DO TROPICAL BIRDS REAR AS MANY YOUNG AS THEY CAN NOURISH?

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I. INTRODUCTION—" THE SIGNIFICANCE OF CLUTCH-SIZE ".

No one can give much attention to the nesting habits of birds in both the temperate zones and the Tropics without being impressed by the fact that, in many families, the tropical birds lay sets consistently smaller than those of their nearest relations in the North or South. The difference in size is often most striking. Thus, to take the example nearest at hand as I write, of the eight species of finches whose nests I find in some abundance on my farm in southern Costa Rica, seven almost invariably lay only two eggs in a set, one often lays three; but I have never once in seven years found four eggs in a finch's nest in this neighbourhood. Yet among the finches of temperate North America and Europe, sets of four, five and six eggs are common, and even larger sets by no means rare. One immediately asks whether the smaller sets of the tropical birds may not be counterbalanced by the production of a larger number of broods, especially in those humid tropical regions where the climate seems favourable to the reproductive activities of birds throughout the year, and individuals of some species are indeed found nesting every month. But longer experience shows that for many species the breeding-season is surprisingly short and the tropical birds, even if they could successfully fledge all the broods they attempted to rear, would actually leave at the year's end fewer offspring than their near relations at higher latitudes. Further experience demonstrates that, especially in the rain-forests, nest losses through predation are far heavier in the Tropics than those that have been commonly reported for extra-tropical regions. Hence we are led to the conclusion that tropical birds, in the rain-forest areas at least, reproduce more slowly than related northern birds; whence it follows that their average life-span must be longer (Skutch 1940).

Birds which nest at high latitudes must each autumn perform a long migratory journey to reach milder regions, or else endure a period of great cold often accompanied by scarcity of food. Whichever alternative they choose is full of perils, and instances of great mortality from both are so familiar to all ornithologists that it is unnecessary to do more than mention this point in passing. Further, it is evident that, in general, the higher the latitude at which a bird breeds, the more severe the winter it must endure if permanently resident, or the longer and more hazardous the journey it must perform to reach milder regions; hence its annual death rate is likely to be higher and it must rear larger families to maintain its numbers—as we actually

observe in the well-known phenomenon of the increase in clutch-size with latitude. One might surmise that predation on adult birds would be higher amidst the more teeming life of the Tropics, but actually this does not appear to be true. Here in Costa Rica, for example, I see fewer hawks and owls than I was accustomed to see in eastern United States, where I spent the early part of my life; and most of the local hawks prey upon reptiles, insects, or even nestlings rather than upon adult birds. I pass whole years without seeing a raptor strike down a bird. It is obvious that in any region a species in order to avoid extinction must, on the average, produce enough progeny each year to replace its annual losses. Students of tropical birds have concluded that in general they rear small families because these suffice to maintain their population constant and even to extend their range. We have assumed that, in some way not clearly understood, clutch-size has through natural selection been nicely adjusted to the reproductive necessities of each species (see Moreau, 1944).

Recently, however, Lack (1947), in an outstanding contribution on the subject, has advanced views which, if admitted as applicable to birds of the humid Tropics, must cause a radical change in our manner of thinking. On the strength of an impressive array of data, Lack concludes 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 ". According to this view, northern birds lay larger sets of eggs because, during the longer period of daylight that prevails during their breeding-season, they can bring more food to the nest than tropical birds limited to little more than twelve hours of diurnal activity. Although it is still evident that tropical birds rear all the offspring that they *need* (since they continue to exist as species with no apparent diminution in numbers), we must add, if we follow Lack's argument, that they also rear all that they *can*. This conclusion, that tropical birds are in many instances unable to rear as many offspring as their relations in the North, and that the difference in their ability to nourish young is of the degree of magnitude that their relative clutch-sizes would indicate, comes as a shock to some of us familiar with conditions in the humid Tropics, and I have thought it worth while to examine it in some detail.

Lack's argument rests upon the proposition that if clutch-size is inherited, those strains within a species which lay more eggs and can, without impairing the strength of the parents, rear normal healthy offspring from them, must come to predominate over their less prolific neighbours merely by virtue of their greater rate of increase. Although he does not make the suggestion, this same argument must apply to variations in number of broods. We do actually observe (for example, in the Neotropic House Wren *Troglodytes musculus*) pairs which produce each year a larger number of broods than is customary in their species, just as we find an occasional female who lays more

eggs than her kind usually does. If these pairs can successfully rear the extra broods, and if number of broods is, as it seems to be, heritable; then the strains with the greater number of broods must, by their very fecundity, come in the long run to predominate in the species. Hence it appears that tropical birds must not only rear families as large as they can properly provide for, but also as many broods as their strength or the environment allows.

This leads us to some amazing conclusions. On the east coast of Greenland, near the Arctic Circle, Tinbergen (1939) found that the usual clutch of the Snow Bunting *Plectrophenax nivalis* was six eggs, and he tells of one female which laid a second set of three after successfully brooding her first family of six. Here on my farm, in a region of evergreen forest nine degrees from the Equator and 2500 feet above sea-level, seven out of eight species of finches can properly feed, during approximately thirteen hours of daylight activity, only one third as many nestlings as the Snow Buntings feed during certainly no more than twenty-four hours of diurnal activity—actually, they appeared to need about two or three hours of sleep each " night " even in June when the daylight was continuous (*op. cit.* : 11). The most prolific of our local finches, the Yellow-faced Grassquit *Tiaris olivacea*, can at best provide for a family half as large as that of the Snow Bunting. More than this, although here frost is unknown and there are at most two months of moderately severe drought—not too severe for many plants to flower and put forth fresh foliage—and even at the height of the rainy season some birds, including tiny hummingbirds, successfully nest, none of the local finches (with the possible exception of *Tiaris*) can in the course of a year rear as many offspring as the Snow Bunting produces in the brief Arctic summer. For none of the local finches breeds throughout the year, nor has a nesting-season long enough for the successful rearing of more than three broods; actually, I have no evidence that any rears more than two. But assuming three broods, they could produce only six offspring; whereas the Snow Bunting may follow a first brood of six by a second of three. The Snow Bunting is by no means exceptionally prolific for a bird of the far North, nor are our local finches less fecund than those of other parts of tropical America for which I have information. If in fact they rear all that they *can*, we must revise our ideas of the relative favourableness for bird-life of the Arctic tundra and the humid Tropics.

The implications of Lack's argument are even more profound. If it be true that, because the more prolific variants within a species must eventually outbreed and " drown out " their less fecund neighbours, birds rear all the young that they can bring up without detriment to the health of either parents or offspring, then it may be supposed that the same law would apply to animals in general, and possibly also to plants. Thus we would have the spectacle of all organisms enslaved to a terrific murine fecundity, dedicating all their available strength to the production of offspring, even though the great

majority of these progeny are not needed to preserve the population of the species at a constant level, and are destined merely to fill the maws of predators or to starve in the lean seasons.

In the present paper I purpose first to give certain observations, made on Central American birds, which seem to prove that they do not rear as many young in one nest as they can properly nourish. Then I shall examine Lack's thesis on theoretical grounds, in an attempt to learn whether it is of general application to birds, or holds merely for populations with the special characteristics of those which he has investigated—that is, for populations which, because of recurrent ecological castastrophes, become periodically expanding populations.

2. OBSERVATIONS ON CENTRAL AMERICAN BIRDS.

Temporary acceleration in rate of feeding.

In many species of Central American birds, especially those of the rain-forest, the normal rate of feeding is surprisingly low. Antbirds (Formicariidæ)—a huge, exclusively Neotropical family—are throughout the continental portions of tropical America among the most abundant birds of the understory of the forest, and with exceedingly rare exceptions they lay sets of two eggs. I have before me a table in which I have summarized the results of 90 hours of watching at 9 nests of as many species, containing nestlings of ages varying from 1 to 9 days, when young antbirds are nearly or quite ready to begin life in the open. Mean hourly rates for the several species and ages of nestlings varied from 1·3 to 5·3 feedings per hour by both parents for 2 nestlings, or 0·65 to 2·65 feedings per nestling per hour. Although they come seldom, antbird parents usually bring morsels quite substantial in relation to the size of the nestlings they are feeding—often just as big as they can manage to force down—and the young develop rapidly, those of some species having the shortest nestling periods I have recorded for purely nidicolous birds in Central America.

Do the parent antbirds bring food so seldom because they can find it no faster ? Certain observations lead me to believe that this is not the case. In early June 1937 I watched a nest of Bridges' Antshrike *Thamnophilus bridgesi* containing two young. During the entire morning of 9 June, when the youngsters were 7 days old, their father, who was the more assiduous attendant, brought food 19 times, or at a rate of slightly less than 3 times per hour. But although the average interval between food-bringing by the male, who had practically ceased to brood, was about 20 minutes, often he returned with food in very much less time—once a minute after leaving the nest, once after 2 minutes, once after 3 minutes, thrice after 7 minutes. At the other extreme there were intervals of 50, 57 and 63 minutes between his appearances at the nest; it is difficult to believe that his luck in hunting was so exceedingly variable that on these occasions he could find something for the nestlings

no sooner. On 12 June, during the first 2½ hours of the morning, I noted intervals of 1, 2, 7 and 9 minutes between his departure from the nest and his return with more food; after that one youngster departed and the father devoted his attention exclusively to it, leaving the mother in charge of the stay-at-home. Thus when the male antbird, after delivering food at the nest, noticed that a little one was hungry, he was able in a short time to find more food and return with it. His habitually slow rate of feeding was not related to his ability to find insects, but adjusted to the requirements of his small brood. His mate, who, in spite of brooding only about ⅔ as much as he, fed only ⅔ as often, was certainly not wearing herself out in hunting.

On 23, 24 and 25 May 1942, I spent much time watching a nest of the Tyrannine Antbird *Cercomacra tyrannina* containing two nestlings, which on 23 May I estimated to be about 4 days old. During a total of 12·5 hours the nestlings were fed 56 times, or at the rate of 4·5 times per hour for the two. The male fed only 19 times to 37 by his mate, a preponderance of activity by the female which is exceptional in my experience with antbirds. From 8.56 to 10.37 on 23 May both parents remained out of sight of the nest, apparently detained by some excitement off in the forest. Returning at the end of this unusually long period of absence, they found the nestlings very hungry and proceeded at once to make amends for past neglect. During the next 69 minutes the mother brought food 17 times and the father 6 times; that is, they were feeding at about 4·5 times the average rate. Their period of most active food-bringing was the quarter hour from 11.00 to 11.15, when they brought food 9 times—8 times as frequently as the average rate. During the whole period of accelerated feeding, the parents brought many insects which were decidedly smaller than those usually delivered; apparently under ordinary circumstances they ate at once the smaller fry discovered in their foraging and took only the more substantial morsels to the nest, while now they brought everything edible that they found. But the far more rapid feeding now more than compensated for the small size of some of the insects, for big ones were also included. After the nestling antbirds showed by their somnolence that they were no longer hungry, the parents fell back to their normal slow rate of food-bringing.

These and numerous other observations made during two decades of watching the birds of Central America have left the net impression that they have little difficulty in finding food, and can usually procure a morsel promptly enough when they need it. The leisurely rate at which so many of them feed their nestlings seems, then, to be caused neither by scarcity of provisions nor by lack of skill in procuring them. A possible advantage of small broods and infrequent parental visits to the nest is the smaller likelihood of betraying its position to enemies. Every bird-watcher knows that the easiest way of finding a well-hidden nest is by following the movements of the parent birds as they carry food to it. In the Tropics, as beyond them, snakes prey heavily

upon the eggs and nestlings of birds; and everything that I know about their habits leads me to believe that they locate the nests chiefly by following with their perpetually open eyes the movements of the parent birds, while themselves lurking unseen amidst the vegetation. The fewer their visits, the less likely are the parent birds to betray the position of a well concealed or inconspicuous nest. This, I think, has led to the habit, so common in forest-dwelling birds, of bringing large offerings at fairly long intervals rather than coming often with small portions of food. Although the difficulty of finding a considerable number of nests, and the rarity of variations in the size of the clutch in so many tropical species, would render the accumulation of statistical evidence most difficult, I believe it not unlikely that a small family may stand a better chance of escaping predators than a larger one of the same species in the same habitat—especially in the undergrowth of the forest, where nest losses are particularly high. In considering rates of increase, we should bear in mind the possibility that a smaller clutch may be more or less compensated by a higher degree of success in nesting.

In the experiment that I am about to relate, I was impressed by how much noisier the nest became at meal-time when it contained three nestlings than when it held two, and when it contained two than when it had a single occupant. When the nestling was alone its cries were silenced with a morsel of food as soon as it opened its mouth; with three nestlings there were at each parental visit two unsatisfied throats to emit noises. However, I infer that by day nests are less likely to be betrayed by auditory than by visual clues—else natural selection would long ago have weeded out the noisy babies—while predators that hunt by night must depend largely upon scent. At all events, were larger broods to become essential to the perpetuation of the kind, it is obvious that existing species must either discover some way to rear them in despite of predators, or else become extinct.

In May 1948 I was fortunate enough to have close by my house two nests of the Song Tanager *Ramphocelus passerinii costaricensis*, each with two nestlings—the almost invariable number in this species—those of the two broods hatched only two days apart. On 21 May, when the nestlings in the older set in Nest 151 were 6 days old, I sat on the porch and watched during the first 5 hours of morning activity (5.30 to 10.30). The mother fed the nestlings 66 times, the father 9 times, making a total of 75 feedings in 5 hours, or at the rate of 7·5 feedings per nestling per hour. That evening I transferred a nestling from Nest 152 to Nest 151, bringing the number of its occupants up to three. (I did not remove both because this would have caused the parents of 152 to abandon their nest.) Next morning I again watched Nest 151 from 5.30 to 10.30. Apparently stimulated by the increased noisiness of the larger family, the male first brought food at 5.59, although on the preceding morning he did not visit the nest before 8.00. He fed 23 times during the 5 hours, the female 83 times, making a grand total of 106 feedings by both

parents, or at the rate of 7·1 feedings per nestling per hour. That evening I transferred two nestlings from Nest 151 to Nest 152, leaving only a single one of the original occupants in 151. Next morning, during the first five hours, the male fed only 8 times and the female 28, giving a total of 36 meals, or 7·2 per hour for the single nestling. After this I returned all nestlings to their proper nests. While these observations were in progress, I put no food on my feeding-shelf close by; and the Song Tanagers, who most of the time made good use of the ripe bananas and plantains that were to be found there, had perforce to depend upon their own resources.

Observations at other nests showed that the rate of feeding varies little during the second half of the Song Tanager's twelve-day period in the nest. These parent Song Tanagers adjusted their rate of feeding to the number of mouths with a nicety which I should hardly expect to see duplicated with a repetition of the experiment. They had no difficulty in increasing their usual rate of food-bringing by fifty per cent to satisfy an extra nestling. I did not leave the third nestling in their nest, because the difference of two days in age and expected time of departure, between this birdling and the original occupants of the nest, would have created a situation unprecedented in my experience with Song Tanagers, and would not have been a fair trial of the parents' ability to rear a larger family.

In this species there is a good deal of variation in the part taken by the male in feeding the nestlings; nearly always he brings some food, but often far less than the female. This is one more example of the great waste in potential food-bringing capacity that we observe in Neotropical birds. Were it of any advantage to the species or to certain strains within it, we might suppose that natural selection would mobilize this wasted bird-power and increase the rate of reproduction. Thus, in the Song Tanager, we find an occasional male who feeds the nestlings almost as actively as his mate, and in the same locality an occasional female who lays three eggs. Conceivably, if greater fecundity possessed selective advantage, the felicitious wedding of the more active males with the more fertile females would give rise to a race of Song Tanagers of which the males took their full share in feeding and the females regularly laid three of more eggs; and this race would gradually " drown out " the now predominant stock of lazy males and two-egg females.

I was surprised that the Song Tanagers with which I experimented brought food at a rate so nearly proportionate to the number of nestlings, because at other nests of this species, as well as at nests of the Northern Yellow-bellied Elænia *Elænia flavogaster*, food was brought to a single nestling slightly more than half as often as to a brood of two; and Moreau (1939, 1940, 1941, 1942, 1947) has collected abundant, though not wholly consistent evidence, that among a number of tropical African swifts, swallows and other birds, a lone nestling tends to receive more food than each member of a larger brood. This does not necessarily imply that the members of the bigger brood,

especially if it be of the size normal with the species, do not receive all the nourishment they need. A possibility that should be kept in mind, while making observations and experiments on variations in the rate of feeding, is the existence of an innate rhythm in food-bringing, adjusted to the number of nestlings normal in the species. Among men, two individuals may have very different rates of working, or walking, or reading; and these rates are apparently the result of early training or of temperamental differences rather than of physiological or structural diversity. If need be, the slower individual can read or walk more quickly, or the more lively man do these things more slowly; but each will experience a feeling of strain while performing at the unaccustomed rate, and slide back to his natural pace when external pressure is removed. So, too, as we have seen, birds can for considerable periods alter their rate of food-bringing in obedience to the requirements of their family, but return to their normal rate as soon as unusual demands are satisfied. The existence of an innate rhythm, adjusted to the normal brood, would explain why each nestling in a smaller brood is fed more often than each one in a family of the usual size. Conversely, if members of an abnormally large brood do not receive as much nourishment as they should, it does not necessarily follow that there is any lack of available food or of parental skill in finding it; it may merely indicate the existence of a hereditary or even an acquired rhythm in the rate of food-bringing.

Abnormally large broods.

Even in species very constant in the number of eggs they lay, one occasionally finds an abnormally large clutch. Thus, for the Song Tanager I have written records of 159 nests, and have seen at least several dozen more of which I made no notes. In only four nests have I known the normal clutch-size of two to be exceeded. One of these nests held four eggs which fell into two pairs, differing so strikingly in size and shape that I had little doubt that they were laid by two females—not surprising in a non-territorial species of which two individuals may occasionally build a few feet or even inches apart. One nest with three eggs actually changed ownership from one female to another, differing markedly in brightness of plumage, while I kept it under observation. This leaves two nests with three eggs that appeared in the same quarter of my dooryard in successive years. From dates of hatching and the uniformity of the eggs in size and coloration, I have no reason to doubt that both of these were true sets produced by a single female—the same, I believe, in both years. In 1946 the nest was in a small orange tree, and here all three nestlings were successfully fledged, leaving when between 12 and 13 days old—the normal age. On 16 May, when the nestlings were 11 days old, I watched during the first five hours of the morning, and saw them fed 40 times by the male and 46 by the female, or at the rate of 5·7 times per nestling per hour. This was somewhat less that the rates—7·1 to 7·5 times per hour—

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at the nest with which I experimented in 1948, but not greatly different from that at other nests with the usual complement of two nestlings. The weather and insect life in 1946 were quite different from those in 1948, and not improbably the tanagers at the two nests were bringing their young food of different character.

Although in 1946 the three eggs all hatched within a period of six hours, in 1947, when the nest was in a *Dracæna* tree 80 feet from the site of the former, the third egg hatched more than 24 hours, and possibly as much as two days, after the first two, resulting in a diversity in age among the nest-mates unusual in Song Tanagers. Under these circumstances, one of the nestlings vanished before it was feathered, and only two were successfully fledged. Also the fact that in 1947 the three nestlings were born five weeks earlier than those in 1946, and at this earlier date food was possibly not so abundant, may have had something to do with the parents' failure to rear all three of the youngsters. The nest with four eggs, mentioned above, was cleaned out by a predator before the eggs hatched; and in the nest with three eggs which changed ownership, two failed to hatch, evidently having been damaged or chilled during the contest which resulted in the change in possession ; hence these nests failed to yield information of present interest.

In 63 nests of the Variable Seedeater *Sporophila a. aurita*, I have only once known the normal clutch of two eggs to be exceeded. The unusual nest with three eggs was situated in the top of a hibiscus bush in front of one of the windows of my study; and here, on 20 August 1944, I watched the three fledglings make their exit, all within $3\frac{1}{2}$ hours. For the very different Caribbean race of this species, the Black Variable Seedeater *S. a. corvina*, I have records of six nests, five of which held two eggs and one three. This last also happened to be outside my window, at a house where I was staying as a guest; and I watched all three fledglings take their spontaneous departure, early on the morning when they were twelve days old.

Although occasionally in northern Central America it lays three, in this part of Costa Rica the Blue Tanager *Thraupis episcopus* regularly lays two eggs in a set. These pretty birds sometimes indulge in the bad habit of stealing the occupied nests of other birds, the Golden-masked Tanager *Tanagra nigro-cincta* being their victim in this neighbourhood. If the stolen nest contains eggs, the thief incubates them along with her own. In one instance, the Blue Tanager hatched a single egg of the Golden-masked Tanager along with two of her own, and with her mate's help reared all three nestlings until they were fledged. The young Golden-masked Tanager, whose nestling period was shorter than that of the Blue Tanagers by three or four days, left first, and then apparently died because its calls failed to attract the foster parents, who continued to attend their own bigger offspring in the nest. In a later year, a Blue Tanager incubated two eggs of the Golden-masked Tanager along with two of her own, in a nest stolen from the smaller bird and situated

in a bunch of plantains; but this interesting natural experiment was abruptly terminated by the visit of some predator. Unfortunately, so far as our present inquiry is concerned, in no part of Central America where I have resided long have there been many parasitic cuckoos or cowbirds, except the Giant Cowbird *Psomocolax oryzivorus*, which drops its eggs into the woven pouches of oropéndolas and related birds hanging inaccessibly high. Hence I have enjoyed small opportunity to learn how often Neotropical birds are successful in rearing the foster child with no loss of their own offspring.

Other attempts to learn whether birds with families exceptionally large for the species would succeed in rearing them were frustrated by predatory interference. But it seems significant that in four out of five such nests which escaped predation, the parents were successful in rearing, at least to the age of fledging, broods fifty per cent greater than normal. Apparently with families of the usual size in these species, the parents are not working up to their limit to nourish their offspring.

Moreau (1947 : 206) relates a most interesting experiment with a pair of Red-throated Rock-martins *Ptyonoprogne fuligula* at Amani, five degrees south of the Equator in Tanganyika Territory. " When their brood of one two-thirds grown young was increased to three, they quintupled the rate of their visits to the nest ; and the result was that the feeding-rate per young bird became one and a half times as great as the next highest of which there is any record " (in 1300 hours of observation on this species). In this instance the stimulus of adding young to the nest caused the parent Rock-martins to over-adjust their rate of feeding. Another pertinent observation was made with the Wire-tailed Swallow *Hirundo smithii* in the same locality. As a rule male and female of this species share rather equally the work of feeding the nestlings. But when the male of one pair died, leaving to the female the sole care of three young, she consistently maintained the feeding-rate at slightly above the average, alone bringing food at least as often as she and her mate would ordinarily have done together. It is obvious that before the loss of her mate this swallow had not been bringing food as fast as she could find it.

Variation in clutch-size with number of parents attending the nest.

The observations which follow are to me the most convincing that I have to offer; they represent what we may look upon as the conclusions reached by Nature as a result of experiments carried on over vast areas during many centuries and involving untold millions of birds. No single observer or even team of observers could hope to accumulate so vast a body of experience.

Among nidicolous birds, species in which a single parent feeds the nestlings are relatively more numerous in the Neotropical than in the Nearctic avifauna. This fact alone suggests that Neotropical birds do not reproduce up to their limit—that a good deal of potential food-gathering power is being wasted. The species in which the female alone attends the nest occur chiefly in

families with highly specialized habits of courtship; they include all hummingbirds so far as known*, all manakins so far as known (especially species of *Manacus*, *Pipra* and *Schiffornis*), some of the cotingas (*Cotinga* and doubtless also species with such spectacular modes of courtship as the bellbirds—*Procnias*, *Carpodectes*, etc.), *Dendrocincla anabatina* among the woodhewers (observations at two nests), *Pseudocolaptes boisonneautii* among the ovenbirds (observations at one nest), a number of American or "tyrant" flycatchers (to be considered later), and many Icteridæ (especially oropéndolas and caciques). The feeding-habits of these birds are extremely varied: the hummingbirds subsist upon the nectar of flowers and minute invertebrates plucked from blossoms or foliage or caught in the air; the manakins eat insects and many berries; the cotingas eat fruits and big insects plucked from the foliage; the woodhewers hunt over the bark of trees and capture fugitives from the army ants; the oropéndolas and caciques subsist upon fruits varied by insects.

If tropical birds rear broods as large as they can properly nourish, we should expect that, on the average, species in which both parents co-operate in feeding the young would lay clutches twice as large as those in which the female attends the nest unaided. Certainly the birds mentioned above provide a fair cross-section of the feeding-habits of the arboreal birds of tropical America. Yet in this heterogeneous group the clutch-size is two, occasionally more, just as it is for birds of the lowland forested regions of Central America in general. To make a more specific comparison, the nests which I most commonly find in the undergrowth of the forest in this region are those of hummingbirds, manakins, antbirds, finches and tanagers. In the first two families the female attends the nest alone; in the last three the male helps to feed the nestlings (among antbirds he also broods); yet in the local nests of all five families two is the number of eggs I almost invariably find.

The American flycatchers are a group of exceptional interest. In the majority of species the male takes a full share in feeding the nestlings, although so far as I have observed he never broods. In a few small and retiring species, however, the male has peculiar habits of courtship, at times resembling those of hummingbirds or manakins but less highly developed, and apparently he never concerns himself in the duties of the nest. The following list gives the clutch-size of some Central American flycatchers with such habits. For comparison, I have placed opposite each one a flycatcher of which both parents attend the nest and which shows some points of resemblance, whether in nidification, habitat, or diet. The high degree of specialization of some of these birds makes close matching impossible; but the species on the right

* The observations of Moore (1947) on the males of certain species of Ecuadorian hummingbirds that took an interest in the nest should certainly stimulate further studies, but they are too fragmentary to allow us to form a picture of the part these male hummingbirds play in the economy of the nest.

side of the list give a fair cross-section of the smaller Central American flycatchers of which both parents attend the nest.

Clutch-size of some Central American Tyrannidæ.

Female alone attends nestlings	Both parents attend nestlings
Red-tailed Flycatcher *Terenotriccus erythrurus* 2×C/2	Slate-headed Tody Flycatcher *Todirostrum sylvia* 5×C/2
Short-billed Flatbill *Rhynchocyclus brevirostris* 1×C/1, 1×C/2	Sulphury Flatbill *Tolmomyias sulphurescens* 2×C/2, 1×C/3
Bent-billed Flycatcher *Oncostoma cinereigulare* and *O. olivaceum* 1×C/2 for each species	Golden-crowned Flatbill *Platyrinchus coronatus* 5×C/2
Oleaginous Pipromorpha *Pipromorpha oleaginea* 11×C/3, 2×C/2	Northern Tyranniscus *Tyranniscus vilissimus* 7×C/2
Royal Flycatcher *Onychorhynchus mexicanus* 4×C/2	Black-hooded Flycatcher *Serpophaga cinerea* 16×C/2
Sulphur-rumped Myiobius *Myiobius sulphureipygius* 5×C/2	Black-crowned Tody Flycatcher *Todirostrum cinereum* 7×C/3, 6×C/2

These records are all original, and all were made in Central America. They might be extended by including the published records of other ornithologists, but the picture as it stands would not be changed; and for those species on which my own data are particularly scanty, there appears to be little that is helpful in print. For both groups of flycatchers, two is the prevalent clutch; and the broods of three of the Black-crowned Tody Flycatcher, fed by both parents , are balanced by the broods of three of the solitary Pipromorpha. In fairness, it should be added here that there are, especially among the bigger and more active flycatchers of open country, and particularly in northern Central America, species in which both parents attend broods of four; but there are also many additional species not listed here in which both parents rarely if ever rear more than two nestlings. The female flycatchers which receive no help from their mates manage to rear families as big as those which are assisted. The size of the brood appears to be adjusted to the mortality of the species, which presumably is not affected by the number of parents which attend the nest, rather than to the parents' ability to nourish their offspring.

In the third part of his study of clutch-size, Lack (1948) points out correlations between the safety of the nest-site, size of the brood and length

of the nestling period. He shows that in Europe birds which place their nests in holes or other situations where losses by predation are likely to be lower than at open, exposed nests, can rear somewhat larger broods, because with the slower rate of development permissible in these relatively safe sites the nestlings require less food *per capita* each day. Since a slow rate of feeding may be compensated by a long period in the nest as a specific character, we may ask whether in those flycatchers of which the female alone attends the young these do not have a longer nestling period. With the exception of the Bent-billed Flycatcher, these normally solitary females build pensile structures which, as I have shown elsewhere (1945 : 29–31), appear to be relatively immune from predation, so that the nestlings may in comparative safety tarry long in their swinging cradles. Hence the parents working together might be able to rear a larger brood than could profitably be undertaken by flycatchers whose more conventional nests are more vulnerable, or the male might be released from domestic cares to engage in other occupations.

Because the majority of these pensile nests are with difficulty accessible to man no less than to four-footed mammals, snakes and other wingless creatures, I have not succeeded in gathering a large number of records of the length of the incubation and nestling periods. With the exception of a few recent determinations, my information on this subject was published in the paper already mentioned. The data on clutch-size are presented in the foregoing list, and those on the nestling periods that are pertinent to our immediate interest may be briefly repeated here. Among species in which the female alone feeds the nestlings, a Red-tailed (=Fulvous-throated) Flycatcher reared a single nestling which flew from the nest at the age of 19 days. A single Short-billed Flatbill stayed in the nest about 23 days. A brood of three Pipromorphas flew out somewhat prematurely when I tried to see them in their snug chamber; they were 19 days old. Royal Flycatchers have a nestling period of 21 to 22 days. At a nest of the Sulphur-rumped Myiobius, the two nestlings left when 22 days old. Turning now to species of which both parents feed the nestlings, we shall confine our attention to those whose nests are strictly pensile, for only these can be fairly compared with the solitary flycatchers with hanging nests. Of these, the Slate-headed Tody Flycatcher had a nestling period of at least 19 days at one nest, and of 21 at another. The Sulphury (=Gray-headed) Flatbill had a nestling period of 20 days or more. Although the records are few, they suggest that when a single parent attends the young the nestling period is at most slightly longer than when two parents feed them. Certainly the differences in the lengths of of the nestling periods are hardly great enough to compensate for the absence of one of the possible attendants, if we suppose that the parents bring food to the limit of their ability.

Comparisons of this sort would be more convincing if made within the limits of a single genus, but so far as I know attendance or non-attendance of

the nest by the male is constant in each genus of flycatchers. The male Pipromorphas, which seem to take no interest in the nests, may during nearly half the year be found daily in definite parts of the forest remote from known nests, tirelessly repeating an absurd little song as they flip up their wings alternately. The Bent-billed Flycatchers have somewhat similar habits. The male Royal Flycatcher guards the nest although he seems never to bring food to it. In the other species where regular mating fails to occur, I have been able to discover no special activities of the males.

Nidifugous birds.

Most instructive in our present inquiry are the nidifugous birds. Since the young of these species leave the nest within a day or so of hatching and, in most groups, pick up their own food under parental guidance, we would expect the size of the brood to be influenced by the length of the parents' working day far less than with nidicolous birds. There is no apparent reason why a " gallinaceous " parent cannot scratch for as large a brood in the tropical forest as in northern woodland or steppe. Actually, there is no class of birds in which clutch-size changes more strikingly with latitude. Compare the family of four chicks of the Marbled Wood-Quail *Odontophorus gujanensis* with the 10 to 18 chicks of the Bob-white Quail *Colinus virginianus* in the United States, or the 9 to 20 of the Partridge *Perdix perdix* in England. The downy chicks of the Wood-quail travel in a small covey in which older birds predominate, and apparently profit by the scratching of both of their parents as well as by the activities of other members of the flock. The difference between the abundance of insects and seeds on the ground in tropical America and that in the North Temperate Zone must indeed be great if it is reflected by the fecundity of these members of the pheasant family. In the Eastern Hemisphere, broods in the Phasianidæ are also much smaller in the Tropics than at high latitudes. The interesting comparison between African and British species given by Moreau (1944 : 318) shows that the clutches of the latter average about twice as great. Rails and their allies also have far larger broods in the North than between the Tropics; but since the parents pick up food for the downy young that follow them about, the force of the argument that we have applied to the Phasianidæ is somewhat diminished.

Time required to gather food.

How many hours a day must a parent bird actually devote to finding food and bringing it to the young ? Naturally this will vary greatly with the age of the young, being at a minimum when they are newly hatched and have small capacity; but here we need be concerned only with the maximum time required, since this will limit the number of young that can be properly nourished. Whether the young require more food during their last days in the nest or after leaving it appears not to be known; but the demand upon the time and energy of the parents will probably for most species be greatest

before the young depart the nest; for then each billful must be carried from where it is found to the nest, but after beginning to move about the fledglings may accompany their parents and make these flights between the nest and the source of food unnecessary. How does the amount of food consumed by older nestlings compare with that required by the parents themselves? Because the nestlings are growing, they would seem to need more food than the parent; but because they lie inactive in the nest, while the parents are very active, they burn up less energy than the old birds. These two factors tend to balance each other; and in the absence of exact measurements, I think it a fair surmise that the food needed by a young bird at the point of fledging is not greatly different from that required by each parent.

We are fortunately able to make an estimate of the time required by an adult bird to find its own food. With some exceptions, most birds continue to eat well during the period of incubation, taking many short recesses or a few long ones and either leaving the eggs uncovered while they forage, bathe and preen, or else sitting alternately with their mates. They that do not scrimp themselves with food is proved by the fact that the Song Sparrow *Melospiza melodia*, doves and doubtless other birds actually gain weight during this period (Nice, 1937 : 27). Since we are able to measure the number of minutes they spend away from the nest, we can set an upper limit to the time they must devote to satisfying their appetite.

Table I gives the number of hours spent away from the nest by 17 incubating females of 8 species of Costa Rican finches. Each nest was watched from concealment from 6 (in one instance 5) to 12½ hours, continuously or at most in two shifts. After computing the average length of the bird's sessions and recesses, the time on the nest and the time off were calculated as percentages. Then, allowing 12·5 hours as the length of diurnal activity at 9 degrees North latitude while the sun is in the northern hemisphere, and multiplying this by the percentage of time spent away from the nest, the total length of each bird's absences during a day was estimated. Each of these finches incubated with no help from the male. The saltators and the *Arremonops* were given occasional morsels by their mates, but these were token feedings and seemed insufficient in amount to cause a significant reduction in the time the females needed to devote to finding their own food.

The time spent by these seventeen females away from their eggs ranged from 2·4 to 5·0 hours per day. A Towhee *Pipilo erythropthalmus* that I watched in Maryland, U.S.A., in early June, gave 4·2 hours to her recesses, as calculated from her spending 27 per cent of my seven-hour observation period away from the nest, and allowing 15·5 hours for diurnal activity at this season. The data published by Nice (1943 : 221, Table xxiii) indicate that the Song Sparrow and other northern birds devote comparable periods to their recesses from incubation each day; expressed as a percentage most of these birds spent less time away from their eggs than my Costa Rican birds, but their

absences were spread over a longer day. Averaging the figures that appear in the right-hand column of Table I, it appears that female finches while incubating devote roughly four hours a day to finding food, preening and other

TABLE I.

TIME DEVOTED BY INCUBATING FINCHES TO FORAGING AND OTHER ACTIVITIES OFF THE NEST.

Species	Hours watched	Percentage of time off nest	Hours off nest per day of 12·5 hours
Striped Atlapetes *Atlapetes torquatus*	9	39·2	4·9
Same—another nest	6·5	35·4	4·4
Orange-billed Sparrow *Arremon aurantiirostris*	12·5	33·5	4·2
Black-striped Sparrow *Arremonops conirostris*	10	24·6	3·1
Same—another nest	12	23·8	3·0
Blue-black Grosbeak *Cyanocompsa cyanoides*	7·5	25·1	3·1
Same—another nest	12	27·7	3·5
Buff-throated Saltator *Saltator maximus*	12	34·0	4·3
Same—another nest	6	33·6	4·2
Same—another nest	5	39·9	5·0
Streaked Saltator *Saltator albicollis*	9	31·5	3·9
Variable Seedeater *Sporophila aurita*	8	25·0	3·1
Same—another nest	9	18·8	2·4
Same—another nest	8	39·1	4·9
Same—another nest	6	34·0	4·3
Yellow-faced Grassquit *Tiaris olivacea*	9	36·0	4·5
Same—another nest	6	29·7	3·7
			Per day of 15·5 hours
Red-eyed Towhee *Pipilo erythropthalmus*	7	27·0	4·2

necessary activities. We shall assume that their time away from the eggs is fully occupied by essential business, although my impression is that they dawdle a good deal.

The male, we have every reason to believe, can attend to all essential matters, such as finding food, preening and bathing, with the same allowance of time as the female. After he begins to attend the nestlings—as he does in all of these species of finches—he sings little, or sings while he forages and as he approaches the nest with his mouth full. Thus, in this region, in April, May and June, each parent has available 12·5 less 4, or 8·5 hours, for feeding older nestlings which no longer require brooding by day. All of the species I have listed, except *Tiaris* and *Pipilo*, regularly lay two eggs; *Tiaris* in this neighbourhood often lays three, and the northern Towhee from three to five. Is it possible that it takes each parent more than twice as long to feed a nestling as to find enough food for itself? We may suppose, however, that although the parent finch's time is not fully occupied in feeding two nestlings, the 12·5 hours of daylight would not permit them to attend three. Together the two parents have available 8·5 times 2, or 17 bird-hours that they can devote to their nestlings. If they could properly nourish their offspring with an allowance of 5⅔ hours for each, the theory that they rear as many young as they can properly provide for would require that they rear three. Hence we must conclude that Costa Rican finches, with few exceptions, cannot bring enough food to their nestlings in less than six bird-hours for each. On the basis of our liberal allowance of four hours daily for all the requirements of the parents, this is hardly credible. Although I chose the finches as the group more familiar to northern readers and more available for comparison, I have an even greater bulk of data for the tanagers which points to the same conclusion, which holds in general for the passerine birds of this region, and for many non-passerines.

For birds at high latitudes, the great variability of length of day with latitude and with date, the varying length of twilight and of the duration of the birds' activity during this period, render it most difficult to make calculations such as we have done for the Costa Rican finches, especially on the basis of the data on clutch-size given in regional bird-guides, which fail to take all these variables into account. But the roughest calculation will show that northern finches often feed their nestlings with an expenditure of less than six-bird-hours for each. Making the same allowance of four hours per day for the necessities of each of the parents, a pair with four nestlings, and 16 hours of daylight available for foraging as at middle latitudes in midsummer, can give six hours to each nestling. With a brood of five, still common at these latitudes, each can receive 4·8 hours of parental attention; with six in the brood, four hours are available for each. Far in the north, where the birds' activity may continue for 20 hours, with a brood of four the parents may devote eight hours to finding food for each; with five they have 6·4 for each; and with six nestlings (by no means rare in the far North) they have 5·3 hours for each. It seems likely that with such prolonged activity and so many nestlings to toil for, the parents themselves must require more food than

tropical birds which are active for little over twelve hours and feed only two or three nestlings. These northern birds often fall off markedly in weight while attending young, indicating that they are depriving themselves in favour of their offspring and not taking as much food as they require. It would be interesting to know if tropical bird parents also lose weight at this period. Nothing would tell us more convincingly whether they are working as hard as they can to feed their young.

Limitation in number of broods.

If we assume that birds rear families as large as they can feed without permanent injury to thenselves or loss of vigour in their offspring, we must also recognize that the operation of the same principle would cause them to raise each year as many broods as they can care for without detriment to their health. Do tropical birds in general produce as many broods as environmental conditions, or their own health and strength, will allow? In many parts of Central America, some birds nest successfully in every month; yet in most species the breeding-season is so restricted that it surprises the new-comer, who supposes that where the climate appears so uniformly favourable, the birds should always be singing and nesting. Likewise, a few individuals of a certain species may rear offspring at a time when the majority of their neighbours of the same species are not engaged in reproduction; for example, in this region a few pairs of Variable Seedeaters *Sporophila aurita* and of Yellow-faced Grassquits *Tiaris olivacea* may nest at the beginning of the drier weather in December, although most breed only in the earlier part of the wet season, from May or June to August or September. Facts like these lead us to believe that many birds might successfully reproduce at seasons when they are resting.

It is sometimes said that birds, like plants, must have a period for rest and recuperation after the exhausting activities of reproduction. Actually, many plants, including the guava, the orange, and the rubiaceous shrub *Hamelia patens*—to name only those in sight as I write—bear flowers or fruit, or both together, through most or all of the year; and individual plants are constantly in some phase of reproduction. Among mammals, too, there are examples of incessant reproduction. In many communities, women become pregnant while still suckling their latest infant, continuing this for perhaps twenty years and never ceasing to perform their household drudgery. In this neighbourhood, the farmers breed their cows again long before they have weaned their calves; and they not only keep their mares constantly in some phase of reproduction, but at the same time ride them over rough mountain roads with little foals trotting along at their heels. Birds in the far north may rear ten or twelve fledglings in two or three broods, moult, then perform a long and exhausting migratory journey or stay and face the rigours of a snowy winter, yet manage to survive. I should think that it would be rather less

than more exhausting for tropical birds to bring up the same number of progeny in five or six broods, even if this keep them engaged through most of the year—especially when we recall that incubation makes no drain upon the organism of a small bird which takes frequent recesses for food and exercise. In Central America some birds, including Rieffer's Hummingbird *Amazilia tzacatl* and the Talpacoti Dove *Columbigallina talpacoti*, do indeed nest, as species, through all or nearly all of the year; but we do not know how long the reproductive period of any single individual may last. The majority of the birds have far shorter breeding-seasons; and these, I believe, are in general adjusted to their annual mortality rather than limited by climatic conditions, or by the ability of the birds to continue to lay or to feed nestlings.

In any general discussion such as this, we must tacitly allow for many exceptions. Among the thousands of avian species of the humid Tropics, it would be surprising if there were not some which must exert all available strength to rear broods big enough and often enough to balance a high mortality, and still others which have become extinct through inablility to replace their losses. We are here considering those common, widespread, successful species which appear to hold their place without devoting every available ounce of energy to reproduction. In commenting by letter on my paper on incubation and nestling periods, Dr. Erwin Stresemann remarked that these tend to be long unless selection pressure keeps them short. Likewise, clutches tend to be small unless natural selection—acting as we shall see through chronic or recurrent low density of population—stimulates them to increase. The principle of acquiring the greatest benefit through the least effort appears to hold in biology no less than in political economy.

3. DISCUSSION—FUNDAMENTAL DIFFERENCES BETWEEN STABLE AND UNSTABLE POPULATIONS.

I have now presented numerous reasons for believing that in the humid Tropics birds do not rear as many offspring as would be physically possible for them. On the other hand, Lack's thesis, that clutch-size in birds is limited only by the parents' ability to nourish their young, is supported by an array of evidence too impressive to be lightly brushed aside. Lack's investigations, however, were made almost entirely with northern birds; he applies his conclusions to tropical birds only by extension. Perhaps there is some radical difference between the populational characteristics of the two groups of birds which will explain our divergent conclusions. Nearly ten years ago I wrote (1940 : 409) : " After a decade devoted largely to the study of the habits of the Central American birds, its seems to me that the most fundamental and far-reaching difference between them and the birds of a region of great annual fluctuation in temperature, such as eastern North America, is that the majority of the tropical species dwell in the same localities throughout the year, while those of the temperate zone are, on the whole,

shifting and migratory. I believe that the chief biological differences, as opposed to those of specific composition, between the bird populations of these two regions are related closely to the extent of their annual wanderings." Let us see whether this view helps us to understand why birds of high latitudes should breed up to their limit, while those of the humid Tropics do not. I wish to emphasize the fact that by " Tropics " in this discussion I refer only to those portions which enjoy a fairly moist and uniform climate, especially those where rain-forest is the climax vegetation. I have slight first-hand familiarity with severely arid regions such as extend over much of Africa and Australia and the narrow Pacific littoral of South America, but believe that in those areas where the rainfall is most irregular and in some years may be insufficient to refresh the vegetation, drought impresses upon the avian population many of the characteristics which at higher latitudes are caused by recurrent seasons of cold.

Birds which nest at high latitudes must either migrate southward in autumn or endure a long period of cold often accompanied by great scarcity of food. Nearly all, even those which do not follow the sun to warmer regions, wander more or less during the coldest months, hence are exposed to the hazards of travel. Even under the most favourable conditions of weather, birds which venture into unfamiliar country are at a disadvantage when compared with those that remain all the year in the same spot, where they are perfectly familiar with every sheltering bush and tree, and know all the local hazards. Whether from storms that overtake them on long migratory journeys, or from recurrent winters of extreme cold and unusual scarcity of food, these northern birds perish in vast numbers and begin the next breeding-season with the population greatly reduced. Thus Lack (1947 : 317) points out that the Heron *Ardea cinerea* and other British birds remain at approximately the same population density for years together, but after a severe winter there is a marked decrease, followed by a rapid return to normal numbers. For migratory species disastrous storms cause similar heavy reductions in the density of the population, which as a rule likewise quickly recovers its normal density. Corresponding fluctuations are observed in northern mammals (Errington, 1946).

These years of greatly reduced population furnish the key to our problem. After each such catastrophic reduction, the survivors form an expanding population. Whether a population expands because it is moving into new territory or because of a preceding high mortality, it presents many of the same features. Intraspecific competition for food and living space are reduced to a minimum; predation is likely to fall off because the survivors are well situated, enjoying good cover, and predators turn their attention, when they can, to other species more easily hunted. Under these circumstances an unusually high proportion of all the young survive to reproduce their kind, and the largest families make the greatest permanent contribution to the

population. In such circumstances, " if some individuals of a species lay four eggs and others five, then, given that clutch-size is inherited, the five-egg birds are bound to predominate rapidly in the population, as they have more descendants, even if this leads to ' over-population '—unless the laying of five eggs instead of four is a disadvantage in itself, either to the brood, or to the parents, or to both." (Lack, 1947 : 318.) If a succession of prosperous years follow upon the year of great reduction in numbers, the population will reach a balanced state of relatively high density, and mortality will be greater than it would have been if a high rate of reproduction had not been favoured by the catastrophic year; but under existing conditions at high northern latitudes these catastrophes are recurrent, and tend to keep the birds keyed up to the maximum rate of reproduction, as Lack's theory holds.

In the rain-forest regions of tropical America, ecological catastrophes affecting wide areas, and comparable in their results to severe " cold spells " in the far north, seem never to occur—or happen only at intervals measured by geologic rather than by human time. Volcanic eruptions devastate only areas whose extent is insignificant when compared with the range of most species; violent winds are rare in most parts of tropical America, local in their disastrous action, and can do no great harm to the woodland birds unless strong enough to flatten the forest which shelters them; floods, although at certain seasons they might destroy many nests situated on or near the ground, are hardly likely to be fatal to birds that can fly. Thus in the humid Tropics conditions are fairly uniform from year to year, and the population density of the birds tends to be constant over long periods. Let us examine the effects of an increase in rate of reproduction, arising as a mutation, in a steady, non-expanding " saturated " population.

The increase in fecundity, which we would consider, is of no advantage to any individual—it affects no bird's ability to escape its enemies nor increases its skill in finding food. Likewise it is of no advantage to the species as a whole, which by hypothesis has fully occupied all the area available to it—or if of advantage, it is only through producing more individuals variable in other respects, upon which natural selection may act. If the mutation of increased fecundity were favourable to any bird individually or to the species as a whole, it would be relatively easy to assess; at best, however, it can favour one sector of the species at the expense of the remainder, which in other respects is no less fit to survive; and this renders our task of appraisal difficult. To simplify our discussion, let us imagine two congeneric, non-migratory species occupying the same area, nesting in the same trees, reproducing at essentially the same rate, widely overlapping yet not fully coinciding in their choice of food. This is no purely hypothetical situation; several such groups of congeneric species regularly nest in my dooryard, including two species of American flycatchers of the genus *Myiozetetes*, two of *Elænia* in the same family, four species of little painted tanagers of the genus *Tanagra*, etc.

Let us suppose that one species of a congeneric pair comes through mutation o reproduce more rapidly than formerly, and consider whether it will now be at an advantage or at a disadvantage as regards its congener which continues to reproduce at the same rate—a rate that for many years has sufficed to maintain both species at a high and constant level in the heart of their ranges.

We shall designate as "A" the species which has increased its clutch-size from two to three, " B " the congener that remains constant to the ancestral two. Experiencing no difficulty in feeding the larger family and at first escaping high predation, A has in a few years effected an appreciable increase in population in the limited area where the mutation occurred. During the period of less abundant food that precedes the breeding-season, it now tends to deplete those articles in its diet which it shares in common with B. The latter then depends more and more upon food of kinds not usually taken by A, while A comes to rely more heavily upon foods not favoured by B. But the higher population of A tends to exhaust these sources, too; and the birds reach the breeding-season in rather poor physical condition, or their nesting is delayed. Species B enters the breeding-season in excellent condition and at the normal time.

Another circumstance also tends to delay the onset of nesting by species A. Like so many tropical birds, it remains paired throughout the year, and at all seasons stays on its nesting territory or at least keeps in touch with it. But now many excess, unsettled individuals give rise to contests over territory and mates—formerly such disputes were few and as a rule resolved long in advance of the nesting-season. At last the birds are paired, their territorial boundaries adjusted, and they settle down to building; but because of over-crowding many must choose inferior sites, and their eggs and young are more readily found by predators. Hence in spite of its increased fecundity, it does not at its higher level of population effect an annual net increase greater than that of B at its lower level. Indeed, after the initial increase in density it may slide back toward its original density, or it may fluctuate more or less rhythmically in the manner of northern birds and mammals with high potentials of reproduction, whose net annual increase is often in inverse proportion to density at the beginning of the breeding-season (Errington 1946). I cannot see that its increase in clutch-size has given A any advantage over B, and in some respects it is at a disadvantage.

This last statement does not rest solely upon theory, but is substantiated by my experience with two congeneric species which for many years I have observed together. Two big, yellow-breasted flycatchers are abundant in this neighbourhood, and often build their bulky, roofed nests in the same orange tree—at times, it seems, preferring to be close together. I have never noticed signs of antagonism between them. In general, their diets are similar; they subsist upon insects caught upon the wing and many small fruits. But one, the Chipsacheery *Myiozetetes similis columbianus*, spends much time stand-

ing on low stones, logs, fence-wires and the like, whence it drops to the ground to pick up food; whereas the related Gray-capped Flycatcher, *M. g. granadensis*, rarely forages from the ground. In fecundity the two species differ somewhat. The Chipsacheery lays four eggs about as often as three, and more rarely two. The average size of 17 sets from this region is 3·2 eggs. The Gray-cap usually lays three eggs, often two, but I have only once known it to lay four. The average size of 36 sets from this same locality is only 2·6. The difference in the number of sets for which I have records does not arise from a greater abundance of nests of the Gray-cap, but from their greater accessibility; although the Chipsacherry often forages nearer the ground than the Gray-cap, it tends to place its nests higher and their contents are not readily seen. The Chipsacheery is the wider ranging and doubtless older species; but here well within the geographical limits of both I cannot see that it has any advantage whatever over the less prolific Gray-capped Flycatcher.

Let us now consider the colony of our hypothetical species A in which three eggs are the rule in relation to the surrounding population of the same species which lays two. This is a flourishing population adjusted through many generations of selection to existing conditions, and suitable habitats are rather fully occupied. If a " territory " is left vacant by the death of its owner, it would be more likely to be filled by the normal increase of the surrounding pairs than by an invading member of the three-egg race, coming from a greater distance. I believe that it would be most difficult for the more prolific race to extend its range at the expense of its less fecund neighbours, even admitting that its net annual increase were greater. If some far-reaching catastrophe reduced the population of this species over a wide area, then the more fecund strain would gain an advantage. But such reductions seem to be of rare occurrence in the humid Tropics, although frequent at high latitudes.

The ornithologist in the tropical rain-forest is often impressed by the abundance of kinds of birds and the paucity of individuals of most of these species. High concentrations of a single kind of organism are likely to cause predators to specialize upon them. Where invertebrates or even small mammals are the victims, this is a well-known phenomenon: Antarctic whalebone whales feed almost exclusively upon the prawn *Euphausia superba*, Everglade Kites *Rostrhamus sociabilis* subsist upon the snail *Pomacea caliginosa*, hawks and owls may specialize upon lemmings, field mice and voles, particularly when these rodents are at high density. Birds of a single species are apparently not often the peculiar prey of a predator; nor do nest-robbing birds, mammals or reptiles usually, so far as we know, confine their attention to a single kind of nest. The only example of this which I recall is that given by Hudson (1920, 2 : 72–73), who tells us that the Common Carrion Hawk *Milvago chimango* nourished its young exclusively with nestlings of Hudson's Spinetail *Synallaxis hudsoni*, which it found in their nests, excellently concealed beneath a cardoon bush, by listening for their shrill, laughter-like notes. Specialized predation of this kind, particularly by an abundant predator, may

well turn a common species into a rare one; and in the long run a moderately abundant bird may stand a better chance of survival than one which becomes so common that enemies are led to concentrate upon it. This, I believe, may explain why in the rain-forest, where the struggle for existence is so keen, there is a great variety of birds with amazingly diversified architecture, yet relatively few individuals of each kind.

The recognition of large broods as a characteristic of populations that are expanding, whether by invasion of new territory or as a result of periodic reductions in numbers, may help us to understand some of the variations in clutch-size in a single species or genus within the Tropics. In northern Central America both of my nests of the Black-chinned Jacamar *Galbula melanogenia* contained four eggs; but in Costa Rica none of my eight nests of this species held more than three, half of these nests only two eggs. Likewise in northern Central America, in the Caribbean lowlands of Honduras and Guatemala, the Rufous-breasted Castle-builder *Synallaxis erythrothorax* lays sets of three or more usually four eggs; whereas in Costa Rica in southern Central America the Slaty Castle-builder *S. brachyura*, closely similar in all its habits, regularly lays two. Both of these genera entered Central America from the south, and their paucity of forms within the area suggests a relatively recent invasion. Apparently in Costa Rica these birds have been resident for a period sufficiently long to bring their clutch-size into balance with the mortality of a settled population, whereas in Guatemala they are still in the expansion phase. This principle, if further studies demonstrate its validity, may help us to understand some increases in clutch-size with latitude in the Neotropic avifauna, which apparently originated chiefly in the vast Amazon–Orinoco region and thence spread north and south. For tropical and subtropical Africa, Moreau (1944) has presented numerous instances of increase in clutch-size with latitude; but I am not sufficiently familiar with this avifauna to know whether the same explanation could apply here.

The situation is somewhat different when birds from regions in which broods tend to be about as large as the parents can properly feed have been introduced by man into new territory. The Little Owl *Athene noctua* reduced its clutch-size as it became well established in England, where the broods of many species are smaller than on the Continent of Europe at the same latitude (Lack, 1947 : 312). Taken from Europe to North America, where it spread chiefly through regions of lower latitude and shorter summer days, the Starling *Sturnus vulgaris* came to lay smaller clutches; but under similar circumstances the House Sparrow *Passer domesticus* possibly made a slight increase in the size of its clutches (Moreau, 1944 *a*).

SUMMARY.

1. The thesis that birds lay clutches of eggs which will produce as many nestlings as they can, on the average, adequately nourish, is considered in relation to the Central American avifauna.

2. Birds whose usual rate of bringing food to the nest is slow can greatly augment this rate if, after an exceptionally long period of neglect, they find their nestlings unusually hungry (examples are given for two species of antbirds), or if an additional nestling is placed in the nest (an experiment with a tanager is described).

3. In four out of five cases, birds of four kinds in which the clutch consists almost invariably of two eggs succeeded in rearing three nestlings.

4. In numerous species of hummingbirds, manakins, cotingas, American flycatchers, Icteridæ, etc., the male does not help to feed the nestlings; yet these birds nearly all rear broods of two, which in the same habitats is the prevalent size among species in which both parents attend the nest. If the latter were rearing as many young as they could properly provide for, we should expect the unmated females to lay clutches only half as big. Among flycatchers, when the female alone feeds the nestlings, their period in the nest is not significantly longer than at comparable nests of species in which both parents feed.

5. Also in nidifugous species, of which the chicks pick up their own food under parental guidance, clutches are far smaller in the Tropics than in the North.

6. On the basis of the time spent away from the nest by 18 incubating finches of 9 species, it is estimated that on the average 4 hours per day suffice each parent to find all the food it needs, preen, bathe, and perform other necessary activities. This would leave each parent, of the tropical species, about 8·5 hours to devote to the feeding of the nestlings; both together would have 17 hours per day. Even allowing $5\frac{2}{3}$ bird-hours for each nestling, the two parents together could attend 3; yet 7 of the 8 tropical species considered regularly lay sets of only 2 eggs.

7. Even when the climate appears to be favourable through much or all of the year, the breeding-season of many tropical birds is short and the number of broods small. The fact that some individuals breed successfully at seasons when most members of the same species are resting from reproduction, points strongly to the conclusion that these birds do not attempt as many broods as they might successfully rear. Neither in the size of their broods, nor in the number per year, do tropical birds in general appear to rear as many offspring as their own powers and the environment would permit. Their rate of reproduction seems to be adjusted to their average annual mortality rather than pushed to the limits of their strength.

8. Two species of Tyrannidæ, *Myiozetetes similis* and *M. granadensis*, are similar in appearance and habits and often build their nests in the same trees, but differ in their rate of reproduction. In the midst of their ranges, it does not appear that the more prolific *M. similis* has any advantage over its congener.

9. In a hypothetical species which with a clutch-size of two keeps its range occupied at a high or optimum density, the fate of a three-egg mutant is considered. It would be difficult for the more fertile genotype to displace the well-established two-egg strain, unless some catastrophe caused a severe reduction in the density of the population. Such catastrophes are rare in the humid Tropics.

10. The situation is radically different in a species expanding into a new area, or in one increasing rapidly in numbers after a great reduction in density of population. In these cases intraspecific competition is at a minimum, and the more prolific strains will tend to predominate. At high latitudes, recurrent drastic reductions in density as a result of great cold, famine, or disasters during migration, are followed by periods of free expansion; and under these circumstances it is likely that the rate of reproduction will be held to near the maximum which combined internal and external conditions allow. Lack's views appear to fit the facts in relation to the northern birds which he investigated, but seem to be in accord neither with observations nor theory when applied to the birds of humid tropical areas, where ecological catastrophes are at most rare and local.

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