

How Birds Handle Their Population Problem

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THE RECENT great acceleration in the growth of the world's human population is causing thoughtful people much concern. Whether the fullest development of the planet's agricultural resources will finally permit it to support three billion people or six is possibly a debatable question, but there can be no doubt that the present rate of increase cannot be long continued, as nations count time, without bringing very disagreeable consequences to mankind and to the living world as a whole. On the one hand, overpopulation, with the inadequate diet, housing and educational facilities which invariably accompany it, causes the physical, intellectual and moral deterioration of men. On the other hand, the steadily mounting human population presses ever more heavily against the wilderness with all its varied life, so that the greater the number of men who inhabit the world, the less of beauty and interest it has to offer them. Thus those who love both their fellow men and the natural world have a twofold reason for wishing to see the planet's population kept within due bounds.

This population problem is not so new as we sometimes suppose. The ancient Greeks were a



fecund race, and after filling their mountainous peninsula, the Aegean islands and the opposite shores of Asia Minor, sent their colonies far and wide about the shores of the Mediterranean. The two leading Greek philosophers, Plato and Aristotle, gave serious attention to the regulation of the number of men in their ideal states. And long before their time, the wanderings of Neolithic peoples, revealed to archaeologists by the changing distribution of their artifacts, suggest that savage and barbarian tribes frequently outgrew their means of subsistence.

It is far easier to recognize the dangers of overpopulation than to prevent it. Perhaps some light might be thrown upon this difficult problem by considering how it has been met by other species of animals, which like men are capable of producing far more progeny than the land can support. If their solutions have not been reached by intelligent planning, but rather through their millennial interaction with their environment,

they are not for this reason less likely to be illuminating to us. And since the goal of all attempts to regulate human population is to maintain it at a steady level, avoiding the plagues, famines and wars that may suddenly and drastically reduce it, we shall turn for enlightenment to those animals which seem to hold their numbers fairly constant over long periods, rather than to lemmings and other northern vertebrates which pass through cycles in which years of tremendous abundance alternate with years of scarcity.

Those who have studied birds in the wetter areas of the tropics, where heavy forests are the natural vegetation, have been impressed by the constancy of the population of the more common birds, which seem to be present in about the same numbers year after year. One reason for this is the absence of great and widespread catastrophes, such as the blizzards which in northern lands take so heavy a toll of those hardy birds which brave the winters, and the adverse winds which often destroy countless thousands of the migratory kinds. Unlike the birds of high

in whatever zone they breed; but in most groups of birds the tropical members lay smaller sets than the extra-tropical members. Here in southern Costa Rica, most of the nests I find contain only two eggs; sets of three are not uncommon; but those of four are rare, and still larger sets exceedingly rare. In the northern United States, on the contrary, sets of two are rare except in pigeons, hummingbirds and goatsuckers, whereas sets of three to five are perhaps the most frequent among small land birds and far larger sets are found in ducks, pheasants and other families in which the young pick up their own food soon after hatching.

This increase in the size of sets with latitude holds good within families, genera and even wide-ranging species. In Costa Rica the Marbled Wood Quail lays four or rarely five eggs, but in the United States the Bob-white Quail lays from 12 to 18 in a nest. In this locality the Southern House Wren lays three, four or very rarely five eggs, but the North American House Wren has sets of six to eight. With us, Gray's

The Russet-capped Nightingale-thrush (left) and her nest (right). Thrushes of tropical America lay about half as many eggs as northern thrushes.

All photographs by the author.

latitudes, most of those of the humid tropics reside the year around in the districts where they breed. Here destructive cataclysms, like volcanic eruptions and hurricanes, are rare and local, not affecting great areas like a devastating winter. Unfortunately, it is difficult to make an accurate census of the birds anywhere, and especially in the heavy vegetation of the tropics; so that our belief that the avian population is fairly constant from year to year is based upon general impressions, or the number of nests in a small area, rather than upon careful counts of whole populations.

The absence in the humid tropics of recurrent spells of severe weather which decimate the bird population is balanced by a low rate of reproduction which cannot increase it rapidly. Ornithologists who visit the tropics from the north are impressed by the small sets of eggs they find. A few avian families, such as pigeons and hummingbirds, lay the same limited number of eggs



Thrush lays two or three eggs, while the American Robin incubates three to five at a time. Innumerable instances of the same sort might be given. There is, however, no abrupt decline in the size of the set as one passes the Tropic of Cancer or of Capricorn; the "latitude effect" holds good within the tropics and beyond them; so that there is in general a slow but steady increase in the size of sets as one passes from the equatorial to the Arctic regions. The wide-ranging Tropical Kingbird (represented in the United States by the race known as Couch's Kingbird) lays sets of four in the South Temperate Zone in Argentina, sets of two or less often three in southern Central America, sets of two to four in

individual has so long a breeding season. Many of the birds in this region raise two or at most three broods, laying two eggs each time, so that they could not possibly equal the output of a finch of the far north, such as the Snow Bunting, which may follow a successful first brood of six young by a second brood of three. But the most prolific of the birds that nest about my house, the Southern House Wren, with its three or four broods of three or four young each, about equals the annual productivity of its northern relative, with two broods of five to seven.

And now for the question most interesting to us from the point of view of the control of population: why do the tropical birds so often lay smaller sets than the most nearly related forms at higher latitudes? Is it, as Dr. Lack has contended, because they cannot adequately nourish larger families? Since birds generally breed when the sun is on their side of the Equator and days

The Ruddy Rail lays 3 or 4 eggs in Honduras, while the northern rails lay much larger sets of 6 to 12 and sometimes even more.

A typical brood of Amazon Kingfishers—four youngsters. Belted Kingfishers in the north make families of five to eight.

northern Central America, and from three to five in northern Mexico and southern Texas. In the Old World, this increase in set size with latitude has been demonstrated for a number of species in tropical Africa by Mr. R. E. Moreau and in Europe by Dr. David Lack.

One at once asks whether the smaller size of individual broods at lower latitudes might not be compensated by a greater number of nesting attempts in the course of a year which, at least so far as temperature is concerned, seems constantly favorable for breeding. Here in Central America a few hummingbirds, antbirds, pigeons and others are known to nest, *as species*, through most or all of the year; but there is no evidence that any

are longer than nights, diurnal species nesting at higher latitudes have a longer period of daylight for gathering food for their families than those of regions near the Equator where day and night are approximately equal at all seasons, and this increase in day-length is progressive until in Arctic regions in June the nesting birds enjoy continuous daylight, although they find it necessary to take a few hours of rest in each twenty-four-hour period.

There is one obvious reason for believing that birds everywhere — and other animals, too — must raise as many offspring as the parents can adequately feed without impairing their own health and strength. In many species we find occasional broods larger than normal, and it seems likely that the capacity to lay these larger sets of eggs is heritable. That race or strain within the species that produced the greatest number of

healthy offspring would multiply more rapidly, and so in the course of generations become the prevailing type. This would seem true even if the more rapid reproduction led to great overpopulation and hence to an extremely heavy annual mortality, which would occur chiefly during the season when food is scarcest and conditions on the whole least favorable. For we have supposed that individuals from larger broods are in no way inferior in strength and vigor to those from smaller broods, so that the two groups should lose the same proportion of their total number.

Dr. Lack's careful studies of Swifts, Starlings and other European birds indicate that broods are

severe. In either case, they confront great hazards which birds of the humid tropics do not know, and from time to time are decimated by adverse weather. After each of these periodic catastrophes they begin the breeding season with greatly reduced numbers, and so resemble a pioneer or freely expanding population, in which large families enjoy an advantage they do not have in more densely populated communities. These occasional depressions in population density give the more prolific strains within each species an opportunity for increasing their number which they would lack if the population remained steadily near its optimum.

We must be careful how we extend to the



normally as large as can be adequately nourished; and when more than the usual number of eggs is laid, if some of the resulting young do not succumb in the nest they are likely to leave it underweight and so begin their active life at a disadvantage. Thus the largest broods do not necessarily produce the greatest number of mature offspring, and over the centuries the fecundity of the females has been so adjusted that in a given region they lay sets of a size which in average conditions will yield the maximum number of healthy progeny. But the birds of central and northern Europe, where these studies were made, must either perform a long migratory journey or else face a winter which is often

tropics the results of studies made in the very different conditions of northern lands. There are several reasons for believing that in the humid tropics birds do not on the whole rear families as large as they can adequately nourish. The nests that I most frequently find in the under-wood of the rain-forest on my farm belong to hummingbirds, manakins, antbirds, finches and tanagers. In hummingbirds and manakins, the male does not share the labors of the nest and to the female alone falls the task of raising the nestlings. In the antbirds, tanagers and finches, the male takes his due part in feeding the young, and the male antbird even helps to incubate the eggs and brood the nestlings. Yet in both of these



The Violet-eared Hummingbird feeds her nestlings in a cypress tree in Guatemala. The few hummingbirds that nest at high latitudes preserve the family tradition of broods of two.

classes, the number of eggs is regularly two. If the solitary manakins and hummingbirds can rear two nestlings, it would seem that with an equal effort the antbirds, tanagers and finches, with both parents cooperating, could raise four instead of the two which I nearly always find in their nests. It might be argued that differences in food account for the smaller number of young for each attendant in the antbirds, tanagers and finches, but I doubt that this is the true explanation. Among the smaller American or "Tyrant" Flycatchers, there are species in which both sexes feed the young and species in which the female alone attends them, yet there is no constant difference in size of broods in the two groups. Taking the tropical American birds as a whole, there are many altricial or nidicolous species of the most diverse feeding habits in which the female alone attends the nest, and most of these lay two or three eggs, like the majority of the females whose mates regularly help to feed the young. This is to me a most convincing reason for believing that when the two parents join in feeding the young, they are not working as hard, or rearing as many offspring, as they might easily do.

Other observations, less convincing in themselves, support the conclusion drawn from the

lack of correlation between the size of the brood and the number of attendants. Rarely a species which normally lays two eggs will produce a set of three; and in four of the five such cases which I studied, the larger family was successfully fledged. Many of the small birds of the tropical forest bring their nestlings big portions of food at rather long intervals; and the advantage of this seems to be that the fewer the visits to the nest, the less likely are the parents to betray its position to predators which rely chiefly upon sight, such as snakes and hawks. Yet if these parents with slow rates of feeding are kept away from their nests until their young are unusually hungry, they can greatly accelerate their rate of food-bringing, as I have seen on several occasions with antbirds. This suggests that food is not hard to find in the rain-forest, and in nourishing their usual brood of two the birds are by no means working to the limit of their strength.

We can hardly escape the conclusion that small birds of the humid tropics do not raise broods as large as they could adequately attend; nor do they seem to attempt as many broods in the course of the year as their own strength and external conditions would permit. Their rate of reproduction seems to be adjusted to their annual losses rather than pushed to the limit of their capacity, as appears to be true of a number of northern birds. Another wholly distinct set of facts reveals that birds as a class do not reproduce as rapidly as they might. Anyone who has

kept domestic quadrupeds, such as horses and cows, knows that they can breed before they have stopped growing, and the same is true of man. But wild birds seem practically always to reach full adult size before they begin to reproduce. Many of the larger birds, as penguins, herons and petrels, delay to breed until several years after they have attained adult stature. The Royal Albatross does not start nesting until nine or ten years of age, and the Fulmar of the North Atlantic not before it is seven years old, or even eight or nine. Like other petrels, the Fulmars incubate one egg at a time, yet in recent decades they have been spreading in a spectacular fashion about the shores of the British Isles, indicating that their slow rate of reproduction is quite adequate for maintaining their numbers and even for rapid expansion.

Is it not remarkable that these birds and numerous others should require a longer period to reach reproductive maturity than many mammals whose size is so much greater than theirs? It appears that after they have completed their growth in stature some inhibiting factor comes into play and delays for one or more years the development of their organs of reproduction; and in view of the fact that these birds are quite capable of maintaining their numbers, it seems that this is an adaptation to prevent superfluous breeding

and overcrowding, with resulting strife between individuals and starvation. It is far more difficult to understand how such an adaptation could evolve than in the case of many modifications which give a more immediate and obvious advantage to the birds which possess them, such as stronger flight or better concealment of the nest. But the subtle interactions between living things, continued for countless generations, produce results which are far from obvious and confound our too facile theories.

To conclude, birds avoid excessive increase in numbers in two distinct ways. Many of the longer-lived species delay breeding for one or more years after they have attained adult stature. Many tropical species lay only two or three eggs in a set although they seem capable of giving adequate care to larger families; and they do not compensate for these small broods by raising a larger number of them each year. These adjustments are not, like late marriage and small families among ourselves, socially determined practices, but are controlled by genetic modifications that have arisen in the course of a long evolution. We know little of the manner in which these adjustments were brought about; but in view of their relevance to one of the most pressing problems of mankind, they seem worthy of our careful study.