BIOLOGY AND BEHAVIOUR OF FRIGATEBIRDS *FREGATA* SPP. ON ALDABRA ATOLL

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The Great Frigatebird *Fregata minor* and the Lesser Frigatebird *F. ariel* nest on Aldabra atoll, Indian Ocean (9° 24′ S, 46° 20′ E). Both are largely Indo-Pacific in distribution, breeding in the Atlantic Ocean on only the two islands of Trinidade and Martin Vas. In many parts of the world, these two frigatebirds breed at different places in the same archipelago; of 21 islands or island groups listed as breeding sites of either by Watson, Zusi & Storer (1963), Watson (1965) or King (1967), both species breed on ten, *F. ariel* alone on five and *minor* alone on six. Mixed colonies of the two species, however, have been found only on North Keeling (Gibson-Hill 1949) and Aldabra.

The present paper gives the results of field work carried out on Aldabra from August 1967 to March 1968, and from March to September 1969. These visits covered the two main climatic periods, the southeast trade winds (roughly March to October) and the calmer wet season or northwest monsoon. During this period I was studying the ecology of ten species of sea-bird, as a member of the Royal Society expedition to Aldabra. The history of the atoll, and the results of the expedition up to March 1968, including a brief account of sea-bird ecology (Diamond 1971a), may be found in Westoll & Stoddart (1971).

NESTING HABITATS AND DISTRIBUTION OF COLONIES

The elongated rim of land which forms the atoll (Fig. 1) is divided into four main islands by narrow channels connecting the sea and the extremely shallow lagoon. The lagoon shore is lined by a belt of mangroves, in most places 200–500 m wide. Frigatebirds nest only in tall stands of mangrove along the lagoon coast of Middle Island and in Bras Takamaka. The majority of each species nested in 'Main Colony' at the eastern end of Middle Island (Tables 1 and 2, Fig. 1). At the time of my study there was also a colony of *F. minor* breeding on islets at the lagoonward end of Gionnet (= Johnny) Channel; this site has since been abandoned, as a result of disturbance by tourists from the M.S. 'Lindblad Explorer'.*

Within the colonies, both species nested principally in trees which were sheltered from the full force of the southeast trade winds. These blow throughout the first 2 or 3 months of the nesting period, and are at their height when nests are being built. Although the general aspect of the northern shore of the lagoon is southerly, the coast is highly indented and dissected into many small islets, providing large areas of north- or northwest-facing mangroves, in which the nests were concentrated.

Nests were distributed not at random but aggregated in groups of up to 20, normally of a single species. With the exception of a few nests of *F. ariel* built in *Pemphis acidula* bushes on small islets surrounded by mangroves, both species nested only in mangroves. Three of the four commonest mangrove species (*Rhizophora mucronata, Bruguiera gymnorhiza* and *Ceriops tagal*) were commonly used but the fourth, *Avicennia marina*, was avoided. *F. minor* often nested in occasional dense patches of low, stunted, flat-topped *Ceriops* bushes, but no *F. ariel* nests were seen in such sites. More *minor* nested in the flat tops of the trees, while greater numbers of *ariel* chose the lower lateral branches

TABLE 1

Census of frigatebirds in 1967

Colony[1]	Date(s)	Total	Immatures	*F. minor* males	*F. minor* females	*F. ariel* males	*F. ariel* females	Total identified	Calculated *F. minor*	Calculated *F. ariel*
Main (a)	Oct./Nov.	4003	363	428	233	699	571	1911	1306	2330
(b)	Oct./Nov.	10 000	908	—	—	—	—	—	3265	5825
Gionnet	11 Oct.	338	17	88	46	0	0	134	338	0
Camp Frigate[2]	24 Nov.	183	24	51	42	0	0	93	183	0
Bras (a)	5 and 17 Nov.		183	24	51	85	111	197	2	295
Takamaka (b)	5 and 17 Nov.	611	44	7	9	95	146	257	38	570
				574	331	879	828	2592	3826	6690

Notes: [1] Main colony (a) sum of ten counting strips, (b) $a \times 2{\cdot}5$ (see Appendix 1).
Bras Takamaka (a) scattered groups, (b) discrete colony in northeastern corner.
[2] Shown as 'Frigate' by Stoddart (1971).

(indeed some *ariel* nests were within 0·5 m of the water-surface at high spring tides), but a majority of both species nested in an intermediate zone of the canopy. The differences in extreme nest-sites of the two species may be related to the greater agility of *ariel*, which is considerably smaller and lighter than *minor*.

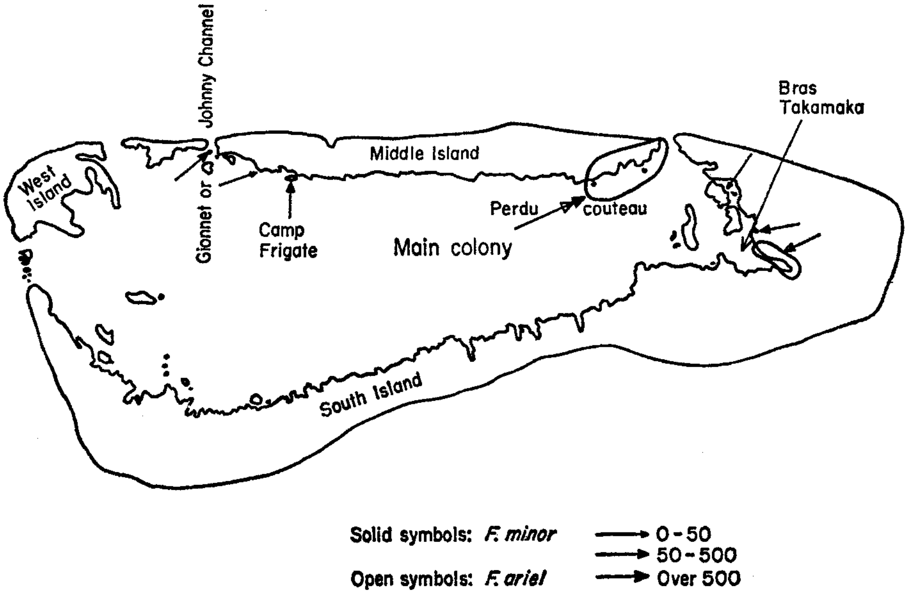

FIGURE 1. Map of breeding colonies.

TABLE 2

Estimations of frigatebird populations in 1967

	F. minor	*F. ariel*
(i) Maximum numbers of individuals		
Calculated totals (Table 1)	3826	6690
Factor to estimate seasonal maximum:	1·3	1·6
	4974	10704
Factor to estimate numbers in air at time of count:	1·7	1·7
Final estimation	8500	18 200
(ii) Numbers of breeding pairs		
Calculated totals (Table 1)	3826	6690
Factor to estimate seasonal maximum:	1·3	1·6
	4974	10 704
Factor to estimate number of nests:	0·365	0·5
	1820	5352

NUMBERS

During the season 1967–68, about 27 000 individuals were estimated to be present in the colonies; the breeding population was estimated as about 1800 pairs of *minor* and 5350 pairs of *ariel*. Full details of the census are given in Appendix 1.

SEASONAL VARIATION IN NUMBERS

A combined plot of periodic counts made in two study areas in Main Colony (in which about 67% and 13% of birds, respectively, were *F. ariel*) is given in Figure 2(a). In both areas, both species showed a peak in numbers in August. A second peak in mid-November 1967 occurred in the first study area but not in the second. The first area had been seriously disturbed by sightseers in September, and many birds lost their eggs; it was probably these birds returning to re-lay which produced the second peak in November.

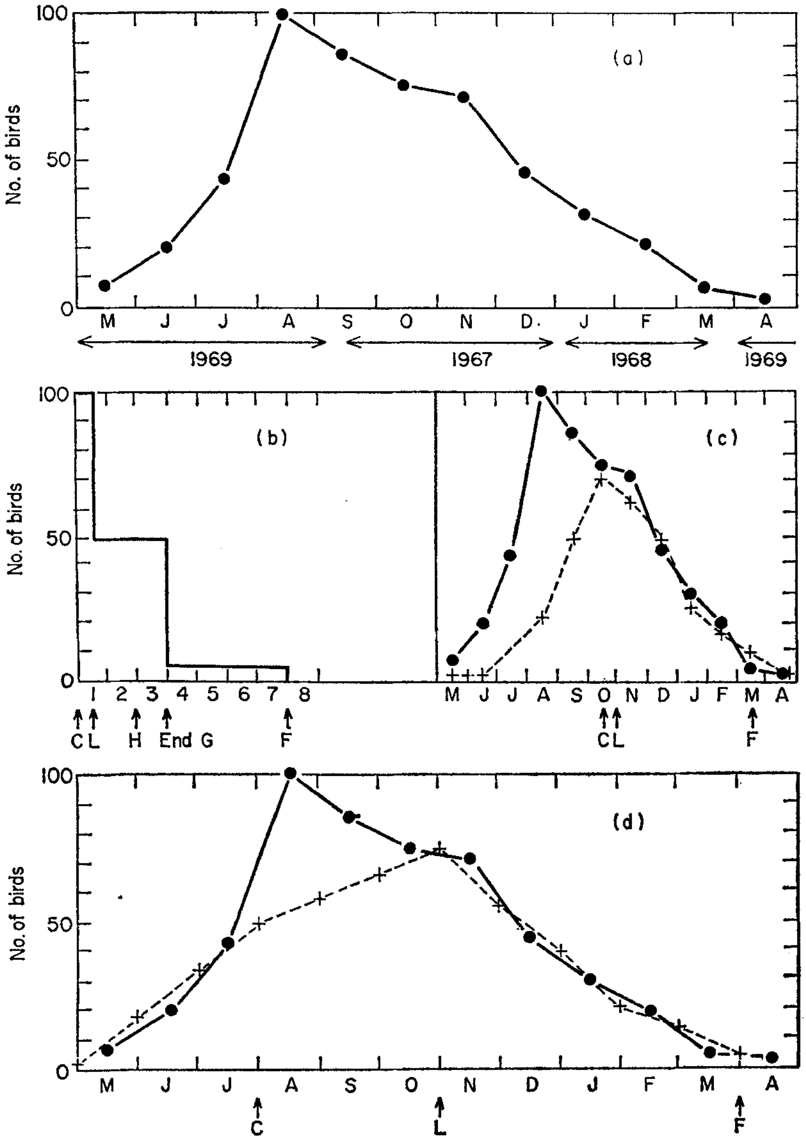

FIGURE 2. Seasonal changes in numbers, and models of changes, in study areas Main 1 and 2. Notes: C = peak of courtship, L = peak laying, H = peak hatching, F = peak fledging, End G = end of guard period. (——●——) observed; (– – + – –) predicted by model. Extent of variation in observed numbers cannot be shown, since usually only one count was made in each month. See text for explanation of models.

Figures 2(b), (c) and (d) show successively better fits to the observed seasonal variation in numbers of three models of changes in numbers, explained in detail below (Discussion). Briefly, they show that the same number of adults is probably resident on the atoll throughout the year and that their stage of breeding, and hence the time each bird spends at the colony, controls the number that can be seen in the colony at different times of year.

BEHAVIOUR

VOICE

Both sexes are silent except when coming in to land, displaying, fighting or chasing. The 'arrival' call (i.e., that given by birds approaching a perch) of the female *F. minor* is an accelerating *wiiiiiick – wiiick – wick – wickwick wick.* The corresponding male vocalization begins with a long, drawn-out call which runs into a rapid series, descending in pitch, *teeeeeuu – teeuu – teu – tutu,* sometimes ending with a short version of the display whinny. In *ariel,* the male's arrival call is a series of short whistles; the female's is similar to that of female *minor* but is hoarser, *chuck – chuck – chuck.* In all cases, the notes accelerate and appear to drop in pitch in the final stages of the bird's descent.

DISPLAY

The display of *F. ariel* is broadly similar to that described by Nelson (1968) for *F. minor.* Males display in groups, usually of one species, to females flying overhead. The male's red throat pouch is inflated, the wings raised, outstretched and usually turned over so that the undersides face up, and are rapidly vibrated. The head and bill are pointed upwards, following the female flying overhead, and the mandibles are vibrated rapidly together to give either a reeling or drumming sound. In *minor,* but not in *ariel,* males also give a vocal 'horse-whinny', best rendered *hoo – hoo-hoo-hoo-hoo,* descending in pitch and accelerating towards the end. It is analogous to, but distinguishable from, the 'warble' described by Nelson (1968) in the Galapagos race *F.m. ridgewayi.* The only call uttered by male *ariel* in display is a rapid whistling, identical to the arrival call, which is sometimes also given to a female coming in to land by a displaying male. In both species, the two sexes indulge in mutual head-waggling, caressing (and nibbling) the other's body with the head (and bill); the female *ariel* sometimes whistles softly while doing so.

Female *minor* registers interest in displaying males simply by hovering above a group, but female *ariel* gives a distinctive 'goose-neck' action when approaching a display group in which she is interested. The head and neck are stretched forward and sharply down, in an action similar to the forward threat posture of many geese, and the wings are vibrated rapidly and the tail wagged from side to side. The wings are stretched out flat and held straight or even bent slightly forward, not back at the wrist as usual. This response lasts for only a few seconds before the bird either flies on or descends to join the group. The goose-neck component may appear without the wing and tail movements, but not vice versa.

MALE-TO-MALE DISPLAY

A male *minor* sometimes responds to the appearance overhead of another male, rather than a female, by giving a low intensity version of the display normally given to a female. The wings are half opened and are waved half-heartedly rather than outstretched and energetically vibrated, cf. 'wing-waving' and 'wing-fanning', respectively described by Diamond (1973) for *F. magnificens.* If the incoming male lands too close to the sitting bird it is repelled by a lunging, snapping bill. Male *ariel* give no comparable display, but simply threaten with the bill open and the neck stretched out toward the intruder.

Males of both species certainly defend from other males the area immediately around themselves (*contra* Nelson 1967, 1968), although this area may be very small.

BREEDING CYCLE

SEASON

Two measures of breeding activity were recorded. First, the proportion of males displaying with inflated throat pouches (Fig. 3). Some birds were seen with inflated throat pouches as early as March and as late as January elsewhere in Main Colony, but in the study area, where the data for Figure 3 were collected, display was seen only between June and December. There was a marked peak of activity in *minor* in August and September; in *ariel* the peak was less evident, but most display took place between early July and early October. There was a significant negative correlation between the proportion of males displaying in the two species in August–September ($r = 0\cdot78$, $P < 0\cdot02$). Probably the excess *minor* males remained unmated, and continued to display after most male *ariel* had paired.

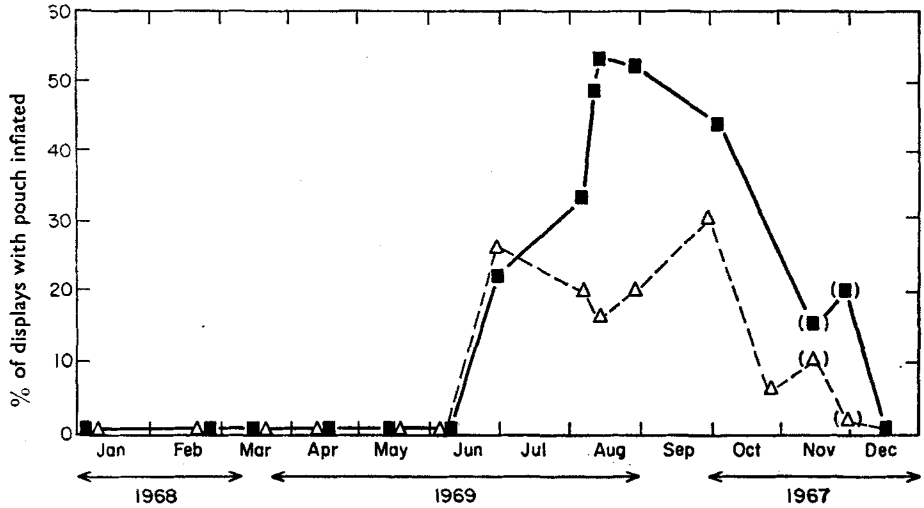

FIGURE 3. Seasonal variation in the percentage of courting males. (——■——) *minor*, (– – △ – –) *ariel*. Bracketed points indicate mean value for the period covered by the brackets. Each point represents a single count.

Secondly, inferred laying dates derived from measurements of the bills of chicks. Because of bias introduced by losses of eggs or chicks, only a rough guide to the laying season can be obtained. Apparent differences between species and seasons are probably due to such bias, and to errors inherent in small samples (Fig. 4).

Measurements of *minor* chicks were taken in Camp Frigate and Gionnet Channel; measurements of *ariel* chicks, and the counts of courting males, in Main Colony. Laying seasons were similar in these areas, but in 1967 birds (mostly *ariel*) in one part of Main Colony—'Perdu Couteau'—laid later than those elsewhere in this colony. A discrete colony of about 600 *ariel*, in the northeast corner of Bras Takamaka, laid at the same time as Main Colony in 1967, but only five young hatched and none survived. According to the local fishermen, frigatebirds had not nested there before.

NEST BUILDING

In both species, males collected nest material and the females built it into the nest. Twigs and leaves of mangroves and the bush *Pemphis acidula* were the commonest materials; *F. ariel* also used a vine which grew profusely over the mangroves in some areas. Some material was obtained by robbing other frigatebirds in flight or, occasionally, Red-footed Boobies *Sula sula*, but the birds also gathered material for themselves, particularly from *Pemphis* bushes growing on the windward side of lagoon islets. Material was also picked off the surface of the water (behaviour interpreted by Morris, 1964, as feeding). Unattended frigatebird nests were frequently robbed of material by males of either species. This behaviour increased when human disturbance drove birds off their nests, but it evidently occurred also in undisturbed parts of the colony, as shown by piles of nest material and broken eggshell on the ground beneath nests in the remotest areas. The relative importance of these different sources of nest material was not assessed quantitatively, but my impression was that robbing of both kinds contributed least nest material to the population as a whole.

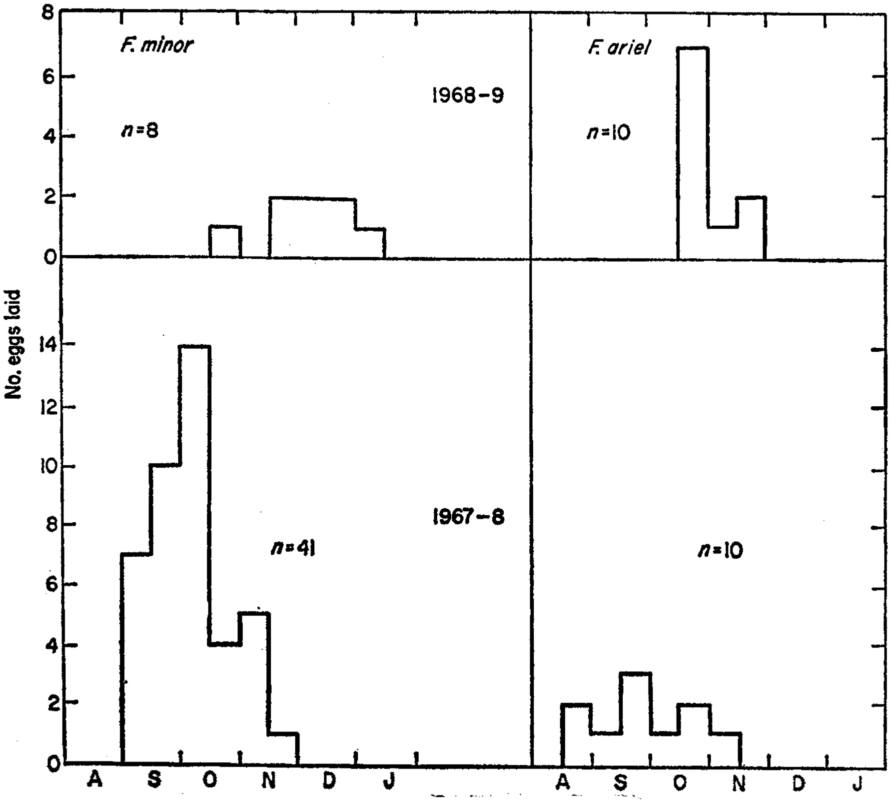

FIGURE 4. Laying dates, calculated from bill-length of chicks.

I only once saw a frigatebird—a male *ariel*—take an egg out of a nest, and I never saw any bird of either species take a chick. This is in marked contrast to the behaviour of *minor* on Christmas Island, Pacific Ocean (Schreiber & Ashmole 1970), or in the Galapagos (Nelson 1967, 1968), where eggs and young are commonly eaten by males and juveniles.

EGG STAGE

The egg weighs on average 5·7% of the body-weight of the female *minor*, *c*. 6·9% of *ariel* (Table 7), compared with *c*. 6% of *aquila* (Stonehouse 1963) and 7·5% or 5·1% of *minor* in the Galapagos (Nelson 1968: 225, 315). Among other birds, only the Sulidae have relatively lighter eggs (3–7%, Nelson 1970).

The sexes were found incubating in equal proportion in both species (39 ♂ : 38♀ *minor*, 21 ♂ : 25 ♀ *ariel*) at various times of day. One female *minor* sat continuously for 6 days, while four stints by *ariel* averaged 3 days (range 1–6), cf. in *minor* about 4 days on Christmas Island, Pacific Ocean (R. W. Schreiber, unpubl.), and 10 or 15 days in the Galapagos (Nelson 1968: 225, 528).

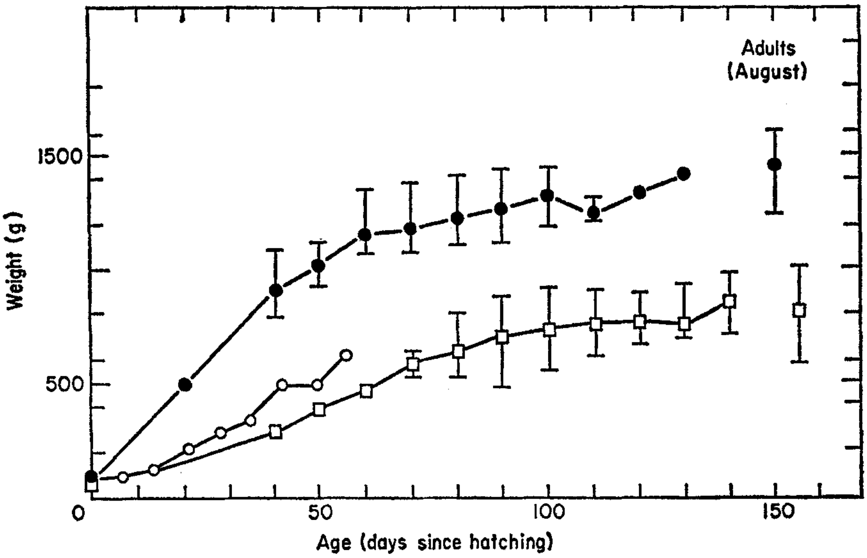

FIGURE 5. Chick growth curves. Ranges indicated by vertical bars. (●) *minor*, Aldabra; (○) *minor*, Galapagos (from data in Nelson, 1968); (□) *ariel*, Aldabra. Sample sizes on Aldabra between 2 and 8 of each species, the smaller samples being at the extreme ends of the curves.

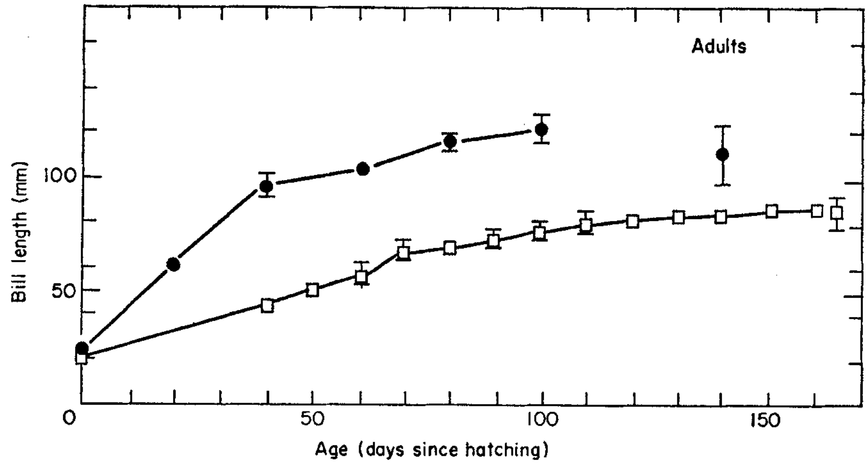

FIGURE 6. Bill growth of chicks. Conventions and sample sizes as in Figure 5.

CHICK STAGE

Growth curves obtained in 1967–68 are shown in Figures 5 and 6. Fledging periods were not determined directly, so estimates were derived from the time taken to reach the asymptote of bill-growth: 120 days for *minor*, 140 days for *ariel*. The faster growth of *minor*, reaching half the asymptotic weight after 30 days, cf. 60 days in *ariel*, is similar to that obtained by R. W. Schreiber (unpubl.) on Christmas Island, Pacific Ocean, but faster than that measured by Nelson (1967) in the Galapagos shortly after a period of severe food shortage. I can trace no published growth data for *ariel.*

Feeding frequencies were measured in two ways. First, on 27 March 1969 I weighed eight *minor* and 11 *ariel* chicks, and re-weighed them on each of the following 5 days. Captive chicks weighed at the same times provided control data on weight loss in an unfed chick. On average each *minor* chick was fed every 1·5 days, *ariel* every 1·8 days (an insignificant difference). Secondly, on 1, 20 and 24 April 1969 one study area was watched, from a hide, from about 06.30 to 18.00 hrs, and the proportion of chicks of each species fed during the day was recorded. The results (Table 3) may be slightly low due to a few overlooked feeds, but these should not affect comparisons between the species. Clearly the feeding frequencies were variable, but the species fluctuated in parallel and there was no significant difference between them. ($P > 0{\cdot}05$, χ^2 test.)

TABLE 3

Feeding frequencies of frigatebird chicks, obtained by observations throughout the day in one colony

Date	Species	No. of chicks	No. of chicks fed	Proportion fed (%)	Calculated feeding Interval (days)
1 Apr. 69	*F. minor*	20	12	60	1·7
	F. ariel	17	11	65	1·6
20 Apr. 69	*F. minor*	16	3	19	5·3
	F. ariel	19	5	26	3·8
24 Apr. 69	*F. minor*	30	14	47	2·1
	F. ariel	9	3	33	3·0
Totals	*F. minor*	66	29	44	2·3
	F. ariel	45	19	42	2·4

The number of feeds given per three-hour period is shown, by sex and species, in Figure 7. The two species clearly differ in this respect ($P < 0{\cdot}001$, Kolmogorov–Smirnov test); *minor* chicks were usually fed between 09.00 and noon, most *ariel* in the afternoon. There were also sexual differences in each species; in *minor*, males gave few feeds in the afternoon, and so gave fewer feeds overall (32) than females (53), whereas in *ariel* the sexes fed the young equally often (males 52, females 51) but males mostly in the early morning and the evening, females chiefly in the late morning and the afternoon.

POST-FLEDGING STAGES

In the Galapagos young *minor* were fed by their parents for at least 6 months after fledging (Nelson 1967), and on Christmas Island, Pacific Ocean, for at least 14 months (Schreiber & Ashmole 1970). On Aldabra, wing-tagged chicks of both species were still being fed 4 months after fledging, when my study ended. In July and August 1969, however, during three all-day watches of wing-tagged juveniles which had first flown 3–4 months before, I found that the frequency with which these fledglings were fed was lower than expected if they were relying on their parents for all food. These young birds spent only 26–50% of their time at the colony, so it is possible that they were catching most of their own food. Alternatively, their parents may have fed them mainly at night, as among *minor* on Christmas Island, Pacific Ocean (Schreiber & Ashmole 1970). From June to October, parties of recently-fledged juveniles were often seen roaming the lagoon but only once were seen feeding (M. J. Penny, pers. comm.).

Of 36 nestlings of both species wing-tagged in February 1968, none were seen in 1969. Probably they had left the colony, but the possibilities that they had all died or lost their tags, though unlikely, cannot be excluded. I saw few young being fed between September and March 1968, so most young probably left the colony 5–12 months after fledging. The highest numbers of immatures were present in the colony between July and early September (Fig. 8). Most were in the first immature plumage (see Appendix 2) which is retained for a minimum of 2½ years, in captivity at least (van Bemmel & Hoogerwerf 1940). During this period there were about twice as many present as could be accounted for by fledglings of the previous season; presumably the extra birds had fledged the year before and were returning to the atoll. The sort of distance that might be travelled in the interval is illustrated by one of 44 chicks tagged just before fledging (*ariel* no. A04), last seen at the nest site on 29 August 1969, which was recovered exhausted near Bombay on 4 June 1970, 4400 km to the northeast (Ali 1970).

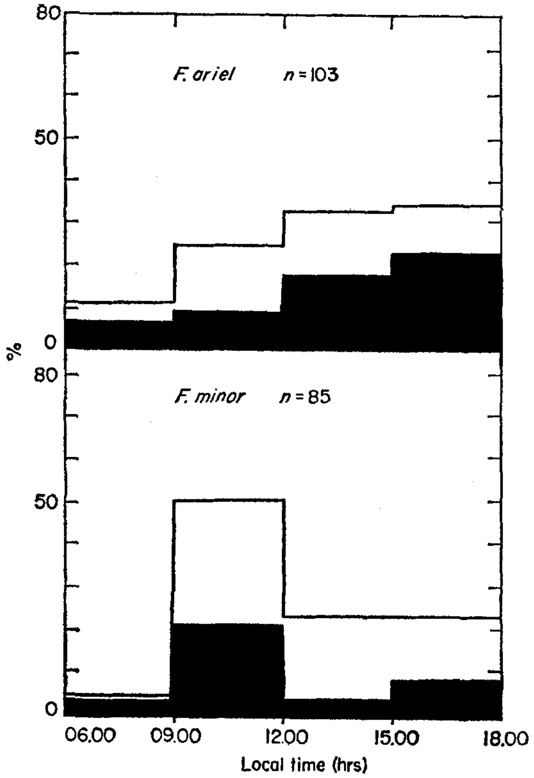

FIGURE 7. Time of day feeds given to chicks. (■) feeds given by males; (□) all feeds.

BREEDING SUCCESS

This could not be measured directly, but a rough guide was obtained by comparing chick counts made in late January 1968 with the estimated number of nests in the same areas the previous November. The figure clearly overestimates fledging success, since it takes no account of subsequent mortality before fledging. Results were very variable (10–83%), averaging 26%, close to the fledging success of *F. aquila* (15–20%, Stonehouse & Stonehouse 1963) and Galapagos *minor* (25%, Nelson 1967).

WEIGHT CHANGES DURING BREEDING

One hundred and twelve adults were weighed during incubation, 35 around the peak of hatching, and 77 during courtship; the mean weights are shown in Figure 9. The only significant change was in weight of males, which were heavier when courting (in August) than at the end of incubation ($P < 0{\cdot}002$ *minor*, $P < 0{\cdot}01$ *ariel*).

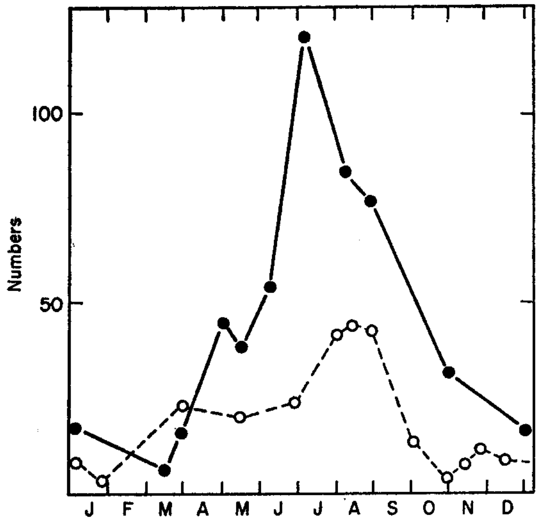

FIGURE 8. Seasonal variation in number of immatures in study areas Main 1 and 2 (– – ○ – –) Main 1 (mainly *ariel*); (——●——) Main 2 (mostly *minor*).

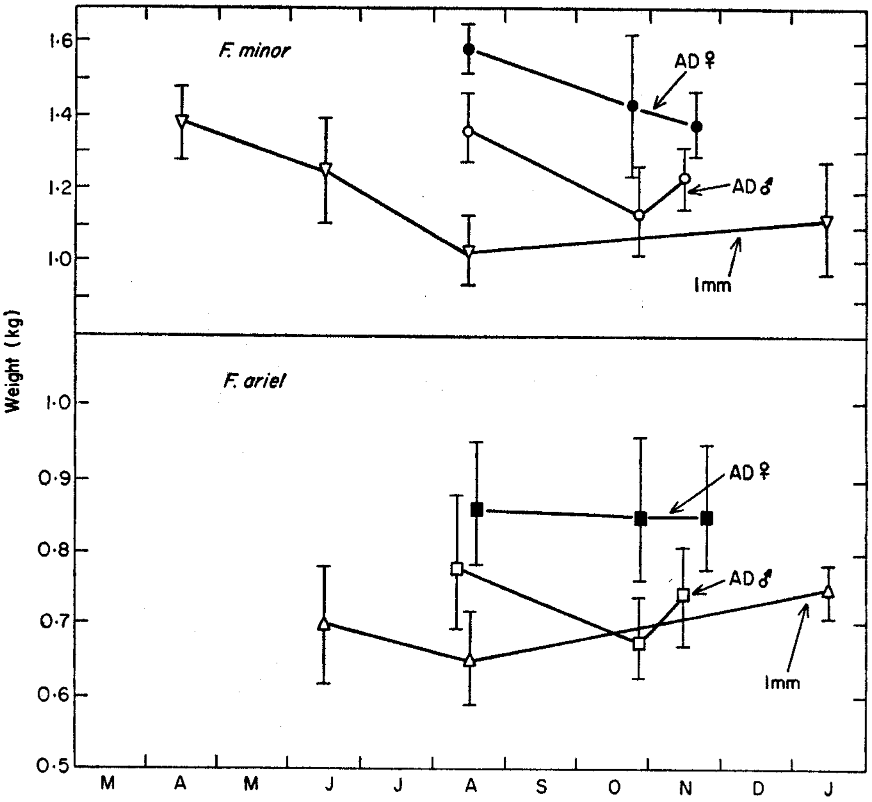

FIGURE 9. Seasonal variation in weight. Ranges shown by vertical bars.

FOOD AND FEEDING

FEEDING BEHAVIOUR AND FEEDING AREAS

The cleptoparasitic feeding behaviour of frigatebirds has been emphasized in the literature. This behaviour is a feature of many sea-bird colonies where frigatebirds are present, whether or not they breed there, but it is not clear how common or successful it is at sea where most frigatebirds obtain their food. At some colonies, e.g., Christmas

TABLE 4

Composition of food samples regurgitated by frigatebird chicks

	Overall		Wet season		Dry season	
	minor	*ariel*	*minor*	*ariel*	*minor*	*ariel*
No. of samples	79	179	27	65	52	114
(a) Frequency (% of regurgitations in which listed items were identified)						
E. volitans	38	29	56	31	29	28
C. furcatus	32	19	30	11	33	24
O. micropterus	4	3	4	3	4	3
All fish	95	94	100	96	90	92
Squid	35	45	50	56	26	40
(b) Number (% representation of each item in all regurgitations combined)						
E. volitans[1]	53	52	66	76	43	52
C. furcatus[1]	43	42	31	19	52	42
O. micropterus[1]	4	5	3	5	5	6
All fish	74	64	84	53	83	69
Squid	26	36	16	47	17	31
(c) Weight (% by weight of all regurgitations combined)						
E. volitans[1]	42	33	53	66	28	26
C. furcatus[1]	49	50	41	26	59	56
O. micropterus[1]	9	16	6	8	13	18
All fish	87	89	88	69	86	96
Squid	13	11	12	31	14	4

Note: [1] Calculated as percentage of all fish identified, not of all food items.

TABLE 5

Statistical significance (χ^2 test) of differences between food samples of the two species of frigatebird

Species	Prey categories compared	Character	*P*
(a) Seasonal changes within each species			
F. minor	*Exocoetus/Cypselurus*	Number	≪0·001
	Exocoetus/Cypselurus	Frequency	<0·001
	Exocoetus/Cypselurus	Weight	<0·001
	Fish/squid	Frequency	just >0·05
F. ariel	Fish/squid	Weight	<0·001
	Exocoetus/Cypselurus	Weight	<0·001
	Fish/squid	Number	0·05> *P*>0·01
	Exocoetus/Cypselurus	Frequency	just >0·05
(b) Differences between species in each season			
Season	Prey categories compared	Character	*P*
Wet	Fish/squid	Number	<0·01
	Fish/squid	Weight	<0·001
	Exocoetus/Cypselurus	Number	*c*0·05
	Exocoetus/Cypselurus	Weight	<0·05
Dry	*Exocoetus/Cypselurus*	Number	<0·001
	Fish/squid	Number	*c*0·05
	Fish/squid	Weight	<0·05

Island, Indian Ocean, the robbing of boobies may provide an important source of food to frigatebirds (Gibson-Hill 1947), but this cannot be so on Aldabra where frigatebirds greatly outnumber boobies.

The commonest victim of this behaviour on Aldabra was the Red-footed Booby *Sula sula*, which frequently escaped. Of 55 attacks in which the result could be seen, in only 10 (18%) did a frigatebird obtain food regurgitated by a booby (cf. 12% in Galapagos *minor*, Nelson 1968; 63% in *minor* on Christmas Island, Pacific Ocean, Schreiber in litt.). Of 95 chasing birds identified, 80 were *minor* and 15 *ariel*. In both species females chased more than males; only one male *ariel* was seen harrying boobies, as against 12 females and two immatures; 54 of the *minor* identified were females, eight immatures and only two males. Females also chased more than males in the Line and Hawaiian Islands (Schreiber in litt.), but in the Galapagos the reverse was true (Nelson 1968). At Aldabra, in almost all cases when males chased other birds (including other frigatebirds), the male's object was to obtain nest material, not food.

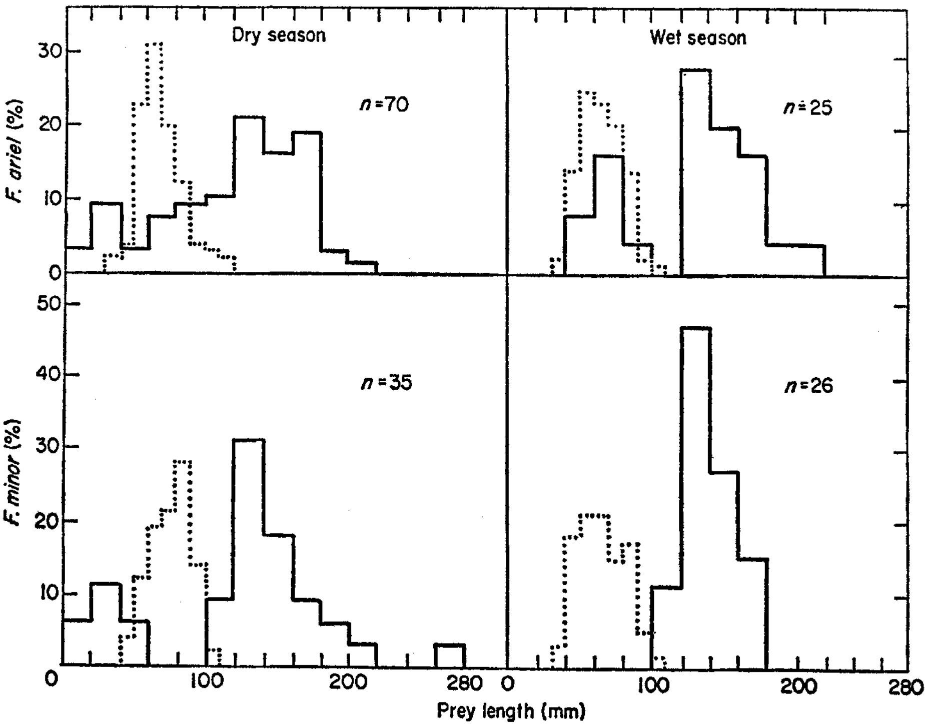

FIGURE 10. Length of prey in regurgitated food samples. (——) fish; (- - - -) squid.

FOOD SAMPLES

The composition of food samples regurgitated by frigatebird chicks is shown in Table 4. The overall composition of the two species' diet was extremely similar. Only when data from the wet and dry seasons are analysed separately do significant differences between the species emerge (Table 5).

In *minor* the proportions of the two commonest genera of flying-fish (*Exocoetus* and *Cypselurus*) differed in the two seasons, but the proportions of fish to squid in the diet remained the same. In *ariel*, the proportions of *Exocoetus* and *Cypselurus* changed in parallel with *minor*, but there was also an equally large change in the relative proportion of fish and squid. The seasonal change in the diet of *ariel* was similar to that of *Sula sula*, which also took fewer squid and more *Cypselurus* in the wet season than in the dry (Diamond 1971b and in press (a)).

In many sea-birds, body size and prey size are positively correlated (Ashmole 1968, Pearson 1968). Since *minor* is on average more than half again as heavy as *ariel* (Appendix 2), one would expect it to take longer prey, but Figure 10 shows that the two species take fish and squid of about the same size ($P > 0{\cdot}05$, Kolmogorov–Smirnov test). Since the squid are usually smaller than the fish, however, and since *ariel* takes a higher proportion of squid than *minor* in the wet season, it takes smaller prey on average than *minor* in the wet season ($P < 0{\cdot}05$) though not in the dry ($P > 0{\cdot}1$, both Kolmogorov–Smirnov test) (Fig. 11b).

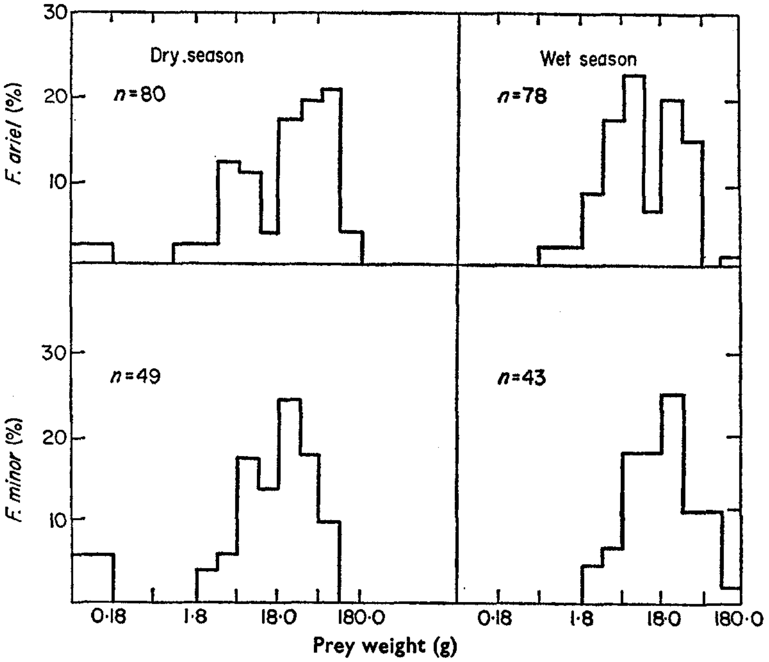

FIGURE 11. Weight of prey in regurgitated food samples, fish and squid combined.

The weight of the average meal fed to chicks can be estimated by multiplying the mean weight of each prey category by the mean number of that category per sample. In the wet season, *minor* meals are nearly twice as heavy as *ariel* meals (mean weights 148 g and 79 g respectively), whereas in the dry season the two species took meals of similar weight (122 g and 115 g respectively). The lighter meals fed to *ariel* chicks in the wet season may help to explain their slower growth during this period.

DISCUSSION

NESTING DISTRIBUTION

The restriction of the breeding colonies to mangrove is unexpected, since large areas of the atoll are covered with dense *Pemphis acidula* scrub which is used by both species elsewhere (e.g., on North Keeling, Gibson-Hill 1949). The most likely explanation is that mangroves, being both tall and situated on the intertidal zone, are less vulnerable to rats *Rattus rattus* than terrestial *Pemphis* scrub. All the larger islands of the atoll are infested with introduced rats, which have affected the nesting distribution not only of tree-nesting sea-birds (frigatebirds, *Sula sula* and the White Tern *Gygis alba*) but also the ground-nesting species (tropicbirds and terns), all of which nest on small, rat-free islets in the lagoon (Diamond 1971a).

The aspect of most nesting colonies—sheltered from strong southeast trade winds—recalls the similarly sheltered nest sites of the Magnificent Frigatebird *F. magnificens* on Barbuda, West Indies. Diamond (1973) attributed this to the birds' difficulty in making an accurate landing on a small perch or nest in a strong wind, which can best be overcome by flying into the wind. The same holds true on Aldabra, where most nests face northwest, and it is during the period of courtship and nest-building, when there is the greatest premium on fine control of flight near the nest, that the southeast trades are at their height. The nests are exposed to the wind only during the northwest monsoon, which is not as strong and steady as the trades and which blows when chicks are in the nest and the adults spend less time in the colony.

Precision in landing is important at the nest but much less so at roosts, which were located with no consistent relation to the wind.

SEASONAL VARIATION IN NUMBERS

The seasonal variation in numbers (Fig. 2) might be due either to birds leaving the colony between September and April or to their spending less time at the colony over that period. With breeding birds, one would expect that both members of a pair would be present for much of the time between pair-formation and egg-laying, that only one would be present during incubation and the short time for which the chick is guarded, and that neither would attend the nest very often during the rest of the cycle. Figure 2 models the changes in numbers that would result in a population of 50 pairs behaving in this way; in Figure 2(b) the birds are completely synchronous; in Figure 2(c) there is a laying spread of 6 months (as observed on Aldabra). In both models courtship is assumed to take 15 days (Nelson 1967, for Galapagos *minor*), incubation and the guard stage together 3 months, and fledging 5 months. During the post-guard stage of the chick's period on the nest, each adult is assumed to spend half an hour at or near the nest each visit, and to visit it once every 2 days (both figures based on my own observations).

The numbers of adult birds in two study areas combined (Fig. 2a) follow a curve similar to that of the second model (Fig. 2c), except that the observed curve is displaced 2 months to the left of the predicted between May and October. This discrepancy is attributable almost entirely to an excess of courting male *minor* in one of the study areas. In Figure 2(d), the courting period is extended from 15 days to 3 months; a much closer fit to the observed curve is obtained, but there is still an earlier, higher peak than predicted. Males move around a good deal when displaying, and probably this peak in observed numbers represents groups of males which courted but did not pair in the area and subsequently moved out. This is supported by the excess of male (80) over female (25) *minor* in one study area in August, which was close to the discrepancy between observed and expected numbers at that time (50).

The closest fit to the observed numbers (Fig. 2d) was obtained by extending the courtship period to 3 months, or 6 times the period recorded for *minor* by Nelson (1967). Nelson (in litt.) agrees that courtship may well be longer than 15 days, but considers it very unlikely to be as long as 3 months in an individual. More likely, a great deal of display does not result in pair formation and subsequent nest-building and egg-laying, especially in *minor* in which males outnumber females so greatly (Table 1). Stonehouse & Stonehouse (1963) also found that much early display of *F. aquila* was ineffective.

Whatever the explanation of the discrepancy, the model shows that most seasonal variation in numbers of adults can be accounted for by changes in nest attendance by breeding birds according to the stage of the breeding cycle, with no need to postulate dispersal away from the colony.

The number of immatures present in the colony showed a sharp peak between July and September (Fig. 8). This is attributed partly to dispersal and partly to a change in pattern of attendance at the colony of a resident population. The number of adults was also highest then, so perhaps the feeding conditions are particularly good at that time of year and the birds need to spend less time in search of food at a distance. That there is some dispersal of immature *ariel* is shown by the recovery of a tagged bird in India (above), but the extent of this dispersal, and whether it occurs in *minor* as well, is not known. Most frigatebirds seen at sea in the western Indian Ocean are immatures (Bailey 1968), which can rarely be identified to species. Studies of these two species elsewhere suggest strongly that immature *ariel* disperse about six months after fledging (Sibley & Clapp 1967), and that immature *minor* either do not disperse at all, or do so when much older (Nelson 1967, 1968, Schreiber & Ashmole 1970). This could be an important isolating factor in the ecology of the two species at Aldabra, and would repay further investigation.

TIMING OF BREEDING SEASON

Frigatebirds on Aldabra lay during the dry season, whereas most of the other sea-birds there lay either all year round or in the wet season (Diamond 1971,a b). Red-footed Boobies laid a little later than frigatebirds, possibly to avoid interference from them (Diamond 1971b, in press (a)). The diet of the boobies was very similar to that of the frigatebirds, so it may be that food resources for both groups are optimal at the same time. The stage of the cycle at which food availability is most critical may be when the chicks are growing, when they fledge, or when they finally have to fend for themselves. I suggest that the height of the trade wind or dry season is the time when food supplies are most critical for the frigatebirds, since it is then that the adults need to accumulate sufficient reserves to last them through the long period of courtship and nest-building. Individual males spend many days, perhaps weeks, displaying in the colony and, having obtained a mate, they must subsequently collect nest material while the female guards the nest. Males of both species were heavier during courtship than at egg-laying (Fig. 9), and the same trend was apparent, though not statistically significant, in female *minor*. In several other species of sea-bird, e.g., the Royal Penguin *Eudyptes chrysolopus* at Macquarie Island (Carrick & Ingham 1967) and the Laysan Albatross *Diomedea immutabilis* on Midway Atoll (Fisher 1967), adults need to lay down fat prior to breeding in order to carry them through the early stages of the reproductive cycle, when they are tied to the colony and have no time to feed.

In general, synchronous breeding is probably related to a seasonal increase in food availability, but it may also be important, in frigatebirds, in reducing the effects of nest-robbing, which is carried out mainly by males collecting material for a nest in which the egg has not yet been laid. 'Predator-swamping' is frequently invoked to explain breeding synchrony in sea-birds (Darling 1938, Cullen 1960, Ashmole 1971) but in this case the predators are other frigatebirds, often conspecifics.

SEXUAL CYCLES OF INDIVIDUALS

Nelson (1967, 1968) pointed out that in *F. minor* in the Galapagos, successful parents cannot nest again the following year, because the population breeds at annual intervals while a successful cycle takes more than one year. Nelson did not stress the importance of moult in still further extending the duration of the cycle. If adults do not moult while breeding, the successful cycle might be as long as two years. None of the breeding adults I caught showed primary moult; but, since those feeding large chicks were impossible to catch, no evidence was obtained to show that moult does not begin while the parent is still feeding young. The length of the breeding cycle in both *minor* and *ariel* on Aldabra, combined with the delay in onset of moult (at least until the latter part of the fledging period), suggest that successful breeders here, as in Galapagos, do not breed annually.

Harris (1969), however, suggested that successful *minor* in Galapagos could move between colonies, since these are out of phase with each other, thereby breeding every 18 months or so. This presupposes a weak attachment both to the nest-site and to the partner, both features of Nelson's (1967) description of the biology of *F. minor*. Further, even successful breeders could breed in successive seasons at the same colony, if they laid early in one season and late in the next, since the spread of laying in the colony is about 6 months. Against this, Nelson (in litt.) has argued that although the total spread of laying is very wide, most eggs were laid within a period of about 2 months. Nest success is so low (about 20%) in frigatebirds that an 'average' pair would be successful only once every 5 years or so. Birds which were unsuccessful could nest annually; the small proportion of clutches laid outside the peak laying period may be those of birds whose previous nesting attempt was successful. Regular biennial breeding not only remains unproven, but is likely to be the exception rather than the rule.

FOOD AND FEEDING RANGE

Both frigatebirds ate fish and squid of the same species and in similar proportions. The striking point about their food is that, in spite of the large size differences between the *F. minor* and *F. ariel*, size *per se* was clearly not important in determining the prey taken. The smaller average size of prey taken by *ariel* was due to a preference for squid rather than fish, not for smaller items of prey.

Frigatebirds have long been regarded as closely tied to land, and hence feeding close to shore (Murphy 1936). However, A. Bombard (quoted by Bourne, 1957) observed *F. magnificens* at points covering the breadth of the Atlantic Ocean between the Canaries and the Antilles, and Sibley & Clapp (1967) quoted observations in the western Pacific of over 40 *minor* more than 200 miles from land and one at over 500 miles. Their recoveries of banded *ariel* in the same region show that birds must often be several hundred miles from land. In the western Indian Ocean, 10% of the frigatebirds seen by Bailey (1968), most of which were unidentified immatures, were more than 320 miles from land, and during the present study I saw several more than 300 miles from Aldabra. M. J. Penny (pers. comm.) saw immatures catching fish in the Aldabra lagoon in April 1969, and they could often be seen feeding in the mixed flocks of terns and boobies outside the reef, so their potential feeding range extends from the lagoon to several hundred miles out to sea. The intervals at which food was brought to chicks (Table 3) suggest that the adults concerned either fed far out to sea, or spent a great deal of time not actually gathering food for the young.

The seasonal comparison of the weights of meals fed to chicks of the two species (above) suggested that feeding conditions were slightly better for *minor* in the wet season and very much better for *ariel* in the dry season. This may reflect the lower wing loading of *ariel*, which would make it more efficient than *minor* at soaring flight. Steady trade winds would enable *ariel* to feed more efficiently in the dry season than in the wet, when it would expend more energy in flapping flight.

SPECIES ISOLATION

In any situation where two congeneric species are sympatric, it is of evolutionary interest to investigate isolating mechanisms, both reproductive and ecological. Genetic isolation is evidently complete in this case, since no mixed pairs or hybrids were seen. The differences in size and display of the two species, described above, aided perhaps by the slight difference in nest-site evidently suffice to prevent interbreeding.

The principle of competitive exclusion (otherwise known as Gause's hypothesis, ecological isolation, etc.) is now widely taken to mean that coexisting species must differ somehow in their ecology. While it is generally true that they do, from an evolutionary point of view it is strictly necessary only that the two species differ in the factors which regulate their numbers. It is rarely possible to demonstrate this strict application of the principle, and even more rarely attempted. This present study is no exception, since I did not discover what factors, if any, regulate the populations of either species. However it is worth noting that the amount of overlap between the two species, particularly in their feeding, is very much greater than has been found in any other study of coexisting congeneric sea-birds. It certainly exceeds the overlap between the two tropicbirds on Aldabra, *Phaethon rubricauda* and *P. lepturus*, which differ more in nest-sites and very much more in food than do the frigatebirds (Diamond 1971b, 1975).

COMPARISONS WITH OTHER STUDIES

Table 6 sets out a number of features of frigatebird biology for all the species which have been studied in some detail. Gibson-Hill's (1947, 1949) studies of *minor* and *andrewsi* on Christmas Island, Indian Ocean, are not sufficiently detailed to be included here. *F. andrewsi* remains the least known of the five recognized species of frigatebird.

TABLE 6

Summary of comparative breeding biology of frigatebirds Fregata spp

Species	*F. minor*	*F. minor*	*F. minor*	*F. ariel*	*F. magnificens*	*F. aquila*
Locality	Aldabra	Galapagos	Christmas Is., P.O.	Aldabra	West Indies	Ascension
Main laying season	*c.* 6 months	*c.* 6 months	*c.* 6 months	*c.* 6 months	*c.* 5 months	8–9 months
Nest dispersion	Groups	Groups	Scattered	Groups	Groups	Groups
Nest density	NR[1]	Mean 0·6m^2	NR[1]	NR[1]	Mean 0·3m^2	0·02–1·2m^2
Nest site	Mangroves	Low bushes	Bushes, low trees	Mangroves	Low mangroves	Ground
Main food	Flying fish, squid	Fish	Flying fish, squid, young terns	Flying fish, squid	Flying fish, squid	Flying fish
Post-fledging parental care	4 months	6 months	14 months (one case)	4 months	4 months	3–4 months
Display:						
♂ call	'Whinny'	'Warble'	NR[1]	Whistle	Whistle	NR[1]
♂ to ♂ display	Yes	No	NR[1]	Threat only	Yes	NR[1]
♀ ritualized aerial response	No	NR[1]	NR[1]	Yes	No	NR[1]
Authority	This study	Nelson (1968)	Schreiber (unpubl.) Schreiber & Ashmole (1970)	This study	Diamond (1973)	Stonehouse & Stonehouse (1963)

Note: [1] NR = Not recorded.

In general, this comparison reveals the extreme uniformity of the family. The main features of the biology and behaviour are similar in all species. Among the Pelecaniformes only the tropicbirds show so little adaptive radiation. This emphasizes the biological interest of those instances where two species of frigatebird are sympatric. These may be said to be the rule rather than the exception, since *aquila* is the only species which does not coexist with another somewhere in its range. *F. minor* and *F. ariel* are sympatric throughout their respective ranges, and *minor* coexists also with *andrewsi* on Christmas Island and *magnificens* in the Galapagos.

The periodicity of breeding is the feature of frigatebird biology which has attracted most attention in recent years (Nelson 1967, 1968, Diamond 1972, 1973). The breeding cycle is so long that successful breeders cannot possibly breed annually; so much is indisputable from the bare details of the nesting cycle. This applies to all species which have been studied, probably including *F. aquila* (which Stonehouse & Stonehouse, 1963: 418, suggested laid every 12 months even if successful, although their other data show the successful cycle to involve an incubation period of 1½ months, fledging period of 5–6 months, post-fledging dependence at least four months and courtship period unknown, i.e., nearly 12 months, and that moult did not overlap with breeding). Nevertheless, the actual periodicity of breeding, in any species of frigatebird, remains to be established with marked individuals.

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SUMMARY

Both species nested in mixed colonies in mangrove trees. The tops of trees were usually occupied exclusively by *minor* and the lower parts by *ariel*, but most nests of both species were in the intermediate parts of the canopy. The main laying season for both species was July to January. A census showed about 27 000 individuals present at the height of the season (1500 breeding pairs of *minor*, 5350 of *ariel*). Seasonal variation in numbers could be accounted for almost entirely by the changes in breeding activity of a resident population. Young of both species were fed at or near the nest-site for at least four months after fledging. A recovery near Bombay of a wing-tagged immature *ariel* shows that this species, at least, undergoes a post-fledging dispersal; it is suggested that young *minor* either do not disperse, or do so later than *ariel*.

Food samples collected from chicks showed no overall difference between the species, but a seasonal analysis showed that *ariel* took more squid than *minor* in the wet season, and in the dry season the two species took different proportions of the two commonest species of flying-fish. Chicks of *ariel* received smaller meals than *minor* chicks in the wet season, but similar-sized meals in the dry season; *ariel* chicks grew more slowly than *minor* chicks. It is suggested that the timing of the breeding season is related to the need for adults to build up fat reserves to carry them through the courtship, nest-building and laying periods, when they are tied to the colony and so have little opportunity to feed.

The evidence for non-annual breeding in frigatebirds is discussed. It is concluded that while successful breeders must breed at intervals of more than 12 months, they could theoretically nest in two successive seasons and that, since breeding success is low, most individuals probably do so.

Existing knowledge of the biology of four of the five recognized species of frigatebirds is summarized, and shows that the family is at least as uniform as the tropicbirds and much more so than other Pelicaniformes.

APPENDIX 1 CENSUS

Methods

In small colonies (300 pairs or less) all birds were counted, but in Main Colony, extending over several kilometres of coastline, this was impossible. Here, the occupied area was plotted on a 1 : 25 000 map, and divided into 1 km squares, each of which was subdivided into five north–south strips 200 m wide. Two strips in each 1 km^2 block were chosen at random and counted in detail. The total number of birds on the colony was then estimated by adding the totals of the counted strips and multiplying by a factor of 2·5.

The birds were counted from a boat anchored about 35 m from the edge of the mangroves, using 8 × 30 binoculars and a hand tally-counter. Most of the lagoon is inaccessible by boat except at high spring tides, which occur around dawn and dusk; the counts were made at dawn. A number of all-day watches showed that there was little diurnal variation in the numbers of birds at the colony. I first counted the total number of frigatebirds visible on the trees, and then identified as many as possible to species and sex. Immatures could rarely be identified to species, and this category in Table 1 covers all frigatebirds showing some white on the head, thus including up to five age-classes of each species.

In addition to the birds counted on the trees, there were large numbers soaring above the colony, some of which took flight only when disturbed by the approach of the boat. Photographs of the birds flying above one isolated counting strip, whose limits could easily be determined on photographs, showed 281 birds in the air *v.* 393 counted directly on the trees, giving a total of 1·7 times the number on the trees alone. Since each category probably differs in sensitivity to disturbance (for example, immatures usually took flight sooner than adults), it cannot be assumed that the proportion of each species, sex or age class was the same in the air as on the trees.

Results

The raw totals of the census are given in Table 1. These need to be corrected for seasonal variation in numbers (see Discussion). The census was made in October and November, when numbers were lower than the maximum (in August). Accordingly the raw totals of the census are multiplied by the ratio of the numbers in August to those in October–November derived from regular counts in two study areas in Main Colony (Fig. 2a). The figure of 27 000 birds so obtained is a minimum, since it excludes birds absent from the colony at the time of the count (e.g., those away fishing). The population is likely to be much higher than this, but is certainly much smaller than some previous guesses (e.g., 'millions', Gaymer 1966).

To estimate the breeding population, counts of nests were made in August 1969. These showed that, in both species, the number of females on the trees corresponded closely with the number of nests. The calculated total number of nests at the time of the census is given in Table 1 and shows that breeding pairs of *ariel* outnumbered *minor* by more (about 3 : 1) than did individuals (about 2·1 : 1), largely because of the excess of males over females in *minor*.

The final adjustment to be made to the estimate arises from the likelihood that successful breeders do not breed in successive seasons. If this holds true for *minor* and *ariel* on Aldabra (see Discussion), then only a part of the population, related to the breeding success the previous year, will breed in any one year. Breeding success averaged *c.* 26%, so that only about three quarters of the population would breed in any year (assuming that failed breeders nest annually and successful breeders biennially). This would bring the calculated breeding populations to about 2000 pairs of *minor* and 6000 pairs of *ariel*.

APPENDIX 2 MORPHOLOGY

Since there is some confusion in the literature about frigatebird morphology, it may be helpful to describe the Aldabra species in some detail.

Adults

Males of both species are black, with a metallic sheen on the mantle which is predominantly green in *F. minor* and purple in *F. ariel*. Male *ariel* also show a broad white patch on each flank. The feet, bill and eye-ring are black in males of both species, though the bill becomes grey and flaky towards the end of the breeding season. Neither species shows a light bar on the upper surface of the wing, though *minor* does elsewhere in its range. The females of the two species are similar in body colour, with dark brown upperparts and head, black belly and white breast. In *ariel* the throat is black, sharply demarcated from the white breast and there is a white collar often reddish on the nape, whereas in *minor* the throat is grey, merging gradually into the breast, and there is no collar. Females of both species have a light wing-bar. The bill, feet and eye-ring are pink in all female *minor* and most female *ariel*, but in about 40% of the latter the bill and eye-ring are blue. This dimorphism appears not to have been recorded as such before, although Pocklington (1965) described some females breeding in the Cargados Carajos group as having a black eye-ring.

The two species are very different in size, and in both the female is larger than the male, although sexual dimorphism in size is more marked in *minor* than in *ariel* (Table 7).

Immatures

In both species, the first plumage (i.e., that assumed at fledging) is generally dark brown with a white belly, black breast band and pale head and wing bar. In *minor* the head is white or creamy, but in *ariel* it is strongly suffused with red; in other parts of its range, juveniles of *F. minor* also have rusty heads. The bill in both species is very pale, either pinkish or bluish, often with a dark tip to the upper mandible. This plumage lasted at least 2½ years in a captive *minor* (van Bemmel & Hoogerwerf 1940) and two years in a captive *ariel* (pers. obs.), though in *ariel* the head became somewhat paler over this period. The black breast-band becomes whiter before there is any other change in the plumage; subsequently the belly (and, in males also the breast) becomes black and the head dark. For convenience, several stages of plumage can be recognized (Fig. 12) but some of these may be arbitrary stages in a continuous slow change. Between the last plumage shown and the fully adult ones, there is a stage in which the bird closely resembles the adult but has a paler head and throat (females) or even some white on the breast (males). Some males will display feebly, and even occasionally attract a female in adult plumage, in a plumage in which the head is largely white and the gular sac very small. The time taken to acquire the full adult plumage is not known, but in Pacific *minor* is at least five years (R. W. Schreiber, pers. comm.).

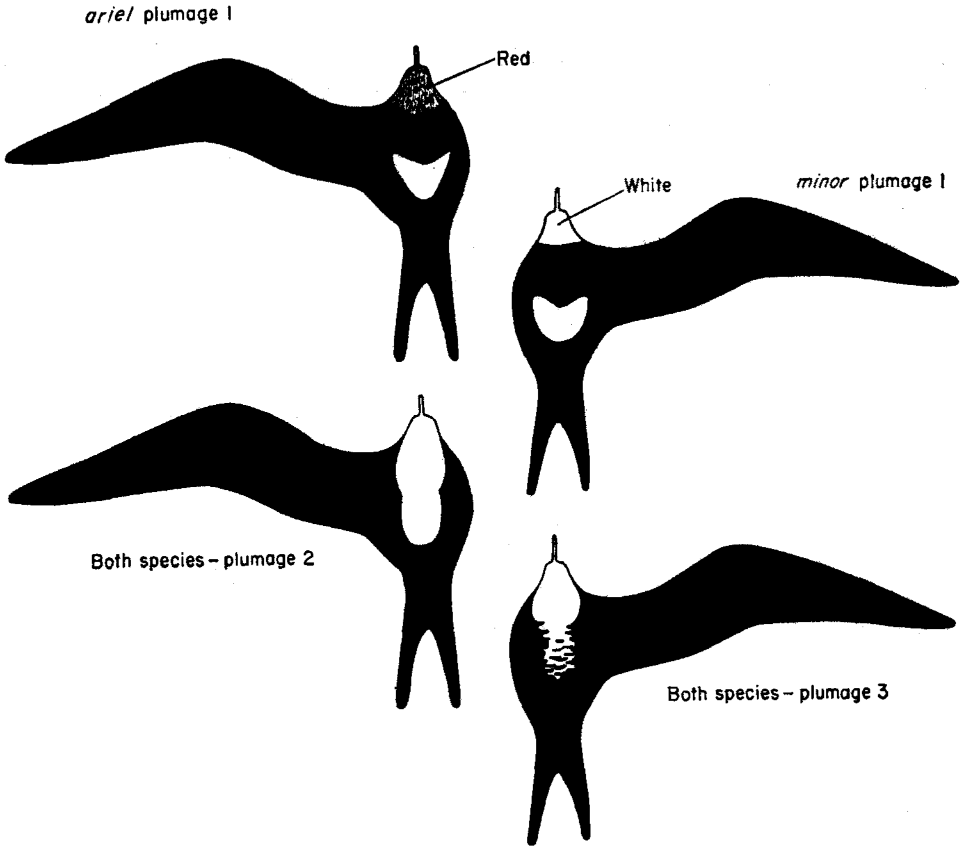

FIGURE 12. Plumages of immature frigatebirds at Aldabra.

TABLE 7

Aldabra frigatebirds: metrical data

(a) Weights (g)

		Number weighed	Range	Mean
F. minor	Male	21	1000–1450	1201
	Female	21	1215–1640	1427
F. ariel	Male	29	625–875	754
	Female	45	760–955	858

(b) Weights and measurements of eggs

		F. minor			*F. ariel*	
	Number	Mean	±s.d.	Number	Mean	±s.d.
Weight (g)	9	81·0	7·5	1	59·0	—
Yolk weight as % of egg weight	2	28·1	—	—	—	—
Length (mm)	8	67·6	1·8	8	60·8	2·5
Breadth (mm)	8	47·4	1·6	8	42·1	0·9

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* In October 1974, A. Forbes-Watson (pers. comm.) found that this area had been recolonized by both species, and that the distribution of colonies was rather different from that described here. Considerable changes in distribution, particularly of *F. ariel* have evidently taken place, and deserve investigation.