

EFFECTS OF SPACING AND SYNCHRONY ON BREEDING SUCCESS IN THE GREAT FRIGATEBIRD (*FREGATA MINOR*)

BARRY J. REVILLE

Department of Zoology, University of Aberdeen, Aberdeen, Scotland

ABSTRACT.—Nearest-neighbor methods of spatial analysis confirmed that colonies of Great Frigatebirds (*Fregata minor*) on Aldabra Atoll were subdivided into clusters of up to 22 nests/cluster. Each cluster arose from a nucleus of advertising, unpaired males. Within a cluster, sites were spaced regularly at intervals of 0.5–1 m. Clusters differed in degree of synchrony of female settlement. Hatching success correlated positively with synchrony of female settlement. The interval between female settlement and laying date decreased as the season progressed. Hatching or fledging success was not significantly affected by date of laying. Breeding success (fledglings/egg) exceeded 50% in both seasons.

Great Frigatebird males formed display clusters one month before females settled, competed for display sites within clusters, and preferred clusters that contained eight or more displaying males. Females settled more readily by males in the larger colony and, early in the season, preferred clusters that already contained nests.

I suggest that usurpation of nests by unpaired males was a principal cause of nesting failure, and that synchronous female settlement within a cluster made the cluster less attractive to prospecting males than one that contained mostly advertising males. Selective mate choice by females appears to be the principal agent inducing spatial clustering by males. *Received 4 May 1987, accepted 23 October 1987.*

LARGE colonies of nesting seabirds are frequently composed of distinct subgroups that can be demarcated by spatial analysis and by social interactions within each subgroup (Nelson 1970, 1980; Parsons 1976; Veen 1977; Gochfeld 1979). In Herring Gulls (*Larus argentatus*), for example, synchrony of egg laying increased with colony size up to about 200 pairs, but decreased in larger units (Burger 1979). Subgroups were also spatially distinct (Burger and Shisler 1980). Synchrony within, but not between, subgroups has now been reported for many species (references in Gochfeld 1980).

Nelson (1967, 1975) described colonies of Great Frigatebirds (*Fregata minor*) as subdivided into numerous distinct nest clusters. Each cluster consisted of 10–30 closely spaced nests and arose from a cluster of displaying males. As in most Pelecaniformes (van Tets 1965), the nest is built on the display site after the male has attracted a female.

Small clusters with high nest density should provide excellent opportunities for synchronized breeding activities. Nelson (1975: 122) proposed that synchronization occurs within clusters and is presumably adaptive. The nature of the adaptiveness, however, has not been determined. Both Nelson (1975, 1985) and de Vries

(1984) commented on the apparent paradox of nesting in dense colonies when conspecifics are the chief predators. In the Galápagos unpaired males seeking a display site usurped nesting pairs and destroyed 75% of eggs and chicks (Nelson 1975). Because predation frequently has been of fundamental importance in shaping the spatial pattern of colonial species (Burger 1982, Wittenberger and Hunt 1985), I suspected that the advantage of greater synchrony would be to minimize conspecific predation.

I attempted to confirm that Great Frigatebird colonies were composed of distinct subgroups of up to 30 nests, that subgroups differed in synchrony of breeding activities, and that differences in synchrony were associated with differences in breeding success. I propose a mechanism that links spatial pattern and synchrony with breeding success through minimal conspecific predation.

STUDY AREA AND METHODS

The birds studied nested on Aldabra Atoll, Seychelles. Aldabra (9°24'S, 46°20'E) is an elevated, coralline limestone atoll ca. 420 km northwest of Madagascar (see Reville 1983: fig. 1). Mangroves fringe the lagoon and many lagoon islets (Macnae 1971). Most of the land mass is covered with dense thicket

dominated by *Pemphis acidula*, a broad-leaved microphyllous, evergreen sclerophyll (Fosberg 1971). Great Frigatebirds nested only in mangrove, principally *Rhizophora mucronata* (44% of cases) and *Bruguiera gymnorhiza* (22%). Nesting colonies were confined to three locations along the southern shore of Ile Malabar. The majority of nests (ca. 80%) were built on west- to north-facing shores, presumably to obtain shelter from the prevailing southeast tradewinds and to assist landing (Diamond 1975). Nests were placed on, rather than under or within, the canopy.

The study lasted from January 1976 to January 1978. Observations (560 h) from a permanent blind were initiated at 8-day intervals, and each stint lasted up to 4 days. Results are for birds never handled or closely approached because Aldabran frigatebirds were very sensitive to human disturbance. This limited accurate estimation of laying dates, so settlement dates of laying females were used to calculate measures of synchrony. The settlement date is the day a female first landed by the advertising male with which she eventually bonded. Detailed descriptions of the study sites and of the observation schedule were given by Reville (1983).

Terminology.—I applied the term "colony" to aggregations of nests found in widely separate localities on the atoll, i.e. Camp Frigate, Middle Camp, and Gionnet. Within colonies the distance between adjacent groups of nests rarely exceeded 100 m, whereas several kilometers separated colonies. Decisions on colony boundaries are typically arbitrary (Nelson 1980). My usage agrees with previous Aldabran studies (Diamond 1975) and does not conflict with other authors who have stressed social integration (Coulson and Dixon 1979) or centralized location (Wittenberger and Hunt 1985). Birds entering or leaving the colony were exposed to the sight and sound of hundreds of neighbors. There was no evidence of frequent visits between colonies.

The term "habitat patch" describes a patch of continuous vegetation in which nests were built. "Cluster" describes an aggregation of active sites within a habitat patch as established by the computer program CLUSTER ANALYSIS OF CASES (see below). The term "active site" was applied to sites occupied by any bird of adult plumage involved in breeding activities initiated in the current season (including advertising males, courting pairs, and sitting birds) or by a nestling hatched in the current season. Standard deviation was adopted as the measure of synchrony. To calculate values for synchrony of settlement and egg laying, only pairs known to have been the first tenants of a nest were considered.

Mapping of sites.—To obtain detailed information on site spacing within a habitat patch, I chose an islet, MC:RM at Middle Camp, with continuous mangrove and open to scrutiny from a permanent blind. The area of habitat appeared adequate for multiple clusters of a size anticipated from the literature. From

photographs of the frontal view of MC:RM taken with an 85-mm lens at 25 m, I made a map of scale ca. 1:50 by tracing the outline and internal relief of vegetation. On each subsequent visit I noted on the map the position of each bird, its species, sex, age, and breeding status. When there was no longer a risk of my intrusion causing chick loss, I measured the length, height, and depth of the habitat patch and photographed the vegetation profile.

Because the initial map was created from frontal-view photographs, it indicated only the vertical distance between nests of different depth. This did not account for the horizontal component caused by the front-to-rear curvature of the vegetation canopy (lateral curvature of the habitat patch was minimal). The actual distance between sites was obtained by measuring the distance between them on the vegetation profile rather than the difference in their heights. Similarly, the surface area of vegetation was expressed as a flat surface with dimensions: length of vegetation profile \times length of habitat patch. A surface area of 217.5 m² was estimated for MC:RM.

A 1-m² grid was then superimposed on the new map and the position of each active site specified by a 6-figure Cartesian coordinate. I encoded these coordinates onto computer file (Honeywell 66, Univ. Aberdeen Computing Center) and used the program "CLUSTER ANALYSIS OF CASES, BMDP-2M" (Engelmann 1977; prepared by Univ. Kansas Computation Center) to calculate the distance between all possible pairs of sites. Simple Euclidean distances were used as the measure of separation between each pair of sites. Distances among 15 advertising male Great Frigatebirds in MC:RM measured from the map for 5 August 1977 were compared with visual estimates (bird lengths) made on that day. No significant differences was detectable ($df = 10$, $T = 38.5$, $P > 0.05$) with the Wilcoxon matched-pairs signed-ranks test (Siegel 1956).

Detecting nonrandomness.—I used the R index (Clark and Evans 1954) to test for significant nonrandomness ($R > 1$ indicates regularity of spacing, $R < 1$ indicates clumping, r_n = mean nearest-neighbor distance) and Thompson's test to the n th nearest neighbor (Thompson 1956) to identify average cluster size. In both analyses the nest sites were treated as points rather than circles. Nest diameter approached half the expected mean nearest-neighbor distance for points (Simberloff 1979); however, the slope of the canopy allowed access without disturbing neighbors.

Identifying clusters.—I used the CLUSTER ANALYSIS OF CASES program to produce clusters of neighboring sites in MC:RM for dates on which there was statistical evidence of contagion. The cluster analysis cannot tell whether the contagion was due to, for example, 10 small or 5 larger clusters. Therefore, average cluster size was determined statistically by assuming that the level of nearest neighbor at which contagion was last detected by Thompson's test cor-

TABLE 1. Nearest-neighbor analyses of Great Frigatebird site distribution in habitat patch MC:RM (R index).

Date	No. of sites	r_s (cm)	R^a	P
All active sites				
23 Oct. 1976	100	60	0.82	<0.001
5 Aug. 1977	72	64	0.74	<0.0002
24 Oct. 1977	110	56	0.79	<0.0002
10 Dec. 1977	68	76	0.85	<0.02
Advertising males only				
5 Aug. 1977	57	78	0.8	<0.001
24 Oct. 1977	19	132	0.78	<0.08
Nests only				
5 Aug. 1977	11	138	0.62	<0.01
24 Oct. 1977	84	63	0.79	<0.0002

^a $R < 1$ indicates clumping of sites.

responded to the average cluster size in the distribution. The cluster-analysis pattern that produced this same average cluster size was then taken to define cluster boundaries.

The complete sequence of steps involved was: (1) select habitat patch large enough to allow multiple clusters; (2) prepare two-dimensional map of sites in the three-dimensional field situation; (3) test for statistical evidence of clumping using R index; (4) produce a variety of possible cluster configurations using the cluster-analysis program; and (5) select correct cluster configuration by comparing mean cluster size with that obtained from Thompson's test.

RESULTS

Nature of spatial pattern.—Great Frigatebirds in habitat patch MC:RM exhibited a consistent and significant tendency to cluster (Table 1). This was so for advertising males before many females had settled (e.g. 5 August 1977), for nest owners at low (e.g. 5 August 1977) and high (e.g. 24 October 1977) nest densities, and for all active sites considered together.

Thompson's test suggested that the average number of occupied sites per cluster differed between seasons and increased as the season progressed, e.g. 14–15 sites (23 October 1976, 5 August 1977) and 22–23 sites (24 October 1977). Because the number of active sites present in MC:RM on 23 October 1976 (100 sites) did not differ significantly from that on 24 October 1977 (110 sites; $\chi^2 = 0.48$, $df = 1$, $P > 0.25$), the distribution of structurally suitable sites in MC:RM did not dictate average cluster size (Fig. 1).

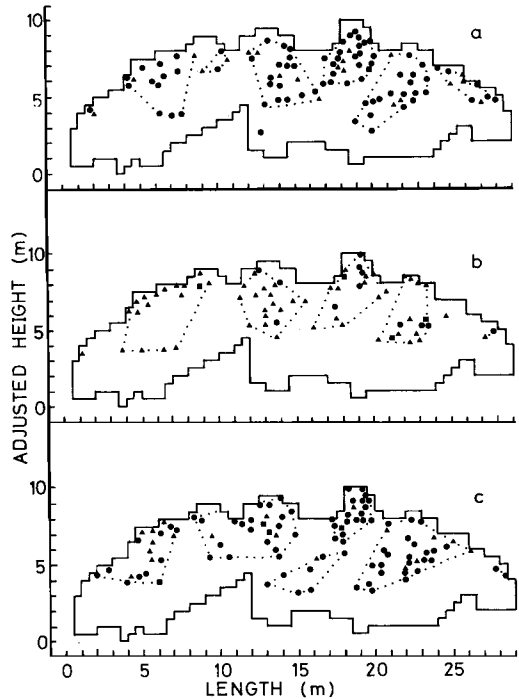


Fig. 1. Distribution of active sites within habitat patch MC:RM with cluster boundaries. (a) 23 October 1976, (b) 5 August 1977, (c) 24 October 1977. Δ = displaying male, \blacksquare = courting pair, \bullet = nest.

I examined the arrangement of sites within a cluster for two clusters of different date and composition. The first contained 16 advertising males and 3 nests, the second 3 advertising males, 2 courting pairs, and 19 nests. Areas (14.1 m² and 18.3 m², respectively) were estimated by the convex-polygon method (Flowerdew 1976). In each case sites were regularly spaced within the cluster ($r_s = 58$ cm, $R = 1.37$, $P < 0.01$; $r_s = 59$ cm, $R = 1.35$, $P < 0.001$).

Temporal patterns.—In 1976 clusters differed significantly in the variance of settlement dates of females that eventually laid eggs (Bartlett's homogeneity of variance, $B_c = 56.96$, $df = 6$, $P < 0.01$). In 1977 differences approached but did not reach significance ($B_c = 9.52$, $df = 5$, $P < 0.1$; Table 2). In 1976 the time between female settlement and egg laying declined from 26 days in early August to 5 days in mid-October ($n = 51$, Spearman $r_s = -0.603$, $P < 0.001$). In 1977 the interval declined from 20 to 5 days between early August and October ($n = 36$, $r_s = -0.508$, $P < 0.002$). The 5 females that settled after 19 October reverted to longer intervals, i.e. 17–30

TABLE 2. Settlement dates of female Great Frigatebirds in clusters within habitat patch MC:RM.

Cluster	No. of females	Mean date	SD (days)
1976			
1	2	14 Aug.	10
2	10	27 Sept.	36
3	7	12 Sept.	38
4	19	13 Sept.	31
5	17	6 Sept.	33
6	22	2 Sept.	25
7	5	11 Sept.	48
MC:RM	82	10 Sept.	32
1977			
1	10	4 Sept.	29
2	19	28 Aug.	21
3	8	30 Sept.	23
4	20	31 Aug.	33
5	21	3 Sept.	23
6	2	16 Aug.	26
MC:RM	80	3 Sept.	27

days. Despite the potential for postsettlement synchronization, synchrony of subsequent breeding events was highly correlated with synchrony of settlement, e.g. SD of hatching dates compared with SD of settlement dates among clusters in 1976 ($n = 7, r_s = 0.929, P < 0.01$). Clusters with higher synchrony of settlement of first-tenant females had significantly higher hatching success (1976: $n = 7, r_s = -0.893, P = 0.01$; 1977: $n = 6, r_s = -0.841, P < 0.05$; Fig. 2).

There was no significant correlation among clusters between mean date of female settlement and any index of breeding success. Hatching or fledging success was not significantly affected by laying date, although the few females that settled after mid-October had lower breeding success (1976: 33% vs. 58%; 1977: 33% vs. 59%).

Nest usurpation.—Relatively high breeding success in 1976 and 1977 (Table 3) reduced the opportunity for viewing nesting failure, and I did not observe the moment of loss of a Great Frigatebird nest. The possibility of nest usurpation by males is suggested by the following observations. First, unpaired male Great Frigatebirds frequently attempted to obtain females by displacing the males of courting Great Frigatebird pairs. They also forced incubating Lesser Frigatebirds (*Fregata ariel*) off nests; hence, some usurpation occurred. Second, more than 80% of nests that failed in the first half of the

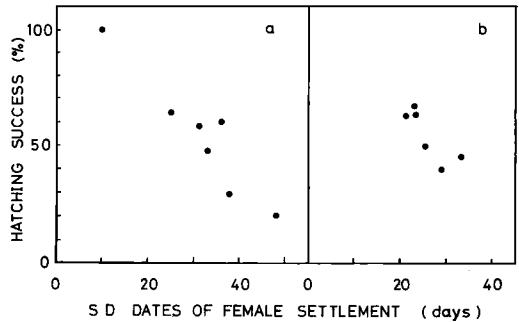


Fig. 2. Hatching success as a function of synchrony (SD) of female settlement dates in clusters in MC:RM. (a) 1976: $r_s = -0.893, P = 0.01$; (b) 1977: $r_s = -0.841, P < 0.05$.

laying season contained a new displaying male or courting pair when first seen after failure, indicating that potential usurpers were available. Third, during an apparent food shortage from mid-August to mid-September 1976, when many unpaired males temporarily deserted the nesting colonies, no incubating pairs lost their sites despite exceptionally long incubation stints (13.5 days cf. 4.3–6.3 days otherwise). Further, in both years there was a steep drop from early October in numbers of unpaired males attending the colonies. The first chicks began hatching about mid-October. Such timing of hatching would be adaptive if young chicks were, as in other populations, targets for site usurpation by unpaired males. This would not be a stratagem against predation of chicks for food because nesting males still attended the colonies.

If prospecting males were attracted to clusters of displaying males rather than to clusters containing mostly nests, then synchronous female settlement would rapidly change the character of a display cluster and discourage invasion by further prospecting males. Clusters with greater synchrony of female settlement would suffer

TABLE 3. Components of breeding success of Great Frigatebirds in habitat patch MC:RM.

	1976	1977*
Eggs	111	100
Hatched	60	55
Fledged	57	*
Chicks/egg (%)	54	55
Fledglings/chick (%)	95	*
Fledglings/egg (%)	51	*

* * = all chicks alive when observations were terminated.

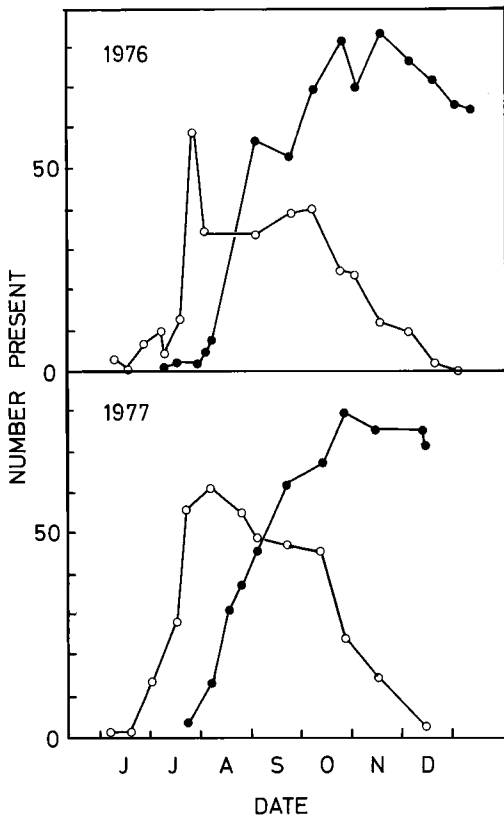


Fig. 3. Attendance of advertising males (O) at and recruitment of nest (●) to MC:RM.

less usurpation. The following factors suggest that males were attracted by other displaying males. First, clusters were established by interactions among advertising males more than a month before females began settling (Fig. 3). Second, there was considerable competition among males for sites within these clusters even when alternative sites, later to receive nests, were unoccupied. Supplanting, threatening, and fighting among advertising males were common, in contrast to the situation in the Galápagos where such events happened only after the acquisition of a female (Nelson 1967, 1975). Third, the numbers of advertising males at larger display clusters were less variable than at smaller clusters, suggesting that clusters where more males displayed were preferred ($n = 14$, $r_s = -0.937$, $P < 0.01$). Variability changed little once cluster size exceeded 8 displaying males (Fig. 4). Larger clusters did not facilitate the display of individual males because the amount of gular presentation per male was independent

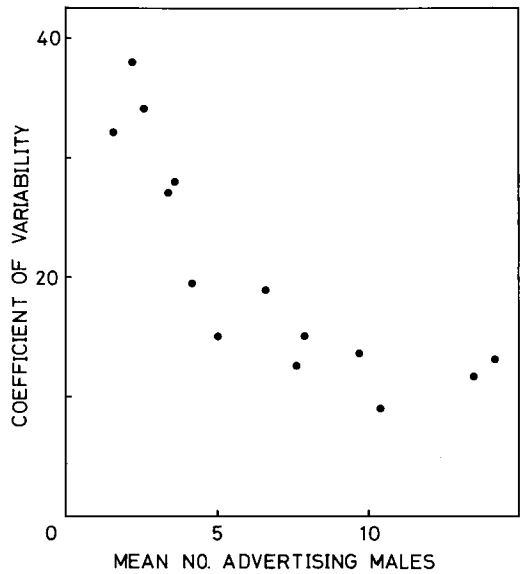


Fig. 4. Relative variability in numbers of advertising males attending clusters that contained different numbers of males. Mean values obtained from counts each 5 min over 4 h.

of cluster size over a wide range of sizes (2-14 males/cluster, 14 clusters, $r_s = 0.23$).

Females appeared to discriminate in their choice of male or cluster. They consistently preferred the larger of the two colonies. At the larger colony (Middle Camp) in 1976, 54 days of advertising were invested $\text{male}^{-1} \cdot \text{nest}^{-1}$ recruited, compared with 78 days per male at smaller Camp Frigate (calculated by measuring the area between the curves for number of males and number of nests vs. date, then dividing by the number of nests recruited). In 1977 the figures were 55 and 91 days, respectively. Further, females did not begin settling and pair bonding until many males were advertising in clusters (Fig. 3). Finally, when prospecting, the female did not hover over a particular male, but swept low over a series of clusters, setting off a wave of display in her wake. In 0 of 5 intervals during the nesting season did the recruitment of nests correlate significantly with the distribution of displaying males among clusters (7 clusters, maximum $r_s = 0.56$). In the early nesting season the recruitment of new nests was significantly correlated with the distribution of existing nests ($n = 7$, $r_s = 0.79$, $P = 0.05$). This suggests that females settling early in the season preferred clusters already containing nests. The mean in-

terval between recruitment of nests declined linearly from 26 days for a 2-nest cluster to 4 days for clusters of more than 11 nests ($n = 7$, $r_s = -0.954$, $P < 0.01$). Females probably visited several males in different clusters before forming a stable pair for the season. Copulation of one male with several females was confirmed by paint-marking, but the effectiveness of the copulations could not be determined. In 11% (10/92) of hatchings the female settled by her eventual mate less than 5 days before the egg was laid.

DISCUSSION

The spacing pattern of Great Frigatebirds on Aldabra resembled that on Tower Island in the Galápagos (Nelson 1967, 1975). The similarity between two distant populations in different habitats suggests that subdivision of a colony in discrete clusters is typical of the species (*sensu* Veen 1977). Differences between the populations included lower breeding success, more frequent site usurpation by conspecific males, and greater synchronization of breeding activities on Tower Island. Identifying the causes of these differences helps clarify the origin of the clustering phenomenon.

Frigatebirds are not the only group that illustrates intraspecific interference (e.g. gulls: Parsons 1971, 1976; Ewald et al. 1980; Schoen and Morris 1984; corvids: Yom-Tov 1975; reviewed by Wittenberger and Hunt 1985); however, the extent of sabotage of nesting attempts by unpaired males has been considered remarkable (e.g. Bent 1922). Recently, de Vries (1984), in an argument reminiscent of group selection, suggested that this behavior contributes to population regulation. Nelson (1985) emphasized the primary role of individual selection and pointed out that "by disrupting breeding pairs, non-breeding males increase the supply of available and experienced females and thereby their own chances of acquiring such a mate."

The argument can be extended to establish when it is advantageous for an unpaired male to attempt usurping the site of a nesting pair. Clearly, there must be some chance for the usurper to acquire a female, and there must be sufficient time remaining in the laying season to initiate a successful breeding attempt. The cost to the usurper is relatively small. There is a risk of physical injury, but this can be minimized

by breaking off the attack if the resident, who cannot move from the nest, resists strongly. In addition, the usurper acquires a ready-built nest platform, an important energy consideration because nest material typically is gathered by the male. During poor conditions the usurper is likely to be in a better nutritional state than a nesting bird because he is not prevented from feeding by long incubation stints. Also, resistance from the resident bird is less probable if it is already stressed by shortage of food. Conversely, good feeding conditions will promote stronger resistance and discourage attempts at usurpation. Consistently poor feeding conditions will also discourage usurpation because the breeding attempt of the usurper is also likely to fail. Thus, usurpation is likely to be most frequent in populations experiencing unpredictable feeding conditions. Conditions may be poor at the time of usurpation, but the usurper gambles, at little cost, that an improvement may soon occur.

On Tower Island incubation stints averaged 10 days and extended to 18 days (Nelson 1975: 153). Nelson (1967) frequently described food availability as "unpredictable." In contrast, incubation stints on Aldabra usually averaged 4.3-6.3 days and extended to 13.5 days in one exceptional period. This difference may account for the higher incidence of site usurpation on Tower Island. Because synchrony of female settlement within the cluster discourages the attraction of potential usurpers to the cluster, it will be most apparent in populations where environmental conditions favor usurpation.

The aggregation of advertising Great Frigatebird males in clusters resembles the spatial pattern of males in many lekking species (review by Bradbury and Gibson 1983). Further parallels are the conspicuous communal advertisement by males, competition between males for positions in display clusters (Diamond 1975; *contra* Nelson 1967, 1975), and development of male epigamic structures (e.g. inflated gular sac) and behavior (e.g. gular presentation; Nelson 1975) used both in male-male threats and in advertisement to females.

Selective mate choice by the females, as in some lekking species (Davies 1978, Halliday 1983), may have forced the males to compete for arbitrary display positions, that is, sites within clusters. (In Great Frigatebirds the display site must also have suitable physical characteristics for supporting the nest.) Because fe-

male Great Frigatebirds visit a number of clusters and males before pair bonding, characteristics of the males probably are assessed as well as composition of the cluster. Female Great Frigatebirds on Aldabra were well placed to exercise such discrimination. In many species there is an advantage in mating early in the season; otherwise, the best mates, the best sites, or the best seasonal conditions may be missed (Perrins 1970, Hunt and Hunt 1976, Hunt 1980). These constraints did not apply to female Great Frigatebirds on Aldabra. There was no significant difference in breeding success for birds laying at different stages of the season, and the quality of nest sites was not physically limited but depended on a repetitive combination of social factors. Most importantly, there was a surplus of males available each season (Reville 1983), so females could delay settlement yet be certain of finding a mate. In species exhibiting a surplus of males, sexual selection is likely to be strong (Halliday 1978).

I suggest that clustering is likely where it can be enforced by female selectivity, as when more males than females are available each laying season. A surplus of males at courtship has been demonstrated only for the Great Frigatebird (Diamond 1975, Reville 1983) and the Magnificent Frigatebird (*F. magnificens*; Diamond 1972). In the latter, females outnumber males overall, but males breed annually and females biennially (Diamond 1972, 1973; Coello et al. 1977; Trivelpiece and Ferraris 1987); hence, fewer females than males are available for courtship in mid-September (Diamond 1972). In *F. ariel* on Aldabra there seem to be equal numbers of males and females available (Diamond 1975, Reville 1983). Insufficient information on sex ratio is available for *F. aquila* or *F. andrewsi*. Whenever females can copulate with a number of males before deciding on an eventual mate, male investment in the chick is likely to be lower than that of the female (Trivers 1972, Burger 1981). Where feeding conditions permit the female to raise the chick alone, it is to the male's advantage to abandon rearing and attempt to breed annually. Consequently, feeding conditions will affect the nature of the spatial pattern through the ratio of males and females available for courtship as well as through the likelihood of site usurpation. Differences in spatial pattern may be expected, not only between different frigatebird species but also between conspecific

populations in different environmental conditions.

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