FRIGATEBIRDS, AGGRESSION AND THE COLONIAL HABIT

by

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Since I first studied Fregata minor on Tower Island (Genovesa) in 1964, establishing that the breeding cycle took considerably longer than a year and suggesting that successful breeding could occur only once in two years (Nelson 1968, 1976), substantial work has been conducted in other parts of the world, particularly the Carribean (Diamond 1975) and on Aldabra in the Seychelles (Reville 1980). To this reason must be added the results of several years' further work in the Galapagos by de Vries and his helpers. This article addresses some of their findings and in particular the interpretation, reported by de Vries (1984). Except where stated otherwise, 'frigate' refers to F. minor, the Great Frigatebird.

One of the functions of aggressive behaviour is to ensure that the breeding unit, usually a pair, has an adequate territory. It may therefore seem anomalous that a species should be both territorial and colonial, spaced-out and concentrated into (often large) breeding aggregations. For seabirds, however, the smallness of the territory implied by their colonial habit is readily understandable since their territory is merely a land-base, a patch on which to establish a pair-bond and then to breed. It need furnish only a meeting place and a site for egg(s) and young. Nevertheless, some seabird species compete extremely strenuously even for such a small patch, implying by the efforts and risks thus involved that adequate sites are to some extent limited. It is often (though not always) plain to see that there are plenty of physically adequate sites and that the competition relates to less obvious features. At this point evidence becomes extremely thin and each species must be assessed within its own particular context. To ascribe the advantages of colonial nesting to social factors merely invites the question: what sort of social factors?

Because of their unusual (biennial) breeding cycle frigates complicate this particular question even more than most seabirds. To begin with, they are highly unusual in that they are in fact notably un-aggressive in defence of their territory. Most seabirds begin to defend a particular site before they build a nest and lay their egg(s). Frigatebirds do not. On the contrary, the males gather into close-contact clusters in which they display to over-flying females, but they do not vigorously defend their display perch. They do not fight in defence of it nor do they possess an aggressively-motivated, site-ownership (territorial) display. Indeed, it would be maladaptive to do so, since the perch is often transitory; it may be abandoned if the male is unsuccessful in attracting a female, in which case he moves elsewhere. As I will describe, this remarkable lack of territorial aggression has important correlates later in the breeding cycle. Once the male has paired, which he does on his display site where he is ‘chosen’ by a female (who thus acquires site and mate in a single response) he does defend that spot, which will shortly hold the nest. He lunges, snaps at and briefly grapples with potential intruders but, even now, he has no ritualised territorial display.

The frigate’s unusual territorial system may be discussed in terms of its causes and consequences. The causes seem clear: at least two of the major advantages enjoyed by highly territorial seabirds are denied to the frigate because the habit of moving his display site precludes (i) above, and this display habit, together with the biennial cycle, precludes (ii). Biennial breeding means that there are two breeding populations (not necessarily or even likely to be halves), one laying, let us say, in years A, C, E, etc. and the other in B. D. F., etc. Thus there can be no guarantee that the site which a particular male used in year A will not be in use, in year C, by another pair whose dependent offspring (egg laid year B) will still be in possession of it. Further, if such a male were to insist on re-occupying his former site he would necessarily forfeit his habit of joining any display group that happened to be elsewhere. And group-display is obviously an important characteristic. So, for the frigate, a semi-permanent territory is simply not an available option and the territorial behaviour which would support it is not necessary. It is important to have de Vries’ concrete evidence from marked individuals, that, as I predicted, frigates do not in fact return to the same site or the same mate in successive cycles.

The biennial cycle which affects so much frigate behaviour is the result of the slow growth of the chick and its prolonged dependence which in turn stems from the extremely demanding circumstances of the frigate’s foraging and feeding mode in the context of the impoverished tropical oceans which it inhabits.
Top: Male Great Frigate-bird displaying; orienting to female flying over, sac mainly deflated.
Bottom: Great Frigate-bird. Male with throat sac inflated, and female.

Photos by J.B. Nelson
One correlate of this notable absence of territorial defence seems to be that interference by conspecific males is extremely common. With the dramatic consequences that I described from my 1964 observations and which others have confirmed. Eggs and young are tossed out of the nest or (in the case of some young) eaten, carried away or simply mauled on the nest. This can happen even if, as is normally the case in pairs with an egg or very small chick, one parent is on or near the nest (incidentally, we still lack evidence that frigate colonies which are completely undisturbed by humans suffer in this way, although it seems likely that they will do so). The advantages to the perpetrators of such behaviour (excluding those which eat the young, an act which, incidentally, is feeding rather than aggressive behaviour) remain totally obscure. It is quite erroneous to use a "preservation of the species" argument, as for instance that such behaviour reduces breeding success and thus regulates the population, since natural selection cannot operate in this way but only through individual or kin-selection (see, for example, Dawkins 1978). Why, then, do they do it? I do not know, but one may speculate that there may be social advantages, such as 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 key to understanding may be to establish the identity and status of the disrupting males.

Clearly, aggressive behaviour in defence of territory is a cost/benefit equation and although the costs of the frigate's system may seem high, either they are bearable (otherwise frigates would not have survived) or the populations which have been studied are atypical, which seems unlikely. But what are the benefits of the colonial habit which, in conjunction with the poor territorial defence, makes interference by conspecifics so easy? There are several possibilities.

(i) Communal display facilitates pair-formation. It is energetically extremely costly for the male to remain on land, displaying. Reduction of this period would confer worthwhile advantage.

(ii) It may be advantageous for a female to be able to choose a mate from a group of displaying males. Female choice evidently is exercised, though on what grounds we have no idea.

(iii) The enhanced synchronisation of egg-laying which results from communal nesting may make the use of temporarily abundant food (as often happens in the tropics) more effective as a proximate timer of laying. That is, more birds are enabled to take advantage of a temporary flush to complete the early and costly stages of breeding. Another potential benefit of synchronisation is that it reduces the period during which interference by conspecifics can occur. Reville (1980) has shown that on Aldabra, where both F. minor and F. arif breed, the former is more synchronised and has greater success than the latter. Yet, of course, colonial breeding itself makes conspecific interference easier — again a cost/benefit equation that applies to both species.

The control of the size of the frigate population is a matter of immense interest. Is it the case that factors external to the frigate, such as food shortages, and inescapable social costs in the cost/benefit equations (such as the one discussed above in connection with territorial aggression) keep productivity low? Or can one plausibly suggest that the frigates themselves "keep" productivity low, implying an element of choice? I adhere firmly to the first of these and do not accept that the second is a viable alternative. In the seabird species that I have studied, and in all detailed work of which I am aware, the evidence supports the contention that each species rears as many young as it can, within the constraints imposed by factors such as the need to avoid damaging stress on adults. In the frigate's case, environmental factors can cause heavy loss of eggs and young and this is compounded by losses due to conspecific interference. Certainly we need to understand the nature of that interference, but I see no justification for interpreting it as a mechanism of population control. The low productivity is a fact and it is the nature of the factors that keep it low which we must investigate. For example, the evidence given by de Vries (1984), even if inconclusive, that frigates may wait three or four years after breeding before attempting another cycle accords well with other evidence that breeding is an extremely demanding process. Such an interval may be necessary to avoid damaging stress on the highly non-expendable adults. It is interesting to note that Abbott's booby (Sula abbotti) which, like the frigate, is one of the very few biennially-breeding tropical seabirds, also takes 'rest' years (Nelson & Powell, in press). There is no need to postulate that these aspects of breeding are mechanisms for reducing recruitment, and every justification for supposing that they have evolved because they maximise lifetime productivity.

In sum: frigates breed in groups (whether one calls such a group a 'colony' or the whole aggregation of groups a 'colony'); they are rarely if ever forced to do so by physical shortage of sites. As a consequence of their particular social system, including biennial breeding, which system itself derives from slow breeding due to ecological factors, frigates are relatively un-aggressive and un-territorial. This exacerbates the
effect of intra-specific interference by non-breeding males, a phenomenon which is not aggressive in the usual 'defence of territory' sense but is a special behaviour whose function we do not understand. Despite this cost, colonial breeding presumably confers important social benefits, some of which I have suggested. Apart from this, all aspects of its breeding biology may plausibly be interpreted as mechanisms which maximise lifetime productivity of individuals, even though this is unavoidably low. However, the frigate has no important enemies except man, it is probably extremely long-lived, and so has become reasonably successful (numerous and widespread).

REFERENCES