Studies in Avian Biology No. 8:73–83, 1983.

GROWTH STRATEGIES IN MARINE TERNS

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ABSTRACT.—Clutch size, brood size, and growth rates of chicks of *Sterna sandvicensis, S. hirundo, S. dougallii,* and *S. paradisea* were studied on Coquet Island, Northumberland, England (a temperate regime) and compared to *S. sumatrana, S. bergii, S. anaethetus,* and *Anous tenuirostris* on One Tree Island, Great Barrier Reef, Australia (a tropical regime). Species and regime-specific differences in these features are related to the general biology of the species, and especially to the role of courtship feeding, inshore or offshore feeding behavior, presence of predators, mobility of young, and the necessity of chicks to withstand periodic food shortage.

Marine terns are specialised larids primarily feeding on shoaling fish or squid, usually nesting colonially in areas free of ground predators. Despite their morphological similarity, they exhibit a number of different strategies when breeding. Tern chicks are semi-nidifugous and at hatching their legs are well-formed and the bodies are down-covered for mobility and thermo-regulation, respectively. Although they show precocial development resembling Galliformes and Anseriformes, they are altricial in that they continue to be fed by their parents up till and beyond fledging. The breeding adults are monogamous and share incubation and feeding duties. Some species nest in trees or cliffs whilst others nest on the ground amongst vegetation or on bare shingle, sand or rock. Various nest densities are adopted, with some species nesting in dispersed colonies with nest, eggs and chicks having cryptic coloration, whilst others nest in dense groups where although the eggs and chicks may appear cryptic amongst the droppings (Croze 1970) the area itself is conspicuous. Cullen (1960) has described the adaptations associated with such nesting with respect to north-temperate species and similar patterns are shown by subtropical and tropical species.

Besides nesting densities, marine terns exhibit variations in clutch size, subsequent brood size and growth rate of nestlings. It has been suggested that brood size is influenced by the food supply which is less abundant in the tropics and liable to fluctuations in offshore- or pelagic-feeding species and as a result these tend to have smaller broods and slower growth rates (Lack 1968). Most tropical and subtropical species have single egg clutches whether offshore or inshore feeders, whereas north-temperate species have larger clutches, with two or three egg clutches frequent in most inshore feeders. Brood size and growth of nestlings are interrelated, and theoretically a species could increase its brood size at the expense of growth and adopt a slower rate, or alternatively reduce its brood size and grow faster. In the tropical and subtropical species, it would appear that single chicks are growing at the maximum rate, determined by the available food and the adult's ability to collect it.

In recent years, there has been an increased focus on the growth rate of birds (see Ricklefs 1967, 1968, 1979a, 1979b; O'Connor 1978), with particular emphasis on the energetic constraints imposed by particular modes of reproduction. Ricklefs (1968) improved the method of measuring growth rate, by considering growth as a percentage of the asymptote, instead of considering a chick's growth from the time of hatching to fledging as used by Lack (1968). Also, it was no longer necessary to interpret chick growth as simply a compromise between chick mortality and the availability of food. Instead, growth rates could be related to adult weight, nestling period, food availability and brood size. Ricklefs (1979b) compared the growth rate of the Common Tern, *Sterna hirundo* with two other non-larid species, one precocial which grew slower and one altricial which grew faster. In the present study the growth rates of several different tern species are examined and the different strategies adopted by temperate and tropical species are compared.

STUDY AREAS

The study areas were confined to two islands: 1) *Coquet Island,* Northumberland, England (55°38'N, 1°37'W) has been described by Langham (1974) and is a breeding site for four species of terns in a north-temperate regime. It is about 2 km from the coast and on the continental shelf in water less than 50 m depth and surrounded by water of not more than 100 m deep. 2) *One Tree Island* (23°31'S, 152°06'E) situated at the southern end of the Great Barrier Reef, Australia, in the Capricorn-Bunker group. It is a coral rubble island with the southern edge consisting of a shelving reef, and the remainder of the island surrounded by a shallow lagoon. The island is close to waters exceeding 180 m. A full description of the island and its vegetation is given by Hulsman (1979) and Heatwole et al. (1981). The island has at least four, and sometimes six, species of terns nesting during the southern summer in a subtropical regime. Although in the subtropics, its period of productivity is spread over eight to nine months of the year (Hulsman 1980) and will be referred to as tropical in the following account as the tern species considered are all found breeding in tropical waters.

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TABLE 1
CLUTCH SIZE AND HATCHING SUCCESS

Species	Clutch size[a]	Hatching success (%)
Temperate		
Arctic Tern	1.82 ± 0.28	77.1
Common Tern	2.45 ± 0.29	75.5
Roseate Tern	1.49 ± 0.17	91.4
Sandwich Tern	1.23 ± 0.04	85.5[b]
Tropical		
Black-naped Tern	1.78 ± 0.39	31.4
Crested Tern	1.01 ± 0.01	69.4
Bridled Tern	1.00	91.2
White-capped Noddy	1.00	46.2

[a] ±1.96 standard error of $\bar{x}$.
[b] Unweighted mean: 73.9%.

TABLE 2
HATCHING AND FLEDGING SUCCESS IN RELATION TO CLUTCH SIZE AND BROOD SIZE

Species	Clutch size	Hatching success (%)	Brood size	Fledging success (%)
Arctic Tern	1	52	1	93
	2	74	2	76
	3	83	3	0
Common Tern	1	41	1	69
	2	67	2	74
	3	76	3	67
Roseate Tern	1	86	1	99
	2	92	2	90
Sandwich Tern	1	57	1	90
	2	70	2	77
Black-naped Tern	1	16	1	25
	2	34	2	67
Crested Tern	1	99	1	85
	2	<1	2	0

METHODS

In both areas, chicks being studied were weighed close to hatching and marked with monel bands soon after so that individual growth rates could be be measured. In this study, growth was measured by weight to the nearest gram using either a pesola spring balance or a torsion pan balance placed in a blind to avoid disturbance by wind. Wing growth was measured after the primaries had sprouted, using a wing-stop rule to measure the longest primary from the carpal joint to the nearest mm. The bill length was measured from the base of the cere to the tip, using vernier calipers to the nearest 0.1 mm. Only growth by weight is considered in this paper.

In those species that nested in a dispersed manner, the nests were marked and the chicks either collected in a partitioned box for weighing and measuring, or weighed on the spot, before returning them to their individual refuges. In dense nesting species, enclosures were sometimes set up to enable the same individuals to be weighed and measured regularly. In some cases, enclosures led to injury or deformity of the bill and these measurements were discounted. Enclosures were removed prior to fledging or during adverse weather conditions so as not to influence chick mortality.

RESULTS

The terns nesting on Coquet Island include the Common Tern, Sandwich Tern, *Sterna sandvicensis,* Roseate Tern, *S. dougallii* and Arctic Tern, *S. paradisaea.* Their general breeding biology in this area with reference to clutch size variation and breeding success has been described (Langham 1974). The growth and survival in Common Tern chicks of different brood sizes have been compared (Langham 1972) and detailed development of this species has been monitored (Ricklefs 1979b). In the following results, the information from Coquet Island is based on three years, whilst the tropical species described: Black-naped Tern, *S. sumatrana,* Crested Tern, *S. bergii,* Bridled Tern, *S. anaethetus,* and the White-capped Noddy, *Anous tenuirostris* are mainly based on one year's results. Only the last species has been the subject of a detailed study of its breeding biology in the tropical Atlantic (Ashmole 1962).

CLUTCH SIZE

Clutch size and hatching success in the different species are given in Table 1. Apart from the Black-naped Tern, most tropical species have a single egg clutch. In temperate species, the clutch sizes are larger, particularly in the Common Tern, with a declining average clutch size in the order Arctic Tern, Roseate Tern, Sandwich Tern. Other tropical species [the Sooty Tern, *Sterna fuscata* (Ashmole 1963a, Robertson 1964), Brown Noddy, *Anous stolidus* (Woodward 1972) and Fairy Tern, *Gygis alba* (Dorward 1963)] lay single eggs. The small clutch of tropical species may be viewed as a result of competition around the colony during the breeding season where there is no marked seasonal fluctuation in food in tropical waters (Ashmole 1963b). The lack of fluctuation in productivity made it possible for adults loosing their eggs early in incubation to re-lay in less than annual periods, either nine months on Ascension (Ashmole 1963a) or six months on Christmas Island, Pacific Ocean (Schreiber and Ashmole 1970).

BROOD SIZE

All species experienced a relatively high hatching success, apart from the Black-naped Tern whose loose colonies along the foreshore were

TABLE 3
GROWTH RATE, WEIGHT, AND BROOD SIZE

Species		*K* (growth constant)	Asymptotic weight (g)	Adult weight (g)	Brood size
Arctic Tern		0.302	115	110	1/2
Common Tern	B/1	0.311	126	126	1
	B/2	0.270	124	126	2
	B/3	0.226 to 0.449[a]	119	126	3
Roseate Tern		0.263	105	124	1/2
Sandwich Tern		0.232	189	230	1/2
Black-naped Tern		0.288	100	110	1/2
Crested Tern	(a)	0.107	279	350	1
	(b)	0.094	318	350	1
Bridled Tern		0.114	128.5	130	1
White-capped Noddy		0.152[b]	117	115	1
Brown Noddy[c]		0.153	160	159	1
Sooty Tern[d]		0.073	205	175	1

[a] $\bar{x} = 0.279$.
[b] Gompertz *a* = 1979/80, b = 1981/82.
[c] Dry Tortugas (Ricklefs 1978).
[d] Kure Atoll (Woodward 1972).

relatively vulnerable to predation by Silver Gulls, *Larus novaehollandae* or wading birds, despite camouflage. In 1979/80, most of the Black-naped Tern clutches were lost through high spring tides associated with strong winds. The Black-naped Tern was the only tropical species to have a number of broods of two chicks (Table 2). It is possible that single eggs in this species had a higher hatching success as some single eggs may represent deserted clutches before a complete clutch had been laid. Only chicks ringed at birth and subsequently seen weighing more than 50 g were deemed to have survived. Although a few Crested Terns hatched two chicks, there was no evidence to suggest they raised two.

Temperate species had brood sizes ranging from one to three (Table 2). The lower hatching success of single egg clutches was probably due to desertion before the clutch was complete, otherwise hatching success was relatively high. The subsequent brood sizes were in a similar proportion except that in the Arctic Tern broods of three were very rare and unsuccessful.

GROWTH RATE

The details of growth are shown in Table 3. Except for the White-capped Noddy, a logistic equation fitted the growth curves of each species. Values were derived from the asymptote adopting the method described by Ricklefs (1967). The growth curves based on these asymptotes were fitted to a logistic or Gompertz curve. Comparison of the t_{50} (or the time it takes to reach half the asymptotic weight) shows a close similarity between the temperate species and the Black-naped Tern (Table 4). It takes longer in the White-capped Noddy and Bridled Tern and longest in the Crested Tern. A similar resemblance is shown in the time taken to reach t_{90} between the Crested Tern and Bridled Tern. Although the Bridled Tern and Noddy reach 90% of their asymptotic weight at about 38 and 29 days, respectively, they do not fledge until about 58–60 and 51–53 days, respectively. In contrast, the Crested Tern, which takes about 38–40 days to reach 90% of its asymptotic weight, fledges at about the same time as it reaches its asymptotic weight. Earlier hatched chicks appeared to complete their growth quicker and were flying at about 35 days. The growth constants of the White-capped Noddy and the Brown Noddy, *Anous stolidus*, are almost identical, although the former had a closer fit to a Gompertz equation.

In the Common Tern there was sufficient information to compare the growth rates in different brood sizes (Table 5). Single chicks and chicks in broods of two showed similar growth rates although the growth constant was slightly lower in broods of two chicks (Table 3). Examination of the growth rates in broods of three chicks showed that the growth rates were similar in the first chick ($K = 0.256$) and the second chick ($K = 0.239$), but that third chicks showed a marked change in growth rate after 10 days (Fig. 1). The first part of the fitted curve gives a very low constant ($K = 0.145$) which indicates that the third chick experiences a shortage in food during that period. However, the second part of the fitted curve follows a different slope, giving a growth constant ($K = 0.312$) that is as high as single chick broods. Although the data on third chicks in broods of three were based on relatively few chicks (see Langham 1972), it suggests that if chicks survived the first 10 days they would attain a similar growth constant ($K = 0.250$) as that shown by first and second chicks over the whole period. However, these third chicks still appeared to fledge at a lower weight than first (83%) and second (95%) chicks which may be critical in post-fledging survival

DISCUSSION

Lack (1968) has said that the clutch size of birds corresponds to the maximum number of young that the parents can raise on average. Although terns are semi-nidifugous, acquiring mobility and the ability to thermo-regulate early in life, they are still fed by their parents as are altricial species. The variation in average clutch size between marine tern species nesting in the same locality presumably evolved to be the most productive. Pelagic species have reduced their clutch size to the minimum possible, one egg,

TABLE 4
SUMMARY OF TERN CHICK GROWTH STATISTICS

Species	Arctic	Common	Roseate	Sandwich	Black-naped	Crested[a]	Bridled	White-capped Noddy	Sooty
Clutch size	1.82	2.45	1.49	1.23	1.78	1.01	1.00	1.00	1.00
Incubation (days)	22	23	24	23	21	28–30	28–30	35	30
Fledging (days)	19	22	22	25+	24	35–41	58–60	51–53	60
Asymptotic weight (g)	115	128	105	189	100	279–318	128.5	117*	205
Adult weight (g)	110	126	124	230	110	350	130	115	175
Feeding zone	inshore	inshore	inshore	inshore	inshore	inshore	offshore	offshore	offshore
t_{10}–t_{90}	14.5	14.1	16.7	26.6	15.3	38–40	38.4	28.9[b]	—
t_{50}	7.5	7.6	7.3	7.8	8.2	16.4–19.6	14.8	10.6[b]	—

[a] 1979/80 and 1981/82 asymptotes, respectively.
[b] Gompertz.

TABLE 5
PERIOD TO ASYMPTOTE AND FLEDGING IN THE COMMON TERN

Brood size	Chick order	t_{10}/t_{90} (days)	Asymptotic period (days)	Fledging period (days)
1	1	14.1	19	19
2	1	17.1	20	24
	2	18.4	20	24
3	1	19.7	23	23
	2	16.9	17	24
	3	30.3/14.6[a]	18	24

[a] First 10 days/after 10 days.

where there is little variation in food abundance through the year. Inshore-feeders have an average clutch size which varies from one to three according to species. It is unlikely that egg production in the inshore feeders is limited by food, although early pair bonding and courtship feeding may be an important influence as demonstrated for the Common Tern (Nisbet 1973, 1977). In marine terns, eggs are normally between 15–20% of adult body weight (Table 6), and food required for egg production will depend on clutch size. In temperate species, and also in the Black-naped Tern and Crested Tern, fish are presented to females prior to egg-laying. In the Bridled Tern and White-capped Noddy, fish and other food items are carried in the crop (pelagic foraging making it uneconomical to return with one or few items carried in the bill), but courtship feeding by regurgitation has been observed in the Bridled Tern (Hulsman and Langham, in prep.).

Clutch size tends to be smaller in those inshore feeders that nest in dense groups: Sandwich Tern, Crested Tern, and Royal Tern (*Sterna maxima*). Although largest of the inshore feeders, their eggs still weigh less than 20% of adult body weight (*S. maxima* from Buckley and Buckley 1972). These species avoid aerial predation by sitting tight on their eggs, but their conspicuous guano-spattered colonies make them very susceptible if ground predators are present. Perhaps a small clutch is less wasteful should it prove necessary to desert the colony to avoid ground predators.

Clutch size determines the subsequent brood size and factors favouring a particular brood size such as feeding rate per chick may be the main selective force determining clutch size. Changing environmental conditions, especially those effecting food supply, may favour different brood sizes in some years, so that females of inshore-feeding species might lay one egg less or more than the mean. The variation in brood size be-

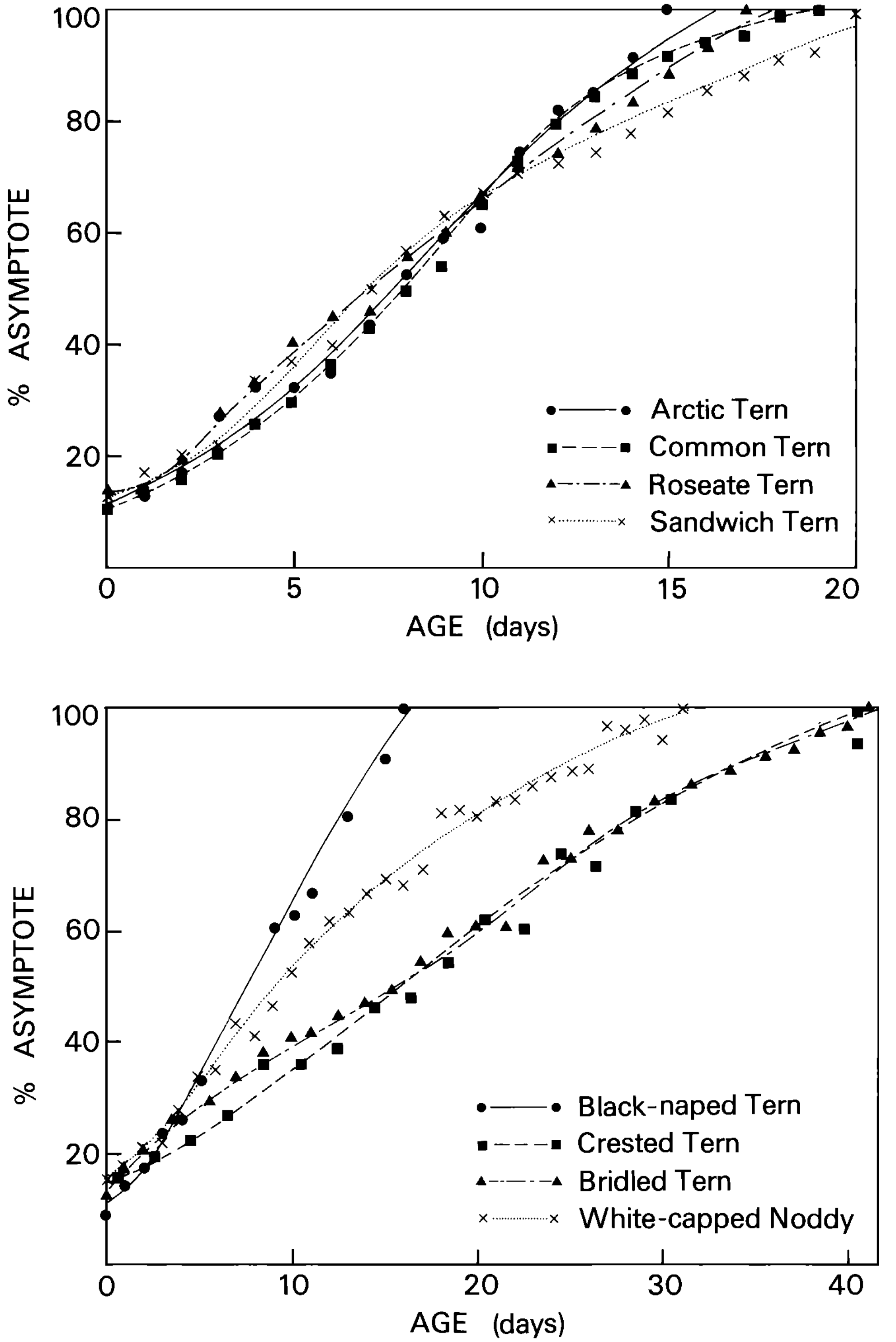

FIGURE 1. Tern chick growth curves as a percentage of asymptote.

TABLE 6
EGG WEIGHT IN RELATION TO BODY WEIGHT

Species	Egg weight (g)	Adult body weight ($\bar{x}$ g ± SD)	Egg weight/body weight (%)
Temperate			
Arctic Tern	19[a]	109 ± 1.30	17.4
Common Tern	20[a]	126 ± 1.82	15.9
Roseate Tern	20[a]	124 ± 2.08	16.1
Sandwich Tern	35[a]	229 ± 2.75	15.3
Tropical			
Black-naped Tern	–	110	–
Crested Tern	55	320 ± 350[b]	15.7–17.2
Bridled Tern	25	131 ± 1.80[b]	19.1
White-capped Noddy	23	114 ± 1.38[b]	20.2
Sooty Tern	34[c]	175[c]	19.4

[a] Lack 1968.
[b] Hulsman, pers. comm.
[c] Stonehouse 1963.

tween temperate nesting species in the same locality in the same season cannot be explained by chick mortality as they are exposed to the same environmental factors, including predators. The Common Tern and Sandwich Tern are both inshore feeders, yet the average brood size of the former is twice that of the latter. The growth constant in the Common Tern is greater in single chick broods, broods of two and three, with the exception of the first 10 days of the third chick, than in the single chick broods of the Sandwich Tern. The differences are not related to the greater adult weight (230 g) or asymptotic weight (189 g) of the Sandwich Tern, as the fitted slope is only steeper in the single chick broods of the Common Tern. In other brood sizes the fitted slope is almost identical with that found in the Sandwich Tern (Fig. 2). Also, the asymptote is reached at about 20 days in both species, with the Common Tern fledging at 22 days and the Sandwich Tern at about 25 days. The actual growth from hatching to asymptotic weight is about 5.65 g/day in the Common Tern and about 8.25 g/day in the Sandwich Tern. This means that with twice the brood size on average, the Common Tern will have collected about 37% more food than the Sandwich Tern, assuming that conversion rates are similar. In the Roseate Tern and Arctic Tern, with smaller brood sizes, the growth rates are about 4.6 g/day and 5.1 g/day, respectively.

Dunn (1979) gives comparative growth of temperate nesting species with K values of 0.300 and 0.258 for the Common Tern and Sandwich Tern, respectively. These values (derived from Ricklefs 1973, taken from Pearson 1968), are comparable to those made on Coquet Island, 28 km south of where Pearson made his observations. On Great Gull Island, North America, Common Terns had a lower constant (0.213) in 1967 and a higher one (0.241) in 1968, than that of the Sandwich Tern, asymptotes being reached earlier at 15 days, but fledging later at about 26 days at lower weight (LeCroy and Collins 1972). However, later studies in years with higher survival the results from Common Terns were more comparable (LeCroy and LeCroy 1974).

On Coquet Island, Sandwich Tern parents raised one and occasionally two chicks to one and a half times the weight of Common Tern chicks. Only broods of two Sandwich Tern chicks would have comparable daily increases in weight (16.50 g/day) with broods of three Common Tern chicks (16.95 g/day). Only in 1967, did these two brood sizes have a high success; in the two earlier years broods of one Sandwich Tern and broods of two Common Tern chicks were most frequent due to high mortality of 2nd and 3rd chicks, respectively (Langham 1972, 1974). In these two years, the daily weight increase of Sandwich Tern chick (8.25 g/day) was intermediate between single Common Tern chick (5.65 g/day) and that of a brood of two Common Tern chicks 11.30 g/day).

The other two temperate species considered, the Arctic Tern and Roseate Tern, appeared to feed mainly out to sea from the breeding colony (Langham 1968), but since this was still over the shallow water of the continental shelf, they were considered inshore-feeding species in contrast to the tropical pelagic-feeding terns. The growth constant is higher in the Arctic Tern with a slightly higher asymptote attained in 15 days. Although a few Arctic Terns lay three eggs, the commonest clutch size is two (76%) and most succeed in raising two chicks. The Roseate Tern lays equal numbers of one-egg and two-egg clutches, both with high success, and so half raise one chick and half raise two chicks. Given this dichotomy, one might expect all Roseate Terns to lay two eggs and have a slightly slower growth rate with a longer fledging period. Although in the three years studied the Roseate Tern enjoyed a high breeding success, it appeared more susceptible to climatic changes, probably because Coquet Island is near the northern extremity of its range (Langham 1974). The data on growth obtained by LeCroy and Collins (1972) is very similar, but the survival of chicks in broods of two was about half that in broods of one, although there appeared to be more two egg clutches. As in the Common Tern, the Roseates suffered from poor survival in 1967 (LeCroy, pers. comm.).

In the tropical species, only the Black-naped Tern had a growth rate similar to that shown by temperate tern species. The commonest clutch was two (78%) and the hatching and fledging successes (Table 2) are underestimates due to the difficulties experienced in locating eggs and chicks on the pebble-strewn beach. Its growth rate bears most resemblance to the Arctic Tern and Roseate Tern. It reaches its asymptotic weight in 16 days and fledges in about three weeks, with a daily weight gain of about 4.7 g/day.

The other three species show a much slower growth rate, including the Crested Tern which was mainly seen fishing in the surf zone near the reef edge, an inshore feeder. The situation on One Tree Island seems to be modified by the increase in Silver Gulls, partly associated with human occupation, as some of these are persistent predators of the Crested Tern, and to a lesser extent, Black-naped Tern eggs. In the case of the Crested Tern, certain gulls have become very adept at robbing adults returning to feed their chicks, and even attacking chicks, trying to force them to disgorge (Hulsman, 1976, pers. obs.). This persistent kleptoparasitism may have a significant effect on growth rate. Another factor is that the measurement of growth rate was made using one of the later subcolonies where conditions may have been less favourable. In this case, the asymptotic weight was not achieved until about 38 days, yet some chicks fledged as early as 35 days. In 1982, using the same asymptotic weight it was estimated the nine chicks, the total produced on One Tree Island, would attain this at 40 days, and were probably fledging at this age.

Although predominantly an inshore feeder, the Crested Tern normally lays one egg, a resemblance to tropical, offshore-feeding species. The other tropical species attain their asymptotic weight at a similar or shorter period than the Crested Tern, but the latter fledges much earlier, normally between 35–40 days. On One Tree Island, Bridled Terns and White-capped Noddies attained their asymptotic weights at about 38 and 29 days, respectively. Yet, the Bridled Tern fledged between 58 and 60 days and the noddy between 51 and 53 days. Ashmole (1962) gives a normal fledging age of about 45 days for the noddy but this may be delayed by shortage of food. Other tropical species feeding offshore have long fledging periods such as the Sooty Tern at about 60 days (Ashmole 1963a) and the Fairy Tern at about 83 days, on average (Dorward 1963). The growth of the two offshore species resemble the Sooty Tern when growth constant (K) is plotted against asymptotic weight in contrast to the other species studied (Figs. 2A,B).

In these slow growing tropical species, only one egg is laid which Lack (1968) thought was a result of sparser food and greater distances involved in fishing to feed young. However, it seems that energy requirements are not markedly affected by changes in growth rate where most energy is being required for maintenance with less than a third being devoted to growth (Ricklefs 1979a). Unlike the Common Tern, Ricklefs (1974, 1979b) found the total energy requirement of the Sooty Tern, a pelagic species with a slow-growing chick, reached a maximum early in growth and remained at that level until fledging. The prolonged period of growth occurs after the energy requirements have reached a maximum.

Ricklefs (1979a) speculates that mobility may be important in dense colonies of Sooty Terns where emphasis is on rapid development of legs followed by a slow growth rate of other body structures including flight feathers. Slower growth rate correlated with mobility might explain that found in Crested Terns as well as Sandwich Terns, in contrast to other inshore feeders, as chicks move out of the conspicuous nesting area soon after hatching. Although mobility is important in Bridled Terns, it is not required in the White-capped Noddy which stays put on its nest until fledging. A similar situation would seem to apply to Brown Noddies and Fairy Terns which are also sedentary until fledging, but have slow growth rates.

Another important aspect of a slow growth rate, is that the chick is less prone to starvation where food supply is liable to fluctuations. The advantage of slow growth rate and reduced metabolism (or torpidity) was mentioned for such species as the Swift (Lack 1956). It has been mentioned for the Sooty Tern on Ascension where some chicks were seen to survive for long periods with little food (Ashmole 1963a). In the present study, a period of cyclonic winds and heavy rain demonstrated that Bridled Tern chicks had a much higher survival than those of Crested Terns, even though the latter were near fledging. The chicks of the White-capped Noddies would prob-

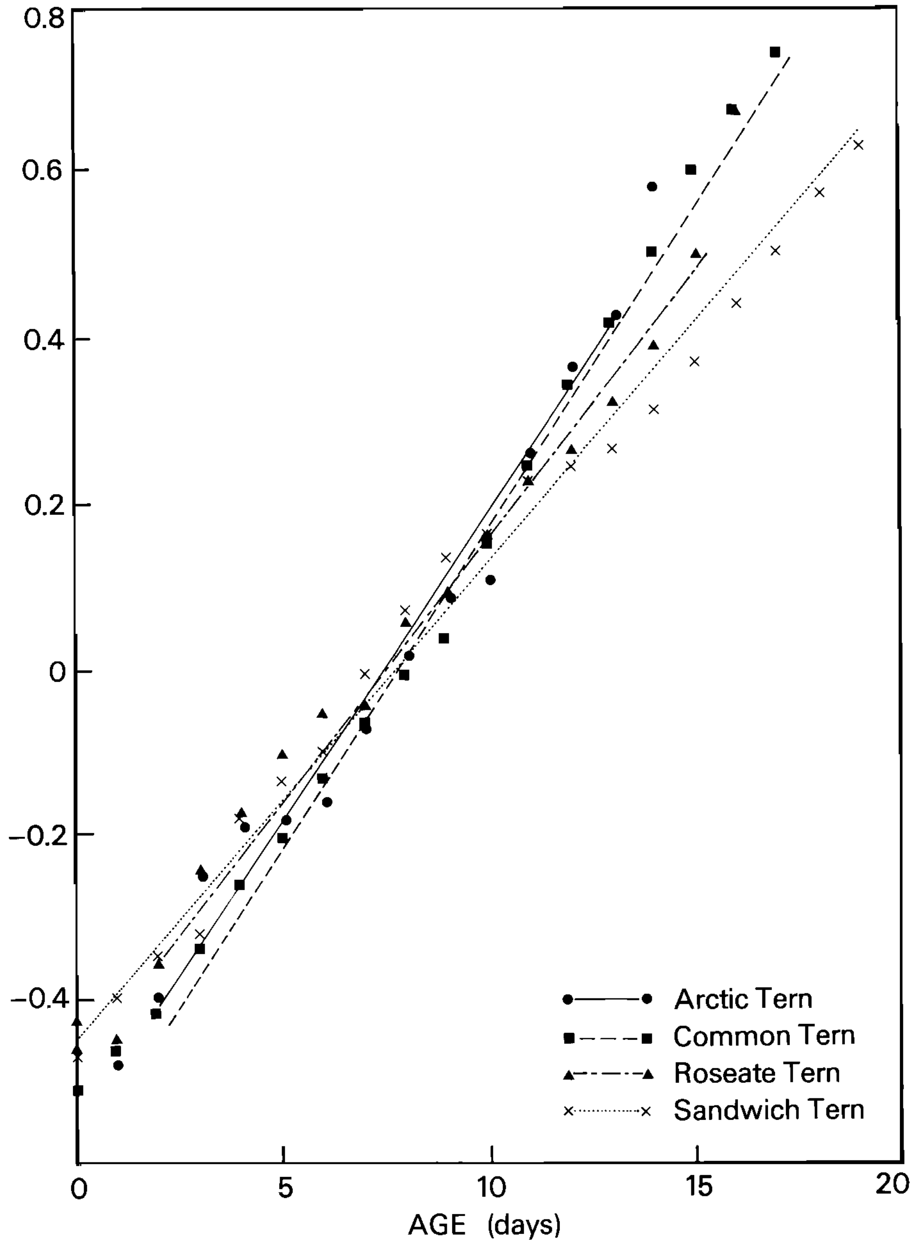

FIGURE 2A. Tern chick growth fitted to logistic or Gompertz curves.

ably have a similar resistance to fluctuating food supply, but the destruction of their nest sites by the cyclonic winds obscured this on One Tree Island. White et al. (1976) reported that Brown Noddies, *Anous stolidus* were unaffected by a storm, and young Sooty Tern chicks which were in more exposed situations died from the loss of insulation caused by the rain and wind, rather than starvation.

Semi-precocial development shown by seabirds such as terns means that parents are soon freed from brooding so that both can be involved in fishing. The chicks of many tropical species have a slower growth rate than temperate species,

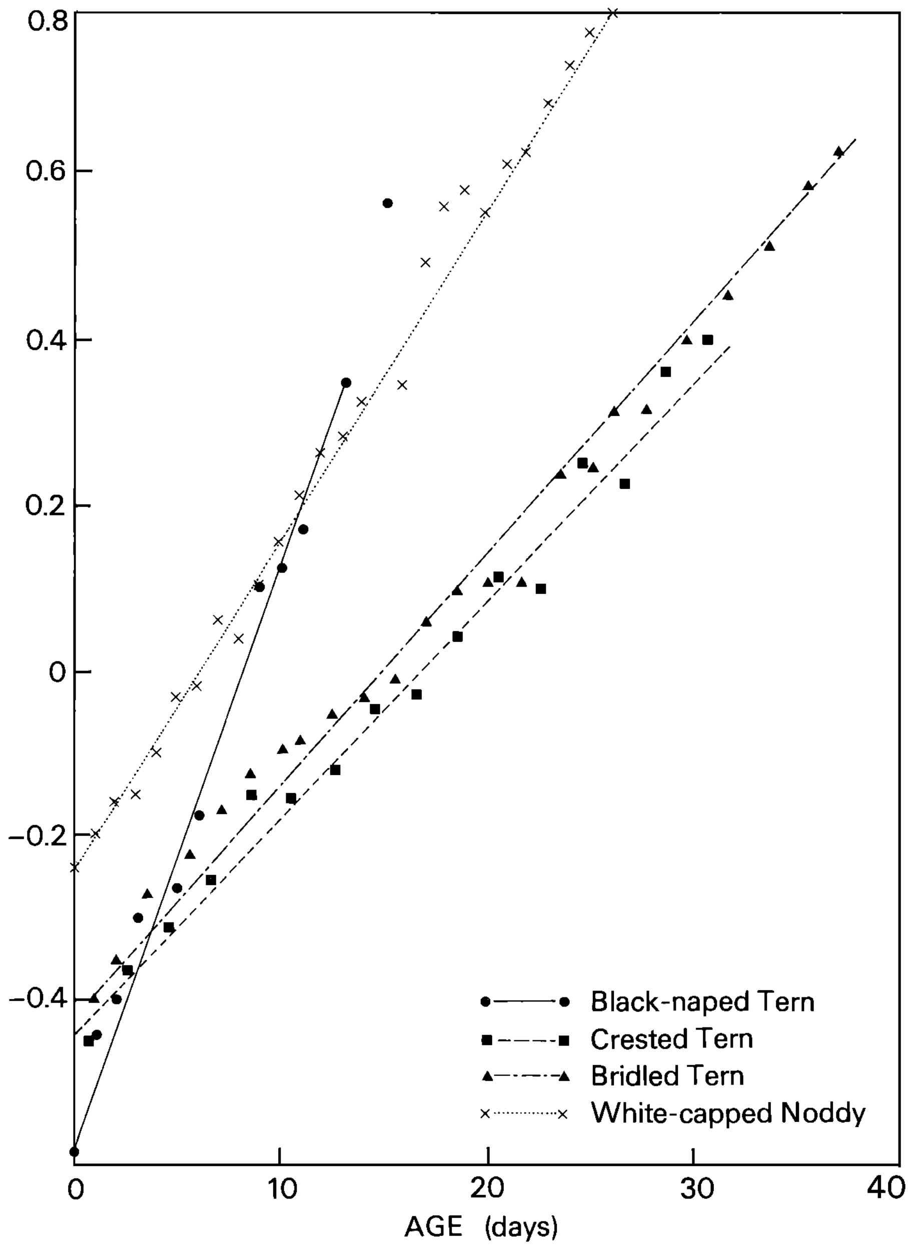

FIGURE 2B. Tern chick growth fitted to logistic or Gompertz curves.

as well as a smaller clutch size and subsequent brood size. These features suggest that predation has been relatively unimportant and that a slow growth rate for species laying a single egg is the only means of reducing food requirements still further (Ricklefs 1968). This is particularly important where food requires foraging over a wide area and is liable to fluctuations. The chicks of tern species rapidly acquire the ability to thermoregulate, and ground-nesting species have advanced development of the legs so that they can move away from the nest site to avoid intraspecific aggression, into cover to escape predators and food robbers, as well as sheltering from inclement weather. The subsequent long period to fledging shown by certain tropical species does not involve a marked increase in weight, since most energy requirements are required for maintenance. The latter part of development involves the growth of plumage, notably remiges and retrices, so that energy requirements remain fairly stable (Ricklefs 1979a). On One Tree Island, the growth rate of the tree-nesting and therefore stationary White-capped Noddy has a faster growth rate in terms of weight to attain asymptote than the Crested Tern or Bridled Tern. Common Noddies have a similar growth rate ($K = 0.153$) to reach asymptote shown by the White-capped Noddy (Ricklefs 1978), with a similar nest site, either a tree or cliff-ledge, involving little necessity for mobility until fledging.

The slower growth rate of offshore-feeding, tropical species is an adaptation to infrequent feeds when parents are required to search over wide areas of ocean where food maybe patchy and daylength short (Hulsman 1980). The Crested Tern has much more frequent feeds (Langham and Hulsman, in prep.) than Bridled Tern or White-capped Noddy, and the slow growth rate to asymptote of the former is accompanied by feather growth and other adult structures so that it can fledge soon after. Unlike the tropical offshore-feeding species, it is not capable of withstanding long periods without food, either because of dispersed food supply or prolonged bad weather, and in this respect resembles temperate marine tern species.

SUMMARY

The growth strategies adopted by marine terns in a temperate and a tropical regime were compared. Tern chicks are semi-nidifugous, being mobile and capable of thermo-regulation soon after hatching, but dependent on their parents for food. In England, the growth rates of Arctic, Common, Roseate and Sandwich Tern chicks were measured. In Australia, Black-naped, Crested and Bridled Terns and White-capped Noddy chicks were considered. The growth rates of all species, except the noddy, fitted a logistic curve. Temperate species lay one to three eggs and raise one to three chicks. The growth to asymptote is completed in all species in about 20 days, and temperate fledging a few days later taking longest in the Sandwich Tern. In the tropical species, the Black-naped Tern has a growth strategy resembling temperate species, with one or two chicks completing asymptotic growth in about 20 days and fledging occurring soon after. In contrast, the asymptotic growth of the young in the inshore-feeding Crested Tern resembled that of the offshore-feeding Bridled Tern, although the former fledges between 35–41 days and the latter at 58–60 days. The White-capped Noddy's single chick completed asymptotic growth in 29 days, but did not fledge until about 51–53 days.

The growth strategies employed are discussed in relation to clutch size and brood size, mobility, feeding rate, duration from asymptote till fledging and the ability to withstand periods of starvation caused by erratic food supply or bad weather.

ACKNOWLEDGMENTS

I am grateful to University of Sydney for use of its research station on One Tree Island, and to Angus and Allison Moore for their hospitality. Kees Hulsman helped in the collection of data. I thank Ralph Schreiber and Mary LeCroy for critical reading of this manuscript. This research was funded by the University of the South Pacific and the Royal Society.

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