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NEST SPACING AND BREEDING SUCCESS IN THE LESSER FRIGATEBIRD (*FREGATA ARIEL*)[1]

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Abstract. Colonies of Lesser Frigatebirds (*Fregata ariel*) contained nesting groups with up to 250 nests per group. Within groups, sites were not arranged in clusters as in Great Frigatebirds (*F. minor*) but were regularly spaced. On Aldabra Atoll, nesting success (fledglings/nest) was inversely correlated with nest density in nesting groups for 1976 but the correlation was not significant for 1977. Breeding success (fledglings/egg) was low (23% and 17%) and varied with date of laying. In 1976, birds laying before the mean laying date were less successful whereas in 1977 birds laying after the mean laying date were less successful. Site usurpation by unpaired males was a major cause of chick loss, especially in 1976. Usurpation of a site resulted in neighboring sites also being lost. Breeding failure in late 1977 was apparently due to abandonment of eggs rather than usurpation. Unlike male Great Frigatebirds, unpaired male Lesser Frigatebirds did not form stable display clusters: they aggregated only at sites of female interest, remained for a short time and did not fight for display sites. Unlike female Great Frigatebirds, female Lesser Frigatebirds performed a ritualized aerial display before landing at an advertising male, began settlement soon after the first male display, and showed no preference for colonies of different size. On Raine Island there appeared to be no site usurpation by unpaired males. The differences between Great and Lesser Frigatebirds in site-selection and nest spacing have probably arisen from differences in food availability, sex ratio and predation.

Key words: Fregatidae; colony; nest spacing; site choice; density; breeding success; Lesser Frigatebird; Fregata ariel.

INTRODUCTION

Each species of seabird appears to have a characteristic spatial pattern of nests (Veen 1977). The pattern may be shaped by habitat characteristics (Buckley and Buckley 1980), predation (Burger 1982), or intrinsic social factors (Gochfeld 1980).

It has been assumed that all frigatebird species share the spatial nesting pattern described for Great Frigatebirds (*Fregata minor*) in the Galapagos Islands (Nelson 1967, 1975). In this population, males advertising for a mate associated in communal display groups; nests were built on the display site, resulting in spatially distinct clusters of up to 20 nests; and site usurpation by unpaired males was a major cause of breeding failure (Nelson 1967, 1975; de Vries 1984).

Anecdotal comments suggest that other frigatebird species form display and nesting clusters (Stonehouse and Stonehouse 1963; Nelson 1972; Diamond 1973, 1975). However, the only published quantitative analysis of nest spacing in frigatebirds is for the Great Frigatebird population on Aldabra Atoll. This study confirmed that clusters rarely exceeded 20 nests, even when extensive habitat was available. Hatching success was proportional to the synchrony of female settlement within a cluster, perhaps because potential usurpers found nesting clusters less attractive than clusters containing displaying males (Reville 1988).

In this paper, I present an analysis of spacing in the Lesser Frigatebird (*F. ariel*), a description of the events leading to site selection and an appraisal of the consequences for breeding success. Comparison with the Great Frigatebird suggests that specific differences in behavior and ecology among frigatebirds are greater than previously recognized.

STUDY AREA AND METHODS

Two populations were studied: Aldabra Atoll, Seychelles (9°24′S, 46°20′E) and Raine Island, Great Barrier Reef (11°36′S, 144°01′E).

Aldabra is an elevated, coralline limestone atoll ca. 420 km northwest of Madagascar (see Fig. 1 in Reville 1983). Lesser Frigatebirds nested in mangroves (30%), principally *Rhizophora mu-*

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cronata and *Bruguiera gymnorhiza,* and shrubs (70%), especially *Pemphis.* Nesting colonies were confined to three locations along the southern shore of Ile Malabar, with most Lesser Frigatebirds nesting at Camp Frigate (Reville 1983). Nests were usually within 10 m of the lagoon, from 0–15 m above highwater. Lesser Frigatebirds nesting in mangrove were usually evicted by Great Frigatebirds, hence results in this paper refer to birds nesting in *Pemphis* or other shrubs which were not used by Great Frigatebirds.

The study on Aldabra Atoll lasted from January 1976 to January 1978. Detailed descriptions of the study sites and of the observation schedule are given in Reville (1983). Detailed information on site spacing within a habitat patch was obtained from an islet at Camp Frigate, which had reasonably continuous *Pemphis* and could be viewed from a permanent blind. The area of habitat (90 m^2) appeared adequate for multiple clusters of a size anticipated from the literature. The habitat patch was photographed and maps made of the position of each bird on each visit. Techniques for estimating distances between nests and subsequent spatial analysis were as described for Great Frigatebirds (Reville 1988). The R index (Clark and Evans 1954) was used to test for non-randomness of spacing ($R > 1$ indicates regular spacing, $R < 1$ indicates clumping, r_a = mean nearest neighbor distance).

A temporary hide was established 3 m from a second islet. From this hide, displaying males were paint-marked using yellow plastic polymer paint manufactured by Imperial Chemical Industries. The paint was delivered on the end of a rubber cork by blowgun. Tests on nesting birds indicated that the paint markings lasted from a few days to six months. The stage of development of the male gular sac and female bill color were useful in determining when nest sites changed ownership. Observations on a wing-tagged male indicated that at least 14 days were required for the gular sac to develop from the inconspicuous patch of skin typical of incubating males to the red, inflatable stage typical of advertising males. In the Aldabran population, female Lesser Frigatebirds have either a pink or a blue bill and eye ring (Diamond 1975). During the laying season, the pink or blue is much richer in unmated females and fades during incubation.

Raine Island is a semi-arid, sand key on the ocean side of the Great Barrier Reef 100 km from the Queensland coast. The island is 27.3 ha in area with a maximum elevation of 6 m. I visited the island between 14–30 July 1982, at the peak of the nesting season (Warham 1961; B. King, pers. comm.). About 900 nests were occupied in 24 nesting groups, each consisting of 1–242 nests. I chose a group with 168 nests on sand among isolated *Lepturus repens* tussocks (tussock density ca. 1 per 15 m^2). Nest positions within a 1 m^2 grid were plotted by running a tape marked at 1 m intervals above the nesting group at right angles to a fixed baseline also marked at 1 m intervals. Measurements were done at night to minimize disturbance. The area occupied by the nesting group (82 m^2) was calculated by the convex polygon method (Flowerdew 1976).

RESULTS

NATURE OF SPATIAL PATTERN

In the Aldabran study group, advertising males or nests tended to be regularly spaced ($R > 1$) whether many or few sites were occupied (n = 54–86 sites, r_a = 73–55 cm respectively), but the tendency was not significant. Within this habitat patch, the *Pemphis* canopy was irregular and its surface area was difficult to measure. On Raine Island, where the birds were ground-nesting and areas easily measured, the regularity of spacing was highly significant (n = 168 sites, r_a = 47 cm, $R = 1.35$, $P < 0.001$).

TEMPORAL PATTERNS

In the Aldabran Camp Frigate colony, there was no significant difference among habitat patches in the timing or rate at which nest sites were settled, until the colony had reached 85% occupancy for the season. Within the intensively studied habitat patch, new arrivals settled between existing nests rather than near each other. In 1977 but not in 1976, females settling later in the season took less time to lay after settlement than did birds nesting earlier in the season (1976: $n = 26$, Spearman $r_s = 0.048$, ns; 1977: $n = 20$, $r_s = -0.462$, $P < 0.05$).

SITE SELECTION

The behavior of unpaired Lesser Frigatebird males differs in several respects from that of Great Frigatebirds (Reville 1988). First, there was no long period of display before a female was attracted. Nests were established when only a few advertising males were present (Fig. 1). Male investment in advertising was much less than in Great Frigatebirds, e.g., 26 days per male per

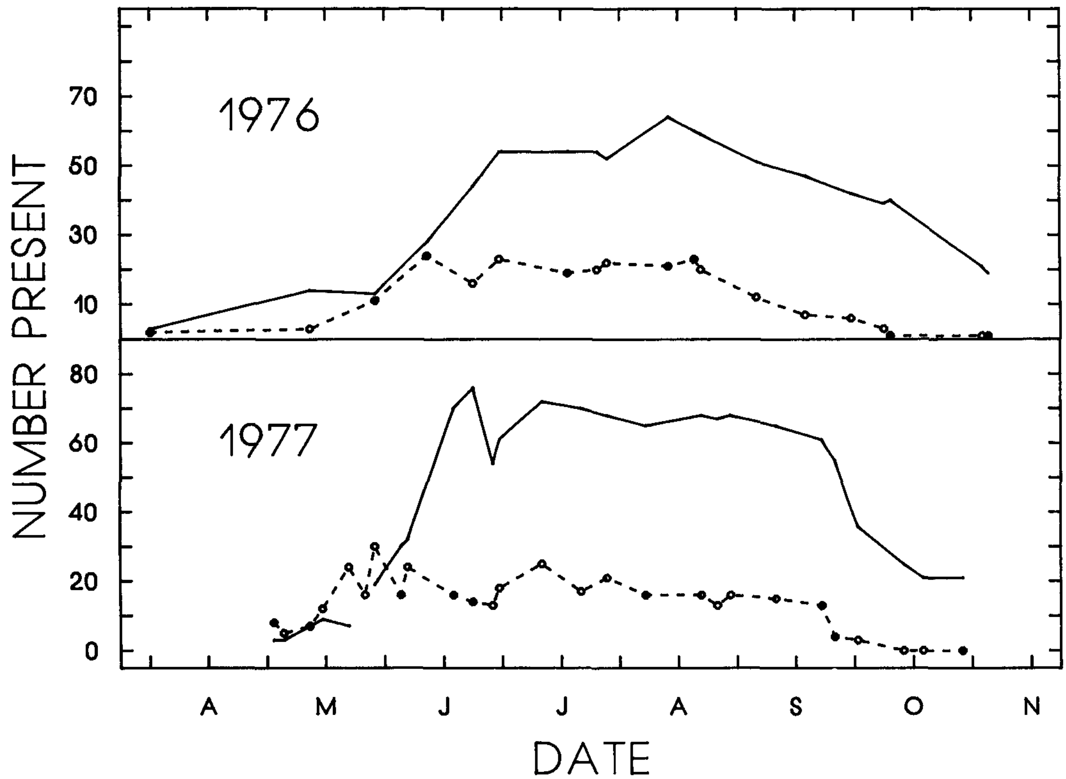

FIGURE 1. Attendance of advertising males (broken line) and number of active nests (solid line) in study group at Camp Frigate.

nest at Camp Frigate in 1977 cf. 54, 55, 78 and 91 days for Great Frigatebirds at various colonies. Unlike Great Frigatebirds, Lesser Frigatebird males were equally successful at small (Middle Camp) and large colonies (Camp Frigate) in attracting females, i.e., 15 and 19 days per male per nest (to 79% colony occupancy, after which point Great Frigatebirds interfered at Middle Camp). Second, the numbers of displaying males were as variable at places where many males were advertising as at places where there were few males, suggesting that there was no preference for joining a "display cluster" containing more males (Fig. 2). Third, the numbers of displaying Lesser Frigatebird males attending a habitat patch fluctuated more rapidly than did numbers of Great Frigatebirds (Fig. 2). This was because Lesser Frigatebird males remained on the display site for much shorter periods. Only 1 of 21 Lesser Frigatebird males spent more than 2 hr continuously on site (2 hr 6 min), whereas 11 of 17 Great Frigatebirds spent more than 5 hr on site. Longest attendances for paint-marked birds were 52% of a 10 hr, 12 min period for a Lesser Frigatebird and 93% of a 6-day period for a Great Frigatebird. Fourth, in 565 hours of observation, no instances of threat or fighting were seen between males which did not involve nest-material or a female. In a comparable period, over 200 instances were noted amongst Great Frigatebird males occupying only display sites.

Recruitment of males to part of a habitat patch was related to the level of display activity of other males at the site. The number of males nearby increased following increased display per male in the preceding 10 min interval ($n = 214$ intervals, $\chi^2 = 6.61$, $P < 0.025$) and decreased after a period of no increased display ($n = 213$ intervals, $\chi^2 = 10.05$, $P < 0.005$).

Areas with a high density of displaying males exhibited a greater amount of display per male than areas of low density, as indicated by three comparisons of large versus small display groups. Observations between the two display groups in

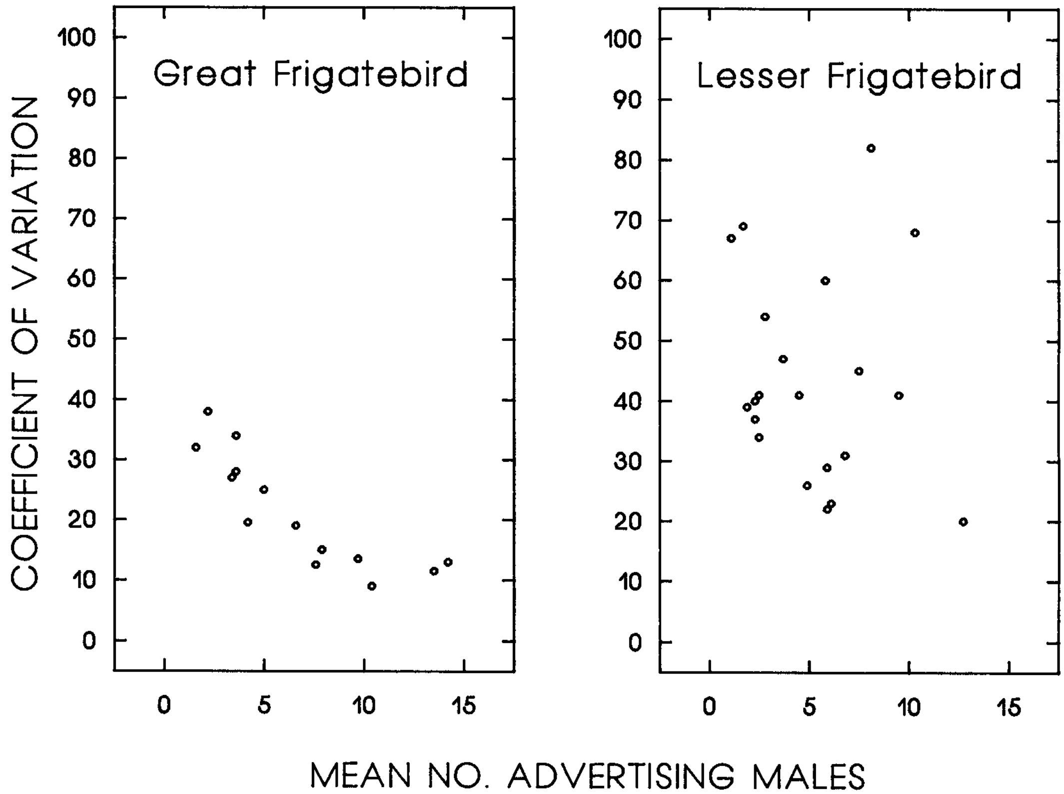

FIGURE 2. Relative variability in numbers of advertising males attending habitat-patches containing different numbers of males. Mean values obtained from counts each 5 min over 4 hr.

each pair were alternated at 5 min intervals over 4, 4 and 3 hr respectively and the number of males in display scored on each minute. The number of display opportunities taken and not taken were then compared for each pair. In each case, males in the larger group displayed more often than males in the smaller group (13 cf. 3 males: $\chi^2 = 4.64$, $P < 0.05$; 12 cf. 5 males: $\chi^2 = 5.22$, $P < 0.025$; 13 cf. 7 males: $\chi^2 = 4.82$, $P < 0.05$). This contrasts with the Great Frigatebird in which the amount of display per male was independent of the number of males per group (Reville 1988).

CONSEQUENCES FOR BREEDING SUCCESS

In 1976, nesting success (fledglings/nest) was inversely correlated with nest density for habitat patches containing only Lesser Frigatebirds ($n = 8$, Spearman $r_s = -0.81$, $P < 0.05$). A similar, but not significant, tendency was apparent in 1977 ($n = 9$, Spearman $r_s = -0.418$, $P < 0.25$) (Fig. 3). In both seasons, breeding success was low and markedly affected by date of laying (Fig. 3). In 1976, females who laid in the first half of the season were less likely to produce a fledgling than those who laid later. This was due to lower fledging success for early layers (Table 1). In 1977,

TABLE 1. Components of breeding success of Lesser Frigatebirds in study group at Camp Frigate before and after mean laying date (24 July ± 43 days in 1976 and 26 July ± 47 days in 1977).

	1976		1977	
	Laid before mean date	Laid after mean date	Laid before mean date	Laid after mean date
Number of eggs	67	69	86	75
Number hatched	17	14	24	4
Number fledged	4	11	18	3
Chicks/egg (%)	25	20	28	5[1]
Fledglings/chick (%)	24	79[2]	75	75
Fledglings/egg (%)	6	16	21	4[3]

[1] Significantly less than before mean laying date $\chi^2 = 12.68$, $P < 0.001$.
[2] Significantly more than before mean laying date $\chi^2 = 7.24$, $P < 0.01$.
[3] Significantly less than before mean laying date $\chi^2 = 8.69$, $P < 0.005$.

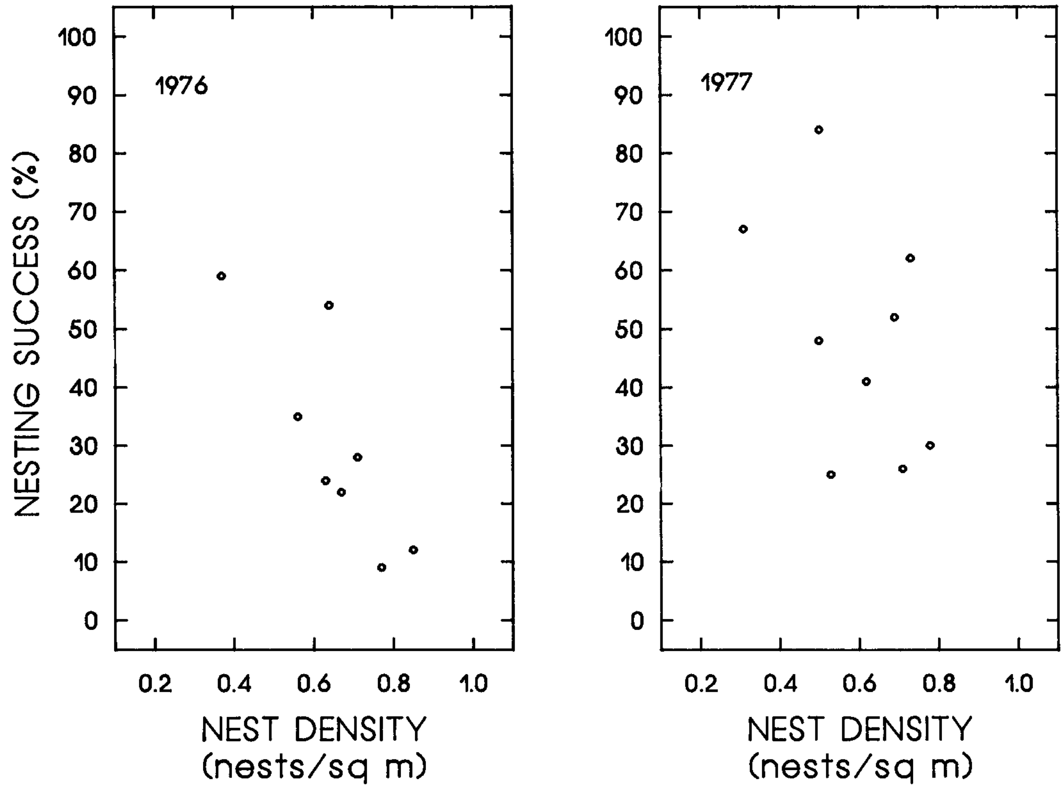

FIGURE 3. Nesting success (fledglings/nest) versus nest density in habitat-patches. (left) 1976: $r_s = -0.81$, $P < 0.05$; (right) 1977: $r_s = -0.42$, ns.

females who laid in the first half of the season were more likely to produce a fledgling than those who laid later. This was due to lower hatching success for late layers (Table 1).

In 1976, 11 of the 16 nestlings lost were killed by usurping males who subsequently attracted a female. In three of these cases the parent was displaced; in the rest, the chick was unguarded. Fewer chicks were lost in 1977 than 1976 (25% cf. 52%), perhaps because chicks were guarded for longer after hatching (33 ± 7 days cf. 28 ± 6 days, 15 chicks, Mann-Whitney *U*, $P < 0.05$). There is no direct evidence as to the cause of loss in other cases, as changes of site ownership were detected only after the event. Changes of site ownership were numerous: new pairs occupied 63% of failed nests in 1976 and 60% in 1977. They produced 11 of the 15 fledglings reared in 1976 but only 4 of the 21 fledglings reared in 1977 ($\chi^2 = 8.49$, $P < 0.005$).

In 1976, nests failing on or about the same day were contagiously distributed in space (Table 2), suggesting that nests were put at risk by the failure of a neighbor. Simultaneous nest-failure in 1977 was rarely of contagious distribution, and not at all in the latter half of the season when hatching success was low (Table 2). Nests failing

TABLE 2. Nearest neighbor analyses of spatial distribution of Lesser Frigatebird nests in the study group at Camp Frigate lost within 2–4 days of each other.

Date	No. of nests	r_a (cm)	*R*	*P*
1976				
1–4 June	10	80	0.53	<0.01
14–18 June	12	100	0.73	<0.08
8–12 July	20	106	0.63	<0.01
8–10 Sep.	10	122	0.82	ns
1977				
3–7 July	18	112	1.43	<0.002
12–15 Aug.	11	111	0.74	ns
11–15 Sep.	19	116	1.07	ns
16–19 Sep.	14	143	1.13	ns

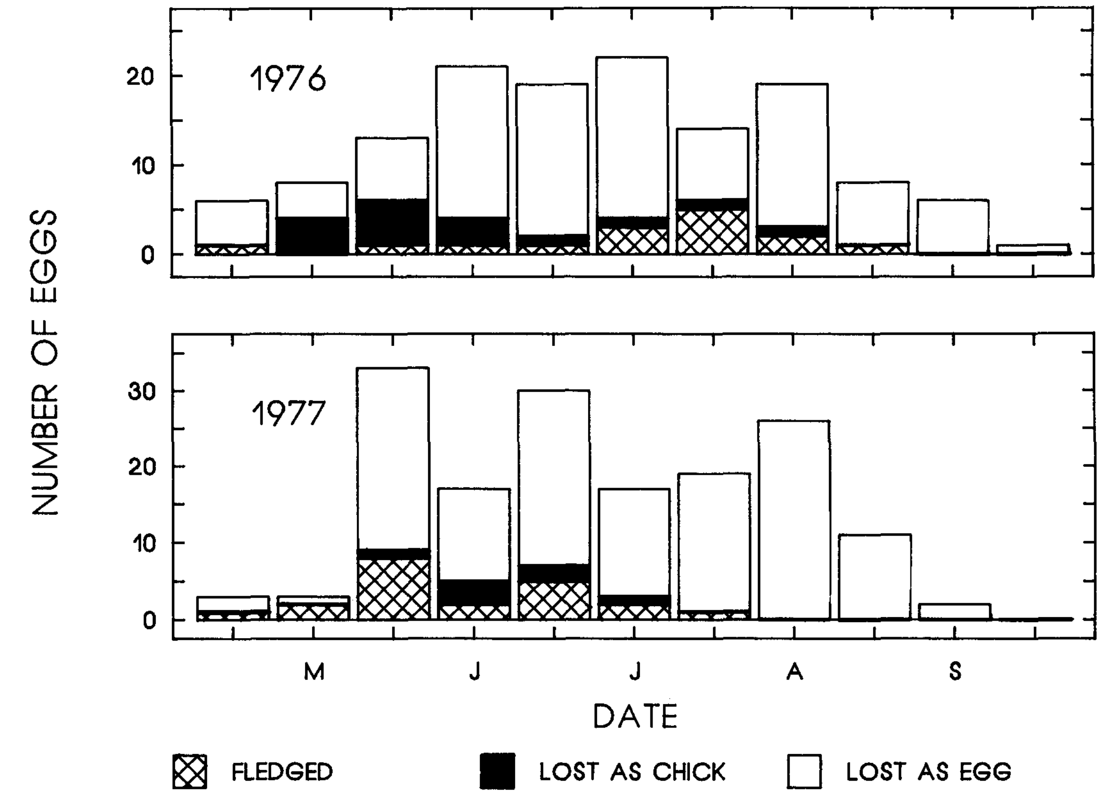

FIGURE 4. Distribution of date of female settlement and subsequent breeding success in study group at Camp Frigate.

during this latter period were usually not occupied by new birds, perhaps indicating that conspecific interference did not cause their loss.

Food may have been scarcer in 1976 than in 1977. Incubation stints tended to be longer in 1976 than in 1977 (6.3 ± 2.9 days cf. 4.9 ± 1.7). Also, the highest loss of chicks (47%) in 1976 occurred between 23 August and 12 September. No measures of feeding or incubation stints for Lesser Frigatebirds were made during this period, however it coincided with a marked temporary decline in nest-settlement by Great Frigatebirds. The two frigatebirds take very similar prey (Diamond 1975).

DISCUSSION

It has been argued that feeding conditions, through effects on sex ratio and the likelihood of site usurpation, have influenced the spatial nesting pattern of Great Frigatebirds (Reville 1988). Similar considerations apply to Lesser Frigatebirds, but quantitative differences have resulted in a different spatial pattern.

The large nesting groups of Lesser Frigatebirds on Aldabra and Raine Island were not divisible into small, spatially distinct clusters of nests typical of Galapagos and Aldabran Great Frigatebirds. The processes of site and mate selection were also different. Compared with Aldabran Great Frigatebirds, male Lesser Frigatebirds did not join male display groups of a particular size, did not remain long on a display site if unsuccessful in attracting a mate and did not fight with other displaying males. The likelihood of remaining at the site was proportional to the level of display by adjacent males and, presumably, to the level of female interest as indicated by the "goosenecking" (Diamond 1975) of overflying females. Overall, this suggests that male Lesser Frigatebirds moved readily from site to site, presumably searching for areas of female interest, rather than attempting to obtain and hold a position within a stable, display cluster.

Such a strategy is explicable given the greater readiness with which female Lesser Frigatebirds settled at a male. In contrast with female Great

Frigatebirds, female Lesser Frigatebirds began pairing as soon as males become available, settled at similar rate in all habitat patches with displaying males and did not distinguish between colonies of different size. Differences in sex ratio may account for this difference in female behavior. On Aldabra, more male than female Great Frigatebirds were available for breeding each season, whereas male and female Lesser Frigatebirds were equally numerous (Diamond 1975, Reville 1983). Consequently, female Lesser Frigatebirds were more likely to have difficulty in finding a mate if they delayed mate selection, than were female Great Frigatebirds.

In frigatebirds, an apparent imbalance in sex ratio can occur through males breeding annually rather than biennially, as suggested for the Magnificent Frigatebird (Diamond 1972, 1973; Coello et al. 1977; Trivelpiece and Ferraris 1987). This demands feeding conditions sufficient for the female to complete the rearing of the chick unaided by the male. There is evidence that Great Frigatebirds were more successful than Lesser Frigatebirds on Aldabra in obtaining food during the wet season, the period coinciding with hatching and maximum growth of the nestling (Diamond 1975). Thus, Great Frigatebirds would be more likely to show an apparent surplus of males than Lesser Frigatebirds.

For Great Frigatebirds, I have argued that female choice has encouraged the evolution of the male display cluster (Reville 1988), aided by the bias in effective sex ratio which has intensified intermale competition (Halliday 1978). The advantage to female Great Frigatebirds in choosing males in clusters appears to be a reduced likelihood of the site being usurped (Reville 1988). In contrast, there seems no obvious advantage for Aldabran Lesser Frigatebirds through nesting regularly spaced in large groups, particularly in relation to site usurpation. Site usurpation was a significant cause of breeding failure, as indicated by the observed killing of chicks, the inverse correlation between density and breeding success in the absence of other predators, and the loss of nearby nests when one nest was usurped. Regular spacing of nests maximizes the distance between neighbors within a habitat patch, which could help prevent being disturbed by advertising males attracted to a nearby usurpation. This might be true early in the season when nests were well-spaced but is of doubtful advantage later when the mean distance between nests was only 60–70 cm.

It is possible that regular spacing of nests within large nesting groups is a spatial pattern which evolved under conditions where site usurpation by unpaired males was less important. Even on Aldabra the importance of site usurpation varied as a cause of breeding failure. In 1976, when chick mortality due to usurpation was high, there was a significant inverse correlation between nest density and breeding success. In 1977, when breeding failure was largely due to poor hatching success late in the season, the correlation was not significant. In the latter case, site usurpation was probably not implicated in the failures since new males had not occupied the failed nests. For Lesser Frigatebirds, as for the Glacous-winged Gull (*Larus glaucescens*) (Hunt and Hunt 1976), adaptive differences in spatial pattern may be realized only when other environmental factors, such as food supply, allow.

On Raine Island, I saw no site usurpation during two weeks of observation of 900 nests. Here, as in many Pacific Ocean populations (Sibley and Clapp 1967), the Lesser Frigatebirds nested on the ground. Nesting in large groups with each group consisting of many regularly spaced nests is typical of many ground nesting birds (Buckley and Buckley 1980) and can have numerous antipredator benefits (Wittenberger and Hunt 1985). Avoiding a peripheral location is the most likely factor relevant to Lesser Frigatebirds exposed to predation by other species, especially ground predators. Lesser Frigatebirds sit closely on the nest and do not "mob" ground predators. They do, however, lunge at animals which come within range of the outstretched bill. On Raine Island, potential egg predators such as the Banded Landrail (*Rallus philippensis*) were always attacked when they ventured amongst the closely packed nests.

Amongst the other species of frigatebirds, the Ascension Island Frigatebird (*F. aquila*) resembles the Lesser Frigatebird in that nest density is inversely correlated with breeding success, which is influenced by site usurpation and interference from neighbors (Stonehouse and Stonehouse 1963). Anecdotal descriptions of spacing in the Magnificent Frigatebird and the Christmas Frigatebird (*F. andrewsi*) suggest that nests are clustered as in Great Frigatebirds (Diamond 1972, 1973; Nelson 1972), but this could be caused by habitat restrictions such as nesting in the canopy of a single tree. Similarly, Lesser Frigatebirds were thought to nest in clusters (Diamond 1975).

Assumptions of similarity between different species of frigatebird or even between different populations of the same species are unwarranted in the absence of quantitative descriptions of spatial pattern, descriptions of site selection behavior and the related consequences for breeding success. The recent discovery that populations of *F. minor* in the Central Pacific differ from each other in sexual size dimorphism (Schreiber and Schreiber 1988) emphasizes that each breeding station can represent a genetically and ecologically separate unit.

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