

THE REGULATION OF NUMBERS OF TROPICAL OCEANIC BIRDS

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It has been argued by Lack (1954) and others, that most bird populations are stable—in the sense that they are not in the process of expanding indefinitely, or of declining to extinction—and that this stability must result from the operation of density-dependent regulating factors: that is, factors which ensure that a population increase results in a lower reproductive rate, or a higher death rate, and so leads to an eventual halt in the increase, and that a population decrease normally results in a higher reproductive rate, or a lower death rate, so that the decrease does not continue to extinction.

I fully accept the contention that in a stable bird population the numbers must be regulated by the operation of density-dependent factors. However, I will in this paper be considering mainly populations of sea-birds, and it must be kept in mind that many of these populations have been very greatly affected, during the last few centuries, by the activities of man and of the predators introduced by him. Since most sea-birds have low reproductive rates, it is likely that the populations of many species have not, since then, achieved stability. Much of the argument which I shall put forward is related primarily to stable populations; it therefore relates essentially to populations in a fully natural state, and should be applied only with caution to particular present-day populations, especially in areas where the interference by man has been greatest.

Factors which are theoretically capable of maintaining stability in bird populations, by exerting density-dependent control of reproductive or mortality rates, include predation, disease, the availability of nest sites, and food supply. The possibility must also be kept in mind that two or more of these factors may in some cases operate together to limit populations. Furthermore, one of these factors, for instance food supply, may affect both the reproductive and the mortality rates, or may have several different density-dependent effects on one or the other.

So far as predation is concerned, it seems certain that at the present time many islands are made uninhabitable for certain species of sea-birds by the presence of introduced predators, notably rats and cats. However, apart from this, adult sea-birds, especially in the tropics, suffer remarkably little predation, and there is no evidence that the numbers of any species of tropical sea-bird are limited by the mortality of adults caused by natural predators. Predation on eggs and young by native predators is sometimes serious, and may in many cases determine the choice of sites for breeding, but it seems unlikely that it is often density-dependent, or that it regulates the size of the populations.

Disease, again, could limit sea-bird populations, but there is no positive evidence that it normally does. Thus, although so little is known about the incidence of disease in sea-birds that the possibility that it is important in some species must be kept in mind, it seems unlikely to operate in most cases.

There are of course some sea-bird breeding stations where only a limited number of nest sites are available. Even here, however, the limitation of nest sites is not completely straightforward. Thus, in a bird population breeding in one of these places, so long as the number of young produced by the birds breeding in available sites outweighs the losses of adults, non-breeding adults will accumulate. At first these surplus birds might be able to emigrate to unsaturated nearby colonies, or to found new ones. But once all the colonies in the area are fully occupied, and there are no suitable sites for new colonies, the non-breeding section of the population must presumably continue to increase, until eventually the point is reached at which the total annual mortality of breeders and non-breeders combined just balances the recruitment into the adult population of birds raised in the available sites. This point must eventually be reached even if the absolute total

production of young, and the proportionate death rate of the adults, remains constant. In practice the point of balance might be reached rather soon, since as the population increased, the intense competition for nest sites would be likely to increase the losses of eggs and young. The situation described by Stonehouse (1962) in the tropic birds *Phaethon* spp. on Ascension Island, suggests that their populations are now limited by nest sites, but that the control is exerted not primarily through the inability of some adults to obtain sites, but through the high losses of eggs and young caused by competition for the sites. Another population which may at present be limited by the availability of nest sites is that of the Great Shearwater *Puffinus gravis* on Nightingale Island (see account by Rowan 1952). However, among tropical sea-birds it is unusual to find nesting colonies occupying all the available ground, and in all the cases where there is excess space available, some other limiting factor must be operating.

While realizing that one or more of the factors just considered can theoretically, and may at times in practice, limit the numbers in bird populations, many recent authors, especially Lack (1954), Southern (1959) and Wynne-Edwards (1962), have argued that the remaining factor—food—limits the numbers of most birds, acting either directly, or indirectly through behavioural mechanisms (especially Wynne-Edwards 1962). In this paper I shall consider the ways in which the food supply could limit the numbers of tropical sea-birds.

If an animal population increases, and no other density-dependent factor intervenes to stop the increase, the animals must eventually run short of food, and density-dependent effects resulting from food shortage will prevent further increase. As already stated, density-dependent limiting factors can operate by reducing the reproductive rate, or by increasing the mortality, as numbers increase. Lack (especially 1947–48 and 1954) argued forcefully that in all birds the reproductive rate, evolved by natural selection, is that which normally gives rise to the greatest number of eventual descendants; this view has been criticized (especially by Wynne-Edwards 1962), but no satisfactory alternative has been offered. Lack also argued that in most species there is little indication that clutch-size is affected by the population density to an extent sufficient to regulate numbers. By implication Lack also rejected nestling mortality as being an important regulating factor, and concluded that it is mainly density-dependent variation in mortality of adults and independent young which must limit most bird populations. He suggested that in birds competition for food is usually the factor which is responsible for this density-dependent variation in the mortality, although predation is apparently the main factor in certain gallinaceous birds, and populations of some species may be limited by a complex interaction of density-dependent mortality factors.

Wynne-Edwards (especially 1962), while agreeing with Lack that food is the factor which ultimately limits the numbers of most birds, suggests that many species have the capacity to control their own population densities, and to keep them as near as possible to the optimum level for each habitat they occupy. He argues that populations can control, to a great or lesser extent, recruitment arising from reproduction, immigration and emigration, and a certain part of their mortality (which he calls “social mortality”). By this means, he suggests, the members of a population, acting together, are able to ensure that the recruitment into the population balances the losses from it, and that numbers remain continually close to the highest level which can be maintained without over-exploiting the food supply.

Among other examples, Wynne-Edwards (1955, 1962) points to the low reproductive rates of many sea-birds, and suggests that in these species, which have low adult mortality, “restrictive adaptations” have been evolved to reduce the reproductive output below that which could be achieved. Thus he says (1955 : 541): “low recruitment is largely a consequence of a series of adaptations, which seem to have been evolved for no other purpose”. The characteristics of the long-lived sea-birds which Wynne-Edwards

considers to be restrictive adaptations are the laying of a clutch of one egg, single-broodedness and the failure to replace lost eggs, the prolongation of the incubation and fledging periods, reproductive cycles exceeding one year, and the deferment of maturity.

It is clear that if these features are present in a species, it cannot have a high reproductive rate, but this alone would not ensure that in a given population the production of young would precisely balance the mortality. This balance could be achieved by variation in the extent of the deferment of maturity (i.e. variation in the age at which breeding starts), but Wynne-Edwards suggests that in addition a "density-dependent brake" can be applied to the rate of recruitment to a population (here not specifically a bird population) in various ways, including, "increasing the losses due to parental neglect, cannibalism, social stress and similar intrinsic causes" (1962 : 527). Again (p. 530) he says "What is produced in an average breeding season [in birds] is sufficient to make good the losses in the stock, or to take advantage of prevailing economic conditions, but the population ordinarily withholds a reserve of reproductive power, to be exercised fully only under exceptional conditions of understocking and regeneration".

The two species of tropical tern which I have studied on Ascension Island (the Wideawake *Sterna fuscata* and the Black Noddy *Anous tenuirostris*), and also the Fairy Tern *Gygis alba* and the Brown Noddy *Anous stolidus* which also breed there, show several of the characteristics of long-lived sea-birds which were pointed out by Wynne-Edwards. In particular they lay only one egg, are single-brooded and often do not replace lost eggs, and have long incubation and fledging periods; we do not know at what age they first breed. The same tendencies are found also in the other groups of tropical sea-birds—the boobies *Sula* spp., tropic birds *Phaethon* spp. and frigate birds *Fregata* spp. They are also shown by both the tropical and temperate-zone species of Procellarii, which are also known in many cases to have long periods of immaturity.

Convergent evolution of these features in nearly all the tropical oceanic members of several different groups, and of some of the same features in temperate-zone species, implies that they are adaptations associated with certain common features of the way of life of the species involved. Like Wynne-Edwards, I believe that the most important common feature is the oceanic habitat and the associated generally low adult mortality. I shall argue that this low mortality is also more or less independent of density, and that, as suggested by Wynne-Edwards, many populations of oceanic birds are regulated by density-dependent variation in the reproductive rate, or in the recruitment of adults to the breeding population. However, I do not agree with Wynne-Edwards that the reduction in the production of young, as the numbers increase, is an adaptation evolved to limit the numbers below the level at which food would run short: I suggest instead that the characteristics of the individuals in the population are adapted to rearing the greatest possible number of young under the conditions prevailing, and that as numbers increase, the production of young per pair falls, and in addition young individuals may be prevented from breeding, as a result of competition for food round the breeding colonies. I therefore believe that it is a forced reduction in the reproductive rate, and sometimes also a forced increase in the deferment of maturity, as numbers increase, which limits the numbers of many oceanic birds, especially in the tropics.

Before presenting my hypothesis in detail, I must say why I feel bound to reject Wynne-Edwards' suggestion that long-lived sea-birds have evolved special characteristics which lower their reproductive rate below the potential rate, especially when the population is high, and so limit the population at a level below that at which it would "overfish" its food supply. My main reason is that it seems impossible that individuals which developed any characteristics which lowered their output of young could compete under natural selection with others that did not develop them, and continued to reproduce at a faster rate. Wynne-Edwards is aware of this difficulty and invokes group selection as an overriding force: he apparently envisages that populations which evolve mechanisms

allowing them to limit their own size and so avoid over-exploiting their food supply will persist for long periods, while populations which do not regulate their own numbers in this way will "overfish" their food supply and dwindle or become extinct, eventually being replaced by colonists from the self-limiting populations.

If populations with the required characteristics did in fact exist, this mechanism might sometimes operate, although in sea-birds it seems unlikely that even a population which was not self-limiting could over-exploit its food supply so drastically that it would itself become extinct: it is more likely that as the population increased, the amount of food obtained by each bird per day would decrease, until the population was stabilized by the competition for food. Furthermore, because of the overpopulation and shortage of food which would occur in the area utilized by the population which was not self-limiting, it is likely that there would be emigration from it into the territory of the self-limiting population: there would thus tend to be gene flow into the self-limiting population from the stock in which the characteristics necessary for self-limitation were not developed.

However, a more fundamental objection to the form of group selection envisaged by Wynne-Edwards is the difficulty of understanding how any self-limiting population could evolve. A crude illustration of the difficulty is the evolution of a clutch of one. Wynne-Edwards considers that the laying of a clutch of one is a "restrictive adaptation", evolved to reduce the reproductive output below the potential level; he points out that it must be a specialization, since all modern birds which lay only one egg must have evolved from species—bird or reptile—which laid more. The evolution of a clutch of one must therefore have taken place through the existence of variation in the size of the clutch laid in the ancestral population, and selection of the genotype which led to the laying of small clutches rather than larger ones. Now, as Lack (1954 : 22) pointed out, "If one type of individual lays more eggs than another and the difference is hereditary, then the more fecund type must come to predominate over the other (even if there is overpopulation)—unless for some reason the individuals laying more eggs leave fewer, not more, eventual descendants." Since in fact the individuals laying the smallest clutches have been favoured by selection (in nearly all oceanic birds) it must be assumed that by doing so they leave more descendants than those laying larger clutches. This conclusion seems to eliminate the possibility that the consistent laying of a clutch of one could be evolved as an adaptation to reduce the reproductive rate below the potential rate.

A similar difficulty arises in relation to the phenomenon of deferred maturity, which plays an important part in Wynne-Edwards theory that many animals have adaptations enabling them to control their own population densities. Wynne-Edwards suggests that populations, especially of those species among the higher animals in which there is a long span of individual life, limit their densities "by holding back a reserve of full-grown adolescents or virgin adults and admitting to breeding status only the number actually justified at the time by circumstances" (1962 : 557). In respect of sea-birds, he argues that there is a "conventional limitation of the number of acceptable sites" (1962 : 157), and that an individual which does not own such a site is inhibited from breeding. The implication is simply that in a population which is well below the food limit all young birds are allowed to join the breeding population as soon as they are capable of breeding, but that when the food limit is approached the breeding adults stabilize the population by preventing (in some way) young adults from achieving breeding status, only allowing in enough to balance the losses of old breeders.

If it operated, such a mechanism could indeed serve to disperse and eventually to limit the population of a colonial sea-bird, and would in the process generally produce a surplus of individuals which, although they were several years old, did not yet breed. However, Wynne-Edwards' suggestion is unsatisfactory in several ways. First, although it is true that colonial sea-birds generally defend the area round their nests, and there is

often competition for nest sites, this appears to be acute only when the number of sites suitable for breeding is limited by the terrain, and I know of no case in which it has been shown that new pairs are prevented by the members of the colony from settling on unoccupied ground suitable for breeding.

This is not to deny that in some highly social species (including the Black Noddy on Ascension—Ashmole 1962) there is an extremely strong tendency for all individuals to try to nest in an existing colony rather than colonizing new areas some distance away, which appear to be almost equally suitable for nesting. There are, however, two reasons why the tendency to choose a nest site within an existing colony might be selectively advantageous, and so be established as a characteristic of the species, even though it may occasionally lead (as it did in the Black Noddies on Ascension) to unsuccessful attempts to breed in an overcrowded colony when successful breeding might be possible elsewhere. First, there may be advantages in breeding among other individuals of the species (for instance reduced predation in species which have a more or less communal defence against predators). Second, it could be that for young individuals choosing a place to breed for the first time, the best indication of a place suitable for breeding is the presence of a colony: it can usually be assumed that places which do not hold colonies are less suitable for breeding than those that are already occupied.

Returning to Wynne-Edwards' hypothesis as to the way in which colony size is limited, it should be mentioned that he implies that birds (especially young adults) which have failed to obtain nest sites within the recognized boundaries of the colony, will normally be inhibited from breeding, even if there are other sites suitable for breeding unoccupied just outside the colony (see, for instance, 1962 : 156–157). I think it unlikely that this occurs, but even if it did, it need not be interpreted as evidence for a self-regulatory capacity in the population: in many species individuals breeding at the edge of a colony are more exposed to predation than those at the centre, so that in some populations individuals which missed a breeding season rather than breed on the edge might not be eliminated by selection.

Finally, considering the deferment of maturity more specifically, it seems clear that if a prolonged period of immaturity was forced on young sea-birds by the members of the breeding population (as it is, for instance, on young males in polygamous species of pinnipedes), selection must favour those individuals which manage to breed soonest. This selection would surely quickly eliminate meek acceptance of a "conventional limitation" to the size of the breeding colony. Since there is no evidence that members of sea-bird colonies employ the alternative of physical force to prevent individuals from breeding outside the "recognized boundaries", it seems necessary to reject Wynne-Edwards' hypothesis that dispersion and regulation of numbers of colonial sea-birds is achieved by the existence of conventional limits to the size of the colonies. I should mention, however, that Lack (1954) has made a plausible suggestion as to the way dispersion could be achieved in those colonial species which do not breed in their first year. If the young spent at least one summer in the vicinity of a breeding colony before starting to breed, they could sample feeding conditions and settle to breed there in the next year if food was sufficiently abundant, or go elsewhere if food was scarce. In fact, in the Swift *Apus apus*, the Heron *Ardea cinerea*, the Rook *Corvus frugilegus* (Coombs 1960) and in many species of sea-birds, the young do visit the breeding colonies in the years before they breed. The mechanism suggested by Lack depends only on different responses by individuals to favourable and to unfavourable conditions, and it could therefore be evolved without the aid of group selection. It could explain dispersion of a population over the available habitat, but does not of course provide a density-dependent mechanism for regulating the size of the whole population.

If we reject Wynne-Edwards' hypothesis as to the way in which sea-bird numbers are regulated, what alternative explanation is available? I suggest that the food supply,

acting directly (not indirectly as postulated by Wynne-Edwards), is the factor most likely to be exerting a density-dependent effect on the numbers of tropical sea-birds, and to be responsible for regulating their numbers; it may also control the numbers of some sea-birds breeding at higher latitudes. If food is the critical factor, it could be exerting its density-dependent effect either on the mortality of adults, outside the breeding season; or on the mortality of fledged young, after they have left the colonies; or on the output of young, by regulating the breeding success and/or the rate of recruitment of adults to the breeding population. As already mentioned, I support the third hypothesis.

I cannot believe that density-dependent mortality of adults from starvation, outside the breeding season, is an important factor in regulating the numbers of most species of sea-birds. Density-dependent factors can operate only when members of the population are competing with one another. Thus if food is the limiting factor, competition is occurring, and can limit the population, only if an increase in numbers makes it significantly more difficult for each individual to obtain enough food. Thus competition will not occur unless the population is appreciably depleting the stock of food. Now when oceanic birds are not breeding they have available to them any feeding grounds rich in the food they are adapted to collect: these feeding grounds are so extensive, and the amount of food in them so great, that I think it is unlikely that the birds are greatly depleting the stock. But unless they are, density-dependent mortality from food shortage cannot occur.

Adult mortality at sea is low, and as I have said, it seems most improbable that it could be density-dependent, except under special circumstances. Mortality among fledged young, after they have left the colonies, is much higher, and may be largely caused by starvation. However, for the reasons given above in relation to adults, I think it is unlikely that in many species the mortality among juveniles after they have dispersed over the most favourable feeding areas, is to a significant extent density-dependent.

The sea cannot, of course, support an infinite number of birds: if the populations were sufficiently large, the total food supply of the species would be depleted and there would be density-dependent mortality among adults or fledged young. I suggest however, that long before their populations reach the level at which this could occur, many species, especially in the tropics, run short of food round the colonies in the breeding season. If so, the resulting competition for food, long before it becomes severe enough to affect the mortality of adults, will lower the reproductive success by preventing the less efficient individuals from rearing young; at the same time young adults, if they are less efficient at collecting food than more experienced individuals, may be prevented from even attempting to breed, thus leading to deferment of maturity and reducing the recruitment to the breeding population. I suggest that these two effects of competition for food round the breeding colonies together regulate the numbers of most tropical oceanic birds, and possibly also those of some species breeding at higher latitudes.

There are three main reasons why I think it is so much more likely that populations of tropical sea-birds are regulated by competition for food round the breeding colonies during the breeding season, rather than at other times. First and most important is the fact that most sea-birds can spread themselves in the non-breeding period over all the suitable feeding areas, but have to breed on land. Therefore their breeding distribution is largely governed by the distribution of islands suitable for breeding, and while breeding they must either use only a small proportion of the total available feeding areas, or they must spend much time flying to and from more distant feeding areas. Second, in order to breed successfully, the birds must collect food more quickly than in the non-breeding period, because of the extra demands of courtship, the production of egg(s), incubation and the feeding of young. Third, while at high latitudes there is generally an enormous flush of marine food in the spring, which must tend to reduce competition for it, in

tropical oceans seasonal fluctuations in food abundance are generally much less extreme, and marine food is unlikely ever to be superabundant, except in certain special areas.

I am suggesting that unless some other factor limits the numbers, competition for food round the colonies will gradually become important as the population increases, so that the birds will be unable to collect so much food per day as when the population was small, and will find difficulty in raising young. Eventually the food shortage will become so acute that the production of young will decrease to the level at which it just balances the mortality of adults and fledged young.

It is of interest that Paludan (1951) in his work on the Herring Gull *Larus argentatus*, has argued that in this species also the population could be potentially controlled by a density-dependent variation in the production of young, operating by increased eating of young by adults, when a high population has made feeding difficult. However, it is not necessary to suppose, in this case, that eating of chicks by adults has evolved, by group selection, as a mechanism for limiting the population; it could have evolved through individual selection favouring those adults which found food for their young, even though it consisted of their neighbours' offspring.

In populations limited in the way I have suggested the reproductive output of the individuals will on average be determined solely by the mortality rate. Now the mortality of adult sea-birds is generally low (most of the few available figures are given by Lack 1954), so that the reproductive output must also be low. It is of course possible that the mere fact that tropical seas are relatively unproductive, might prevent some species from rearing more than one chick, even in the absence of intraspecific competition for food. However, the evolution of a clutch of one would be inevitable even in the case of a bird species which, when first introduced into a virgin area, was able to collect enough food to raise several young. As the population increased, competition for food round the colonies would reduce the breeding success, and finally, if the adult mortality was sufficiently low, the stage would be reached at which a clutch-size of one was more productive than larger clutches, because the collection of food would take so long that parents trying to raise several chicks would end by raising none.

Since most sea-bird populations before the arrival of man were presumably generally stable and saturated, it is not surprising to find that virtually all tropical sea-birds, and many species breeding at higher latitudes, lay only one egg. This merely implies that their adult mortality is so low that a balanced population is only attained when each pair produces less than one chick per season.

However, the evolution of a clutch of one cannot by itself regulate the numbers in a population, since if the population can maintain itself with a clutch of one, its numbers will still tend to increase indefinitely, though slowly, unless some additional factor halts the increase by reducing the reproductive rate yet further, in a density-dependent manner. If one was not the minimum clutch, the population might be regulated by further, density-dependent reduction in the clutch-size as numbers went up. Since this is not possible, all the pairs have to try to raise a whole chick each season; as a result, breeding success may be very low, as it was in several species on Ascension (see Dorward 1962). My suggestion is that the extra density-dependent control is provided by the increased difficulty in collecting food, and the consequent lower breeding success, as numbers increase. If so, it is primarily density-dependent variation in the breeding success which controls the size of the population.

In a population regulated in this way, the birds will normally be working near the limits of their food-collecting capacity, even if they lay only one egg. (This is inevitable on my hypothesis, since if they were not, reproductive success would be high, and the population would increase until competition reduced the success.) One might therefore expect short-term and even slight fluctuations in the availability of food to have a profound effect on the breeding success in particular seasons or parts of seasons.

In fact, periodic mortality of chicks from starvation, of the kind we observed on Ascension among Black Noddies (Ashmole 1962), Wideawakes (Ashmole 1963) and Brown Boobies *Sula leucogaster* (Dorward 1962), is recorded in a number of populations of tropical sea-birds. In the Wideawake, starvation of chicks has been reported in the Kermadec Islands (Guthrie-Smith 1936) and on Christmas Island, Pacific Ocean (Gallagher 1960); on the other hand Bartsch (1922) suggested that an epidemic had caused the death of the adult and young Wideawakes whose corpses he found on Midway Island. Among other tropical sea-birds there is less evidence for starvation, although this may be due to lack of observations. Richardson & Fisher (1950) record the death of many young Brown Noddies, apparently from starvation, on an island off Oahu, Hawaii, while Hoogerwerf (in van Bemmelen & Hoogerwerf 1940) records deaths, apparently from starvation, in young Red-tailed Tropic Birds *Phaethon rubricauda* and Brown Boobies on Goenoeng Api in the South Banda Sea; Galtsoff (1939) mentions the death from starvation of many young Laysan Albatrosses *Diomedea immutabilis* on Pearl and Hermes Reef, Hawaii. There are doubtless other examples scattered in the literature.

For the present argument, it is not only the occurrence of occasional mass starvation of chicks which is of interest. It is important to know whether mortality of chicks from starvation is regular among populations of tropical sea-birds laying clutches of one, and if so, whether it is on average density-dependent, as it was shown to be in the Tawny Owl *Strix aluco* (Southern 1959). Since fluctuations in the food supply from year to year will result in high breeding success in some years even when the population is large, and in low success in some years with a small population, long-term studies of populations changing in size would be needed to show a density-dependent effect: the build-up of a population from a low level, after the cessation of predation by man, might provide an ideal opportunity for such a study.

It is clear that if competition for food round the breeding colonies of tropical oceanic birds is always severe, and chicks often die of starvation or fledge underweight, there will be almost continuous and extremely severe selection for the ability to raise a chick under adverse conditions. It is this selection which I consider to be responsible for the presence, in so many oceanic birds, of the peculiarities to which Wynne-Edwards (1955) has drawn attention, and which will now be considered in greater detail. The presence of these characteristics is difficult to explain on any other hypothesis, and I regard their widespread occurrence as striking evidence that the numbers of many sea-birds, including some outside the tropics, are limited in the way I have suggested.

I have already discussed the evolution of the laying of a clutch of one, and have concluded that it results inevitably from the inability of the parents to feed more than one chick, because of competition for food. The boobies (*Sula* spp.) are unusual among tropical sea-birds in that some of them lay clutches of more than one: Murphy (1936) gives the clutch as normally two in *Sula dactylatra*, one to three (normally two) in *S. leucogaster*, one to three in *S. nebulosus* and one to four in *S. variegata*. The last species inhabits the rich waters of the Humboldt current, an area where periods during which food is extremely plentiful are punctuated by disastrous seasons in which marine conditions change entirely, and many adult birds die (Murphy 1936, Lack 1954); *S. nebulosus* replaces *variegata* further north, and is probably also affected by the catastrophes. These two species may therefore have rather high adult mortality, coupled with generally rich food supplies, and their population dynamics are probably not typical of tropical sea-birds. *S. dactylatra* and *S. leucogaster* are more typical tropical species, and it is of interest that although they normally lay two eggs, on Ascension at least they hardly ever raise two young. Dorward (1962) found that when both eggs hatched, the younger chick was almost invariably found dead outside the nest within a few days; he concluded that the elder chick ejected the younger from the nest. Experiments suggested that in the young of these boobies special behaviour has been evolved which

usually enables the first-hatched chick to eliminate the second, which might otherwise compete with it for food. An explanation for the laying of two eggs is therefore required, and Dorward suggests that the second egg is an insurance against the loss of one during incubation, or the failure of one to hatch.

It could be argued that if it is worth while for a booby to lay an extra egg as an insurance policy, other tropical sea-birds should also lay two eggs. However, in most other species the single egg is far larger relative to the bird than in the boobies (Stonehouse 1963); this could mean that in the boobies, selection has favoured the laying of an insurance egg, but that in other species in which it is for some reason important to have chicks which are large at hatching, it is more advantageous to lay a single large egg.

The next of the peculiarities mentioned by Wynne-Edwards is single-broodedness and the failure to replace lost eggs. The raising of only one brood in a season is so general among species in which the incubation and fledging periods are long that it does not require a special explanation. The failure to replace lost eggs is a striking characteristic of the Procellarii, which normally do not lay again even when the first egg is lost early in the incubation period (for a few exceptions see Davis 1957). Except in this group, however, failure to replace lost eggs is not closely correlated in its occurrence with the other peculiarities which contribute to the low reproductive rate of sea-birds. Some bird species which lay large clutches do not replace them if they are lost, and some tropical sea-birds which lay only one egg yet often replace it (for instance the Black Noddy—Ashmole 1962).

I would suggest that the extent to which lost eggs are replaced is related primarily to the length of the season favourable for breeding, and that if the season is short there is no point in laying a replacement egg, since the chick will hatch too late to have a reasonable chance of fledging successfully. If this is the correct explanation, one would expect to find that eggs lost early in incubation were more often replaced than those lost later: this is at least generally true. One would also expect a lower rate of replacement in species in which the manufacture of the egg takes a long time, and it is probably no coincidence that in the Procellarii, which do not normally lay replacement eggs, there is evidence suggesting that several weeks may be needed for the production of the egg (cf. Wynne-Edwards 1962 : 489). Thus in several species of Procellarii the female, and sometimes also the male, is generally absent from the colony for a considerable period immediately before laying: presumably the female needs to spend this time in intensive fishing, in order to produce the egg. In the Short-tailed Shearwater *Puffinus tenuirostris* both sexes desert the colony entirely for three weeks, returning on the night of laying (Marshall & Serventy 1956). When they return, the females, which have just completed the production of an egg weighing about 16% of their body weight, have some fat, but the males, which take the first incubation shift of eleven to fourteen days, have a large quantity. Another case is that of the Dove Prion *Pachyptila desolata*, in which the female rarely visits the nest during a period of seven to fourteen days before laying, although the male returns each night to the burrow, keeping it clear of snow (Tickell 1962). Tickell has also collected records referring to several other species of Procellarii.

The fact that in the species just mentioned, all of which breed in seas which in the breeding season are much richer than most tropical seas, the production of the egg requires a special feeding effort over a considerable period, suggests that food round the colonies is by no means superabundant. One might expect the production of the egg in tropical species to be much more difficult. Relevant information is scarce, but the fact that in Wideawakes and Black Noddies on Ascension replacement eggs are laid about two or three weeks after loss (Ashmole 1962, 1963), and in Yellow-billed Tropic Birds *Phaethon lepturus* 23–30 days after loss (Stonehouse 1962), suggests that in tropical sea-birds the production of the egg requires a considerable period of intensive feeding.

Before leaving the subject of the failure to replace lost eggs, it should be mentioned that in species in which the incubation shifts are long (as in most Procellarii), the infrequent

meeting of the members of the pair during incubation could lead to difficulty in achieving the re-coordination of the sexual cycles of the birds which would be necessary for re-laying.

Long incubation and fledging periods are other characteristics of all the Procellarii, of many tropical sea-birds in other groups, and of some large land-birds. Wynne-Edwards (1955), commenting on this peculiarity, suggests that because of the high losses of eggs and young "the conclusion cannot easily be avoided that if the incubation and fledging periods were shorter, egg and chick mortality would be less". It is true that if fledging periods were shorter, mortality caused by predation and some other factors would normally be lower, but it is reasonable to suppose that deaths of chicks from starvation—which could well be more important—would be higher in most cases. This is because the faster a chick grows the more food it will need each day; if the parent can collect food only slowly, there will, as suggested by Lack (1947–48), be selection for a slow rate of growth, to spread the load of food collection over a long period. However, the chick before it can fly is exposed to various hazards, so that, as Wynne-Edwards pointed out, a long fledging period will increase some forms of mortality. The observed result of these conflicting pressures is that, while the fledging period is very long in most sea-birds laying clutches of one, it is also more or less flexible, so that the birds can take advantage of periods when food is abundant by growing rapidly, but can survive for long periods with negligible growth, when food is short. This is also the adaptation evolved by the Swift *Apus apus* (Lack 1956).

We saw on Ascension an instance in which the flexibility of development in the Wideawake was brought into play, and apparently was responsible for the fact that a few chicks fledged successfully even in the second breeding period we observed, when food was evidently very short: the chicks grew much more slowly than in the previous breeding period, but some of them did survive (Ashmole 1963). On the other hand the Black Noddy chicks, which were also capable of surviving for long periods with very little food, did not benefit from it in the season we observed, since all the chicks hatched early in the season grew rapidly and fledged successfully, while later food shortage was apparently so acute that all the late chicks eventually died (Ashmole 1962). Even the shortest fledging periods which we observed in the Wideawake (about eight weeks), in the Black Noddy (about six weeks) and in the Fairy Tern (not less than about nine weeks—Dorward 1963) are long compared with those found in the terns of temperate regions, which also differ in laying larger clutches. For instance young Sandwich Terns *Sterna sandvicensis* can fly at five weeks, Common Terns *S. hirundo* at four weeks, and Arctic Terns *S. macrura* at three weeks (Witherby *et al.* 1941). There are also indications that the fledging period may differ in different parts of the range of a single species: the best evidence is that given for the Fairy Tern by Dorward (1963), but the Wideawake seems to show similar variation (Ashmole 1963).

An extended fledging period in birds which have a clutch of one is an expected corollary of the hypothesis which I have put forward; on the other hand the long incubation periods shown by many species with exceptionally long fledging periods are more difficult to understand. Lack (1947–48) pointed out that there is a general correlation between the lengths of the incubation and fledging periods in different groups of birds, and suggested that while it was difficult to see how selection could favour the lengthening of the incubation period as such, it was possible that slow development of the young bird, as just discussed, might be most easily evolved by the reduction of the rate of development as a whole. It is reasonable to suppose that pre-hatching and post-hatching development are so closely linked physiologically that it would be difficult for selection to change the rate of one without affecting the other.

Reproductive cycles exceeding one year are included by Wynne-Edwards (1955, 1962 : 489) among the other characteristics which he suggests have been evolved to reduce the reproductive rate below that which could be achieved. Such cycles occur in the

Royal and Wandering Albatrosses *Diomedea epomophora* and *D. exulans*, where they are probably merely the consequence of extreme lengthening of the fledging period through selection of the kind already discussed. The King Penguin *Aptenodytes patagonica* also has a reproductive cycle exceeding one year (Stonehouse 1956, 1960), but the Emperor Penguin *A. forsteri* does not. Wynne-Edwards implies that since the Emperor Penguin can rear a chick in less than a year, the King Penguin could also do so, but Stonehouse (1956 : 61-63), considering this problem, concluded that the different breeding cycles in the two species were related to differences in their environments, and that "King Penguins, like Emperors, have adopted the only mode of life possible to them".

Finally, we may return to the problem of deferred maturity, one of the most striking features of the biology of many sea-birds (although it occurs also in some land-birds), and one for which no satisfactory explanation has been advanced in the past. Wynne-Edwards (1962 : 572) has listed the species in which the phenomenon is best documented, but a few others may be mentioned. In the Manx Shearwater *Puffinus puffinus* there is no precise information, but most individuals apparently do not return to their colonies until they are at least three to four years old, and it is quite likely that they do not breed in the first year when they are back on the breeding colonies (Orlans 1958). On the other hand among smaller Procellariii the deferment of maturity seems to be less extreme : Richdale (1949) found three Diving Petrels *Pelecanoides urinatrix* occupying burrows as yearlings, and seven birds, including these three, reared chicks when two years old; in Leach's Petrel *Oceanodroma leucorhoa* Gross (1947) records that two yearling birds were seen in burrows, while three-year-old birds were known to breed. Wodzicki & Stein (1958) found that young New Zealand Gannets *Sula bassana serratior* first began to appear at their home gannetry at the age of three years, but that the youngest birds breeding were 4-5 years old, and that at the age of 6-7 years still only about half the birds were breeding.

Since nearly all the birds in which deferred maturity occurs have completed most of their growth even before they can fly, it seems likely, as Lack (1954) suggested, that sexual maturity in the first year of life could have evolved if it was advantageous. Every year spent before starting to breed must increase the chances of dying without offspring, and this must result in strong selection for breeding when as young as possible. This selection could be neutralized if breeding when very young reduced the expectation of life of the birds concerned, and this was the basis for Lack's suggestion that the strain of breeding would be so great for young individuals that, through natural selection, the age of first breeding has been retarded: however, I do not think that this can be the only reason for the deferment of maturity. I have already discussed the difficulties in accepting Wynne-Edwards' alternative hypothesis that the age at which young birds first breed is controlled primarily by the older (breeding) members of the population, in such a way that when the numbers in the population are high further increase is prevented by limitation of the number of new recruits allowed to enter the breeding population.

I suggest instead that the reason for the long deferment of maturity in many sea-birds lies in the fact that food is so short in the area of the colonies that only the most efficient individuals in a population can raise a chick successfully: I would suppose that efficiency in collecting food continues to increase over several years, with experience, so that young birds would have virtually no chance of breeding successfully, even if they tried. In all bird populations there must be strong selection for efficiency in collecting food. Lack (1954) has suggested that the fact that yearling birds of many species may lay slightly smaller clutches than older individuals, is an adaptation related to the (presumed) greater efficiency of old birds in collecting food. In birds laying clutches of several eggs even the least efficient individuals may be able to raise some young: staggered hatching, where it occurs, must aid this (cf. Lack 1954 : 40-41), but even in some species in which the young hatch at roughly the same time, the weakest member of the brood may die of

starvation before the rest of the brood are seriously underweight (e.g. tits, Gibb 1950). But with a clutch of one, success or failure must be complete: on my hypothesis young birds attempting to breed for the first time will be competing directly for food with more experienced birds, and a high proportion even of the latter will sometimes be unable to collect enough food for their chicks.

It is not necessary to assume that, for instance, a Diving Petrel two years old is much more efficient than a yearling, or that a New Zealand Gannet ten years old is much more efficient than one six years old: a very slight increase in efficiency might raise the chances of a bird being able to rear a chick from a level so low that on average it would not be "worth while" (in the biological sense) for it to make the extra effort, and to take the extra risk, involved in breeding, to a level at which it would just be worth while to try. This explanation is fully in accord with the observed fact that even within a single population different individuals start breeding at different ages: I would postulate simply that more efficient individuals can breed with a reasonable chance of success when younger than less efficient ones. It is also possible that the tendency to start breeding at a particular age is to some extent genetically controlled, in which case variation in the availability of food (and consequent variation in breeding success) from year to year could conceivably give rise to a persistent polymorphism in respect of the age at which individuals first attempted to breed.

Furthermore, the observed sequence of events in the lives of young individuals is roughly what one might expect on my hypothesis. The evidence suggests that most Procellarii, especially the larger ones, and at least some other sea-birds with low reproductive rates, spend several years away from the colonies, feeding, at any rate in some species, in areas where they do not have to face the severe competition for food which I postulate as occurring round the colonies in the breeding season. During this period they must gain experience in hunting, and presumably become more efficient at it. Many of them then spend one or more seasons round the breeding colonies, not making serious attempts to breed, but no doubt becoming familiar with local conditions, finding enough food to keep themselves alive, and sometimes investigating nest sites. Only after this do they start their breeding life.

There remains for consideration the question of what determines the extent to which breeding shall be deferred, in a particular population. First, Wynne-Edwards' table suggests that deferment occurs mainly in species with a low clutch-size, and that it may generally be most extreme in those laying clutches of one. If so, the explanation is implicit in what has been said already: in species which lay large clutches, young individuals, even if they are less efficient than older ones, can compensate by laying fewer eggs and still rear some young; this course is not open to birds whose normal clutch is only one.

In a stable population of birds laying clutches of one, and regulated in the way I have suggested, both the extent to which breeding is deferred and the reproductive success will depend on the mortality of adults and of fledglings after leaving the breeding colonies. If mortality independent of density is fairly high, the production of young from clutches of one will hardly exceed the deaths during the year, and even a small density-dependent reduction of the output of young will balance the population. One would therefore expect on average few deaths of chicks from starvation, and little or no deferment of maturity. In a population with lower mortality, stability in numbers will be achieved only when competition for food results in the death of many young from starvation; the chicks of the least efficient parents will rarely survive, and deferred maturity will result. In the species with the lowest mortality, breeding will be so difficult that only the most efficient and experienced adults will be able to rear chicks, and long periods of immaturity will be the evolutionary result. It is thus not surprising to find that the Royal Albatross, which has the lowest adult mortality so far recorded in any bird (about 3%: Lack 1954, from Richdale's figures, but based on a very small sample), also has the longest known period of immaturity (about nine years: Richdale 1952).

This discussion has referred to stable populations, limited by competition for food round the breeding colonies in the way I have suggested, but it is clear that in populations which are expanding, or which are limited in other ways (including predation by man), the situation will be very different. Competition for food may then be less severe or even insignificant, deaths of chicks from starvation may be rare, and young individuals may be able to breed successfully. No sea-bird population of this kind has been studied intensively, but Carrick, Csordas & Ingham (1962), studying the Southern Elephant Seal *Mirounga leonina*, showed that in the large unexploited population on Macquarie Island both males and females grow more slowly and have a longer period of immaturity than in the exploited population on South Georgia. It is suggested that the precocity of young bulls on South Georgia results mainly from reduced intrasexual competition, since the older bulls are removed by man; but that the precocity of the females there must be related to the reduced competition for food in the area round the breeding stations. The authors argue, as I have done for tropical sea-birds, that it is competition for food in the vicinity of the colonies which limits numbers in the unexploited populations.

It is clear that in sea-birds, as in the Elephant Seal, variation in the age of first breeding may be expected to be an important density-dependent factor tending to raise the reproductive rate if the population density decreases, or if food becomes more abundant, and to reduce it when the population nears the food limit. I would suggest that it is an important supplement to variation in reproductive success in regulating the numbers of long-lived tropical sea-birds.

In this paper, I have been considering mainly sea-birds breeding in the tropics: however, many oceanic birds breeding even in the richer waters of higher latitudes also lay one egg, some have strikingly long fledging periods, and some show deferred maturity. I have argued that in the tropics the laying of only one egg results not only from the general poorness of tropical waters, but also from the fact that adult mortality is low and apparently independent of density, and no other factors appear to limit the populations, so that numbers increase until competition for food round the breeding colonies prevents the adults from raising more than one chick. It is clear that this mechanism could operate also in populations of birds breeding in much richer waters (mainly in high latitudes), provided only that mortality is low and independent of density, and other factors (such as limitation of nest sites) do not intervene to limit the population at a lower level. Under these circumstances the final result will not be higher clutches in rich waters, but a greater density of birds, since more food will be available round the breeding colonies. Similar reasoning can be used to explain the long fledging periods and deferred maturity found in some species breeding in rich waters.

Looking at this argument from an evolutionary viewpoint, it can be seen that so long as mortality in a species away from the breeding colony is not density-dependent, the reproductive rate will be determined by the mortality. If the mortality is sufficiently low, competition for food even in a rich habitat will prevent birds from raising more than one chick, and a clutch of one will be evolved. Thus a sufficient explanation of the fact that all Procellarii lay only one egg might be that their way of life gives them a low mortality after fledging.

However, one other factor must be considered. I have mentioned that most tropical seas are poorer than those at higher latitudes, but it is also generally true that in high latitudes seasonal variation in the sea is much more extreme than in the tropics. These differences are reflected in the fact that in the tropics it is not unusual to find some sea-birds breeding at all times of year, as on Ascension, while at higher latitudes nearly all sea-birds breed in the spring or summer of the hemisphere concerned, and the breeding seasons of particular species are often short. It is evident that if sea-birds breeding at high latitudes are timing their breeding to coincide with an enormous seasonal increase in the food supply, their numbers will have to be very large before competition for food

round the breeding colonies will become severe. It is therefore likely that the numbers of some sea-birds breeding under these circumstances are limited by other factors before they reach the level at which competition for food round the colonies would produce density-dependent effects sufficient to limit them. Nest sites are doubtless sometimes limiting, and it is also possible that in some species numbers may become so high that competition for food away from the colonies, in the seasons when it is least abundant, may be the limiting factor: as I have already argued, this is unlikely to be the case in the tropics.

Since the way in which a population responds to changes in its environment must depend largely on the factors which originally limited its size, it is perhaps worth considering briefly, in conclusion, how environmental changes will affect populations regulated in the way I have suggested. I have argued that if populations of tropical sea-birds are regulated by competition for food round the breeding colonies, the breeding success, and the extent of the deferment of maturity, when the population is stable, will depend largely on the mortality of fledglings and of adults. If this mortality is low, the population must increase until it is checked by a large density-dependent reduction in breeding success, and/or a large increase in the average extent to which breeding is deferred. But if mortality is higher, and the birds can only just maintain themselves with a clutch of one, a very slight or very infrequent density-dependent reduction in the breeding success, and/or a slight increase in the average deferment of maturity, will suffice to stabilize the population.

From this it follows that the extent to which density-dependent factors originally affected the breeding success and/or the deferment of maturity, will determine the effect on the population of changes in the environment. Most of the striking changes in birds' environments are caused by man, so that the implications for the conservation and cropping of bird populations are important.

Populations in which the original balance was reached only after a large change in the reproductive rate had been caused by density-dependent factors will be likely to survive even heavy regular losses of eggs, young or adults, since if the population begins to decrease, the breeding success of the remaining undisturbed pairs will be substantially increased by the reduction in competition, and individuals may be able to breed at an earlier age, as in the Elephant Seals already mentioned. Such a population may be described as being "well buffered" by density-dependent regulatory factors. On the other hand, populations in which density-dependent factors regulated the numbers by relatively slight effects (which are of course the populations which are only just able to maintain themselves in their environment) will be easily reduced to extinction by any new losses of eggs, young, or adults.

Another type of change which must often occur in a bird's environment is a change in the abundance of food, not caused by the bird's demands on it. It is clear that this must alter the stable density of any population, but while well buffered ones will normally survive at lower densities, others will become extinct. On the other hand a poorly buffered population may be as likely to survive the effects of interspecific competition as one that is well buffered.

Although I have considered only populations of sea-birds regulated by density-dependent variation in reproductive success and/or in the deferment of maturity, similar reasoning can be used in considering the effect of changes in the environment on populations of any animal regulated in any way by density-dependent variation of either the reproductive rate or the mortality.

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This paper has developed over a long period (it appeared in its essentials in my thesis—Ashmole 1961), and throughout this time I have benefited from discussion with many people, to all of whom I owe a debt; in particular I must mention Dr. David Lack, J. M. Cullen, and my wife. At a late

stage I was greatly stimulated by Professor Wynne-Edwards' book (1962), and by the discussion on bird populations at the Edward Grey Institute student conference in January 1963. I am grateful to Dr. Lack, R. E. Moreau and my wife for reading and criticizing the manuscript.

SUMMARY

The ways in which the numbers of tropical sea-birds might be limited are considered; it is argued that food is the only factor likely to be generally effective in limiting numbers, but it seems improbable that food shortage could exert a density-dependent control of the mortality of the birds outside the breeding season.

Wynne-Edwards' hypothesis that colonies of sea-birds are able to keep their own numbers below the level at which food shortage would become acute, primarily by exerting control on the output of young, is rejected as unproven and improbable.

It is suggested that colonies of tropical oceanic birds deplete the food in the waters round them, and that as the populations increase competition for food becomes more intense, and relatively fewer adults succeed in raising chicks. This would provide a density-dependent control of the output of young and could regulate the numbers of the birds.

The peculiarities of long-lived sea-birds (e.g. clutches of one, long fledging periods, deferred maturity) which Wynne-Edwards suggests are adaptations evolved in order to lower the reproductive rate until it balances the mortality, apparently could not be evolved as such; they are more probably adaptations enabling the birds sometimes to raise single chicks in spite of competition for food that makes it impossible to raise more than one. It is considered that variation in the age of first breeding provides an important supplement to variation in reproductive success in regulating the numbers of long-lived tropical sea-birds.

The possible applications of this hypothesis to sea-birds breeding in higher latitudes are briefly considered, as are its implications in relation to conservation and exploitation of populations of sea-birds.

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POSTSCRIPT

I have suggested in this paper that around some sea-bird colonies any increase in the number of birds in the population may reduce the amount of food that each individual can collect for its young—i.e. there may be effective competition for food—and that the numbers of the birds may be regulated in this way. I argued that competition could be effective only if the birds were depleting the stock of food in the area round the colony. Recently, while on fishing vessels near Oahu (Hawaii) and Christmas Island (equatorial Pacific) I have had opportunities to watch some tropical sea-birds feeding, and I now realize that there may be competition for the *available* prey animals even if these are only a small proportion of the total stock, and even if this stock is not being depleted significantly by the depredations of the birds.

Noddies *Anous* spp., Sooty Terns *Sterna fuscata* and probably many other species of tropical sea-birds which feed on small fish and squid, apparently catch these mainly or entirely when they are driven to the surface by schools of large predatory fish, especially tuna. These schools are very thinly spread over the tropical oceans (see Murphy & Ikehara 1955, U.S. Fish & Wildlife Service, Spec. Sci. Rep. Fisheries No. 154), and near sea-bird colonies it seems that almost every one has its accompanying flock of birds. When a large flock is fishing over a school, competition between individual birds will occur if the number of birds is high relative to the number of prey animals available at the surface at a given moment. My own brief observations on dense flocks of noddies feeding over fish schools suggest that such competition does in fact occur. If so, it could limit the populations of the birds concerned by reducing their reproductive output in the ways I have discussed. The numbers of the birds would then be determined by the abundance of the predatory fish which make food available to them, as well as by the abundance of the food animals themselves.

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