# THE BIOLOGY OF TROPICBIRDS AT ALDABRA ATOLL, INDIAN OCEAN

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ALDABRA (9° 24′ S, 46° 20′ E) is a large atoll of raised limestone lying about 640 km off the east coast of Africa and 420 km northwest of Madagascar. It is unique among elevated atolls both in its relatively undisturbed condition and in its ecological diversity. In 1967, in response to a proposal by the British government to build a military staging post there, the Royal Society sent an expedition to Aldabra and later set up a research station. Westoll and Stoddart (1971) documented the history of the atoll and of the first part of the expedition, and Diamond (1971a) gave a brief account of the seabirds.

The seabird community on Aldabra, one of the richest in the Indian Ocean, is more or less unaffected by man. I studied 10 of the breeding species from August 1967 to March 1968 and from March to September 1969 (Diamond 1971b). This paper reports studies on the two species of tropicbirds that breed there, the Red-tailed Tropicbird (*Phaethon rubricauda*) and the White-tailed (or Yellow-billed) Tropicbird (*P. lepturus*).

The atoll is about 34 km long and 14.5 km wide, elongated east-west with a large, shallow central lagoon (Fig. 1). The land rim is divided into four main islands by narrow channels, and consists of deeply eroded limestone raised up to 5 m above sea level. The lagoon is enlarging at the expense of the land rim (Fryer 1911, Stoddard and Wright 1967), and active erosion of the lagoon-facing cliffs has isolated a great many small islets, which provide the tropicbird nesting sites. The islets are least numerous along the south shore of the lagoon, where the coast is sheltered from the southeast trade winds by South Island and is least influenced by the strong tidal currents in the channels. The islets are deeply undercut, often resting on a narrow pedestal; this has given rise to the local creole term *champignon* (mushroom), which is also used to describe the more deeply dissected of the limestone landforms.

The climate is strongly seasonal. From April to October (the dry season) the southeast trade winds blow with an average strength of 7 m/s (16 mph), and from November to March (the wet season) winds are light and variable, most rain falling toward the end of this period. Temperature varies little throughout the year, mean monthly maxima varying between 27.2°C (July) and 32.2°C (December) in 1967-68 (Farrow 1971).
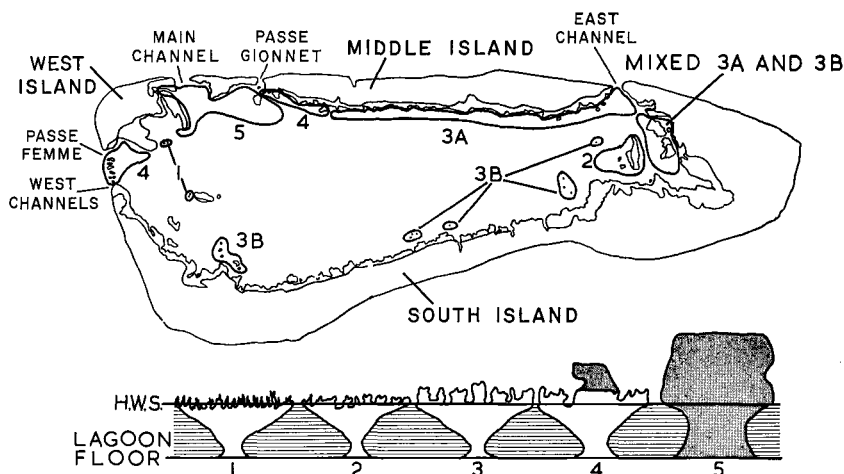
Fig. 1. Distribution and structure of the major types of lagoon islet. Shaded rock: poorly consolidated reef-debris limestone. Unshaded: well consolidated reef limestone. H.W.S.: water level at normal high-water spring tides. Figures indicate islet types (see text).

## MORPHOLOGY

Table 1 gives the weights and measurements of adult tropicbirds. The larger species, *rubricauda*, is the largest of the three tropicbird species (*rubricauda, aethereus*, and *lepturus*). Unlike Caribbean and Atlantic populations of *lepturus* (Gross 1912, Stonehouse 1962, pers. obs.), no individuals were seen at Aldabra with orange or red bills or with any reddish or brown in the tail streamers. A few showed a faint pink suffusion on the breast, and one was strongly washed with the apricot color characteristic of *P. l. fulvus*, which is endemic to Christmas Island, Indian Ocean (Gibson-Hill 1947a). The sexual dimorphism shown by the Ascension population of *lepturus* (most males pink and most females white, Stonehouse 1962) was not present in the Aldabra population.

## NESTING DISTRIBUTION

Both species usually nested only on lagoon islets; the few *rubricauda* attempting to breed on South Island were unsuccessful, perhaps because of introduced rats (*Rattus rattus*).

The lagoon islets differ in lithology, degree of dissection, height of the surface above sea level, and vegetation—all of which are important in determining tropicbird nest sites. For the purpose of estimating the numbers of seabirds nesting on them, the islets were classified into five

TABLE 1

Weights and Measurements of Adult Tropicbirds on Aldabra

|  | Weight (g) | Wing (chord) length (mm) | Exposed culmen length (mm) | Bill length[1] (mm) | Tarsus length (mm) |
|---|---|---|---|---|---|
| *P. rubricauda* | 762 (18)[2] | 337 (17) | 64 (19) | 24 (14) | 29 (13) |
| *P. lepturus* | 334 (59) | 273 (56) | 49 (59) | 18 (21) | 22 (36) |

[1] Measured at base of bill.
[2] Figures in parentheses show the sample size.

types, whose structure and distribution are shown in Fig. 1. Type 1 consists of a few low level, extremely dissected *champignon* islets of very restricted distribution, and we never found tropicbird nests on islets of this type. Islets of type 2 are more massive and less dissected, but still sufficiently low (relative to high-water spring tides) to endanger the nests even of surface-nesting birds. Not surprisingly, very few tropicbirds nested on these islets. Most islets are of type 3, composed of relatively thick *champignon* riddled with holes (solution cavities), occasionally with a flatter, cemented surface. The islets along the north coast of South Island tend to rise rather higher above high-water spring tides than those along the shore of Middle Island, and are separated as

TABLE 2

Number of Occupied Sites of Tropicbirds on Four Main Islet Types and Estimate of Total Aldabra Population

|  | 3a | 3b[1] | 4 | 5 | Total |
|---|---|---|---|---|---|
| Number of islets in study area | 4 | – | 6 | 14 | 24 |
| Number of occupied sites: |  |  |  |  |  |
| *rubricauda* | 11 | – | 9 | 28 | 48 |
| *lepturus* | 21 | – | 11 | 12 | 44 |
| Mean no. occupied sites per islet: |  |  |  |  |  |
| *rubricauda* | 2.75 | (2.13) | 1.50 | 2.00 |  |
| *lepturus* | 5.25 | (3.54) | 1.80 | 0.86 |  |
| Total no. islets in lagoon | 515 | 175 | 140 | 76 | 906 |
| Calculated total no. occupied sites: |  |  |  |  |  |
| *rubricauda* | 1416 | 373 | 210 | 212 | 2211 |
| *lepturus* | 2704 | 620 | 252 | 91 | 3667 |
| Calculated total no. pairs (no. occupied sites less 15% *rubricauda* or 31% *lepturus* (see text)): |  |  |  |  |  |
| *rubricauda* |  |  |  |  | 1879 |
| *lepturus* |  |  |  |  | 2530 |

[1] No study area included islets of type 3b, which were sampled only during the second half of the study. These islets were intermediate in structure between types 3a and 4, and the number of occupied sites was estimated to be the mean of the number on types 3a and 4.

TABLE 3

DISTRIBUTION OF OCCUPIED NEST SITES OF THE TWO TROPICBIRD SPECIES
AMONG THREE TYPES OF LAGOON ISLET

| Islet  type | No. islets visited | %I[1] | %R | %L | Preference index | |
|---|---|---|---|---|---|---|
| | | | | | R | L |
| 3 (East Channel) | 4 | 16.7 | 22.9 | 47.7 | 1.37 | 2.86 |
| 4 (Passe Femme) | 6 | 25.0 | 18.8 | 25.0 | 0.75 | 1.00 |
| 5 (Gionnet) | 14 | 58.3 | 58.3 | 27.3 | 1.00 | 0.47 |

[1] % I is the percentage of each islet type, as the proportion of all the islets regularly visited. % R is the percentage of the 31 *rubricauda* sites, and % L of the 41 *lepturus* sites. The choices of islet type are highly significant ($\chi^2$ test: $P < 0.001$, *rubricauda*; $P < 0.001$, *lepturus*).

type 3b. Type 4 islets have a basal layer of *champignon* capped with remnants of an upper layer of poorly consolidated limestone composed largely of coral debris. The islets south of Passe Gionnet are composed entirely of this latter rock type, frequently capped by solution pans and rising to 1.5 or 1.8 m above high-water springs (type 5).

Table 2 shows the number of nest sites occupied by each species in each study area. Table 3 gives estimates of preference for each islet type by a "preference index" similar to that Dunnet and Patterson (1968) used, calculated by dividing the percentage of nest sites of each species found on islets of a given type by the percentage of all islets searched of that type. It was not practicable to allow for possible differences in islet sizes of different types, but inspection suggested any such differences were small. Table 3 shows clearly that both species selected type 3 islets but differed in the types they avoided.

The choice of islet type by each species can be related, in part at least, to the nest sites available on each type (Fig. 2). In general *rubricauda* occupied larger cavities than *lepturus*; few solution cavities were large enough for *rubricauda*, which usually nested on the surface under cover of vegetation. The smaller species usually nested either in solution holes or on the surface between tussocks of the grass *Sclerodactylon macrostachyum*; the latter sites closely resembled solution cavities except that the roof and sides were formed of thick grass rather than rock. Shallow cavities between the two layers of limestone on type 4 islets were particularly favored by *lepturus*, but were not available on islets lacking the upper limestone layer.

The type of nest site most frequently used differed in each species, but taking into account the numbers of each type of islet in the lagoon, the overlap in nest sites in the total population, estimated by Morisita's (1959) index,

$$C_\lambda = \frac{2 \sum\limits_{i=1}^{s} x_i \cdot y_i}{\sum\limits_{i=1}^{s} x_i^2 + \sum\limits_{i=1}^{s} y_i^2}$$

is about 78% (Diamond 1971b). This implies that some interspecific competition for sites could occur, though it does not prove this is so unless it can be shown that nest sites are in short supply. This cannot be proved, though it seems likely on Aldabra. In the Galápagos, Harris (1969) found that *P. aethereus* competed for the best sites even when there was an apparent superabundance of sites. Probably both inter- and intraspecific competition for sites occurs, though the relative importance of the two processes cannot be assessed.

## NUMBERS OF BREEDING BIRDS

From Table 2 the mean number of occupied sites per islet for each species can be found for each islet type in the study areas. The total
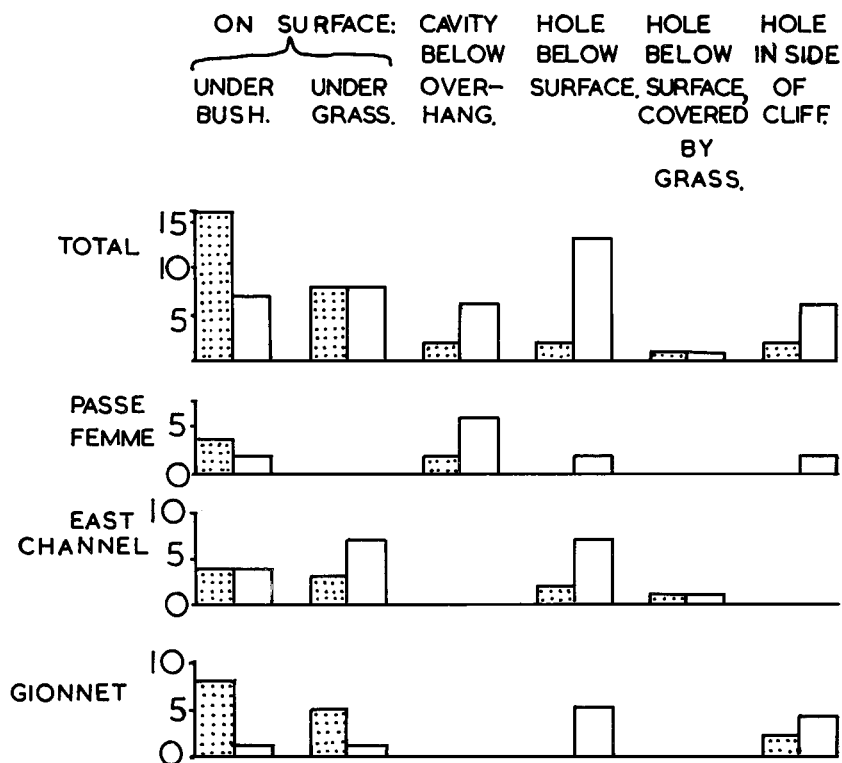


Fig. 2. Number of nest sites of each type occupied by tropicbirds in the three study areas. Stippled: *rubricauda*. Plain: *lepturus*.

number of islets of each type was counted from aerial photographs after the distribution of islet types in the lagoon had been determined in the field, and simple multiplication gave the total number of sites each species occupied (Table 2).

Totals for the two study periods cannot simply be added together to give a total for 1 year, as some individuals nested in both study periods. Six of 39 (15%) breeding *rubricauda* and 13 of 42 (31%) breeding *lepturus* were known to have bred in both study periods. Thus 15% and 31% respectively have been subtracted from the total numbers of *rubricauda* and *lepturus* to estimate the numbers breeding in one calendar year (Table 2).

Figures for the two species are not strictly comparable. Because *rubricauda* is larger than *lepturus* and nests more often on the surface, it is more conspicuous; it also draws attention to itself by calling harshly when disturbed. Thus more *lepturus* than *rubricauda* are likely to have escaped detection. These differences were particularly important on the more densely vegetated islets (types 4 and 5) where the vegetation was so thick and the ground so rough that the islets could not always be searched completely in the time available. The relatively long interval between successive visits also introduced errors by allowing unsuccessful breeders to occupy and desert a nest between visits and so escape detection. This bias is likely to underestimate the numbers of *rubricauda* more than *lepturus*, which had a higher breeding success. It is not possible to give confidence limits for the breeding population estimates of about 1880 and 2530 pairs of *rubricauda* and *lepturus* respectively (Table 2), but they are unlikely to be in error by more than ± 30%.

## THE SEXUAL CYCLE

*Breeding season.*—As laying dates could not be calculated for many nests, the seasonality of breeding is expressed in terms of nests occupied by an egg or a chick, rather than in terms of laying dates. The number of sites occupied by each species in each month of the study is shown in Fig. 3. Clearly breeding was aseasonal, but both species showed slight peaks between December 1967 and February 1968 and in April and May (*rubricauda*) and June and July (*lepturus*) 1969.

*Courtship, laying, and incubation.*—As I visited nests irregularly and briefly, and most were either below ground or well hidden by vegetation, I saw very little display at the nest. But aerial display was conspicuous in both species, involving between 2 and 20 birds at a time. Loose groups of birds flew in wide circles at heights up to 100 m, calling rapidly and harshly. Two or three *rubricauda* would frequently leave the group and glide downward, wings held stiffly above the body, to within a few
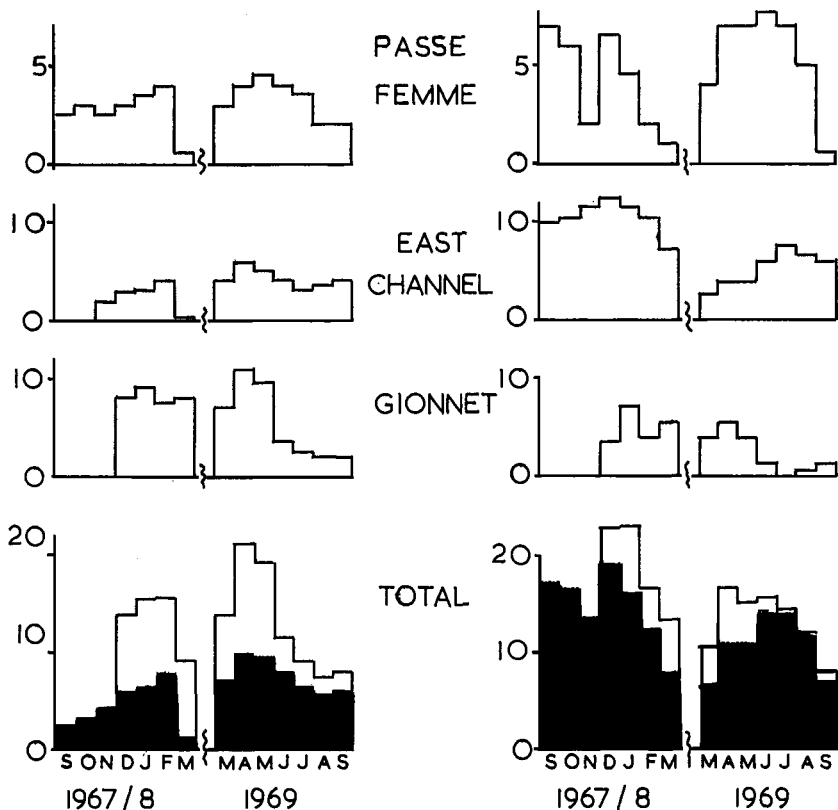
Fig. 3. Number of tropicbird nest sites occupied per month. Left: *rubricauda*. Right: *lepturus*. Solid shading: total excluding Gionnet study area, which was not visited until December 1967.

meters of the ground or water before leveling out, calling loudly through-out. This action might be repeated many times before the birds either disappeared or landed to prospect a nest site. This display was very similar to that Brattstrom and Howell (1956) described in the Red-billed Tropicbird (*P. aethereus*), except that in *aethereus* the upper bird holds its wings down rather than up. The dark innermost underwing coverts were not conspicuous in *rubricauda* on Aldabra, and did not appear to feature prominently in display as van Tets (1965) suggested they do on Laysan Island. The aerial display of *lepturus* was similar to that of *rubricauda*, except that the close gliding descent of two birds was much less frequent. I did not see the upper bird attempting to touch the lower with its tail, as described by Worth (1935). It is unlikely that the aerial display of either species serves to indicate nest sites as van Tets

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TABLE 4

WEIGHTS AND MEASUREMENTS OF TROPICBIRD EGGS ON ALDABRA[1]

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|  | Weight | | | Length | | | Diameter | | | Weight as % adult weight |
|---|---|---|---|---|---|---|---|---|---|---|
|  | n | x̄ | SD | n | x̄ | SD | n | x̄ | SD |  |
| *P. rubricauda* | 10 | 77.4 | 7.2 | 8 | 65.1 | 2.5 | 8 | 46.4 | 1.4 | 10.2 |
| *P. lepturus* | 10 | 43.4 | 7.0 | 10 | 53.2 | 3.3 | 10 | 39.0 | 1.7 | 13.0 |

[1] n = number in sample, x̄ = mean, SD = standard deviation.

(1965) suggested, as it is performed over open water and dense vegetation on the main islands as well as over the islets used for nesting.

It is possible that some of the birds seen in aerial display, and subsequently prospecting nest sites, were nonbreeding birds. This has been suggested for *lepturus* in Bermuda (Wingate pers. comm.) and *aethereus* in the Galápagos (Harris pers. comm.). In both cases it is supported by the observation that display is most common after, and not before, the peak of laying. On Kure Atoll, Fleet (1972) found that aerial displays preceded breeding in a seasonally breeding population of *rubricauda*. As no laying peak was discerned at Aldabra, it is not possible to decide whether the displaying birds there are also nonbreeders. This possibility, if it were confirmed, would explain an anomaly noticed both on Ascension and at Aldabra, namely that a number of nests remained unoccupied after the occupants had apparently been evicted by prospecting birds. If the culprits had been breeders, they would be expected to occupy a site from which they had successfully ousted the occupants.

Table 4 gives egg weights and measurements. One *rubricauda* egg, hard-boiled and then dissected, had weights of yolk 18 g, albumen 47 g, and shell 7.5 g. No comparable data are available for this species or for *lepturus*, but for *aethereus* in the Galápagos Harris (1969) gives weights of 18 g, 32.5 g, and 5.5 g respectively.

Incubation periods were not determined. Stonehouse (1962) found the average incubation period of *lepturus* on Ascension to be 41 days, and I used this figure in interpolating laying dates for this species on Aldabra. Four *rubricauda* eggs, one of which was known to have hatched subsequently, were incubated for at least 51 days on Aldabra, but Fleet (1972) recorded incubation periods of 42-46 days on Kure Atoll. The Aldabra periods may have been longer than normal because the eggs were left unincubated; *aethereus* eggs are known to be capable of hatching after being unattended for as long as 5 days (Harris pers. comm.).

Incubation shifts were measured by marking one bird of an incubating pair with red paint and visiting the nest daily to record the incubating

TABLE 5
ATTENDANCE OF ADULT TROPICBIRDS TO CHICKS[1]

| Age groups (weeks) | P. rubricauda | | P. lepturus | |
|---|---|---|---|---|
| | No. of visits | % of visits adult present | No. of visits | % of visits adult present |
| 0–1 | 22 | 100 | 26 | 90 |
| 1–2 | 7 | 86 | 15 | 60 |
| 2–3 | 7 | 100 | 13 | 30 |
| 3–4 | 11 | 45 | 13 | 24 |
| 4–5 | 6 | 33 | 8 | 0 |
| 5–6 | 2 | 50 | 11 | 0 |
| 6–7 | 8 | 0 | 9 | 0 |
| 7–8 | 5 | 0 | 7 | 14 |
| 8–9 | 2 | 0 | 10 | 0 |
| 9–10 | 6 | 17 | 8 | 0 |
| 10–11 | 3 | 0 | 5 | 0 |
| 11–12 | 4 | 0 | 2 | 0 |
| 12–13 | 5 | 0 | 1 | 0 |
| 13+ | 2 | 0 | 0 | – |
| TOTAL | 90 | 43.3 | 128 | 31.3 |

[1] The difference in attendance by the two species over the first 6 weeks of the chick's life is highly significant ($\chi^2$ test: $P < 0.001$).

bird's identity. Most incubation shifts were longer than the number of successive days that could be devoted to this task, so most shifts measured were incomplete. One complete shift of 6 days and incomplete ones of 3, 4, 5, and 6 days were recorded for *lepturus*, and incomplete shifts of 4 and 6 days for *rubricauda*. From these data it is possible to say only that on Aldabra shifts of *lepturus* were probably slightly longer than those of 3 to 4 days on Ascension (Stonehouse 1962), and those of *rubricauda* were probably similar to those of "about six days" on Christmas Island, Pacific Ocean (Ashmole and Ashmole 1967).

*Chick growth.*—Chicks of both species were brooded for the first few days of life. Their eyes were often closed for the first 2 or 3 days, but a chick's ability to open its eyes was not a sound criterion of age.

Table 5 shows the number of visits I paid to chicks of different ages and the percentage of those visits on which an adult was also present. Clearly *lepturus* chicks were left unaccompanied much earlier than *rubricauda* chicks. Stonehouse (1962) found a similar difference in chick attendance between *aethereus* and *lepturus* on Ascension, although there the difference continued up to 70 days after hatching. He suggested that the greater attendance *aethereus* showed its young chicks might be important in achieving this species' greater nesting success. Harris (1969) also suggested that attendance of chicks by adult *aethereus* in the Galápagos might help to reduce nest mortality resulting from intraspecific competition. This seems unlikely both on Ascension and
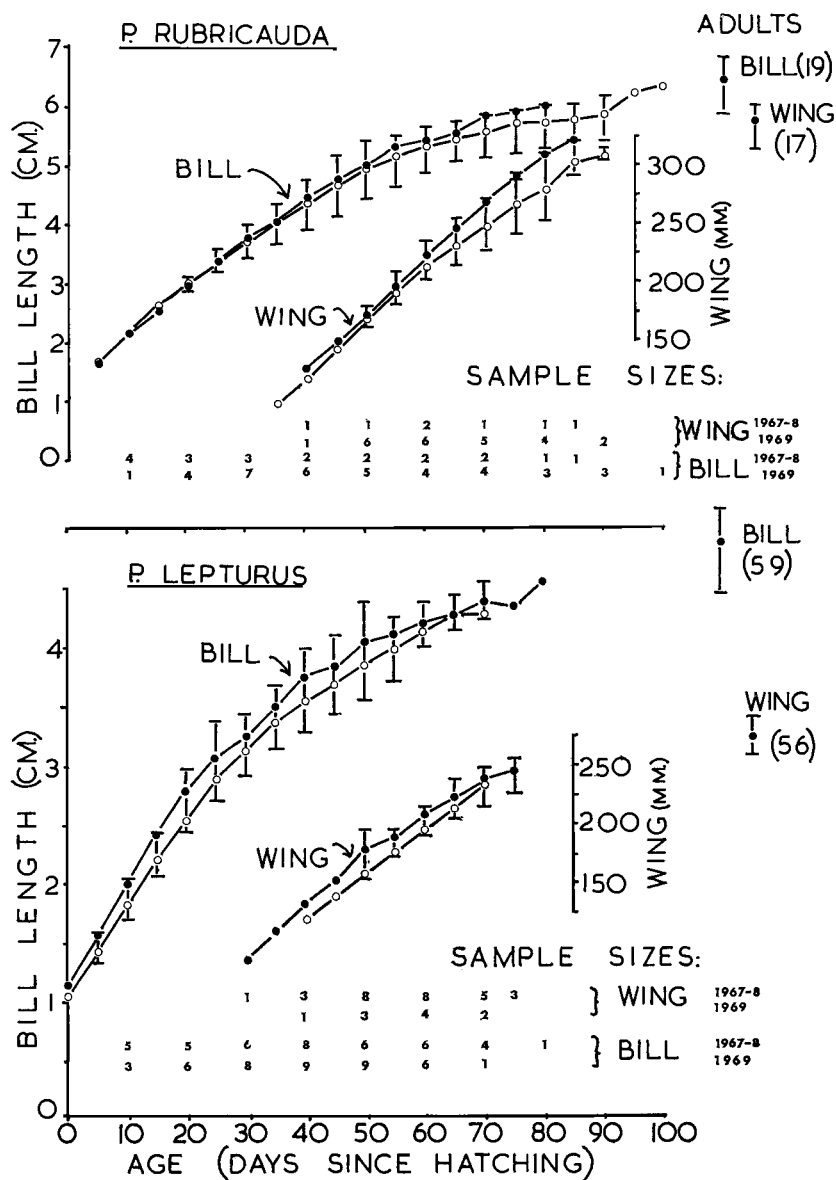
Fig. 4. Bill and wing growth of tropicbird chicks. Solid symbols: 1967–68. Hollow symbols: 1969.

at Aldabra, as the species showing greater chick attendance (*aethereus* and *rubricauda* respectively) actually suffered higher chick mortality than the other species (*lepturus* in both places). It could still be that more nests might fail if the adults attended their chicks less often.

Figs. 4 and 5 show chick growth and include all chicks younger than 60 days (*rubricauda*) or 45 days (*lepturus*) when first found. Older birds could not be aged accurately ($\pm$ 1 week); chicks that were weighed daily for several successive days to find the frequency with which they were fed were also excluded, as they often regurgitated their last meal and so presumably grew more slowly than normal.

Chicks of both species attained maximum weights considerably greater than that of adults (121% of the mean adult weight in *lepturus*, 115% in *rubricauda*). Although much of this excess weight was lost before the young disappeared, most young probably fledged at or slightly above the mean adult weight. From the growth curves, fledging periods (i.e. the average period between hatching and the time the chick was last found in the nest) were estimated as 80 days in *lepturus* and 90 in *rubricauda*. These periods are similar to those recorded in *lepturus* and *aethereus*, respectively, on Ascension (Stonehouse 1962). Samples are too small to compare growth in the two study periods, but the data suggest that growth may have been slightly slower in both species in 1969 than in 1967–68.

The feeding intervals of chicks were estimated by weighing them on successive days at approximately 24-h intervals. Weight increases between my visits clearly showed that chicks had been fed. The distribution of these weight increases was unimodal and so all weight increases were assumed to result from a single feed. Weight decreases were more difficult to interpret, as a small chick might lose weight over 24 h if given only a small meal (Harris 1966). Chicks that lost 10 g or less between weighings were scored as having been fed. Feeding intervals in the two species were similar, averaging 1.4 days in *rubricauda* and 1.5 days in *lepturus* (in 59 and 58 chick days respectively), though they varied more in *rubricauda* than in *lepturus*.

On two occasions I watched an adult *rubricauda* feeding its chick. As soon as the adult landed, several meters from the nest, the chick set up a shrill, persistent rattling call with the bill partly open, resembling the sound made by a fisherman's reel, and rarely paused to take breath. As soon as the parent came within range the chick lunged at its bill, and after half a minute or so the adult turned its head on one side to put its beak into the chick's gape and regurgitated a fish into the chick's throat. The chick called continuously, though less strongly after being fed, until the adult flew off about 5 min after first landing.

After fledging, young tropicbirds do not return to land until they have assumed adult plumage. No information on how long this process may take is available, though in *aethereus* the adult red bill color is attained within 6 months of fledging (Harris 1969).
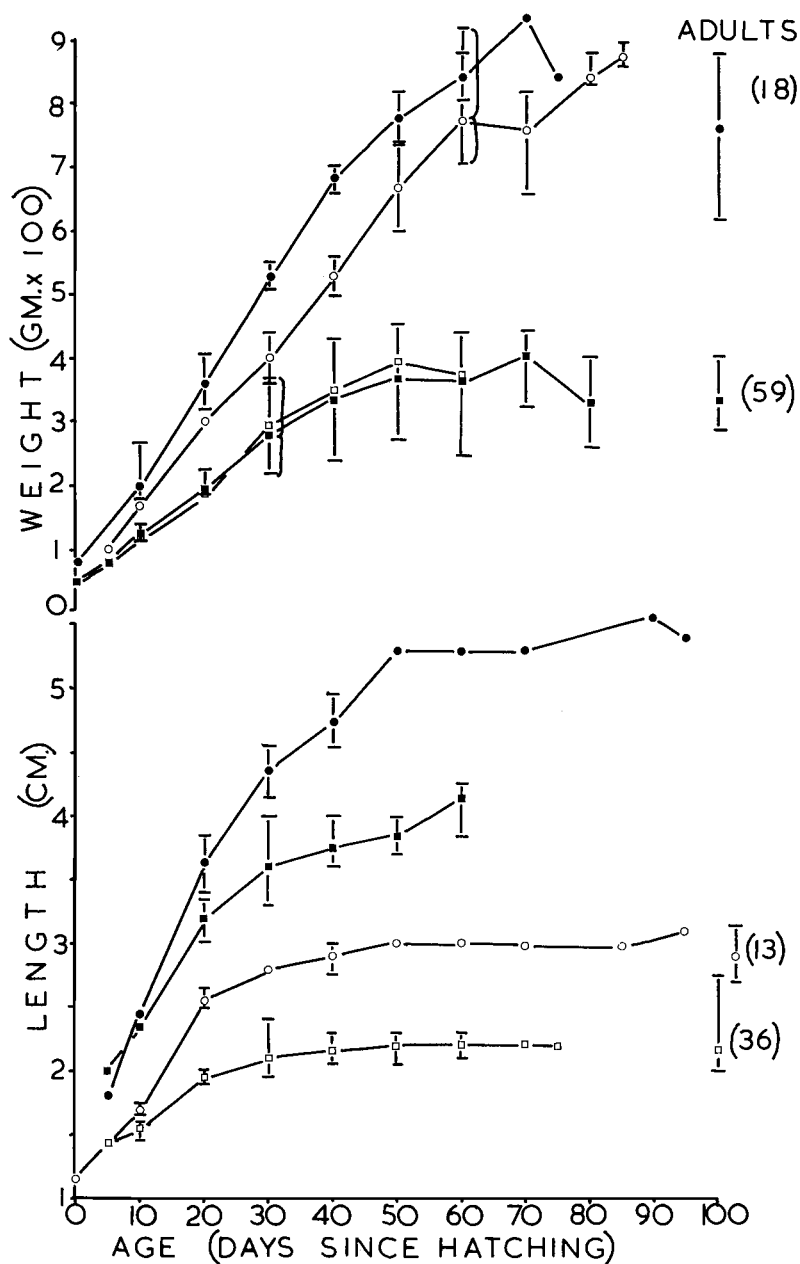
Fig. 5.  Weight increase and growth of toe and tarsus of tropicbird chicks. Circles: *rubricauda*. Squares: *lepturus*. Upper figure: solid symbols, 1967–68; hollow symbols, 1969. Lower figure: solid symbols, toe; hollow symbols, tarsus.

TABLE 6

NEST MORTALITY OF TROPICBIRDS

| | *P. rubricauda* | | | *P. lepturus* | | |
|---|---|---|---|---|---|---|
| | 1967–68 | 1969 | Total | 1967–68 | 1969 | Total |
| Data from all nests in which date of failure known: | | | | | | |
| No. losses of eggs and chicks < 5 weeks old | 17 | 15 | 32 | 10 | 15 | 25 |
| No. of losses of chicks > 5 weeks old | 4 | 2 | 6 | 0 | 0 | 0 |
| Data from all nests in study areas only: | | | | | | |
| No. nests failed | 22 | 10 | 32 | 7 | 14 | 21 |
| No. successful nests | 1 | 8 | 9 | 7 | 12 | 19 |
| No. fate unknown | 2 | 2 | 4 | 8 | 0 | 8 |
| % nests successful | 4.4 | 44.4 | 21.9 | 50.0 | 42.9 | 47.5 |

*Breeding success.*—Counting all nests in the three study areas in which eggs were known to have been laid during the study, the overall nesting success (i.e. young fledged as a percentage of eggs laid) was 21.9% in *rubricauda* (4.4% in 1967–68, 44.4% in 1969) and 47.5% in *lepturus* (50.0% in 1967–68, 46.1% in 1969) (Table 6). These figures are maxima as they exclude birds that laid and lost their egg between my visits to the nest. Breeding success showed no clear pattern in relation either to the month of laying or to the breeding activities of the other tropicbird species.

It was rarely possible to determine the cause of failure; usually a nest that had been occupied at one visit was empty at the next. Sometimes, particularly in *rubricauda* nests, the remains of an egg or chick were found trampled in the floor of the nest scrape, though it was not clear whether the offspring had been squashed before or after death. Some nest losses may have been due to predators such as coconut crabs (*Birgus latro*), which were present on many of the Gionnet (type 5) islets, but general observations suggested that many nest losses may have been caused by intraspecific fighting over nest sites.

Table 6 shows that most nests that failed were occupied by an egg or young chick. No *lepturus* chicks that survived to the age of 5 weeks were known to have died subsequently, but several *rubricauda* chicks died after reaching this age.

The extremely low success of *rubricauda* nesting attempts in 1967–68 was unlikely to have been caused by food shortage, as chicks grew at least as well as and possibly slightly faster than in 1969. More likely the extremely hot, calm weather of the wet season drove incubating and brooding adults from their nests and the exposed egg or young chick

became overheated. Similar effects of heat stress on *rubricauda* were recorded on Midway Island by Howell and Bartholomew (1962) and on *lepturus* on Ascension by Stonehouse (1962). Such a marked seasonal difference in nesting success cannot be normal, as selection against nesting in the wet season would be strong. Probably the wet season of 1967–68 was unusually dry. Certainly the vegetation on the islets was much drier and less luxuriant, affording tropicbird nests less shade than in 1969. Nest sites of *lepturus* are mostly below the surface and much better protected from the heat than those of *rubricauda*. This may explain why breeding success did not vary seasonally in *lepturus*.

Other nest losses may have been due to intraspecific competition for nest sites. Inter- and intraspecific competition are known to be important causes of nest failures in tropicbirds elsewhere (see Discussion). Interspecific competition did not seem to be important on Aldabra, partly because the two species were able to use different types of nest sites; only 6% of the nest sites in the study areas were used by both species during the study. We have no direct evidence for the importance of intraspecific competition. In four of the nine *lepturus* nest sites where both adults were ringed in the first study period, at least one of the adults was different in the second study period; but this may have been due to weak site attachment or adult mortality rather than to intraspecific competition for sites. The only relevant data for *rubricauda* concern one adult ringed in 1967 that laid in a different nest site in 1969. On many occasions groups of birds involved in aerial display were seen coming down to an occupied site, apparently trying to dislodge the occupant. When such nests are occupied only by an egg or chick, intrusion by prospecting birds could easily destroy the nest contents. Prospecting birds seemed more attracted to occupied sites. One reason well-grown chicks were sometimes lost from nests of *rubricauda* but not *lepturus* may be a large chick's greater conspicuousness to prospecting birds in the more exposed nest sites *rubricauda* favored.

Relaying after the loss of an egg or small chick was recorded in six cases. The intervals between the failure of one breeding attempt and laying the next egg were: between 40 and 56 days, not more than 47 days, and not more than 71 days in three pairs of *rubricauda*; and 47 ± 5 days, not more than 41 days, and not more than 51 days in three pairs of *lepturus*. Comparable figures from other areas are between 1 and 2 months for *rubricauda* on Christmas Island, Pacific Ocean (Schreiber and Ashmole 1970) and 23–30 days for *lepturus* on Ascension (Stonehouse 1962).

*Sexual cycles of marked individuals.*—Successive nesting attempts by marked birds could not be followed because the interval between my two

visits to Aldabra was a year. In a few cases the laying dates of marked birds in both study periods were known; the fate of the breeding attempt in each study period was known, but that of the intervening breeding attempt was not. One *rubricauda* bred successfully in the first study period, and laying dates in the two periods were 21 months apart. No published information exists on the length of the sexual cycle in this species; but it is probably similar to that of *aethereus*, which averages 11 months on Ascension (Stonehouse 1962), 12 months in some colonies in the Galápagos, and possibly less in others (Snow 1965, Harris 1969). The laying interval of 21 months on Aldabra might represent either twice the length of the successful cycle, or the sum of one failed and one successful cycle. Single laying intervals following a failed attempt and one of unknown fate were 13 and 12 months respectively.

One pair of *lepturus* bred successfully in both periods with a laying interval of 19 months. On Ascension the successful cycle length averaged 9½ months (Stonehouse 1962). Thus the 19-month interval recorded on Aldabra probably represents twice the successful cycle length. Two intervals following failed breeding attempts were 19 and 15 months, and one following an attempt of unknown fate was 13 months.

Stonehouse (1962) pointed out the interval between breeding activity peaks in the population correspond closely with the length of the successful cycle, or if breeding success is low, the individual's unsuccessful cycle. Fig. 3 shows Aldabra breeding peaks were approximately 14–15 months apart in *rubricauda* and 19 months in *lepturus*. As breeding success in the first study period was low in *rubricauda* but reasonably high in *lepturus*, these intervals probably correspond to twice the unsuccessful cycle length (or one failed and one successful cycle) in *rubricauda*, and twice the length of the successful cycle in *lepturus*. These suggestions must remain tentative, as at least one breeding peak for each species presumably occurred between my visits to Aldabra.

*Molt.*—Molt could not be studied in detail, as it could be detected only by catching birds on nest sites. Very few birds of either species were in active wing molt when incubating or attending a chick. Table 7 shows the stages in the breeding cycle at which molting birds were found. Because no adults were found on empty nests from which young were known to have fledged recently, I have assumed that birds found at empty sites were prospecting birds, at the beginning rather than the end of a breeding attempt. On this assumption, Table 8 shows that *lepturus* often began courting but rarely laid before primary molt was complete; and *rubricauda* did not normally begin courtship until primary molt was complete. Primary molt in *rubricauda* began while the chick was still being fed. The lack of records of molting *lepturus* at

TABLE 7

NUMBER OF TROPICBIRDS IN ACTIVE PRIMARY MOLT AT EACH STAGE OF BREEDING

| Species | Stage of breeding cycle | | |
|---|---|---|---|
| | Empty nest[1] | Egg | Chick[1] |
| *P. rubricauda* | 0    (12)[2] | 1.3  (77) | 13.9  (36) |
| *P. lepturus* | 23.7  (38) | 1.2  (84) | 0    (39) |

[1] The difference between the two species in these columns is statistically significant ($P < 0.001$).
[2] The first figure is the percentage of these birds that were in active primary molt. The figure in parentheses is the number of individuals handled at each stage of the breeding cycle.

this stage may be because of the very small numbers of adults handled while attending large chicks (Table 5). The relation between molt and breeding in *lepturus* was similar to that in both *lepturus* and *aethereus* on Ascension (Stonehouse 1962). On Christmas Island, Pacific Ocean, Schreiber and Ashmole (1970) found that primary molt in *rubricauda* overlapped with breeding more at the beginning of the breeding cycle than at the end.

Table 8 gives details of primary molt in all individuals in which it was recorded. Feathers that were being replaced tended to be at a later stage of growth in *lepturus* than in *rubricauda*, supporting the suggestion that the former were finishing molt and the latter beginning

TABLE 8

PRIMARY MOLT OF TROPICBIRDS

| Species | Date | Nest Contents | Growth stage of each primary[1] | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| *P. lepturus* | 23 Nov. 1967 | Empty | · | 4 | · | · | 4 | · | · | 3 | · | · |
| | 11 Jan. 1968 | Empty | · | · | · | · | · | · | · | · | · | 4 |
| | 12 Mar. 1968 | Empty | · | · | · | · | · | 3 | · | · | · | · |
| | 1 Feb. 1968 | Egg | · | · | · | · | · | 1 | · | · | · | · |
| | 8 Feb. 1968 | Empty | · | · | · | · | · | · | · | · | · | 4 |
| | 10 Feb. 1968 | Empty | · | · | · | 4 | · | · | · | · | 4 | · |
| | 30 Jan. 1968 | Empty | · | · | · | · | · | · | 4 | · | · | · |
| | 20 Mar. 1968 | Empty | · | · | · | · | · | · | · | 3 | · | · |
| | 18 Aug. 1969 | Empty | · | · | · | · | · | · | · | · | · | 4 |
| | 25 Mar. 1969 | Empty | · | · | · | · | · | · | · | · | · | N |
| *P. rubricauda* | 4 Feb. 1968 | Chick | · | · | · | · | · | 2/1 | 0 | 0 | 0 | 0 |
| | 9 Jul. 1969 | Egg | · | · | · | · | · | · | · | · | · | 4/0 |
| | 14 Jun. 1969 | Chick | · | · | 1 | · | · | · | · | 1 | · | · |
| | 1 May 1969[2] | Egg | · | · | · | · | · | · | · | · | · | · |
| | 1 Jul. 1969[2] | Chick | · | · | · | · | · | 3 | · | · | · | · |
| | 28 Apr. 1969[3] | Egg | · | · | · | · | · | · | · | · | · | · |
| | 11 Jun. 1969[3] | Chick | · | · | · | · | · | · | · | 4 | 0 | 0 |
| | 8 Jul. 1969 | Chick | · | · | · | 2 | 0 | 0 | 0 | 2 | 0 | 0 |

[1] Primaries are numbered from the innermost to the outermost. Growth stages as in Ashmole (1962). · represents a fully grown feather of uncertain age; N and O present new and old feathers, respectively.
[2] Same individual.
[3] Same individual.

it, and two birds of each species showed more than one wave of primary molt in progress. Multiple molt waves have been found in *lepturus* on Ascension (Stonehouse 1962) and *rubricauda* on Christmas Island (Schreiber and Ashmole 1970). In the two adult *rubricauda* that were retrapped (Table 8), primary molt began with primaries 5 or 6 and 7 or 8, respectively, suggesting that each molt wave begins not at the innermost primary but probably where it finished before breeding. Schreiber and Ashmole (1970) documented this in *rubricauda* on Christmas Island. Tropicbird molt is thus almost certainly a "Staffelmauser" (Stresemann and Stresemann 1966) or "(interrupted) continual stepwise moult" (Ashmole 1968).

## FOOD AND FEEDING

*Feeding areas.*—The few arrivals of adults at nests that I saw suggested that *lepturus* usually arrived between 0800 and 1100 and *rubricauda* in the afternoon, but I have no firm data to show whether or not there was a specific difference in the time of return. Several chicks of both species that were weighed twice daily were fed almost exclusively during daylight. Tropicbirds rarely collect food within sight of land, even when breeding. The length of the incubation shift and the feeding interval give some idea of the distance to which the adults may fly for food. The incubation shifts of several days and the feeding intervals of about 1½ days are similar in the two species and support the view that they are pelagic rather than inshore feeders. When regurgitating their last meal, *rubricauda* chicks usually produced a bolus of tightly packed food items entirely covered in thick, sticky mucus, whereas *lepturus* chicks usually regurgitated the food items separately with little or no mucus. Ashmole and Ashmole (1967) noticed that food regurgitated by adult Sooty Terns (*Sterna fuscata*) was often in strikingly good condition and was frequently covered in mucus. They suggested that in this species, which is an oceanic feeder, the mucus might retard the digestion of food in the adult's crop. If this is so, the use of mucus by *rubricauda* but not *lepturus* might indicate that the former species feeds farther from land than the latter, in spite of their similar feeding intervals.

Probably breeding birds feed as near to the colony as possible, even though out of sight of land. The tropicbirds seen several hundred kilometers from the nearest colony, even during the breeding season (e.g. Bailey 1968, King 1970), may well be nonbreeding birds.

*Food samples.*—An analysis of regurgitated food samples is presented in Table 9. The major differences between the two species are the greater frequency of squid taken by *lepturus,* the greater frequency of

TABLE 9

COMPOSITION OF FOOD REGURGITATED BY TROPICBIRDS

| | *P. rubricauda*[1] | | | *P. lepturus*[1] | | |
|---|---|---|---|---|---|---|
| | % Frequency | % Number | % Weight[2] | % Frequency | % Number | % Weight[2] |
| Total | 62 | 119 | 48 | 36 | 118 | 41 |
| FISH | 88.7 | 42.0 | 73.4 | 63.9 | 42.0 | 15.2 |
| Exocoetidae (unidentified) | 46.8 | 32.8 | 17.3 | 30.6 | 14.3 | 1.0 |
| *Exocoetus volitans* | 4.8 | 2.5 | 8.8 | 5.6 | 2.5 | 7.8 |
| *Oxyporhamphus micropterus* | 1.6 | 0.8 | – | 2.8 | 0.8 | 3.9 |
| *Cypselurus furcatus* | 21.0 | 10.9 | 37.0 | 2.8 | 0.8 | 2.5 |
| *Cypselurus ?nigripennis* | 0 | 0 | 0 | 2.8 | 0.8 | – |
| All Exocoetidae | | 47.0 | 63.1 | | 19.2 | 15.2 |
| Hemirhamphidae | 1.6 | 0.8 | 1.5 | 2.8 | 0.8 | – |
| Tylosuridae | 8.0 | 4.1 | 5.7 | 0 | 0 | 0 |
| Coryphaenidae | 0 | 0 | 0 | 2.8 | 0.8 | – |
| Carangidae | 4.8 | 2.5 | – | 0 | 0 | 0 |
| Gempylidae | 0 | 0 | 0 | 16.7 | 6.7 | – |
| Scombridae | 1.6 | 2.1 | – | 2.8 | 0.8 | – |
| Gonorhynchidae | 0 | 0 | 0 | 5.6 | 13.4 | – |
| Stromateidae | 1.6 | 0.8 | 3.1 | 0 | 0 | 0 |
| CEPHALOPLDS | | | | | | |
| Ommastrephidae | 37.1 | 40.3 | 21.3 | 72.2 | 58.0 | 84.8 |
| *Tremoctopus violaceus* | 3.2 | 2.5 | 5.1 | 0 | 0 | 0 |

[1] *P. rubricauda* samples were from 27 adults, 35 chicks. *P. lepturus* samples were from 27 adults, 9 chicks.
[2] Some items were in such poor condition that they could not be weighed or measurued; these are scored – in the % weight column.

flying fish taken by *rubricauda,* and the larger size of *rubricauda* prey (Figs. 6 and 7). Clearly the separation between the two species in size of prey is almost complete. The largest overlap in diet was in small squid, but even here *rubricauda* took larger prey than *lepturus* ($t$-test, $P < 0.001$). The distributions of prey weight (Fig. 7) show a sharp cut-off in the region of overlap between the two species. This seems likely to have been brought about by competitive exclusion acting either through the two species' feeding behavior or through their structure. *P. rubricauda* weighs more than twice as much as *lepturus* and has a longer and heavier bill (Table 1) and so would be expected to take larger prey.

The fish and squid proportions in the *rubricauda* diet were similar to those at Christmas Island, Indian Ocean (Gibson-Hill 1947b); squid were more important in both places than at Christmas Island, Pacific Ocean (Ashmole and Ashmole 1967). Aldabra *lepturus* took more squid than did those at Christmas Island, Indian Ocean (Gibson-Hill 1947b).

Samples from *rubricauda* contained several prey species not found in samples from any other seabird on Aldabra. These included three specimens of the pelagic octopod *Tremoctopus violaceus*, which is usually found at the surface and is sometimes washed ashore during storms

## P. RUBRICAUDA

( N = 51 )



## P. LEPTURUS

( N = 41 )



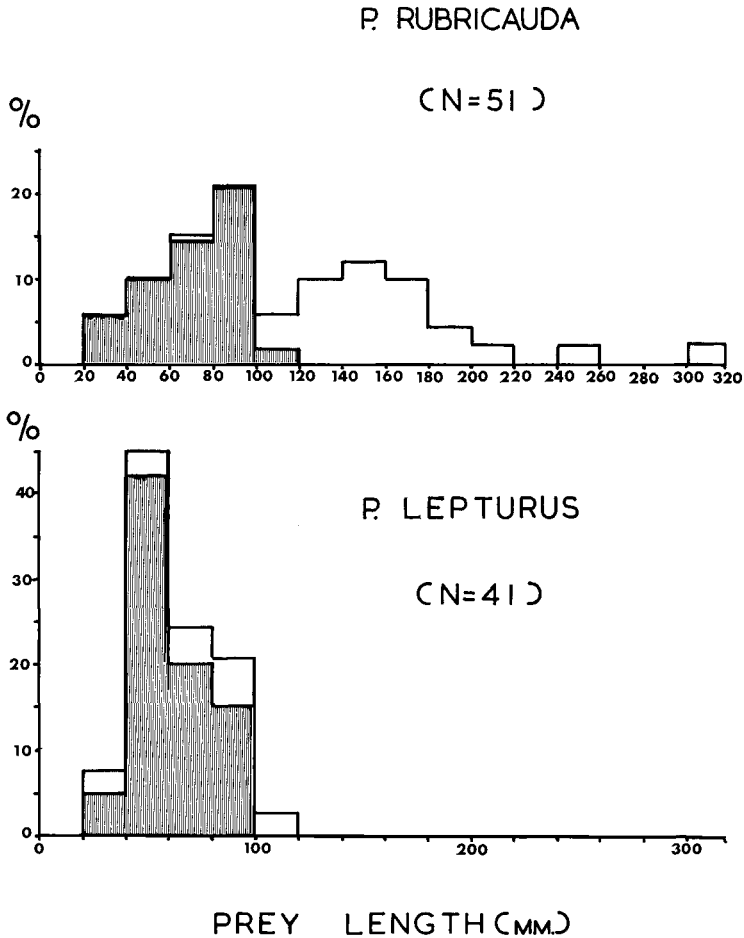## PREY   LENGTH (MM.)

Fig. 6.  Length  distribution  of  tropicbird  prey.  Unshaded:  all  items.  Shaded: cephalopods.

(Clarke pers. comm.); several shells of the deep-water cephalopod *Spirula* sp.; one specimen of the squid *Thysanoteuthis rhombus;* and shells of two species of shallow-water gastropods characteristic of clean sandy parts of the sea bed, or of beds of the marine grasses *Thalassia* sp. and *Cymodocea* sp., which are very extensive on Aldabra. These gastropod remains suggest inshore feeding by *rubricauda,* but they might also have been taken from the stomach of a bottom-feeding fish the tropicbird caught farther out to sea.

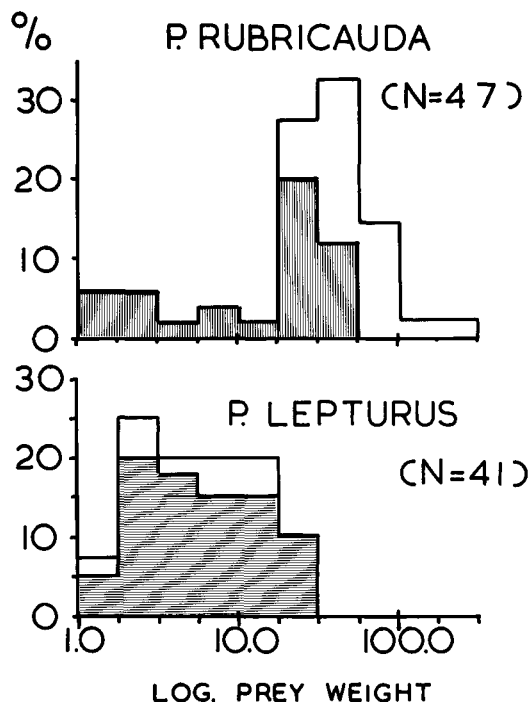The only seasonal difference in food that was detected was an increase

Fig. 7. Weight distribution of tropicbird prey. Unshaded: all items. Shaded: cephalopods.

in the proportion by weight of cephalopods in the diet of *lepturus* in the wet season (90.7%) compared with the dry (46.1%; $\chi^2$ test on weights, $P < 0.001$). I found similar changes in Red-footed Booby (*Sula sula*) and Lesser Frigatebird (*Fregata ariel*) diets on Aldabra (Diamond 1971b).

## DISCUSSION

Present knowledge of the family Phaethontidae is summarized in Table 10, which enables comparisons to be made both within and between the species. The extreme uniformity of the group is evident, differences between species usually follow well-established relationships, such as that relating increasing fledging period to increasing body size (Lack 1968). Some of the apparent intraspecific differences, such as the high body weight and short fledging period of *lepturus* on Bermuda, rest on small samples and may prove atypical. Clearly this family has not succeeded in radiating into a diversity of niches to the extent that some other Pelecaniformes, such as the boobies (Sulidae) (Nelson 1970) and cormorants (Phalacrocoracidae), have done. In the uniformity of their ecology and behavior tropicbirds resemble frigatebirds (Fregatidae).

TABLE 10

COMPARISON OF BREEDING BIOLOGY IN TROPICBIRDS

| Species and location | Breeding regime[1] | Breeding success (%) | Incubation period (days) | Fledging period (days) | Incubation shift (days) | Feeding interval (days) | Chick attendance (%) | Egg weight (g) | Body weight (g) | Egg weight as % body weight | Main food[2] |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *P. lepturus* | | | | | | | | | | | |
| Christmas, I. O. | S | – | – | – | – | – | – | – | – | – | Fc |
| Ascension | N[3] | 30 | 41 | 75 | 3–4 | – | 28 | 41 | 300 | 13 | Fc |
| Bermuda | S | – | – | 62 | – | – | – | 40 | 407 | 10 | Cf |
| Aldabra | N | 48 | – | 80 | 3–6+ | 1.5 | 30 | 43 | 334 | 13 | Cf |
| *P. rubricauda* | | | | | | | | | | | |
| Aldabra | N | 4–44 | 51[4] | 90 | 4–6+ | 1.4 | 40 | 77 | 762 | 10 | Fc |
| Christmas, I. O. | S | – | 44+ | 100 | – | – | – | – | – | – | Cf |
| Christmas, P. O. | S | – | – | 86 | 6 | – | – | – | 665 | – | FC |
| Midway | S | – | – | – | – | – | – | 62 | – | – | – |
| Kure | S | 17–38 | 44 | 89 | – | – | – | – | – | – | – |
| *P. aethereus* | | | | | | | | | | | |
| Ascension | N[5] | 52 | 43 | 95 | – | – | – | 68 | 750 | 9 | Fc |
| Galápagos: | | | | | | | | | | | |
| Daphne | N | 32 | – | – | – | – | – | – | – | – | – |
| South Plaza | S | 55 | – | – | – | – | – | – | – | – | – |
| South Plaza | S | 44 | 42 | 85 | 6 + | 1.5 | 81 | 59 | 642 | 9 | Fc |

[1] S = seasonal, N = nonseasonal.
[2] F = fish, C = cephalopods. Most frequently taken class of food shown in capitals. Sources: Gibson-Hill (1947b), Christmas, I. O.; Stonehouse (1962, 1963), Ascension; Gross (1912), Bermuda; present study, Aldabra; Ashmole and Ashmole (1967), Schreiber and Ashmole (1970), Christmas, P. O.; Howell and Bartholomew (1962), Midway; Snow (1965), Daphne; Harris (1969), South Plaza (lower line); Lévêque (1964), South Plaza (upper line).
[3] Nonseasonal, but peaks when fewest *aethereus* breeding.
[4] Probably anomalous (see text).
[5] Nonseasonal, but peaks when fewest *lepturus* breeding.

Other studies of tropicbirds (Gibson-Hill 1947a, Stonehouse 1962, Snow 1965, Harris 1969, Schreiber and Ashmole 1970) have shown that many populations, even very near the equator, breed at annual intervals. Where nest sites are scarce and competition for them is intense, breeding may be continuous with individuals returning to breed not annually but at intervals corresponding to the length of the individual sexual cycle, i.e. they breed as often as possible. Stonehouse (1962) showed with a theoretical model that tropicbird populations with low breeding success develop unsynchronized laying with strongly damped oscillations in breeding activity, whereas in populations with high breeding success, breeding is more highly synchronized and the interval between successive peaks is determined by the length of the sexual cycle of the particular species. In fact the latter type of breeding regime has not been found; the only populations described nest either all year round or annually.

Snow (1965) described two populations of *aethereus* in the Galápagos that demonstrate Stonehouse's principle. On Daphne Island, which has a shortage of nest sites and a large population, intraspecific competition for nest sites is high, and the breeding season is continuous and breeding success low (32%), whereas on South Plaza Island, only 25 km away, competition for nest sites is light, breeding is annual, and nest success is higher (55% in 1962-63 (Snow 1965), 44% in 1965-67 (Harris 1969)). Harris found some competition for the best nest sites even on South Plaza, but did not dispute Snow's hypothesis.

A similar comparison can be made between Aldabra, where *rubricauda* and *lepturus* both nest all the year round, use similar nest sites, and are very numerous (and thus presumably compete for sites to some extent), and Christmas Island, in the eastern Indian Ocean, where the same two species nest in completely different sites (*rubricauda* on cliff ledges and *lepturus* in holes in forest trees), lay mainly between May and October, and are much scarcer (Gibson-Hill 1947a). It remains to be shown that nest success is lower in both species at Aldabra than on Christmas Island, as Stonehouse's model predicts.

The tropicbirds resemble some other species on Aldabra (*Sula sula* and Crested Terns, *Thalasseus bergii*) in demonstrating by their continuous breeding regime that any seasonal increase in food supply that may occur is slight enough to be overriden by other selective factors, in this case possibly intraspecific competition for nest sites.

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## SUMMARY

The Red-billed Tropicbird (*Phaethon rubricauda*) and the White-tailed Tropicbird (*P. lepturus*) were studied in 1967–68 and in 1969 at Aldabra Atoll. Approximately 1900 pairs of *rubricauda* and 2500 pairs of *lepturus* breed on the islets in the lagoon. The islets are of sufficiently complex structure that the tropicbird species are able to choose slightly different types of nest sites, although with considerable overlap. Breeding occurs in all months of the year with minor peaks at intervals coinciding with the probable lengths of the sexual cycle in each species. Breeding success was between 40% and 50% in each species except in *rubricauda* during the wet season of 1967–68, when it was only 4%, possibly because of overheating during unusually hot, dry weather. Both species fed on fish and squid, *lepturus* mainly on small squid and *rubricauda* chiefly on large fish. There was very little overlap in the weight of prey taken by the two species.

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