

## The breeding of the Sooty tern *Sterna fuscata* in the Seychelles and the effects of experimental removal of its eggs

CHRISTOPHER J. FEARE\*

*University of Aberdeen, Culterty Field Station, Newburgh, Ellon, Aberdeenshire, Scotland*

*(Accepted 9 December 1975)*

*(With 18 figures in the text)*

In the Seychelles the eggs of the Sooty tern *Sterna fuscata* are collected for human consumption. A reduction in the number of Sooty terns breeding in exploited colonies has been attributed to over-exploitation of the eggs. However, the population decline has been over-estimated and factors other than exploitation have led to a reduction in the land area available to breeding colonies.

In the study colony, on Bird Island, egg laying was highly synchronous, and birds which laid at peak laying time had a higher reproductive success than those that laid early or late. The higher success of these birds was due to their being at the same stage of the reproductive cycle as their neighbours: this reduced losses of eggs to predators and losses of chicks due to pecking by adults and other chicks. Birds which laid late, which included young birds and birds which had lost their first egg and laid a replacement, were therefore penalized.

The ability to lay a replacement egg after loss of the first, was found experimentally to be much greater than previous estimates had suggested, and some individuals were induced to lay a third egg. Both the ability to relay and the success of replacement eggs declined seasonally. The laying of a replacement egg did not seem to place extra strain on the parents, and the lower weights of most replacements compared with first eggs was due to seasonal factors rather than to the inability of adults to produce a large second egg.

The food brought by the parents to the chicks consisted mainly of fish and squid, but frequent and abrupt changes in the species composition of the food suggested that food supplies were unpredictable. In 1973 chick growth was interrupted by two periods of food shortage, and although late hatched chicks experienced this food shortage early in their lives, starvation did not appear to be a major source of mortality.

The regulation currently in force in the Seychelles imposing a close season for egg collecting protects only late-laid eggs, and since these have a very low success rate and can contribute little to future generations, there is no biological foundation for continuing this restriction. Adult mortality and age at first breeding are not known for Seychelles Sooty tern populations, and exploitation should be restricted to 10–20% of the birds that lay during the main laying period.

### Contents

	Page
Introduction .. .. .	318
Aims of the investigation .. .. .	318
The study colony .. .. .	319

\* Present address: Ministry of Agriculture, Fisheries and Food, Pest Infestation Control Laboratory, Field Research Station, Tangle Place, Worplesdon, Guildford, Surrey, England.

**Contents—continued**

Part I. Breeding biology of Sooty terns on Bird Island	..	..	..	..	320
Methods	..	..	..	..	320
Seasonal pattern of laying, and colony size	..	..	..	..	320
Egg survival	..	..	..	..	321
Chick growth and survival	..	..	..	..	321
Parental care of the egg and chick	..	..	..	..	323
Results	..	..	..	..	324
Colony size and the seasonal pattern of laying	..	..	..	..	324
Duration of incubation shifts	..	..	..	..	325
Parental care of the egg	..	..	..	..	326
Incubation period	..	..	..	..	327
Seasonal changes in egg weights	..	..	..	..	328
Hatching success	..	..	..	..	328
Chick growth	..	..	..	..	331
Chick mortality in the marked squares	..	..	..	..	336
Other sources of chick mortality	..	..	..	..	337
Parental care of the chick in the colony	..	..	..	..	338
Post-fledging parental care	..	..	..	..	342
Adult mortality during the breeding season	..	..	..	..	342
Part II. The effects of taking eggs	..	..	..	..	343
Methods	..	..	..	..	343
Results	..	..	..	..	343
Proportion of birds that relaid	..	..	..	..	343
Time taken to relay	..	..	..	..	344
Sites of replacement layings	..	..	..	..	344
Weights of first and replacement eggs	..	..	..	..	349
Survival of replacement eggs	..	..	..	..	349
Chick mortality	..	..	..	..	349
Chick growth	..	..	..	..	352
Discussion	..	..	..	..	352
Summary	..	..	..	..	357
References	..	..	..	..	358

**Introduction***Aims of the investigation*

The eggs of the Sooty tern *Sterna fuscata* L. (and to a lesser extent those of the Brown noddy *Anous stolidus* L.) in the Seychelles have been collected for human consumption for many years. The Sooty tern population is said to have declined since the beginning of this century, and much of this supposed decline has been attributed to over-exploitation of the eggs (Vesey-Fitzgerald, 1941; Cott, 1954; Ridley & Percy, 1958).

Ridley & Percy (1958, 1966) proposed several recommendations for the cropping of eggs in order to reduce exploitation to a level which would provide a sustained yield in the future, and to improve the quality of eggs reaching Mahé. Low egg quality, involving the arrival in Mahé of a high proportion of broken or bad eggs, can be improved using common sense rather than biological information. Ridley & Percy (1958, 1966) only spent short periods in the Seychelles and many of their recommendations concerning the extent of cropping (quotas), islands to be cropped, and the imposition of a close season, were of necessity intuitive.

The aims of this study were (a) to provide relevant information on the breeding biology of Sooty terns in the Seychelles in order to discover what factors limit the output of young from breeding colonies, and (b) to discover the effects of cropping the eggs on the breeding regimes of the parents and on the output of young. Both of these problems were studied on Bird Island (3° 53'S, 55° 12'E), an expanding colony which is no longer exploited commercially, in 1972 and 1973. In 1972 I was present on the island on 8 June, 14 to 23 June, and from 10 August to 11 November, while in 1973 I lived on the island for the entire breeding season, from 28 May to 23 October. In 1974 a further visit was made to Bird Island from 9–12 July, and other Sooty tern islands were visited in that year. The short duration of this study precluded the collection of data on age at first breeding and on post-fledging and adult mortality.

#### *The study colony*

The ecology of Bird Island is discussed elsewhere (Feare, in press). In the first decade of this century Bird Island was mainly a bird colony, with Sooty terns occupying the centre of the Island (Fryer, 1910), but no realistic estimates of the number of birds exist. The Sooty tern colony became restricted to the north-west corner when coconuts *Cocos nucifera* L. were planted over most of the island. Most of the decline in the Sooty tern population must therefore have been due to the extension of the plantation, and not to over exploitation of the eggs, even though Bird Island was one of the most important egg producing islands up to 1955.

From 1933 to 1937 *c.* 65,000 pairs of Sooty terns nested (Vesey-Fitzgerald, 1941). In 1955 Ridley & Percy (1958) estimated the population at 8300 pairs, but later (1966) they corrected this to 18,000 pairs. In 1966 they estimated 120,000 pairs.

After 1967 the area available to the birds was increased by tree clearance (Fig. 1) and the birds rapidly occupied this space. In 1973 the population was estimated at about 395,000 pairs (see below), and the rapid increase (*c.* 19% pa) since 1955 probably involved recruitment of birds from other colonies (Feare, 1973).

The vegetation of the original part of the colony consists mainly of *Portulaca oleracea* L. with limited areas of *Boerhavia repens* L., *Tribulus cistoides* L., and bushes of *Tournefortia argentea* L., *Scaevola taccada* L. and *Suriana maritima* L. (Fig. 1), while the area recently cleared of coconuts was covered mainly by grasses (Graminae) in 1972–1974. During these three years, however, the amount of grass diminished, and *Portulaca*, *Boerhavia* and *Tribulus* were spreading within the grass area. To encourage this spread, the grass was burned off at the end of the 1973 season (Sooty terns nested at a lower density in the grass than in the *Portulaca*—grass  $2.3 \pm 0.2$  eggs/m<sup>2</sup>, *Portulaca*  $4.2 \pm 0.1$  from 17 and 18 25 m<sup>2</sup> sample areas respectively,  $P < 0.001$ ). In addition to this form of management large *Tournefortia* and *Scaevola* bushes growing within the colony are cut down at the beginning of each season to leave more space for the terns.

Although many migrant birds feed in the Sooty tern area (Feare, 1974) only Turnstones *Arenaria interpres* L. are present in sufficient numbers to be regarded as important egg predators (Crossin & Huber, 1970). Cattle egrets *Bubulcus ibis* L., take eggs and small chicks, and chase well-grown chicks to make them regurgitate. Rats *Rattus rattus* L. only reached Bird Island in 1967 but are now abundant and take eggs and chicks, while land crabs are important scavengers. Flies (Diptera) infest the island for short periods each year, mainly in July and August.

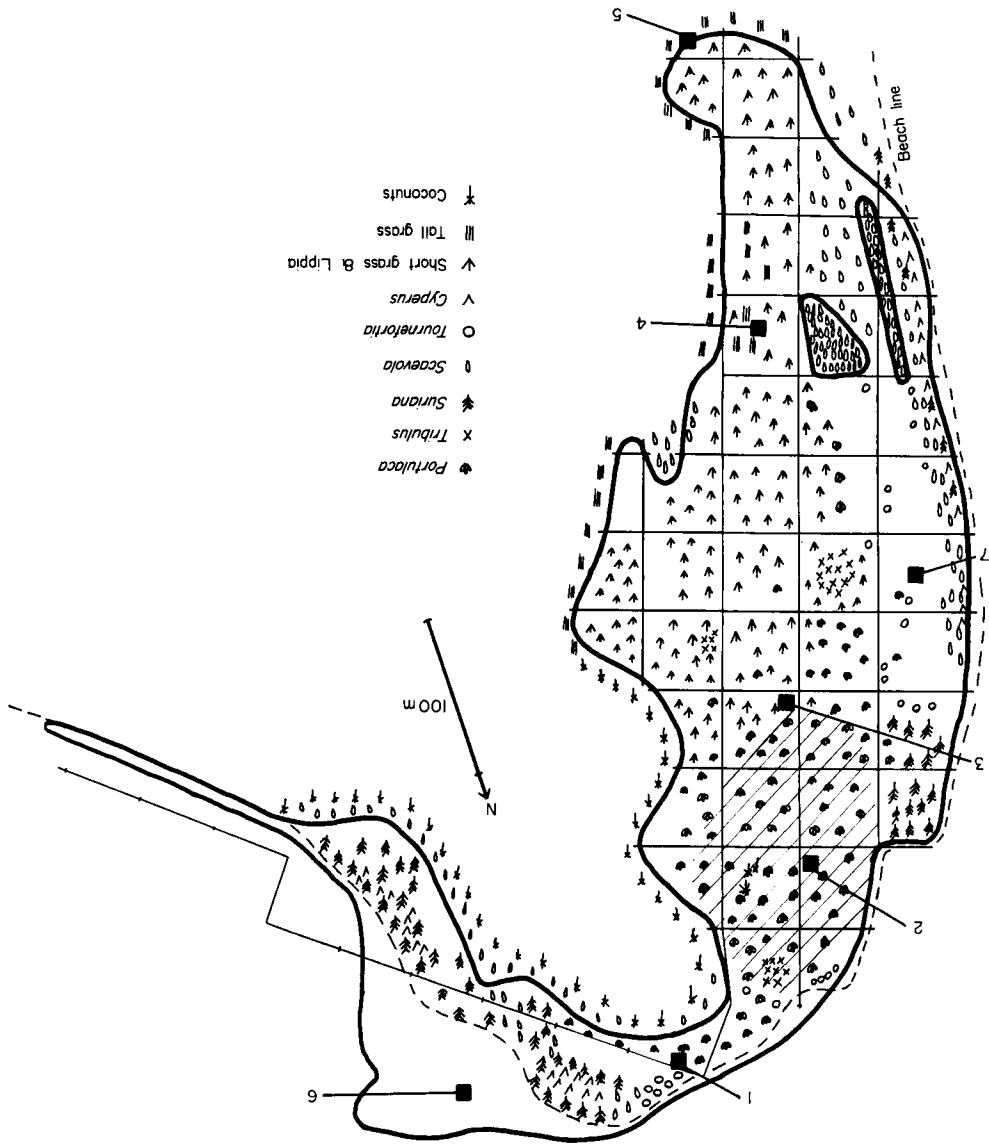


FIG. 1. The Sooty tern colony in 1973, showing the grid used during egg counting, and the seven marked squares (see text). The area of *Portulaca* around square 2 (hatched) represents the original part of the colony, and the grassy area to the south of this is the area cleared of coconuts since 1967.

## Part I. Breeding biology of Sooty terns on Bird Island

### Methods

#### *Seasonal pattern of laying, and colony size*

Before the birds began laying in 1973 a 50 m grid was marked out in the colony with numbered posts (Fig. 1). Within each 50 m grid square 2 further marked posts were positioned at random. To count the eggs around these posts 2.82 m of terylene cord was fitted with wire loops at each

end, such that one loop would fit over and rotate around the post, and the other loop could be held by a finger. By walking 360° round the post the cord passed over 25 m<sup>2</sup> of the colony, in which all eggs were counted. Sixty-two posts were used, and counts were made daily between 06.00 and 08.00 hrs local time (GMT-4h), from the day that eggs were first found in the colony until no further laying was recorded. Daily increases in the number of eggs counted were net increases since this method did not account for eggs lost between checks.

The area of the colony was found by plotting the grid on graph paper. The outline of the colony was found by measuring from the grid posts to the limits of the colony in early July, when laying had almost stopped, and marking these points on the map. The outer points were connected by a line fitted by eye, and the outline of the colony was then cut out and weighed. The total area was found by weighing a piece of the same sheet of graph paper corresponding to a known area (see Feare, 1970).

### *Egg survival*

Six 25 m<sup>2</sup> squares were marked with corner posts and string before laying began. The positions of these squares (referred to later as the "marked squares") were selected to cover the centre and edge of the colony, but square 4 (Fig. 1) was not occupied by birds.

Each square was visited between 09.00 and 12.00 hrs daily throughout laying. The position of each new egg (generally, but not always, in a scrape) was marked with a wooden label bearing the square number, site number and date laid. The egg was weighed to the nearest gram. On each subsequent day every labelled site was checked until the egg was lost or hatched. The eggs themselves were not marked, so that if an egg was lost after a check and a new egg was laid in the site before the next check, the loss of the first egg would not be recorded. This resulted in only a small error; out of 246 eggs that hatched only 1 showed an unusually prolonged incubation period (43 instead of 28 days) indicating that an egg had been lost and replaced between counts. By clearing eggs from 50 marked sites elsewhere in the centre of the colony, the interval between the loss of an egg and its replacement in that site (by another adult) was found to be  $6.2 \pm 0.4$  days (range 2-11 days,  $n=37$ , the remaining sites being unoccupied) showing that egg loss and replacement between checks would be rare.

### *Chick growth and survival*

The daily checks on the 25 m<sup>2</sup> marked squares were continued until all the eggs hatched or were lost. When a chick was first found, i.e. within 24 h of hatching, it was given a numbered British Trust for Ornithology ring, and a spot of yellow dye (Auromine ON 150 dissolved in 70% ethanol) on its back. Even on dark chicks the dye was readily visible, and could be used to identify ringed chicks from a distance. (No check on the effect of this dye on chick predation was possible, since undyed ringed chicks would be difficult to find, but the chick predators, cattle egrets and rats, probably hunted weak and unguarded chicks rather than conspicuously coloured ones.)

Each chick was also weighed to the nearest gram, and its right wing (flattened) and culmen were measured to the nearest mm.

On the daily checks only new chicks were processed as above, but on every third day all marked chicks that could be found were caught, weighed and measured, ascribed to one of the plumage categories in Fig. 2 and re-dyed. If a chick was noticeably weak, pecked or showed other abnormalities, these were recorded. Catching and checking all the chicks in a square was a full morning's work, and each square was done every third day, i.e. day 1, square 1; day 2, square 2; day 3, square 3; day 4, square 1, etc. No eggs hatched from squares 4 and 6, and 4 chicks which hatched in square 5 died within 2 days, so that in order to increase the sample of birds hatching late in the season a 7th square was added when chicks began to hatch there. Most chicks were fed in the afternoon, evening or night, and chicks handled at these times frequently regurgitated. To

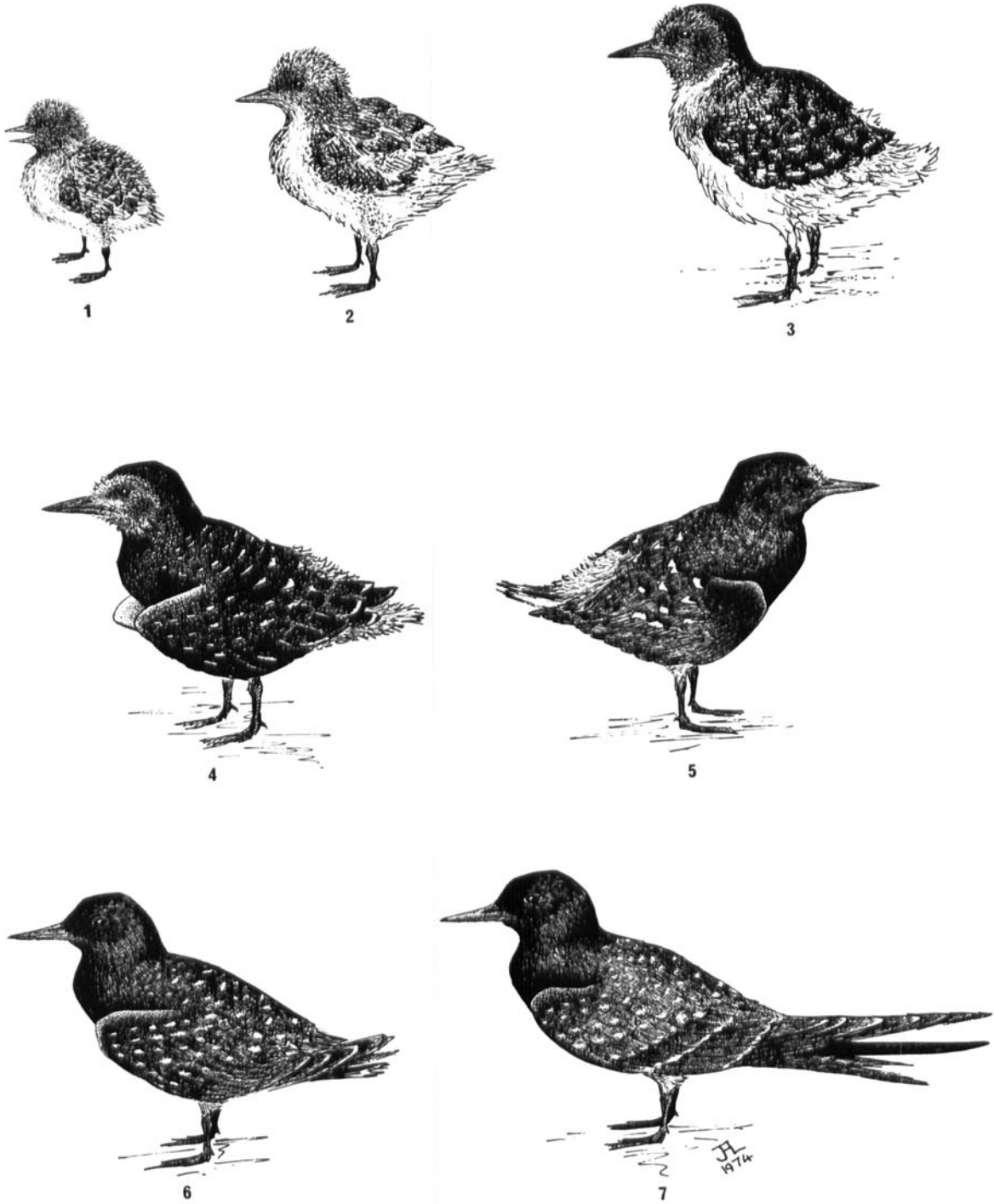


FIG. 2.

prevent this all catching and checking was done between 09.00 and 12.00 hrs, except for birds from square 7 which were done between 06.00 and 09.00 hrs on the same day as square 1.

Dyed chicks were caught by hand after a brief chase, and placed in wooden holding pens which on hot days were shaded. When a search of the square and its surrounding area, usually by 2 but sometimes by 3 people, produced no further dyed chicks, the chicks were removed from the holding pen, processed and released, whereupon most returned straight to their scrapes.

This method of catching obviously caused much disturbance, and a simple check on its effect on survival was made. While walking through the colony to check the squares, certain paths were strictly adhered to. Some of these went through the 25 m<sup>2</sup> egg counting areas, and on 18 July 1973 (approx. 14 days after hatching began in the colony) these were searched for dead chicks. Similar counts were made at posts which had not been visited since laying stopped. Only sample areas which had contained *c.* 100 eggs in the centre of the colony, where chicks were unlikely to have been removed by cattle egrets, were used for this check. At this stage of the season rats and land crabs did not seem to be removing chicks, and decomposition was sufficiently slow for corpses to be identifiable several weeks after death. In disturbed areas,  $5.1 \pm 0.5$  (1 standard error,  $n=11$ ) dead chicks/25 m<sup>2</sup> were found, compared with  $2.6 \pm 0.6$  ( $n=7$ ) in undisturbed areas ( $P < 0.002$ ). My disturbance therefore increased the mortality of downy chicks by 97%, a factor which is used to correct estimates of chick mortality found in the marked squares.

Most chicks which died were found and identified by their rings, but some disappeared. On each check over 95% of chicks known to be alive were caught. The distribution of the frequency of absences of birds known to be alive on the 3-day checks (Patterson, 1965) showed that if a chick was absent for 3 successive searches there was at least a 95% probability that it was dead: no chicks were found alive after an absence of 4 checks. When chicks were leaving the colony successive absences could mean that a chick had left or had died without being found. The following criteria were used: if a chick was above 160 g and had wings over 200 mm when last seen it was considered to have flown; if it weighed less than 160 g, had been losing weight rapidly, was weak, or had wings less than 200 mm at the last check it was considered to have died. Most chicks which complied with one or more of the "presumed dead" yardsticks above were subsequently found dead.

#### *Parental care of the egg and chick*

Direct observations on diurnal variations in behaviour associated with incubation were made from a viewing platform *c.* 2 m above the colony, on a tree. This did not appear to disturb the birds. The proportions of birds involved in pre-laying activities, incubation, etc., were found by hourly counts of the number of birds performing each activity in a marked area of the colony close to the viewing platform. The number of feeds and drinks seen in this marked area was recorded during 5-min observation periods each hour.

The duration of incubation shifts by each member of pairs of birds was found by fitting patagial wing tags (Anderson, 1963 and subsequently modified by Patterson *et al.* (1971) and E. K. Dunn (pers. comm.)) to one member of each of 23 pairs. These birds were also ringed, as were 11 of their mates. All tags were fitted within 2 days of laying, and the nest sites were marked with wooden

---

FIG. 2. The stages of plumage development used in this study. 1. *Downy*—chick covered with down; 2. *Small wings*—scapular feathers appear; 3. *Head moulting*—feathers appear on the crown, mantle and breast; 4. *Down on face*—down restricted to face, lower belly and rump; 5. *Tail cocked*—tail coverts grow and tail appears "cocked"; 6. *Short tail*—rectrices all about same length, wings < 200 mm; 7. *Tail forked*—outer rectrices considerably longer than inner, wings > 200 mm.

labels on which the tag number was clearly written, so that both tags and nest labels could easily be read with binoculars from the viewing platform. The presence or absence of the tagged bird at its scrape was checked at 09.00 hrs daily throughout incubation.

These tags were invaluable for the study of parental behaviour, but they undoubtedly increased the mortality rate of the birds. Of the 15 pairs whose eggs hatched none of the mates died, while one tagged bird was found dead with its bill caught in the tag pin and 2 others disappeared, presumed dead. Thus although useful for short-term observations, tagging could not be used on Sooty terns to estimate adult mortality, as was done in rooks *Corvus frugilegus* L. (Dunnet & Patterson, 1968).

The frequency of feeding of the chicks was obtained by regular weighings of the ringed and dyed chicks of the tagged adults, once direct observation of feeding and subsequent weighing had established that a measurable increment in weight corresponded to a feed. Food composition was obtained from food regurgitated by chicks handled in the evening in a part of the colony not used for other observations, since periodic deprivation of food could have altered their growth and behaviour.

## Results

### *Colony size and the seasonal pattern of laying*

The estimated area of the colony in 1973 was 11.69 ha, and the density of eggs was  $3.38 \pm 0.16/m^2$  (range 0–5.48,  $n=64$ ), giving a total population of about 395,000 pairs.

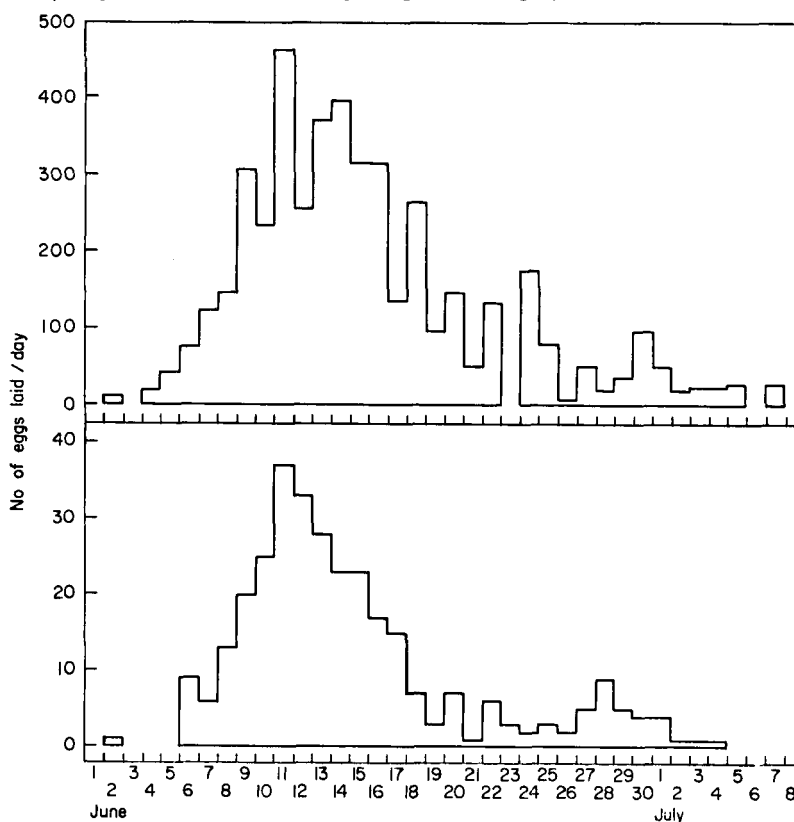


FIG. 3. The seasonal pattern of laying in the colony in 1973, as shown by the egg count circles (a) and the marked squares (b).

Figure 3 shows the seasonal pattern of laying in the colony in 1973, as derived from the 25 m<sup>2</sup> counting circles and from the 25 m<sup>2</sup> marked squares, indicating that the pattern of laying in the marked squares was representative of the colony as a whole.

Laying began at several nuclei in the main *Portulaca* covered area of the colony, and spread from these until the whole colony was occupied. In each part of the colony laying was highly synchronous, and this "mass laying" continued at the extremities of the colony, outside the counting circles, until 12 July. Sporadic laying, perhaps of replacement eggs, continued until the end of July, but in the colony as a whole 75% of the eggs (c. 300,000) were laid in the 9-day period 8–17 June. Laying appeared to be bimodal (Fig. 3) with a main peak on 11–12 June and a much smaller peak possibly of replacement eggs round 28–30 June.

Hourly counts of the number of eggs in selected areas showed that 94% of the eggs on Bird Island were laid between 12.00 and 18.00 hrs, and 82.3% of afternoon layings (77.7% of all layings) occurred between 13.00 and 16.00. Thus laying was diurnally as well as seasonally synchronous, as shown by Ridley & Percy (1958), Ashmole (1963) and Dinsmore (1972).

#### *Duration of incubation shifts*

With eggs laid during the peak laying period 57% of the incubation shifts were of 1-day duration (Fig. 4), the pair usually attending the egg on alternate days. 2-, 3-, 4- and 5-day shifts occurred with decreasing frequency. The incubation regimes adopted by pairs were

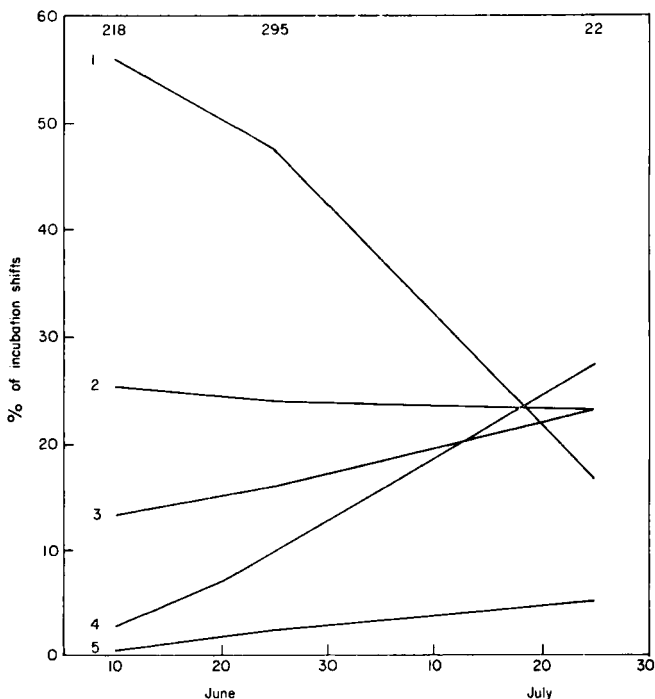


FIG. 4. Seasonal change in the frequency of incubation shifts from 1 to 5 days duration. Figures at the top of the graph are the number of incubation shifts measured in each sample.

usually regular (1 day on, 1 day off or 2 days on, 2 days off), although some were highly irregular. One bird (1E) was not seen after its ringed mate relieved it on 27 June after 16 days of incubation, but the mate completed incubation, and the egg hatched successfully. On 5 July 1973 a young bird, with entirely smokey-grey underparts, except for white under tail coverts, and black upperparts with no white spots, was found incubating. It was mated with a normal adult, and was presumably breeding for the first time. Although the incubation regime of this pair was regular, the shifts were much longer than those of the tagged birds, involving 4 shifts of 5–6 days (only 14 out of 535 shifts of older birds were of this duration).

Incubation shifts became longer towards the end of the laying season (Fig. 4). The data for birds laying on 25 June and 25 July were from dyed birds incubating replacement eggs (see Part 2 below). They were therefore not young birds breeding late in the season (Harrington, 1974), but it is possible that the production of a second egg had altered their feeding regimes and/or their incubation shifts. However, it is probable that the increasing length of shifts was a genuine seasonal phenomenon, since the tagged birds showed a tendency to longer incubation shifts as incubation progressed. The frequencies of shifts of 1 to 5 days' duration during the first 14 and last 14 days of incubation were: 1-day, 64.4% and 57.6%; 2-day, 21.1% and 29.3%; 3-day, 13.3% and 9.8%; 4-day, 1.1% and 2.1%; 5-day, 0% and 1.1% (sample sizes 90 and 92 respectively).

Out of 66 timed changeovers, 60 (91.0%) occurred during the night, 3 (4.5%) in the morning and 3 (4.5%) in the afternoon. Most adults returned to the colony in the evening (and presumably at night): between 06.00 and 16.00 hrs the proportion of birds (sample 200 nests) with their mates present at the scrape ranged from 1 to 7%, but at 18.00 hrs this rose to 23%.

A few of the tagged adults or their ringed mates were weighed on successive days of incubation, and they lost weight as follows: day 1— $13.2 \pm 0.8$  g ( $n=18$ ), day 2— $9.7 \pm 0.8$  g ( $n=6$ ), day 3— $7.7 \pm 0.7$  g ( $n=3$ ). Weight loss during the first day of an incubation shift was significantly greater than on succeeding days ( $P < 0.001$ ), but on average incubating birds lost about 10 g day, or *c.* 5% of body weight.

#### *Parental care of the egg*

When the egg was first laid the adult attending it usually flew off at any disturbance. During incubation aggressiveness increased until, when eggs were about to hatch, some adults repeatedly attacked any approaching human. At hatching the egg is most sensitive to environmental factors (Howell & Bartholomew, 1962).

Besides being protected from potential predators, the egg must be maintained at the correct temperature and humidity. At night and in shade eggs are incubated, but in the sun the adults stand over the egg, facing into the wind with carpal joints drooped and the mantle feathers raised, keeping the egg in their shadow. In the early afternoon on sunny days all adults shaded the egg, but where nest sites were close to large trees adults began to incubate soon after the shadow of the tree reached them, only to recommence shading when they were in the sun again. On cloudy or rainy days eggs were incubated continuously.

Even around midday, however, some eggs were not attended and this appeared to be related to brief flights by the adults to the sea, close inshore, where they dipped the bill, belly or feet. On returning to the scrape they either trod on the egg and turned it or briefly settled on it before resuming shading; after this the egg was wet.

The frequency with which the adults dipped their bills, bellies or feet varied seasonally. During the pre-laying period 86.8% of 696 water contacts were by the bill (drinking), but on 15 June when most of the birds had eggs, belly (13.3%) and especially foot, (36.9% of 777 contacts) dipping became frequent. After hatching drinking (94.7% of 924 contacts) again became the main purpose of dipping, water being required by both adults and chicks (see below).

#### *Incubation period*

The incubation period of 234 eggs in the marked squares was  $28.1 \pm 0.05$  days (range 26–32). Of these, 160 (68.4%) hatched on the 28th day, 19 (11.9%) on 27th day, and 23 (14.4%) on 29th day. The incubation periods of eggs laid after the main laying period were more variable than those laid during it: for eggs laid before 17 June the mean incubation period was 28.14 days, with a variance of 0.56 ( $n=192$ ), while for eggs laid after 17 June the mean was 28.18 days with a variance of 1.06 ( $n=42$ ). In this last sample the proportions hatching on 27th, 28th and 29th days were 31.0%, 41.4% and 20.7% respectively. The

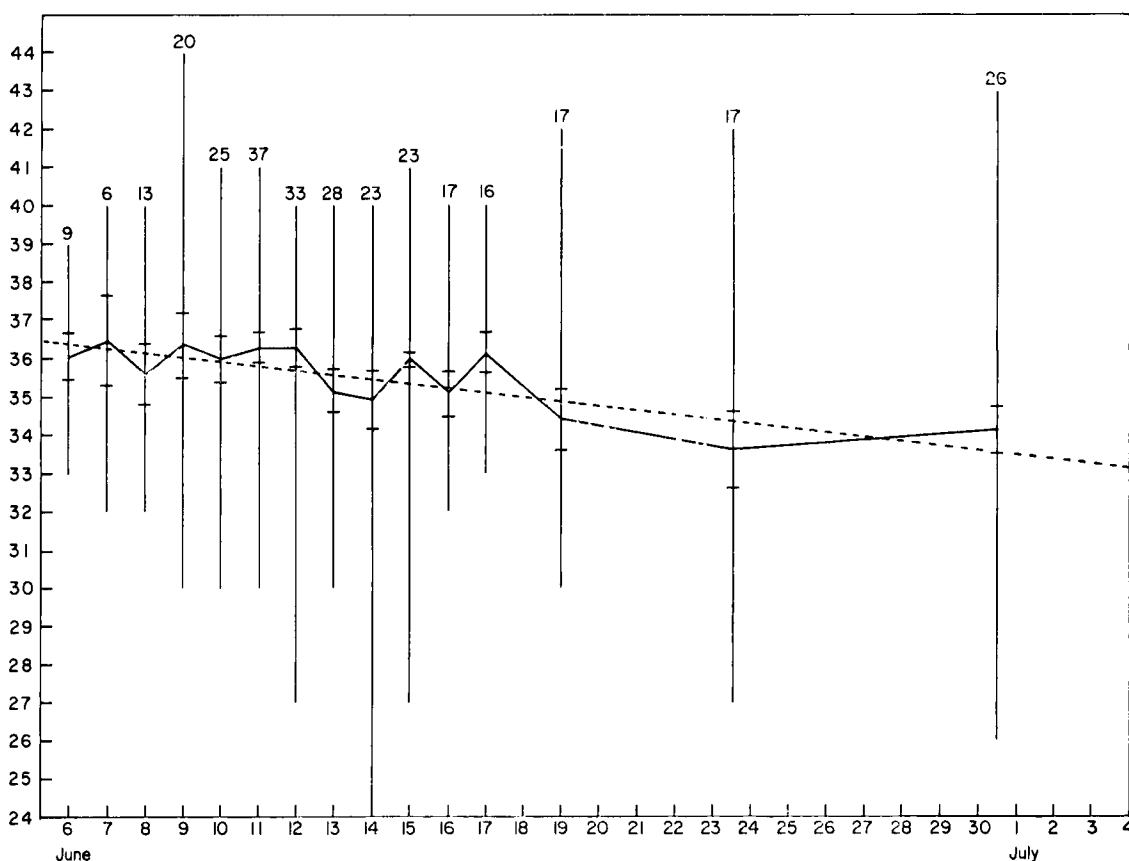


FIG. 5. Seasonal change in the weights of eggs laid in the marked squares. From 6 to 17 June mean weight, standard error (horizontal bars) and range (vertical lines) were calculated daily, but eggs laid on 18–20 June, 21–25 June and 26 June–4 July were grouped. Figures above the lines are the number of eggs in each sample. Regression equation  $y = 37.02 - 0.11x$ ,  $r = 0.79$ ,  $P < 0.001$ .

cause of this increased variance is not known. There was no relation between egg weight and incubation period, but a factor which did prolong the incubation period was the presence of two eggs in a scrape. Five 2-egg clutches occurred in the marked squares, but of the 10 eggs laid only three hatched, with incubation periods of 29, 30 and 32 days. Double clutches resulted from an adult rolling a second egg (usually an accidentally laid egg not in a scrape) laid within its territory into its scrape. Of the seven eggs which failed to hatch, two clutches were deserted, one egg of a pair disappeared, and the other two eggs failed to hatch once the first eggs in the scrapes had hatched. The prolonged incubation periods of the eggs which did hatch, and the failure of most, presumably resulted from the parents' inability to incubate two eggs. The rarity of 2-egg clutches (1.2% of 422 nest sites) indicates that they contributed little to the increased variance of the incubation period at the end of the season.

#### *Seasonal changes in egg weights*

The mean weight of eggs on the day of laying in the marked squares was  $35.9 \pm 0.2$  g, but egg weight declined seasonally (Fig. 5). The weights of samples of fresh eggs collected for human consumption on 3 and 22 June and 5 and 10 July were  $36.2 \pm 0.2$  ( $n=117$ ),  $34.0 \pm 0.2$  ( $n=149$ ),  $35.0 \pm 0.3$  ( $n=80$ ) and  $31.8 \pm 0.2$  ( $n=74$ ) respectively.

#### *Hatching success*

In the centre of the colony hatching success was about 75% (Table I), while at the extreme edge (where few eggs were laid in the squares) only 10% of the eggs hatched. The majority of the losses occurred within the first few days of incubation (Fig. 6), when adults were not very aggressive to intruders.

All of the losses in squares 5 and 6, on the edge of the colony (i.e. the edge of the entire colony, rather than the dynamic edge as the colony expanded from the nuclei of first

TABLE I

*Total losses of eggs from the marked squares (no eggs were laid in square 4, and square 7 was not established until the eggs hatched)*

Marked square	Position in colony	No. eggs laid	No. lost	% lost
1	Centre	98	29	29.6
2	„	112	23	20.5
3	„	100	25	25.0
5	Edge	39	36	92.3
6	„	23	20	87.0

laying) were due to predation. In the centre of the colony predation accounted for 41.6% of egg losses, the remaining losses being broken eggs (12.2%), chicks dead on hatching (4.2%) and eggs that failed to hatch (43.0%,  $n=77$ ). The "failure to hatch" category included desertion by the parents, egg infertility and probably mortality due to incorrect temperature and humidity maintenance during incubation. These were impossible to separate as by the 28th day these eggs were usually bad. In a few cases the adoption of a second egg also led to losses (see above).

The relative importance of the three egg predators on the island was not determined: both rats and Cattle egrets either removed the egg, or ate it where they found it leaving a broken shell in or close to the scrape, while Turnstones pecked a small hole in the shell. Eight (40%) of the eggs lost from square 6 were taken by Turnstones, and the remainder were assumed to have been taken by rats as Cattle egrets were not seen in this part of the colony. In square 5, close to the settlement, and in squares 1, 2 and 3, no Turnstone predation was seen. Of the 32 eggs taken by predators in squares 1, 2 and 3, 12 (37.5%) had not been laid in scrapes and were presumably "accidental" layings. (This could result from disturbance when the birds were about to lay nearby (pers. obs.), and some of these

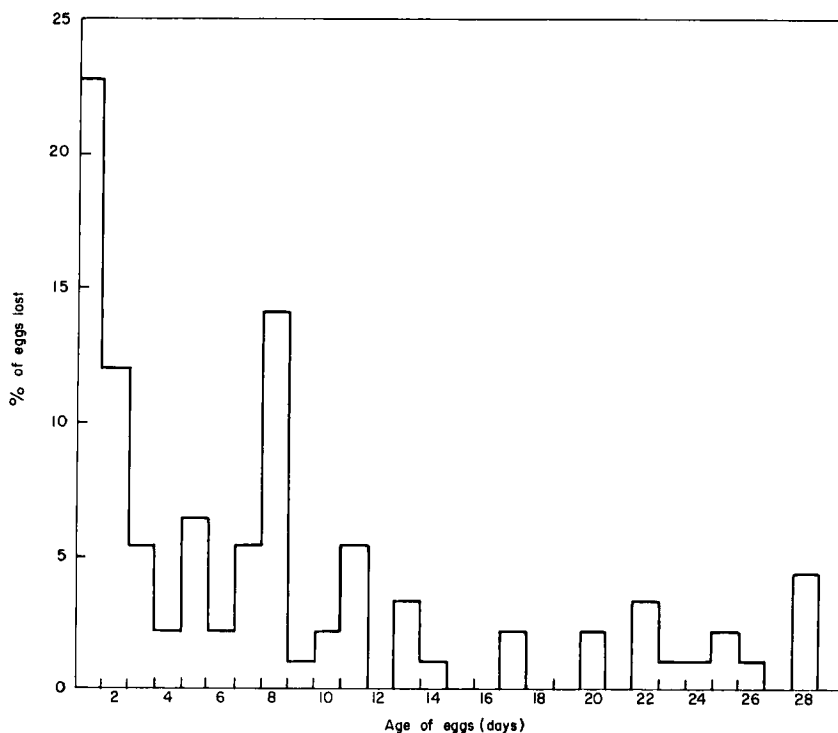


FIG. 6. The age (days after laying) that eggs from the marked squares were lost ( $n=133$ ).

could have been due to my activities). Of a further four eggs which were laid outside scrapes in these squares, three were adopted to form 2-egg clutches, and the fourth was not incubated.

Other causes of egg loss in the colony, but not in the study areas, were the collection of eggs for local consumption (around 10,000), the desertion of part of the colony after an infestation of ticks *Ornithodoros capensis* Neumaan (c. 5000 eggs, Feare, 1976), and the crushing of a few eggs by Green turtles *Chelonia mydas* L. which laid in the colony. Since the assessment of egg losses involved checking nest sites daily it was not possible to estimate the effects of my disturbance, but this probably increased losses where repeated observations were made.

The proportion of eggs laid each day which were lost varied seasonally. The earliest



eggs (the first were seen on 29 May, but did not occur in any of the study areas) suffered high predation from Turnstones and Cattle egrets. Before mass laying began, Sooty terns on the ground were extremely nervous, and the few birds with eggs took off with the other birds during disturbances. Turnstones and Cattle egrets quickly found the eggs. Only when many birds had eggs together did the nervousness of birds which had not yet laid cease to affect incubating birds.

Losses of eggs laid during the main laying period (6 to 18 June) were relatively small (Fig. 7): 47 (18.4%) of 256 laid, but thereafter losses were greater: 33 (64.7%) of 51 laid. As with the earliest eggs, later eggs tended to be lost earlier during incubation than those laid during the main laying period (Fig. 8).

Eggs which were lost tended to be lighter than those which survived. The 234 eggs which hatched weighed  $35.9 \pm 0.2$  g, while the 77 which failed weighed  $34.4 \pm 0.4$  g (difference not significant). As later eggs were lighter (Fig. 5) and survived less well (Fig. 7) than earlier eggs, a possible seasonal influence was eliminated by comparing only eggs laid on 10 to 12 June, which again showed a tendency for lost eggs to be lighter (hatched  $36.4 \pm 0.3$  g,  $n=79$ ; lost  $34.9 \pm 0.8$  g,  $n=15$  n.s.). There was no significant difference between the weights of eggs which were predated ( $33.9 \pm 0.6$  g,  $n=32$ ) and which "failed to hatch" ( $34.6 \pm 0.6$  g,  $n=36$ ).

Eggs lost weight during incubation, and egg weight at laying and chick weight at hatching were correlated ( $r=0.69$ ,  $P<0.001$ ), the chicks weighing  $72.5 \pm 0.9\%$  ( $n=230$ ) of the initial egg weight.

#### *Chick growth*

For the construction of growth curves (Figs 9, 10 and 11) the chicks that survived to fledging were divided into five groups according to their date of hatching: group 1, chicks that hatched 3–5 July; group 2, 6–8 July; group 3, 9–11 July; group 4, 12–14 July; and group 5, 15 July to 2 August (this group is therefore not directly comparable with the other groups of chicks hatched over 3-day intervals).

In all groups weight increase was rapid over the first 30–35 days and growth rates over this period were not significantly different. However, the mean maximum weights attained by the groups after the rapid growth declined: group 1–187 g, group 2–178 g, group 3–178 g, group 4–165 g and group 5–130 g. Birds of groups 1 to 4 then lost weight as food became scarce (see below), and the decline in the weight attained after the rapid growth reflects the earlier onset on this food shortage in later-hatched birds.

Following this food shortage weights increased again, and during this increase group 1 birds flew well enough to avoid being caught. Birds from later groups became uncatchable as a second period of food shortage began, and the mean weights of these birds when last caught (Fig. 9) declined. However, the marked chicks of the tagged adults remained in the colony for an average 17 days after they became uncatchable, and the final weights recorded for groups 1–5 may not be the weights at which these chicks left the island. Nevertheless, the lower weights of later birds, and the greater ages at which they became uncatchable (Fig. 9) suggest that later-hatched birds may leave the colony less fit than early ones.

Weights at all ages were significantly correlated with weight at hatching, including the weight when the chicks were last caught. However, although the correlations were significant,  $r$  values were small, and so the relation between hatch weight and growth rate over

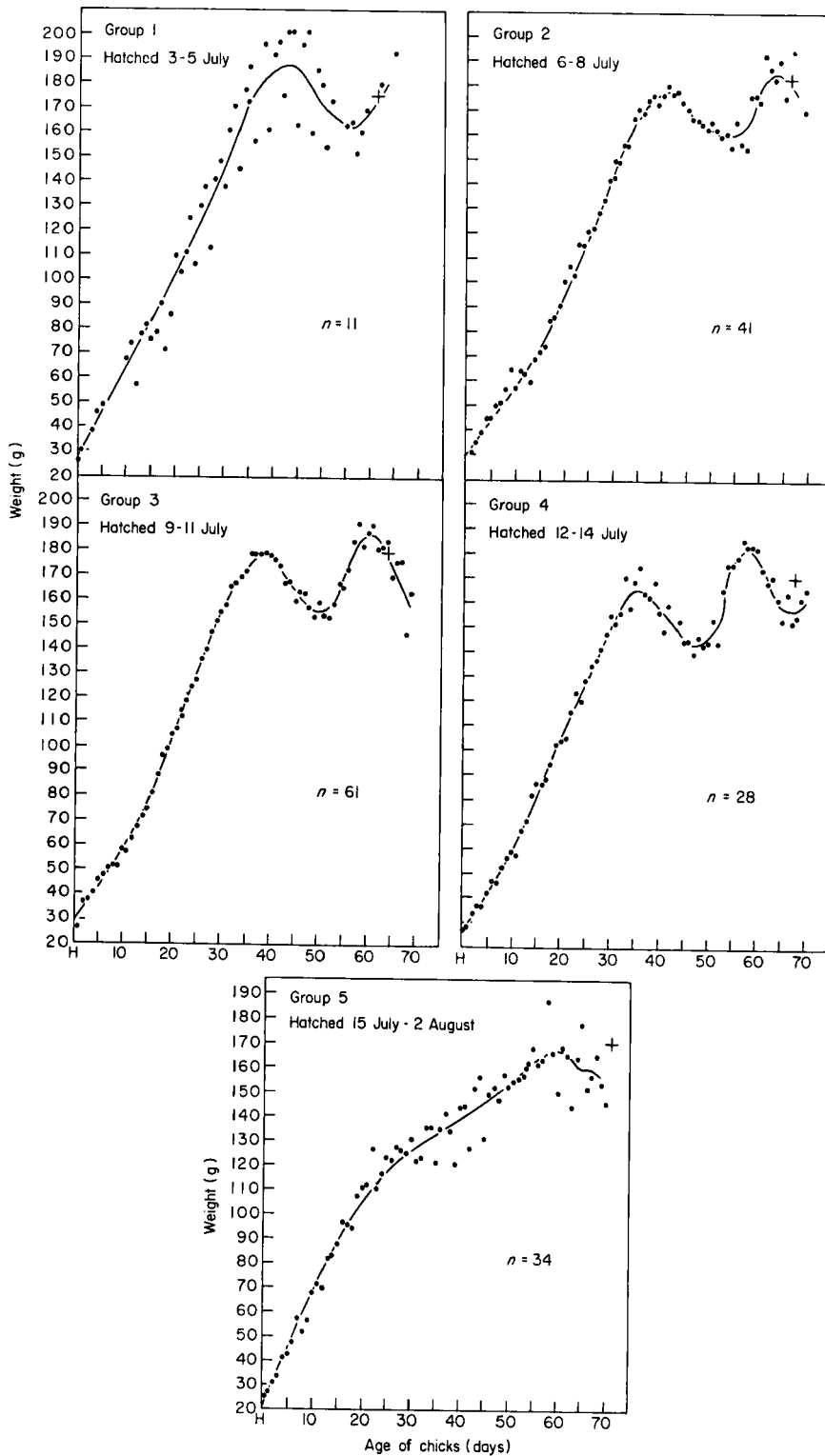


FIG. 9.

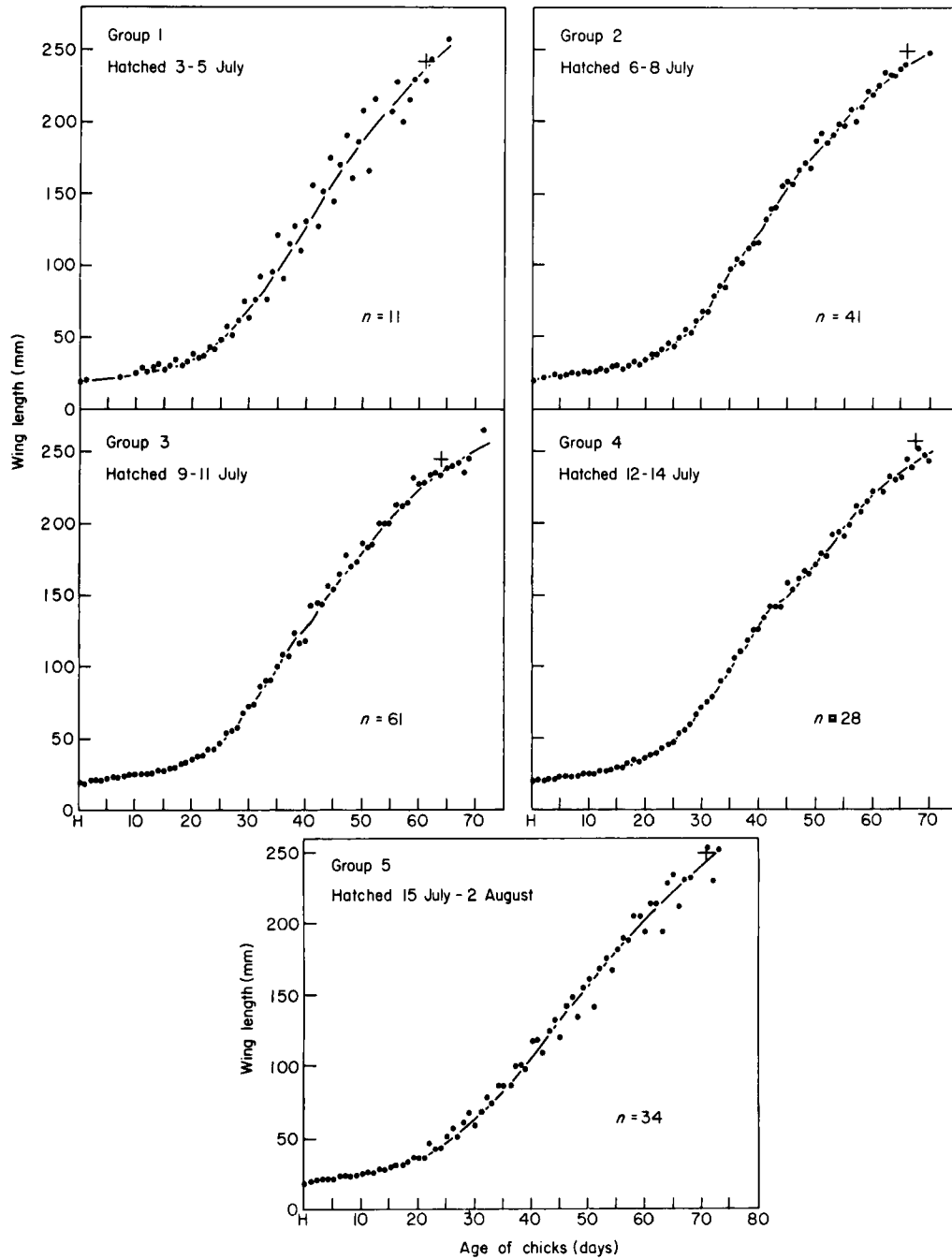


FIG. 10. Wing growth in the five groups of chicks. For explanation see legend to Fig. 9.

FIG. 9. Growth in weight of the five groups of chicks. Each point represents the mean weight of chicks at each age. The cross in the top right corner of each graph is the mean weight and mean age at which the chicks were last caught. Curves were drawn as running means over five points.

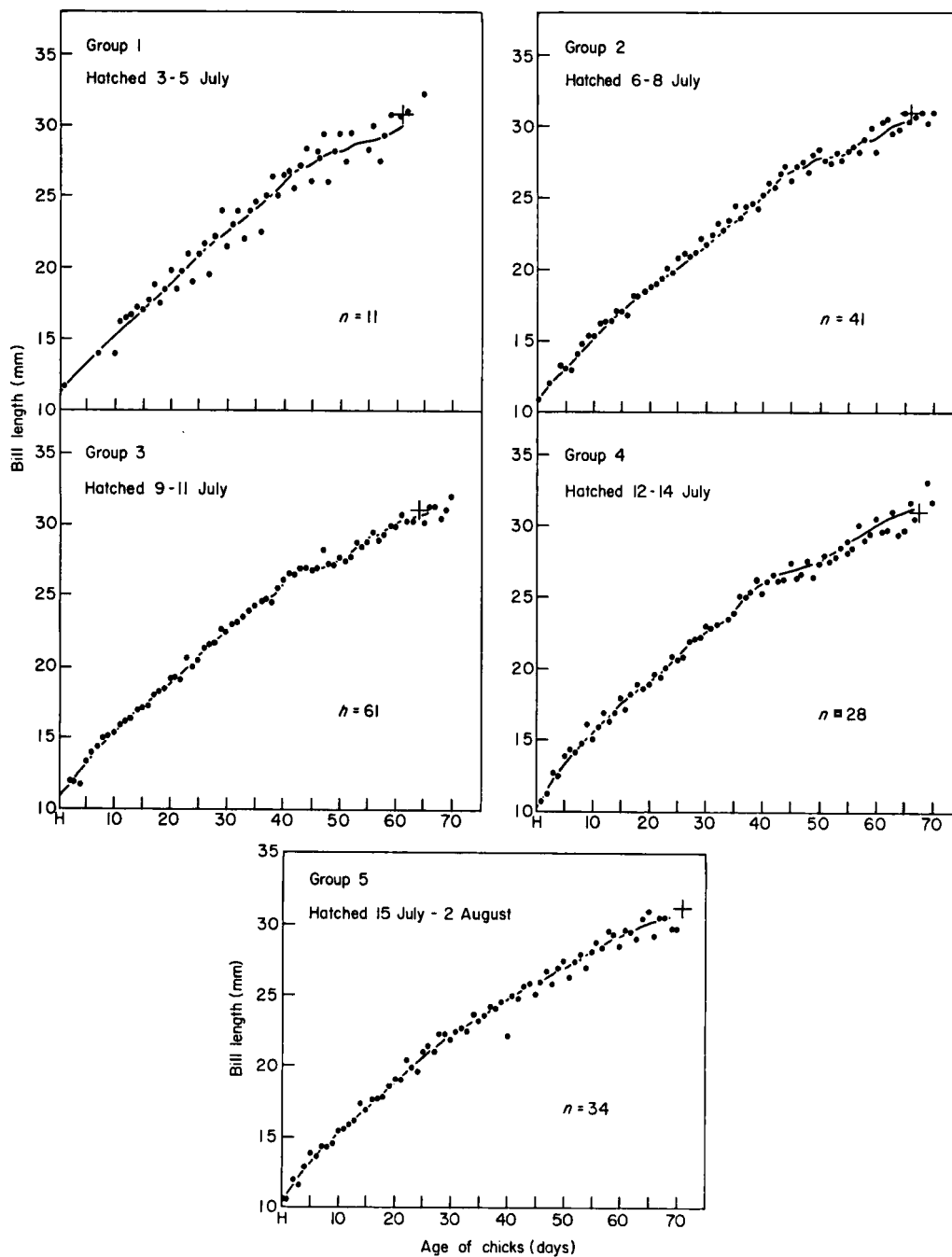


FIG. 11. Culmen growth in the five groups of chicks. For explanation see legend to Fig. 9.

the initial rapid growth phase was investigated in the heaviest and lightest chicks at hatching (Fig. 12). Chicks which hatched at 29–34 g had a significantly ( $P < 0.001$ ) higher rate of weight increase than those which hatched at 20–23 g. The heavy chicks at hatching were also heavier when last caught ( $185.5 \pm 3.5$  g compared with  $172.0 \pm 3.4$ ,  $n = 29$  and  $28$ ,  $P < 0.01$ ) and became uncatchable earlier ( $64.0 \pm 1.3$  days compared with  $71.3 \pm 1.5$  days,  $n = 29$  and  $28$ ,  $P < 0.001$ ) than lighter chicks.

No differences were apparent in the rates of wing or bill growth in the five groups (Figs 10 and 11), nor was there any indication that food shortage influenced these rates.

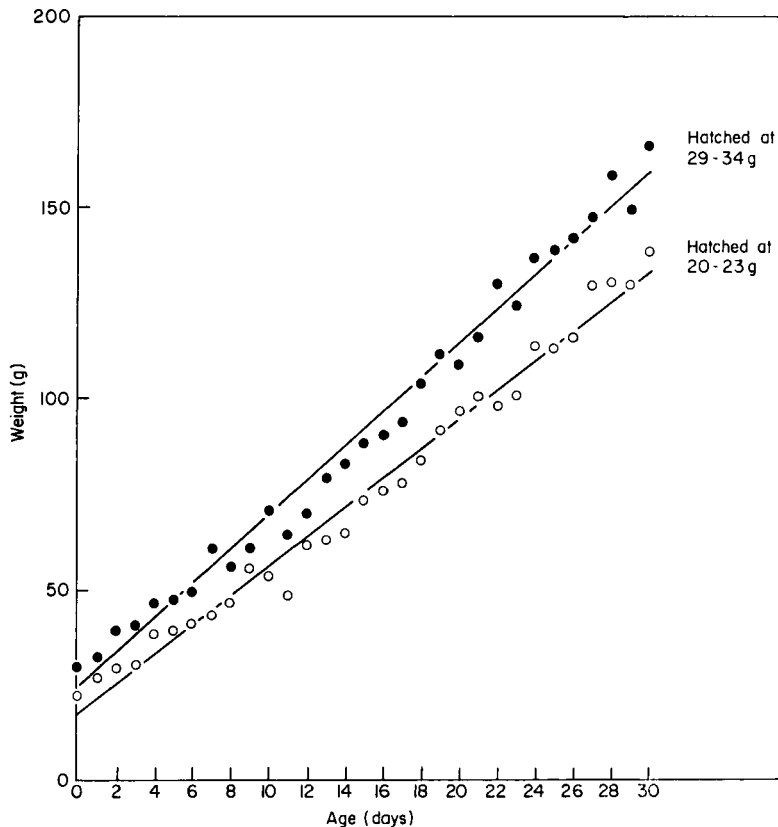


FIG. 12. Growth in weight over the first 30 days of chicks of low (20–23 g) and high (29–34 g) hatch weights. For low group  $y = 17.76 + 3.82x$ ; high group  $y = 24.10 + 4.48x$ ;  $t = 3.69$ ,  $P < 0.001$ ; for each group  $n = 29$ .

Despite differences in the weights and ages at which chicks of the five groups became uncatchable, wing and bill lengths of the birds when last caught were similar. Both the wing and bill continued rapid growth after the birds became uncatchable in the colony: the wing and bill measurements of 10 flying chicks mist netted on the beach as they were flying out to sea were  $280.7 \pm 2.5$  mm and  $33.0 \pm 0.4$  mm respectively (cf. breeding adult ♀ wing  $293.4 \pm 1.4$  and bill  $41.8 \pm 0.3$ ; adult ♂ wing  $294.3 \pm 1.5$ , bill  $43.3 \pm 0.4$ ).

The age at which transition from one plumage stage (see Fig. 2) to the next occurred showed wide variation (Fig. 13) but on average the stages were of approximately equal

duration in all groups, except for stage 3 ("head moulting"). This stage was the longest, and it tended to be longer in later than in earlier hatched chicks.

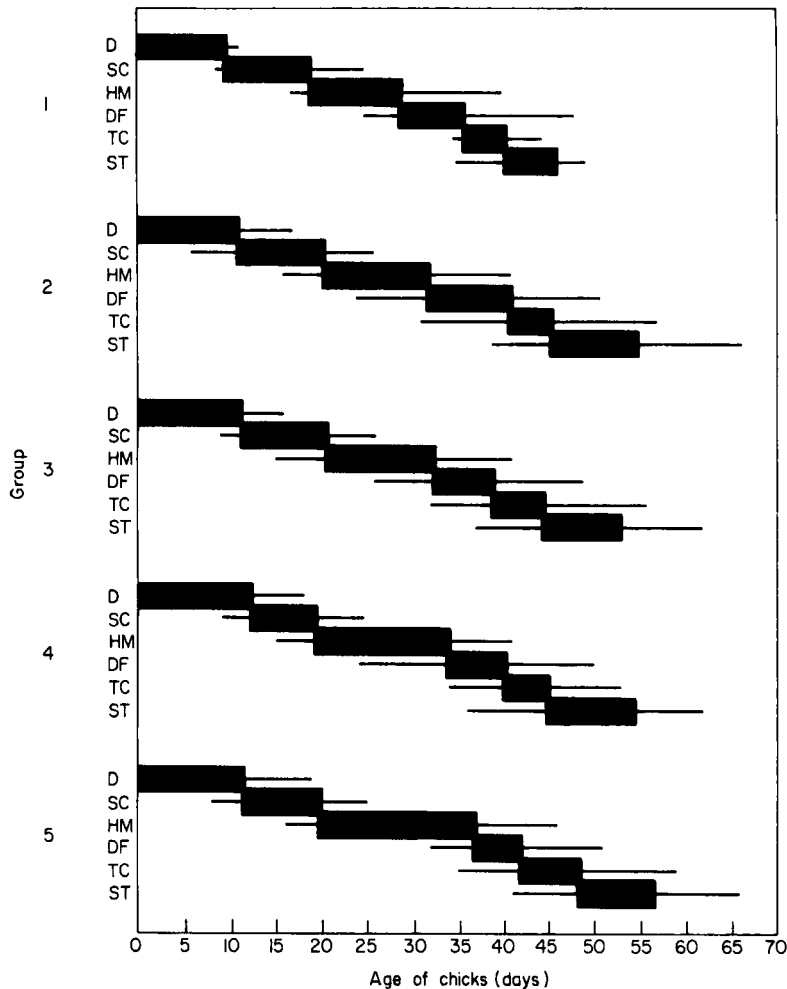


FIG. 13. The duration of each stage of plumage development in the five groups of chicks. The end of a horizontal bar is the mean age at which the chicks changed from one stage to the next, and the horizontal lines indicate the range about this mean. For descriptions of the plumage stages see Fig. 2: D = downy, SW = small wings, HM = head moulting, DF = down on face, TC = tail cocked, ST = short tail, TF = tail forked.

#### *Chick mortality in the marked squares*

Of 264 eggs that hatched in the marked squares, 172 produced flying young, a mortality of 34.8%. This mortality varied seasonally, and those that hatched later in the season suffered higher mortality than early chicks (Table II). Most of this mortality occurred within the first 10 days (Table II), and while the proportion of group 5 birds dying within 10 days is low compared with other groups, this is simply because mortality was high in older chicks in this group.

Cause of death was difficult to establish, and in the five groups only three categories were recognized: (1) *Pecking*. When disturbed, adults flew up and their chicks ran in an attempt either to hide or to move away from the disturbance, depending on their age. After the disturbance the adults settled again and the chicks started to return to their nest sites. As they passed through territories of other birds they were pecked, often lost down and bled, and sometimes sustained more serious injuries (e.g. blindness, or broken or dislocated wings—this only became apparent when the primaries grew). Some chicks were more prone to being pecked than others, and were regularly found bleeding; the reason for this is unknown. Chicks which were found dead or which disappeared after being badly pecked when last seen were regarded as having died through pecking. (2) *Starvation*. When chicks were found dead or disappeared after several days of losing weight, they were

TABLE II  
*Mortality, age at death and cause of death of chicks from the five groups*

Group	Date hatched	No. hatched	No. (+ %) died	No. (and %) died		Cause of death		
				<10 days	>30 days	Pecked	Starved	Unknown
1	3-5 July	14	3 (21.4)	0 (0.0)	0 (0.0)	2 (66.7)	0 (0.0)	1 (33.3)
2	6-8 July	49	9 (18.4)	5 (55.5)	2 (22.2)	6 (66.7)	1 (11.1)	2 (22.2)
3	9-11 July	81	21 (25.9)	11 (52.4)	6 (28.6)	7 (33.3)	5 (23.8)	9 (42.9)
4	12-14 July	53	25 (47.2)	18 (72.0)	4 (16.0)	14 (56.0)	2 (8.0)	9 (36.1)
5	15 July-2 August	67	34 (50.7)	13 (38.2)	14 (41.1)	16 (47.1)	8 (23.6)	10 (29.4)

considered to have starved. (3) *Unknown*. Many chicks died or were presumed to have died with no cause being apparent.

In none of these causes of death was there a seasonal change, but a high proportion of deaths were due to pecking (Table II). Much of this mortality was undoubtedly due to my disturbance when catching chicks. My disturbance was estimated to have increased mortality by 97% (see above) so that had chicks in the marked squares not been disturbed the number that died through pecking would be reduced from 45 to 23, and the overall mortality of these birds would then have been 26.6%, instead of 34.8%.

Despite the seasonal decrease in egg weight (Fig. 5), the hatch weights of the five groups of chicks did not show a seasonal decline (group 1,  $25.6 \pm 0.5$ ; 2,  $25.3 \pm 0.4$ ; 3,  $25.9 \pm 0.4$ ; 4,  $25.9 \pm 0.3$ ; 5,  $24.4 \pm 0.7$ ). Heavier chicks at hatching survived better than lighter ones (mean hatch wt of survivors  $26.1$  ( $n=172$ ), mean hatch wt of those that died  $24.7$  ( $n=92$ ,  $P < 0.001$ ) but there was no relation between weight at hatching and age at death.

#### *Other sources of chick mortality*

Elsewhere in the colony other causes of death were seen, some of which could have contributed to the "cause unknown" category above.

#### *Predation*

Predation by Cattle egrets of small downy chicks was not detected in the marked squares as the egrets carried the chicks away, and ringed chicks would have disappeared. The only other predators were rats; these were mainly nocturnal, and appeared to eat their prey under bushes where yellow dyed feathers were easily seen and rings usually found.

Apart from unattended young chicks, predation appeared to be secondary to other causes of loss. Some chicks which had been weakened by pecking were found dead under bushes, and, especially at the end of the season, starving or injured birds were killed by rats. In 1973 only six chicks (6.5%) from the marked squares were known to have been killed by rats, and they had all been losing weight before they died. Predation therefore appeared to be an insignificant cause of mortality on Bird Island.

### *Weather*

Sooty terns are well adapted to cope with high temperatures (Howell & Bartholomew, 1962), but they appear badly adapted to cope with rain. During rain, incubating adults remained on the egg, but adults with chicks flew up calling loudly and shaking their wings presumably to prevent their feathers becoming waterlogged. Rain showers frequently caused a mass exodus of adults, and chicks were left standing at their scrapes or sheltering under bushes. These chicks became waterlogged, and large chicks normally capable of flying were prevented from doing so. Most chicks were capable of withstanding wetting, but those which had lost down through pecking rapidly became weak, probably through chilling, and some died. In 1973 heavy showers fell on only six days between 28 May and 21 October, with light rain on a further eight days, and rain caused few deaths. In 1972, however, 703 mm of rain fell between 15 August and 5 November, and after 90 mm on 30/31 August all of six badly pecked ringed downy chicks were found dead. In 1973 many similarly badly pecked chicks eventually flew.

Rain also led to weight loss in chicks. In 1972 43 ringed chicks were caught on 25 and 28 August (before rain) and on 1 September after 90 mm of rain on 30/31 August. These chicks showed a weight increase of  $3.0 \pm 1.3$  g between 25 and 28 August, but a loss of  $8.2 \pm 2.1$  g between 28 August and 1 September ( $P < 0.001$ ). This weight loss during rain may be due to the adults finding difficulty in locating food when rain falls over a wide area on the sea surface, and it could increase mortality in chicks already weak through pecking and chilling.

During the wet 1972 season mortality also resulted from the accumulation of wet guano off the ground on the primaries of some chicks. The guano solidified, and rendered affected chicks flightless. They were deserted by their parents at the end of the season.

### *Deformity and feather loss*

In 1972 one chick was found with primaries missing, three with curved upper mandibles, and one with a third foot at the top of the tarsus. In 1973, 9 out of 198 (4.5%) of the ringed chicks shed remiges and/or rectrices, most of these birds being late-hatched chicks. In addition 2 (1.0%) lost their ability to coordinate and balance and eventually died (Feare, 1976).

### *Parental care of the chick in the colony*

The 15 chicks which hatched from eggs laid by the tagged birds remained at or very close to their marked nest sites (except when disturbed) until they left the colony.

For the first two days all chicks, except two which had lost one parent, had an accompanying adult almost continuously. Of the 13 pairs of adults, 10 changed over at hatching, but most were changing daily during incubation. After hatching, changeovers became more frequent and occurred throughout the day.

Some three-day-old chicks were left for several hours, when they generally hid under vegetation, sometimes digging holes under *Portulaca* and *Boerhavia*, in which they sheltered. By day 15 parents spent very little time with their chicks, usually only returning in the afternoon or evening to feed them.

Of the two birds which had lost their tagged mates, one (IE) had been incubating continuously for 12 days before hatching, and the day after hatching this bird was absent all day and returned in the evening to feed its chick—a pattern which was followed until the chick flew. The other adult (11) had been incubating continuously for five days, and it left its chick on the second day after hatching.

### *Feeding*

Most chicks appeared to be fed within 24 hours of hatching. Small chicks were fed several times by the same adult without the adult leaving, so that the parent must have brought back enough food for several feeds. The weight increments (Table III) of downy chicks showed that only small quantities of food were given. As the chicks grew and they received more food at each meal, the frequency of feeds fell from approximately 2 feeds/day shortly after hatching to one feed/2 days after the period of rapid weight increase (30 days onward, Fig. 9). During the first period of food shortage this dropped to one feed in 3 days, and the amount of food given also dropped resulting in weight loss (Table III).

During the first few days of life, when chicks were being fed most frequently, feeds were observed throughout the day, but especially in the evening and at night. The proportion of feeds occurring during the night increased in older chicks (Table III). Every evening there was a massive influx of adults into the colony: the number of feeds counted during 10 m observations of *c.* 200 chicks was 0 at 12.00 hrs, 5 at 15.00 hrs, but 24 at 18.00 hrs.

Much of the food regurgitated was well digested, and the intact food items which were preserved for subsequent identification and measurement are undoubtedly biased in favour of squid, which appeared to take longer to digest than fish, some regurgitations containing intact squid amongst well-digested fish. Also, small fish may be digested more rapidly than large ones. Although Sooty terns may possess a mechanism to retard digestion (Ashmole & Ashmole, 1967; Ashmole, 1971) so that they can carry food over long distances, samples obtained in colonies may nevertheless be more representative of food items caught nearby than of food obtained further away.

The range of foods taken was small. Samples contained three families of squid, with most individuals being Ommastrephidae, but including one individual each of Enoploteuthidae and Chirotentidae. Seven families of fish were represented: Carangidae (*Decapterus* sp.), Mullidae (2 species?) Engraulidae (?*Stolephorus* sp. post-larvae), Hemiramphidae (*Hemiramphus* sp.), Emmelichthidae (*Emmelichthys nitidus* Richardson), Clupeidae (*Sardinella leiogaster* Valenciennes) Scombridae, and Exocoetidae (*Exocoetus volitans* L.). Of these Exocoetidae, Emmelichthidae and Mullidae were the only fish brought back regularly and in large numbers. The small Engraulidae post-larvae were brought back to the colony in vast numbers on 3 and 4 August and 2 and 4 September, 1973, but were not seen at other times. In addition to these fish and squid, carapaces of decapod crustaceans and crab megalopa larvae were occasionally brought back by some adults.

The size of food items given to chicks did not increase as the chicks grew, and even small downy chicks were given flying fish approaching the maximum size regurgitated by all ages of chick: the mean length of fish given to downy chicks was 59.4 mm (range 25–126) while

TABLE III  
*Number of feeds received, weight increments per feed and the times during the growth of 15 marked chicks in 1973. (The figures of 26 August to 2 September are during the first period of food shortage—see text)*

Date	10-11 July	24-25 July	9-10 August	26 Aug-2 Sept	5-11 Sept
Age of chicks (days)	3-4	17-18	32-33	49-56	59-65
Av. no. feeds/day/chick	1.87	0.97	0.47	0.33	0.45
Wt increase/feed (mean $\pm$ s.e. and range)	5.0 $\pm$ 0.4 (2-12)	11.9 $\pm$ 0.9 (7-22)	19.0 $\pm$ 3.7 (5-59)	13.1 $\pm$ 1.1 (5-31)	13.7 $\pm$ 1.7 (6-36)
Wt. of chicks g. (mean $\pm$ s.e.)	29.3 $\pm$ 1.3	70.9 $\pm$ 3.7	153.3 $\pm$ 6.4	139.2 $\pm$ 8.4	171.6 $\pm$ 6.8
No. of feeds/interval of the day					
06.00-08.00 hrs	0				
08.00-10.00 hrs	5	4			
10.00-12.00 hrs	11				
12.00-14.00 hrs	8				
14.00-16.00 hrs	6	8	4		
16.00-18.00 hrs	10				
Night	15	16	6		

As chicks grew older and ran faster and further, catching involved more disturbance. The number of catches and weighings per day was therefore reduced in the 17-18 and 32-33 day old chicks, and these chicks were not caught more than once per day after this.

fish given to chicks about to fledge was 62.7 mm (33–150). Small chicks found these large fish difficult to eat because the adults presented them tail first, having presumably themselves swallowed them head first, and the large pectoral fins of flying fish sometimes prevented small chicks from swallowing them. When all chicks were small, rejected fish were left on the ground, but if larger chicks were present they were quickly taken. Daily records of the main prey species brought back to the colony showed considerable variation, with sudden changes in diet.

Many of the Bird Island Sooty terns fed between Silhouette and Mahé, 80–100 km to the south. This feeding area was shared by Sooty terns from Aride Island and also by noddies *Anous stolidus* (L) and *A. tenuirostris* (Temminck) and Audubons and Wedge-tailed shearwaters *Puffinus lherminieri* Lesson and *P. pacificus* (Gmelin).

During feeding it was essential that food passed quickly from adult to chick. On the few occasions seen where passage from adult to chick was slow, other chicks attempted to steal the food, and sometimes succeeded. Adults and chicks attacked other chicks which came too close, even if this meant the adult swallowing the food again.

### *Drinking*

After hatching, dipping flights continued with most of the adults drinking. When the chick begged on the adult's return to the nest site, the adult regurgitated a string of clear mucus which the chick swallowed. No food was passed, and the mucus presumably served as a drink for the chicks since they have no other source of water except for that in the food. The mucus itself may have some nutrient value (Ashmole, 1971), but its major function in this context is probably to reduce water spillage. On Bird Island the giving of drinks to chicks was a conspicuous part of adult behaviour, and the 2–3-day-old chicks of the tagged adults received a drink every 1.4 hours, while 18-day-old chicks received a drink every 2.5 hours. The rate of drink giving by adults was highest around midday.

### *Cooperation between adults in rearing chicks*

The chicks of the tagged birds begged to adults other than their parents, and obtained drinks, and occasionally food, from them. This usually happened when both of the chick's own parents were away, and therefore became more common as the chicks grew older and were left alone for longer periods. With 3-day-old chicks 14.4 % of 97 drinks were obtained from adults other than their own parents, while 58.5 % of 41 drinks were obtained from other adults by 18-day-old chicks. At 18 days old 13 of the 15 chicks of the tagged adults were seen to take drinks from other adults. Adults with chicks of their own attacked other chicks which begged to them, and two tagged birds which had lost their own chicks (and did not re-lay) confirmed that it was mainly failed breeders that gave this "assistance". A chick was also seen being fed by an immature bird with dark breast markings, and it was known that this bird had not attempted to breed.

This assistance from other adults, elicited by the begging of the chicks, was of great survival value to some chicks, especially where one of its parents had died as in the cases of birds 11 and 1E. None of the neighbours around the site of 11 lost their eggs or chicks, and chick 11 rarely received drinks from other adults. With only one parent caring for it this chick died when 47 days old. The neighbours of 1E deserted their egg shortly after chick 1E hatched, and this pair was seen giving drinks to chick 1E on its first day, its own parent being absent. Subsequently chick 1E frequently took drinks from this pair, and was

also fed by them. This chick was last caught when 59 days old when it weighed 193 g (above the average for group 2 birds hatched at the same time (Fig. 9)). It left the colony at 74 days old, compared with an average of 83 days for the other chicks of the tagged birds.

#### *Twinning experiment*

To see whether a pair of Sooty terns could raise more than one chick, on 24 July six pairs of twins were prepared using wet, recently hatched chicks. In three of these pairs one chick died within the first two days; in a further two pairs one of the chicks was adopted by a neighbour. In the only pair that remained as twins both chicks grew slowly, one dying on the 10th and the other on the 34th day. This inconclusive experiment, together with the failure of bird 11 to raise a chick without assistance, suggests that a pair of Sooty terns cannot raise more than one chick, but further study is required.

#### *Post-fledging parental care*

When chicks could fly well they frequently flew over the colony with their parents, adults and juveniles continually calling to each other. These chicks were still being fed by their parents, both on the ground and occasionally in the air (Feare, 1975). These calls were heard through the day and night, and were also heard between juveniles and their presumed parents at sea. Although juveniles appeared to leave the colony with their parents (see Gould, 1974), three tagged birds were seen to spend a short time at what had been their nest sites 2, 5 and 6 days after their chicks had left. Juvenile dependence upon adults for food may be short-lived since a bird which hatched on Bird Island on 17 July 1973 and was last caught on 29 September was recovered in Northern Australia on 13 January 1974, indicating an extensive dispersal of juveniles.

#### *Adult mortality during the breeding season*

During the 1973 season 50 adults were found dead or dying. Most deaths occurred during the first half of the season, and 31 (62%) involved birds with broken or dislocated wings. Of these 31, 1 was found in the colony, 1 in the sea, and the remainder on the beach (some were wet, suggesting they had swum ashore). How these injuries occurred is not known, but the finding of so many on the beach suggests that they occurred at sea, possibly resulting from collisions with other birds or with waves. Other causes of death were oiling (1 bird), blindness (1), caught in *Cassythra filiformis* L. (4), starvation (2) and cause unknown (11). Birds in the "cause unknown" category were not underweight, and it is unlikely that they had starved. In addition to birds found dead on the island some may have died at sea. On 10 July an incubating bird was found covered in blood with the skin from one side of its neck torn away. On 19 July a weak adult was found with a gash in its belly and bleeding badly. These wounds may have been fish bites, sustained while the birds were feeding.

Adult mortality during the breeding season was low. All of 28 birds ringed shortly after their eggs were laid were known to be alive when their chicks left the colony. Similarly, all of 30 dyed adults, which had lost their first egg and subsequently relaid, were alive when their chicks could fly.

## Part II. The effects of taking eggs

### Methods

The commercial method of egg collecting is to remove all eggs from a given area daily during laying to ensure that all eggs collected are fresh. In this study eggs were removed experimentally in areas of the colony in which laying was just beginning, and egg freshness was checked by examining the germinal disc.

Incubating adults were caught by hand or a hand net, and their eggs collected. The adult was ringed, weighed and dyed on the neck, breast and under the wings, using Auromine ON 150 or Magenta P 150 dyes dissolved in 70% denatured ethanol. Auromine (yellow) dye was still clearly visible at the end of the season, 5 months after application, but the magenta was visible for only 3–6 weeks. The egg was weighed to the nearest gram. The following experiments were carried out:

R1—131 fresh eggs removed and adults dyed yellow on 7–9 June (the mates of 5 of these birds were also ringed and dyed).

R2—On 6–8 June 74 fresh eggs were marked with labels, and the adults were caught and marked (yellow) and their eggs removed on 20–21 June, after 15 days incubation (the mates of 10 of these birds were also ringed and dyed).

R3—150 fresh eggs removed and the adults marked (magenta) on 22–23 June.

R4—81 fresh eggs removed and the adults marked (yellow) on 5–6 July.

R1 (2)—The fresh replacement eggs of 52 birds from experiment R1 were removed and the adults re-dyed (yellow) on 19–22 June.

Once the first group of birds had been dyed the colony was searched daily for marked birds with eggs. When one was found, the scrape was marked with a wooden label, the egg weighed to the nearest gram, and a description of the site recorded for subsequent location. Every effort was then made to catch the marked bird and identify the ring, but in a few instances eggs were predated before the adult was caught, in which case the adult was not identified.

After discovery, every replacement egg was visited daily and the identity of the incubating bird (i.e. dyed or not) was recorded. This was continued until the egg disappeared or hatched, and the date of laying was taken as 28 days prior to hatching. If an egg was lost prior to hatching, and the appearance of the egg had not been observed following the establishing of a territory by the adults, then the date of laying of the replacement egg was unknown.

On the day of hatching the chick was ringed, and its growth (weight) and survival followed as described in Part I above. Replacement eggs were laid throughout the colony, and visiting each site to search for and catch each chick took a long time and caused much disturbance. In order to reduce both time and disturbance linear measurements were not taken.

### Results

#### *Proportion of birds that relaid*

Table IV gives the numbers of marked birds from each experiment that were subsequently found incubating second eggs. (In the first three days after removal of the first egg, four marked birds of experiment R1 adopted eggs. These four birds were left to incubate their adopted eggs, but in subsequent experiments the adopted eggs of two other birds were removed.)

The proportions of birds found with replacement eggs are minimal because it is unlikely, in such a large colony, that all of the incubating dyed birds were found: all of the birds from R1 may have re-laid.

The results of experiment R1, R3 and R4 show a marked seasonal drop in the tendency of birds to re-lay. The proportion of R1 birds which laid a third egg (experiment R1 (2)) was the same as the proportion of R3 birds that re-laid, and their eggs were laid at the same time. Some of the R3 birds may have laid previously, but as the colony was not heavily exploited for eggs in 1973 most of the R3 birds must have been laying their first eggs. The laying of a previous egg had therefore not affected the ability of the R1 (2) birds

TABLE IV  
*The proportions of birds found on replacement eggs after the removal of the first egg*

Experiment	Date eggs removed	No. removed	No. found on replacement eggs	% found on replacement eggs
R1	7-9 vi	127*	118	94.0
R1 (2) (third eggs)	19-22 vi	52	20	38.5
R2 (incubated 14 days)	20-21 vi	74	49	67.5
R3	22-23 vi	150	59	38.7
R4	5-6 vii	81	8	9.7

\* Excludes the four pairs which adopted eggs.

to re-lay again, and that the proportion laying third eggs was simply following the seasonal pattern.

A considerably higher proportion of R2 birds (whose eggs had been incubated for 15 days) re-laid than with R3 and R1 (2) birds, the eggs of all three groups of birds being removed around the same time.

#### *Time taken to relay*

Figure 14 gives the interval between egg removal and its replacement for individually known birds in the five experiments. The mean interval between the first and second eggs in experiment R1 is calculated assuming that all eggs laid after 20 days following the removal of the first egg were in fact third eggs, the second having not been found (the earliest replacement eggs were laid after 10 days, and presumably no third eggs would therefore appear before 20 days: the earliest known third egg was in fact laid 22 days after the first had been removed). No birds from later experiments were found on what may have been third eggs. The time taken to re-lay did not differ significantly between experiments, showing that neither the stage of the laying season nor previous laying history affected this time. None of the pairs in which both birds were marked split up before re-laying, as found by Ashmole (1963).

#### *Sites of replacement layings*

In experiment R1 replacement eggs were laid when the colony was still expanding, and were found all over the colony with no marked tendency to lay close to their original sites (Fig. 15). R3 birds tended to lay in the general area, but not in the same sites, as the first eggs (Fig. 16) but between the experimental removal of the first eggs and the laying of replacements this area had been exploited by labourers. Consequently when these dyed birds were ready to re-lay this area was one of the areas of heavy laying in the colony at the

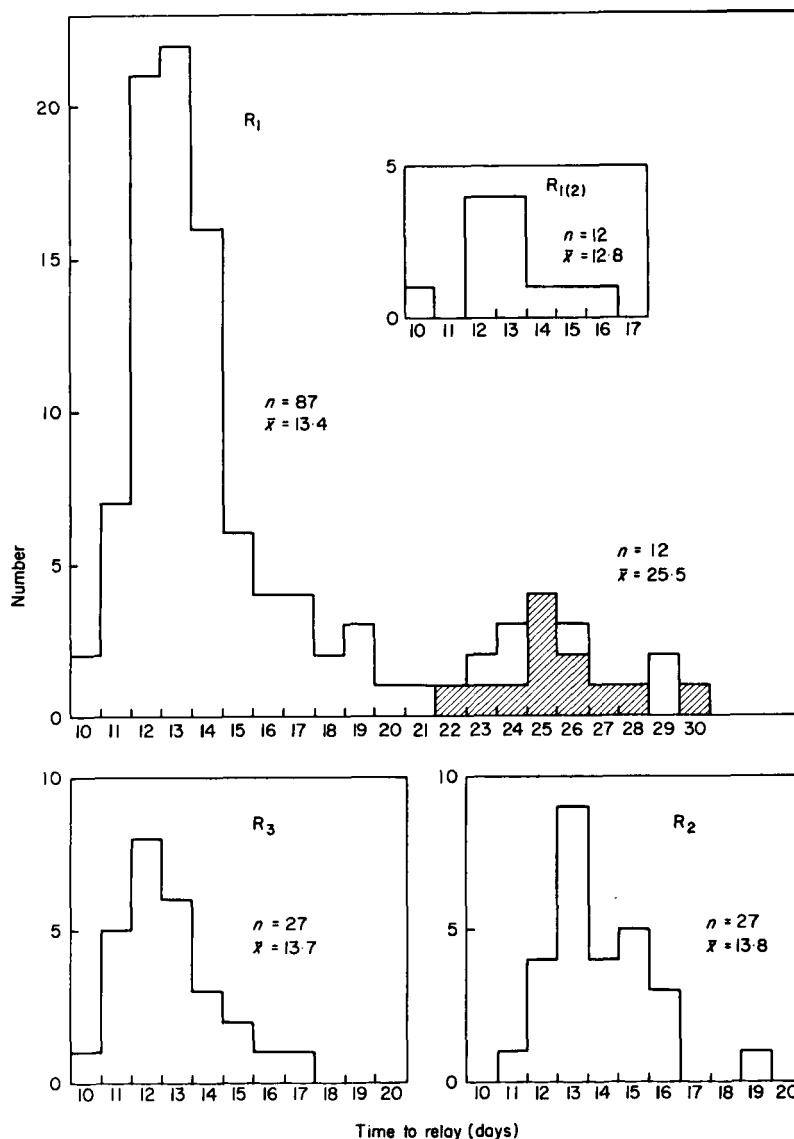


FIG. 14. The interval between removal of the first egg and the laying of a replacement in each experiment. The hatched columns in the histogram of experiment R<sub>1</sub> are eggs which were known to be third eggs, and the interval between removal of the second and laying of the third egg is shown in the inset of this graph (i.e., R<sub>1</sub>(2)).

time. This tendency for replacement eggs to be laid where mass laying was proceeding, and therefore to be laid amongst eggs of about the same age, was marked, and was also shown by R<sub>1</sub> (2) birds laying third eggs, many of these being laid in the north-east corner of the colony (Fig. 15). The eight replacement eggs laid in mid July, when mass laying had stopped, were scattered throughout the colony (Fig. 16).

R<sub>2</sub> birds, which had been incubating for 15 days, tended to re-lay where their first eggs

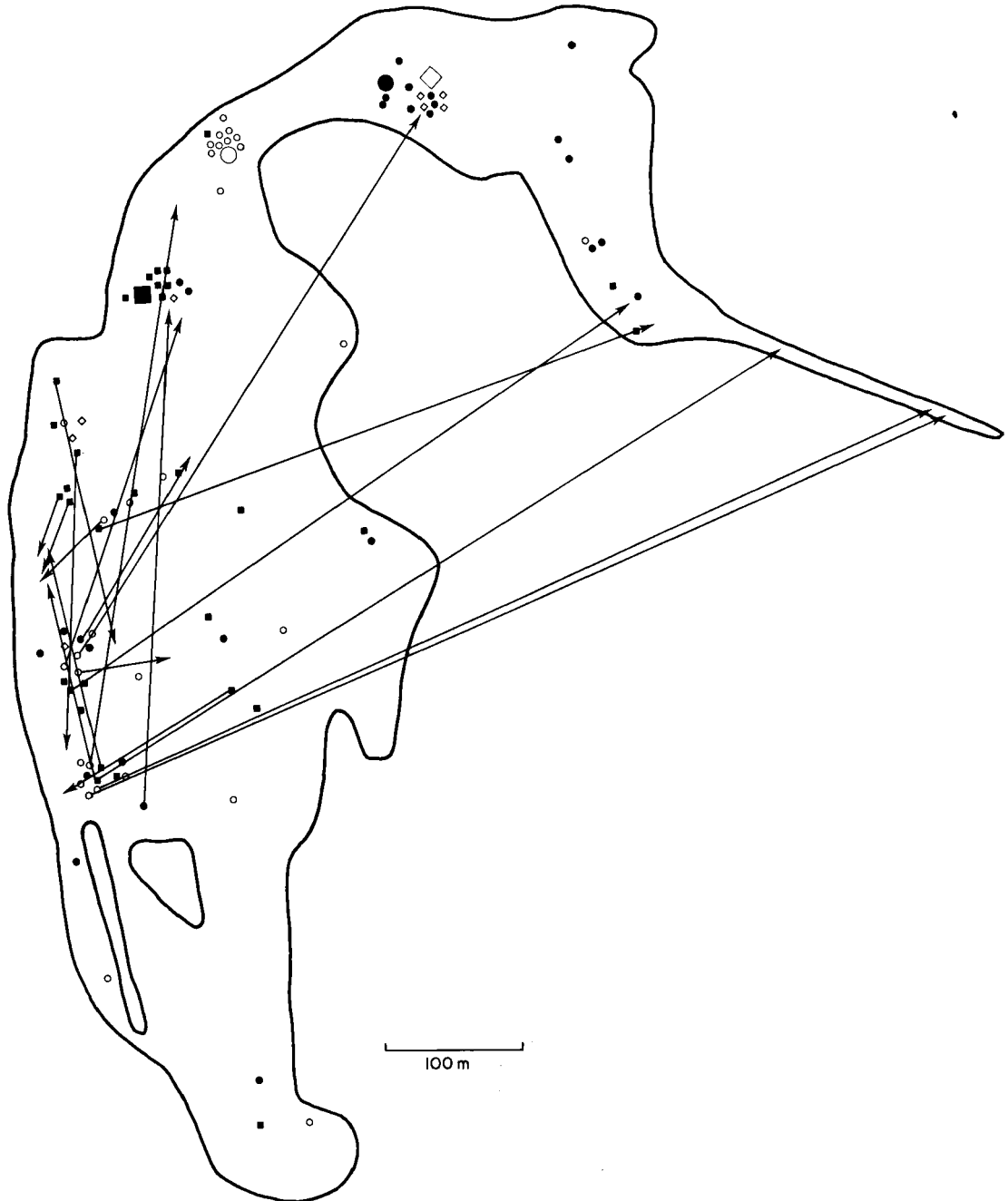


FIG. 15. The sites of laying of replacement eggs (small symbols) in relation to the four sites from which first eggs were removed (large symbols) in experiment R1 (eggs removed 7–9 June 1973). Arrows show where third eggs were laid when the second egg was removed.

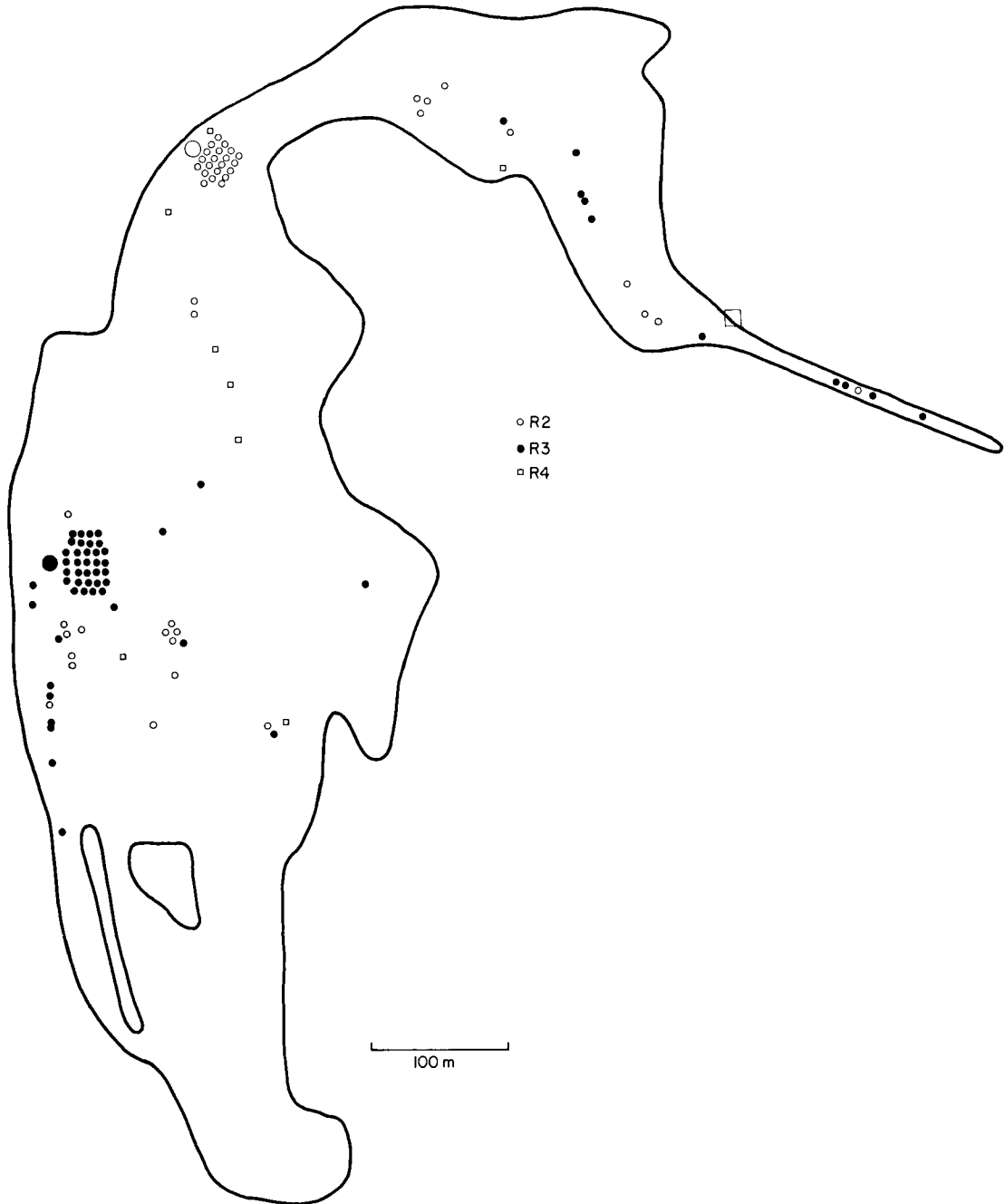


FIG. 16. The sites of replacement eggs (small symbols) in relation to the site at which the first egg was removed (large symbols) in experiments R2 (half incubated eggs removed 20–21 June), R3 (fresh eggs removed 22–23 June) and R4 (fresh eggs removed 5–6 July).

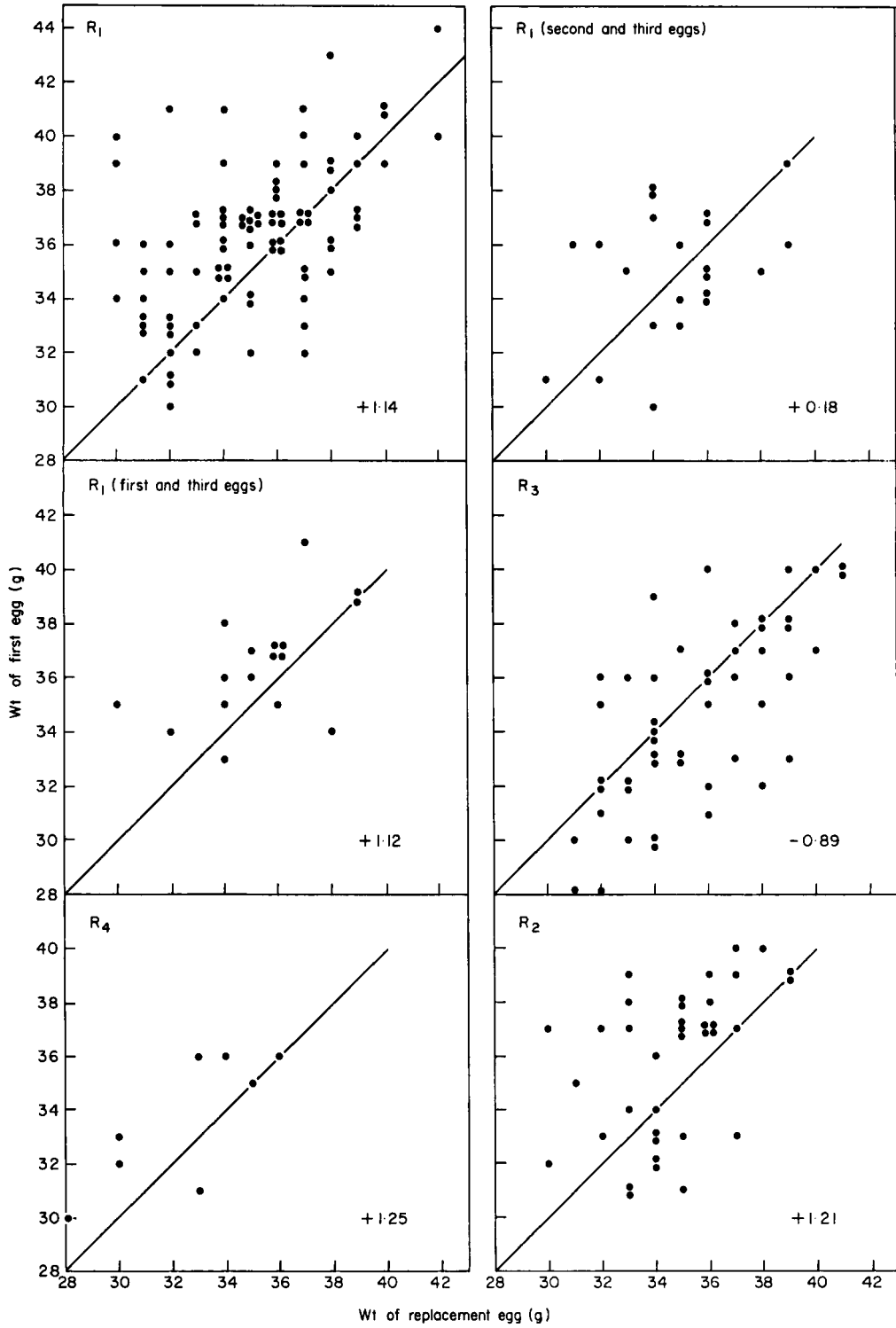


FIG. 17.

were laid, and in the interval between egg removal and replacement many dyed birds were seen in the area where the eggs were collected. Where fresh eggs were removed, dyed birds quickly left the area. Birds which had half incubated their eggs had presumably formed a strong attachment to their nest sites and defended them against birds attempting to settle there. This may explain the high proportion of R2 birds that re-laid in comparison with R3 and R1 (2) birds. R2 birds which re-laid elsewhere tended to do so in areas of mass laying.

#### *Weights of first and replacement eggs*

In Fig. 17 the weights of first and replacement eggs in each experiment are plotted against each other. The scales of the axes are the same, so that if the weights of the two eggs were the same, all points would fall on a 45° line. If the first egg was heavier than the replacement the point would fall above the 45° line and *vice versa*. In all experiments except R3 the replacement egg was on average about 1 g lighter than the first egg, but in R3 the replacement averaged 0.89 g heavier than first eggs. These replacement eggs were laid on 2–7 July, while the first eggs were laid on 22–23 June. Eggs collected for human consumption on 5 July were heavier than those collected on 22 June (see above) and Fig. 5 suggests that egg weights were tending to rise at the end of June. The weights of replacement eggs therefore appeared to follow the seasonal trends of egg weights, and the lower weights of most replacement eggs are probably not indicative that females were unable to produce heavy eggs as a result of having previously laid an egg.

#### *Survival of replacement eggs*

In the marked squares late eggs survived less well than early ones and this seasonal effect also applied to replacement eggs. R1 eggs survived less well (70.8% of 49) than eggs laid 7–9 June (Fig. 7) when the first eggs of the R1 birds were laid, and the survival of later replacement eggs was even lower (R3—42.4% of 59; R4—0.0% of 8).

In all experiments a higher proportion of eggs that were laid amongst older eggs was lost (average 64.0%) than of eggs laid amongst eggs of the same age (i.e. in areas of current mass laying—average 34.6%).

#### *Chick mortality*

The mortality of chicks from replacement eggs was also higher than chick mortality from eggs laid on 7–9 June (Table V) following the seasonal pattern of mortality (Table II). As in the later chicks from the marked squares, mortality in the chicks from replacement eggs was high in older chicks, rather than being concentrated in the first 10 days of life as found in chicks that hatched from eggs laid in mid June.

Although chicks from experiments R3, R1 (2) and R2 all hatched at about the same time (31 July–7 August), the mortality of R3 chicks was considerably lower than the other two

---

FIG. 17. The relative weights of first and replacement eggs in the experiments (see text for explanation). Figures in the lower right corner of each graph show the relation between the mean weights of the first and second eggs e.g., in R1 first eggs averaged 1.14 g heavier than replacement eggs.

TABLE V  
Mortality of chicks which hatched from replacement eggs

Group	No. hatched	No. (and %) died	No. (and %) died <10 days		No. (and %) died >30 days		Laid with eggs of same age		Laid amongst older eggs		Cause of death	
			No. (and %) died	(and %)	No. (and %) died	(and %)	No. laid	(and %)	No. laid	(and %)	Pecked	Starved
R1	35	14 (40.0)	5 (35.7)	5 (35.7)	9	6 (66.7)	26	8 (30.8)	4 (28.6)	2 (14.3)	8 (57.1)	
R3	25	12 (48.0)	6 (50.0)	3 (25.0)	24	11 (45.8)	1	1 (100.0)	1 (8.3)	2 (16.6)	9 (75.0)	
R1 (2)	8	6 (75.0)	2 (33.3)	3 (50.0)	4	2 (50.0)	4	4 (100.0)	1 (16.7)	0 (-)	5 (83.3)	
R2	26	18 (69.2)	5 (27.8)	5 (27.8)	6	2 (33.3)	20	16 (80.0)	7 (38.9)	1 (5.6)	10 (55.6)	

groups. In these groups, (but not in R1) mortality was higher in chicks that were not among chicks of approximately the same age than in chicks from eggs laid in areas of mass laying (Table V). Chicks from R1 eggs laid amongst older eggs were only about a fortnight younger than their neighbours, while the chicks from later groups were about a month younger, and this age difference appeared to reduce survival.

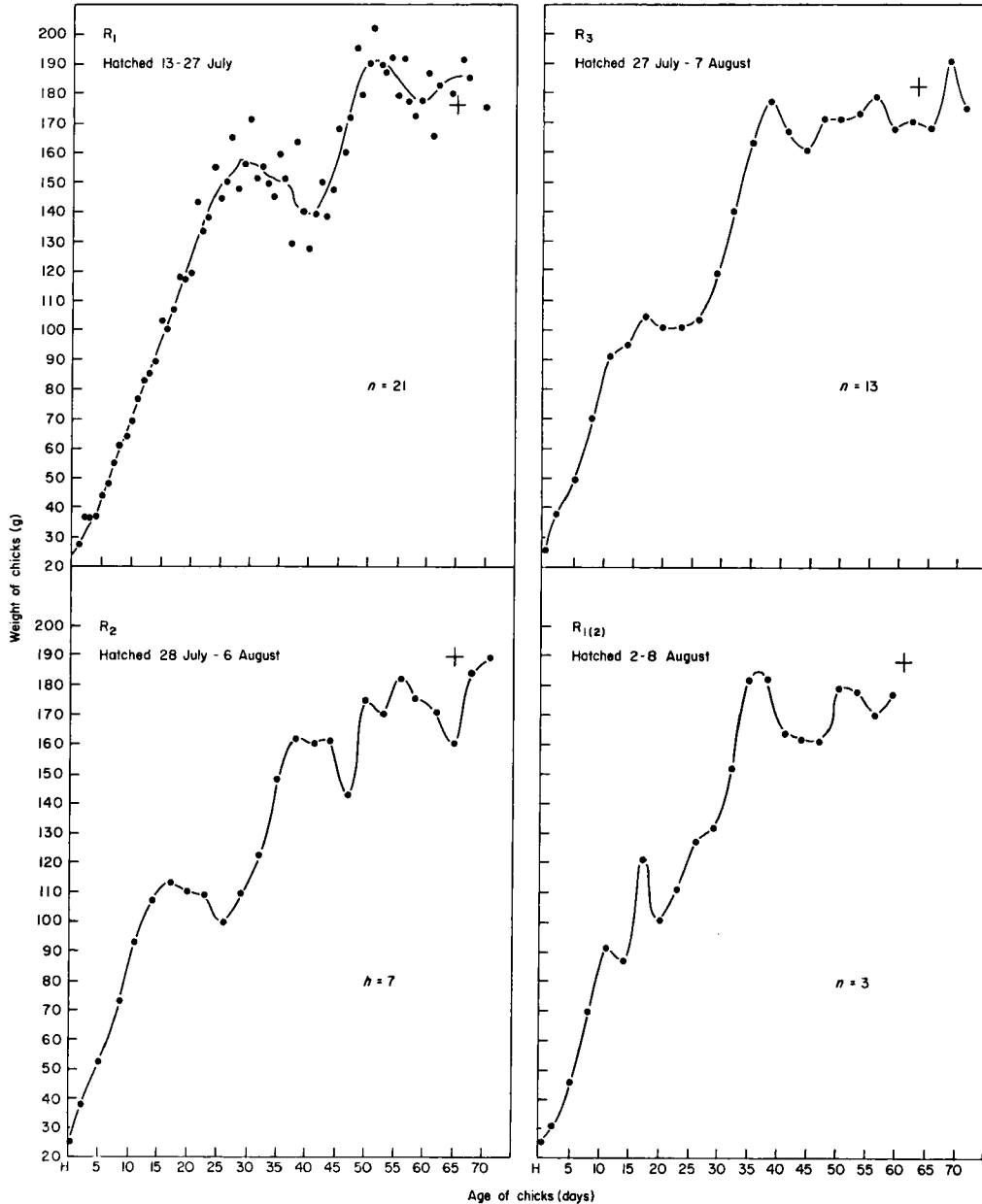


FIG. 18. The growth in weight of chicks which hatched from replacement eggs. For explanation see legend to Fig. 9.

Thus birds laying replacement eggs stand a greater chance of rearing a chick if they lay in areas of mass laying than if they lay in already densely colonized areas, and 66.8% of birds which re-laid while heavy laying was still occurring did so in areas of mass laying (excluding R2 birds as mentioned above).

### *Chick growth*

Owing to small samples the growth curves of groups R3, R2 and R1 (2) (Fig. 18) are drawn from the average weights over 3-day periods. The curves followed the pattern shown in the birds from the marked squares (Fig. 9), i.e. a phase of rapid growth ended at the first period of food shortage, which occurred at a lower weight and earlier in later hatched groups of chicks. After a second period of rapid growth weights fluctuated, but in these surviving chicks the early experiences did not appear to affect the ages and weights at which these birds became uncatchable (Fig. 18, cf. Fig. 9). In fact ages were lower and weights higher than in the group 5 birds from the marked squares, and the chicks from replacement eggs may have become uncatchable at a time of food abundance. Alternatively, the higher

TABLE VI

*Mortality of chicks of different hatch weights from eggs laid in the main laying season and from late replacement eggs*

Hatch wt (g)	% dying ( <i>n</i> in brackets)		Increase in % dying
	Main season	Late replacement	
18-24	47.3 (91)	66.7 (21)	19.4
25-28	27.4 (124)	62.1 (29)	34.7
29-34	29.8 (47)	40.0 (10)	10.2

mortality of these later chicks may have selected against all but the fastest growing ones, which are likely to be the heaviest at hatching (Fig. 12). This suggestion is supported by Table VI, which shows that although the mortality of chicks of all hatch weights was higher in the latest groups, the main increase in mortality was suffered by birds in the middle hatch weight class.

### **Discussion**

Many aspects of Sooty tern biology in the Seychelles, e.g. incubation period, diurnal synchrony of laying, and diet are similar to what has been found elsewhere (Ashmole, 1963; Ashmole & Ashmole, 1967; Potthoff & Richards, 1970; Robertson, 1964). Dinsmore (1972) found much higher feeding frequencies on the Dry Tortugas than observed in the Seychelles and suspected by Ashmole (1963) on Ascension. However, Dinsmore did not mention chicks drinking, and since his chicks took 8-9 weeks to fly, as in the Seychelles, some of the feeds he observed may in fact have been drinks. Differences between Bird Island and Ascension appear to be related to poor food supply on the latter island, leading to longer incubation shifts, slower chick growth which affected wing and bill length as well as weights, and much higher chick mortality due to starvation. Food scarcity may also have led to the increased time taken for pairs to re-lay on Ascension (16-20 days cf. 12-13 days on Bird Island). After losing an egg the pair must meet, presumably at the colony, to recommence courtship and stimulate ovulation. On Bird Island most pairs, at least

early in the laying season, changed over on the egg every day, so that after egg loss the pair would meet within 24 hours. On Ascension incubation shifts averaged 5–6 days, and assuming the non-incubating member of the pair did not return to the colony during this time, it would take much longer for the pair to meet. Once the pair has met, the female must accumulate sufficient food to produce another egg, and if necessary the pair must select and establish a territory.

The proportions of birds found to have laid replacement eggs in all of the Bird Island experiments except R4 are greatly in excess of those found by Ridley & Percy (1958) on Desneufs (6–29 % average 16.5 %) and by Ashmole (1963) on Ascension (13 %). Ashmole's experiments were performed late in the egg-laying season (which may also account for his finding that eggs lost late in incubation were less likely to be replaced than eggs lost earlier, in contrast to the Bird Island observations) but the relation between Ridley & Percy's experiments and peak laying is unknown. Ridley & Percy also found dyed birds on other islands, and the terrain on Desneufs is less amenable to the finding of marked birds than is that of Bird Island (pers. obs.). These factors would all reduce the proportion of re-laying birds that was discovered, but the timing of experiments in relation to the timing of the laying season is of overriding importance.

The synchronous laying found in Sooty terns also occurs in many other seasonally and non-seasonally breeding birds, and the timing of laying (i.e. of peak laying) is often thought to be related to a certain level of food availability—that which permits females to produce eggs (Perrins, 1970). In some species food intake of the female prior to laying may be increased by courtship feeding (Royama, 1966; Nisbet, 1973), thereby permitting earlier breeding, but this is rare in Sooty terns (at least at the colony). While many species may breed when food availability reaches the required level, and thus have a degree of synchrony forced on them, the synchrony found in certain colonial tropical seabirds requires more explanation, especially where breeding seasons do not appear to be related to cyclical abundances of food, e.g. Sooty terns on Ascension (Ashmore, 1963).

Ashmole & Ashmole (1967) found that on Christmas Island (Pacific) different seabirds with similar diets bred at different times of year, and a similar situation prevails in the Seychelles where four kinds of breeding occur:

- (i) year-round breeding *Gygis alba*, *Phaethon lepturus* Daudin (and possibly *Anous stolidus* on some islands),
- (ii) extended annual breeding (no marked synchrony)—*Anous stolidus*, *A. tenuirostris*, *Puffinus lherminieri* (*Sula dactylatra* and *S. leucogaster* (Beddaert) may also fall into this category or (i) above),
- (iii) restricted annual breeding—*Sterna fuscata*, *S. dougalii*, *Puffinus pacificus* (and possibly *Sterna sumatrana* Raffles),
- (iv) restricted non-annual breeding—*Sterna anaethetus* Scopoli (approx. 8 month cycle—Diamond, in press).

Although the diets of these species have not been studied it can be inferred from the Ashmoles' (1967) study that they are probably similar. Of the non-annual breeders it is not known whether breeding numbers or success vary seasonally (in *Gygis alba* fledging time varies seasonally—D. Lloyd pers. comm.) but the predominance of breeding during the south-east trades (May to October) suggests that food may be more abundant during

this season. In the seas around Seychelles primary, secondary and tertiary production are higher during the south-east trades than during the usually calm north-west monsoon (Cushing, 1971). At sea in the Indian Ocean, Sooty terns are more abundant in areas of strong winds (Bailey, 1968), and wind may be a factor restricting their breeding to the south-east trades. If wind is important, then adults may spend the non-breeding season to the south of Seychelles, where the south-east trades blow continuously. However, the occurrence of both extended and restricted (i.e. synchronous) breeding during the south-east trades suggests that the extreme synchrony of Sooty terns is not due entirely to the seasonal nature of the food, and although food may be more abundant during the south-east trades, this study has shown that there may be periodic shortages. These shortages did not cause mass starvation and they were not sufficiently severe or prolonged to reduce the rate of wing and bill growth (cf. Ashmole, 1963). Even when food appeared plentiful sudden changes in diet, and the feeding of large fish to small chicks, suggest that adults were catching what was available rather than selecting fish appropriate to their needs. In this situation the pecking of chicks which wander into other adults' territories is presumably an adaptation to reduce the chances of these adults "wasting" food on chicks other than their own, rather than preventing adoption of other chicks (Ashmole, 1963).

The synchrony observed in Sooty terns appears to be of social significance, since both egg and chick survival were higher where eggs had been laid at approximately the same time as the surrounding eggs than where they were laid among partly incubated eggs. Reduced losses of eggs in areas of mass laying appeared to be due to more effective parental care by birds all at approximately the same stage of breeding. Early breeders lost eggs to predators through being excessively wary and prone to panic flights, while late breeders may have had reduced success through laying among birds whose eggs were about to hatch, and whose extreme aggressiveness at this time may have disturbed the incubation shifts of the late birds. This could also account for the increased variability of incubation periods observed in birds breeding late. However, a decline in egg weight and a lengthening of incubation shifts with later breeders, both of which were shown to be seasonal effects rather than due to young birds breeding late (Harrington, 1974) and laying smaller eggs (Richdale, 1954), indicate that some seasonal factors may have contributed to losses of later eggs. Sooty tern egg and chick weights were correlated, as in woodpigeons and domestic hens (Murton, Westwood & Isaacson, 1974; Skoglund, Seeger & Ringrose, 1952), but the hatching success of heavy eggs in this study was not significantly higher than that of light eggs. Chicks among others of about the same age suffered lower mortality due to pecking, and possibly also due to predation, than chicks among older ones. This could result from several factors: (i) during disturbances, late, and less mobile, chicks would tend to get isolated and be more liable to predation (Cattle egrets were seen carrying chicks more frequently at the end of the hatching season than at its peak, due both to this isolation of young chicks as older ones ran away, and to the lower number of adults in the colony); (ii) after disturbances the younger chicks took longer to get back to their nest sites, and on the way back were pecked by adults and large chicks; (iii) as the vegetation (especially *Portulaca*, *Tribulus* and *Boerhavia*) was killed by guano, much potential shelter for chicks was lost; (iv) young chicks take a long time to swallow large food items, and large chicks sometimes robbed them of their food—if this happened frequently the young chicks might starve. However, in later chicks an increased mortality of older birds again suggests that late breeding may be disadvantageous with respect to (unknown) seasonal factors. Thus

synchrony increased the chances of successful breeding, as did early laying, and on both of these counts birds that relaid were at a disadvantage. Table VII shows the production of flying juveniles by birds which laid during the main laying period (groups 1–4 in marked squares 1, 2 and 3: this does not take into account the high egg losses around the edge of the colony, but this edge represented only a small proportion of the total area of the colony of which squares 1, 2 and 3 were representative), compared with that of birds which laid replacement eggs. Output decreased from 0.58 chicks per pair of adults in the main season to none in the latest replacement layings.

The age of first breeding of Indian Ocean Sooty terns is not known, but in Atlantic and Pacific colonies it ranges from 4 to 9 years (Robertson, 1969; Harrington, 1974), most birds probably first breeding when six years old. The small number of birds with dark markings on the breast (which Harrington (1974) found to be up to five years old) which bred on Bird Island, suggests that age at first breeding here is similar to that elsewhere, although Carrick, Csordas & Ingham (1962) in mammals, and Johnson & Hardy (1962) and Orians (in Lack, 1968) in birds, have shown that individuals may breed earlier in exploited or expanding populations. The Bird Island colony has been exploited and is still

TABLE VII

*The output of fledged juveniles from the main laying season (groups 1–4) and from the re-lay experiments*

	No. of eggs laid	No. young fledged	Proportion fledged
Main season	250	145	0.58
R1	49	23	0.47
R2	49	11	0.22
R3	59	13	0.22
R1 (2)	20	2	0.10
R4	8	0	0.00

expanding, and the discovery of a young bird with wholly dark underparts incubating in 1973 shows that in this population a few very young birds may breed.

Between fledging and first breeding further mortality will occur, especially when juveniles become independent of their parents, a time which is critical in Great frigate birds *Fregata minor* (Gmelin) (Nelson, 1967). Robertson (1969) found that the ranges of adult and juvenile Sooty terns diverged about two months after they left Dry Tortugas colonies, the juveniles crossing the Atlantic while adults remained in the Caribbean area. Juveniles therefore have only two months in which to learn to feed themselves, a shorter time than in many other terns (Feare, 1975). In seabirds body colour and bill size appear to be related to feeding methods (Ashmole, 1968; Ashmole & Ashmole, 1967; Cowan, 1972; Feare, 1967; Phillips, 1962; Simmons, 1972), and the dark ventral surfaces of juvenile Sooty terns (cf. white in adults) and their shorter bills suggest that they may feed in a different way from adults (e.g. by "contact dipping" rather than "chasing"—Feare, 1975) during their early independent life. Nevertheless, gaining independence is likely to be hazardous, and more late than early-hatched young may die at this time, as in Manx shearwaters *Puffinus puffinus* (Brunn.) (Harris, 1966; Perrins, 1966), Herring gulls *Larus argentatus* Pontopp. (Nisbet & Drury, 1972), Franklin's gulls *Larus pipixcan* Wagler

(Burger, 1972) and the South African gannet *Sula capensis* (Lichtenstein) (Jarvis, 1974). Mortality during the first year is therefore likely to be higher than in succeeding years, a situation demonstrated in gulls (Coulson & White, 1959; Patterson, 1965; Brown, 1967), terns (Austin & Austin, 1956) and other seabirds and land birds (Lack, 1954, 1966). Adult mortality in Sooty terns is likely to be low, as they are known to survive for at least 32 years (Clapp & Sibley, 1966; Austin, 1965 and pers. comm.), but there is evidence that mortality rate increases after the 29th year (Austin, pers. comm.).

In a stable population the egg production of one age group throughout its life is equal to one year's production from all age classes in the population. Thus if 1000 eggs are laid in one year, the birds produced from these eggs must in their lifetime lay 1000 eggs.

In Sooty terns that laid during the main laying season 1000 eggs produced 580 flying chicks (Table VII). Before breeding these birds would suffer a high post-fledging mortality and then 5 years (assuming age at first breeding 6 years) of lower mortality. If an upper limit to their lives is put at 31 years the birds will have a potential breeding life of 25 years, during which they will die at a rate similar to that in the 5 years before breeding, and each will produce 0.5 eggs/year. In Table VIII these figures are used to calculate the egg production of a cohort of 1000 eggs at different levels of post-fledging and adult mortalities. Post-fledging mortalities for several larids have been estimated at 30%–50% (Coulson & White,

TABLE VIII

*The estimated production of eggs during their lives of Sooty terns that hatched from 1000 eggs laid during the main laying season in 1973 at different levels of post-fledging and adult mortality. These figures assume an age of first breeding at 6 years and a maximum age of 31 years i.e. a breeding life of 25 years*

Adult mortality (%)	Post-fledging mortality (%)				
	30	40	50	60	70
5	2313	1983	1657	1322	991
10	1110	961	800	640	480
15	591	507	423	338	253

1959; Patterson, 1965; Brown, 1967) and large aerial pelagic birds appear to have adult annual mortalities of 3%–7% (Ashmole, 1971) but this may be somewhat higher in smaller birds.

Until the mortalities of Seychelles Sooty terns are known it is impossible to estimate what proportion of the eggs laid represents an excess (i.e. over 1000 in Table VIII) and can be cropped, but it appears from Table VIII that a low (10%–20%) level of exploitation will be allowable. Eggs laid after the main season are less productive (Table VII), and eggs laid by birds in experiments R2 and R3, of which only 22% survived to fledging, could not maintain a stable population even with post-fledging and adult mortalities as low as 30% and 5% respectively (output per cohort of 1000 eggs as calculated above would be 878 eggs).

The commercial system of exploitation differs from my experimental exploitation in that all eggs in a given area of a colony are removed. Eggs that are eventually left to hatch will all be laid with eggs of about the same age, and may therefore stand a better chance of success than the experiments indicated, even though they are laid late. In Herring gulls the removal of the main crop of eggs effectively prolonged the laying season (Nisbet & Drury,

1972), but although many flying young resulted from the re-nesting attempts, post-fledging mortality in these juveniles was exceptionally high. Robertson (1969) suggested that the migration route of juvenile Dry Tortugas Sooty terns was that which gave them the most favourable weather conditions for their Atlantic crossing. If this is true also of Seychelles birds, then the timing of the migration in relation to the southerly retreat of the south-east trades in October–November, and the occurrence of cyclones south of Seychelles in the southern summer, could be critical for the survival of late birds.

The productivity of late laid eggs is therefore probably very low, and the replacement eggs may not in fact contribute to future generations. It is precisely these eggs that the present close-season regulations protect, and on biological grounds these regulations could therefore be withdrawn without detriment to the birds. However, exploitation of eggs laid during the peak laying period should be carefully controlled, and until data on age at first breeding and post-fledging and adult mortality are available for Seychelles populations, these parameters must be assumed to be high in order that egg losses due to cropping are kept at a level which the Sooty tern can tolerate.

### Summary

The aims of this study of the breeding ecology of Seychelles Sooty terns *Sterna fuscata* were to discover factors that limited the output of young from unexploited colonies, and how this output was affected by the removal of eggs, following claims that over-exploitation of the eggs had led to considerable reductions in the size of tern colonies.

Egg laying in the Bird Island colony (c. 395,000 pairs in 1973) was highly synchronous. Most pairs changed over regularly during incubation, but incubation shifts tended to lengthen as the season progressed. Incubating birds lost c. 5% of body weight/day. The incubation period was 28 days. Hatching success averaged 75% in the colony centre, but only 10% at the edge where predators accounted for all losses. Chicks grew rapidly for the first 30–35 days, but this period of rapid growth was curtailed by food shortage. Heavy chicks at hatching grew faster, and flew earlier and at a greater weight than light chicks. Food shortage did not affect rates of bill and wing growth. Overall chick mortality, after correcting for the increased mortality due to observer disturbance, was 26.6%, but early-hatched chicks survived better and flew earlier and at a greater weight than late-hatched birds. Most losses were due to pecking by adults, and starvation and predation were not important. Rain increased mortality, especially of pecked chicks.

Chicks were fed mainly on fish and squid. The size of food items brought by the parents did not increase as the chicks grew; this, together with frequent and sudden changes in diet, suggested that adults were taking what they could get, and not selecting preferred prey. Chicks were regularly given drinks, often by adults other than their own parents. Sooty terns appear unable to raise more than one chick. Post-fledging parental care lasts only two months, and young Sooty terns may feed in a different way from adults.

Ability to relay after egg loss declined seasonally, and eggs lost early in the season were probably all replaced. Replacement eggs were laid 12–13 days after loss of the first, and some birds laid three eggs in the 1973 season. Birds tended to relay in areas of current mass-laying: this enhanced egg and chick survival. Previous laying history did not affect the weights of replacement eggs, as the lower weights of most replacements merely reflected seasonal trends of egg weights.

In the Seychelles the south-east trade wind period (May–October) appears to be a period of high food availability, but there may be unpredictable shortages.

Age at first breeding, post fledging mortality and adult mortality are not known for Seychelles sooty terns, but by extrapolation from other areas it is suggested that only 10–20% of eggs laid during the main laying season should be cropped. The present regulations relating to a close season for egg collecting could be withdrawn.

This work was made possible by a Natural Environment Research Council grant to Professor G. M. Dunnet which allowed me to hold a Research Fellowship at the University of Aberdeen. I am grateful to NERC for this financial support, and to Professor Dunnet for making the initial arrangements and for continuing assistance with the grant while I was in the Seychelles. Professor Dunnet was a constant source of encouragement throughout the project, and he gave invaluable advice and practical assistance at the start of the 1973 season, this made possible by a grant from the Royal Society. Professor V. C. Wynne-Edwards and Professor Dunnet provided facilities for planning, analysis and writing at Culterty Field Station.

In the Seychelles Messrs G. R. A. Savy and R. Delorie kindly allowed me to live and work on Bird Island. My wife, Chris, Mrs Marie-France Savy and Mr Norman Lindsay were able and hard-working field assistants. The Director of Agriculture, Mr S. M. Savy, provided office facilities in the Department of Agriculture on Mahé, and Mr Ian Frost gave encouragement and assistance on many occasions. Lindblad Travel were helpful in many ways, especially in operating a postal service.

Dr I. J. Patterson wrote computer programmes for the analysis of growth data, and Mr J. A. Love made the excellent chick drawings for Fig. 2. Fish samples were identified by Dr P. J. P. Whitehead, squid and crustaceans by Drs A. L. Rice and R. Aldred, and ticks by Drs H. Hoogstraal and M. N. Kaiser.

The manuscript was greatly improved by critical and constructive comments from Professor Dunnet, Drs N. P. Ashmole, R. S. Bailey and W. R. P. Bourne, and any faults that remain are entirely my own.

To all of these people I am extremely grateful.

#### REFERENCES

- Anderson, A. (1963). Patagial tags for waterfowl. *J. Wildl. Mgmt* **27**: 284–288.
- Ashmole, N. P. (1963). The biology of the Wideawake or Sooty tern *Sterna fuscata* on Ascension Island. *Ibis* **103b**: 297–364.
- Ashmole, N. P. (1968). Body size, prey size and ecological segregation in five sympatric tropical terns. *Syst. Zool.* **17**: 292–304.
- Ashmole, N. P. (1971). Sea bird ecology and the marine environment. In *Avian biology* **1**: 223–286. Farner, D. S., King, J. R. (Eds). London: Academic Press.
- Ashmole, N. P. & Ashmole, M. J. (1967). Comparative feeding ecology of seabirds of a tropical oceanic island. *Bull. Peabody Mus. nat. Hist.* **24**: 1–131.
- Austin, O. L. (1965). Longevity and mortality in the Sooty tern. AOU Abstracts, 83rd meeting, August 23–27, 1965.
- Austin, O. L. & Austin, O. L. Jr. (1956). Some demographic aspects of the Cape Cod population of Common terns (*Sterna hirundo*). *Bird Banding* **27**: 55–56.
- Bailey, R. S. (1968). The pelagic distribution of seabirds in the western Indian Ocean. *Ibis* **110**: 493–519.
- Brown, R. G. B. (1967). Breeding success and population growth in a colony of Herring and Lesser black-backed gulls *Larus argentatus* and *L. fuscus*. *Ibis* **109**: 502–515.
- Burger, J. (1972). Dispersal and post-fledging survival of Franklins gulls. *Bird Banding* **43**: 267–275.
- Carrick, R., Csordas, S. E. & Ingham, S. E. (1962). Studies on the Southern elephant seal, *Mirounga leonina* (L.) IV. Breeding and development. *C.S.I.R.O. Wildl. Res.* **7**: 161–197.
- Clapp, R. B. & Sibley, F. C. (1966). Longevity records of some central Pacific seabirds. *Bird Banding* **37**: 193–197.

- Cott, H. B. (1954). The exploitation of wild birds for their eggs. *Ibis* **96**: 129–149.
- Coulson, J. C. & White, E. (1959). The post-fledging mortality of the kittiwake. *Bird Study* **6**: 97–102.
- Cowan, P. J. (1972). The contrast and colouration of sea-birds: An experimental approach. *Ibis* **114**: 390–399.
- Crossin, R. S. & Huber, L. N. (1970). Sooty tern egg predation by Ruddy turnstones. *Condor* **72**: 372–373.
- Cushing, D. H. (1971). *Survey of resources in the Indian Ocean and Indonesian sea*. Roje: Indian Ocean Fishery Commission, F.A.O.
- Diamond, A. W. (in press). Subannual breeding and moult in the Bridled tern *Sterna anaethetus* in the Seychelles. *Ibis* **118**.
- Dinsmore, J. J. (1972). Sooty tern behaviour. *Bull. Fla St. Mus. biol. Sci.* **16**: 129–179.
- Dunnet, G. M. & Patterson, I. J. (1968). The Rook problem in north-east Scotland. In *The problems of birds as pests*: 119–139. Murton, R. K. & Wright, E. N. (Eds). London: Academic Press.
- Feare, C. J. (1967). Feeding enhancement in certain members of the family Laridae. *Seabird Bull.* **3**: 45–46.
- Feare, C. J. (1970). The reproductive cycle of the dogwhelk *Nucella lapillus*. *Proc. malac. Soc. Lond.* **39**: 125–137.
- Feare, C. J. (1973). Research on Sooty terns in Seychelles. *Biol. Conserv.* **5**: 236–238.
- Feare, C. J. (1974). Unexpected visitors to the Seychelles. *Biol. Conserv.* **6**: 218–219.
- Feare, C. J. (1975). Post-fledging parental care in Crested and Sooty terns. *Condor* **77**: 368–370.
- Feare, C. J. (1976). Desertion and abnormal development in a colony of Sooty terns infested by virus-infected ticks. *Ibis* **118**: 112–115.
- Feare, C. J. (In press). The ecology of Bird Island, Seychelles. *Atoll Res. Bull.*
- Fryer, J. C. F. (1910). Bird and Denis Islands, Seychelles. *Trans. Linn. Soc. Lond. (Zool.)* (2) **14**: 15–20.
- Gould, P. J. (1974). Sooty tern (*Sterna fuscata*). Pelagic studies of seabirds in the central and eastern Pacific Ocean (Ed. W. B. King). *Smithson. Contr. Zool.* **158**: 6–52.
- Harrington, B. A. (1974). Colony visitation behaviour and breeding ages of Sooty terns (*Sterna fuscata*). *Bird Banding* **45**: 115–144.
- Harris, M. P. (1966). Age of return to the colony, age of breeding and adult survival of Manx Shearwaters. *Bird Study* **13**: 84–95.
- Howell, T. R. & Bartholomew, G. A. (1962). Temperature regulation in the Sooty tern (*Sterna fuscata*). *Ibis* **104**: 98–105.
- Jarvis, M. J. F. (1974). The ecological significance of clutch size in the South African gannet (*Sula capensis* (Lichtenstein)). *J. Anim. Ecol.* **43**: 1–17.
- Johnson, R. F. & Hardy, J. W. (1962). Behaviour of the Purple martin *Progne subis*. *Wilson Bull.* **74**: 243–262.
- Lack, D. (1954). *The natural regulation of animal numbers*. Oxford: University Press.
- Lack, D. (1966). *Population studies of birds*. Oxford: University Press.
- Lack, D. (1968). *Ecological adaptations for breeding in birds*. London: Methuen.
- Murton, R. K., Westwood, N. J. & Isaacson, A. J. (1974). Factors affecting egg weight, body weight and moult of the Woodpigeon *Columba palumbus*. *Ibis* **116**: 52–73.
- Nelson, J. B. (1967). Etho-ecological adaptations in the great frigate-bird. *Nature, Lond.* **214**: 318.
- Nisbet, I. C. T. (1973). Courtship feeding, egg size and breeding success in Common terns. *Nature, Lond.* **241**: 141–142.
- Nisbet, I. C. T. & Drury, W. H. (1972). Post-fledging survival in Herring gulls in relation to brood-size and date of hatching. *Bird Banding* **43**: 161–172.
- Patterson, I. J. (1965). Timing and spacing of broods in the Black-headed gull *Larus ridibundus*. *Ibis* **107**: 433–459.
- Patterson, I. J., Dunnet, G. M. & Fordham, R. A. (1971). Ecological studies of the Rook (*Corvus frugileus* L.) in north-east Scotland. Dispersion. *J. appl. Ecol.* **8**: 815–833.
- Phillips, G. C. (1962). *Survival value of the white colouration of gulls and other seabirds*. D.Phil. thesis, University of Oxford.
- Perrins, C. M. (1966). Survival of young Manx shearwaters *Puffinus puffinus* in relation to their presumed date of hatching. *Ibis* **108**: 132–135.
- Perrins, C. M. (1970). The timing of birds' breeding seasons. *Ibis* **112**: 242–255.
- Potthoff, T. & Richards, W. R. (1970). Juvenile bluefin tuna *Thunnus thynnus* (Linnaeus) and other scombrids taken by terns in the Dry Tortugas, Florida. *Bull. Mar. Sci.* **20**: 389–413.
- Richdale, L. E. (1954). Breeding efficiency in Yellow-eyed penguins. *Ibis* **96**: 207–224.
- Ridley, M. W. & Percy, R. (1958). *The exploitation of sea birds in Seychelles*. London: H.M.S.O.
- Ridley, M. W. & Percy, R. (1966). *Report on the exploitation of sea birds eggs in Seychelles*. Seychelles: Govt Printer.

- Robertson, W. B. Jr. (1964). The terns of the Dry Tortugas. *Bull. Fla St. Mus.* **8**: 1-94.
- Robertson, W. B. Jr. (1969). Transatlantic migration of juvenile Sooty terns. *Nature, Lond.* **223**: 632-634.
- Royama, T. (1966). A re-interpretation of courtship feeding. *Bird Study* **13**: 116-129.
- Simmons, K. E. L. (1972). Some adaptive features of seabird plumage types. *Br. Birds* **65**: 465-479, 510-521.
- Skoglund, W. C., Seeger, K. C. & Ringrose, A. T. (1952). Growth of broiler chicks hatched from various sized eggs when reared in competition with each other. *Poult. Sci.* **31**: 796-799.
- Vesey-Fitzgerald, D. (1941). Further contributions to the ornithology of the Seychelles Islands. *Ibis* (14) **5**: 518-531.