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THE BIOLOGY OF THE SEABIRDS OF THE INDIAN OCEAN CHRISTMAS ISLAND*

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ABSTRACT

Eight seabird species (two of them endemic) of four families breed on Christmas Island. Between them they utilise at least 11 distinct breeding niches. They nest at different seasons and their species-specific breeding cycles differ in several basic ways.

The object of this contribution is to analyse these factors, with particular reference to the families Sulidae and Fregatidae. Of the three sulids (*Sula abbotti*, *S. sula* and *S. leucogaster*) the endemic *S. abbotti* is particularly important because of its rarity and the fact that so little has hitherto been discovered about its numbers, distribution on Christmas Island and breeding biology. Attention is particularly appropriate in view of the probable future destruction of its habitat. The extremely slow growth and consequent alternate year breeding of *S. abbotti*, together with its one-egg clutch, would impose severe restraints on the recuperative power of the population (now around 2,000 pairs).

Of the two frigate (*Fregata andrewi* and *F. minor*) the status of the former is of considerable interest; its biology and prospects will be discussed.

The emphasis throughout this contribution will be on the breeding biology of the species concerned, particularly in relation to conservation prospects.

INTRODUCTION

THE heavily forested, coralline limestone Christmas Island in the Eastern Indian Ocean (Lat. 10°25′S, Long. 105°42′E) is of outstanding interest in its geology, botany and zoology and particularly in its bird life. Andrew (1900) wrote the first account of the natural history, while Gibson-Hill (1949) reviewed its history and described its topography and climate and provided most of the existing information on its zoology, particularly its crabs and birds.

The seabirds have been investigated in some detail by Gibson-Hill (1947) and Chasen (1933). Two of them (*Sula abbotti* and *Phaethon lepturus fulvus*) at the present time breed nowhere else and a third (*Fregata andrewsi*) is not certainly known to do so. Their numbers and distribution need to be known to provide a basis for conservation. Secondly, knowledge of the breeding biology of *S. abbotti* completes our records of the breeding ecology and behaviour of an entire family (the Sulidae). Thirdly, comparing a species' biology in different parts of its range can add to our understanding of some basic phenomena, such as the adaptive patterns of reproductive regimes within different zoogeographical areas.

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This contribution, which is based on a visit to the island between March and September 1967, attempts to establish the present-day numbers and distribution of the seabirds of Christmas Island and their breeding regimes, in particular those of the sulids (*S. abbotti, S. sula, S. leucogaster*) and the two frigates (*F. andrewsi* and *F. minor*), and finally to make some general comparisons of seabird breeding biology. In addition the prospects for Christmas Island's seabirds are discussed.

Other contributions to this Symposium particularly those of Bourne and Bailey, provide the background against which Christmas Island can be compared with other Indian Ocean Islands.

That material for this paper was gathered is due almost entirely to the kindness and co-operation of the Phosphate Commissioners, to whom I am most grateful. No less is due to my wife, for hundreds of hours help in the field. David Powell (Christmas Island Surveyor) helped a great deal by putting his unrivalled knowledge of the island and his frequent observations of *S. abbotti*, at our disposal.

I am grateful, also, to Aberdeen University for the Visiting Research Fellowship during which the work was done and for a Parliamentary Grant-in-Aid.

W. R. P. Bourne and, especially, R. S. Bailey, criticised and improved the manuscript, for which I thank them.

The Numbers, Distribution and Breeding Seasons of Christmas Island Seabirds

On Christmas Island there are three species of booby (*Sula sula, S. leucogaster*, and *S. abbotti*), two frigates (*Fregata andrewsi* and *F. minor*), two tropic birds (*Phaethon rubricauda* and *P. lepturus fulvus*) and one tern (*Anous stolidus*).

Sula leucogaster (the Brown Booby)

This species nests on the shore terraces, at the top of the sea cliffs and on the edge of the inland cliff (Fig. 1). Its colonies are patchily distributed and vary in size from a few pairs to between 100-200. Gibson-Hill estimated there to be 5,000 to 6,500 pairs and thought it was the most numerous sulid. My estimate for the east coast, based on extrapolation from several counts was 2,250 pairs. Since it nests, though thinly, all round the perimeter of the island, according to D. Powell and R. Bishop, who know the island better than anybody, its total breeding population would thus be around 7,000 pairs, a figure which is close to Gibson-Hill's.

Gibson-Hill states categorically that *S. leucogaster* breeds all the year round, although laying mainly between March and May. The breeding regimes of our study groups, numbered in Fig. 1, are given in Table 1, and Fig. 2.

None of the groups other than those listed in Table 1 were large enough to merit detailed analysis, but it may be said that the small groups (nos. 5 & 6) both laid in May, that group 7 of about 75 nests laid chiefly in April and May and that in sporadic visits to other parts of the coast all observed clutches had been laid between

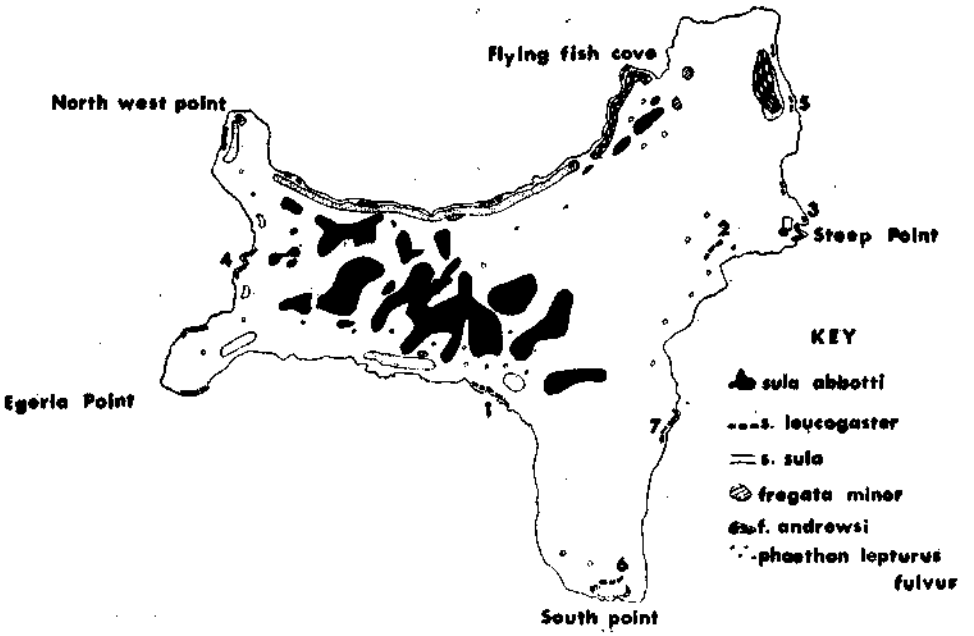

Fig. 1. Map of Christmas Island (Indian Ocean) showing the distribution of six of its eight seabirds.

Note.—(1) The distribution given have been compiled from positive records and DO NOT represent the total areas occupied by the species concerned, (2) In the case of *S. abbotti* only the most densely occupied areas have been depicted, (3) In the case of *F. andrewsi* it is unlikely that there are any other groups of significant size, and (4) The numbers given for some of the *S. leucogaster* colonies are referred to in Fig. 2 and Table 1.

TABLE 1. *Seasonal distribution of egg laying in* S. leucogaster *on Christmas Island**

Group	Area (sq. m)	No. of pairs	Mimnium number of clutches started in								Total clutches recorded
			J.	F.	M.	A.	M.	J.	J.	A.	
1 South shore terrace	6000	55	2	3	4	7	4	0	0	1	21
						15					
2 Lip of inland cliff	500	36			0	6	17	4	1	0	28
						23					
3 Shore terrace & inland cliff		70		3	2		28		0	0	33
4 West shore terrace		66	0	2	10	25	10	0	0		47
						45					

* It is possible that before our arrival, at the end of March, some clutches had been laid and lost; we could only work back from existing young. Consequently figures for Jan.-March may be too low if many chicks died and left no trace.

about March and May. Unless heavy mortality of eggs or chicks occurred the general conclusion must clearly be that few eggs were laid between August/September 1966 and March 1967, otherwise we should have found young birds or eggs in March 1967, and in 1967. It is also probable that very few eggs were laid in September/October 1967 because in August *leucogaster* showed no signs of preparing for a new wave of breeding. Although it may be possible to discover isolated cases of *leucogaster* laying in almost all months, in 1967 there was a very strong tendency to lay mainly in April and May, different areas of Christmas Island showing little difference in this respect (Fig. 2).

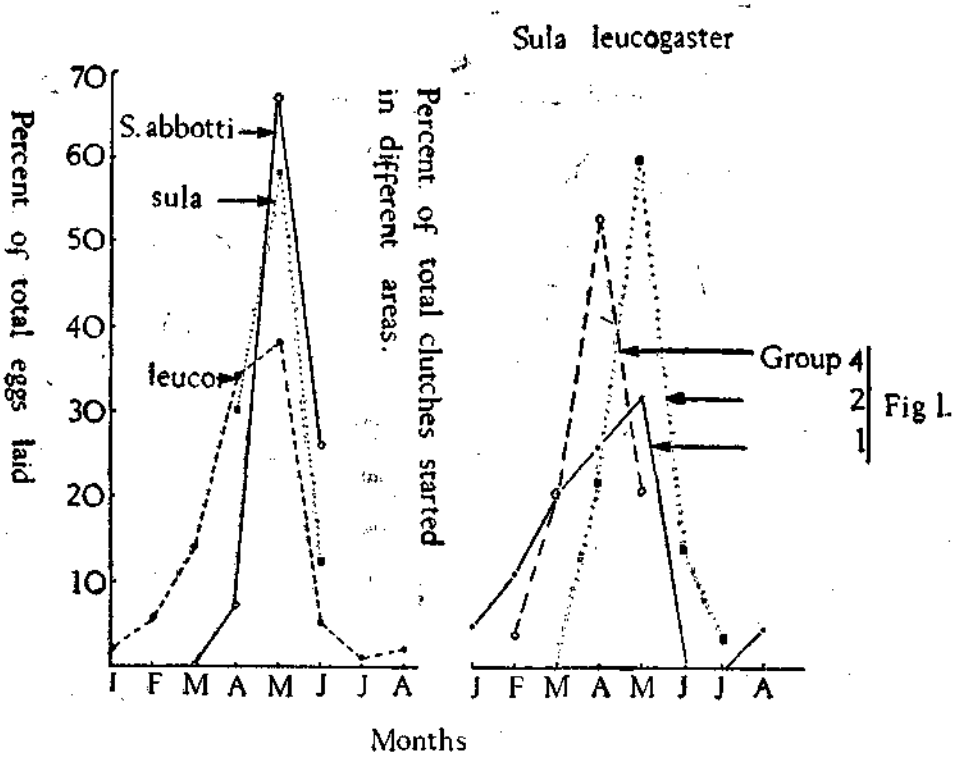

Fig. 2. a. The three sulids of Christmas Island compared with respect to the months in which they lay ; b. Three groups of *S. leucogaster* compared with respect to the months in which they lay. *Note.*—(1) *Sula sula* and *S. leucogaster* figures are based on more than 50 clutches, *S. abbotti* on 15 clutches, and (2) The group numbers for *S. leucogaster* refer to their position shown in Fig. 1.

On Christmas Island, as elsewhere, clutches consisted of 1 or 2 eggs (57% c/1) but the brood was always reduced to one by the death of the younger chick. Since there is only one known case of two young surviving anywhere, it seems almost certain that the two-egg clutches of both *S. leucogaster* and (elsewhere) *S. dactylatra*, do not owe their retention within the population to an ability to produce two independent young. Nevertheless, clutches of two gave rise to a considerably higher percentage of young than did clutches of 1 : 15 chicks fledged from 19 clutches of 2, and only 13 chicks fledged from 33 clutches of 1. These data support Kepler's (1969) findings that two-egg clutches of *dactylatra* produce more young than one-egg clutches. The mechanism by which one young from a two-egg clutch survives

better than one from a single-egg clutch remains unknown (but see discussion); however, the second egg may contribute to breeding success largely by replacing the first born chick should this die in the 5-day interval between the hatching of the first and second eggs.

The brown boobies of Christmas Island showed a surprising agility among and beneath trees and bushes, frequently nesting in most awkward and inaccessible sites. They seemed at least as competent among twigs as the more traditionally arboreal *S. sula*. In general, their behaviour agreed with the descriptions given by Dorward (1962b) and Simmons (1967). A comparison with that of all other sulids has recently been published by Nelson (1970).

Sula sula (The Red-footed Booby)

S. sula (all of them the white form) is probably more numerous than *S. leucogaster*. It nests, at a height of 30′ or more, in trees on the shore terrace region around much of the island and particularly on the mid-north coast, around North West Point and at South Point (Fig. 1). Human predation has eliminated the habit of nesting low down, as it used to do in the Lily Beach area (pers. comm. from several long term residents). Its total numbers cannot have been less than 5,000 and may have been very many more. I guessed that the north coast alone held at least 3,000 pairs and there were many other areas holding several hundreds.

The local Malays esteemed *S. sula* as food (whereas they held *leucogaster* in low regard) and informants estimated that at certain seasons 200-400 adults and large young were taken per week. Over 2-3 months this could amount to more than 2,000 birds, perhaps mainly juveniles.

In all the groups (Fig. 1) laying occurred in late April or May and in the group studied in detail (South Point) predominantly in the first half of May. Because our visits were confined to one or two main areas it would be unjustifiable to say that there was no laying *anywhere* on the island outside the period April-May-June, but this species certainly laid almost entirely in these 3 months in 1967. Also, it had not laid between September and December 1966, or there would have been young birds present in March 1967 (always providing that there had not been massive mortality). So this species like the Brown booby, tends to produce eggs mainly in May (Fig. 2). By contrast, on Aldabra which lies at about the same latitude in the Western Indian Ocean *Sula sula* lays mainly between November and April (Diamond 1971).

Sula abbotti (Abbott's Booby)

One of the rarest and the least known of Christmas Island's seabirds is *S. abbotti*. It is thought, to have formerly nested on Assumption Island, (see Stoddart *et al.*, 1970) but has not done so since early this century. I have recently concluded that *abbotti* probably never, in fact, nested on Assumption but certainly nested on Rodriguez in the Mascarenes (Central Indian Ocean). This island used to be forested and a 17th Century French account describes a booby which could have been no other than *abbotti* (Nelson, in press). Its sole nesting

locality is now Christmas Island, and the main object of our work there was to investigate its numbers and distribution and compare its breeding biology and behaviour with that of other members of the same family. The details are presented elsewhere (Nelson, 1971) and may be repeated here.

Sula abbotti nests almost exclusively in large trees on the central plateau of Christmas Island [up to the two highest points Ross Hill (1,060′) and Murray Hill (1,170′)]. Although these are the most densely occupied areas (Fig. 1) it occurs over much of the island at lower densities.

Population

Pearson's (1966) opinion that *S. abbotti* might number less than 100 pairs, following Gibson-Hill's (1947) estimate of 500-700 pairs, suggested that the species was in danger of extinction (the ' Red Book ' ; I.U.C.N.). At the time of Pearson's stay on the island, 90% of its 64 square miles was trackless jungle, much of which, if not impenetrable, could be reached only by trekking for days. Even then, because of the obscuring growth, only haphazard observations were possible.

The population in 1967 was estimated by *direct search*. As a check numbers were estimated from counts of birds made as they returned to the island in the evening. Fortunately, they flew in high from the N.W., over a very narrow front, which made counting from a suitable vantage point relatively simple.

Four categories were accessible to methodical search along survey lines.

1. Nests could often be seen high up in the first few ranks of trees on either side of a line.

2. Free-flying juveniles regularly return to the precise site of the nest, itself often disintegrated. Parents return to feed them there mainly during the last two hours of daylight when the juveniles maintain an unmistakable calling which reveals a high proportion otherwise hidden by foliage.

3. Pairs re-uniting at the nest-site call loudly, particularly during courtship display, incubation and the first half of the chick's time in the nest. They rarely greet each other when the juvenile is free-flying, so there is little or no overlap with category 2, even when the record is purely auditory. Meetings of adults are also most frequent in the last two hours of daylight.

4. Fresh excreta beneath perches indicates a juvenile, single adult or pair.

The results of all searches made during our visit from March to September whether positive or negative were marked on a large-scale map of the island. By this method, we located 410 calling pairs, 112 juveniles and 264 nests, totalling 786 pairs.

The exactness of our grand total depends on the correctness of the estimate of *undiscovered* pairs both in the areas searched and in those we could not comb in the time available. Assuming that our search disclosed 70% of the nests actually there,

and estimating the number of pairs in unsearched areas from our knowledge of adjacent ones, the total figure becomes 1,844 pairs. In fact, a figure of 20% almost certainly overestimates the success of our search and the total population is probably at least 2,300 pairs and may be 3,000 or more. In addition, the current year's juveniles and the dispersed immatures should be added to arrive at the world's total of *abbotti*. On the basis of 1,850 pairs, 282 juveniles and an estimated 200 immatures, a figure of around 4,200 individuals is obtained. Based on 2,300 pairs the total becomes around 5,100 individuals.

To check we counted the number of birds flying in to the island during daylight. From the actual figures obtained in the field : (865 incomers from 16.00 to 18.00 hrs. on 1 August ; 1,850 from 05.30 to 18.00 on 2 August ; 1,188 from 16.00 to 18.00 on 3 August ; and 700 from 16.10 to 18.00 on 1 September) one may calculate the population. We took into account the proportion of incomers that would (from our knowledge of the breeding situation) have been returning to an incubating or guarding mate, and would therefore represent a pair, the proportion that would have been returning to an unguarded juvenile and which would therefore simply count as individuals, not pairs, and lastly the proportion of incomers that would themselves be juveniles. Incorporating these corrections into the calculation (below) gives a figure of 3,500 to 4,500 individuals. Again, this is probably a low estimate since in the calculation we assume that we spotted a high proportion of the incomers and also apply certain correction factos (given above) which themselves result from a conservative estimate of the total population, i.e. correcting depending on estimates which include, for example, the uncounted areas in the direct search. The result nevertheless agrees well with that obtained by direct search.

TABLE 2. *Estimation of the population of Abbott's Booby on Christmas Island in August* 1967, *from counts of incoming birds*

Basis : approximately 2,000 incoming individuals each day.

Assumptions :

(1) Adult population roughly in two halves, breeding in alternate years. This is more than an assumption since observations proved that the same pair could not breed successfully in two successive years.

(2) Of the pairs which laid in 1966, 80% assumed successful and still visiting the nest, the remaining 20% permanently at sea at the time of the count.

(3) For every ten breeders there is one current non-breeder visiting the island, and non-breeder pair members return on alternate days (at the time of the counts non-breeders were usually seen singly at the nest-site).

(4) 1967 breeders will, each day, have one bird on the nest and one bird returning (supported by observations).

(5) In pairs with juveniles, both members will return daily (supported by observations).

(6) 75% of juveniles, at time of count, assumed to be free-flying and returning daily.

Calculation : On the assumptions and observations given above, the incoming birds will consist of the following categories :

	Proportions	Comments
Non-breeders	1	Only half the non-breeders return each day.
1967 breeders	5	10 1967 breeders for every 10 1966 breeders, but 50% of 1967 breeders on nest.

1966 breeders	8	20% of 1966 breeders failed and absent.
Juveniles	3	75% of juveniles from 80% of 1966 breeders arrive daily.

Applying these proportions to the 2,000 incomers :

Non-breeders	118
1967 breeders	588
1966 breeders	941
Juveniles	353
Total	2,000

Population composition at time of count, as individuals :

Non-breeders (2×118)	236
1967 breeders (2×588)	1,176
1966 breeders with juveniles	941
1966 breeders away at sea	236
1966 juveniles (353+25%)	441
Total	3,030

Distribution and habitat

S. abbotti occurs mainly above the 500' contour and most of the population is concentrated in the hillier and more irregular western half of the Island. There is no simple relationship between distribution and type or height of tree. As the number of pairs marked on the map grew, the impression was that *S. abbotti* tended to concentrate on spurs and the sides of small valleys even when these were not obvious to us on the ground. On the other hand, whilst in some areas the correlation between *S. abbotti* distribution and map contours is very clear, in others it is poorer, but this is often because there are quite significant topographical irregularities which contours do not reveal.

The type of tree cover is also important. Typically, *S. abbotti* nests at a height of 60 feet or more, in trees which are either fully emergent or contain large gaps for access. The nests are placed on a broad limb beneath a section of canopy or among thinner lateral branches, never, in our experience, right up in the crown. This provides shelter for the chicks from rain, wind and sun.

S. abbotti generally occupies dense jungle. Areas sparsely covered with poor trees as in the extreme southwest and many parts of the east of the island are unoccupied, as also are poor trees on drier, stony slopes within the generally favoured areas. Yet there are large areas of magnificent trees under the right topographical conditions that are extremely thinly populated or empty. The eastern half of the island is, in many places, covered with fine trees but lacks the irregularly dissected topography of the favoured western half. The canopy on the extreme eastern slopes, exposed to the prevailing southerly winds, tends to be more closely knit and so less suitable for *S. abbotti*. The entire eastern seaboard lacks *S. abbotti* even above the 500-foot contour, though they occur in small numbers nearer the centre, the first pairs just inland of the inner cliff.

This booby is certainly the least gregarious of all sulids. Many pairs are solitary, but it does not occur randomly even within favoured areas ; some pairs nest in small loose clumps and occasionally two or three nests may be found in the same or adjacent trees. This is to be attributed to a slight tendency to nest in colonies rather than to a clumping of the best sites.

Nest and egg

S. abbotti constructs a deep well-woven and substantial nest of living twigs. One or more of the supporting branches may penetrate the base, giving good stability in winds. *Abbotti* lays a single egg weighing approx. 112 g., which is 7.1% of the female's weight. This percentage is 2% more than that in *S. sula* in the Galapagos, the species with the nest highest ratio of egg to body weight. Large eggs are usually a feature of species whose chicks are well-developed on hatching and which grow relatively slowly, and *S. abbotti* shows both these features.

Breeding Regime

I must remind the reader that the following accounts is based on only part of a year and although it is highly probable that we obtained reasonably full data on laying in 1967, and that our reconstruction of events in 1966 is correct, the possibility that freak circumstances wiped out all traces of a breeding attempt late in 1966 or very early in 1967 cannot be entirely excluded. If this had occurred it would of course radically alter our conclusions, and whilst there is absolutely nothing to suggest that it did, the basis for our conclusions must be made clear. The two crucial points are that *abbotti* apparently lays only between April and August and that the whole breeding cycle, excluding the rest period, occupies more than 12 months [the supporting details for this statement are given in Nelson (1971)]. It therefore follows that *S. abbotti* breeds once in every two years (or theoretically even less often, though this is improbable).

The months in which it laid we could of course establish only for the year of this study (1967) when laying was confined between April and July with a clear May peak. There is little likelihood that eggs were laid after we left in September, since we could find no pairs courting and building, activities which take 2-3 months at least. A similar breeding season must also have occurred in 1966, for an extensive search in March and April 1967 disclosed only fully grown juveniles, apart from some pairs in early courtship. Working back, the eggs must have been laid earlier than the preceding August but (from later-gained knowledge of the length of time that young take to grow, and are fed as juveniles) probably later than March/April ; that is, probably between April and July 1966. No eggs had been laid between approximately August 1966 and April 1967. *S. abbotti* thus shows the same tendency to lay in May as do the other two sulids.

Young S. abbotti

The most remarkable features of the young are their extraordinarily slow growth and the fact that their juvenile plumage is almost exactly like that of an adult male. No other juvenile sulid shows a comparable resemblance to the adult (juvenile Red-footed boobies of the brown form are deeper brown than adults and have black instead of blue bills, and blackish instead of red feet) and in one (*S. bassana*) the juvenile's plumage is about as different from that of the adult as it could be. In the only available identification manual for the Indian Ocean (Watson *et al.* 1963) the juvenile *S. abbotti* is depicted as a dull, nondescript bird, but this is incorrect.

The slow growth of *S. abbotti* is of particular interest, since that of some other Christmas Island seabirds is considerably quicker than that of the same or related species in some other places. Compared with *S. sula* and *S. leucogaster*, *S. abbotti* grows very slowly, taking over ten weeks to reach 90% of the adult's weight whereas *leucogaster* reaches adult weight in about seven weeks. The fledging period is probably at least 24 weeks and the period over which the fully-grown and free-

flying young continues to be fed by the parents almost as long, or perhaps longer (Nelson 1971).

Behaviour

The breeding behaviour of *Sula abbotti* is very different from that of other sulids. Its main features are that, remarkably, there is no overt aggression (fighting or jabbing); the main displays are conducted with the partners distant from each other, whereas those of all other sulids involve contact; and the begging of the young is highly restrained. In addition some behaviour patterns, notably appeasement, found in one form or another in all other sulids, are absent and some (notably false sleeping and ritualised preening) are found only in *S. abbotti*. It would involve too much digression to give the full interpretation here but all these features support the suggestion that *S. abbotti's* behaviour has been shaped by the dangers of its tree-top breeding environment. To fall through the canopy to the ground would be fatal and selection pressure has brought about a marked reduction in contact-behaviour, especially aggressive behaviour, probably by raising the internal threshold for aggression. This, in turn, has rendered certain behaviour unnecessary. This interpretation also makes sense of the otherwise puzzling fact that *S. abbotti's* juvenile plumage is identical with that of the adult male, the suggestion being that distinctive juvenile plumage in birds has, as one of its functions, inhibition of attack by adults, by not presenting the appropriate releasers. In *S. abbotti*, however, a high internal threshold for attack renders such morphological inhibition unnecessary and since there are probably advantages in having a black dorsal surface and a white ventral one (the plumage of the adult) the juvenile can benefit from these without danger. By contrast, the gannet has an extremely low internal threshold for aggression (Nelson 1965) and its juvenile plumage is entirely different from that of the adult.

Fregata minor (Great Frigate Bird)

Fregata minor is widely distributed in the tropics and is often sympatric with *F. ariel*, although on Christmas Island it occurs with *F. andrewsi*. *F. minor* is not common on Christmas Island, where its small and widely scattered nesting colonies (Fig. 1), occur both on the shore terrace and above the inland cliff. There is an association, even closer than the Figure suggests, between this species and *S. sula*, but none with *F. andrewsi*.

In 1967 display was in full swing by late March and continued until late May and eggs were laid chiefly in April, May and June. On Aldabra, *F. minor* lays mainly between September and December (Diamond 1971).

Rough counts of a number of breeding groups gave a total population of about 300-500 pairs, but the true figure is probably higher, around 500-1,000. No nests were accessible to full investigation and so a comparison with the *F. minor* studied on Tower Island, Galapagos, (Nelson 1968) was impossible except for the length of incubation stints, which were less than half as long as in the Galapagos. If shorter stints reflects shorter foraging periods at sea this then supports the general picture, revealed by the sulid comparison, of more easily accessible food around Christmas Island. Nevertheless, from the length of its fledging period, there is every reason to think that, like *F. andrewsi*, *F. minor* breeds less than once every year.

Fregata andrewsi (Christmas Island Frigate Bird : Andrews Frigate Bird)

At the present time *F. andrewsi* is not known to nest elsewhere although it might be too dogmatic to say that it definitely breeds only on Christmas Island. It has been recorded from the Cocos Keeling Islands, was common in the Anamba Islands and strays to Java, Ceylon, the Malabar Coast of India and Sarawak (Chasen 1933). Gibson-Hill (1947) concludes from Chasen's observations that ' there can be little doubt that it is resident somewhere in the Anamba-Natuna group '.

It has fairly well-defined preferences on Christmas Island (Fig. 1). The two main nesting areas are behind the golf course and along a two-mile strip near the north-east tip of the north coast. In both these areas it nests fairly well down on the shore terrace. It almost certainly numbers less than 2,000 pairs on Christmas Island.

Like *F. minor*, most *F. andrewsi* nest in fairly dense groups with adjacent pairs sometimes only two or three feet apart. These are founded around nuclei of displaying males after a proportion of them have attracted mates. Typically, between 10 and 30 pairs form a fairly discrete group, clearly separated from the nearest adjacent one. Often, they nest in partly dead trees though never on thin dead branches.

Display begins in late January or February (D. Powell, pers. comm.) and is probably at its peak in March, declining by mid-April and virtually finished by mid-May. It is similar to that of *F. minor* (Nelson 1966) but because *F. andrewsi* is larger the movements are slower. This applies, also to the vocalisations, which at first sound entirely different, but in fact are deeper and slower versions of those used by *F. minor*. Thus, the fast, high-pitched warble of *F. minor* emerges from *F. andrewsi* as a deep and slow ' kow-wow-wow '.

Eggs were laid from late March to late May and possibly later, since *F. andrewsi* will lay a replacement egg if it loses the first one.

On Christmas Island, *F. andrewsi* grows much faster than *F. minor* in the Galapagos. Thus at ten weeks *F. andrewsi* chicks had almost reached adult weight, whereas in the Galapagos *F. minor* at ten weeks weighed little more than half adult weight. This represents an enormous difference in the amount of food brought to the young (Fig. 3).

The fledging period of *F. andrewsi* was not accurately determined but was probably at least 27 weeks. The free-flying young are then fed for at least a further six months because we saw juveniles which (if the '66 laying season was like '67) must have fledged during October 1966, being fed in May 1967. This means that the species can breed only once in two years ; an intermediate frequency is ruled out by the observation that display and, therefore presumably, egg laying are confined to the same few weeks each year (D. Powell, pers. comm.). It would now appear probable that *all* frigates breed at more than annual intervals probably as an adaptation to their highly specialised hunting behaviour, which requires the free-flying young to be subsidised for the considerable period they take to become proficient.

Although protected by law, adult *F. andrewsi* are taken by the resident Malays in considerable numbers. We found the remains of 40 beneath one display area in April 1967, including one alive but with a broken wing. This represents a very

significant toll of the world's population and the species certainly requires tighter protection (see Discussion).

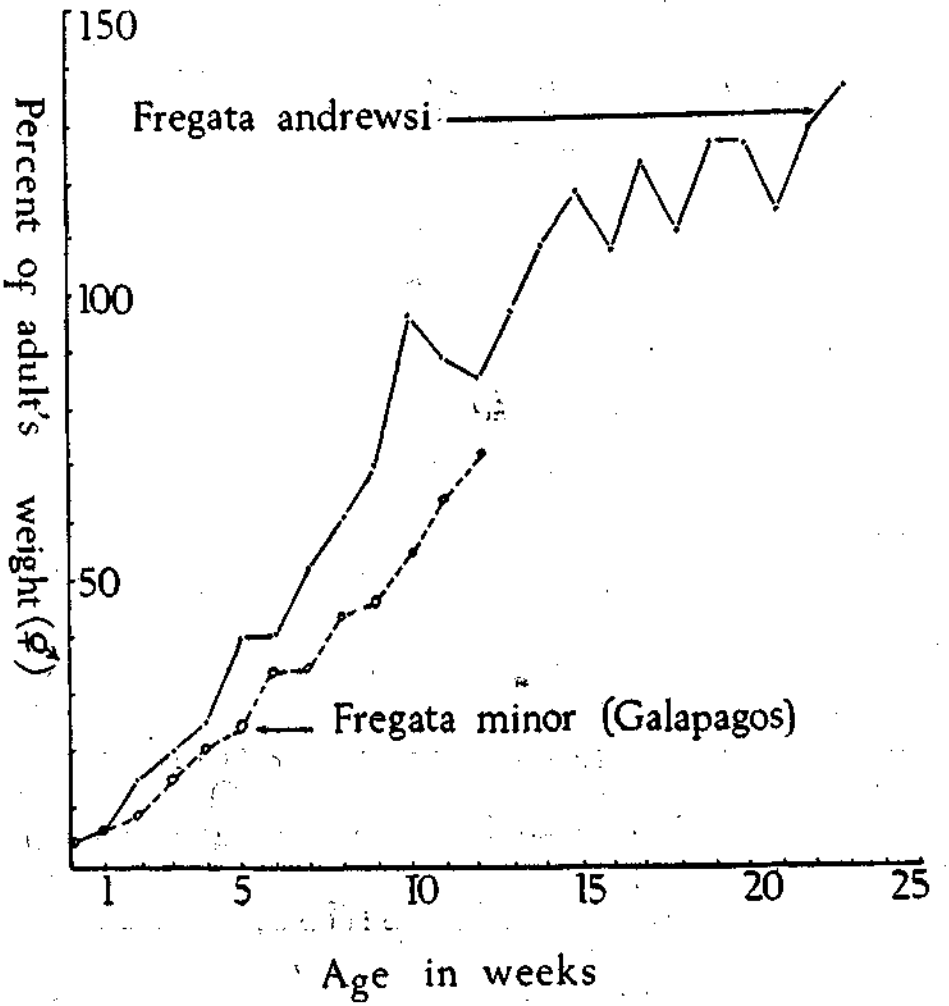

Fig. 3. The growth rates of *Fregata andrewsi* (Christmas Island) compared with *F. minor* (Galapagos). The adult weight is based on the average of male and female weights which for *F. andrewsi* were only one each.

Phaethon rubricauda and Phaethon lepturus fulvus

(Red-tailed and Golden Tropic-birds)

Our few observations on the two Christmas Island tropic birds concern only their numbers and breeding seasons. Gibson-Hill's estimate of 400-600 pairs of *P. rubricauda* is probably low. One thousand or more would be nearer the true figure and perhaps still an underestimate. I corroborated Gibson-Hill's main areas and found *P. rubricauda* particularly plentiful at Steep Point, South Point and on the north-east segment, but the entire north coast also holds them.

Our observations also supported Gibson-Hill's conclusion that the main laying period is May and June but, at least in 1967, the spread was greater than he implies. A five-week-old chick discovered in April proved that some eggs may be laid in March and the fact that courtship display continued until we left in late September suggested that some might be laid in later in the year, although it is possible that this display came from non-breeding birds. Gibson-Hill similarly recorded communal fighting all year round. On Aldabra, large numbers of this species lay in all months of the year (Diamond 1971).

The Golden Tropic-Bird *Phaethon lepturus fulvus* is certainly commoner and more widely distributed than Gibson-Hill reported. It is the most difficult of all Christmas Island's seabirds to study since it nests deep in tree holes in the forest. An accurate census was impossible but, from the wide areas over which I saw it (Fig. 1) and the size of the display parties (up to 14 in the air together), there were certainly more than 1,000 pairs and possibly two or three times that number. It is not strictly confined to tree holes; we discovered one nest in a cliff hole and suspected from the appearance of some of the sites visited that it occasionally used deep crotches between trunk and branch. That it should use such dangerously inaccessible nesting sites was to me its most remakable feature. To see parties of adults weaving and dodging among the branches emphasised this, but not nearly so dramatically as did the large number of dead and dying grounded juveniles. To fly straight from a hole, climb through the canopy and then fly one to five miles or more down to the sea seems a supremely difficult test for a juvenile tropic bird and suggests that the selection pressure that led it to adopt the tree nesting habit must have been very strong. Competition with the larger *P. rubricauda* might have excluded it from cliff holes. Elsewhere *P. lepturus* and *P. rubricauda* often breed sympatrically and may compete for nesting sites. They (or *P. lepturus* and *P. aethereus*, which is very similar in size to *P. rubricauda*) are frequently on record as nesting in close association but preferring slightly different sites. On Ascension, the breeding success of *P. lepturus* is much affected by competition for sites from *P. aethereus* (Stonehouse 1962).

Like Gibson-Hill, we deduced the breeding season from records of stranded juveniles. He concluded that eggs were laid mainly between June and October. Some, however, must certainly have been laid at least as early as February 1967 for we found juveniles in late April. On Aldabra *P. lepturus* like *P. rubricauda* was markedly non-seasonal.

The two Christmas Island tropic birds (and particularly *P. lepturus*) thus showed less tendency than the other seabirds to lay around May in 1967.

So far as we knew *P. lepturus* was not taken for human food, but *P. rubricauda* was shot occasionally.

Anous stolidus (Common Noddy)

Gibson-Hill estimated the Common Noddy population to number 4,000-5,500 pairs. It utilises a far wider variety of nesting habitats than he records however, and may therefore be more numerous. In addition to ledges on the sea cliffs all round the island and at several points on the inland cliff (e.g. Steep Point and South Point) it nests in considerable numbers in the tops of Pandanus and Aringha Palms and in trees at least half a mile inland, up to a height of 800 feet above sea level.

The breeding season given by Gibson-Hill (beginning of April to end of September, with most eggs laid in May) was correct for 1967. On Aldabra, this species laid mainly between the beginning of December and early March (Diamond 1971).

Noddies are eaten by the Malays, though in what numbers we were unable to ascertain.

A Comparison Between the Indian Ocean Christmas Island and Some Other Tropical Islands with respect to Adaptive Aspects of Breeding Regimes

An obvious theme concerned with a general understanding of Christmas Island seabird biology requires comparison between its populations and those of the same species elsewhere. I refer not to other Indian Ocean Islands (a theme covered by R. S. Bailey, this symposium), between which some degree of correspondence might be expected, but to islands with a different set of environmental conditions. This is not the place for a detailed comparative review, covering a large number of islands, but rather for a statement of the main contrasts between Christmas Island frigates and boobies,in particular, and those from one or two apparently very different areas, namely the Galapagos Islands, Ascension and Aldabra, where intensive work has been carried out during the last decade (Nelson 1966, 67, 68 ; Dorward 1962a, b ; Stonehouse 1962, Ashmole 1962, Simmons 1967). The issues involved emerge better from a few clear contrasts than from a mass of relatively inconclusive comparisons.

The comparison will concern the timing, duration and frequency of breeding and associated adaptations.

Evidence presented in this paper together with earlier accounts, strongly suggests that with the partial exception of *Phaethon lepturus* and perhaps *P. rubricauda* all the seabirds of Christmas Island lay mainly between March and June with a peak around May. This markedly seasonal breeding contrasts strongly with the Galapagos situation in which :

(*a*) *Sula sula* on Tower breeds in any month, though with a tendency to lay each year in April/May and September/October (Nelson 1969a).

(*b*) *Sula nebouxii* on Hood Island (Nelson 1968a), *Creagrus furcatus* on Tower (Nelson 1968b), *Puffinus lherminieri* (Harris 1969) and *Phaethon aethereus* (Snow 1966, Harris 1970) lay in any month, though irregular peaks may occur.

On the other hand, *Fregata minor* on Tower lays chiefly in March/April (Nelson 1966) ; *Sula dactylatra* on Tower mainly in August/October and *S. dactylatra* on Hood mainly in October/November (Nelson 1967).

Similarly on Ascension, the seabirds (two species of booby, two tropic-birds, three terns, two frigates) show no strong tendency towards seasonal breeding (Dorward 1962, Ashmole 1962, Stonehouse 1962) ; and on Aldabra non-seasonal breeding is the rule among the very same species which breed seasonally on Christmas Island.

Among Christmas Island seabirds, the two frigates and *S. abbotti* take a long time to fledge and are fed as free-flying juveniles for a further long period. Since their breeding regimes are adjusted to produce seasonal laying, individual birds must breed every two years, at least when they have bred successfully.

In the Galapagos a similar situation exists in that *F. minor* takes at least 15 months from beginning courtship to finally ceasing to feed its offspring (Nelson 1966) and *S. sula*, at least, sometimes takes more than a year (several months longer than on Christmas Island). The former, however, breeds biennially whilst the latter often breeds at intervals of between one and two years. Thus, the difference between the two areas is that Christmas Island birds, if their cycle takes more than a year, breed seasonally and biennially whereas comparable Galapagos and Ascension species breed *either* seasonally and biennially (*F. minor*) or aseasonally and irregularly (*S. sula*).

Conversely, it appears that no Christmas Island species breeds at intervals of less than a year despite the fact that *S. sula* and *S. leucogaster* each take less than nine months from the beginning to the end of successful breeding. In the Galapagos, however, *Sula nebouxii* breeds at 9-10-month intervals (Nelson 1970), *Creagrus furcatus* breeds at around 9-month intervals (Snow & Snow 1967), *Puffinus lherminieri* at approximately 9-10-month intervals (Harris 1969) and *Phaethon aethereus* at 10-month intervals (one instance, Snow 1965).

S. leucogaster is absent from the Galapagos, but in some areas, such as Ascension in the South Atlantic, it breeds at intervals of 8-9 months (Dorward 1962a). Again, seasonal breeding is maintained on Christmas Island but not on the Galapagos or Ascension.

Since some species breed seasonally on Christmas Island, despite the fact that they take either much less or much longer than a year, whilst the same and/or closely-related species on the Galapagos and Ascension may breed *either* seasonally *or* aseasonally, one presumes that the difference is connected with climate, oceanographic features and food supply, which are probably linked. The obvious implication is that food is significantly more available at certain times of year in the foraging area of Christmas Island and that their breeding season is geared to this. In the Galapagos, on the other hand, this is either not so, or less so, hence the flexibility in breeding season which is permissible or even advantageous. In this context it is interesting to note that the area N.W. of Christmas Island, on the Continental shelf, is an area of enhanced biological productivity (50+mg. of organic matter per cu. m./yr), and Wyrtki (1962) describes an upwelling area between Java and Australia during the S.E. Monsoon between May and September. It is in this area that the South Equatorial current of the Indian Ocean is formed and Wyrtki points out that although this takes most of its water from the current off the N.W. cape and the Timor Current these are together insufficient to form the strong South Equatorial current which leaves the area near Christmas and Cocos Islands. He concludes that a contributory upwelling (which in other oceans accompanies the formation of the zonal equatorial currents) is present off the coast of Java and Sumbawar, that is, to the N.W. of Christmas Island. I suggest that Christmas Island seabirds have evolved their seasonal breeding regimes with dependent young mainly between June and September, to take advantage of this upwelling with its associated fauna. A supporting point is that all returning *Sula abbotti* without exception came into the island from the N.W.

On the other hand, this speculation must be highly tentative because we do not know how long a time elapses before the upwelling results in food suitable for seabirds, nor how far the water will have moved by then, so there is no direct proof that food is more abundant or available during the breeding season. Nevertheless, breeding most probably *is* seasonal, and the seasonal nature of the upwelling is one factor that may affect its timing. A further factor may be the danger to fluffy young, with inadequate thermo-regulation, associated with the strong winds and rains of the N. & N.E. monsoons (Nov.-April). Even if it could be shown that around Christmas Island food was most accessible at a particular season and that this was not the case in the Galapagos, it would prove nothing about the *absolute* amount, nor its *relative abundance*, in the two areas. However, the evidence (breeding success ; rate of growth of young etc.) very strongly suggests that the two areas *do* differ markedly in the amount of available food they contain, the Indian Ocean around Christmas Island being much richer than the Pacific around the Galapagos. As Figure 3 and Table 2 shows, the same and closely related species grow faster on Christmas Island than in the Galapagos. Also they suffer very much lower mortality due to starvation in the nest (Nelson 1969a & unpublished). Further, one can point to intra-specific (inter-population) differences such as egg size, period of post fledging dependence of young etc., which are probably correlated with the relative abundance of food.

Thus the most interesting feature emerging from a comparison of the breeding biology of *S. sula* on Christmas Island and on Tower Island in the Galapagos, is that the two populations seem to have evolved significantly different adaptations. In the Galapagos the species is adapted to an environment in which food is scarce and erratic for variable and unpredictable periods. Putting it the other way round, there are no seasons or periods during which it can depend on food being adequate (Nelson 1969a). Under these circumstances it has evolved :

(*a*) non-seasonal breeding which is *proximately* triggered by a period of relatively abundant food (Nelson *loc. cit.*) ;

This at least ensures that the energy consuming activities of courtship and nest-building and (for the female) the metabolic effort of egg production are appropriately timed. Harris (1969) has shown a similar adaptation in *Puffinus lherminieri*, which moults at times of relatively plentiful food and is then released into a new breeding cycle. It remains unknown whether there is also *on average* a positive correlation between plentiful food early in the cycle and again later when needed for feeding young, but we know that *often* there is no such correlation and the young die. By contrast, there is no reason to suppose that food acts in this proximate way on Christmas Island seabirds or, if it does, then there is also a strong positive correlation between abundant food early and later in the cycle.

(*b*) relatively large eggs, presumably to ensure that the newly hatched young are in a relatively more advanced state ;

(*c*) extremely slow growth (though it is of course possible that this is a purely phenotypic effect of food shortage).

The Christmas Island population, on the other hand, has :

(*a*) seasonal breeding, with the non-breeding (recuperative) period apparently falling in the rainy period (Nov.-March) ;

(*b*) an egg which is significantly lighter, both in absolute terms and as a proportion of the female's weight, than in the Galapagos ;

(*c*) and, in 1967 at least, a fledging period approximately five weeks less than that normally found in the Galapagos population.

These facts strongly suggest that it enjoys a much better food supply in the breeding season and this is borne out by the breeding success (in 1967, on Christmas Island, more than three times as high as in 1964 in the Galapagos).

Whilst the foregoing may provide acceptable interpretations for most of the differences between the two populations of *Sula sula*, it also raises the question of why some Galapagos seabirds breed seasonally in an apparently seasonless environment. *F. minor* breeds biennially in the Galapagos, since there is apparently little if any apparent seasonal difference in availability of its food, though the only 'evidence' is inferential. The seasonal breeding may simply reflect the fact that 24 months is about the time required for a complete cycle plus recuperation. The same (on a 12-month basis) might be true for *S. dactylatra* and in fact inter-island differences in this species' breeding season in the Galapagos tend to support this against the alternative, namely that there may be slight seasonal differences in the food items of these two species (but not, or less, in that of others). However, we simply do not know anything about local differences in currents and food etc. in the Galapagos.

In connection with the subject of seasonal breeding, it may be mentioned that none of the Galapagos seabirds show closely synchronised breeding either (even if they did, its survival value could, of course, be quite unconnected with food). Thus the two phenomena, first that the different species breed at different times of year and second that there is very considerable spread within most species can be interpreted to mean that there is no seasonally concentrated exploitation of food.

In comparing the breeding regimes of seabirds on Christmas Island and Aldabra, we are dealing with islands in the same ocean and within a degree of the same latitude. Both are seasonal in climate. From April to October both Aldabra and Christmas Island are swept by the dry South-east Trade Winds. On Christmas Island these frequently shift to the north or north-east in the early months of the year, when they become strong to gale force, bringing rain, most of which usually falls between January and June. December is the warmest month, with a mean maximum temperature of about 32°C—about the same as that on Aldabra. The rainy season on Aldabra is, similarly, between November and March. Both islands vary considerably from year to year but an important difference between them is that Christmas Island gets a longer period annually of the south-east trades.

Despite the similarities between the islands, Diamond (1971) has shown that some seabirds on Aldabra are non-seasonal in their breeding whilst on Christmas Island most are markedly seasonal. The most likely explanation of the differences again seems to be that the Christmas Island seabirds are within foraging distance of seasonal upwellings or downsinkings not present in the Aldabra area. In addition to the upwelling between Java and Australia already mentioned, two other upwelling areas have been described by Rochford (1962) in the eastern Indian Ocean—one along the shelf of north-west Australia (previously postulated by Wyrtki (1962), though he later described it as less important than the Java one) and another along the shelf and slope region of the eastern Arafura Sea. All three have their maximum upwelling period before August or September. Whilst we do not know the temporal or spatial relationships between maximum upwelling and the production of organisms high in the food chain, it seems possible that by laying around May Christmas

Island seabirds meet the heaviest demands of their offspring when the upwellings within their feeding range have produced more food than can be found at other seasons.

CONSERVATION

Since 1958, Christmas Island has been a territory of the Australian Government. The Christmas Island Act 1958-1963, administered by the Minister of State for Territories, provides for protection of wildlife, but since, in practice, it depends on the efforts of about three police officers to patrol 64 square miles of island, in addition to other duties, it is hardly implemented.

Nevertheless the cessation of wholesale slaughter of some indigenous birds, attributable largely to this Act, has been of benefit. For example, the Imperial Pigeon used to be sold in large numbers, became scarce and is now increasing. My personal experience leads me to believe that only Andrews Frigate suffers severely from human depredation. Since, however, this is one of the world's rarest seabirds it justifies much more effective protection than it gets. Its main colonies are down on the shore terrace and relatively near the village, and therefore easier to protect (as also to predate!) than if they were in the centre of the island. A major psychological obstacle is that Malay policemen are loath to enforce with full vigour a protection law to which they are unsympathetic and which sets them against their fellow islanders.

The main danger to Christmas Island wildlife comes from the inevitable destruction of habitat which accompanies phosphate mining, the island's only industry. To extract phosphate the vegetation and the top soil must be entirely removed. After extraction only the limestone pinnacles remain and in this arid and highly alkaline habitat hardly any regeneration can take place. The pinnacles themselves would frustrate any attempt to replace top soil which would in any case be a prohibitively expensive operation and, moreover, pointless so far as the existing wildlife is concerned, since to replace the present jungle would presumably require at least 100-200 years.

Accepting the inevitability of continued large-scale extraction of phosphate, there seem three possibilities. First, the areas to be worked may 'accidentally' (i.e.—other than as a deliberated policy) leave enough untouched jungle to support viable populations of the three most important Christmas seabirds, namely, *Sula abbotti*, *Fregata andrewsi* and *Phaethon lepturus fulvus*. This would depend on at least two unknown factors, which are, to what extent the lower grade phosphate will be exploited and thus how much of the island's cover will be destroyed, and how well the seabirds would adapt to a reduced habitat. The exploitation will be influenced by the extent and location of phosphate deposits found in Australia, which (with New Zealand) is the main market for Christmas Island phosphate. Second, the extent to which *abbotti* in particular (but *lepturus* also) could adapt itself to nesting in tree cover different in character from that which it always uses at present is highly debatable. Could it possibly utilise sparser smaller trees at lower altitudes? Some such areas are bound to remain untouched. This unfortunately will be discovered only after large-scale destruction of habitat has taken place, and a negative answer would then allow of no redress.

The other possibility for conservation would be the deliberate preservation of several quite large areas of jungle holding the main concentrations of *abbotti* (and

some *lepturus*), notwithstanding the loss of phosphate which would be entailed. The areas that should be safeguarded can now be drawn on the map and the size of a viable 'unit' of forest, though not easily ascertained, could be estimated. This proposal should receive serious consideration if a future survey were to show a marked decline in the population of *abbotti* and reveal no evidence of adaptability to the destruction of habitat by a change in distribution.

Many islands hold distinct races of birds ; indeed Christmas Island has its own subspecies of White-eye (*Zosterops*), Pygmy Owl, (*Ninox forbesi natalis*), Sparrow-hawk (*Accipter fasciatus natalis*), and others. *S. abbotti*, however, is a full species which not only is entirely confined to Christmas Island, but differs markedly from all other members of its family. Should the *Zosterops* go, or even *P. lepturus fulvus*, other subspecies remain elsewhere but if *S. abbotti* goes, nothing remotely similar will exist. *F. andrewsi* would seem to be in a better position, if the depredations of the inhabitants could be controlled, since its present habitat is unlikely to be cleared under the present programme of mining.

Valuable information might be obtained by putting up high poles with resting platforms on top, in areas which held *abbotti* before the trees were destroyed. If the boobies accepted these as nesting sites their prospects would be much improved. Similarly, it is likely that *P. lepturus* would use nest-boxes and this possibility certainly ought to be explored.

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