BROOD REDUCTION IN THE CURVE-BILLED THRASHER

By Robert E. Ricklefs

Lack (1954; 40–41) has pointed out that in species of birds which have asynchronous hatching, brood size may be adjusted to temporal fluctuations in food availability. Parents generally feed the most active of their brood, that is, the largest (oldest) and the strongest. When such nestlings are replete, they become inactive and food is then passed on to the smaller members of the brood. When food availability is high, the parents are capable of satisfying all of the brood; when low, only the largest or first hatched are satisfied and the others starve to death. Thus, because of size differences due to asynchronous hatching, the parents are able to distinguish their young and can distribute limited food resources to the best advantage. If differentiation were not possible, food would be distributed randomly with each nestling having equal probability of being fed. During a poor year, all of the young would be underfed, a condition presumably less advantageous than having fewer well-fed young. Brood reduction is generally thought of as being prevalent in the hawks and owls and in some sea birds. It is the purpose of this paper to demonstrate the phenomenon in a passerine, the Curve-billed Thrasher (*Toxostoma curvirostre*).

Up to a point, the parent can increase its rate of food delivery to the young by increasing its own effort. When food availability is low, it presumably takes a greater effort to deliver food at a given rate than during a more favorable period. It is convenient to think of the rate as being constant for any given level of food availability. Although probably unrealistic, this assumption is not impractical if we consider that regardless of the food availability there is an optimum effort which the parent can devote to gathering food. For different resource levels, this optimum effort will yield different rates of food delivery to the young.

The energy requirement for the growth of the nestling increases with age up to a certain point after which it decreases (fig. 1). Thus, the parents are increasingly taxed not only with the addition of more young to the brood, but also with time. In a good year, the parents are able to keep up with the increasing demands and can deliver food at the maximum rate required by a full brood of nestlings. In a poor year, the requirement of the entire brood may exceed the delivery capacity of the parents long before the peak requirement is reached. When this happens, the smallest receives no food and dies. If, several days later, the requirement of the reduced brood again exceeds the delivery capacity of the parents, the smallest of the remaining birds has already been starved to death. It is theoretically possible that not one nestling would end up well fed in extremely hard times, but the birds would not be likely to breed under such conditions.

Clutch size and breeding success.—The Curve-billed Thrasher is a common and conspicuous bird of the Sonoran Desert of the southwestern part of the United States and northern México. It usually builds its deep, cup-shaped nest in cholla cacti (*Opuntia* sp.) and lays two, three, or four eggs. In the Tucson region in Arizona, where this study was made, the average clutch size of about 2.8 shows no evidence of variation between years nor over the long breeding season which generally lasts from February through early August (Bent, 1948; Hensley, 1959; Jim Ambrose, pers. comm.). My study was made during the months of June and July, 1964. Judging from the breeding success and the nutritional state of the young, food availability was con-

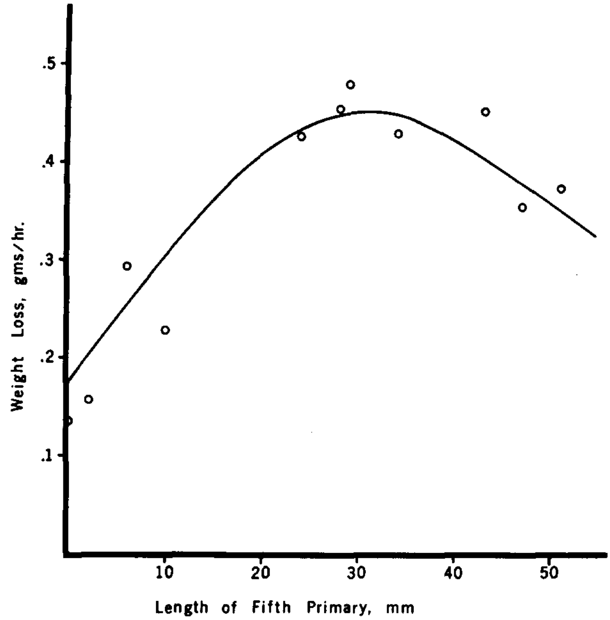

Fig. 1. Metabolic rates of growing Curve-billed Thrashers.

siderably lower than normal. Complete clutches found were 4 of 2 eggs, 10 of 3, and 1 of 4 (15 clutches averaged 2.8 eggs). Brood sizes at hatching were 3 of 1 young, 4 of 2, 6 of 3, and 1 of 4 (14 broods averaged 2.4 nestlings at hatching). None of the unhatched eggs showed any development; two eggs failed to hatch in each of three nests, and a fourth nest with two unhatched eggs was found after young had fledged. Because I was collecting the nestlings for another study, my data on fledging success indicate the number of young that would have left the nest had I not collected them, and thus are optimistic: 4 fledged no young, 5 fledged 1, and 9 fledged 2 (18 nests averaged 1.3 fledged per nest). There was no concrete evidence of either disease or predation playing a role in the disappearance of young from the nest. Of interest are several cases of brood reduction.

Energy requirements.—Metabolic rates of nestlings were approximated by weight loss during a period when they were not being fed. This is a measure of the amount of fat and protein oxidized plus the water lost during respiration, and it is directly proportional to the rate of energy consumption. Measurements made immediately upon bringing nestlings in from the field were high and were taken to be those of the actively growing bird. After a period of usually an hour or more, the rate characteristically dropped and leveled off at basic diurnal metabolism. Rates during the night were somewhat lower than this. Weight loss was plotted in figure 1 as a function of the length of the fifth primary. This measurement was chosen as an indication of the age and size of the bird because in some cases the true age was not known.

The peak energy requirement comes during the last half of the second week after hatching. Age was determined by comparison with Rand's (1941) data on feather length and age.

Begging behavior.—The period of increasing energy requirement determines the competitive phase of nestling behavior (Ricklefs, in press) which is characterized by

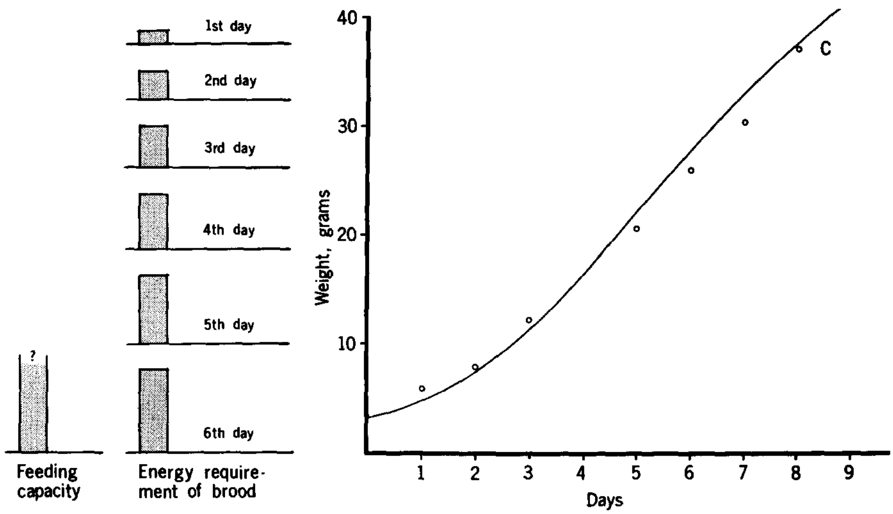

Fig. 2. Nest T-18, one egg hatched. Solid line represents average growth curve of thrashers (Rand, 1941), serving as a reference curve of a typical, well-fed nestling. Vertical solid bars are estimated energy requirements of brood on successive days; feeding capacity of parents at optimum effort shown by the single bar at far left. "C" marks time when brood was collected.

begging with extreme vertical stretching and extension. The effect of competitive begging is to accentuate size (=age) differences within the brood, perhaps most critically the height to which the nestling can raise its gaping mouth. It is likely that this is the principal feature which attracts the feeding activities of the parent and enables it to distinguish individual nestlings. After the peak energy requirement is passed, a noncompetitive phase ensues which is characterized by begging that lacks pronounced stretching and is more flexible in direction.

Asynchronous hatching.—Rand (1941) states that "one of the young in a thrasher's nest was usually twenty-four hours older than the other or others." My limited observations on hatching indicate that one, or two, of the young were often a day older, but that in several cases, any age differences must have been less than a day. The degree of asynchrony required for brood reduction must depend on the sensitivity of the parents to age differences within their brood. In the cases given beyond, parents were able to distinguish nestlings whose age differences could not have been more than twenty-four hours.

Brood reduction.—Two model examples of brood reduction, for which I have growth data, were observed in the nestings followed, and many others were suspected. None of the nests which hatched three or more eggs (50 per cent of all nests) would have fledged more than two nestlings.

In the cases illustrated by figures 2, 3, and 4, both parents were known to be alive throughout the period of observation. The weights on the graphs were those taken at dusk.

At nest T-18 (fig. 2) the parents had no difficulty keeping up with the energy requirement of the single nestling and therefore the growth curve is typical. At nest T-1 (fig. 3) the smallest of the brood of three hatched as much as a day later than the other two and was starving within a day. After the fifth day, the needs of the

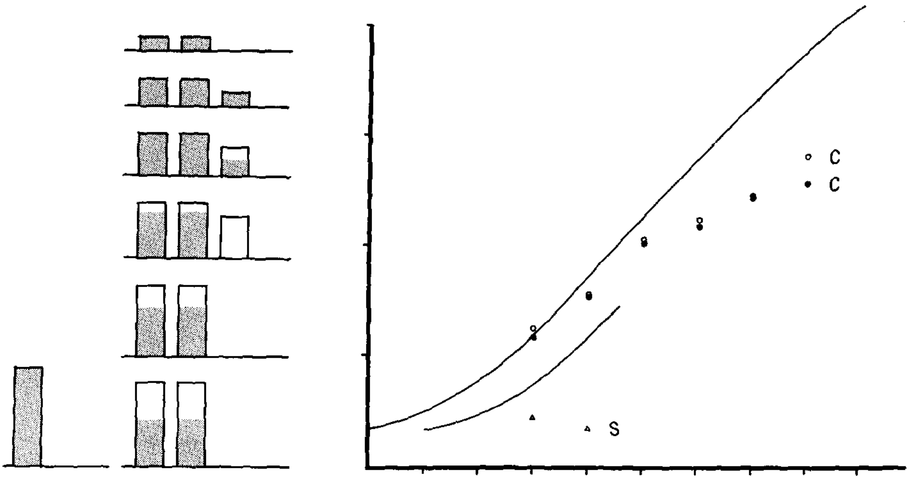

Fig. 3. Nest T-1, three eggs hatched. Legend as in figure 2, but separate columns of vertical bars represent each of the three nestlings. A fully solid bar represents fulfillment of the requirements of the young, and the open part of the bars the deficit in feeding. The total shaded areas for fulfillment of young equals the area of the feeding capacity bar. A separate reference curve is given for the younger member of the brood. "C" indicates young collected; "S" indicates died of starvation.

two remaining nestlings again exceeded the feeding capacity of the parents. As the nestlings were apparently of the same size they could not be distinguished and were both poorly fed from this time on. When these nestlings were collected on the ninth day, their fifth primaries measured 28 and 29 mm, indicating similar size. At nest T-10 (fig. 4) four eggs hatched, the third a day after the first two, and the fourth, a day later. The youngest and next to youngest had died of starvation when two and four days old, respectively. A few days later, the requirements of the remaining two birds again exceeded the feeding capacity of the parents, but in this case, the parents could distinguish the two nestlings and one was starved. On the evening of the ninth day, the larger bird fell out of the nest. By the following midday, the remaining nestling had gained a considerable amount of weight. This indicates that there was nothing physically wrong with the starved bird except that it was not effectively competing with the other for the feeding activities of the parents.

Discussion.—Being able to adjust brood size enables birds to raise the greatest possible number of young at any level of food availability. This can be accomplished by adjusting the clutch size. Many species of birds lay smaller second clutches than first, and presumably this reflects a predictable reduction of the food supply toward the end of the breeding season. Clutch size can be selected to correspond to the average conditions at a particular time of the season, or, it is also possible that the female is capable of "evaluating" the food availability just prior to laying and adjusts the clutch size at this time. For passerines, there is a lag period of at least two weeks between the time of possible evaluation prior to laying and the onset of feeding activities, and another week or more before the peak energy requirement is reached. Thus it may be almost a month between the time of evaluation and the critical feeding period. Evaluation may be an effective strategy when the food supply is stable, or changes predictably, over long periods. However, where food availability may increase

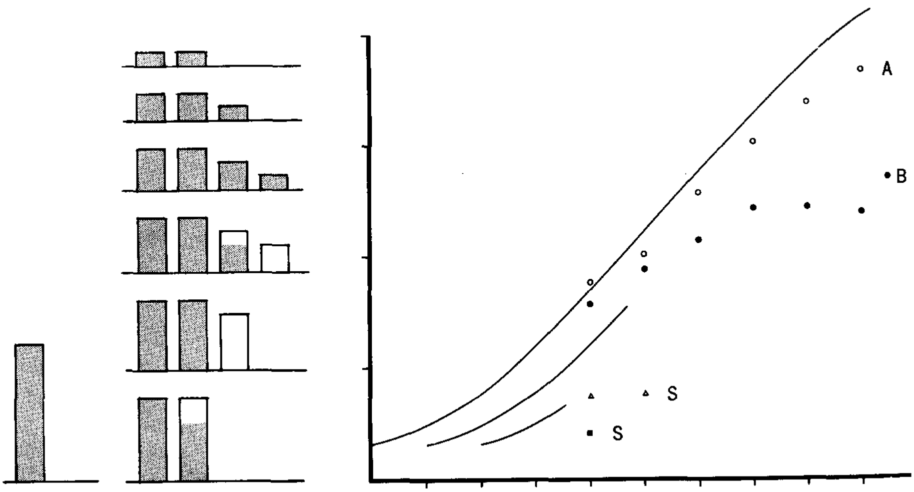

Fig. 4. Nest T-10, four eggs hatched. Legend as in figure 3. "A" indicates nestling fell out of the nest, probably shortly after being weighed in the evening; "B" the nest tipped over at about midday—the nestling was found dead on the ground and was weighed.

or decrease unpredictably, and rapidly with respect to the lag period, the accuracy of the evaluation, and thus the effectiveness of the evaluation strategy, is reduced.

In large raptorial birds, two months or more may pass between the time of laying and the peak energy requirement of the nestlings. In order to make the critical feeding period correspond to the peak food availability, laying may be forced to occur too early in the season to make a meaningful evaluation possible.

The advantages of brood reduction lie in its having no lag period. Brood size can be adjusted to changes (decreases) in food availability almost immediately. This strategy will permit clutch size above the normal optimum to correspond to favorable conditions which occur frequently enough to give added productivity.

It is also apparent that the strategy is wasteful, because young which will eventually starve to death are hatched and fed with the expenditure of valuable energy. Therefore, equilibrium clutch size will be reached when the conditions for a further increase in brood size are so rare that the added inefficiency of brood reduction more than balances the fitness gained when the requirements of the larger brood can be met.

Brood reduction should be suspected in any species whose average food availability while feeding young shows temporal fluctuation without corresponding variation in the clutch size. Also, the strategy is useful to species adjusting clutch size where the accuracy of evaluation is not high: the two strategies are by no means mutually exclusive.

In conclusion, I would suspect that the phenomenon of brood reduction is much more widespread among altricial birds than has been indicated and is a significant factor in determining the clutch size of these species.

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SUMMARY

The mechanism of brood reduction is described, and the phenomenon is demonstrated in the Curve-billed Thrasher. A general discussion is given of two strategies of adjusting brood size to correspond to food availability: evaluation and brood reduction. The evaluation strategy of adjusting clutch size is useful when the availability of food at the time that nestlings are being fed can be predicted with reasonable accuracy from an evaluation of the food availability, or other environmental conditions, prior to egg laying. Brood reduction is advantageous when the food supply is unstable and its fluctuations are unpredictable, or when the eggs are laid before the female can meaningfully evaluate the season's food availability.

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