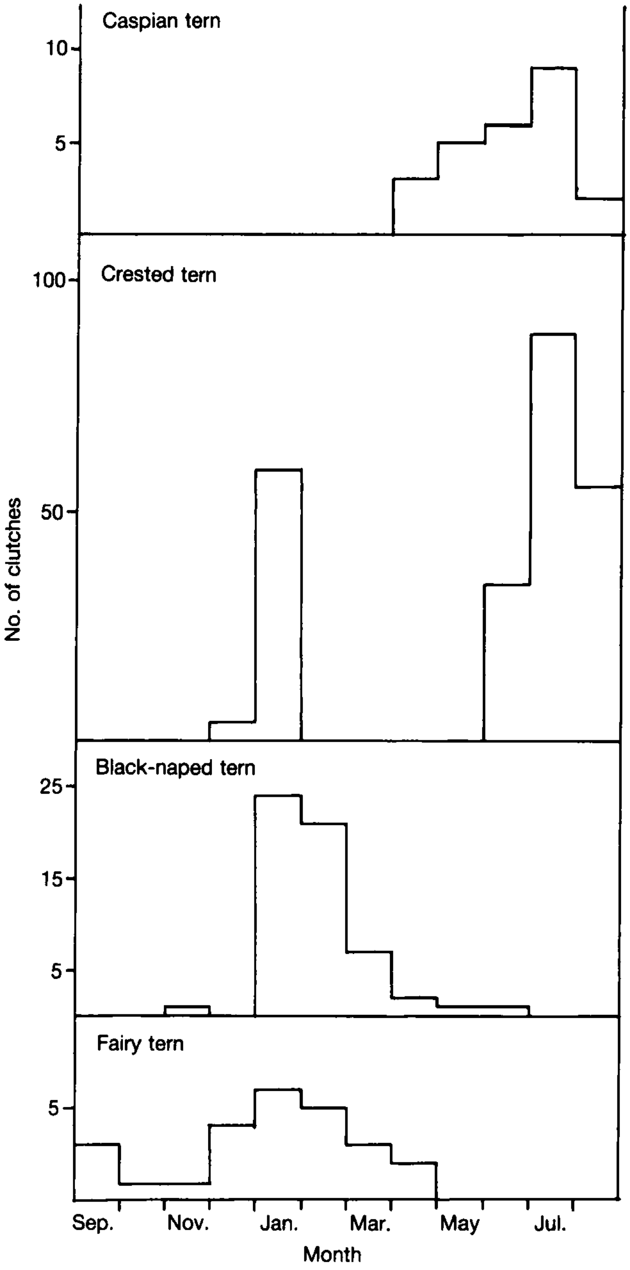

FIG. 3. Laying chronology for Caspian, Crested, Black-naped and Fairy terns. Records backdated to probable month of laying.

Feeding

The short incubation shifts and absence intervals indicate that Caspian terns on Aldabra are inshore foragers. Neither of us, however, saw individuals feeding in the lagoon, although in April 1969 M. J. Penny (pers. comm.) photographed several feeding on small fish trapped in shallows behind a mud bar at low tide. Our own observations all involved Caspian terns diving into water under one metre deep along the seaward reef flats of the south-western coast between the Research Station and Dune Jean Louis, i.e. the coastal area closest to the Îles Moustique breeding site.

Crested tern

Distribution and numbers

Crested terns were recorded breeding on seven islets (nos. 2, 4, 5, 6, 8, 11 and 13 in Appendix I), all of structural types 3 or 4 (Fig. 2). The hearsay record of Gillham (1977) regarding a nesting site on Îles Moustique may reflect confusion with Caspian terns. Outside the nesting season birds roosted at low tide on sand banks, coral rubble and pebble beaches and at high tide on various small islets and in trees around the lagoon shore. Counts at major low tide roosts in 1968 totalled 80–100 birds, roughly twice the maximum number of nests recorded as active simultaneously (see below). Allowing for birds missed during roost counts and for possible non-breeders, a population of *c.* 150 was suggested by Diamond (1971*a*), but this may be too low if the birds are not resident year-round (cf. Feare, 1975), or if individuals do not breed every six months (cf. Dunlop, 1985; and see below). Gillham (1977) recorded 'several hundred birds' frequenting the mangroves of Île Esprit during early 1970, but may have confused Crested with migrant Lesser crested terns *Sterna bengalensis* which utilize this site (Diamond, 1971*a*).

Breeding cycle

The overall pattern of breeding is shown in Fig. 3. The evidence that two laying periods normally occur per year, at roughly six-month intervals in December/January and June–August, is strengthened by the constancy of the observed timing over a number of years. During 1976, when we obtained our most comprehensive records, there were three breeding periods corresponding closely to the overall trend (Fig. 4). Data supplied by S. Hnatiuk (*in litt.*) for July 1973–August 1974 also show laying at *c.* six-month intervals in early August 1973, January 1974 and July 1974. Whether successful pairs can breed again six months later is not known, but the extended post-fledging dependence of chicks and the time required for moult (see below) suggest not, as do the analogous data of Dunlop (1985). Probably the situation resembles that in populations of Sooty terns *Sterna fuscata* which have six-month laying cycles, in which successful breeders miss the next breeding period and return after 12 months (Ashmole, 1965).

In colonies on grassy islets, e.g. Champignon des Os, eggs were laid on the grass with no attempt at nest construction. On other islets, the eggs were laid either in patches of the halophyte *Sesuvium portulacastrum* or on bare rock, with occasionally a few pieces of fine gravel chippings as a 'nest'. Most nests were in small, closely-packed colonies of up to 40 pairs; inter-nest distances in a colony of 20 pairs on Table Ronde in 1969 averaged *c.* 50 cm. All but three of 167 clutches contained only a single egg; the remainder contained two. Occasional clutches of two eggs have also been recorded elsewhere (Storr, 1964; Gerhart & Turner, 1978; Langham, 1984), but it is not clear whether these are the product of more than one female. Eggs varied greatly in base

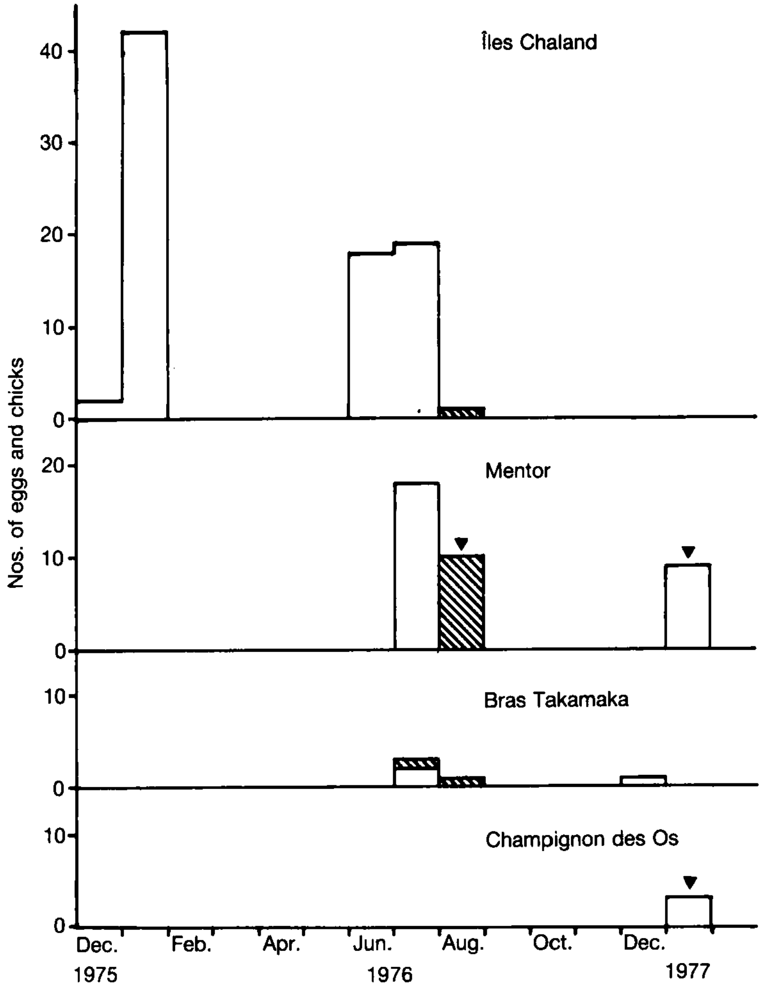

FIG. 4. Recorded breeding by Crested terns on Aldabra between December 1975 and January 1977. Unshaded (□) = eggs; shaded (▨) = chicks; ▼ = minimum estimates made from boat.

colour and markings, from pale with almost no spots to dark and extremely heavily spotted. Intact eggs were not preyed upon even when deserted, but broken eggs were rapidly consumed by the littoral crab *Grapsus tenuicrustatus* which was common on the islets.

Even in situations of minimal human disturbance, total or near-total failures of breeding colonies were not infrequent, e.g. at Îles Chaland in 1976 (Fig. 4). Efforts to observe colonies at close range invariably caused adults to desert eggs or small chicks and move elsewhere to re-lay, whereas large chicks formed creches which took to the water if approached. During 1969, however, a colony on an islet at Coffee Camp was watched by telescope from a hide on another islet *c*. 250 m away. Knowledge of the number of chicks present and counts of the number of adults bringing fish per hour enabled the mean feeding frequency of each chick to be calculated. In 1190 minutes of observation, 87 feeds were given to an average of 7·5 chicks aged *c*. two weeks old, averaging 0·58 feeds per chick per hour.

Birds in immature plumage were fed by adults for several months, although they could also be seen fishing for themselves during this time. Extreme records included one immature being fed in late January by an adult, and another begging in August from an adult which was feeding a small chick. These juveniles must have fledged a minimum of four to five months previously, confirming Feare's (1975) suggestion that post-fledging parental care lasts at least four months.

Moult

One adult in January 1968 and two in June 1969 had almost completed primary moult, each having the distal primary about three-quarters grown; one of the latter birds was resighted a month later in the nesting colony at Coffee Camp. An adult caught in August 1969 showed no sign of moult. These few observations suggest that adults complete wing moult near the onset of a laying period. An immature examined in January 1968, which must have fledged four to five months previously, had the four innermost primaries new, the fifth growing and the rest old; thus wing moult probably begins within a month or two of fledging.

Feeding

Most observed feeding involved birds diving into very shallow water (< 1 m) over the seaward reef flats and along the lagoon shore at low tide (*cf.* Gaymer, 1967), but they would also forage on occasion over deeper lagoon waters. Birds normally fed singly or in small groups, but concentrations of fish could bring groups of 10–20 together.

Black-naped tern

Distribution and numbers

With a single exception on the eastern tip of Middle Island, all nest-sites found were on small lagoon islets, predominantly type 4 and adjacent to the channels joining lagoon and sea. Normally, only one pair bred on any islet, the maximum found being three. The species was difficult to census because it is inconspicuous and breeds solitarily, and estimates of 70 breeding pairs and a total population size of 160 (Diamond, 1971*a*) must be minima.

Breeding cycle

Over 75 % of recorded clutches were laid during January and February (Fig. 3), with the remainder between March and early June, except for a single November clutch found by Gaymer (1967). Most nest sites were on bare rock, a few in small tussocks of coarse grass; Gillham (1977) describes an unusually well vegetated site. The lining, where present, was of fine rock fragments, occasionally embellished with a few twigs and leaves. Minimum inter-nest distance was *c.* 4 m, and mean recorded clutch size 1·5 eggs ($n = 49$, range 1–2). Elsewhere, clutch sizes averaging 1·6 eggs have been recorded at comparable latitudes in the Maldives (Phillips, 1958) and the Gulf of Thailand (Dickinson & Tubb, 1964).

Seventeen complete incubation shifts by one pair in 1968 averaged 62 min (range 15–210). Thirty-four absence intervals for two pairs with downy chicks averaged 25 min (range 2–80), and duration of absence interval was negatively correlated with reef-edge tide height ($r = -0{\cdot}50$, $n = 34$, $P < 0{\cdot}01$). Parent birds did not invariably return with food, and the feeding interval for chicks averaged 34 min. One chick was seen to fly unsteadily at 26 days old, indicating a similar fledging period to the 24–28 days recorded in Australia (Hulsman, 1980; Langham, 1984).

Juveniles could be distinguished from adults for about a month after fledging, during which time they remained associated with their parents but were not seen being fed.

Moult

Primary moult patterns of six adults are shown in Table I. Two features are striking: first, that adults with both eggs and chicks were in active moult; secondly, that the bird feeding a chick apparently had two cycles of moult occurring simultaneously. On Christmas Island, Pacific Ocean, Ashmole (1968) also found that moulting Black-naped terns had growing feathers at two or even three widely-separated points in each wing, but implied that his birds did not moult while breeding.

TABLE I

Primary moult of adult Black-naped terns

		Proximal									Distal
		Growth stage of primaries*									
Date	Status	1	2	3	4	5	6	7	8	9	10
22 January	At roost	.	.	.	.	.	.	2	.	.	.
22 January	At roost	.	.	.	.	.	2	.	.	.	.
25 January	Incubating	.	.	.	.	.	1	.	.	.	.
18 April	Incubating	.	.	.	.	.	5	.	.	.	4
20 April	At roost	5	5	5	5	5	5	4	0	0	0
26 May	With chick	.	.	.	1	.	.	.	.	3	0

* After Ashmole (1962). Dots denote full-grown feathers of uncertain age.

Feeding

Black-naped terns were seen feeding throughout the lagoon, and up to *c.* 1 km offshore. Unlike Crested terns, they rarely foraged over very shallow water; at low tide when Crested terns were fishing over the barely submerged reef flats, Black-naped terns flew past them to feed beyond the reef. This division of feeding area by water depth was particularly obvious at Passe Houreau, separating Middle and South Islands, where both species fed frequently on the falling tide. Black-naped terns fished in the deeper water of the central channel and adjacent areas of coral heads, while Crested terns foraged over the surrounding shallow flats covered by the sea grasses *Thalassia* and *Cymodocea.* An uncommon behaviour pattern among Black-naped terns, seen only around mid-tide along the edges of the channels, involved individuals perching on rocky overhangs from which they would repeatedly dip the metre or so to the water surface and then return to their perch; even at close range no prey could be seen, but possibly they were obtaining small items swept past by the tide.

Fairy tern

Distribution and numbers

Breeding pairs were scattered widely through the mangrove areas surrounding the lagoon and on islands within it, although none was found along the southern lagoon shore. Smaller numbers bred along the oceanic coast of Polymnie and Middle Islands, and along the channel (Gionnet) separating them, as well as on the Passe Femme islets at the western end of the lagoon. The main nesting habitat of mangrove was so difficult to census that the population estimate of 750 birds given by Diamond (1971*a*) is probably accurate only to an order of magnitude.

Breeding cycle

All 28 recorded breeding attempts refer to eggs laid between early September and early April (Fig. 3), and there was no indication that breeding might have occurred outside this period. M. E. Gillham (*in litt.*) found 'eggs and large young' in February and March 1970. Clutch size was invariably one. Breeding sites were usually on trees, less commonly on bare ground; no attempt at nest construction was made in either situation. Most tree sites were in mangroves, on a horizontal branch or projection from the trunk, in a convenient crevice (often a knot hole), or on the slight fork formed by two twigs crossing one another. All sites were well below the canopy and often directly above water. Occasional pairs nested in *Casuarina* trees and one incubating bird was found on the horizontal branch of a *Sideroxylon* tree. Three out of five recorded ground nests were on the flat rock surface of small islets, a situation identical to that favoured by Black-naped terns, and the other two on rock ledges above water. Nesting success was not measured but was clearly low.

Moult

None of seven incubating adults examined between September 1967 and March 1968 was moulting any primaries. However, of five adults of uncertain breeding status examined at the end of the breeding season in late April 1969, four were in active primary moult and the fifth had primaries 4 and 8 in its right wing, and 5 and 9 in its left, newly grown. In two individuals, two waves of primary moult were apparently proceeding simultaneously. Ashmole (1968) also found that Fairy terns tend to cease primary moult during breeding but then carry on from the same points subsequently in a continual stepwise moult.

Feeding

Our few records of feeding were mainly of birds which joined large mixed-species flocks feeding in deep water beyond the reef edge, but individuals also fed in the lagoon and along the reef edge in similar fashion to Black-naped terns. Most foraging must be undertaken out of sight of land.

Brown noddy

Distribution and numbers

Brown noddies at Aldabra nested colonially on many of the lagoon islets. The biggest reliably documented colony, on an islet at Coffee Camp in January 1974, held *c.* 600 nests with eggs and young (S. Hnatiuk, *in litt.*). The larger colonies were always found on type 3b islets, but smaller colonies could be found on islets of all structures from type 2 to type 5. Islets used for nesting tended to be sparsely vegetated: average numbers of plant species on type 2 and type 3a islets were 2·2 and 4·6, respectively, but islets of these types on which Brown noddies nested between 1967 and 1969 averaged zero and 1·3 plant species, respectively. This paucity of plant life is at least partly caused by the Brown noddies, whose colonies may have pronounced effects on vegetation structure and composition (Gillham, 1977).

Some Brown noddies roosted on nesting islets when not breeding, but most roosted elsewhere,

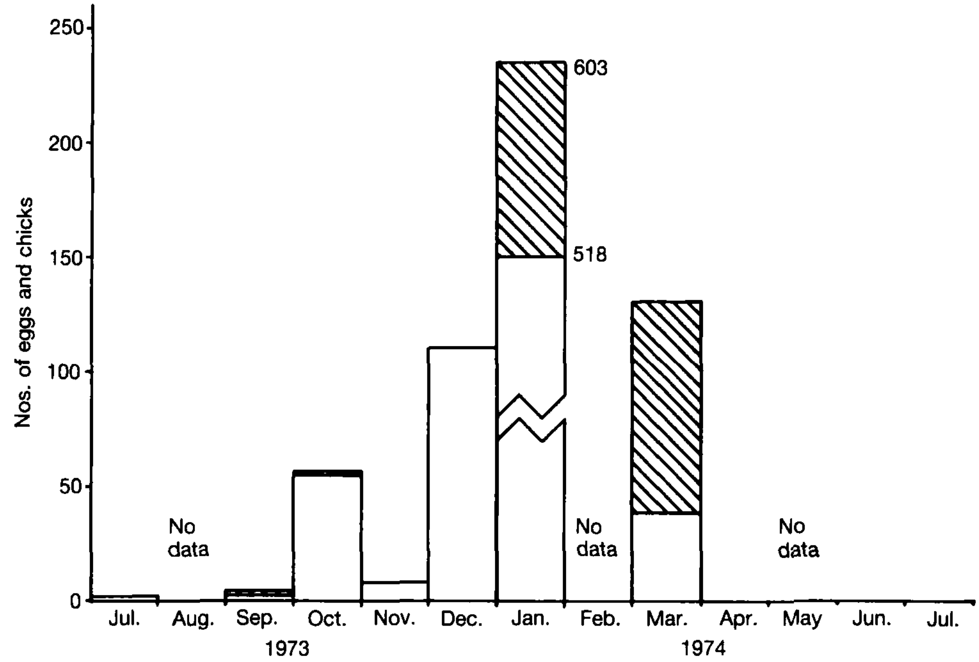

FIG. 5. Recorded breeding by Brown noddies on Aldabra between July 1973 and July 1974 (data from S. Hnatiuk, *in litt.*). Unshaded (□) = eggs; shaded (▨) = chicks.

especially on *Pemphis acidula* bushes along the Polymnie lagoon coast, around Passe Gionnet, in the southern parts of the West Channels, and on several islets around Île aux Cedres and Île Michel. Smaller numbers of birds roosted in mangroves. Diamond (1971*a*) estimated a total population of 3,500 birds, based on roost and nest counts; this is best regarded as a minimum figure as some birds were inevitably missed.

Breeding cycle

The first evidence of breeding on Aldabra was obtained by W. L. Abbott, who found large numbers of Brown noddies nesting between September and December 1892 (Ridgway, 1895). No further records are available until the late 1960s. During a brief visit in late February and early March 1967, Beamish (1970: 95) found 40-50 nests with eggs or chicks in the Coffee Camp area. We found few eggs between September and November 1967, but much larger numbers, *c.* 800 in all, in four main colonies (islets 4, 7, 8 and 10 in Appendix I) and other minor ones between early December 1967 and early March 1968. In late March and early April 1969, there were nearly 100 eggs, over 100 chicks, and many fledged juveniles spread through a number of colonies, indicating laying from at least December 1968. However, we recorded no further laying between mid-April and mid-September 1969. Gillham (1977) observed breeding during her stay on Aldabra between February and May 1970, but gave no details.

Detailed islet censuses in all but three months from July 1973 to July 1974 (S. Hnatiuk, *in litt.*) showed a major laying peak in December/January following a smaller one in October, and minimal laying between April and September (Fig. 5). Similar censuses we conducted between

December 1975 and January 1977 revealed laying peaks in November/December 1975, February 1976 and September/October 1976, with indications of another peak developing in January 1977 but very limited laying at other times (Fig. 6). Summarizing all available evidence, most laying occurs between September and March, with very little at other times. Considerable variation in the pattern of laying within different breeding seasons is at least partly a product of frequent mass losses of eggs and chicks and subsequent re-laying (see below).

Brown noddies constructed substantial nests, consisting largely of sea-grass, old mangrove leaves and twigs, and other debris collected from the ground or water surface. On most islets, nests were on open rock, often in slight depressions; on the high type 5 islets, nests could also be found on ledges and in cavities around the sides. On one islet, Table Ronde, where the woody herb *Achyranthes aspera* grew vigorously, Brown noddies nested both on the ground beneath it and also on the plants themselves (see also Gillham, 1977). In large colonies, nests averaged *c.* 50 cm apart.

All except 11 of 864 clutches examined between 1967 and 1969 contained one egg only; of the exceptions, 10 contained two eggs and one held three. Nine of these multiple clutches contained only one fresh egg, and should probably be viewed as successive single egg clutches where replacements had been laid alongside old eggs. However, in a small colony on Ros L'Eglise in March 1976 we found two nests which each contained two small chicks of the same age. It is therefore possible that a tiny percentage of Brown noddies on Aldabra lay two-egg clutches.

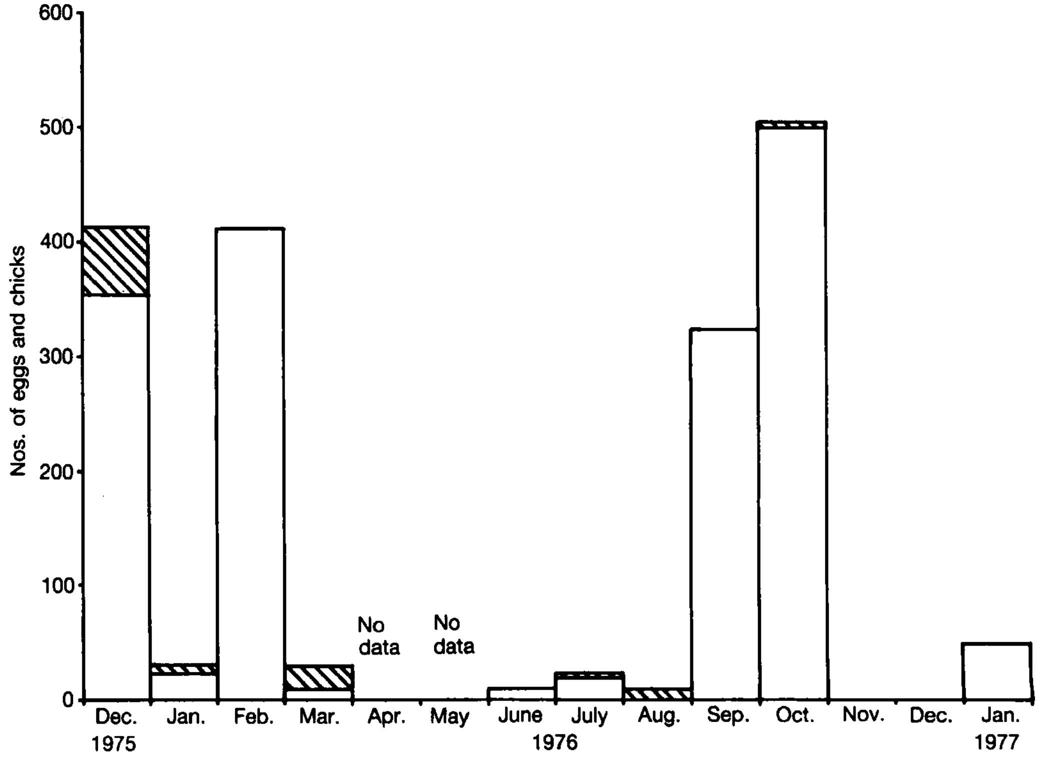

FIG. 6. Recorded breeding by Brown noddies on Aldabra between December 1975 and January 1977. Unshaded (□) = eggs; shaded (▨) = chicks.

Downy chicks were polymorphic in colour, varying from pale grey to almost black (cf. Dorward & Ashmole, 1963), and were guarded continually by one parent. Feeding frequency was estimated by weighing 11 chicks three times over a 24-hour period. During this time, seven were fed at least twice and the other four at least once, implying feeding intervals averaging considerably less than one day. Juveniles could be seen at nesting colonies for at least a month after fledging, by which time they had become indistinguishable in the field from adults.

Overall breeding success was low, with losses often extending to all eggs or chicks in a colony. This tendency for entire colonies to fail and then re-lay caused marked peaks and troughs in the numbers of eggs and chicks present at different times within the main breeding season (e.g. Fig. 6), although some colonies did include pairs differing greatly in the progress of their nesting cycle. Major causes of nesting failure can be grouped under four headings:

1. *High tides*: Nests on the very low-lying, type 2 islets west and south of Île Michel were constructed only a few centimetres above normal high water level. Exceptionally high tides tended to flood these islets, washing away the small colonies present.

2. *Weather*: Torrential rainfalls (> 100 mm within 24 h), with accompanying wind squalls, which occurred between 9 and 11 January 1976 and on 10 March 1976, caused the almost total destruction of successive breeding attempts by large colonies of Brown noddies at Coffee Camp and Mentor (Fig. 6). A census at both sites on 17 January revealed the presence of large numbers of intact, abandoned eggs and a few dead, uneaten chicks; a similar census on 17 March again revealed numerous abandoned eggs, many of which contained chicks which had died in the process of hatching. Assuming an incubation period of 32–35 days (Ridley & Percy, 1958), this indicates synchronized re-laying at both colonies about one month after the initial loss; this corresponds well with documented re-laying periods for this species (Ridley & Percy, 1958). The Coffee Camp and Mentor breeding sites were both flat, largely unvegetated islets, situated well away from the lagoon shore. A small colony on Ros L'Eglise, well protected on three sides by tall mangrove forests, survived the March storm essentially intact, suggesting that the exposed situation of the other colonies was an important contributory factor in their destruction.

3. *Predation*: The main predators noted were Pied crows *Corvus albus*, which have a population of *c.* 75 individuals on Aldabra (Benson & Penny, 1971, pers. obs.). Most evidence for this was deduced from the characteristic signs of numerous broken eggs and occasional remains of partially consumed chicks and adults at Brown noddy breeding sites, and confirmed by infrequent direct observations of predation. Between 1967 and 1969, attacks by Pied crows were limited to a few small colonies along the lagoon coast of Middle Island, but in 1975 and 1976 they occurred on such a scale that all observed breeding attempts by Brown noddies in the north-east sector of the lagoon (islets 7, 8, 9 and 10 in Appendix I) ended in total failure. These attacks appeared to be largely the work of a few 'specialist' Pied crows whose area of activity was centred on the east end of Middle Island, and predation was only rarely observed elsewhere.

The Grey heron *Ardea cinerea* may also be a predator; a large pellet found on Table Ronde and containing the remains of several Brown noddy chicks, including three ringed individuals, must have been produced by a bird considerably larger than a Pied crow. Until recently, human use of Brown noddy eggs for food also occurred (*e.g.* Beamish, 1970: 96), but this custom ceased with the opening of the Research Station in 1971.

4. *Unknown causes*: Colonies occasionally disappeared between censuses in inexplicable fashion. The most striking example was at Coffee Camp in 1976: on 23 October a colony of over 300 pairs on eggs was present, but by 20 November it had disappeared without trace, despite

calm weather throughout the intervening period. Another colony on Mentor also failed over the same period, but here the characteristic signs of Pied crow predation were present. The Coffee Camp islets are too high to be washed over by any tide, and it is difficult to envisage another cause of failure which would obliterate all evidence of its action.

Moult

Adults checked for primary moult between 1967 and 1969 showed several unusual features (Fig. 7). First, primary moult began in many individuals while they were incubating eggs. Incubating birds handled in late December 1967 and early January 1968 were all in fresh plumage, but by late January and early February some had initiated primary moult, and by April this moult was well under way. Secondly, birds caught in roosts throughout the year were always in more advanced stages of primary moult than any nesting individual caught. Thirdly, all nesting birds had only one primary per wing growing at any time, but most roosting birds had two growing simultaneously (mean = 1·7, n = 22), indicating more rapid moult among individuals that were presumably not breeding. Fourthly, whereas most birds replaced their primaries in an ordered descendent sequence, two individuals had two primaries growing simultaneously at different points in the same wing. The conclusion that flight feather moult and breeding proceed independently among Brown noddies (Glutz von Blotzheim & Bauer, 1982) clearly does not cover the complexities of the situation on Aldabra.

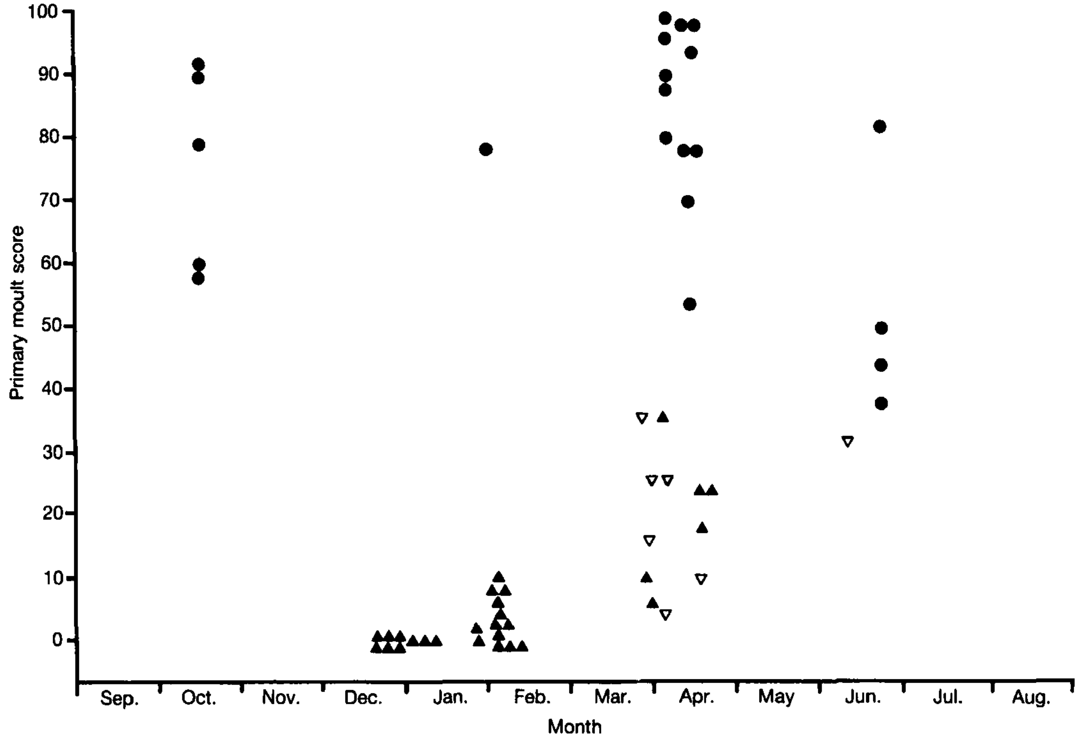

FIG. 7. Primary moult scores of Brown noddies on Aldabra. ▲ = incubating birds; ▽ = birds with chicks; ● = roosting birds. Data collected between October 1967 and February 1968, and from March to June 1969.

Feeding

Brown noddies were never seen to feed in the lagoon, although they often picked nest material off the water there. Much of their foraging probably occurred well out to sea, but they could on occasion also be seen feeding just seaward of the reef edge. At such times, they usually formed part of large mixed-species flocks with frigatebirds *Fregata* spp., Red-footed boobies *Sula sula* and, less commonly, Sooty, Black-naped and Fairy terns, all taking advantage of concentrations of prey driven to the surface by schools of large predatory fish. Watches at the channels revealed conspicuous peaks of movement out of the lagoon at dawn and into it at dusk, suggesting that Brown noddies fed mostly by day. The observations of feeding flocks, short inter-feed intervals of chicks, and evidence that most birds spend the night hours ashore, all support the notion that most feeding is conducted within a few tens of kilometres of Aldabra.

Discussion

Distribution and abundance in relation to foraging ecology

The islands of the Seychelles fall naturally into four geographical groups (Fig. 8): Central Seychelles, on the Seychelles Bank (mainly high granitic islands, but including coralline Bird and

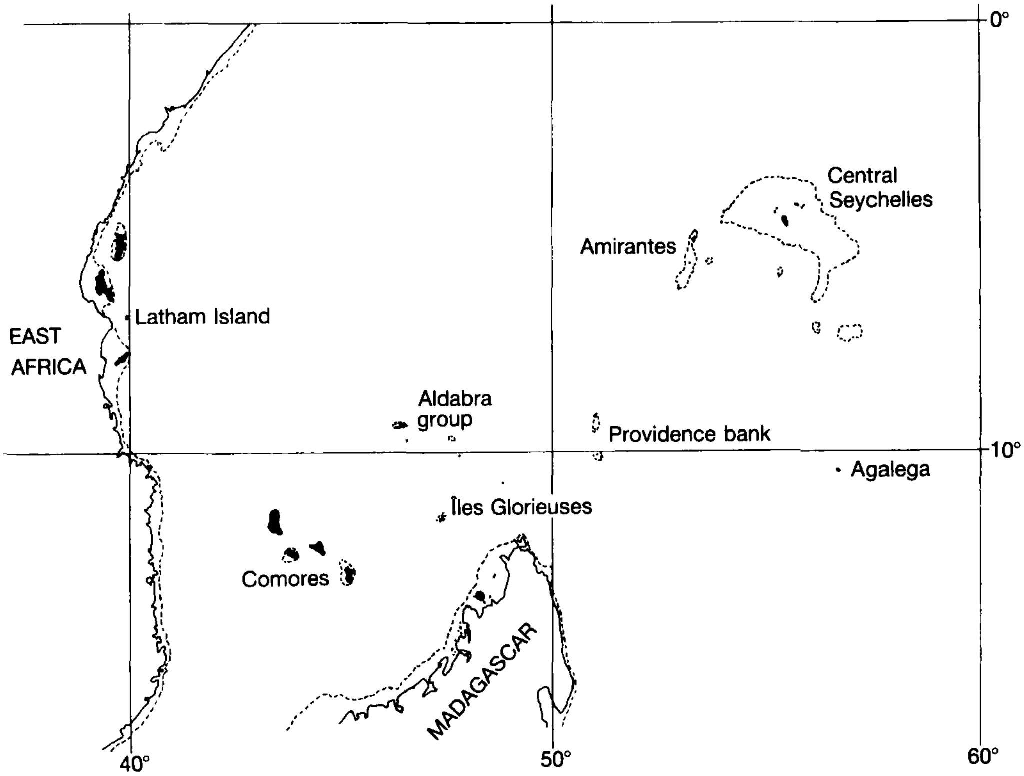

FIG. 8. Map of the Seychelles and adjacent regions. Dotted areas = shallow (< 200 m deep) submarine banks (source = General Bathymetric Chart of the Oceans, map 5·09, 1982. Ottawa: Canadian Hydrographic Service).

Denis); the coralline Amirantes; islands of the Providence Bank, including the large atoll of Farquhar (all low-lying and coralline except for the raised limestone island of St. Pierre); and the Aldabra group of raised limestone islands including Aldabra itself, Assumption, Astove and Cosmoledo. Nine species of tern are known to breed among these islands: the five species on Aldabra, plus Bridled *Sterna anaethetus* and Sooty tern, which both nest elsewhere in the Aldabra group, and Roseate tern *S. dougallii* and Black noddy *Anous stolidus*, which do not. Claims that Little terns *S. albifrons* breed in the Seychelles (Betts, 1940; Loustau-Lalanne, 1963) have not been substantiated; the species is a common migrant that winters throughout the region (Feare & Bourne, 1978; Prŷs-Jones, 1984) but hearsay breeding records probably stem from confusion with Black-naped terns which share the same local name 'dyaman' (Cheke, 1982).

Table II summarizes the known breeding distribution and abundance of terns in the Seychelles. Data from the smaller or outlying islands are often inadequate; to reflect this we give population estimates only to orders of magnitude. In addition, massive human interference over the last two hundred years has undoubtedly altered population sizes and distributions (Feare, 1976*a*, 1978; Prŷs-Jones, Prŷs-Jones & Lawley, 1981). These limitations to the data are important, but are unlikely to bias them in relation to the natural factors which we suggest have shaped current patterns of distribution and abundance.

In Table II, we further classify each species according to its foraging range during the breeding period, using our own data and published records from the region. Most species are easily

TABLE II

Distribution, abundance and foraging range of terns breeding in the Seychelles

		Population size			
Species	Feeding range	Central Seychelles (*c*.4° S; 55° E)	Amirantes (*c*.6° S; 53° E)	Providence Bank area (*c*.10° S; 51° E)	Aldabra group (*c*.10° S; 47° E)
Caspian tern	R				10^1
Crested tern	R		$10^1/10^2$	$10^1/10^2$	10^2
Black-naped tern	I/R		+	+	10^2
Bridled tern	I	10^3	+	+	+
Roseate tern	I	10^4	10^2	+	
Black noddy	I(O)	10^5	10^2		
Fairy tern	I/O	10^4	+	+	$10^2/10^3$
Brown noddy	(I)O	$10^4/10^5$	10^4	$10^3/10^4$	10^3
Sooty tern	O	$10^5/10^6$	10^6	10^5	10^4
Total species breeding:		6	8	7	7

R = reef/lagoon (water < 5 m deep); I = inshore (within sight of land, but water > 5 m deep); O = offshore (out of sight of land).

Abundance data are given to order of magnitude categories (i.e. 10^0 = 1–9, 10^1 = 10–99, etc.); diagonal slashes indicate probable population size lies near the boundary between the two categories shown. + = breeding recorded, but no population estimate available.

Sources for evidence of breeding and population estimates:

1) Central Seychelles: Betts (1940), Brooke & Houston (1983), Dawson (1966), Diamond (1975*c*), Feare (1976*a*, 1979*a*), Ridley & Percy (1958), Warman (1979), Warman & Todd (1984).

2) Amirantes: Feare (1976*a*, 1979*b*), Gadow & Gardiner (1907), Parker (1970), Ridley & Percy (1958), Stoddart & Poore (1970*b*), Vesey-Fitzgerald (1941).

3) Providence Bank area: Farquhar (1900), Feare (1976*a*), Gadow & Gardiner (1907), Parker (1970), Stoddart (1967), Stoddart & Poore (1970*a*), Vesey-Fitzgerald (1941).

4) Aldabra group: Bayne *et al.* (1970*a*, 1970*b*), Parker (1970), Prŷs-Jones *et al.* (1981), Vesey-Fitzgerald (1941), present paper.

classified, but three are not. Black noddies feed closer to shore than Brown noddies (Bailey, 1968; Diamond, 1978, 1984), which often feed well away from land. Fairy terns are the most problematical; they are rarely seen foraging, being usually solitary at sea (Feare, 1981) and also feeding perhaps partly at night (Ashmole & Ashmole, 1967; Gill, 1967). Seychelles populations have usually been described as predominantly inshore feeders (Penny, 1974; Diamond, 1978; Feare, 1981), but we rarely saw them feeding close to Aldabra and suspect that their feeding range there is similar to that of the Brown noddy (*cf.* Bailey, 1968). On Cousin Island (Central Seychelles), the Fairy tern's diet was more diverse than that of any other tern, most resembling that of the White-tailed tropicbird *Phaethon lepturus* and, among the terns, the Brown noddy (Diamond, 1984). Other studies of Fairy terns in the Pacific (Ashmole & Ashmole, 1967; Harrison, Hida & Seki, 1983) confirm that this species is unusually flexible in its foraging habits.

Breeding distribution and abundance are clearly related to foraging range in two respects. First, the reef-feeding species do not breed in the Central Seychelles, and reach maximum diversity in the Aldabra group. Secondly, the species that forage further from land show the opposite trend: they are scarcest in the Aldabra group and most abundant in the Central Seychelles. The Amirantes and Providence Bank areas are intermediate in both respects. These two trends relate to the different marine environments of the island groups. The distribution of reef-feeding terns corresponds with the greater areas of reef and lagoon shallows around coralline islands, especially the large atoll of Aldabra. Consequent on its proximity to the Mozambique Channel, an average tide at Aldabra has over twice the range of one in the Central Seychelles (Farrow & Brander, 1971). The predominance of deeper-water feeders in the Central Seychelles corresponds with the presence of the huge Seychelles Bank (Diamond, 1979), where depths of 44–65 m extend for about 43,000 km^2 (Braithwaite, 1984). Such areas of shallow water (deeper than that used by reef-feeders, but much shallower than most of the ocean) are not found within the Aldabra group (Fig. 8), whose islands are the tips of sea-mounts around which the sea floor drops to oceanic depths within a couple of kilometres of the coast (Diamond, 1979). The Amirantes and Providence Bank areas are intermediate in these environmental features, just as they are in their tern communities. Sooty terns feed over the deepest oceanic waters as well as over banks and so are abundant throughout the region.

The submarine banks and their associated upwelling currents (Piton, 1976) provide richer feeding grounds than the deep ocean, which is relatively infertile by comparison (Gill, 1967). The banks attract concentrations of tuna and other predatory fish (Sund, Blackburn & Williams, 1981), which drive smaller fish to the surface where seabirds can reach them. Discussing the seabirds breeding at Christmas Island (Pacific), Ashmole & Ashmole (1967: 58) pointed out that '. . . probably all the tern species . . . are dependent on the presence of marine predators such as tunas to make potential prey available at the surface.' The presence of large submarine banks should therefore greatly increase the abundance and diversity of seabirds breeding in the local area.

Breeding seasonality

Bailey's (1974) summary of seabird breeding seasons in the western Indian Ocean lacks analysis at the species level and requires revision in the light of more recent work, whereas Feare's (1981) review refers only to the Central Seychelles. Here we summarize the breeding seasons of Seychelles terns as far as the data allow us. Their quality is uneven and, though we have discarded information given without source or not clearly derived from personal observation, difficulties remain. First, descriptions often refer only to 'breeding'; since the breeding period of an individual tropical tern can extend for several months, such records allow seasonality to be assessed only roughly. Secondly, few islands have been visited either in enough months of the year, or in enough different years, to be sure of the months when laying normally occurs, or of the periodicity of successive breeding peaks; this problem is particularly acute at Providence Bank. Thirdly, eggs and young of seabirds in the Seychelles have traditionally been taken for food or bait; this can not only distort the breeding patterns recorded on casual visits, but might potentially shift the breeding season from its 'natural' timing if sufficiently regular, heavy and long-lasting (Moreau, 1950; Britton & Brown, 1974).

Caspian terns nest in the region only in the Aldabra group (which is probably their only oceanic breeding site world-wide), where the well-defined laying season is similar to that in northern Madagascar (Milon, 1950; Milon, Petter & Randrianosolo, 1973). The other strictly shallow-water feeder, the Crested tern, has two laying periods each year at Aldabra, and fragmentary evidence of eggs in July and November in the Amirantes (Vesey-Fitzgerald, 1941; Feare, 1979*b*) suggests that this regime may be typical of its whole Seychelles range. In northern Madagascar, Crested terns begin to lay in April (Milon, 1950), whereas at Latham Island (Fig. 8), eggs have been recorded in October and November (Gerhart & Turner, 1978). Aldabra may thus form an interface between populations having breeding peaks about six months apart. Such a situation would parallel that in Australia, where Crested terns breed between September and December in the east and south, between March and June in the north, and during both periods in the west (Serventy, Serventy & Warham, 1971; Dunlop, 1985).

The other three species which breed at Aldabra have very different breeding regimes elsewhere in the Seychelles. Sparse data on Black-naped terns from Providence Bank and the Amirantes suggest laying there between July and November (Gadow & Gardiner, 1907; Vesey-Fitzgerald, 1941; Ridley & Percy, 1958), not January to April as on Aldabra. Brown noddies breed mainly from March to October in Central Seychelles (Feare, 1981; Diamond, 1984; Warman & Todd, 1984), in the Amirantes (Ridley & Percy, 1958; Newman, 1965; Bourne, 1966; Bailey, 1968), and probably also on Providence Bank (Farquhar, 1900; Parker, 1970; Stoddart & Poore, 1970*a*). This regime contrasts markedly with that on Aldabra, where laying is concentrated between September and March. Fairy terns also lay at this time on Aldabra, whereas in Central Seychelles they breed throughout the year, having peaks during the south-east monsoon in some years (Feare, 1979*a*, 1981; Diamond, 1984) but during the north-west monsoon in others (Bathe, 1982; Wilson, 1982). There is unfortunately no reliable information on Fairy tern breeding seasonality for either the Amirantes or Providence Bank.

These results indicate that those terns which feed beyond the reef edge breed during the north-west monsoon at Aldabra, but largely or entirely in the other half of the year elsewhere in the Seychelles. Roseate terns and Black noddies, which do not breed in the Aldabra group, also forage beyond the reef and they, too, breed during the south-east monsoon throughout their Seychelles range: Roseates between June and August in the Amirantes and Providence Bank (Farquhar, 1900; Feare, 1979*b*), and starting about a month earlier in Central Seychelles (Vesey-Fitzgerald, 1941; Ridley & Percy, 1958; Dawson, 1966; Warman, 1979); Black noddies mainly between March and October in Central Seychelles (Feare, 1981; Brooke & Houston, 1983; Diamond, 1984; Warman & Todd, 1984), and probably over the same period in the Amirantes, though the records here do not span the whole year (Ridley & Percy, 1958; Stoddart & Poore, 1970*b*).

Both Bridled and Sooty terns nest within the Aldabra group, although not on Aldabra, but their breeding seasons there are not recorded. Bridled terns have an apparently unique breeding cycle at the only colony in Seychelles that has been studied. On Cousin Island, in Central Seychelles, the colony laid three times in the two years 1973-4 (Diamond, 1976); earlier casual records (Newman, 1965; Dawson, 1966; Penny, 1974) and subsequent continuous records (Diamond, 1980 and unpubl.), confirm that this eight-month cycle is normal and has continued for over 20 successive breeding 'seasons'. Enormous and economically important colonies of Sooty terns in the central Seychelles and Amirantes have a highly synchronous annual laying season in June and July (Ridley & Percy, 1958; Feare, 1976*a*, *b*), and colonies on Providence Bank appear to breed at a similar time (Farquhar, 1900; Stoddart & Poore, 1970*a*; Feare, 1976*a*). However, on Îles Glorieuses, 250 km south of Aldabra (Fig. 8), there are records of large-scale laying in January/February, March/April and August/September in different years (Benson, Beamish, Jouanin, Salvan & Watson, 1975). Sub-annual breeding cycles are well documented for Sooty tern populations in the Atlantic and Pacific (Ashmole, 1965) and, whatever the precise regime may be on Îles Glorieuses, it is clearly different from any yet recorded in the Seychelles.

An explanation for differences in tern breeding seasonality in the Aldabra/Îles Glorieuses region relative to the rest of the Seychelles is suggested by the seasonal movements of oceanic currents and the associated migrations of the tuna that make prey available to seabirds. Piton & Magnier (1975) showed that the boundary between the South Equatorial Current and the Equatorial Counter-current lies at 6-7 °S (the latitude of Central Seychelles and the Amirantes) during the austral winter, but shifts south to 9-10 °S (the latitude of Aldabra) during the southern summer. Boundaries between currents often generate oceanic 'fronts' where plankton is abundant and tuna and seabirds congregate to feed (Brown, 1980; Sund *et al.*, 1981), and this appears to be true of the zone of divergence between these two Indian Ocean currents (Piton & Magnier, 1975). Peak catches of tuna in the region are made at this boundary and shift seasonally with it (Uda & Nakamura, 1973). Thus Piton (1976) recorded large concentrations both of surface-feeding tuna and seabirds along the edges of the Seychelles and Amirantes Banks in May and June. Conversely, in the Aldabra region, the daily rate of sighting tuna, and the daily weight of the tuna catch, were each over twice as high from November to March as between April and October (Stequert, Marcille & Piton, 1975).

In conclusion, we consider that the seasonal latitudinal shift in the divergence zone between the South Equatorial Current and the Equatorial Counter-current, acting through associated seasonal shifts in prey species and game-fish abundance, may contribute importantly towards the observed tendency for terns which forage beyond the reef edge to breed during the south-east monsoon in the Central Seychelles and Amirantes but during the north-west monsoon in the Aldabra region. Available data from Providence Bank, lying at the same latitude as the Aldabra group, do not conform with this interpretation, but lack of published observations during the north-west monsoon highlights the need for closer study before any definitive conclusions can be reached. Finally, it may be noted that the documented contrast in tern breeding seasonality between the Aldabra area and the Central Seychelles is paralleled by striking differences in the breeding seasonality of their landbirds (Prŷs-Jones & Diamond, 1984), although the causative factors are apparently distinct.

A.W.D. thanks Cho-Cho, Jean-Baptiste Croiset, Celestine Laporte, Harry Stickley and Willem Tambara for field assistance, G. M. Dunnet and H. Milne for supervision and advice, and Aberdeen University and the Royal Society for financial support; his work was part of a PhD study at the Zoology Department of Aberdeen University. R.P.P-J. thanks Francis Alcindor, Harry Charles, Antonio Constance (Mazarin) and Marilyn Prŷs-Jones for field assistance, D. Snow and D. Stoddart for advice, and the Natural Environment

Research Council for financial support; during the course of the work he was attached to the British Museum (Natural History). Both authors are extremely grateful to the Royal Society for facilities provided on Aldabra, and to S. Hnatiuk for permission to make use of the considerable information she collected.

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