NOTES ON THE BREEDING BIOLOGY AND BEHAVIOR OF THE MAGNIFICENT FRIGATEBIRD

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Of the five species of frigatebirds currently recognized, four have been studied in some detail: *Fregata aquila* on Ascension Island (Stonehouse and Stonehouse 1963); *F. minor* in the Galapagos (Nelson 1967, 1968), on Christmas Island, Pacific Ocean (Schreiber and Ashmole 1970) and, with *F. ariel*, at Aldabra Atoll, Indian Ocean (Diamond 1971 and unpubl.); and *F. andrewsi* on Christmas Island, Indian Ocean (Nelson unpubl.). Although it is the only species breeding in North America (and also in the Cape Verde and the Galapagos Islands, along the coasts of northern South America and throughout the Caribbean), the Magnificent Frigatebird (*F. magnificens*) has so far escaped detailed attention. This paper reports studies made on the breeding colony of *F. magnificens* at Barbuda in the Lesser Antilles, on irregular visits totaling 10 days, between March and September 1971. Only brief comparisons will be made with other species since a more thorough investigation of this and other species is planned.

THE STUDY AREA

Barbuda, lying about 56 km N of Antigua at about 17°35′ N and 61°45′ W, is a low-lying island of raised limestone, 90 km^2 in area (fig. 1). The western part is occupied by a large shallow lagoon, bounded to the west by a narrow ridge of sand and to the north by a large expanse of swamp edged by low mangroves. Along the edge of the channel between the lagoon and the sea, the mangroves are mainly *Rhizophora mangle*, but further from the channel *Avicennia nitida* is dominant and it is here that the birds nest. The narrow zone of *Avicennia* bushes, rarely more than 2.5 m high, abuts immediately onto the lagoon shore, and behind the *Avicennia* is a zone of very low halophytic vegetation, principally *Sesuvium portulacastrum* and *Batis maritima*, on soft, deep mud interspersed with shallow pools of open water.

POPULATION

The breeding colony is restricted to a small area of the lagoon-fringe of the swamp, but birds roost in mangroves to the north and south of the nesting area. The colony occupies about 500 m of shoreline and a total area of about 22,500 m^2. On 14 June 1971, a count of occupied nests was made in an area of about 2825 m^2 at the northern end of the colony. Extrapolation of this count (160 occupied sites) gives a breeding population of about 2500 pairs, after making allowances for variations in nest density and for nest losses before the count was made. The largest colony of *F. magnificens* recorded by Eisenmann (1962) was an estimated 2500 nests at Isla Desterrada (Yucatan), so the Barbuda colony is among the largest in existence.

NESTING

All nests were built on top of low vegetation (extreme heights 0.3 and 2.6 m), normally *Avicennia*, though one was on ground vegetation (*Batis*). Nests were in isolated clumps of suitable vegetation separated by areas of *Batis*, *Sesuvium*, and bare mud subject to periodic inundation, or in the continuous fringe of *Avicennia* bushes along the lagoon shore. A minimum estimate of nest density, obtained from two clumps of stunted *Avicennia* containing five and seven nests, is 0.28 nests/m^2. Eisenmann (1962) gave a density of 212 nests in a 40-ft square, which is equivalent to 1.3 nests/m^2. Nest densities in other *Fregata* species are lower; 0.06 nests/m^2 in *F. minor* in the Galapagos (Nelson 1967) and between 0.11 and 0.5 nests/m^2 in *F. aquila* on Ascension (Stonehouse and Stonehouse 1963).

The comment has often been made (e.g., Murphy 1936) that frigatebirds nest on the windward side of islands, and that this helps them to take off, since with their enormous wingspan and short legs, they may have difficulty getting airborne without assistance from the wind. However, frigatebirds are quite capable of taking flight from trees or bushes in perfectly calm conditions. They can do so even from the water provided that they do not stay on the surface long enough to become waterlogged (pers. observ. of *F. magnificens*, *F. minor*, and *F. ariel*). It was noticed on

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[1] Present address: Cousin Island, Seychelles, Indian Ocean.

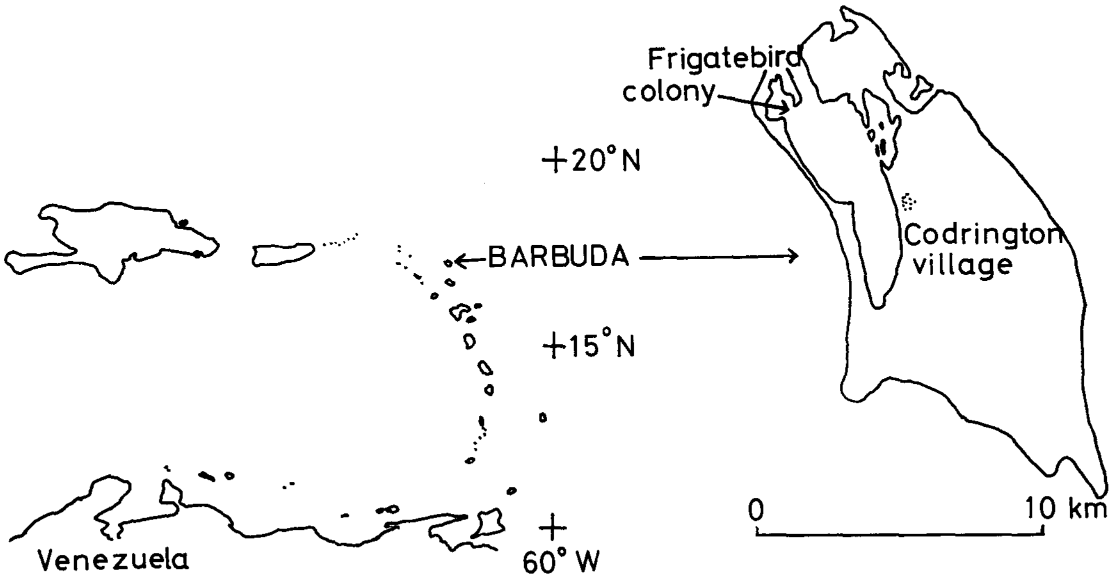

FIGURE 1. Map of eastern Caribbean showing position of Barbuda, and map of Barbuda showing location of frigatebird colony.

Barbuda, and also in the colonies of *F. minor* and *F. ariel* at Aldabra (Diamond 1971 and unpubl.), that although colonies are situated on the side of the lagoon which is exposed to the trade winds, the nests themselves are placed on the sheltered side of the trees. The fully exposed side is used, if at all, only for roosting. The explanation for this dispersion pattern does concern the lift that the birds gain from the wind; its importance is in landing, not in taking off. To take flight, the bird needs only to get into the air, and if its perch is at all springy, it can do this easily. In landing, however, the bird has to alight precisely by, or on, the nest or perch. It can achieve the fine control necessary to do this only if it can reduce its groundspeed while maintaining its airspeed, by approaching the nest upwind like a tanker docking against the tide. A few minutes spent watching the attempts of an adult to land by a hungry, begging chick on a thin twig, in a 15-knot wind, will convince anyone of this point. Nesting on the sheltered side of the trees may also reduce the chances of the egg being blown out of the nest. However, this is evidently not the primary factor determining the choice of the nest site or the birds would nest on the sheltered side of the lagoon.

LAYING SEASON

On my first visit in late March 1971, most nests contained small chicks, though a few still had eggs. Forty-one chicks were measured, and from subsequent records of the growth of a few chicks in marked nests, it was possible to estimate the hatching dates of these young. Laying dates were then estimated using a hypothetical incubation period of 50 days; the true incubation period is not recorded for this species. Fifty days was used because it is between the periods of 44 days in *F. aquila* (Stonehouse and Stonehouse 1963), 41 days in *F. ariel* (Serventy and Whittell 1962), and 55 days in *F. minor* (Nelson 1967).

The laying dates estimated for these 41 birds are shown in figure 2. The apparent bimodality of the distribution of these dates cannot be explained. Note that the median laying date is at the end of November or beginning of December and that there is a spread of at least 2.5 months on either side of this point. (Some nests contained eggs in

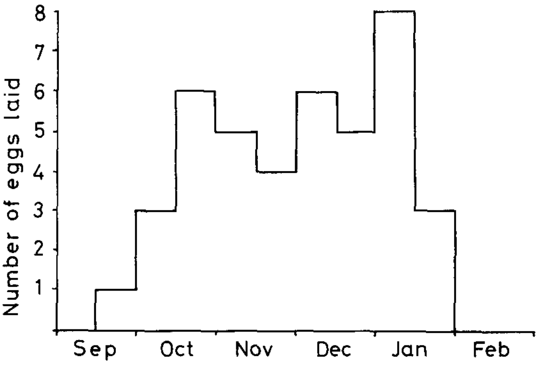

FIGURE 2. Egg-laying periods in 1970–71, calculated from bill lengths of chicks (see text).

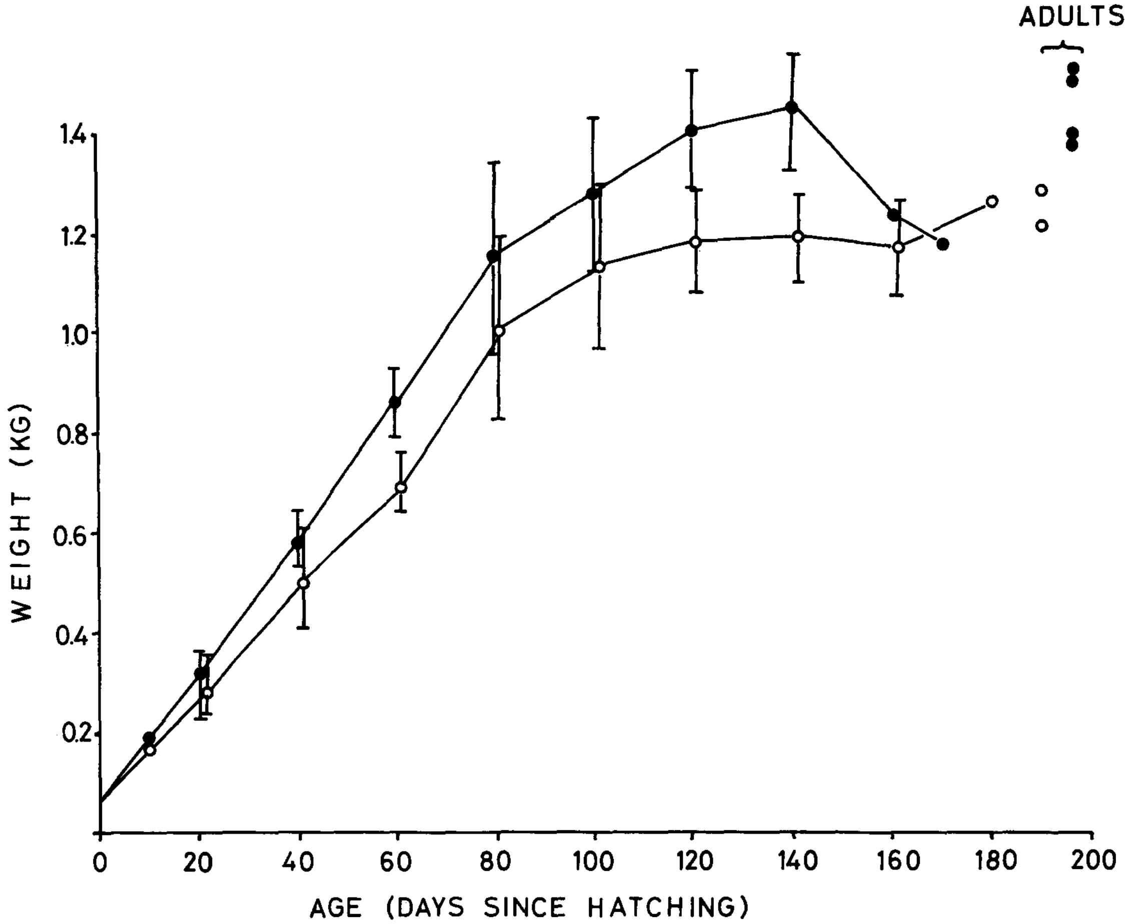

FIGURE 3. Weight increase of male and female chicks. Solid circles indicate mean weight of females, and open circles indicate mean weight of males. Vertical bars show range of weights.

late March, and these eggs must have been laid later than the last laying date shown, i.e., sometime between early February and late March.)

The data available (Eisenmann 1962) are insufficiently precise to enable the laying season on Barbuda to be compared with those elsewhere. The only more recent information is from Monito, off Puerto Rico, where C. and A. Kepler (pers. comm.) found young about to fledge in early June, which suggests that the laying period on Monito was very similar to that on Barbuda.

To what extent laying occurs at the same time each year on Barbuda is impossible to say after only one-half season's observations. No eggs were laid between late March and late August (or at least none stayed in the nest long enough to be observed by me.) The males began to display in late August but had not reached their peak when observations ended in mid-September. By analogy with *F. minor* (Nelson 1967, 1968) and *F. aquila* (Stonehouse and Stonehouse 1963), egg laying occurs from 3 weeks to a month after display begins. Therefore, the peak of laying could not have occurred sooner than early October, and since the peak of display had not been reached by mid-September, the peak laying period would have been much later than this, probably not before the beginning of November (i.e., about the time of the first laying peak in 1970, see fig. 3). From these observations, it seems likely that laying occurred at about the same time in 1970 and 1971.

CHICK GROWTH

The growth of six chicks was followed from late March 1971, and the growth of another nine from late April. Both groups were followed until the end of August. Since adult males are smaller than adult females, and this difference is noticeable in chicks 100 days old, it is possible to determine the sex of chicks that live at least 100 days. The growth of the 11 chicks whose sex could be determined from the bill length at fledging is shown

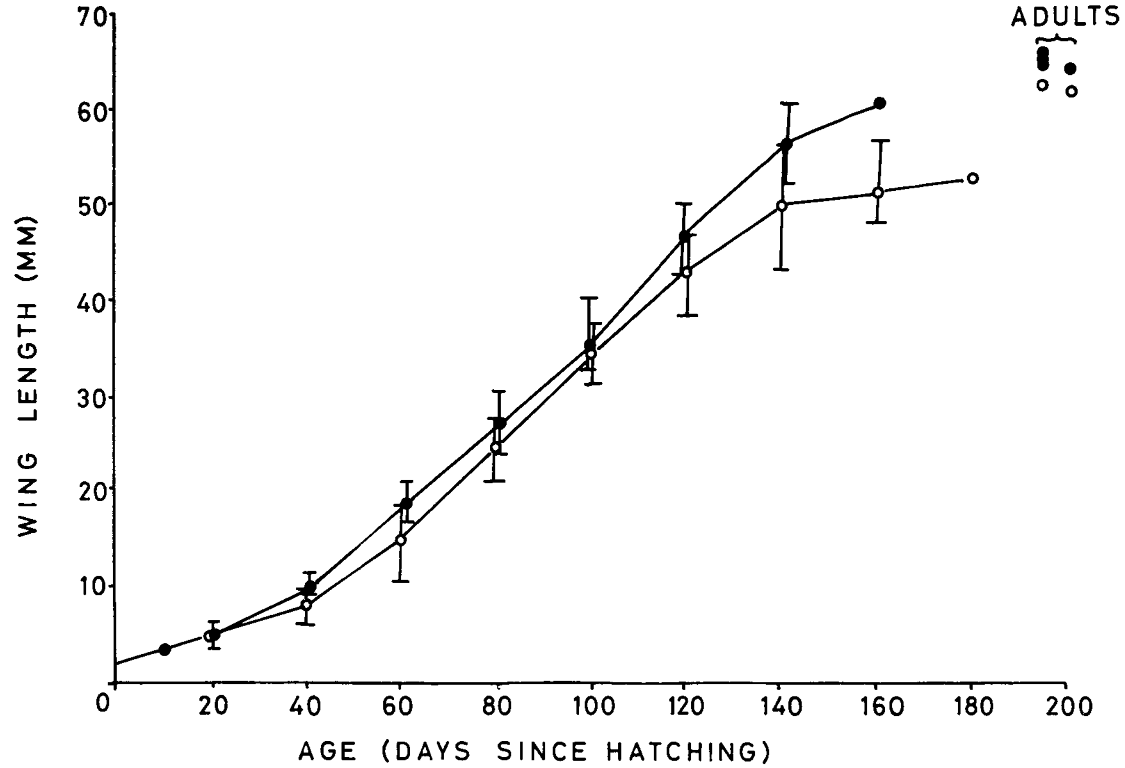

FIGURE 4. Wing growth of male and female chicks. Solid circles indicate mean wing length of females, and open circles indicate mean wing length of males. Vertical bars show range of wing lengths.

for males and females separately in figures 3, 4, and 5. These curves are similar to those for *F. aquila* (Stonehouse and Stonehouse 1963) and *F. minor* and *F. ariel* (Diamond 1971), except that neither of these studies showed the growth of the sexes separately. Clearly, only bill length is reliable for separating the sexes, since weights are variable and the winglengths of adults are very similar. (Although only seven adults were measured in this study, females' bills are consistently longer than males' in specimens of this and all other *Fregata* species. Although there is a little overlap in bill length between adult male and female *F. magnificens*, chicks whose measurements fell in the area of overlap were excluded from the growth analysis.) The variability of weights is probably not due to any great extent to differences between chicks which had been fed recently and those which had not, since birds which had recently received food usually regurgitated it before they were weighed. Further, almost all feedings were given at the end of the day (fig. 9), and chicks were weighed in the late morning.

Both sexes brooded the young for the first few weeks of its life, but thereafter the chicks were visited only to be fed. The average age of the five oldest chicks seen being brooded by adults was 40 days (range 30–50 days).

FLEDGING PERIOD

The calculated fledging periods of 9 of the 11 chicks whose growth was followed to fledging averaged 166 days (range 149–207); males averaged 168 days, females 163. These differences presumably were due to chance. These periods can be compared with others reported: 130–160 days for *F. minor* in the Galapagos (Nelson 1967) and *F. aquila* on Ascension (Stonehouse and Stonehouse 1963); about 145 days for *F. minor* on Christmas Island, Pacific Ocean (Schreiber, pers. comm.); about 120 days in *F. minor* and 140 days in *F. ariel* at Aldabra (Diamond 1971); and about 155 days in *F. andrewsi* and *F. minor* on Christmas Island, Indian Ocean (Gibson-Hill 1947).

SEX RATIO OF CHICKS

During my June visit to Barbuda, my wife pointed out that small-billed chicks (presumed males) had browner wing-bars than large-billed ones (presumed females). This point was checked by recording the bar on the upper surface of each chick's wings as either "white," "brown," or "intermediate."

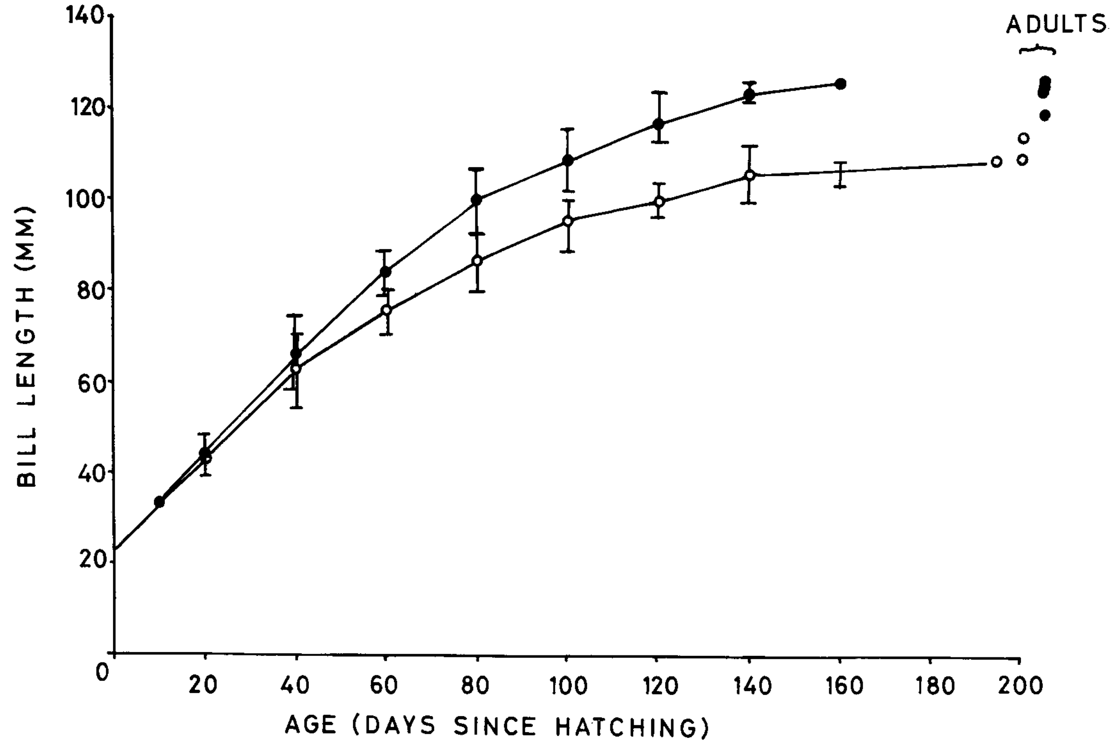

FIGURE 5. Bill growth of male and female chicks. Solid circles indicate mean bill length of females, and open circles indicate mean bill length of males. Vertical bars show range of bill lengths.

The bill lengths of fledglings (i.e., birds attempting to fly when approached, but unable to fly strongly enough to evade capture) identified as "white-winged" or "brown-winged" before capture, are shown in table 1, which supports the validity of this character in sexing fledglings. It is unlikely to be useful in older birds, since the whiter appearance of the females' wing-bars is caused by broad white edges to the brown wing coverts, and these edges probably abrade rapidly once the bird makes regular sustained flights. The wing-bar, as Murphy (1936) pointed out, is not caused by abrasion but, on the contrary, may be reduced by abrasion; Stonehouse and Stonehouse (1963) attributed the alar bar of *F. aquila* to feather attrition but this is certainly not true in *F. magnificens*.

TABLE 1. Bill lengths (in mm) of fledglings with ♂ ("brown") and ♀ ("white")-type wing-bars.

	Brown type	White type
Number measured	9	10
Range	102–111	117–124
Mean	105.8	120.9
Standard deviation	3.2	2.5
"t" for difference between means	11.6 ($P < 0.001$)	

Using wing-bar color as a criterion of sex, fledglings in three different parts of the colony on 28 July 1971 were found to have a sex ratio of 1.8 females:1 male (71 females, 39 males, 16 undetermined—most "undetermined" birds that could be caught proved, on the basis of bill length, to be females). Possible reasons for this ratio will be discussed in the next section.

TWINS

The normal clutch of frigatebirds is one. However, in March 1971 two nests were found each containing two young; whether these chicks came from eggs laid by one female or by two is not known. The growth of wing and bill were comparable with normal chicks but the "twins" were well behind normal young in weight increase. Both sets of "twins" had disappeared by my June visit, long before they could have fledged, suggesting that the parents were unable to feed two young.

DIVISION OF LABOR BETWEEN THE SEXES

Table 2 shows the number of adults of each sex incubating or brooding in March and April 1971. Two points are suggested by these figures: first, that the proportion of females

TABLE 2. Number of adults of each sex incubating or brooding small chicks.

Date	Time	♂♂	♀♀
22 March	09:00	27	24
22 March	13:50	38	63
20 April	11:00	10	25
20 April	15:50	7	19

incubating and brooding increases during the day; second, that males were less attentive in April than in March. This drop in male attendance foreshadowed an almost complete absence of males from the colony at my next visit, in mid-June, when I saw no more than three males in the whole colony. In late July, about 10 males were present in the colony, and by the end of August there were as many males as females. The number of females remained more or less constant throughout this period.

It seems reasonable from these observations to assume that the majority of males left the colony during April and May, and that most probably returned during October (since many had not returned by mid-September, when observations ceased). Therefore, males spend on average only 6 months at the colony. They presumably undergo a complete molt during the other 6 months since they apparently do not molt while breeding. This assumes, of course, that males breed at annual intervals: females cannot breed annually since they feed the young for at least 4 months after the chicks have fledged. I showed this by marking about 20 chicks, at or shortly before fledging, with numbered plastic wing tags, and recording the whereabouts of these birds on subsequent visits. One bird, tagged on 20 April when it could just fly, was fed by a female on 12 September at or close to its nest site, i.e., 20.5 weeks after fledging. Moreover, there was no sign that females were beginning to desert their young, since the number of feedings given per hour in mid-September, though not measured, appeared to be similar to that recorded in July. Unless the females begin to molt when the males leave the colony, which could not be checked since adults feeding well-grown young are very difficult to catch, they evidently cannot breed at annual intervals. Since breeding in the colony evidently recurs at approximately yearly intervals, the females cannot breed more often than once in 2 years. Although proof is still lacking, the implications of such a unique system are considered in detail elsewhere (Diamond 1972). Here it is relevant only to note that this breeding regime appears to maximize chick production and is possible only where food is predictably abundant; it can hardly be a coincidence that one of the Caribbean Sea's richest fishing areas, at the edge of the Barbuda Bank, lies only 8 miles to the west of the colony. The system does, of course, require females to outnumber males in the breeding population. While this cannot be verified directly, since the whole population is not assembled at one time and place, the excess of females at fledging, already described, provides strong circumstantial evidence that a disparate sex ratio exists in the adult population.

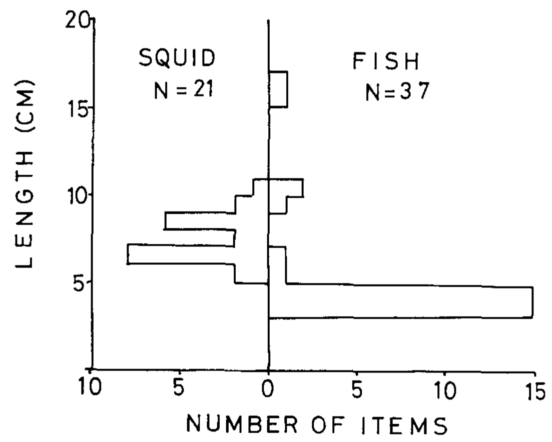

FIGURE 6. Size distribution of prey in food regurgitated by chicks.

FOOD

The most popular English names of the Fregatidae—frigatebird, Man-o'-War—refer to the birds' habit of robbing other sea birds of their food. While all species do this to some extent, the importance of this source of food varies from colony to colony. At the breeding grounds of *F. magnificens* on Little Cayman, for instance, frigatebirds frequently chase Red-footed Boobies (*Sula sula*). No boobies nest on Barbuda, but Brown Pelicans (*Pelecanus occidentalis*) and Laughing Gulls (*Larus atricilla*) probably do and I saw none being chased by frigatebirds. Probably most food is caught directly from the surface of the sea.

Chicks frequently regurgitate their last meal when approached. Ten such food samples are detailed in table 3, and the lengths of the food items which could be measured are shown in figure 6. The distribution of fish lengths is atypical since it is dominated by 30 small fish larvae found in one sample. The squid are of a similar size to those taken

TABLE 3. Contents of ten food samples regurgitated by chicks.

	Squid		Fish			
Sample	Ommastrephidae	Others	Exocoetidae	Lutianidae	Balistidae	Scombridae
1		1				
2				1		
3						1
4	2	1				
5		3				
6			1	2		3
7			10			
8	13	6				
9			2			
10	2		2+		1	

Note: Ommastrephid squid identified by shape of funnel-locking cartilage (Roper et al. 1969). "Other squid" includes unidentifiable cephalopod remains so may include some Ommastrephids.

by both *F. minor* and *F. ariel* off Aldabra (Diamond 1971).

In addition to the samples analyzed in table 3, many chicks regurgitated boluses, showing no recognizable remains except the pectoral spines of flying fish. However, these samples are not included since these spines are (1) very resistant to digestion, (2) are easily identifiable at a late stage of digestion, and (3) their inclusion would lead to an over-representation of Exocoetidae in the diet.

BEHAVIOR

No detailed analysis of behavior patterns was made, but the calls and more obvious behavioral features of both sexes are described below.

CALLS

Frigatebirds are usually silent, calling only when coming in to land, in display, and when begging for food. The arrival call is similar in the two sexes, being a rapid rattle descending in pitch and increasing in speed as the bird descends to its perch. The female's call is deeper and hoarser than the male's, but the difference is not nearly so marked as in *F. minor* or *F. ariel* (Diamond, unpubl.). When circling above the nest or roosting site, the female often calls more slowly in two-syllable bursts, but the notes run together into the familiar rattle once the bird starts to descend. Young birds have a harsher note, similar to that of the female.

In display, males give three types of calls, referred to here as drumming, reeling, and purring: (1) drumming was heard only from birds with the pouch inflated; it is a deeper, more resonant sound that the other two, and no doubt owes some of its quality to the resonant properties of the pouch. (2) Reeling, which resembles the sound made by the spokes of a turning bicycle wheel, can be given by birds with the bill held at any angle with either a deflated or an inflated pouch. Birds in full display to a female alternate reeling with drumming. (3) Purring is self-descriptive; it was heard rarely, only from birds with the pouch partly inflated, and may be the sound which results when a bird in such condition tries to drum. It was given to males, females, immatures, and in the absence of any audience, so its function is not clear.

Perhaps the most important feature of the male's acoustic display is that it lacks the vocal "warble" (Nelson 1968) or "whinny" (Diamond, unpubl.) found in *F. minor.* All the sounds made by male *F. magnificens* are to a large degree mechanical in that they are accompanied by, and presumably in part produced by, rapid bill vibrations; in this *F. magnificens* is similar to *F. ariel* but contrasts with *F. minor.*

The only call heard from a female in a sexual context, a rapid twittering accompanied by vibration of the mandibles, was given by a female which had recently landed near a male.

The begging call of the young is harsh, rhythmic, insistent, and plaintive, and is more porcine than avian.

DISPLAY

The general features of the courtship display are similar to those described by Nelson (1968) for *F. minor.* Males display in groups, commonly of four to eight, to birds flying overhead. The full display, with outstretched wings rapidly vibrated, head thrown back, and pouch fully blown out, is reserved for females, but what is probably a low-intensity version of this display is given to incoming males as well. This version differs from the full male-to-female display in the following

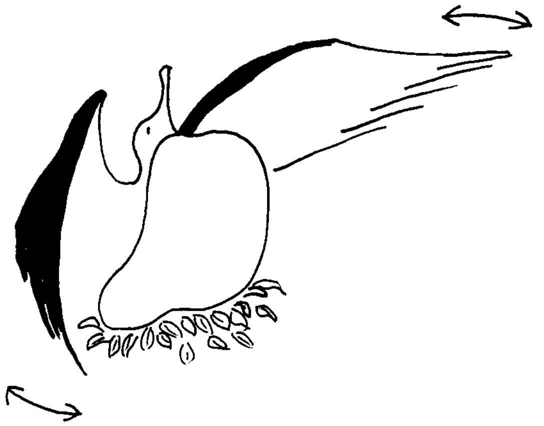

FIGURE 7. Diagram of ♂ – to – ♀ display. Arrows show direction of movement of wing tips in wing-fanning.

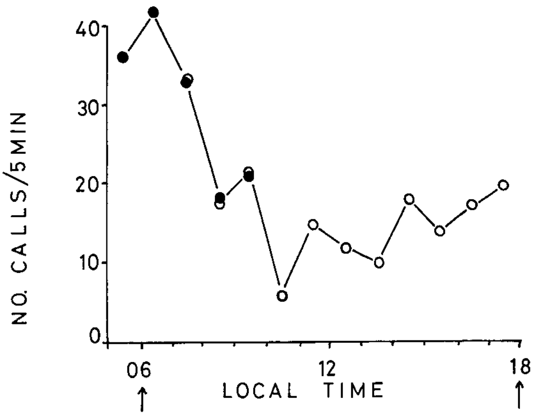

FIGURE 8. Diel periodicity of display calls given by males. Open circles: 15 September. Solid circles: 16 September 1971.

respects: (1) the wings are not fully outstretched and are flopped or waved half-heartedly; in full display they are extended sideways, raised well above the substrate, and vibrated rapidly back and forth (fig. 7). I suggest the term "wing-fanning" be used for the full-display wing movements and "wing-waving" for the actions used in a male-to-male context. (2) The displaying male does not throw back his head and raise the scapulars to nearly the same extent as when displaying to a female. (3) When a female pauses overhead to inspect a group of males (females flying directly over are often ignored), every male in the group at once goes into full display. When a male flies over, and particularly when one attempts to land in or next to the group, usually only the nearest one or two males react with the low-intensity version of the display; the others pay no visible attention. (4) When a male does land, the nearest male in the group lunges at him with bill-snapping and frequently drives him off. Thus although there is no ritualized site-ownership display, the male certainly defends the area immediately around his display site (cf. Nelson 1968, 1970).

Male-to-male display has hitherto been recorded in Pelecaniformes only in the Masked or Blue-faced Booby (*Sula dactylatra*) in the Pacific (Kepler 1969).

Once a female has landed by a male, he continues the full display intermittently, often accompanied by one or two, but rarely all, members of the group, and alternates display with bouts of head-shaking with the female. She responds with the twittering already described, bending her neck around to nibble the male's flanks or stretching across to rub her head along his pouch, and passing her head across his in mutual head-snaking. Contrary to the description of frigatebird display given by van Tets (1965), the female does not have a display similar to the male.

A female flying over a group of displaying males would, if attracted by the display, hover above the group before flying on or descending. This hovering was apparently identical with that used to maintain position in other situations, e.g., before landing by a chick or on the nest; there are no ritualized wing or neck actions characteristic of females answering a male's display such as are found in *F. ariel* (Diamond, unpubl.).

A measure of the diurnal variation in display activity is given by the number of "reeling" and "drumming" sounds heard in a given time interval. This is shown, for parts of 2 days in September, in figure 8. There is an early morning peak and a late morning trough, followed by a steady rise to about half the dawn value at dusk. Some display was heard after dark.

FEEDING THE YOUNG

Display groups form on and around the nest sites which are still being used by young birds and females of the previous breeding cycle. However, by the time display gets under way, most of these young do not spend all day at the nest but return to it in the afternoon to be fed. If they find their perch occupied by a male, they may sit nearby, but if they persistently try to land on their own perch, the male usually gives way. When a female flies over a group of young, intending to land, several young adopt the hunched begging posture, with half-open wings, and begin to bob the head and shoulders and to give the plaintive

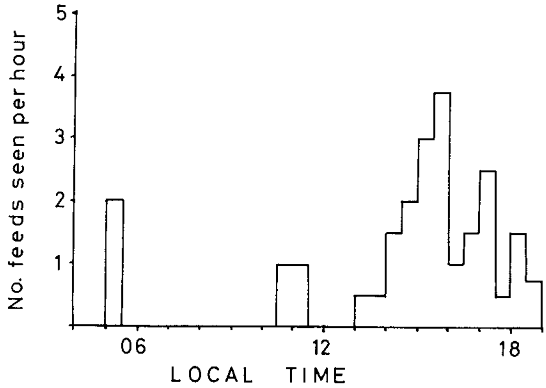

FIGURE 9. Diel periodicity of feeds given to young. From 40 feedings recorded on 13 and 14 June, 29 July, 25 and 26 August 1971.

begging call. Soon, however, unless the chicks are very hungry, only one is left begging and it is this one to which the female descends. Apparently the young can recognize its mother since often only one bird responds to a female flying overhead and, if the female lands some distance from the chick, the young bird may fly across to her to be fed. The female presumably also recognizes her young, rather than simply returning to her own nest site, since a female on several occasions fed a wing-tagged juvenile 80 m from its nest.

Feedings were not recorded systematically until June, but during my visits then and in late July, late August, and mid-September, 40 feedings were seen of which only one (on 14 June) was by a male. Thus the female alone feeds the chick from the time when the males leave the colony (when the chick is about 100 days old) until several months (at least 4) after the chick has fledged. Figure 9 shows the time of day at which feedings were seen and shows that most were given in the late afternoon. The distinctive sounds of feeding—repeated plaintive begging by the chick, followed by the female arrival call and the choking gurgle as the chick puts its head down the female's gullet—were often heard after dark, up to midnight. However, it is not possible to compare the rates of feeding before and after dark since most of the former were seen rather than heard. Not all the chicks visible from the blind were fed during daylight each day, but some at least were fed after dark.

Feeding the young was often complicated by interference from Laughing Gulls. Sometimes two or three gulls would hover over a female feeding a chick and would try to snatch food from the chick's gullet; they rarely succeeded in this but would sometimes surprise the young bird, causing it to accidentally drop part of its food on which the gulls then pounced. Immature frigatebirds which could fly well also picked up dropped food, and in August and September flying young, whose plumages indicated they were older than first-year birds, tried several times to snatch food being passed from adult to fledged young.

DISCUSSION

Most features of the biology and behavior of *F. magnificens* are similar to those of other *Fregata* species. *F. magnificens* differs in details of behavior, but the main difference from other species is the disparate roles played by the sexes in rearing the young, and presumably the unequal sex ratio of fledglings (though the latter has not been measured in other species). These points need to be investigated in greater detail, and with marked birds. If they are confirmed, they may well be related to the unusually rich food supply (Diamond 1972). This is probably not a characteristic of the Barbuda population alone, since most colonies of this species are coastal (unlike those of other *Fregata* species, in which almost all colonies are on oceanic islands) and presumably also have rich food supplies close at hand. It is especially interesting to note that many of the features of frigatebird biology, which Nelson (1967, 1968) suggested were adaptations of the birds he studied to a poor and unpredictable food supply, are also present in a species with a much richer and more dependable source of food.

SUMMARY

About 2500 pairs of *F. magnificens* were estimated to breed on Barbuda in 1970–71. The nests were grouped in low clumps of mangrove (*Avicennia*), few being higher than 3 m above the ground. Most of the eggs were laid between September and March. The young were attended by both sexes until they were about 3.5 months old, when the males left the colony. The males spent 6 months away from the colony, and it is suggested that they molted then, returning to breed every year. Although annual breeding by males is not proved, it is the most likely explanation of the males' 6-month absence from the colony. The females fed the young for at least 5 months after fledging and so cannot breed more often than once every 2 years, unless they molt while feeding the young. The fledging period averaged 166 days. Growth of the young is described; the sexes are separable by bill length after 100 days. They can also be sexed by the whiter wing-bars of the females, and the sex ratio was unequal, 1.8:1 in favor of females, in 1971. It is suggested that the breeding population produces more females than males, and thus achieves the unequal sex ratio which is necessary if the sexes are to breed at different time intervals. Two sets of natural "twins" failed to fledge. The components of a few food samples, mostly squid and fish, were identified and measured. Voice and behavior are described. The special breeding regime which this species appears to show on Barbuda is probably related to a rich, local food source. It is suggested that this breeding regime may also occur in other colonies of this species, most of which are in coastal waters and so probably also have a dependable food supply.

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