FEEDING ECOLOGY OF THE BENGALEE, *LONCHURA STRIATA* VAR. *DOMESTICA* (ESTRILDIDAE)

2. Time expended by the parent on feeding the nestling

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In my previous paper dealing with the amount of the two kinds of foods fed to the nestling of the Bengalee *Lonchura striata* var. *domestica* by the parents, I reported that the marked difference between the pattern of change in the amount of the seed of the foxtail millet fed to the nestlings and that of the leaf of the cabbage was recognized (SUZUKI 1967).

The parent birds spend more time for the feeding activity during the nestling period than during any other periods. If there exists an optimal time and energy budget for various activities of a species in a given environment (ORIAN 1961), it must also be seen in the case of feeding activity during the nestling period. The behaviour of the Great Tit feeding the young was reported by ROYAMA (1966, 1970). The time budgets of various birds during the breeding period have been studied by several workers (ORIAN 1961, SCHATZ and ZIMMERMAN 1971, VERBECK 1972 and VERNER 1965) in the field. However, the time expenditure on feeding and the change in the amount of time spent every day during the nestling period have not been estimated sufficiently.

As the ability of the thermoregulation of the nestlings of the altricial bird only gradually develops after hatching, the parent bird must brood them for some time of a day or all day long until they become to be able to control their body temperature by themselves. If other conditions such as food availability are favourable, the time of brooding by the parent in which heat is supplied to the nestling may be particularly dependent on the ability of the thermoregulation of it, the brood size, nest construction and the air temperature.

During the nestling period, a pair of bengalee must spend some time of a day on the self-maintenance and the brooding and some of the remaining on taking foods for the nestlings.

This paper, following the previous one, deals with the time expenditure and its change of the parent bengalees during the nestling period.

METHODS

The Bengalees used, the method for rearing birds and the experimental conditions were the same as those mentioned in my previous paper (SUZUKI 1976).

Measurement of brooding time. Parent Bengalees brood their nestlings by turns in the daytime or lighted time, and sleep together in a nest in the night or dark time. The brooding time was measured with a wrist watch on the minute basis for an hour for one nest every nestling day, and the maximum number of nests on which measurements were made in a day was eight. The brooding time for an hour was multiplied by 14 to get that for the whole lighting time. Thus calculated value was regarded as the amount of time spent in brooding in the daytime. The parents sometimes fed nestlings while brooding and/or brooded while feeding. In such cases it was difficult to divide the activity of the parents into brooding and feeding. The brooding time stated here means the duration when at least one parent was present in a bottle-shaped nest. Therefore some overestimation would occur especially in the later period when the parent seldom broods.

Measurement of time expended on food collection. Time spent in taking food was measured by a stop watch on 0.2-second basis on the birds raising the nestlings.

When a bird continuously took more than ten seeds, the number of the seeds taken and the time spent in taking them were recorded at the same time.

Fig. 1. Daily change in the brooding time. Brood size was from 3 to 6.

Fig. 2. Daily changes in the time spent by the parents in taking foods for a nestling. Time spent in taking millet seeds is 15.3 min. per g dry wt. and that in taking cabbage leaves is 162.6 min. per g dry wt. ○ millet, X cabbage, △ total

The dry weight of one hundred millet seeds was measured and the dry weight per ten seeds was calculated. Time spent in taking one g dry weight of millet seeds and that in taking them in a day were calculated from above mentioned data.

As stated in the previous paper, the supplied foxtail millet seeds had been artificially husked. Time spent in taking one seed, therefore, mainly consists of the time of picking and swallowing, though birds occasionally behaved as if the husk of the seed existed, that is, showed husking behaviour.

The weighed cabbage leaves were given, and the length of the time when the parent bengalees took them was measured. The time was recorded for the individual male and female. After the total time reached 20–30 minutes, measurement was stopped and the remaining leaves were removed from the cage. Time spent in taking cabbage leaves a day was calculated, using the relationship between the dry weight of cabbage leaves taken and the time spent in taking them.

RESULTS

(1) Brooding time

The change in brooding time is shown in Fig. 1. The parent bengalee brooded nestlings for longer time in a day during several days after hatching of them, but the brooding time abruptly decreased after about a week. This decline in the brooding time seems to correspond to the development of the thermoregulating ability of the nestlings. DAWSON *et al* (1957) reviewed the thermoregulation of several species of the altricial birds. The nestlings possess the function of effective temperature control from 7–11 days after hatching at moderate (20–25°) temperature, differing according to the difference of species.

Although both a male and a female brooded, the brooding time of a female amounted to 67.4% (S.D. =22.4, n=90) of the daily amount of time spent in brooding from the first to the 13th day.

Fig. 3. Daily change in the ratio of time spent in taking cabbage leaves to the total time spent in taking both millet seeds and cabbage leaves.

Fig. 4. Daily changes in the time spent in taking foods when time spent in taking millet seeds is 19.6 min. per g dry wt. and that in taking cabbage leaves is 162.6 min. per g dry wt. $\circ$ millet, $\times$ cabbage, Δ total

(2) Time expenditure on taking foods

The mean times spent in taking one g dry weight of the millet seed and the cabbage leaf in minute with S.E. were 15.3 ± 0.52 ($n=52$) and 162.6 ± 14.08 ($n=11$) respectively. The mean dry weight of 100 kernels of the foxtail millet was 188.4 ± 0.25 mg ($n=10$).

The mean time spent in taking one g dry weight of the cabbage leaf was 10.6 times as long as that in taking one g dry weight of the millet seed. Since a pair consumed daily 4.29 g dry weight of millet seeds and 0.21 g dry weight of cabbage leaves, each adult must spend 32.8 min. daily in taking millet seeds and 17.1 min. in taking cabbage leaves on the average. The proportion of time spent in taking cabbage leaves to that in taking the total foods was 34.3%.

The parents eat foods and store them in their crops, and they give them to their nestlings by regurgitation. Therefore, the time needed to take the unit weight of food for nestlings is about the same as what the parents need to take the unit weight of food for themselves.

The time to take the unit weight of each food was multiplied by the amount of each food fed to a nestling. This value was considered to be the amount of time spent in taking each food for a nestling. The calculated values are shown in Fig. 2.

The total amount of time spent in taking two kinds of food increased during the early period, but the increment stopped about on the 13th day and time was nearly constant from the 13th to the 17th day. Thereafter it decreased a little for a few days and then the decreasing ceased. It became constant after about the 20th day.

The change in the ratio of the time expended on taking cabbage leaves to that on taking total foods with age is shown in Fig. 3. The proportion of the former changed from 64% to 38%.

DISCUSSION

The amount of time spent in taking the unit dry weight of millet seeds was very much different from that of cabbage leaves. For example, the ratio of the amount of time spent in taking cabbage leaves daily to the total amount of time spent in taking both foods was 34.3% in the case of adults. This is very high ratio in comparison with that of the amount of cabbage leaves to all foods taken on dry weight basis (4.7%).

The pattern of change in the total time spent in taking foods for a nestling (Fig. 2) was different from that in the total amount of foods for the same reason.

The time spent in taking the millet seed was based on the time spent in taking the artificially husked seed in this study. The time spent in taking the millet seed with husk was measured under the same conditions and with the same procedures by adding the husking time. The adult raising the nestling spent 19.6 min. (S.E.=0.45, $n=56$) to take one g dry weight of kernels. This was only 1.28 times as long as what was spent in taking husked seeds amounting to 15.3 min. If it is assumed that the amount of kernels gained from non-husked seeds is the same as that of the husked seeds and that the amount of collected cabbage leaves does not also change, then it can be said that the total time spent in taking foods for nestlings increased, while the pattern of change in the total time expenditure does not vary fundamentally (Fig. 4).

The relationships between the amount of millet seeds and cabbage leaves fed to a nestling and the time expended on taking them are summarized in Fig. 5. The figure represents clearly that if the bengalees take the millet seed only, they can take much more food in dry weight in a given time.

The measured time implies the "eating time" only. It is the total of the picking and the swallowing times in the case of the millet seed and the total of the tearing, the grinding and the swallowing times in the case of the cabbage leaf. The measured times spent in taking foods are the minimum ones, because other times expended on such behaviour as moving from the cabbage to the millet and *vice versa*, selecting the feeding part of the cabbage leaf and, if any, searching for food *etc.*, are omitted there. It was difficult to measure the time spent upon such activities. However, if the amounts of time spent in taking millet seeds and cabbage leaves were proportional to the dry weight of them, Fig. 5 shows that the time spent in taking the food of a nestling by the parents does not increase after the 13th day under the condition that the resultant ratio of time spent in taking cabbage leaves to that in taking millet seeds is more than 4.645. This is also true in the case where the amount of each food changes if the pattern of change in the amount of each food does not change.

Consequently it may be concluded that the decrease in the amount of green leaves fed to the nestlings after the middle period of the feeding of young secures the increase in that of seeds taken in a definite time. That is, it results in the increase in the total amount of foods without the increase in the total time spent in taking them for the nestlings, and in the secure gain of a certain quantity of green leaves.

It is supposed that the characteristic of decreasing the amount of green leaves has developed in connection with the nutrient requirements of nestlings, the nutrient constituents of seeds and green leaves and with the foraging efficiencies of them.

According to WARD (1965), foods of the nestling Black-faced Dioch *Quelea quelea* are mainly grass seeds, but insects are also fed to the nestlings during the early stage. The highest proportion of the amount of insects in dry weight to the total amount of foods was found on the second day of the nestling stage. Afterwards the proportion of insects decreases and it become to almost nil after the 7th day. He states that the presence of animal food in the diet is correlated with the high protein needs of the growing birds, or perhaps more importantly, their requirements of specific amino acids such as lysine and arginine not found in sufficient quantity in grass seeds.

Though he did not describe the amount of the foods fed to nestlings, it seems that the amount of fed animal foods increases at the beginning of the nestling period and then decreases,

Fig. 5. Interrelation among the amounts of millet seeds and cabbage leaves fed to a nestling and the time spent by the parents to take each of them. T_m is a factor (min./g dry wt.) to gain the unit weight of millet seeds and T_c is that of cabbage leaves. Solid circles indicate the amount of millet seeds and cabbage leaves fed to a nestling in each nestling day dated. Broken lines are isoquanta lines (0.4, —, (2.8) g dry wt.), solid lines are isotime-budget lines ((10), —, (80) min.) when T_m is 15.3 min./g dry wt. and T_c is 162.6 min./g dry wt. Dotted line is isotime-budget line when $T_c/T_m = 4.645$. This figure shows, for instance, that if the parents take the cabbage leaf only they can take about 0.18 g dry wt. of it for 30 min., and if they take the millet seed only they can take about 2 g dry wt. of it in the same time.

while that of fed grass seeds increases from the beginning till the end. It can be supposed that if *Q. quelea*'s adult consumed more time to gain the unit weight of animal foods than to gain that of grass seeds, it may increase exceedingly the amount of gain of grass seeds in a given time by decrease in that of animal foods. This may be very important in this species in which the time available to take foods for nestlings by the parent is clearly limited.

The foraging efficiency and the nutrient constituent of the food item and the nutritional requirement of an animal exert an influence upon the choice of the food item by the animal (Emlen 1973, Pulliam 1975, Rapport 1971, Westoby 1974). No matter how it may take very much time or energy to collect a food item, an animal must gain it if the animal can not easily alternate it with the other because of the requirement of some essential nutrients.

That the proportion of one food item in the diet is small does not imply that it is less important. It can be very important nutritionally and furthermore may necessitate much time or energy to take it. Therefore it should be noticed that taking such a food item might effect on the amount of time or energy which an animal can allocate on other activities including the collection of other food items.

The time that the parents can utilize for their activity includes the time to take foods for nestlings, the time to spend on the self-maintenance and that on the brooding. The birds investigated in this study were reared under the 14-hour photoperiod. Daily total amount of the time which the parents could utilize was 14 hour times 2, i.e. 28 hours.

The amount of available time other than that spent in feeding for the parents themselves and in brooding is shown Fig. 6. It was calculated on the assumption that the amount of food consumed by the parents was constant during the nestling period.

Fig. 7 shows the ratio of time spent in taking foods for a nestling to the available time mentioned above. The feeding activity for the parents themselves is a part of the activities for the self-maintenance. But it is the most important and fundamental part of the parent lives and the pattern of change in the ratio is represented clearly in Fig. 7. The ratio increases monotonously till the 4th day. Afterwards it does not change almost at all till the 15th day and then decreases to some extent. The decline in it during the later period seems to reflect the decline in the total amount of the time spent.

It is not yet clear whether or not the relatively constant proportion of time spent in taking foods for nestlings is profitable for the life of this domestic bird, because the parents possess

Fig. 6. Daily change in the time available to the activities other than feeding for the parents themselves and for brooding. Daily brooding time was calculated from the points of the curve in Fig. 1.

Fig. 7. Daily change in the proportion of the time spent in taking foods for a nestling to the time available to the activities other than feeding for the parents themselves and brooding.

surplus time available. If, however, the wild birds of this species had also such a characteristic, the above thing may be profitable to them during the feeding of young, because the parents can allocate, if necessary, remaining available time on other activities, such as feeding to fulfil the increase in energy requirement of them, in proportion to the time spent in taking foods for nestlings, and/or they may use the available time fully to feed for the nestlings.

SUMMARY

The time budget of the parent Bengalees for taking foods consisted of the seed of the foxtail millet and the leaf of the cabbage for the nestlings was studied.

The time spent in taking one gram dry weight of the artificially husked seeds of the millet was 15.3 min. and the time spent in taking the same amount of cabbage leaves was 162.6 min. The pattern of change in the total time spent by the parents for feeding nestlings per day was different from that in the total amount of food. The above time increased till the 13th day, after that the increase ceased in spite of the increment of the total amount of food fed to the nestlings, owing to the pattern of the change in the amount of cabbage leaves fed and to the more time consumed in taking the unit dry weight of cabbage leaves than in taking millet seeds.

The total amounts of time usable for the parents other than for feeding for themselves and for brooding were estimated. The ratio of the amount of time spent in taking foods for nestlings to the total amounts of time above mentioned increased monotonously for several days but afterwards the increase almost ceased.

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ジュウシマツの摂餌生態

2. 親鳥の給餌活動に費やす時間について

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筆者は、前報(1976)で、ジュウシマツの親鳥がヒナに与える種子(アワ)と緑葉(キャベツ)の量が、ヒナの生長とともにどのように変化するかについて、報告した。本論文では、親鳥がヒナの食物を採るために費やす時間について、報告する。

親鳥が乾重1gのむきアワを採る時間は、15.3分であった。また、乾重1gのキャベツを採る時間は、162.6分であった。

ヒナに与えられるキャベツの量が育雛中期以降減少するために、1日当りの給餌量(アワとキャベツを合計した量)自体は増えているにもかかわらず、親鳥によってヒナの食物を採るために費やされる1日当りの時間は、孵化後13日目頃から増加しなかった。

両親が抱雛と彼ら自身のための食物採集に費やす時間が求められた。それ以外の活動に使える時間のうち、ヒナの食物を採るために費やされる時間の割合は、孵化後4~5日目頃からほとんど増加しなかった。