CONTRASTS IN BREEDING STRATEGIES BETWEEN SOME TROPICAL AND TEMPERATE MARINE PELECANIFORMES

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ABSTRACT.—The climatic and feeding conditions to which marine pelecaniforms are subject largely determine the nature of each species' breeding strategy. An individuals lifetime strategy 'should' (presumably) be to produce the greatest number of fit young at the least cost. To achieve this a complex set of breeding adaptations must evolve such that everything the individual does enters the equation between the energetic cost and the net result of the activity. Thus viewed, we may investigate the nature of the differences in breeding strategy between temperate and tropical pelecaniforms. These include deferred breeding, frequency and timing of breeding, size of egg, clutch and brood, the detailed composition of the breeding cycle, the nature of the attachment to breeding area, breeding site and partner and the size and spatial and social characteristics of the breeding group. Few of these relate exclusively to temperateness or tropicalness. Foraging mode (inshore and distant) is a critical determinant of breeding strategy and does not relate exclusively to latitude. But the adaptive advantage of flexibility in breeding under tropical feeding conditions and of predictability under temperate markedly affects breeding regimes and the behavior systems which subserve them.

The breeding strategies employed by an individual largely determine its life's productivity. In genetic terms, this includes its contribution to the breeding success of relatives, with whom it shares genes (Hamilton 1963, 1964, 1970). Breeding strategies must be subject to strong selection pressures. Therefore we may expect that environmental conditions, which so greatly affect foraging and feeding for example, will play an important if not decisive role in shaping breeding strategies. Tropical and temperate regions impose widely different foraging methods and selection pressures. This contribution aims to examine the nature of some of the adaptive responses in the marine pelecaniforms.

Breeding strategies are only part of a species' web of adaptations, evolving along with hormones, respiration, egg-physiology, the shape of wings, beaks and feet and the entire behavioral repertoire of the species. The Great Frigatebird *Fregata minor* of the Galapagos occasionally incubates for 17 days continuously, but, whilst this may be required in order that its partner may forage widely to locate food, the species' physiology must enable it to withstand long periods without food or water. Lack (1967) called this intricate web of relationships 'a new and exciting development in ornithology.' Since then, the complexity has been confirmed but the web has not been untangled.

In elucidating these relationships and the nature of breeding adaptations there can be no substitute for long, detailed and genealogical field studies. In addition, such studies provide the only means by which conflicting theories about evolutionary mechanisms can be resolved. For example, the argument about whether population control occurs by optimal productivity and density-dependent mortality or by intrinsically (socially) controlled recruitment (Lack 1954, Wynne-Edwards 1962) can be fully resolved only through reliable data about the phenomena involved. *Do* some seabirds take "rest" years? Precisely what is the phenomenology of deferred breeding? These and scores of similar questions need answering before interpretation is possible. And in the field of sociobiology, where interpretation tends to precede facts, it would be useful to know *which* individuals are most successful, and why. Life-history data can be used, also, to suggest why certain strategies, for example cooperative breeding and lekking, are common in landbirds but absent in seabirds.

Pelecaniforms are excellent subjects for such comparative ecological and behavioral research because they breed in colonies with great intraspecific variability, thus offering opportunities to study social aspects of breeding success; many species are widely distributed, offering opportunity to study the relationship between breeding and different climatic and environmental conditions; and many aspects of breeding biology vary widely within, and especially between, families. Additionally, once breeding haunts are reached, colonies are usually accessible, with readily quantifiable ecological and behavioral parameters.

In this limited survey of breeding strategies, I include all activities which are a necessary part of breeding, as against merely the maintenance of life in general. Breathing, defecating, preening, thermo-regulation, feeding, etc. are thus excluded, but activities preceding laying, which are often unjustifiably ignored, are here included. Every component of breeding costs time and energy, and thus may involve risks and has potential rewards. As mentioned above, the nature and availability of food is a major determinant of breeding strategy. Other factors, such as climate,

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predation and availability of nest sites can also be important but are usually of more local significance.

My objective is to bring out the nature of adaptive differences in breeding strategies of marine pelecaniforms by means of examples, with special reference to the role of tropical and temperate conditions. I have excluded most pelican species and the anhingas because their inland and fresh water feeding habits introduce complications and their omission does not affect my theme. At the end of each section I provide a brief conclusion, which facilitates cohesion between sections.

Breeding strategies involve: 1. Age at which breeding is first attempted. 2. Activities which precede the first breeding attempt. 3. Frequency of breeding. 4. Timing of breeding. 5. Size of egg, clutch and brood. 6. Composition of the breeding cycle (site-establishment, pair-formation, nest-building, incubation, care of young from hatching to fledging, postfledging care of young). 7. Nature of attachment to breeding area, breeding site and mate. 8. Size and spatial characteristics of the breeding group.

AGE OF FIRST BREEDING

For maximum productivity a seabird "should" breed as soon as it is fit and competent, in terms of hunting ability, local lore and social behavior. This rejects deferred breeding as an intrinsic regulator of recruitment, which is inconsistent with individual and kin selection, and because a simpler explanation exists. The difficulty lies in assessing 'full' fitness. We cannot yet assess physiological fitness to enable us to compare breeders, non-breeders and pre-breeders, and except by inference, we will never be able to assess "skill" and "lore." Nor would it be enough merely to demonstate that individuals of a given age *can* rear young, but that many do not attempt to do so. Some 5 or 6 years olds may be "fitter" than others.

Some phalacrocoracids and pelecanids can breed when two years old (e.g., Brown, Urban and Newman 1982) and none absolutely require more than three years before breeding. Yet it is thought that frigates do not breed before they are seven and may require up to eleven years (Diamond 1975a). In between, Red-billed Tropicbirds *Phaethon aethereus* breed when four or five (Harris 1969a), boobies between two and four and gannets between three and six (Nelson 1978). Within the sulidae, circumstantial evidence (Nelson and Powell, unpubl. data) suggests that the far-foraging Abbott's Booby *Sula abbotti* has the longest deferred breeding period. It also has the slowest growth. The other sulids with slow growth, notably the Red-footed Booby *Sula sula* but to some extent the Masked Booby *Sula dactylatra* also have longer deferred breeding periods and are more pelagic than their inshore congeners, notably the Blue-footed *Sula nebouxii* and Peruvian *Sula variegata* Boobies.

Long-deferred breeding does not correlate with size and weight, feeding mode, nesting habitat, colony size and density or social complexity. It does, however, correlate with foraging habit. With one exception, the Atlantic Gannet *Sula (s.) bassana,* all pelecaniforms which delay breeding until they are five years old or more have in common the habit of foraging far from the colony. This in turn means that tropical marine pelecaniforms tend to show longer deferred breeding periods than temperate ones. Pelagic feeders forage over ocean areas which are often vast and apparently impoverished. Within these areas they must find perhaps transiently productive zones, presumably using many subtle cues. Long experience may count for more, here, than in species which forage in restricted, often rich areas. The Atlantic Gannets' intense competition for a breeding site, unique within the order, may prevent younger individuals (especially males) from breeding (Nelson 1978). Sex differences in age of first breeding (females usually breeding before males) remain to be explained but may have to do with the latter's site-establishing role.

Conclusion

The length of the deferred breeding period correlates positively with the tendency of breeding adults to forage far from the colony and is usually, therefore, longer in tropical than in temperate marine pelecaniforms.

ACTIVITIES PRECEDING FIRST BREEDING ATTEMPT

CLUBS

In general clubs are gatherings of non-breeding (usually pre-breeding) individuals, including many in immature plumage. Sometimes they contain off-duty breeders. Usually club birds congregate near to, but separate from breeders. They are distinguishable from roosts and aggregations of "loafers" by the territorial and incipient nest building activities which occur there. At roosts and loafing areas the main activities are preening, bathing and sleeping and any agonistic behavior is merely to maintain individual distance. In no pelecaniform is it known that permanent pair bonds are first formed in the club, after which the pair transfers to a breeding site, though this is claimed for some gulls. A review of clubs in seabirds remains to be written.

Within the pelecaniforms they are reasonably well documented only in Atlantic Gannets, where they are highly conspicuous. In this species they may contain more than 2000 individuals, packed more densely but less regularly spaced than in the breeding colony to which they are adjacent. Club members perform the species full repertoire of agonistic and sexual behavior, including copulation. They land and depart frequently, with attendant risk of injury, and Gannet clubs cannot be dismissed as mere aggregations of resting birds. There is no special relationship between clubs and either tropical or temperate pelecaniforms. Two possible predisposing factors may be large colony size and complex social structure. The latter may include relatively permanent attachment to site and mate since clubs may facilitate, by practice, site-establishment and pair-forming behavior.

PROSPECTING, AND PRE-BREEDING OCCUPATION OF SITE

The establishment of a breeding site and pair proceed in steps which, though little known (see Hunt 1980, for a recent review of mate selection and mating systems in seabirds) are clearly very different in different pelecaniforms. Prospecting for the 'right' colony and segment within the colony is a preliminary step but because that activity is essentially part of site establishment and this links closely with pair-formation, the whole process is considered under those headings. Most pelecaniforms and indeed most seabirds attempt to breed in the first season in which they establish an adequate site. Only where the site is unusually important would it be worth spending a full season establishing it. This is known to happen only in the Atlantic Gannet. It would be practicable only where seasonally predictable food allows the owner to return predictably to re-occupy the site. In impoverished tropical areas in particular, the cost, in time taken from foraging, would be high. It may be that the Atlantic Gannets' combination of circumstances is unique.

CONCLUSION

No pelecaniform is known to form definitive pairs in "clubs." No tropical marine pelecaniform invests a season in occupying a definite nest site before breeding on it. At least one temperate sulid (the Atlantic Gannet) does so.

BREEDING FREQUENCY

SUCCESSFUL BREEDING

Although in seabirds an annual seasonal cycle is normal in temperate latitudes, many tropical seabirds, including pelecaniforms, have modified the length of their breeding cycles and there-fore their breeding frequency, to suit local conditions. Some tropical pelecaniforms breed more than once a year, thus increasing the number of cycles within their lifetime whilst others are compelled as a consequence of their particular feeding adaptations, to breed less than once a year. For almost all species, data from banded individuals and pairs are lacking. The Flightless Cormorant *Nannopterum harrisi* may attempt to breed several times within a calendar year (seven times within 24 months for one male and eight clutches within 36 months for a female, Harris 1979). In some areas Brown *Sula leucogaster* and Blue-footed boobies fit more than one breeding cycle into a calendar year (Nelson 1978). In several cormorants, for example Little Black, *Phalacrocorax sulcirostris,* Black-faced, *P. fuscescens,* Pied, *P. varius,* Little Pied, *P. melanoleucos,* Long-tailed, *P. africanus,* Bank, *P. neglectus,* and Cape, *P. capensis,* according to area, the population breeds either continuously or at two seasons of the year, though more than annual breeding has not been proved for identifiable pairs. The Common Cormorant *P. carbo* breeds more or less continuously in tropical Australia (Serventy, Serventy, and Warham 1971) but strictly annually and seasonally in Britain and western Europe (e.g., Cramp and Simmons 1977).

Six pelecaniforms (the five frigate species and Abbott's Booby) breed only once every two years, although the male Magnificent Frigatebird *Fregata magnificens* on Barbuda probably breeds more often by abandoning one cycle part-way through and beginning another with a new female (Diamond 1972). The same species can be an annual seasonal breeder in one area (Red-footed Boobies on Christmas Island, Indian Ocean), but breed less often than once a year and largely aseasonally in another (Red-footed Boobies on Tower Island, Galapagos) (Nelson 1969, 1978). However, no pelecaniform is known to breed successfully both more *and* less than once a year, in different localities.

Breeding frequency depends partly on the length of the cycle and this correlates chiefly with the time taken to rear offspring to independence, which is longer in pelagic than inshore feeders. Thus, the seven marine pelecaniform species (five frigates and two sulids) which breed less often than once a year are all pelagic feeders, usually tropical with scarce and/or unpredictable food and therefore with slow growing young.

Some frequent breeders with relatively short rearing periods are inshore feeders (cormorants, some populations of Blue-footed Boobies) or species with readily available and dependable food (gannets, Peruvian Boobies). The Brown Boobies of Ascension Island appear to be a special case (Simmons 1967) in that, although living

under extreme tropical, blue-water conditions, with unpredictable food shortages, most pairs occupy their breeding sites continuously. Pairs without eggs or chicks then lay whenever food becomes plentiful. Thus, although in extreme cases young are dependent for longer than those of almost any other sulid, in general this population breeds more frequently than any other sulid. Several tropical marine pelecaniforms, which are also pelagic feeders (tropicbirds, Masked Boobies and several populations of Red-footed Boobies) breed only approximately once a year, but as populations only very loosely seasonally. There apparently are no predictable advantages to strictly seasonal breeding.

The evidence uniformly suggests, as Lack (1954) predicted, that despite different strategies, each species rears as many young as it can feed. There is no positive evidence to the contrary. However contra Lack there is nothing to support the idea that the number of young reared is always density-dependently controlled. In fact, whilst density-dependence is difficult or impossible to prove, it can sometimes readily be demonstrated that the number of young reared, at least to independence, is NOT density dependently controlled. For example. both in tropical pelagic feeders such as frigates and Red-footed Boobies on the Galapagos, and in inshore feeders of more productive areas such as the Peruvian Boobies, Guanay Cormorants *Phalacrocorax bougainvillea* and Chilean Pelicans *Pelecanus (O.) thagus* of the Humboldt Current, the food shortages which occur are unequivocally *not* due to the size of the bird population. Oceanographic factors and not birds cause the temporary disappearance or shortage of food, which often suddenly reappears. The size of the bird population is supremely irrelevant either in causing the shortage or in coping with it.

FAILED BREEDING

The response to a failed breeding attempt is another aspect of breeding strategy. Options are: remain on site and replace the clutch or brood within the time required to develop new eggs (genuine replacement); abandon the attempt, disperse, perhaps molt and return again at the normal seasonal time if there is one; or lay again *before* this would otherwise have happened but later than genuine replacement would require.

The first option is adopted by most if not all temperate marine pelecaniforms. However, replacement clutches are useful only if young are not produced, or thrown on their own resources, at an impracticably hostile time and if the energy cost to the female can be readily met (or, if it cannot, stress is acceptable). In highly seasonal latitudes there is a cut-off point beyond which lost clutches or broods are not replaced. In the Atlantic Gannet on Bass Rock 70% of eggs lost to experienced females were replaced if lost within a month after laying. After 43 days of incubation, replacement laying did not occur. When (as here) the egg is only 2.9% of the female's weight and food is abundant, the cost of each egg is small. Late eggs are not replaced, presumably because the chicks would fledge too late to have a reasonable chance of surviving. Similarly, Shags (*Phalacrocorax aristotelis*) replace half incubated clutches but do not re-lay after losing a brood (Snow 1960). Tropical pelecaniforms by contrast, are largely free from seasonal constraints. Presumably as a consequence, the first and third options are most commonly adopted by them. Replacement laying within two or three weeks of egg loss may occur in all three pan-tropical boobies and Blue-footed Boobies on the Galapagos. On the other hand failed breeding attempts may be abandoned, and a variable period may ensue, in, for example, the Galapagos Red-footed Booby, the Ascension Island Brown Booby, the Flightless Cormorant and the Red-billed Tropicbird of the Galapagos. Dispersal, return and laying at a strictly pre-determined seasonal period, as in temperate pelecaniforms, could be positively *maladaptive* for tropical species, since it removes the opportunity of using food as a proximate stimulus for initiating a new breeding attempt and thus responding sensitively to its unpredictable fluctuations (Nelson 1968).

Replacement laying remains to be conclusively demonstrated in Great Frigatebirds or most pelecaniforms. My own evidence with Galapagos birds was circumstantial and Reville (1980) claims emphatically that on Aldabra this species and also the Lesser Frigatebird *Fregata ariel* did not replace lost eggs. Apparent replacements were laid by second females. Stonehouse and Stonehouse (1963) however showed with marked individuals that Ascension Frigatebirds *F. aquila* re-layed in 20–25% of instances. The environmental circumstances of frigates seem to point to replacement laying as a predictable strategy. Thus the egg is but a fraction of the cost of the offspring which adults were 'prepared' to meet. Seasonal constraints are mild and largely irrelevant since the offspring will be fed for more than a year and, finally, the biennial breeding regime and long-deferred breeding already minimize lifetime productivity and to wait even one year instead of replacing the egg would further decrease this.

Nevertheless, all five frigate species are either markedly or loosely seasonal breeders and if, for some as yet unidentifiable reason, replacement laying is usually ineffective, their seasonal programming would lead them to wait until the following year.

On occasions, all tropicbirds lay new eggs to

replace lost eggs or small chicks, but appear to require longer than other marine pelecaniforms (1–2 months, Red-tailed *Phaethon rubricauda* on Christmas Island, Pacific Ocean, (Schreiber and Ashmole 1970), 23–30 days, White-tailed (*P. lepturus*) on Ascension (Stonehouse 1962), 40–56 days, Red-tailed on Aldabra and 42–51 days, White-tailed on Aldabra (Diamond 1975b)). The proportion doing so is not known but was at least 10% on Aldabra and few on Ascension. The Red-billed Tropicbirds of the Galapagos sometimes adopt the 'intermediate breeding' strategy. On Daphne Island, for example (Snow 1965), many nests failed due to competition for sites and many of the failed adults nested again after 3–4 months, although interestingly, they did not display this flexibility on nearby Plaza Island (Harris 1969a).

"REST" YEARS

Do experienced adults refrain from breeding despite retaining last season's site and mate? Good data are extremely scarce, but on Ascension Island, Dorward (1962) had good evidence that some Masked Boobies did. Kepler (1969), on Green Island (Kure Atoll) reported that all such pairs *attempted* to breed but Woodward (1972) recorded 20 birds that bred one year, turned up again the following year, but didn't breed. Among those, it is almost certain that there would be both individuals from previous pairings though there is no hint that they remained together in the non-breeding year. Some 90% of Masked Boobies on Kure changed sites, and often territories, in successive years (Kepler, loc. cit.) and many pairs were disrupted. This is the best available data for any tropical pelecaniform and falls short of demonstrating that intact pairs take "rest" years. For the Atlantic Gannet the data, now extending 21 years for a marked group, is quite unequivocal: rest years do not occur in intact pairs (Nelson, unpubl. data). Non-breeding years enforced by loss of mate or site are another matter.

There are many indications for a wide range of seabirds that adult weight and breeding success are positively correlated and that pre-breeding feeding conditions affect laying date. It is conceivable that pre-breeding feeding might be too poor to raise some individuals to a required physiological threshold. The probability of success, below this threshold, could be too low to justify a breeding effort. Critical physiological data are needed. Since it is now possible to record accurately and automatically the weight of an adult every time it comes to the nest, exciting advances should be made concerning adult fluctuations in weight and fine details of chick growth. I suspect that species differ in the height of the "fitness threshold," below which they will not breed. I speculate that those adults in which stress

and reduced longevity is a "fair price" for increased productivity (probably the inshore feeders with large broods) will breed when further below normal weight than do the tropical pelagic pelecaniforms. There are subjective data (Kortlandt, unpubl. data) for the Common Cormorant, that breeding does severely stress adults of some species. However, other evidence also suggests that in some tropical pelagic feeders (frigates, Abbott's, Masked, and Red-footed Boobies, Nelson 1966, 1969, 1978) the adults maintain body weight even when the young are starving. Presumably natural selection operates by taking into account pre-breeding mortality (it is of relatively little benefit to rear a chick which is 95% likely to die before breeding); life-expectancy of adults; capacity of the female to respond to fluctuations in food by modifying brood-size; readiness with which adults can regain lost-condition outside the breeding season; and many other factors.

There is scope here for the mathematic modeller and I suggest that although increasing productivity by "allowing" adults to stress themselves is likely to be a valid strategy in some inshore, temperate pelecaniforms which tend towards the "r" end of the 'r- and K-selected' spectrum, it is not valid for most tropical, pelagic pelecaniforms.

However it is increasingly clear that non-breeding years, where they occur, are not devices for reducing recruitment but for maximising it, by mitigating stress or re-stabilizing social relationships after disruption.

CONCLUSION

Tropical and temperate pelecaniforms contrast strongly in breeding frequency, both as regards successive, successful cycles and also in strategies adopted in response to failed attempts. There is no equivalent among temperate, marine pelecaniforms to the tropical pelecaniform strategies of breeding successfully more than once a year, less than once a year and strictly only once every two years. As regards failed breeding, tropical pelecaniforms have more options available than do temperate ones, due to lack of seasonal constraints.

THE TIMING OF BREEDING

SEASONALITY

Birds lay at those times of year which produce the most survivors to breeding age (e.g., Lack 1966). This, at one point or another, is most often determined by food. In strongly seasonal latitudes breeding seasons are sharply defined by changes in photoperiod and temperature. Most seabirds' mean annual laying dates are remarkably consistent, albeit at the level of local pop-

ulations rather than species. Laying dates may coincide with a flush of food, often for rapidly growing young. For example, the period of most rapid growth of Shags on Lundy Island, England, coincides with the movement of sand-eels, *Ammodytes spp.* into the area (Snow 1960); the young of most seabirds on the Farne Islands hatch in June and early July, coinciding with the arrival inshore of *Ammodytes tobianus* and *A. lanceolatus* (Pearson 1968); the growing period of the young of both British and Canadian gannets coincides with the arrival inshore of the mackerel (*Scomber scomber*) shoals. As mentioned, local differences in food affect laying dates. Bass Rock Gannets lay two to three weeks earlier than birds on Ailsa Craig; Shags from southeast Scotland lay two weeks earlier than Shags from southwest Scotland (Potts 1969) and puffins (*Fratercula arctica*) from the Isle of May (southeast Scotland) lay two or three weeks earlier than birds from St. Kilda (northwest Scotland) (Harris 1978). These differences also affect growth rates in some species. Post-fledging survival is often age-specific in the first year, thus providing strong selection pressure for early laying.

By contrast, all tropical pelecaniforms show a wide spread of laying times. In some cases laying may seem entirely aseasonal but in fact usually favors certain months. For example, on the relatively aseasonal Christmas Island (Pacific Ocean), Schreiber and Ashmole (1970) show that the six breeding pelecaniforms, (Red-tailed Tropicbird, Masked, Brown and Red-footed Boobies, Great and Lesser Frigatebirds) may all have eggs in any month. Nevertheless each species has a detectable, albeit broad peak, or peaks. That of the tropicbird, for example, lasted six months, three of which consecutively produced by far the most eggs.

Where waves of laying in tropical pelecaniforms are triggered by an upturn in food there can be no guarantee that favorable conditions will last. Subsequent abandonments of breeding, or mass starvation of chicks, are on record for marine pelicans, boobies, tropicbirds and frigates. On a practical point, chick-banders waste much extremely valuable information on age-dependent mortality if they fail to note estimated age of chicks which they band.

Some interesting points emerge from a comparison of timing in the Atlantic Gannet (temperate) and Abbott's Booby (tropical). The gannet (at the local population level) has a highly consistent mean annual laying date varying by only ±5 days. Its chick, fed on a seasonal flush of oily mackerel, grows faster than that of any other sulid, despite being the heaviest. This hastens fledging and provides substantial fat deposits, in place of postfledging feeding. I have suggested that early fledging is so important that competition for a socially adequate site, which facilitates this, dominates the gannet's breeding behavior. To acquire and maintain its site, the gannet attends it for three or more months before laying and for an equivalent period after offspring have departed. Furthermore, gannets sustain their site-defense displays to an extent unparalleled among seabirds. If early laying is so important, the spread of laying (late March to early July on the Bass Rock) may seem anomalous. However, the appropriate adaptation to a variable environmental factor is a variable response, not a fixed one. In many seabirds, clutch size is variable because the factors which determine breeding success are variable. In some years smaller clutches outproduce larger ones and this maintains a stable polymorphism. The same argument applies to the spread of laying. The main cause of mortality among recently-fledged Atlantic Gannets is starvation due to bad weather. In the North Sea and North Atlantic weather is highly variable. No fixed laying date is practicable and could avoid bad conditions. In some years, birds fledging earlier or later than the mean will survive best, hence the maintenance of the spread of laying. In addition, the later-laying of first-time breeders contributes to the variability.

Abbott's Booby's unusual breeding strategy does precisely the opposite in that instead of fledging young in time to avoid the monsoons (on Christmas Island, Indian Ocean in November-March) laying is so late and chick growth so slow that by November the chick is still downy (Nelson, 1971). This leaves two options, both apparently maladaptive: It could launch its energetically-costly single fledgling without post-fledging care and without fat deposits, into the monsoonal Indian Ocean in December or January, presumably with little chance of survival. This assumes post-fledging care at sea is impractical. Certainly no sulid shows it. Or adults could try to feed the chick on the island, through the monsoons, until conditions improve in April/May. The chick could then be restored to good condition by August/September when it could become independent at 56–60 weeks, compared with the gannet's 12–13. Abbott's Booby has adopted this second option. Between January and March, 60–90% (it varies from year to year) of dependent, fully grown young starve to death. Each chick represents some 8 months investment by its parents. Moreover, this long cycle means that Abbott's Booby can breed only once every two years. The key to the entire strategy is the timing of laying (mainly June/July) coupled with extremely slow growth. If Abbott's Boobies laid in March and grew at the normal rate for a pelagic sulid the chick could fledge before the

monsoons, as do Brown and Red-footed Boobies on this same island. Presumably a relatively slight shift in weather pattern could significantly affect the survival rate of fledglings between December and April. The strongly-postulated southward drift of Christmas Island due to plate tectonics might conceivably have had an effect by distancing Abbott's from its major feeding area. Perhaps Abbott's now-aberrant breeding strategy accounts for its relict status.

SYNCHRONY

Some 93% of seabirds are colonial (Lack 1966). All pelecaniforms with the partial exception of Abbott's Booby are colonial and their colonies without exception known to me, show at least sub-group synchrony in laying.

One may distinguish between types of synchrony, causes and functions. First, synchrony may, but need not, imply seasonal timing. It represents clustering in time and this may be seasonally consistent, as in temperate species, or largely non-seasonal as in tropical pelecaniforms. Second, clustering can be in relation to the whole colony ("Colony" is a difficult concept/fact to define.) or to parts of it (sub-group synchrony). There is an important difference between these two. A colony may show only slight overall synchrony but marked sub-group synchrony. This is partly because most colonies of seabirds are not homogeneous but are spatially sub-divided. I know of no pelecaniforms for which this is not true except some colonies of Gannets (all three allo-species). But even in topographically homogeneous colonies of Gannets in which nests are regularly distributed (a rare phenomenon but closely approached in some Atlantic and Australasian (*Sula* (*bassana*) *serrator*) gannetries) there is still sub-group synchrony. It is possible to demarcate 'clusters' of chicks whose ages are closer to each other than is the average 'closeness' within the whole colony. Sub-group synchrony is so widespread in colonial seabirds that one may suspect it to be universal.

In marine pelecaniforms of high latitudes the principal 'coarse' timer of reproductive behavior is presumably photoperiodic. Local availability of food certainly affects yearly timing (onset, spread and mean annual date of laying) at the local level but there have been no investigations of differences in timing, between years in the same colony, and linked to food. Social factors are also involved, especially in sub-group synchrony, for example in the Atlantic Gannet (Nelson 1978). Social synchronisation requires far more critical study than it has so far received. It may be regarded as a 'fine' timing mechanism, reducing the spread of laying by bringing laying forward in potentially late females (its probable role in bringing forward the whole group is a separate consideration).

One factor which may be involved in the initiation of sub-group synchrony is the initial attraction ('peer' attraction) between individuals which are all at the same, early stage of breeding. Knopf (1979) has indicated that this occurs in the White Pelican (*Pelecanus erythrorynchos*) and Burger (1979) has analysed it more fully for the herring gull (*Larus argentatus*). That peer-attraction is a widespread phenomenon emerges from many incidental observations in the seabird literature (e.g., Nelson 1970, 1978). Once such a peer group has formed, tighter synchrony can develop. The role of behavioral facilitation in this has remained almost totally unanalysed because of the difficulty of isolating and quantifying its contribution, but videorecording and time-lapse photography now provide useful tools. We need standardised behavioral profiles for different social groupings of the same species. These would have useful applications, for instance, in relating behavior to the probability of egg-laying.

In tropical pelecaniforms, photoperiodic timing presumably does not apply. An internally controlled circannual rhythm could presumably provide 'coarse' timing if this is adaptive but we need to know much more about the possibility of broadly rhythmic fluctuations in external factors. Sudden changes in the availability of food certainly initiate (and terminate) waves of laying in several Galapagos seabirds, including some pelecaniforms (Nelson 1969, Harris 1969b, Nelson and Snow, unpubl. data) but these are not of an annual nature. The tropical marine pelecaniforms have, therefore, a more flexible timing system than temperate species. Socially mediated synchrony is almost certainly involved in sub-groups and a pioneer analysis of this phenomenon in the Great and Lesser Frigatebirds of Aldabra, by Reville (1980) is worth summarizing here.

Overall, colonies of all five frigate species can be seen to consist of sub-groups within which (usually) they seem to be further sub-divided into clumps or clusters, often related to discontinuities in the habitat. I suggested (Nelson 1968) that the clumps of nesting Great Frigatebirds on Tower Island, Galapagos, resulted from nuclei of displaying males. Diamond (1975a) similarly described Great and Lesser Frigatebirds on Aldabra as nesting in groups. Reville's analysis, however, showed that the Lesser Frigatebird did *not* clump when occupying an unbroken stretch of suitable habitat in which there were no Great Frigates. Instead they tended to be regularly spaced, whereas Great Frigatebirds clumped at 15–23 sites per clump. This difference correlates with the two species' different criteria for selecting

sites and affects subsequent synchrony and breeding success. Simply, Lessers fill the patches of suitable habitat which they are going to use, simultaneously. That is, social factors (such as the number and density of displaying males in each patch) do not cause other males, and subsequently females, to prefer some patches over others. In Great Frigates this is emphatically not so and females chose patches with initially many males rather than those with few. Patches of Great Frigates therefore filled up one after the other sequentially rather than simultaneously and the distribution of nests follows the same pattern as the distribution of the (initially clumped) displaying males. Lesser Frigate males, however, continued to settle among pairs that had already formed, until regular dispersion, whether at high or low density, resulted.

The function of synchrony depends on the species. It may (theoretically) 'swamp' predators, reduce interference by conspecifics or have no major function as such but merely result from laying to a tightly-defined mean seasonal date, the seasonality rather than the synchrony being adaptive.

For differential mortality related to time (seasonal) of fledging there is in temperate birds as a whole, abundant evidence. Emlen and Demong (1975) stress the role of information transfer as the benefit of close synchrony in Bank Swallows, (*Hirundo riparia*) those individuals fledging either early or at the peak of synchrony emerge to find a stream of conspecifics flying between the colony and local, ephemeral food sources. Ward and Zahavi (1973) claimed information-transfer as perhaps the function of coloniality but it probably applies much less widely to seabirds than they propose. In my view, neither colonial breeding nor synchrony function in this way in most seabirds, especially pelagic ones.

In the frigates of Aldabra, the two contrasting spatial patterns permitted comparison of synchrony and breeding success in the two species. In the Lesser Frigate, females settling later did not subsequently require less time before laying, whereas in the Great Frigate they did. Therefore laying in Great Frigates was more synchronized than in Lessers. The increased synchrony in Greats, Reville suggests, reduced conspecific interference and increased hatching success (54.5% over two years in the Great Frigate, 20.1% in the Lesser). Moreover, in the Great Frigate, the most synchronized groups had the highest hatching success. Reville suggests that clustering makes a localised group of nests less attractive to potential usurpers and so reduces conspecific interference.

On the major question of why the Lesser Frigate does not cluster Reville comments that the female cannot afford to be as male-selective as the female Great Frigate, because there appear to be more males than females in the Great population but a 1:1 ratio in Lessers. Coupled with Diamond's (1972) discovery of the skewed sex ratio in the Magnificent Frigate (*Fregata magnificens*) this piece of work appears to provide fresh insight into frigate breeding strategies. Why the sex ratios differ in frigate species is another question.

CONCLUSION

Temperate marine pelecaniforms exhibit seasonal timing, and synchrony of laying. Tropical pelecaniforms are relatively non-seasonal but nevertheless show marked sub-group synchrony. The functions of sub-group synchrony (as opposed to seasonal timing) may be several and do not relate especially to either tropical or temperate conditions but more to social phenomena common to both.

THE SIZE OF EGG, CLUTCH, AND BROOD

The pelecaniforms exhibit a wide range of egg and clutch size, presumably reflecting their great adaptive radiation into different feeding and breeding niches. The correlation between large eggs (in relation to female weight) and small clutches (usually one egg) and far-foraging is well known. Conversely, inshore feeders lay relatively smaller eggs and larger clutches. So tropicbirds and frigates are invariably uniparous and lay relatively large eggs, pelicans and cormorants are almost invariably polyparous and lay smaller eggs, whilst gannets and boobies fall in between. Within the sulidae it is not only the range (1–4) of clutch size that is interesting but the fact that some species never lay more than one egg per clutch, others never more than two, whilst yet others lay clutches of variable size. Within this family, a major correlation between clutch size and foraging simply mirrors the general one within the order. The same principle may be further demonstrated by the fact that even within uniparous boobies such as the Red-footed (and also in tropicbirds), egg size varies with locality; eggs are larger where food is scarcer (Snow 1965, Nelson 1969).

Because far-foraging is a widespread adaptive response to breeding in blue-water tropical regions (though not necessarily confined to such) it is to be expected that tropical marine pelecaniforms will tend towards relatively larger eggs and smaller clutches. This is so, although there are important exceptions, principally concerning tropical pelecaniforms with notably inshore feeding habits (all tropical cormorants and pelicans and three tropical boobies). Conversely, temperate marine pelecaniforms are, with the

exception of the three gannet allo-species, po-lyparous inshore feeders. These generalisations and exceptions may be pursued using specific examples.

Tropicality and foraging method interact instructively within the sulidae. All six breed largely or entirely within the tropics although four (the Red-footed, Masked, Brown, and Abbott's) are essentially more tropical than the Blue-footed, and Peruvian. The latter two breed within or close to colder, more productive waters and breeding birds forage less widely than the other four. Consequently the four tropical boobies are all strictly single-chick species although only the Red-footed and Abbott's are actually uniparous. In the Masked and Brown Boobies, which lay either one *or* two, the two-chick broods are always reduced to one by fratricide, the essential point being that the elimination of the younger chick by its sibling is early in life, by active persecution and in no degree dependent on the food available at the time. Thus whether by laying one relatively large egg as do the Red-footed and Abbott's Boobies, or two smaller ones which, if both hatch, are soon reduced to a single chick, as in the Masked and Brown Boobies, these four tropical pelagic sulids are adopting essentially comparable strategies.

The Blue-footed (1–3 eggs) and the Peruvian (2–4 eggs) not only lay these larger clutches but may rear 2 chicks (Blue-footed) or even 4 (Peruvian). Even where the Blue-footed breeds on the same island as the Masked, or the Brown, it does not exhibit obligative brood reduction as they do, although in times of food shortage the smaller sibling may starve. Obviously, the food-scarce blue-water environment and associated foraging habits of the Masked and Brown Boobies have converted facultative into obligative brood reduction by penalising those pairs in which both young survived, even if only for a few days. The Peruvian Booby normally loses none of its brood, although in Niño years, the whole brood and its parents normally starve to death. Clearly in all six boobies, the size of the brood which is reared is low in tropical far-foragers and higher in the less-tropical, more inshore foragers.

It might be expected that the 3 gannet allo-species (Atlantic, Australasian and African (*Sula (bassana) capensis*) would be polyparous but, instead, they are strictly uniparous. But they are not truly inshore feeders. Although they are not truly pelagic either, they forage at considerable distances from the breeding colony. Moreover, they endow their offspring with considerable fat reserves in lieu of post-fledging care and (at least in the Australasian and African) this makes it difficult for them to feed more than a single offspring.

Brood reduction, both through sibling murder and through differential starvation is found in other pelecaniforms. In the White Pelicans (*Pelecanus onocrotalus*) of Dassan Island (South Africa) the older chick actually kills its sibling (Cooper 1980) whilst differential starvation occurs in the Brown Pelican (Schreiber 1979) as it does, also, in many phalacrocoracids (e.g., Kortlandt *in litt.* for the Common Cormorant, Snow (1960) and pers. observ. for the Shag).

Obligative brood reduction may be seen as a mechanism to optimise productivity. If both chicks were allowed to grow strong during a period of plenty, they would later compete strenuously when food became scarcer and before one succumbed both would be weakened. If the probability of temporary food shortage is high enough, natural selection will ensure that chicks which have not been thus weakened survive best. To interpret brood reduction as a mechanism for reducing production is precisely the opposite of the case. Although brood reduction by competition for food among siblings is widespread in birds, for example in raptors, corvids and herons, (see O'Connor, 1978) it is, in these birds, never completely obligatory within the first few days. This is understandable since no land bird is subject to selection pressures comparable to those facing highly pelagic, blue-water seabirds.

Conclusion

Tropical marine pelecaniforms tend to have larger eggs and smaller broods than have temperate members. This correlation exists largely as a result of the differing foraging methods used in these two environments. Therefore it is subject to many exceptions, since inshore and offshore foraging do not correlate precisely with temperate and tropical environs respectively.

COMPOSITION OF BREEDING CYCLE

Although breeding frequency is partly determined by the length of the breeding cycle, cycles of equal length may be sub-divided differently. It is the investment in each component that amounts to a strategy. When comparing these components in different pelecaniforms the premise is that natural selection shapes the details of energy-expenditure on a lifetime basis. Most fieldwork is unavoidably crude by comparison with the admirable physiological studies of, for example, Whittow (1980) on the correlates of prolonged incubation, Dunn (1980) on the energy allocated to feeding nestlings or Ricklefs (1974) on the energetics of clutch-size and chick-growth. However, behavioral field data can facilitate interpretation. Whilst it would be interesting, for example, to know what it costs a

gannet to spend 5 months of each year displaying on its empty site, thereby performing roughly 15,000 display-acts, in comparison with a frigatebird's few days of display, the conclusions which may be drawn do not depend on such quantification. Here, I will contrast some tropical and temperate marine pelecaniforms with respect to the characteristics of the following components of the breeding cycle: (i) pre-laying activities, (site-establishment, pair-formation and nest building), (ii) incubation, (iii) care of pre-fledged young, (iv) care of post-fledged young and (v) post-breeding activities.

PRE-LAYING ACTIVITIES

In tropical pelecaniforms pre-laying breeding activity is highly compressible whereas those of more seasonal latitudes spend longer on this component. Full comparative data are extremely patchy so it is appropriate to select examples. In the Brown Pelican the male selects the site (Schreiber 1977), as is the case in most other pelecaniforms (certainly in sulids, frigates and at least some phalacrocoracids). In 1–4 days, during which he is seldom absent, the male Brown Pelican attracts a female. After a further 4–10 days the nest has been built (material gathered solely by the male) and 1–3 days after this (some 6–17 days after he first stations himself on site) the first egg is laid. During this brief period there is little overt fighting between neighbors, no frequent, ritualised threat and no specific site-ownership display. This may be a phylogenetically primitive procedure, brief, labile and lacking a complex repertoire of behavior. The male finds a suitable perch, sits on it using a simple head-swaying display until a female joins him, bonds almost immediately and quickly builds a nest. Pelicans in general are not faithful to a particular site nor usually to a breeding area (Vestjens 1977, Knopf 1979) and correspondingly they invest little in it.

Great Frigates show this relationship between site and effort even more clearly. Males display in groups, each on his perch, and those which are unsuccessful in attracting a female fly off and join, or initiate, a group elsewhere. Thus the display site may not be, initially, a firmly established, potential breeding site. It is far more labile than in any other pelecaniform. Almost all the frigate's pre-laying activities are sexual, directed to females and not territorial, directed against other males. The site changes with each breeding attempt and little effort is devoted to its maintenance. There is, for example, no special site-ownership display. A male may join a display group, attract a female, form a pair and build a nest all within a few days (Reville 1980, Nelson 1968).

Similarly, in the Flightless Cormorant pre-laying activities may take as little as 10 days from the first display by the male, on the sea, to egg-laying (Harris 1979). Here, too, site establishment and pair-formation take place anew with every breeding attempt, of which there may be several in one year.

By contrast, some high-latitude pelecaniforms, for example, Common Cormorants, Shags, Atlantic, and Australasian Gannets, spend weeks or months attending and refurbishing their sites. In these species the pre-laying period is never highly compressed. Moreover, the incidence of strictly territorial activity may be extremely high. For example, the male Atlantic Gannet attends his site on average 60% of all daylight hours in the six weeks before laying. During this period he fights several times with intruders or neighbors and performs both a ritualised threat display and the complex and energetic site-ownership display approx. 1500 times each (these figures derived from standard checks extrapolated to a 15-hour day). In addition he makes more than 100 visits with nest material. This is a considerable investment of time and energy, repeated in each of the 15–20 years for which an Atlantic Gannet keeps his site.

The Shag begins to attend either the precise site of former years or the same locality, perhaps a ledge or gulley, up to 70 days before laying (Snow 1960), the mean period being 38 days. Territorial display is frequent.

Species which have permanent sites usually have permanent pairs and the site, established by the male, is used by him for sexual display, first to attract a female and in succeeding years as the focus for reunion. This scenario is highly appropriate for consistently seasonal breeders, which is presumably why it applies so widely to seabirds of high latitudes. Conversely, the pre-eminent adaptation to the extreme tropical regime is flexibility in the timing of breeding and in its components, so that these can be modified when food dictates. This opportunism is inconsistent with fidelity either to site or mate and consequently affects the behavior which subserves such fidelity. The adaptive strategy is to abandon the fixed annual cycle, take advantage of upturns in food, use these as proximate timers and evolve the capacity to buffer fluctuations in food by retarded growth, large-egg (to give starvation resistant chick), brood-reduction, and extensive post-fledging feeding. However, many tropical areas are by no means aseasonal and correspondingly, breeding may be loosely seasonal.

The concomitants of these two basically different strategies are that those behaviors which maintain site and pair-bond are extensively de-

veloped in species in which attachment to site and mate is highly durable, e.g., Atlantic Gannet, Abbott's Booby, Shag; and less developed or minimal where it is ephemeral, e.g., all frigates, Brown Pelicans, and tropicbirds. Some pelecaniforms, for example most boobies and cormorants, fall somewhere between the two extremes, as indeed does the strength of their attachment to site and mate.

The frigates do not have permanent sites because these are incompatible with their biennial cycle, in which essentially two populations use the same breeding area, and those pairs which are absent from the colony are in no position to maintain their sites. The shifting nuclei of displaying males are incompatible with the reunion of former partners. Males readily accept females soon after display begins. They attend display sites almost continuously for days on end (some are present for a month before pairing) and the odds are heavily against a former partner coming to the colony and finding "her" male, at the previous site and still unattached. So pairs usually last for only one breeding attempt, and, after the first 3 or 4 days following the initial encounter, and the short nest-building period, there is no pair-bonding behavior. During these first three days Reville (1980) observed that the time which the pair spent together decreased from 90% to 44% of each day and that male sexual display (beak clattering) decreased by half in day two to none in day three. After nest-building, incubation and intensive chick care, the frigate's lengthy foraging absences and brief visits to the nest make meeting somewhat improbable. Despite this apparent lack of pair-bonding behavior the bond between parent and offspring is strong enough to ensure that parents feed their young for longer than almost any other seabird.

In tropicbirds, too, sites and pairs are notably impermanent and pair formation is flexible. Red-billed Tropicbirds in the Galapagos breed at different times on different islands, and on some islands laying occurs all year round. Harris (1969a) showed that on Tower Island sudden scarcity of food caused some adults to desert their young and delayed the onset of breeding in others. This fluidity, together with strong competition for holes, is not conducive to regular re-occupation of sites and re-formation of pairs. Territorial and pair-bonding behavior is so minimal that no worker has commented on anything other than the overt competition for holes and the well-known flight-display, which establishes, rather than maintains, the pair-bond.

In the Brown Pelican, egg-laying in a single colony can occur over a period of at least six months and at many colonies birds remain all year. The records of pelican colonies changing

location, and the state of flux within colonies as new breeders arrive and breeding continues, show that sites and pairs last merely for one breeding attempt. Pelican courtship is relatively simple and its undifferentiated nature is well captured by Schreiber's (1977) account. The male selects the site and displays to females but after pair-formation, as in frigates and tropicbirds, there is no specifically pair-bonding behaviour.

Most pelecaniforms with impermanent sites and pairs invest relatively little in them, behaviorally, but the Flightless Cormorant is an exception. Its nest-relief ceremony, involving ritualised presentation of seaweed, is well documented (Eibl-Eibesfeldt 1960). Correspondingly, although it readily shifts site and changes its mate, it frequently does retain the same site and mate in successive nestings ($^{57}/_{112}$ and $^{52}/_{136}$ males and females respectively remained in the same nesting place for successive nestings; in 31 instances the same partners nested together twice and in one case three times (Harris, 1979). It is, of course, highly sedentary and its foraging absences are short. Both factors increase the likelihood of re-pairings, compared with frigates and tropicbirds.

In sulids the male establishes the site and displays both territorially and sexually on it. Unlike the frigates, tropicbirds and pelicans, sulids have evolved not only a sexual advertising display by which males attract females but also an extensive repertoire of displays performed by the pair on the site, particularly before egg-laying but also at the nest-relief ceremony. Correspondingly, attachment to the site is strong and the pair bond often endures for successive nestings. Abbott's Booby compares interestingly with the frigates in that it, too, nests in trees and breeds only once in two years. Yet is has a permanent site and keeps the same partner. It can do so because, unlike the frigates, it is a dispersed breeder with a precise location to which partners can return. Although the nest itself usually disintegrates in the monsoons, the exact location is used in successive nestings. Return to the island is highly seasonal and the partners therefore have both the environmental timer and the precise location necessary for reunion.

In the Atlantic Gannet 94% of pair bonds remain intact from year to year. Extreme aggression is shown in defence of site and, both overtly and in ritualised form, by male to female. This aggression, by becoming linked to sexual behavior, may actually strengthen the pair bond. Consequently, aggressive males, which presumably are more successful in site competition, are not penalized in the pair context. Copulation is accompanied by vigorous nape-biting *only* in the Gannets (three allo-species) and the act itself lasts

on average 24 seconds, which is 3–6 times as long as in any other pelecaniform. It is accompanied by massive tactile stimulus (tramping movements of the webs on the female's back). Also, the Gannet's elaborate meeting ceremony is preceded by napebiting and the display itself incorporates ritualised aggression. This simple example illustrates the sort of interactions—here between site-attachment behavior and pair-bonding behavior—which must operate on an unimaginably complex scale in the evolution of breeding strategies. The Gannets system works only because the feeding environment allows reliable and early return to the site each year.

The third pre-laying activity is nest-building and associated behavior. The practical functions, in pelecaniforms, are to provide sites for copulation and to protect and insulate eggs and young. The function of nest-building in those species in which the structure is of no practical use is to strengthen the pair-bond. Even where, as in the Atlantic Gannet, the nest is obviously valuable, its pair-bonding function should not be overlooked. On Ailsa Craig the act of landing was the commonest cause of death accounting for more than 300 adults in one season, (Wanless 1979). Yet Gannets bring in nest material far more than appears to be necessary. The pair-bond must justify these visits. Conversely, frigates build flimsy, barely adequate platforms of dead twigs. The young frigate has prehensile feet and nest building probably has little pair-bonding function, so the minimum suffices. Also, frigates have considerable temperature-regulation problems and the open lattice work may help air-flow over egg and young chick. Abbott's Booby needs a substantial nest to give the chick a stable footing as far into the monsoon period as possible. Its bulky cradle is built from large, living twigs plucked with great effort and significant risk from the jungle canopy. In addition, each return with nest material involves mutual greeting and a highly ritualised presentation of the twig, after which both partners build it into the nest structure. Presumably this helps to cement the pair-bond which is highly durable (Nelson and Powell, unpubl. data).

The same combination of practical and symbolic factors applies to the many cormorants and to the pelicans. As nidicolous species, all require a structure, be it land vegetation, twigs, seaweed, pebbles, flotsam or guano. Many phalacrocoracids, however, use nest material in mutual building interactions and continue to build through incubation and part of the nestling period. Correspondingly, nests are often re-used and in some species pair-bonds may endure for more than a season.

As part of breeding strategy, therefore, one may view nest building in relation to the pair-bond (and therefore the relative permanency of the site) as well as in relation to the physical functions of the nest. Through this link, it relates to opportunism in breeding, or the lack of it. Tropical marine pelecaniforms, being mainly opportunistic and with transitory attachments, are constrained largely by the availability of material, the energetics of building and the physical functions of the nest. Temperate species, with more durable bonds, add the social (pair) dimension to their nest-building activities.

INCUBATION

Aspects relating to incubation include: the method, egg-recognition, duration of incubation, length of individual incubation stints and interactions between partners. Of the fact that gannets, boobies, cormorants and pelicans have no brood patch and incubate eggs beneath webs (gannets and boobies) or on them (cormorants and pelicans), whilst frigates and tropicbirds have a median brood patch, I can say little in relation to breeding strategies. Obviously, the small feet of frigates in particular, but also tropicbirds, could not incubate the large egg. Of the difference between sulids and phacrocoracids one may note that the reduced clutch of all the sulids with the partial exception of the Peruvian Booby, permits incubation underfoot whereas this becomes difficult with more than two or three eggs and many phalacrocoracids, as inshore feeders, lay clutches of four or even more. But there is no evidence that incubation beneath the webs is more efficient than on top. The only pelecaniform in which individuals apparently recognise their own egg is the Red-tailed Tropicbird (Howell 1978) which in 27 out of 35 choice-tests retrieved its own rather than another egg. These eggs are variable in color whereas most pelecaniform eggs are plain, stained or nondescript. The competition for nest holes which occasionally leads to the deposition of two eggs in one hole many select for recognition. The duration of incubation is positively correlated with the yolk reserves of the egg and large eggs, in turn, correlate with slow growth of the young. Both large eggs and slow development are adaptations of far-foraging seabirds and will be discussed later in this section.

Long incubation stints, also, go with pelagic rather than inshore feeding and can be used as a measure of foraging behavior. Frigates, tropicbirds and Masked and Red-footed Boobies are often recorded far from the nearest breeding station. In areas such as the Galapagos where evidence of periodic and severe food shortages is incontestable, incubation stints in all pelagic species are unusually long when compared with those of conspecifics elsewhere. There is no rea-

son to doubt that birds absent from the colony are indeed foraging. Within a species, populations with longer incubation stints also have chicks which grow more slowly than others—for example, chicks of Great Frigates on Tower Island (Galapagos) with mean incubation stints of 10 days grow more slowly than those on Aldabra, with incubation stints of 6.5 days. Similarly, Red-footed Boobies on Tower Island have incubation stints 2 or 3 times as long as their congeners on Christmas Island (Indian Ocean) and their chicks take 140 days as against 105 to fledge.

Within the marine pelecaniforms, long incubation stints predictably correlate with low clutch and brood size since both are adaptations to pelagic feeding. All uniparous pelecaniforms have incubation stints well in excess of 24 hours, many exceed 48 and some average more than 5 days. With the exception of two sulids, both of which are single-chick species even though they lay clutches of two, no polyparous pelecaniform averages as much as 24 hours.

There are two possible functions (pair-bonding and coordination of change-over) of the ritualised behavior which may occur at nest relief and these are sub-served by distinct displays. Some marine pelecaniforms show no special behavior at change-over. Incubating frigates and tropicbirds simply vacate the nest to the incomer. Brown Pelicans, at least in early incubation, interact briefly and simply and usually without contact, head-swaying and bowing (Schreiber 1977). This interaction diminishes as incubation and the guard stage progress. Among phalacrocoracids there is no marked greeting ceremony but there is a distinctive pre-flight display. In all four families, with a few exceptions amongst the cormorants, pair bonds are for only one season and pair bonding displays weak or absent. Among sulids, nest relief is much more elaborate, incorporating both pair-bonding display and ritualised pre-departure display. The most marked cases are the Atlantic Gannet and Abbott's Booby in both of which the ecstatic mutual greeting display is prolonged, noisy, and elaborate. In both species, pairs are permanent or highly durable and their nest-relief display may be considered to be an extension of the bonding behavior which they show during pair-formation. The pre-departure behavior in the Atlantic Gannet is also highly conspicuous but its function is to ensure that the partner (as shown by its own behavior) "registers" this intention and therefore remains behind. Departure of both birds could easily result in the loss of egg or chick. It seems anomalous that cormorants and sulids presumably require pre-departure display (since they have evolved them) but frigates, for example, do not. No direct link with foraging and the tropical or

temperate habitat can explain this difference which may relate to the vulnerability of the temporarily unguarded nest of ground-nesting pelecaniforms to predation and stealing by conspecifics. But frigate nests are also vulnerable.

The adaptive aspects of the different degrees and forms of pre-departure behavior are not understood. Complex greeting behaviour at nest relief, however, does appear to relate to permanence of site.

PRE-FLEDGING CARE OF YOUNG

The length of the intensive guard spell during which the young are seldom or never unattended, the frequency of feeding and the period for which young are fed before fledging all lend themselves to adaptive modification in relation to food and foraging behavior.

In pelecaniforms with nidicolous altricial young (all of them except the Phaethontidae, which probably is the most primitive family) some intensive brooding is inescapable. The common practise is to brood the young until they can thermoregulate, which is approximately between 4–6 weeks. But they are still highly vulnerable to attacks from conspecifics and predators such as raptors and introduced mammals. There is now considerable evidence that, among seabirds, interference by conspecifics, either predatory (as in some gulls) or social (as in sulids) is of major significance. In frigates (Nelson 1968, 1976, Stonehouse 1962, Diamond 1975a and Reville 1980) the intrusion of adult males, presumably non-breeding or intending to breed out-of-phase with the main body, causes loss of eggs and of unattended chicks on a large scale. In tropicbirds (Snow 1965, Harris 1969) eggs and chicks are lost as a result of competition for sites and it may be that the unusually long guard spell in these species is to protect chicks from intraspecific interference. The downy young, protected from extremes of temperature in their holes or beneath vegetation, would otherwise seem to need less brooding.

Adults which invest less time in intensive guarding obviously have more time to forage and in tropical pelagic species this is of paramount importance. Nothing else could account for frigates or Masked Boobies, for example, leaving their defenceless young (30–35 days old) as soon as these can thermoregulate. Among temperate species the Gannet's unique investment in guarding its offspring continuously until it leaves the nest and colony (which it does abruptly and with no return) is notable. That it is even possible for one of the parents to remain constantly on guard, thus halving the food-gathering potential of the pair, depends on the timing of breeding such that chicks grow during the period when the shoals

of the exceptionally nutritious and principal prey, mackerel, move inshore and become available. But this does not, in itself, explain why Gannets should trade away half their food-gathering potential. What is the benefit? The only convincing suggestion is that in a dense colony of such a highly territorial species, in which there is intense pressure on breeding sites, unattended nests, and their contents, would be under serious threat. Also, even pilfering of nest material by neighbors would greatly jeopardise small chicks. For these reasons, extended guarding, made possible by abundant food, has evolved. I know of no comparable case in any other seabird.

The habit of forming crêches or pods of unfledged young is entirely restricted among pelecaniforms to pelicans and some cormorants. The function of pods is not clear but may relate to temperature control. Feeding is strictly of one's own offspring. Pods can form only where parents will feed their young away from the nest site. Apparently (and excluding the hole-nesting tropicbirds) all pelecaniforms, except two sulids will do so. Only the Gannet superspecies and Abbott's Booby restrict feeds to the nest, or in Abbott's Booby when the nest disintegrates, to the precise location of it. The reasons are, however, very different in these two cases. In Gannets it is impracticable for young to move off the nest. On cliffs, they might fall, and on flatter ground the attacks of densely packed breeding adults would be fatal. Also, given their method of fledging (one abrupt, irrevocable departure) there would be no gain. In Abbott's Booby where free-flying young are fed for 9 months and most die of starvation, there must be extremely strong selection pressure against feeding intruding young. Restriction to the precise nest site should help prevent this. As in the Gannet, the adults' attachment to their site is strong and highly durable, which will tend to focus feeds on the site.

Perhaps the most obvious difference in chick care to be expected between tropical pelagic pelecaniforms and temperate (and tropical) inshore feeders is that the former will return with food much less frequently than the inshore feeders. As a result, the chicks of the former grow more slowly and single-chick broods are the rule. The frequent feeds, rapid growth and large brood size of inshore feeding Peruvian Boobies, with abundant anchovies *Anchoveta engraulis* in the Humboldt upwelling contrast markedly with the three pan-tropical pelagic sulids and make the point that it is food and foraging which control these parameters. The marine phalacrocoracids, inshore feeders and predominantly temperate, simply emphasise this point. They feed their young frequently and these grow quickly compared with all the tropical pelagic pelecaniforms.

As this contribution repeatedly demonstrates, a principal casual factor in determining breeding strategy is the nature of foraging—inshore or pelagic—and often (but not always) this in turn correlates with temperate or tropical distribution.

POSTFLEDGING CARE OF YOUNG

Post-fledging care, whilst in one sense an extension of incubation and pre-fledging care (and the duration of these three components correlate positively) is nevertheless a very important variable in breeding strategy, with complex costs and benefits. Seabirds have four options in the care they give to their fledged young. Parents can: continue to feed the free-flying juvenile at the site, matching the period to the difficulty of the juvenile's transition to independence; take it to sea, free-flying or otherwise, and feed it there; provide it with reserves to fuel it during the transition to independence; or do nothing for it after fledging and provide no reserves. These options are not independent of prefledging care, which in seabirds may last anywhere from 2 days to 11 months (reviewed by Burger 1980). The procellariforms feed their single young for up to 11 months (Wandering Albatross *Diomeda exulans*) but none feed young after fledging. Penguins either provide fat reserves or launch their offspring to coincide with a seasonal flush of readily-caught crustacea; but adults do not feed young after fledging even if they are not fully grown by then. Some gulls and terns favor extensive postfledging feeding (Ashmole and Tovar 1968). Some auks go to sea with their young, which in some cases carry out most of their growth there (see Sealy 1973). Not surprisingly, no seabird unequivocally adopts the fourth option (above). It would be maladaptive to invest so much in producing a chick only to fail with near certainty at the final stage. The reason lies in the nature of seabird feeding which, even in the simplest cases, is more difficult to perform than in birds (or mammals) whose young receive neither reserves nor post-fledging (or equivalent) care. These are all herbivores, gramnivores, omnivores or insectivores. Either the food is stationary and beneath their noses, or abundant and obtainable by stereotyped, innate or quickly learnt (by rapid trial and error) behavior. Also, the young of such species are usually led to feeding areas by their parents. Among land birds the best parallel to seabirds is the raptors, where post-fledging feeding is, as in many seabirds, prolonged.

Pelecaniforms adopt the first and third of the four options listed above. The phylogenetically primitive strategy in pelecaniforms, in conjunction with a clutch of several eggs (uniparity being

derivative) may have been to feed the mobile, free-flying or free-swimming young for a variable period at, or away from the site. The cormorants and pelicans still do this, though only the former extends feeding to free-flying young. Tree nesting populations of the Brown Pelican do not feed their young once these have left the nest (Schreiber 1977) but the young at 11–12 weeks are late in flying, and may have accumulated reserves (my speculation only). Many pelecaniforms, however, have departed from this simple pattern of feeding mobile young on- or off-site and prolonging the period where and when necessary. All tropical, pelagic pelecaniforms except tropicbirds have evolved long periods of post-fledging feeding. In the classic example, the frigatebirds, with up to 14 months post-fledging feeding and commonly 9–12 months, this huge parental investment demonstrably relates to the great difficulty experienced by newly independent young in securing prey for themselves. Nelson (1968) documented a drop in body weight to 640 gm for juvenile Great Frigates on the Galapagos even after several months of post-fledging support by their parents. Similarly, in all four tropical boobies (Masked, Red-footed, Brown and Abbott's) postfledging feeding is either on occasion or (in the case of Abbott's) always, more than 6 months in duration. The tropicbirds are seemingly anomalous in being classically tropical, pelagic and specialised (plunge divers) and yet lacking post-fledging feeding. Harris (1969a) *contra* Fleet (1974) makes this clear for the Red-billed and certainly the Christmas Island (Indian Ocean) race of the White-tailed did not feed their fledged young (Nelson, unpubl. data). However, Red-billed Tropicbirds, even in the Galapagos, reached weights of 120% adult weight, so presumably they fledge with reserves. I speculate that there are strong inhibitions preventing young of hole-nesting species from returning there, once fledged.

The most extreme departure from post-fledging care and concomitant provision of reserves and fat for their offspring is found in the Atlantic Gannet (Nelson, 1978). Laden with up to 1500 gm of perivisceral and sub-cutaneous fat, the young Gannet literally throws itself from the cliff top and flies for a variable distance before landing on the sea, from whence it is unable to rise until it becomes lighter. Its parents remain behind on the site. Australasian and Cape Gannets are intermediate between this extreme and the practice, amongst all boobies, of some post-fledging care. Some Australasian juvenals wander to the edge of the colony, exercise, and return to be fed for up to three days before fledging (Nelson, unpubl. data) after which they are on their own. Neither of these two allo-species fledge with as much fat as the Atlantic and both are less adapted

to cliff nesting, which makes return impossible (details in Nelson 1978).

As mentioned earlier, the adults of pelagic feeders, those pelecaniforms with the typical syndrome of single-chick broods, slow-growth, long-deferred breeding and high chick mortality, do not lose weight when feeding young even when these are starving. It would not pay off for a long-lived, slow-reproducing adult to stress itself in any one breeding attempt. For inshore feeders, with a different adaptive syndrome, the trade-off will be different and, using hypothetical but reasonable figures, this difference can readily be demonstrated. For them, it may be worthwhile to stress the parents and thereby produce more young.

ATTENDANCE AT BREEDING AREA AFTER DISPERSAL OF YOUNG

Adults which leave the site immediately after the young are independent save energy and gain nomadic foraging time, and can better exploit dispersed and patchy food offshore. All tropical pelagic pelecaniforms therefore abandon the breeding colony at this time. Even frigates, which require land for roosting, wander widely, roosting on many islands where they do not breed. The frigates that are always in evidence at some colonies are probably pre-breeders, breeders and immatures rather than immediately post-breeding adults. Tropical pelagic sulids turn up thousands of kilometres from the place where they last bred (Nelson 1978).

The implications of this essential requirement of tropical pelagic seabirds to spend significant periods of time as nomadic feeders have perhaps been largely overlooked by seabird workers. It is an item that has to be budgeted for in the reproductive lifetime strategy. It is especially important that the newly independent young of such seabirds have a long period during which they can wander at will, feeding opportunistically, unrestricted by the need to spend time and energy returning systematically to a fixed point. I would suggest that this requirement, more than any other, explains why seabirds lack cooperative breeding. Cooperative breeding is common among land birds especially those in rigorous, food-poor environments. Tropical pelagic seabirds would appear to be ideal subjects for cooperative breeding, but an essential prerequisite is that the young do not disperse, but remain in the parent's "territory" (= "breeding colony") and help with subsequent breeding attempts. This, I suggest, is precisely what the young of pelagic seabirds cannot do without serious risk of starvation. They need a larger foraging area and maximum time to forage if they are to survive. I am not aware that the almost complete absence of this major breed-

ing strategy, among such seabirds, has received comment, though it surely deserves it. Even among the inshore feeding marine cormorants and pelicans, there is considerable movement of adults and even greater movement of young birds, presumably for the same reason.

The only pelecaniforms which have incorporated into their breeding strategy a lengthy period during which the site is not only occupied but displayed-upon at high frequency and intensity are the gannets, especially the Atlantic Gannet. This species' three-month period of occupying the site after offpsring have departed is merely consistent with other evidence of the site's importance, which I relate to social stimulation and the timing of breeding.

ATTACHMENT TO BREEDING AREA

I refer here to a species' tendency to restrict further breeding to a precise locality, having once bred there. Philopatry, or the tendency of off-spring to return to breed where they were born is a separate phenomenon. Both are part of breeding strategy but in different ways. The former enables an individual to adapt to local conditions by learning, whilst the latter, theoretically, holds the possibility of genetically adapted local populations. Philopatry is important in the context of group selection, one of the main requirements of which is that local populations should be adequately isolated. The other requirement is that groups should go extinct often enough to make it a viable alternative to individual selection. There is some data from pelecaniforms on the first of these issues.

Species with permanent sites and mates obviously cannot change breeding localities but those with ephemeral attachments have this option. Conversely, if any factor compels a species to change its breeding locality at intervals, then a permanent site and mate would be ruled out. This seems rarely to apply to pelecaniforms.

The substantial advantages of remaining faithful to a locality in which one has bred successfully may be its safety and the knowledge of local feeding areas and conditions. The disadvantages may include denial of the opportunity to discover a better area, perhaps less crowded or safer, or nearer to good feeding areas and possibly (with time) increased risk of predation. An appropriate strategy might be for an individual to explore in the pre-breeding phase, visiting perhaps several colonies, but to remain settled once a choice has been made. Many seabirds do precisely that, and of course range extension and recolonization demand such pioneers. Perhaps because the advantages of remaining true to a locality having once bred there are great, and the strategy so widely adopted, there are no clear correlations

between this habit and the tropical or temperate regime.

Among phalacrocoracids, Guanay Cormorants constantly shift breeding locality (Murphy 1936, Hutchinson 1950). This is partly due to extensive human disturbance but perhaps also to the build-up of parasites in these teeming colonies. Common Cormorants and Shags, by contrast, are strongly attached, as individuals, to traditional localities though pre-breeders move between localities. Some marine (Brown) pelican colonies are traditional (Schreiber 1979) and presumably the same individuals remain there for life. Among sulids, the same individual adult Red-footed Booby has been captured whilst breeding on two widely separated islands (Woodward 1972) in different years. This sort of information is so extremely difficult to obtain that it might be unwise to assume that it only rarely happens. Masked and Brown boobies do commonly shift their territories within the colony (Kepler 1969, Nelson 1978) but this is not a colony shift. The Atlantic and Australasian gannets do not change colonies once they have bred; the proportion of marked individuals which return each year shows this unmistakably (Nelson 1978; Robertson, pers. comm.). Among frigatebirds, the Great and Lesser on Aldabra congregated densely in favored localities but, between years, did move several km. The possibility has been canvassed (Harris 1969b) that in the Galapagos and perhaps elsewhere, experienced breeding individuals of the Great and Magnificent Frigatebirds may move between colonies which are temporally out-of-phase and thus breed more frequently than once in two years. This seems unlikely if only because of the extreme length of the period of parental care and the need for breeding adults to moult and rest. The argument that such extremely K-selected species would be strongly disadvantaged if adults stressed themselves applies forcibly here.

The restriction of the *fulvus* race of the White-tailed Tropicbird to the Indian Ocean Christmas Island shows that it doesn't change breeding locality, but in the Galapagos the existence of different breeding regimes among Red-billed Tropicbirds on adjacent islands (Snow 1965, Harris 1969a) suggests that some interchange may occur. For example, birds returning for a new breeding attempt may be expected to go where there are most available sites and conspecifics in the appropriate phase of reproduction.

The tendency of pre-breeders to explore and attach themselves to a colony other than the one in which they were born is probably much stronger than that of experienced breeders to change colony. Banded cormorants, Shags, Atlantic Gannets, Red-footed, Masked and Brown

Boobies have all been recovered at non-natal colonies. Moreover, in the Atlantic Gannet the population increases at several colonies demonstrate, beyond doubt, the influx of very substantial numbers of immigrants (details in Nelson 1978). A study of Ailsa Craig Gannets (Wanless 1979) appears to show that many pre-breeders establish, defend and consistently attend sites among breeders for a season and then leave the colony and (presumably) go to another one. This finding, if corroborated, would have several important implications, not least for demography, but as yet is not fully acceptable. Undoubtedly, however, large numbers of pre-breeding gannets (as do many other seabirds) visit non-natal colonies and many settle there. On Clipperton Island, after pigs had been exterminated, the population of Masked Boobies rose dramatically within two or three years, presumably by an influx of pre-breeders.

Conclusion

Marine pelecaniforms show variable but usually strong attachment to a breeding colony, having once bred there, although many species move sites within the colony. Usually they return to breed in the colony of their birth but many visit other colonies as pre-breeders and may cause sudden and large increases in the breeding population. The degree of attachment to a colony and of philopatry is extremely difficult to determine but may be weakest in opportunistic breeders, which are usually tropical species.

SIZE AND SPATIAL CHARACTERISTICS OF THE BREEDING GROUP

The marine pelecaniforms congregate in colonies which may number less than 10 pairs (many phalacrocoracids) to several millions (mixed cormorant/booby/pelican colonies in Peru). Obviously, new colonies begin with one or two pairs but even long-established colonies, within most pelecaniforms, range greatly in size. Given the apparent lack of stringent selection pressure on absolute colony size, can any guiding principles be discerned? First, are colonies merely imposed by lack of sites, conferring, otherwise, no special advantages? Clearly this is not the case, since colonial seabirds are strongly attracted to colonies as such. The advantages may be proven safety and also social in nature. If social advantages are important, what are they and would they (and the safety factor) be expected to lead to ever-increasing colony-size until some limiting factor intervened? Such factors could be shortage of sites and density-dependent pressure on food within the colonies' foraging areas. Are small colonies as successful as large colonies? Are there differences in their respective social structures?

These questions move well into little-researched territory which requires a fuller review than is possible here. I will merely suggest some answers to these questions with particular reference to tropical versus temperate marine pelecaniforms.

A social advantage in large colonies is the greater pool of individuals available, for example, to newly established males "advertising" for females and to females prospecting for site-owning males. This saves time and effort and, if there is a mechanism for assessing individual fitness, a large colony applies this differential to a greater number, thus optimizing its effectiveness. It is not known whether, in seabirds, males or females are able to differentiate between "fit" and "less-fit" potential partners but some mammals and birds can make astonishingly subtle distinctions. Male Wood Pigeons (*Columba palumbra*), for example, can distinguish between females that have recently been courted by another male and those that have not (Rissman 1983). Among gulls there are significant differences in breeding potential between individuals. Thus, for example, the age of the male Red-billed Gull (*Larus novaehollandiae*) affects the female's clutch size (Mills 1973). Also, larger colonies presumably provide greater social stimulation and so colony size may help determine the timing of breeding and its synchrony in ways favoring larger colonies. Conversely, large colonies presumably increase interference by conspecifics. Social advantages, however, appear undeniably too slender to account for the presence of very large colonies. But, together with safety and limited availability of breeding locations, they could favor large colonies, the limits on which may then be imposed by site availability and by food. These are often impossible to disentangle.

First, sites themselves may run out. This clearly happened in several Peruvian seabird islands and operates in some Atlantic gannetries. Here enters the little-studied matter of site-quality. Seabirds undoubtedly select sites on the basis of many features. A cliffnester such as the Shag, although breeding on sites with a wide range of qualities such as distance from and above the sea, width and inclination of ledge, presence of protuberances and cracks, nearness to conspecifics, and other factors, is nonetheless applying different criteria than Gannets nesting on the same island. Optimal sites may run out. In tropicbirds, site requirements are such that demand outstrips supply. This accounts not only for the small size of tropicbird colonies but also for the notable competition (intra- and interspecific) and thus for the tendency of tropicbirds to utilize unsuitable sites such as holes in dense-jungle trees far inland on Christmas Island, Indian Ocean. Another population of this species nests in cliff

crannies miles inland in the Waimea Canyon of Kauai (Hawaiian Islands) and yet others on the open ground beneath *Casuarina* trees.

Second, food may limit colony size. The incontestable logic of the inevitability of density-dependent competition is one of degree rather than of decree. Species which forage close inshore must fairly soon begin to compete for food unless this is superabundant. Thus Common Cormorants normally form colonies of less than 200 pairs, whereas colonies of Quanay Cormorants of the rich Humboldt Current commonly number 200,000 or more. The one is probably in density-dependent competition for food, whilst the other probably is not. Among highly pelagic pelecaniforms density-dependent competition for food is also highly unlikely to be a factor in determining colony size. There is clear evidence that the role of food, vital though it is in determining breeding success in many tropical pelecaniforms, operates via oceanographic influences independently of bird numbers. In sum, therefore, the wide range of colony size in many pelecaniforms arises because a wide range of factors determine it and these operate in different combinations for different species and circumstances. There is a correlation between colony size and foraging habit, but loosely, if at all, between colony size and tropical or temperate distribution.

Is breeding success higher in larger colonies? Probably there is a difference only between very small colonies and larger ones. The breeding success of a very small and inaccessible Atlantic gannetry in Britain (at Bempton) increased with colony size but only until the colony reached about 40 pairs (Nelson and Fairhurst, unpubl. data). There is no reason whatsoever to suspect that large colonies of any species are, because of size, less successful than very large ones.

There may be differences in social structure between colonies of different size in at least some pelecaniforms. The Bempton colony of Atlantic Gannets, which was growing rapidly, contained a higher proportion of immature individuals, adult-plumaged pre-breeders and young breeders than did certain sub-sections of the Bass colony. But that was a function of growth rather than colony size, and in fact a rapidly-growing part of the Bass also exhibited the Bempton syndrome. No comparisons have been made between stable large colonies and stable small ones. Existing studies of colony structure in seabirds have all concentrated on ecological factors such as breeding success in relation to edge/centre position, age and experience, body-weight, pair-status and the spatial pattern of the breeders. Most of these are on gulls. In pursuit of the role of social structure and social stimulation we need also ethological longitudinal studies of the differences in

frequency and intensity of named behavior patterns in individuals of different social status (age, experience, position, nature of pair-bond, etc.).

Colony density is much more consistently species-specific than is colony size. Large or small, colonies of all pelecaniforms show recognizable typical densities. Topography places obvious constraints upon density but the latter is nevertheless under strong selection pressure in its own right. It cannot relate to food since it can make no difference whether Atlantic Gannets nest one meter apart or two. But they always choose the former. Where density is intra-specifically variable it may relate to available space. Thus, on some islands Cape Gannets pack much closer together than on others, but Atlantic Gannets maintain the standard spacing regardless of available space. Rather than food or space, social factors are most likely to "explain" observed density at the proximate level. These, however, have been largely neglected and I am unable to quote a single reference which relates the two (see below).

Conclusion

Colony size, enormously variable within and between species, relates to availability of sites, foraging mode, and social factors, rather than directly to tropical or temperate regime. Density is more species-typical and relates more strongly to social factors and colony size, but remains largely unexplored in terms of social behavior.

FUTURE WORK

I suggest that the following areas deserve study:

1. A comparative approach to breeding and stress. It must be significantly more worthwhile for breeding adults of some species, than for others, to subject themselves to harmful stress for the sake of increased productivity in the short term. Data are required on:

(a) The characteristics of first-time and experienced breeders (age, weight, behavior profiles) and their breeding success in temperate and tropical regimes. If field-cum-physiological data could establish quantifiable differences between breeders and non-breeders, and between breeders at the beginning and end of a cycle, we would have a powerful tool.

(b) The relationship between parental weight throughout a breeding attempt and egg/clutch size and chick growth.

(c) The nature and role of "rest" years on a widely comparative basis. The objective of these studies would be to understand the cost/benefits of the alternative strategies of higher productivity involving stress and a shorter breeding life or lower productivity but avoidance of stress and a longer breeding life. These may be studied be-

tween species and in relation to tropical (aseasonal) or temperate (seasonal) breeding regimes and also, possibly, within a species, where different strategies could comprise local adaptations. Group-selection may again become an issue in seabird biology.

2. The hitherto unremarked but intriguing absence of cooperative breeding in seabirds invites comment. There must be compelling reasons for this and my suggestion (that newly independent juvenals would be too heavily handicapped if they were to remain within the limited foraging area available to colony-attached birds rather than wandering more widely during this critical period) is only one.

3. Social behavior (discrete, defined and quantifiable behavioral items) in relation to colony size and density, social status, overall and subgroup synchrony, permanence of site and pair bond and productivity should be studied over the lifetime of known individuals.

The social aspects of coloniality remain little understood and, in conjunction with a more sophisticated approach to the matter of site-quality in physical terms, could help to define the causes of colony-size and spacing in seabirds, at the proximate level. Perhaps the most conceptually important data will come from that demanding and time-consuming project, the long term study of local populations and marked individuals, for which the pelecaniforms are so well suited.

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