

RAIN, FEEDING BEHAVIOR, AND CLUTCH SIZE IN TROPICAL BIRDS

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THAT avian clutch size generally decreases with latitude has been demonstrated repeatedly (Moreau 1944; Lack 1947, 1948; Skutch 1949, 1967; Lack and Moreau 1965). Several theories have been put forth to explain this. Two of the most diametrically opposed are those of Lack (1947, 1966) and Skutch (1949, 1967). Lack proposed that clutch size represents the average number of offspring that parents can nourish adequately so that the maximum number will survive to reproduce. In the tropics, presumably, parents can feed fewer young than can parents in temperate regions because of decreased daylength and increased competition and predation. Hence, they have lower clutch sizes. Adults still produce as many young as they can, and mortality is adjusted to balance natality.

In view of this, the remarks of several ornithologists that tropical birds appear to have more time available for feeding young than they use are of interest (Skutch 1949, 1967; Wagner 1957; Miller and Miller 1968), particularly because Lack (1947) has suggested that decreased daylength in the tropics significantly decreases the time available for feeding young and thereby affects clutch size. Skutch on the other hand suggested that tropical birds do not rear as many young as they are capable of nourishing. According to his theory of adjusted reproduction, natural selection and density dependent regulating factors favor reduced clutch size in order to keep birth rate in balance with average annual mortality, which presumably is lower in the tropics. The birds do not produce as many young as they can, and natality is adjusted to balance mortality. One line of evidence that Skutch supplied to support this idea is an analysis of the time budget of tropical birds in relation to daylength. He showed that tropical parents should be able to feed at least one additional young. However his analysis contains an important fallacy in the assumption that all hours of daylight are equally usable by the birds. The present paper reviews Skutch's analysis to clarify the nature and usability of free time available.

THE TIME BUDGET OF TROPICAL BIRDS

In his very enlightening analysis, Skutch (1949) outlined the time that parents require each day to find food and bring it to their young. Using as an example several species of fringillids in which both male and female rear the young, he cited the following figures. (It is assumed that these figures could be adjusted to fit species in which only a single

parent feeds the young.) In Costa Rica at about 9° N during April, May, and June (usual peak breeding months), daylength averages about 12.5 hours. Assuming that each adult requires approximately 4 hours each day for his own essential activities (feeding himself, preening, territorial defense, etc.), then 17 bird-hours remain per day for reproduction, i.e. feeding nestlings, which probably requires more time than any other reproductive activity. He indicated that northern finches often feed their nestlings while devoting less than 6 bird-hours to each one. Thus according to his calculations, tropical finches ought to be able to rear three young. Apparently he has comparable data for tanagers and in fact concludes that these figures hold equally well for the other passerines and nonpasserines in his part of Costa Rica. However the most common average clutch size for tropical species is two.

Skutch's analysis contains an important oversight in assuming that all of the 12.5 hours of daylight are equally available to the birds. In many tropical land birds (Davis 1945, Moreau 1950, Voous 1950, Marchant 1959, Snow and Snow 1964, Brooke 1966), including a number of those in Costa Rica (Skutch 1950, Foster pers. obs.), breeding is closely correlated with the wet season. It is timed with the rains so that the young birds hatch at a period of peak food abundance, both plant and insect. Apparently the rains have a two-sided effect on food availability. They are at least indirectly responsible for the large increase in food at this time, but also they must interfere on occasion with the ability of the birds to obtain it. Anyone who has spent time in the tropics can vouch for the often torrential nature of the daily rains. That such rains inhibit the activity of insects, particularly aerial forms, as well as insect-feeding by birds, is well-documented (Moreau and Moreau 1939, Moreau 1940, Freeman 1945, Fowle and Fowle 1954, Cloudsley-Thompson 1969). Leck (1972) noted that resident Panamanian frugivores continue feeding or foraging but at a much reduced rate during a light rain, reduce activity further during a moderate rain, and suspend activity and seek shelter during a heavy rain. Certainly, the decrease in activity of birds of all feeding types is considerable during a heavy tropical rain. With regard to this it is interesting to note that many studies of avian reproductive periods emphasize that breeding stops during or begins after that part of the year in which the rains are the heaviest (Moreau 1950, Thomson 1950, Voous 1950).

In many localities rains occur daily, lasting from 1-2 hours or often longer (Koeppel and De Long 1958). Considering an area where the average daily duration is 1½ hours, then 3 bird-hours must be subtracted from the total available for feeding of young as calculated by Skutch. This leaves approximately 14 hours or 4¾ hours per day per nestling with a clutch size of three, substantially below the 5¾ hours

per day suggested by Skutch for each nestling. Even in regions where heavy rains occur only every second or third day, one must assume that the nestlings in a clutch of three would be underfed on at least one-third to one-half of the days. And it should be emphasized that the selectively important feature is the fledging of the most young in *good* condition. Thus it would appear, on the basis of Skutch's estimates, that birds with a clutch size of two, whose breeding seasons substantially overlap a rainy period, may be rearing as many young as they can nourish adequately. However Skutch used the time an incubating bird spent off the nest as an estimate of the time it required for its own essential activities. Therefore the time budget supplied is only suggestive as it is becoming increasingly apparent that many tropical birds do not devote all available time to such activities but may have considerable free time (Miller and Miller 1968, Foster pers. obs.).

DISCUSSION

It appears from the above analysis that tropical birds do have more time available for feeding young than they use. Considering a region where it rains every day and assuming a minimum requirement of $5\frac{1}{2}$ to $5\frac{3}{4}$ hours per day per nestling for proper feeding, then each parent of a two-egg clutch still has from $1\frac{1}{3}$ to $1\frac{1}{2}$ additional hours per day when it can feed young. In places where rain does not fall every day, then periodically this figure will be even larger. Ricklefs (1969) has noted that because clutch size is smaller in the tropics, it may be less closely matched to food supply than in temperate regions. With time, natural selection should favor closer adjustment of energy requirements and energy availability through changes in clutch size, requirements of the young (e.g. for increased growth rates), etc. Alternatively, energy from food gathered during this additional time may be channeled into nonreproductive activities (Foster 1974).

Birds that occupy more arid tropical regions have larger clutches than their counterparts in the humid tropics (Marchant 1960, Lack and Moreau 1965). This may reflect a decrease in the number of hours of rain per day. An analogous situation is presented by birds that breed during the dry season. They should have enough time to gather sufficient food for another nestling, but clutch sizes of such species also are small. This probably reflects the reduced availability of insects during the dry season or in drier habitats, so that more time is expended per unit of food gathered. Both of these groups still rear fewer young than comparable temperate forms.

Finally it should be emphasized that a reduction in time available for feeding young in the tropics by decreased daylength or increased rainfall is only one of many factors affecting clutch size and probably not the

most important one. Thus on the basis of the above analysis we cannot conclude that birds in the tropics are rearing as many young as they can nourish adequately. Undoubtedly individuals of some species rear as many young as they are capable of feeding; individuals of other species do not.

ACKNOWLEDGMENTS

I thank Charles E. King, Joe R. Linton, Roy W. McDiarmid, Ralph W. Schreiber, and Glen E. Woolfenden who read an early draft of the manuscript and provided helpful comments.

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