

ADAPTIVE LIMITATION OF THE REPRODUCTIVE RATE OF BIRDS

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INTRODUCTION

The study of regional and seasonal variations in the number of eggs which birds lay led Lack (1947: 331) to the conclusion that "in most species clutch-size is considered to be ultimately determined by the average maximum number of young for which the parents can find enough food". This simple principle provides a reasonable explanation of many of the observed fluctuations in clutch size. The increase in the size of broods with increasing distance from the equator, observed in many (but by no means all) groups of birds, becomes explicable when we recall that, in the milder part of the year when most birds breed, days are longest near the poles, and a longer working day permits parent birds to gather more food for their young. A similar explanation applies to seasonal changes in clutch size in a single region. In a number of European birds which raise more than one brood, clutch size tends to increase from March to early June and thereafter to decrease, and these variations in the size of the brood are correlated with the changes in the duration of daylight before and after the summer solstice in middle and high latitudes.

Lack's views, worked out in great detail and applied to numerous species in a whole series of papers (see references in Lack 1954) clarify some otherwise puzzling observations. But, as so often happens in the enthusiasm of applying a fertile theory to an ever-widening array of facts, there has been a tendency to work it too hard. So, at least, it seemed to the present writer who, noticing that this theory took no account of how many offspring a species might need to produce in order to maintain its population at a favourable level, raised the question whether tropical birds do indeed rear as many young as they can nourish (Skutch 1949). A number of facts then known to me led me to conclude that they do not. In cases of need, such as when the parents, somehow kept away from their nest for an unusually long interval, return and find the nestlings hungry, they can supply food at a rate far greater than normal, indicating that their usual slower rate of feeding is not due to their inability to find food more rapidly. Occasionally a species which nearly always lays two eggs produces a set of three, and the parents succeed in rearing, at least to the stage of nest leaving, a family 50% greater than normal. A number of other arguments were adduced in support of my thesis, but the one which I considered strongest was that, when we compare species in which both parents feed the nestlings with species in which only the female attends the nest, we find, by and large, that the two parents together rear no more young than the single parents do. Among birds of similar size, diet and habitat, there is no correlation between the size of the brood and the number of adults attending it.

In the concluding section of my paper, I pointed out some circumstances in which birds—and other organisms—tend to produce as many offspring as they can adequately nourish. This will occur in populations which are periodically decimated by natural catastrophes. Each drastic reduction in numbers is followed by a period of free expansion, during which the more prolific genotypes make the largest contribution to recovery, thereby gaining such a numerical preponderance over the less prolific genotypes that eventually, with repetitions of these conditions, they supplant the latter. This course of events occurs at high latitudes, where unusually severe winters, or disasters during migration, from time to time decimate the population of many birds. In the wetter parts of the tropics, especially in evergreen rain forests, where catastrophic reductions in

the avian population over considerable areas are practically unknown, the more prolific genotypes should find it more difficult to supplant genotypes that reproduce more slowly, so long as the latter breed at a rate adequate to replace annual losses. Hence, in these more stable environments, Lack's theory would not apply.

In his comments on my paper, Lack (1949) rejected this modification of his theory. He still insisted that "tropical birds (as well as others) raise not only all the offspring that they need, but also all that they *can*". He gave his theory the widest possible application; not only to the size of broods but to the number of broods per year; not only to birds, but to other animals as well. He too lightly dismissed the fact, which other naturalists have found cogent, that, among birds of the tropical American forests, broods tend to be of the same size whether one or both parents attend them. Nevertheless, the belief that birds everywhere are reproducing as rapidly as they can continues to be widely held by ornithologists, with the notable exception of Snow (1963) who, significantly, has made outstanding studies of the population dynamics of birds in just the kind of environment that has influenced my own thinking on this subject. Other recent writers have overlooked the limitation of my argument to the more humid parts of the tropics where avian populations remain stable over long periods and, applying my views to situations to which they were never intended to apply, have, not surprisingly, found these views untenable.

There is scarcely any question in biology more fundamental than whether the reproductive rate of animals is always maintained by natural selection at the maximum level that their ability to produce and adequately nourish young permits, or whether it is adjusted to the losses which each species must replace to maintain its population at a favourable level. Hence it seems proper to re-examine this question, attempting to clarify views which have too often been misunderstood, and treating the whole problem more thoroughly than was done in a paper that was explicitly limited to the situation in the wetter parts of the tropics.

ADJUSTED VERSUS MAXIMUM REPRODUCTION

It is obvious that, in order to avoid extinction, a species must, on the average, produce enough offspring to replace its annual losses, with perhaps a small surplus to meet emergencies and to permit the occupation of new territory, if this becomes available. From this it may be deduced that a species which reproduces slowly does so simply because its mortality is low and because it has no need to beget more offspring, whereas a rapid rate of reproduction is an indication of high annual losses. This view, which might be called "the theory of adjusted reproduction", seems to have been rather widely held not long ago. I am not aware that it has ever been subjected to exacting scrutiny; but it was not, for that reason, necessarily false. If the opposing theory has done nothing else, it has forced the proponents of adjusted reproduction to examine the foundations of their belief, and for this it deserves our gratitude. This opposing theory, which maintains that animals produce all the progeny they can, no matter how many they need, may be briefly designated as "the theory of maximum reproduction". In recent times it has been closely associated with the name of Dr. David Lack, who has diligently collected a great mass of evidence in its support.

According to the theory of adjusted reproduction, the number of progeny is determined primarily by the death rate. Maximum reproduction does not necessarily exceed adjusted reproduction, for in some cases an animal, by exerting to the utmost its reproductive powers, may barely succeed in maintaining its population. But in many cases maximum reproduction will yield far more progeny than the habitat can support, and the excess individuals will succumb to starvation, fall victim to predators, or die of disease. Now the mortality, instead of determining the rate of reproduction, is itself determined by the rate of reproduction. A fundamental difference between the two opposing

theories is just this: that according to the theory of adjusted reproduction, the reproductive rate is determined by the average annual mortality; whereas it follows from the theory of maximum reproduction, that the annual mortality is determined by the reproductive rate, whenever this exceeds the adjusted rate.

Where maximum reproduction prevails, the population is likely to show fluctuations of great amplitude, with a high peak at the end of each breeding season, a deep valley at the outset of the following season. Adjusted reproduction should give a much flatter curve. This suggests that maximum reproduction is to be expected in a region of pronounced seasonal changes in climate, with accompanying fluctuations in the abundance of food; whereas adjusted reproduction would be expected in a more equable climate.

The difference between an adjusted and a maximum rate of reproduction will be greatest in species which, during their breeding season, enjoy very favourable conditions, with abundant food for the young, but at some other period of the year face severe shortages. Where the reverse conditions hold, and the scarcity is felt chiefly by the breeding birds, the population curve is necessarily much flatter. Such conditions are evidently confronted by tropical sea-birds, which, when not breeding, forage over vast expanses of the oceans and apparently experience no lack of food, but when nesting are concentrated in thousands or millions of pairs on small islands, so that they must either compete keenly for the limited food available in the immediately surrounding waters or else spend much time and energy flying afar to forage (Ashmole 1963). In such circumstances, adjustment will take the form, not of limiting the number of young produced (which in any case is limited by the parents' ability to supply food), but of restraining the reproductive effort, so that the birds will not squander their resources by attempting to rear far more young than they can nourish.

The theory of maximum reproduction is likely to appeal strongly to those who, concentrating on the genetic and numerical aspects of the situation, conclude that the more prolific genotype must prevail because it contributes more individuals to the population. The theory of adjusted reproduction attracts biologists who believe that a population cannot, by becoming excessively numerous, press too heavily upon its environment without being penalized in certain ways which will handicap it in competition with a neighbouring population of the same species that reproduces more conservatively.

What would be the optimum rate of reproduction? One is tempted to define the optimum rate of reproduction in terms of the optimum density of population, saying that it is that rate which most economically maintains this optimum density. But the definition of optimum density itself presents difficulties. Were it merely a question of the relation of an animal to such features of the environment as food resources and cover, we might define the optimum density as that at which a species occupies its habitat "without making any parts so crowded as to subject the inhabitants to privation, or leaving other parts needlessly empty" (Wynne-Edwards 1962: 4). But in addition to finding adequate food and cover, an animal must contend with predators, parasites, and diseases. It may be that a density considerably below that which the food resources of a habitat could support will prove more favourable to some species in the long run, because of the reduced incidence of predation or disease. In view of the difficulty of deciding what is the optimum density, it seems best to define the optimum rate of reproduction in terms of the reproductive rate itself. *The optimum rate of reproduction is the rate beyond which any increase would be balanced, in an average year, by increased mortality.* A reproductive rate above the optimum produces more young but it does not maintain the population at a higher level, because the excess individuals are soon removed by death in one of its many forms. It is a wasteful rate. According to this concept, a perfectly adjusted rate of reproduction is the optimum rate. It seems that in nature such a rate may be approached, but rarely realized.

UNPROVED ASSUMPTIONS OF THE THEORY OF MAXIMUM REPRODUCTION

The reasoning that underlies the theory of maximum reproduction has been succinctly stated by Lack (1954: 22): "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". The critical word in this sentence is the indefinite "eventual". If the statement means that the genotype which comes to predominate is that which maintains the population at the highest sustained level over the years, it is sound evolutionary theory and I have no quarrel with it. But if this is what is meant, Lack here diverged from his distinctive view that animals beget the largest number of young that they can adequately nourish *up to the time of attaining independence from parental care*. The latter is the view which Lack's statistical analyses and writings, as likewise those of his students and followers, seem, on the whole, intended to support. It is the view which has been successfully used to account for certain variations in clutch-size; and it is the view whose too general application I am challenging in the present paper. When, in the following pages, I use the terms "maximum reproduction", "most prolific genotype", and similar phrases, I mean what they obviously imply, the rate of reproduction which yields the greatest number of normal, healthy young at the time of attaining independence, not at some indefinite future date.

Proponents of the theory of maximum reproduction tend tacitly to assume that mutations for increased fecundity will not be lacking, so that in fact most species are reproducing at the maximum rate, irrespective of their need of recruitment (see quotation in first sentence of this paper). The truth of this view is contingent on the truth of three other propositions that need to be examined: (1) That when a species of bird is not rearing as many offspring as it can, an increase in clutch size is more likely to occur than some other mutation which, directly or indirectly, affects the birds' reproductive capacity. (2) That a population (or genotype) breeding at a rate above the optimum can increase at the expense of another population (or genotype) of the same species breeding at a more nearly optimum rate. (3) That an unnecessarily high rate of reproduction is not harmful to a species. We shall consider these assumptions in order:—

(1) When we consider birds as a whole, it becomes evident that variations in clutch size are by no means so common as one who knew only the inland birds of northern lands might suppose. In whole families and orders, the clutch size remains constant despite great diversity in size, appearance, habitat, and mode of life of the component species. Thus a single egg is the rule throughout the whole order Procellariiformes, from little storm petrels to great soaring albatrosses. Among pigeons and doves, a few of the larger species lay one egg and all the rest lay two. Two eggs are almost invariably found in hummingbirds and manakins, two or (less often) one in goatsuckers. In these groups, three or more eggs are so rarely found that whenever they occur there is a suspicion that more than one female has laid in the same nest. In many genera of tropical passerines, including Oscines no less than Tyranni, the set regularly consists of two eggs. In the Charadriiformes, the set hardly ever exceeds four. Considering the great stability of clutch size in numerous groups of birds, it does not seem likely that this character is more subject to mutation than some other character, such as the male's attendance at the nest, which might also affect the reproductive rate. We shall return to this in the next section.

Probably one reason why certain groups of birds were more successful than others in colonizing the new lands that became available in the north, as the ice retreated at the end of the last glaciation, was that their clutch size was more labile, and they could more readily make the adjustments demanded by the adoption of the perilous migratory habit or by the high mortality often associated with a severe winter. Oscines and ducks, which have contributed so many migratory species, readily adjust their clutch size to

changing conditions. Even within the tropics, the flycatchers (Tyrannidae) show greater variability in clutch size than manakins and antbirds, and this is doubtless associated with the fact that many flycatchers have become long-distance migrants, while no species of the two related families, very numerous in tropical America, has done so.

(2) That individuals breeding at the adjusted or optimum rate will be supplanted by others of the same species that reproduce at a higher rate may be true if we assume inter-individual selection but seems unlikely to occur if intergroup selection occurs. The concept of intergroup selection seems not to be popular among biologists, who insist that individuals, not groups, are selected. This is in general true, but it is likewise true that an individual's chance of surviving is more or less dependent upon the character of the population of which it is a part. An individual in a too-dense population that is starving is less likely to survive than one in a population better adjusted to its means of subsistence; and it is obvious that the survival of a group depends on the survival of the individuals who compose it. I do not know all the implications that the term "intergroup selection" may have for others, but to me it is simply a recognition of the ecological truth that a population cannot make excessive demands upon its environment without feeling the adverse effects of the resulting scarcity, so that it will not easily expand at the expense of a neighbouring population that is better adjusted to its environment. Among nomadic organisms, intergroup selection could hardly be effective and inter-individual selection must prevail; whereas in more stationary organisms, intergroup selection can operate. Perhaps this is one of the reasons why in evergreen tropical woodlands, where many birds appear to be quite sedentary, intergroup selection has tended to hold reproduction to the adjusted rate, while among the more widely wandering birds of regions subject to severe winter or drought it has been less effective.

The mutations which increase clutch size will doubtless occur sporadically in certain spots, giving rise to local populations that reproduce more rapidly than neighbouring populations of the same species. The question is whether these more rapidly reproducing groups can spread at the expense of adjacent groups which, although they have a lower rate of increase, manage to keep their habitat rather fully occupied. To displace the established population, the overflow from the pockets of more rapid reproduction would, it seems, need to consist of better-nourished, stronger individuals. This is discussed further below.

(3) It seems likely that an unnecessarily high rate of reproduction is harmful to the species. It is well known that, particularly among altricial birds, rearing a brood can be an exhausting process, making great demands on the energy of the parents and often causing them to lose weight. The larger the brood, the greater this drain. Not only do the parents of large broods come through the nesting season with their strength somewhat impaired, but the young themselves may not be so well nourished as those of small broods—although the number of meals brought to the nest increases as broods grow larger, this increase is rarely proportional to the increase in the number of mouths.

We have also to consider to what degree an oversize population may deplete its food resources. It is well known that grazing or browsing animals in excessive density may so damage their range that many die of starvation, and the vegetation requires years to recuperate. Here we are dealing with the destruction of vegetation that is visible at a glance, but it is conceivable that smaller animals may deplete their food resources no less drastically, yet in a way that escapes casual notice. Insectivorous birds may so reduce the breeding population of the insects on which they chiefly feed, or fish-eating birds that of fish, that years of scarcity will follow. Probably the only birds that cannot damage their sources of nourishment are the fruit-eaters, which disseminate the seeds of the berries or other fruits that they devour.

Finally, there is the problem of the relation to predation and disease of the population reproducing at a rate above the optimum. Predators tend to concentrate on species

that are numerous and easily captured. Ease of procuring food enables them to raise more progeny, which in turn will bear still more heavily on the animals that are providing meals for them. This is known to occur in owls and other rodent-eaters in years when their prey is excessively numerous, and it could well happen with bird-eating raptors if smaller birds become temptingly abundant and often stray from cover in their search for a diminishing food supply.

Thus the birds which produce an excess of progeny seem to be injuring themselves by squandering their energy in rearing many young, by depleting their food resources, by encouraging predators to specialize on them, and by furnishing a fertile ground for the spread of disease. Is it likely that this weakened, spendthrift population can spread at the expense of a thriftier, sturdier population of the same species? Especially among birds which throughout the year live in pairs on their territory, as is true of many tropical species, it seems improbable that starving refugees could displace well-established residents or often gain a foothold in a fully occupied district. It has never, to my knowledge, been proved that they can.

ALTERNATIVE MUTATIONS AFFECTING THE RATE OF REPRODUCTION

It is a commonplace of evolutionary theory that all the characters of organisms, structural, physiological, and behavioural, may be altered by randomly occurring mutations. It is obvious that in a population of birds which, by making the fullest use of its reproductive capacity, barely manages to maintain its numbers, any mutation which reduces this capacity will be rigorously removed by natural selection. But let us consider the case of a population which thrives without employing its full reproductive potential (which depends on the number of eggs the parents lay and hatch as well as on their ability to rear their young), or one which is reproducing at a rate above the optimum. What mutations might arise, and be preserved, in such a population?

(i) In a population that is reproducing at a rate above the optimum, a mutation that reduces the number of eggs is likely to persist, and even to spread, because it increases the birds' adaptation to their environment. This has evidently occurred in Central American populations of large pigeons of the genus *Columba*, which as far as is known lay only a single egg, even in species, such as the Scaled Pigeon *C. speciosa*, which in other regions lay two eggs (Skutch 1964). Certain Old World species of *Columba* also lay only one egg. By this reduction in fecundity, these pigeons may avoid the high mortality of some pigeons that lay two eggs, which for the Woodpigeon *C. palumbus* is sometimes as high as 59% between breeding seasons (Murton 1965). It is evident from the data in Murton's book that the Woodpigeons he studied in Cambridgeshire, England, could maintain a higher stable population if they drastically cut their reproductive rate. The chief cause of mortality is starvation during the autumn and winter. Those pigeons that perish from hunger have already made substantial inroads on the limited food supply, reducing its capacity to support the remainder. If, at the beginning of the season of scarcity, the population were more closely adjusted to the food resources, a considerably larger number of pigeons might be sustained through the winter. It could be argued that the Cambridgeshire Woodpigeons live in an environment that has changed so rapidly that they have not had time to adjust their rate of reproduction to it.

(ii) The number of broods may be reduced. Sometimes this reduction seems to be the inevitable consequence of the prolongation of the incubation and nestling periods until the breeding season is too short for rearing two broods, as in the Procellariiformes and many other sea-birds, large raptors, and other big birds. But many smaller birds of more rapid development raise only a single brood, even when they have time to rear more. Although in El General the Golden-naped Woodpecker *Tripsurus chrysauen* rarely attempts to raise a second brood, this limitation seems not to be due to the shortness of the favourable season, for occasionally a pair produces two broods between March

and July. Wood-warblers (Parulidae), too, are often single-brooded, despite the rapid development of their young.

Most birds, including many that are single-brooded, will lay again, and often repeatedly, if their first brood is destroyed; but some species have more drastically reduced their reproductive potential by the loss of this capacity. In the Procellariiformes, the replacement of the single annual egg is most exceptional and has been recorded as an occasional occurrence only in two species of storm petrels (Wynne-Edwards 1962: 488), which are among the smallest members of the order, and in the Manx Shearwater *Puffinus puffinus* (Harris 1966). The Thick-billed Murre *Uria lomvia* replaces eggs that are lost during the first two to four days of incubation, but not thereafter (Tuck 1960). The cave swiftlet *Collocalia esculenta* does not lay again if its eggs are lost (Medway 1962). On two occasions, Fiery-billed Araçaris *Pteroglossus frantzii* failed to lay again after the loss of their single annual brood.

The greatest reduction in reproductive potential occurs in species that not only produce a single egg but breed in alternate years, as in the larger albatrosses, or twice in three years, as in the King Penguin *Aptenodytes patagonica* (Stonehouse 1960). Whether the omission of breeding in every second or third year is an adaptive limitation of the reproductive potential depends upon whether the slow development of the young, which obliges the parents to omit nesting in the following year, can be regarded as an adaptation in this sense. Single-broodedness in species that could rear two broods in a season is more obviously an adaptive limitation of the reproductive potential.

(iii) The male may cease to attend the young, and this may be followed by failure to form pairs; or the latter condition might arise at once by a radical mutation, in a species in which both parents fed the nestlings. In the Tyrannidae, the male Royal Flycatcher *Onychorhynchus mexicanus* remains with his nesting mate but does not help her; in a number of other genera, including *Myiobius*, *Terenotriccus*, *Rhynchocyclus*, and *Pipromorpha*, pairs are not formed and the nesting female is quite alone. In all manakins (Pipridae) as far as known, most humming birds, many cotingas, and some woodcreepers, as well as among the bowerbirds and most birds of paradise, the males remain aloof from the nest, with a corresponding reduction of the labour force available to supply food to the young. In many of these groups, we find leks or courtship assemblies, in which a number of males, assembled in the same locality, compete for the attention of the females, who come to have their eggs fertilized and then go off to rear their young in solitude. This system, whereby the more attractive males may become the fathers of many broods in a single season, gives these outstanding individuals a great selective advantage that promotes the rapid evolution of bright colours, adornments, and striking displays. To this method of reproduction we owe some of the most beautiful, as well as some of the most bizarre, male birds in the whole avian class. That these gains (at least from our point of view) can be won with no serious loss of population is attested by the fact that manakins and hummingbirds are among the most abundant birds in the lowland forests of the tropical American mainland. By combining insects and berries, or insects and nectar, in their diet, the solitary females can without difficulty rear their broods of two, which is as many young as one will find in most neighbouring nests of such conventionally paired birds as tanagers, finches, honeycreepers, and antbirds. This low rate of recruitment is adequate because the parents are long-lived. Snow (1962) found that adult male Black-and-white Manakins *Manacus manacus* in Trinidad have an annual survival rate of 89%; this is far higher than that of any small bird in the north whose survival rate is known.

True polygamy, in which the male forms lasting attachments to more than one female, also results in a reduction of the parents' ability to supply food to the young. The polygamous male may take no part in feeding the nestlings, he may divide his attention between several nests, or he may help only a single female, often his latest acquisition,

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to attend her family. Polygamy can arise only among birds which do not require the full effort of two parents to feed the brood.

(iv) The age of attainment of reproductive maturity may be deferred. We know too little about the age at which wild birds begin to breed, but there is abundant evidence that in many instances it is far longer than one would expect from the time it takes these birds to attain adult size. After ceasing to grow in a matter of weeks or months, the bird may wait several years before it attempts to rear young. This delay tends to be especially long in sea-birds, which begin to breed at three years in the case of the Arctic Tern *Sterna macrura* (Cullen 1957); two or (more often) three years in the Yellow-eyed Penguin *Megadyptes antipodes* (Richdale 1951); six years in the Short-tailed Shearwater *Puffinus tenuirostris* (Serventy 1956); five or more years in the Black-footed Albatross *Diomedea nigripes* (Rice & Kenyon 1962); and 8–11 years in the Royal Albatross *D. epomophora* (Richdale, in Wynne-Edwards 1962). For a growing number of land-birds, direct or indirect evidence of the deferment of breeding has been accumulating, but this seems rarely to be so long as in many sea-birds; even the Common Rhea *Rhea americana*, far larger in body than any flying sea-bird, attains sexual maturity at the age of two years (Thomson 1964).

Delayed maturity evidently has a genetic foundation, although the length of the delay seems subject to some degree of modification by external conditions, so that more abundant food or reduced competition for nest sites may stimulate the birds to breed somewhat earlier than they would do in years when food is scarce or competition for nest sites severe. Ashmole (1963) believed that certain sea-birds do not begin to breed until a rather advanced age because competition for food is keen in the neighbourhood of populous breeding colonies, especially in tropical waters, and the young birds require several years to gain the proficiency in foraging that will enable them to compete with older individuals and procure enough nourishment for their young. To me it is incredible that a bird whose skill in fishing increases so rapidly that it can feed itself after a few weeks at sea should thereafter improve so slowly that several additional years must elapse before it develops sufficient proficiency to nourish, with the help of its mate, the single nestling that most of these oceanic birds rear. Certainly the acquisition of physical skills as a rule follows no such course. There is, indeed, growing evidence that older parents are more efficient, and can rear larger broods, than those breeding for the first time; but their increased proficiency most probably comes from practice in the exercise of parental offices, which they could not get before they started to nest, rather than greater skill in the foraging, which they have long been practising. Rather than viewing the delayed breeding of these sea-birds as due to some impediment that prevents the steady improvement of skill up to a maximum, I think that we must regard it as an adaptation, originating in a mutation of a series of them, which, by helping to adjust the rate of reproduction to the mortality of the species, improves its adjustment to its environment.

(v) Territorialism may develop to limit the number of breeding birds, or the number of young that each pair can raise. The effectiveness of territory in regulating the density of birds has been questioned, because in many species territories are compressible, the pressure of newcomers often forcing the earlier occupants greatly to contract their original claims; and because the defence of territories may be relaxed or abandoned after the young hatch or when they leave the nest—just at the time when the family requires most food. Neither of these objections is fatal to the view that territory helps to regulate population. The more a bird's territory shrinks before the demands of newcomers, the more stubbornly he defends it. These territorial disputes may drag on for days or, as I have seen in the tropics, even weeks, during which nesting is delayed. Even if territorialism never prevented any bird from breeding in a given season (which sometimes it certainly does), by delaying the start of nesting, and hence the effective length of the

bird's breeding season, it reduces the number of breeding attempts that pairs which engage in protracted territorial disputes can make. Since many pairs try again and again before they succeed in raising fledglings, this reduction in the time available for breeding cannot be without effect on the total reproduction of a population already so dense that territorial disputes are frequent, and it may mitigate the situation in the following year.

As to the breakdown of territorial boundaries after the young hatch, it is of little importance. If territorialism early in the season limits to ten pairs the breeding population of an area of woodland or meadow where otherwise 20 pairs would have settled, there will be twice as much food for each family, whether each remains on its own plot of ground or whether they roam freely over the whole area.

The question of the relation of territory size to brood size requires elucidation. Probably in some instances an undersized territory, by supplying too little food, limits the number of young which the parents can raise. The observation that certain birds can successfully nest on a freshwater island that is much smaller than the territories claimed by pairs of the same species on the mainland, suggests that some birds are holding territories far larger than they need (Beer *et al.* 1956). However, the birds would have to be extraordinarily accomplished ecologists to calculate in spring just how much land they must claim to meet the food requirements of their prospective family in the summer. Since the food supply fluctuates from year to year, the adjustment of territory size to the actual requirements of the breeding pair can at best be only approximate. Although we should not expect territorialism to effect too fine an adjustment between a population and its food supply, it is the sort of development that is not likely to have arisen until birds became so successful and numerous that they began to press hard upon their means of subsistence. Like the other developments we have been considering, it evidently arose through a series of mutations that were preserved because they improved the adjustment of birds to their environment. Its effectiveness in the regulation of population density has been demonstrated by Tompa (1962), working with Song Sparrows *Melospiza melodia*.

(vi) Breeding may be restricted to certain traditional localities, even when other suitable sites are available. This situation is well known in sea-birds, whose colonies on small islands or inaccessible cliffs may contain many thousands or even millions of pairs and remain occupied for centuries. Such exaggerated colonialism must increase the difficulty of procuring suitable nest sites, especially by young birds breeding for the first time; and by forcing parents to fly afar in their quest for food, it seems to add immensely to the labour of rearing the young; yet these very difficulties may prevent the sea-birds from becoming so numerous that they deplete their sources of food on the high seas. Colonialism of this sort is one of the best examples of the social conventions which, in the view of Wynne-Edwards (1962), have arisen among birds (and other animals) to prevent disastrous competition for the primary requirements of life.

The mutations which gave rise to this condition are evidently not irreversible. Salomonsen (1965) regarded the breakdown, through genetic alterations, of this strong attachment to ancestral nesting grounds as the indispensable prelude to the recent spectacular spread of the Fulmar *Fulmarus glacialis* in northwestern Europe. In other instances, the attachment to the traditional breeding ground has persisted despite great overcrowding. On Nightingale Island in the Tristan da Cunha group, where Great Shearwaters *Puffinus gravis* occupy every burrow in their populous colony, hundreds of thousands of burrowless birds deposit their eggs on the surface of the ground, where they fail to hatch. The wastage of reproductive potential may run as high as 10% of that of the whole colony; yet breeding grounds on neighbouring islands are more sparsely occupied, and other apparently appropriate areas are quite neglected (Rowan 1965). If Great Shearwaters are indeed pressing hard on their sources of subsistence on the

wide oceans, this stubborn adherence to social conventions and traditional sites is a highly effective means of reducing the pressure.

(vii) When a species of bird is not forced to apply all its energy in the breeding season to rearing enough young to replace annual losses, it may, through mutations, develop unusual styles of architecture. The most elaborate nests are almost confined to tropical birds, although a few non-migratory birds of extra-tropical lands, such as the bush-tits and penduline tits, may also build them. Long-distance migrants cannot spare the time and energy for such luxurious constructions. It is difficult to assess the effect of elaborate nests on the reproductive potential. The season's first nest may be started weeks or months before the date for laying, so that its time-consuming construction need not curtail the period available for rearing broods. Even the most cunningly contrived nest is not, however, wholly immune from predation and other disasters, and if it must be replaced in the midst of the breeding season, this will take several times as long as the fabrication of a simple nest, with a corresponding reduction of the interval available for rearing replacement broods.

The reproductive efficiency of such constructions depends, then, upon whether they increase the safety of the eggs and young to a degree which compensates for the longer time required for their replacement in the midst of the breeding season whenever this becomes necessary. Since these elaborate nests often hang far above reach, or else are so well enclosed that one cannot learn what they contain without undue disturbance, it is most difficult to obtain an index of their success. My impression is that the pensile nests of certain American flycatchers, like the similar constructions of certain African weavers (Ploceidae), are so difficult for many kinds of predators to reach and enter that they substantially increase reproductive efficiency. On the other hand, the castles of interwoven sticks, often huge in proportion to the ovenbirds (Furnariidae) that make them, are far more conspicuous than more modest nests without being too difficult for slender predators like snakes to enter or for larger mammals to tear apart. I believe that some of these ambitious constructions decrease the breeding efficiency of their builders. They are luxuries which these industrious birds can afford because the maintenance of their population at a favourable level places no great strain upon their energy.

In all these ways, and doubtless a number more about which we know too little for profitable discussion, the evolutionary process limits the reproductive potential of birds which might otherwise become too numerous for their habitat to support. Probably some of these females who receive no help from their mates, some of these sea-birds that do not become sexually mature until an advanced age, or some of these intensely colonial sea-fowl that must vie with myriads of close neighbours for food, are rearing as many offspring as, under the limitations imposed upon them by prior mutations that reduce their reproductive potential, they can. But this is vastly different from a regime that condemns every living thing to procreate to the limit of its capacity, under penalty of being overwhelmed by more fecund genotypes, as the theory of maximum reproduction implies. These mutations which help to adjust the reproductive rate to the actual need for recruitment are just as truly adaptations as any other mutations which give organisms a more perfect adjustment to the conditions in which they live and reduce the stresses to which they are subjected.

RELATION OF BROOD SIZE TO THE NUMBER OF ATTENDANTS

In my earlier paper (Skutch 1949), I called attention to the fact that in tropical America there are a number of birds which regularly fail to form pairs, with the result that the female alone builds and attends the nest. In this class fall all manakins, as far as is known, practically all the hummingbirds that have been carefully studied, *Dendrocincla anabatina* among the woodcreepers, *Cotinga*, *Lipaugus*, *Cephalopterus*, and

probably other genera of the Cotingidae, a growing list of American flycatchers, and the grackles, oropéndolas, and some caciques (*Cacicus*) in the Icteridae. The feeding habits of these birds which do not form lasting monogamous pairs are diverse and, except in the case of the nectar-sipping hummingbirds, can be matched by those of their monogamous neighbours in the same woodlands. Yet these females who rear their families alone lay, on the whole, sets as large as those produced by neighbouring females whose mates take their full share in rearing the young. As already pointed out, two is the number of eggs most commonly laid by both classes of birds. The unmated flycatchers build hanging nests of various types, and a comparison of their clutch size with that of regularly mated flycatchers with similar nests shows no significant difference in the two groups. The unmated flycatcher *Pipromorpha oleaginea*, a widespread and common bird, frequently raises a brood of three; this is as large as I have found in the pensile nest of any mated flycatcher.

On the theory of maximum reproduction, we should expect pairs of birds which cooperate in feeding their young to rear, on the average, broods twice as large as can be raised by unmated females of more or less the same size and foraging habits in the same environment. Yet we find nothing of the sort. This points to the conclusion that the mated pairs are by no means working as hard as they might to feed their young, as on the maximum reproduction theory they should be doing. Of the various kinds of evidence that I gathered to show that tropical birds do not raise as many young as they can nourish, this was the most convincing to me, as it has been to others.

In comments on my paper, Lack (1949) dismissed this evidence as inconclusive, because the feeding habits of birds in different genera tend to differ, and I could not compare mated and unmated species of the same genus, but only (as in the Tyrannidae) different genera in the same family. I still can cite no instance of a genus of tropical American birds in which some species regularly form pairs and other species regularly fail to do so, although it seems probable that when Neotropical birds have been studied as intensively as northern birds, examples will be found.

Meanwhile, however, von Haartman (1955) has made good the deficiency. Among buntings of the genus *Emberiza* and warblers of the genus *Phylloscopus*, there are species in which both parents feed the young and other species in which the male takes little or no share in attending them. In two illuminating tables, von Haartman shows that, in each genus, there is no significant difference in the clutch size of these two groups. From two other tables, one of which lists one Holarctic and eight North American wrens and the other six North American Icterids, it is clear that there is no correlation between the size of the brood and the number of parents that attend it. From Europe, North America, and tropical America, a growing volume of evidence points to this same conclusion: there is little correlation between the size of the brood and the number of adults that feed it. If brood size is correlated with anything, it must be correlated with mortality, which in birds of about the same size in the same habitat is probably about the same, whether both parents attend the nest or only one does. This kind of evidence is so embarrassing to the theory of maximum reproduction that its proponents have, understandably, preferred to ignore it.

HOLE-NESTING BIRDS

The question of the clutch size of hole-nesting birds requires re-examination. As is well known, birds which nest in holes in trees, burrows, and other protected situations tend to have larger broods and longer nestling periods than birds of about the same size with open nests. This poses a problem for the theory of maximum reproduction, which maintains that the size of the brood is limited only by the parents' ability to supply food. Since it is not evident that a nest in a hole confers special advantages for finding food, hole-nesters ought not to have larger broods than other birds. One way out of the

difficulty is to suppose that the nestlings, which remain long in their safe nooks, grow more slowly, hence each requires less food per day than a nestling of the same size in an open nest. The hole-nesters raise larger broods than the open-nesters because they can afford to take more time to do it (Lack 1948). This explanation rests upon a misconception. Hole-nesting passerines gain weight as rapidly, or almost as rapidly, as nestlings of about the same size in open nests. In both classes, the period of most rapid gain in weight commonly covers the first 10–12 days of life. The difference is that the young in open nests leave at a much earlier age, finding safety in dispersal, while those that grow up in holes have a better chance of survival if they linger in their safer nests until their plumage is well developed and they can fly well. During their final days in the nest they often lose weight, after having surpassed that of their parents. Barn Swallows *Hirundo rustica*, for example, when ten days old weigh about 19.5 gm., as much as their parents. Their maximum weight of about 21 gm. is attained at the age of 12 days, but this declines to about 17.5 gm. while the young swallows remain in the nest for nearly a week longer (Stoner 1935). Similar growth curves have been published for many other hole-nesters (Gibb 1950, Paynter 1954, von Haartman 1957, etc.). Even hole-nesting Willow Tits *Parus atricapillus*, with their large broods of seven young, do not work at their utmost capacity gathering food for them (Kluyver 1961).

If clutch size is determined simply by the parents' ability to supply food to the young, it is hard to understand why it should be larger in hole-nesters than in open-nesters. If, on the other hand, it is determined by the species' need for recruitment, perhaps an explanation can be found. Von Haartman (1957) pointed out that, among north European passerines, there is a greater proportion of non-migratory species among the hole-nesters than among the open-nesters, and that the winter mortality of the resident birds is much heavier than that of species that migrate to warmer climates. Thus the hole-nesters need larger broods to recuperate from their winter losses.

This is probably not the whole explanation, for even in the tropics hole-nesters, notably swallows and house wrens *Troglodytes musculus*, lay more eggs than one will often find in open nests. I suggest that hole-nesters raise large families to compensate for the difficulty of finding nest sites. A bird that builds in the open finds an adequate site in almost every well-foliaged tree or shrub. For hole-nesters, obtaining a home site is a more acute problem. Even for those that carve or dig their own holes, such as woodpeckers and barbets, motmots and kingfishers, this problem may be difficult: a flourishing forest contains many more living trees and branches than dead ones, and exposed banks may be scarce over large expanses of territory that are otherwise favourable for burrow-nesters. Birds dependent on ready-made holes or burrows are in even worse plight; they may wait long until some woodpecker or kingfisher brings forth its brood and releases a suitable cavity, or they may fight for the possession of one, either with the makers or with another pair of birds in the same predicament as themselves. These fights for holes sometimes leave casualties, especially at high latitudes. In the tropics I have seen no real fighting for the possession of holes, but I have watched birds such as Masked Tityras *Tityra semifasciata* waste weeks of time while arguing without violence over the possession of a nest cavity (Skutch 1946).

When a hole-nester is finally installed in a suitable cavity, it must, in many cases, make up for lost time, and also raise enough young to compensate for other members of the same species that have failed to procure an adequate nest site, or perhaps have lost their lives while fighting for one. It is aided in this endeavour by the substantially higher success in breeding of hole-nesters as compared with open-nesters, which has been demonstrated for numerous species (Nice 1957). But evidently this advantage is not enough to compensate for the delays and frustrations which hole-nesting entails for many species. For hole-nesting to be a profitable habit, the species which practice it must lay more eggs as well as rear their broods with fewer losses. Nevertheless, hole-

nesters are, in most parts of the world, fewer in species and individuals than birds which, by building in the open, enjoy a vastly greater choice of nest sites.

THE RELATION OF CLUTCH SIZE TO THE NUMBER OF FLEDGED YOUNG

The central postulate of the maximum reproduction theory is that clutch size is labile and changes rather rapidly (in the evolutionary sense) to conform with the largest number of young that the parents can adequately nourish. It should neither exceed nor fall short of this number; birds should not waste their resources by laying too many eggs, although, in the view of those who uphold the theory, the far greater waste involved in rearing an excessive number of healthy offspring is of no consequence. Any divergence between the number of eggs in the nest and the number of sturdy fledglings which the nest produces, if it remains undisturbed, is so damaging to the theory of maximum reproduction that its proponents have lavished much thought and patient research to reconciling such divergence with their views.

A difficulty is presented by such facts as that several species of boobies, including the Brown *Sula leucogaster* and the White *S. dactylatra*, regularly lay two eggs but only rarely rear two young (Simmons 1965). When the hatching of more nestlings than can often be raised is spread over several days, as in the boobies and a number of raptorial birds, an ecological explanation is available. This system provides flexibility and enables the parents to adjust to a fluctuating food supply the number of young that they rear. When they bring insufficient food to the nest, the younger nestlings lose in the competition for it and succumb; when the supply is abundant, most or all of the brood can be fledged.

This explanation of the value of asynchronous hatching certainly fails to hold in many cases, for the older hawk or owl may murder its younger nest mate(s) long before all of them together require as much food as a single nestling will later need. Rowe (1947) watched a three-day-old Verreaux's Eagle *Aquila verreauxi* attack its newly hatched sibling: by repeated savage attacks, by squatting on and smothering it, and by depriving it of food, the older eaglet killed the younger in the course of a few days. Such fratricide has been reported for over 20 species of hawks and owls, and it is commonly followed by cannibalism (Ingram 1959, 1962). No matter how abundant the food supply, the parents of such savage young are not likely to rear all their brood; often the precocious development of predatory ferocity prohibits the rearing of more than one. In such cases, staggered hatching cannot be regarded as a device which facilitates the adjustment of brood size to a fluctuating food supply. We can hardly view the situation as other than a glaring case of maladjustment, or else the crudest possible method of regulating the reproductive rate.

Routine observations suffice to reveal that the parents have frequently failed to raise all their brood. When the disparity between the number of young and the parents' ability to fill their needs is in the opposite direction and the adults could very well nourish one or more additional nestlings, the fact is more difficult to demonstrate. Usually it is necessary to resort to experiment, although sometimes an exceptionally large brood provides the information we seek. Although Scarlet-rumped Black Tanagers *Ramphocelus passerinii* and Variable Seedeaters *Sporophila aurita* very rarely lay more than two eggs, I have known both these species to fledge broods of three healthy young. By combining two broods of House Finches *Carpodacus mexicanus* or of Yellow-eyed Juncos *Junco phaeonotus* in Mexico, Wagner (1957) demonstrated that the parents could raise double their usual number of offspring with no detriment to their rate of development or condition on leaving the nest. Working with birds very different from these finches, Nelson (1964) proved by multiple tests that a pair of Gannets *Sula bassana*, a species which regularly lays a single egg, could, if given an extra nestling of the same age as their own, attend the two young so adequately that their development lagged only

slightly behind that of single chicks. In this case, the objection usually raised against experiments and observations of this type, that the young of these abnormally large broods leave the nest under-weight and are likely to succumb, was effectively answered by experiment. Thus in the single genus *Sula* we find species which lay two eggs but ordinarily rear only one young, and a species that lays a single egg but is quite capable of bringing up two young.

To sift the great mass of evidence that in recent years has been accumulating on the relation between brood size, food supply, and the weight and survival of the young, would exceed the limits of this paper. Enough has already been presented here to show that some species produce broods larger than they can rear, whereas others have families smaller than they could adequately nourish. This being true, even with a random distribution of clutch sizes we should expect that many would contain just the number that the parents could, by the utmost exertion, adequately nourish. This subject is exceedingly complex, and we shall need vastly more observations and experiments, in different parts of the world, before we can draw any sound conclusions. The only verdict that we can pass at present is that any strict correlation between clutch size and the feeding capacity of the parents is decidedly unproven.

SOME MISCONCEPTIONS

It is not in species with thin, precarious populations, but in those widespread, successful species that make full use of their habitat, that adaptive limitations to reproduction seem most often to be operative, provided these successful species have long been established in a fairly stable environment and have not recently been in an expansive stage. These conditions seem to apply to many species of the moister forests of tropical America, which extend widely on both sides of the equator and are fairly abundant over much of their range. As already remarked, manakins and such flycatchers as *Pipromorpha* and *Myiobius*, which in the male's aloofness from the nest have developed an obvious limitation of feeding capacity, are widespread, common birds. If the species of manakins have more restricted ranges than many other Neotropical birds, this is because their mode of courtship favours rapid change in the adornments and display patterns of the males, by which the species are largely differentiated.

Rare birds may well be employing their full reproductive potential without succeeding in maintaining a high density of population; or it may be that certain subtle, still unanalysed reactions with their environment make a sparse population advantageous to these species. There seems to be fundamental agreement between the theory of adapted reproduction and the theory of maximum reproduction that the genotype which can make the fullest use of the habitat, without causing its deterioration, will prevail. The difference between these two views is that the first-mentioned theory holds that the genotype which achieves this result most economically will prevail, whereas the second theory maintains that the most wasteful genotype will supplant thriftier ones. Yet there is a strong tendency among our contemporaries to emphasize the need for animals to economize their time, energy, and resources in order to succeed in the struggle for existence; a number of recent papers (Orians 1961 a; Brown 1964) argue convincingly that the reproductive or the territorial system that is most economical will be selected. I do not understand how this point of view can be reconciled with the present popularity of the theory of maximum reproduction.

Long ago, I announced the discovery that in White-tipped Brown Jays *Psilorhinus mexicanus* and Banded-backed Wrens *Campylorhynchus zonatus* individuals that are apparently yearlings help mated pairs to attend their nests (Skutch 1935). Later I pointed out that the delayed breeding of these helpers and of other birds is a means of population control (Skutch 1953, 1961 a). In a recent publication, Selander (1964), who found helpers rather widespread in the genus *Campylorhynchus*, challenged my

interpretation of their significance. An adherent of the maximum reproduction school, he believed that the delayed breeding of these wrens could persist only if their total production of progeny in the course of their lives is increased by their failure to breed when about one year old. Selander thought that helpers would be likely to arise in a species which rather fully and consistently occupied a stable tropical environment and had a relatively low and invariable mortality. In such circumstances, a young bird would have a greater chance of surviving, and gaining valuable experience, if it remained for another year with its parents and helped to attend their nest, than if it went forth alone into unknown country and contended with strangers for territory. With this I fully agree. But I fail to see why it is necessary to suppose that the bird who spends an extra year without breeding should finally leave more descendants than if it became a parent when only one year old. This would only aggravate the crowding that delayed breeding relieves. If a species can maintain a full population economically, what can it gain by doing so wastefully?

Ward (1965 b) presented evidence that in the African weaver *Quelea quelea* the most common clutch size of three was also the greatest number of nestlings that the parents could normally feed. He believed that this told against my views on the limitation of the reproductive rate in tropical birds and supported Lack's theory of maximum reproduction. On the contrary, *Quelea* is just the sort of bird in which I should expect maximum reproduction to occur. It lives in a climate with pronounced seasonal changes, it annually faces a season of great food scarcity in which many individuals die, and it is migratory (Ward 1965 a). In my earlier paper, I clearly stated that my views on the limitation of clutch size applied to resident birds in a stable environment, and that I would expect birds that are subject to periodic catastrophes which greatly reduce the population to raise as many young as they could nourish. It is hardly fair to test a theory on the reproductive rate of tropical birds by a species the like of which is certainly not to be found in the American tropics, and which has few parallels anywhere.

Verner (1965) compared the breeding biology of Long-billed Marsh Wrens *Telmatodytes palustris* at two localities in the State of Washington, U.S.A. The first was near Seattle, where in a mild maritime climate ice rarely formed on the marshes in which the wrens were permanently resident. The second locality was near Spokane, in the interior of the state, where in a continental climate ponds and marshes are normally frozen for long periods each winter and the wrens are migratory. At Seattle clutches averaged 5.2 eggs in one year and 4.4 in another; near Spokane the average clutch size was 6.0; and the difference was proved to be statistically significant. Verner believed that clutches were larger in the interior locality because food was more abundant; he thought that each population was raising as many young as could be properly nourished, and that his data supported the maximum reproduction theory, although he cited other observations in Georgia that seemed not to accord with this conclusion. However, he took little account of the fact that one population was migratory and the other permanently resident. The population resident in a mild climate was probably fairly stable, with rather constant annual losses to which the recruitment rate could be adjusted. The migratory population was doubtless subject to those catastrophes which seem from time to time to overtake all migrants; and such periodic decimations will, as I have long maintained, favour the maximum rate of reproduction.

DENSITY-DEPENDENT ADJUSTMENTS OF THE RATE OF REPRODUCTION

In the foregoing pages, we considered certain evolutionary developments which, arising by mutation in successful species of birds which did not need to employ their full reproductive potential in order to survive, reduced this potential, thereby adjusting the species more perfectly to the conditions in which it lived and diminishing the stress to which its members were subjected. Among these developments we recognized reduction

of clutch size, reduction in the annual number of broods, the male's aloofness from the nest, the deferment of breeding, the rise of territorialism, the restriction of breeding to traditional sites, and the time-consuming construction of elaborate nests. There may be doubt as to the origin of some of these developments and how effective they are in limiting reproduction. It is not impossible that the single-egg set of certain species of *Columba*, for example, was the original condition in the pigeon family, from which the predominating two-egg set was derived, but it is more likely that the reverse is true. Delayed reproduction may also be the original rather than the derived condition in certain avian groups, but this seems most unlikely in small passerines like Banded-backed Wrens. But we can be certain that the male's aloofness from the nest, especially in passerine families like manakins, cotingas, American flycatchers, and birds of paradise, is a derived rather than an original situation, and we can be equally certain that this development could never have occurred in a species obliged to exert its full reproductive capacity in order to survive, or in a genotype threatened with extinction if it failed to reproduce as rapidly as any other genotype of its species in the same region.

Although these adaptive limitations to reproduction reduce the waste of energy, food resources, and life that are inseparable from excessive breeding, it is doubtful whether, singly or in combination, they often produce a rate of reproduction that is exactly optimum in the sense earlier defined; nor is it desirable that they do so. Even the most stable environment is subject to cyclic or secular changes; it appears that everywhere more favourable years alternate with less favourable ones. A reproductive rate exactly adjusted to an average year might be incapable of meeting the demands of a series of less propitious years, with lamentable consequences to the species too closely adjusted to the average conditions. Moreover, such a tightly tailored reproductive rate would leave no margin for range extension, if the opportunity for this arose. Genetically determined characters of the sort we have been discussing evidently require many generations to become established in a population, and they cannot be quickly altered to meet emergencies. To be safe, a species must in its more favourable years reproduce slightly in excess of its needs, or it must be so organized genetically that it can make a different reproductive response to the different demands for recruitment of varying years. All that I have been claiming is that we find in birds a strong tendency to adjust reproduction to the mortality, and that the more stable the environment, the more the birds are shielded from widespread disasters, the closer this adjustment tends to become, although it may never become mathematically exact.

If the reproductive rate of an organism is even slightly higher than it need be, it will, given a series of exceptionally favourable years in the absence of opportunity for range expansion, yield a population that is too high in the sense that it bears too heavily on its food resources, faces a shortage of adequate nest sites, or is particularly vulnerable to predation or disease. When this occurs, the population will be readjusted to its environment by some means that is density-dependent, that is, which acts the more powerfully the higher the density becomes. Such density-dependent adjustments are supplementary to the primary regulatory arrangements, which are inherent or genetically determined. The two means that have been envisaged are density-dependent reproductive effort and density-dependent mortality.

To Wynne-Edwards (1962) we owe the most careful inquiry into the occurrence, character, and significance of all those gatherings and communal activities of animals which might, by social means, regulate the intensity of their reproductive effort in a given season, making it density-dependent. He applied the term "epideictic" to the gatherings and displays whereby the members of a population make each other aware of their presence, thereby providing an index to their numerical density and, presumably, influencing the intensity of the reproductive effort they are about to put forth. Examples of epideictic displays among birds are the synchronous singing of all the male birds of a

district at special times of day, as of thrushes at dawn and in the evening; the gathering in a communal roost of birds that forage dispersedly; the mixed flocks of small birds that roam the woodland searching for food; the courtship assemblies of manakins and hummingbirds. Although it is hardly doubtful that gatherings of this sort provide birds an opportunity to assess the local abundance of their kind, to what extent they do so, and whether their reproductive effort is influenced by the resulting impression of abundance or scarcity, remains to be investigated.

In a number of insects, small rodents, and small fishes, it has been demonstrated in the laboratory that crowding decreases fertility. In titmice *Parus* spp. an inverse correlation between population density and clutch size has been demonstrated (Lack 1958), but more studies are needed to discover the prevalence and significance of this phenomenon in birds. In those birds whose clutch size varies with the food supply, we should expect a reduction when the population becomes so dense that the supply is depleted; but such depletion is just what the social regulation of animal numbers is supposed to prevent. And in colonial species which may exhibit the "Fraser-Darling Effect", not a low but a high density of individuals stimulates the greatest reproductive effort, so that thin populations should become thinner and dense ones denser. This seems a truly dysgenic arrangement, which might hasten the extinction of a species whose numbers fall below a certain level. However, the reality of the Fraser-Darling Effect, and the extent of its occurrence, are far from being well established (Orians 1961 b). There is need for much more knowledge in this field. Wynne-Edward's book is full of stimulating suggestions whereof the value can be ascertained only by years of patient field work by many investigators.

The rival view, that populations of animals are kept under control chiefly by density-dependent mortality, whether of adults, eggs, or young, is the one upheld by Lack and his school. Density-dependent mortality is one of the most obvious facts in nature: fatal diseases spread more rapidly, predation is more severe, starvation more frequent in times of scarcity, in dense populations than in sparse ones. Yet in some recent literature there appears a perverse obstinacy to attribute to density-dependent factors more than is due. In a crowded colony of sea-birds, for example, the parents are having difficulty feeding their single nestling, and many nestlings succumb. Density-dependent mortality is evidently operative here. But let us not lose sight of the fact that without such genetically determined, adaptive limitations as small clutch size, delayed reproductive maturity, and perhaps also the restriction of nesting to traditional sites, this colony would be in far worse plight and much more severely chastized. All that density-dependent mortality is doing here is to make the last fine adjustment to the local, seasonal conditions, which a genetically determined limitation cannot, by its very nature, achieve.

The subject of the regulation of the reproductive rate is far too complex to be susceptible to explanation by some simple, universally applicable rule, such that the more prolific genotype will inevitably supplant the less fertile genotypes of the species and keep the reproductive rate at the highest possible level. Certainly various "principles" are operative in this context, doubtless with different intensities in diverse situations. The theory of maximum reproduction appears to explain much, especially among northern birds subject to periodic catastrophes that place a premium on rapid recovery, but even in this field it leaves us with many perplexities. If pairs of northern birds are rearing as many young as they can adequately nourish, how does it happen that solitary females so often raise just as many? If open-nesting birds have families as large as they can well attend, how does it happen that hole-nesters in the same locality so often bring up a larger number of young, which grow just as fast although they stay longer in their safer nests? Turning to the more humid parts of the tropics, where adjusted reproduction seems to prevail over maximum reproduction, how can we account for the manifestation of the latitude effect within only 12 or 16 degrees of the equator? Both in Africa (Moreau

1944) and America, certain groups exhibit a definite increase in clutch size within this range, yet neither the slightly longer day in the breeding season, nor the increased perils to which the birds are exposed, seems adequate to account for this. Lack, Wynne-Edwards, and others have given us valuable suggestions, but only more field work, especially in the tropics, will provide convincing answers. Meanwhile we should keep our minds open and our thoughts flexible.

A UNIQUE EVOLUTIONARY PROBLEM

It has long been recognized by naturalists that one general trend of evolution in the Metazoa is to produce fewer young and take better care of them. This trend, already observable in arthropods and fishes, reaches its climax in mammals and birds. Extreme cases are those fishes and frogs which spawn hundreds or even millions of small eggs which they totally neglect, and those mammals and birds which produce one or two young at a time and carefully attend them for months or years. Except on the improbable assumption of a sudden radical change in a whole series of interrelated characters, it is difficult to understand how this reduction in fecundity with concomitant improvement in parental care could have occurred, if the more prolific genotype always prevails, as the theory of maximum reproduction holds.

To demonstrate the relation between reduced fertility and improved parental care, it is not necessary to compare widely separated groups of animals, such as oviparous fishes and birds; we can discern it within orders and genera of birds, sometimes even in a single species. It has frequently been shown that as broods become larger, the rate at which the parents bring food to the nest does not increase proportionately, so that the young of the smaller brood are better nourished. The small broods of tropical birds often remain in the nest until they are older and better developed than are the larger broods of closely related northern birds when they leave (Skutch 1945, and later observations). Moreover, these tropical birds, especially when they are single-brooded, frequently continue to feed their fledged young much longer than has been recorded for related birds at high latitudes; and sometimes, too, they install their fledglings in snug dormitories at nightfall (Skutch 1961 b). When finally they separate from their parents, the young of these tropical birds are more mature, more experienced, better equipped to take care of themselves, because of their longer association with the adults. Their chances of survival should accordingly be better: they must be better to compensate for the smaller families that are closely associated with this superior parental care.

Only if slightly less prolific genotypes, able to provide slightly better parental care for their smaller families, can hold their own against more prolific genotypes of the same species, does this whole complex of inter-related developments seem possible. The theory of adjusted reproduction is in harmony with the fact that evolutionary advance has been accompanied by the production of ever fewer offspring which receive ever more adequate parental care. The theory of maximum reproduction is difficult to reconcile with this fact.

Before concluding, it seems proper to call attention to the unique nature of the problem we have been discussing. Probably no evolutionist doubts that the mutation which persists and spreads is one which gives some advantage to the individual in which it arises and secondarily to the species through which it diffuses. Examples are mutations which improve efficiency in foraging, promote effective self-defence, or impart greater resistance to some environmental stress. But a mutation that increases the reproductive rate of a species that already has an adequate rate benefits neither the individual in which it arises nor the species as a whole. It does not benefit the individual because the individual does not ordinarily benefit itself by reproducing; by providing for its eventual replacement by its progeny, it "signs its own death-warrant, makes its will, and institutes its heir," as George Santayana so well said. Only if the young remain with the parents

and help them in some way, as in White-tipped Brown Jays and Banded-backed Wrens, or if the parents derive pleasure or satisfaction from attending their offspring, can reproductive activity be said to benefit them. But for the young to help their parents is rather exceptional among birds; and if birds do consciously enjoy their parental role, this is probably more satisfying when the family is smaller and they do not need to work so hard, just as among men. Aside from this, the reproductive effort is of no benefit to the individual who engages in it; the parent squanders its strength and makes itself more vulnerable by attending to its offspring rather than to its own needs and safety.

The species in which excessive fecundity arises is benefited as little as the individual. The spread of the mutant gene exposes it to all the results of overpopulation: exhaustion of the food supply; greater vulnerability to predation and disease; for most individuals a harassed life cut short by an early death. The only individuals who might be said to benefit from this excessive fertility are those who otherwise would not have been born; but since the majority of them are destined to die early, it doubtless would have been better for them had they never existed.

Yet it is undeniable that this mutation which harms rather than benefits both the individual and the species has a tendency to spread through the population, as no other mutation in the same category has, simply because it can multiply itself faster than its alleles. As evolutionists have repeatedly noticed, mutations, which occur at random rather than in response to needs, are mostly harmful, and this is certainly a case in point. The gene(s) for excessive fertility might be compared to a pathogenic virus (which has some of the characteristics of genes) that passes from individual to individual through a population without benefiting anything, except its pernicious self. The unfortunate species in which such a mutation arises seems to be caught in a mathematical trap from which there is no escape. What can stop the triumphant march of the more rapidly reproducing genotype through the species? One answer is that it might become the victim of its own success. The spendthrift population in which it prevails may be so weakened by misuse of its strength and resources that in time of stress it suffers heavy losses, and far from continuing to encroach upon genotypes with more conservative rates of reproduction, it is forced to recede before them. Possibly in some species the strength of numbers and the strength of a sound economy are constantly in a state of dynamic tension, alternately encroaching upon and receding before each other. In a stable environment, the sound economy is likely to prevail. But in a species subject to periodic catastrophes the reverse may be true; each time that the population is decimated, the more fertile genotype will enjoy the advantage of rapid multiplication without, for a while, its penalties. The most prolific genotype may then become the saviour of its species.

SUMMARY

Some biologists have held that the rate of reproduction in birds tends to be adjusted to the average annual mortality; others, that it is limited only by the parents' ability to raise sturdy young. The latter theory, that of maximum reproduction, is likely to be true only if three related propositions are true: (1) that an increase of clutch size is more likely to occur than some other mutation affecting the rate of reproduction; (2) that a genotype with a wastefully high rate of reproduction can supplant a genotype with a more conservative but adequate rate; and (3) that an excessive rate of reproduction is not harmful to the species. None of these assumptions has been proved.

In a population not obliged to employ its full reproductive potential to maintain itself at a favourable level, mutations which limit this potential may arise and persist. They may effect this limitation by means of: (i) reduction in clutch size; (ii) reduction in the number of broods; (iii) failure of the male to attend the nest, often followed by failure to form pairs; (iv) deferment of reproductive maturity; (v) developments in territorialism that limit the number of nesting birds or the number of progeny they can rear; (vi) restriction of nesting to traditional sites; and (vii) the time-consuming construction of elaborate nests. These limitations of the rate of reproduction must be regarded as adaptive because, like other adaptations, they adjust the birds more perfectly to the conditions in which they live and reduce the stress to which they are subjected.

In both tropical and temperate regions, species in which only the female feeds the nestlings have broods as large as species in which both parents feed them. It follows that the two parents are not rearing as many young as they could nourish.

The view that hole-nesting birds can rear larger broods than open-nesters because their young develop more slowly, and require less food per capita per day, is untenable. Nestlings raised in holes and burrows gain weight about as rapidly as those in more exposed nests, but for safety they remain longer in their protected abodes. The larger broods of hole-nesters evidently compensate for the difficulty of obtaining nest sites, which delays the breeding of some pairs and prevents that of others.

Clutch size is by no means closely adjusted to the number of young the parents can raise. If given additional nestlings, some birds attend them adequately. In other species, young are rarely fledged from all the eggs. In many cases, asynchronous hatching is not, as has been claimed, an arrangement which permits the parents to adjust to a varying food supply the number of young that they rear. In many raptors, fratricide and cannibalism reduce the size of the brood, sometimes to a single nestling, regardless of the abundance of food.

The more stable the environment, the more closely the reproductive rate tends to be adjusted to the mortality; the more a population is subject to catastrophic reductions, the more the rate will approach the maximum.

Primarily, the reproductive rate is controlled by heritable characters, which can adjust the rate to a stable environment but rarely respond to short-term fluctuations in external conditions or population density. The last fine adjustment of a population to its habitat is effected by processes that are density-dependent: either density-dependent regulation of the reproductive effort, or density-dependent mortality of adults or young, or a combination of the two.

The general evolutionary trend in the Metazoa is toward producing fewer offspring and taking better care of them. This would hardly be possible if the more prolific genotype always prevails over those which raise smaller families and in consequence can attend their young somewhat better. The regulation of the rate of reproduction is a unique evolutionary problem, because a mutation conferring greater fertility, although often detrimental to the species, tends to diffuse through it as no other harmful mutation can. Yet it is counteracted by many factors, chiefly ecological, which operate subtly and are more difficult to appreciate than the force of numbers.

REFERENCES

- ASHMOLE, N. P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103 b : 458-473.
- BEER, J. R., FRENZEL, L. D. & HANSEN, N. 1956. Minimum space requirements of some nesting passerine birds. *Wilson Bull.* 68: 200-209.
- BROWN, J. L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* 76: 160-169.
- CULLEN, J. M. 1957. Plumage, age and mortality in the Arctic Tern. *Bird Study* 4: 197-207. Abstract in *Ibis* 102: 336, 1960.
- GIBB, J. 1950. The breeding biology of the Great and Blue Titmice. *Ibis* 92: 507-539.
- HARRIS, M. P. 1966. Breeding biology of the Manx Shearwater *Puffinus puffinus*. *Ibis* 108: 17-33.
- INGRAM, C. 1959. The importance of juvenile cannibalism in the breeding biology of certain birds of prey. *Auk* 76: 218-226.
- INGRAM, C. 1962. Cannibalism by nestling Short-eared Owls. *Auk* 79: 715.
- KLUYVER, H. N. 1961. Food consumption in relation to habitat in breeding chickadees. *Auk* 78: 532-550.
- LACK, D. 1947-1948. The significance of clutch-size. *Ibis* 89: 302-352; 90: 25-45.
- LACK, D. 1949. Comments on Mr. Skutch's paper on clutch-size. *Ibis* 91: 455-458.
- LACK, D. 1954. *The Natural Regulation of Animal Numbers*. Oxford: Clarendon Press.
- LACK, D. 1958. A quantitative breeding study of British tits. *Ardea* 46: 91-124.
- MEDWAY, LORD. 1962. The swiftlets (*Collocalia*) of Niah Cave, Sarawak. *Ibis* 104: 45-66.
- MOREAU, R. E. 1944. Clutch size: a comparative study, with special reference to African birds. *Ibis* 86: 286-347.
- MURTON, R. K. 1965. *The Wood-Pigeon*. London: Collins.
- NELSON, J. B. 1964. Factors influencing clutch-size and chick growth in the North Atlantic Gannet *Sula bassana*. *Ibis* 106: 63-77.
- NICE, M. M. 1957. Nesting success in altricial birds. *Auk* 74: 305-321.
- ORIAN, G. H. 1961 a. The ecology of blackbird (*Agelaius*) social systems. *Ecol. Monogr.* 31: 285-312.
- ORIAN, G. H. 1961 b. Social stimulation within blackbird colonies. *Condor* 63: 330-337.
- PAYNTER, R. A., JR. 1954. Interrelations between clutch-size, brood-size, prefledging survival, and weight in Kent Island Tree Swallows. *Bird-Banding* 25: 35-58, 102-110, 136-148.
- RICE, D. W. & KENYON, K. W. 1962. Breeding cycles and behaviour of Laysan and Black-footed Albatrosses. *Auk* 79: 517-567.
- RICHDALE, L. E. 1951. *Sexual Behaviour in Penguins*. Lawrence: University of Kansas Press.
- ROWAN, M. K. 1965. Regulation of sea-bird numbers. *Ibis* 107: 54-59.
- ROWE, E. G. 1947. The breeding biology of *Aquila verreauxi* Lesson. *Ibis* 89: 387-410, 576-606.
- SALOMONSEN, F. 1965. The geographical variation of the Fulmar (*Fulmarus glacialis*) and the zones of marine environment in the North Atlantic. *Auk* 82: 327-355.
- SELANDER, R. K. 1964. Speciation in wrens of the genus *Campylorhynchus*. *Univ. Calif. Publ. Zool.* 74: i-iv, 1-259.

- SERVENTY, D. L. 1956. Age at first breeding of the Short-tailed Shearwater *Puffinus tenuirostris*. Ibis 98: 532-533.
- SIMMONS, K. E. L. 1965. Breeding periodicity of the Brown Booby at Ascension. Ibis 107: 429.
- SKUTCH, A. F. 1935. Helpers at the nest. Auk 52: 257-273.
- SKUTCH, A. F. 1945. Incubation and nestling periods of Central American birds. Auk 62: 8-37.
- SKUTCH, A. F. 1946. Life history of the Costa Rican Tityra. Auk 63: 327-362.
- SKUTCH, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91: 430-455.
- SKUTCH, A. F. 1953. Delayed reproductive maturity in birds. Ibis 95: 153-154.
- SKUTCH, A. F. 1961 a. Helpers among birds. Condor 63: 198-226.
- SKUTCH, A. F. 1961 b. The nest as a dormitory. Ibis 103 a: 50-70.
- SKUTCH, A. F. 1964. Life histories of Central American pigeons. Wilson Bull. 76: 211-247.
- SNOW, D. W. 1962. A field study of the Black-and-white Manakin, *Manacus manacus*, in Trinidad. Zoologica N.Y. 47: 65-104.
- SNOW, D. W. 1963. The evolution of manakin displays. Proc. XIII Int. orn. Congr. (Ithaca): 553-561.
- STONEHOUSE, B. 1960. The King Penguin *Aptenodytes patagonica* of South Georgia. I. Breeding behaviour and development. Falkland Islands Dependencies Survey, Scientific Reports No. 23. London: H.M. Stationery Office.
- STONER, D. 1935. Temperature and growth studies on the Barn Swallow. Auk 52: 400-407.
- THOMSON, A. L. (Ed.). 1964. A New Dictionary of Birds. London: Nelson.
- TOMPA, F. S. 1962. Territorial behaviour: the main controlling factor of a local Song Sparrow population. Auk 79: 687-697.
- TUCK, L. M. 1960. The Murres. Their Distribution, Populations and Biology. Canadian Wildlife Series: 1 (Ottawa).
- VERNER, J. 1965. Breeding biology of the Long-billed Marsh Wren. Condor 67: 6-30.
- VON HAARTMAN, L. 1955. Clutch size in polygamous species. Acta XI Int. orn. Congr. (Basel, 1954): 450-453.
- VON HAARTMAN, L. 1957. Adaptation in hole-nesting birds. Evolution 11: 339-347.
- WAGNER, H. O. 1957. Variation in clutch size at different latitudes. Auk 74: 243-250.
- WARD, P. 1965 a. Feeding ecology of the Black-faced Dioch *Quelea quelea* in Nigeria. Ibis 107: 173-214.
- WARD, P. 1965 b. The breeding biology of the Black-faced Dioch *Quelea quelea* in Nigeria. Ibis 107: 326-349.
- WYNNE-EDWARDS, V. C. 1962. Animal Dispersion in Relation to Social Behaviour. Edinburgh: Oliver & Boyd.

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