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Parental Feeding Rate in Relation to Begging Behavior in Asynchronously Hatched Broods of the Great Tit *Parus major*

An Experimental Study

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Summary. Variations in the begging behaviour of the nestlings of altricial birds can provide the parents with information about the nestlings' nutritional needs and thus influence the parental feeding rate. In a series of four experiments, the stimulus situation encountered by great tits on their feeding visits to the brood was manipulated to explore its effect on feeding rate.

A higher feeding rate was observed under the following conditions: (1) after a period of food deprivation, as compared with both normal conditions and satiation through artificial feeding; (2) in periods when recorded begging calls were played during feeding visits, as compared with control periods; (3) after temporary removal from the nest of heavier, as compared with lighter, siblings. The lighter nestlings in the brood benefitted more – in terms of gain in weight – from the increase in parental feeding rate following the playing of begging calls than did the heavier nestlings. Differences in weight spread within broods did not affect the amount of food the parents brought.

We conclude that parental feeding rate is affected not simply by the begging of the hungriest nestling, but rather by the behaviour of all the nestlings in the brood, which makes possible an adjustment of the feeding rate to the average hunger level of the brood. The effects of hatching asynchrony and sibling competition on parental feeding rate are discussed.

Introduction

In altricial birds the offspring are dependent on the parents to feed them after hatching. The quality and amount of food brought to the brood by the parents are factors of crucial importance for the nestlings' chances of survival.

In an ultimate sense, parental feeding effort has been interpreted as balancing food conditions, brood size, and the adult birds' physical condition so as to maximize the number of viable offspring. Proximate factors influencing parental feeding effort, however, have received little attention empirically. Recently, Drent and Daan (1980) proposed that adult birds may monitor their rate of energy expenditure. In a review of relevant literature, these authors indicate evidence that a level of four basal metabolic rates is not more than temporarily exceeded by the parent in its feeding efforts.

Other factors found to be related to parental feeding effort are the age (Gibb 1950; Kluyver 1961; van Balen 1973), size (Royama 1966) and satiation (Perrins 1965) of the brood. Both reduction and artificial enlargement of brood size are followed by adjustments in feeding rate (von Haartman 1953). A ceiling effect can be observed in cases where nestlings are added to a brood in that the number of feeding offers per nestling decreases (von Haartman 1954; Henderson 1975; Tinbergen 1981). Further evidence of adjustment of parental feeding rate to the food requirements of the brood is an increase in the frequency of parental visits after heavy rainfall (Keil 1967) and observation that, if one parent deserts or falls victim to predation, the remaining parent sharply increases its foraging intensity (Gibb 1950; Kluyver 1950). Other findings point in a similar direction. Feeding frequency and the size of the prey is inversely related (Royama 1966), and van Balen (1973) observed that in pinewoods where food conditions are worse than in oakwoods, great

tit parents extended feeding activities into the evening hours.

These findings as a whole suggest that the parents in some way receive information about the nutritional needs of the nestlings. The hunger level of the nestling is reflected in its begging behaviour, which involves both a visual and an acoustic component, each of which changes with age and with deprivation time. Henderson (1975) demonstrated with glaucous-winged gulls (*Larus glaucescens*) that the nestlings' calling rate increased with deprivation time and nestling age; also the spectral properties of the calls and the average sound intensity change with the age of the young birds (Andrew 1957; Muller and Smith 1978; Rydén 1982). The begging call thus contains graded information related to the nutritional needs of the nestlings.

By playing recorded begging calls it has been possible to induce the parents to feed more often (Khayutin and Dmitrieva 1976, 1979). Thus, it appears that the begging behaviour of the young is an important proximate factor in the control of parental foraging intensity. However, evidence that hungrier nestlings can induce the parents to feed more often than less hungry nestlings is mostly indirect. Accordingly, one experiment in the present study is aimed at exploring whether the number of feeding visits change when the hunger level of the brood is manipulated.

In the great tit, early broods hatch within 1–3 days and broods later in the breeding season hatch with successively greater asynchrony (Gibb 1950; Neub 1979). The ensuing weight spread within the brood may affect parental feeding behaviour. In the present study effects of hatching asynchrony on the parental feeding effort and the distribution of feeds within the brood were explored in three ways: by playing recorded begging calls to the brood at parental feeding visits and comparing weight changes in small and large nestlings on experimental versus control days; by temporarily removing small or large nestlings and comparing the subsequent changes in parental feeding rate; and by comparing weight development in pairs of artificial broods of the same size and total weight where the weight spread had been minimized or maximized.

Materials and Methods

Great tit (*Parus major*) pairs inhabiting nest-boxes in deciduous woodland were observed in 1978, 1979 and 1981. The broods were located in two areas 5 and 15 km E of Lund (55°42′N/13°10′E).

Effects of Replayed Begging Calls on Parental Feeding Rate and Distribution of Food. Three broods, containing 8, 8 and 10 nestlings, were studied. The third of these broods originally contained only seven nestlings and was enlarged with three nestlings to allow the effects on parental feeding effort of an artificial stress on the adult birds to be studied. In this brood one nestling died on the second day of observation, another two on the sixth day of observation, and two more several days after the completion of the experiment.

The nestlings were individually marked with non-poisonous color and weighed to the nearest 0.5 g with 10 and 50 g Pesola spring balances each day at 10.00 a.m. and 3.00 p.m. The experiment was initiated when the broods were 7–8 days old. The begging calls from one of the broods were taped with a Sony Micro Cassette-Corder M-102 when all the nestlings were begging intensely. The recording was later played back with a Philips 2235 tape recorder through a 4-Ω loudspeaker (frequency response: 3–17 kHz) attached below the nestbox. The recordings made were of the begging calls of 7–8 and 9–10 days old nestlings, in order to match the age of the nestlings studied. In playing them back the experimenter operated the tape-recorder by remote control while located about 8 m from the nest. During a 3-h period between 10.00 a.m. and 3.00 p.m. the tape was started each time an adult bird approached the nest and was played continuously during its visit. The amplitude was constant and was set at a level subjectively perceived as corresponding to the response of an intensely begging brood. Begging calls were replayed every second day, the intervening days serving as controls. In broods 1 and 2 the begging calls were presented on two different days, and in brood 3 on three different days, involving 21 h. Parental feeding rate was monitored during the experimental sessions as well as for 3 h on the intervening days. This design made it possible to compare the weight gains of the individual nestlings during a 5-h period when the begging calls of an insatiated brood were replayed with those during a period of the same length on the intervening days; two broods were raised under favourable and one brood under strained conditions.

Parental Feeding Rate as Related to Brood Size and Degree of Food Deprivation of the Young. Four broods, approximately 2 weeks old, were selected for study. Three brood sizes, namely 6, 9 and 12 young, were artifically created by moving young between nests. Feeding frequency was observed under three conditions: (1) when a brood had been starved for 4 h, (2) when it had been richly fed with minced meat by the experimenter, (3) when no intervention had been made. Adding or removing young aroused only temporary alarm in the adult birds, who usually resumed normal feeding behaviour within half an hour after their broods had been manipulated. During food deprivation the nestlings were kept in a separate nest-box where they could not be heard by their parents. The removed young were replaced by young from other broods to keep constant the number of nestlings fed by the adult birds before and during the observation period. Parental feeding rate was monitored during 1-h observation periods, between 9.00 a.m. and 4.00 p.m., during which time feeding rate does not change systematically (e.g. Stierhof 1963).

To investigate the validity of the obtained results for changes in begging intensity in only part of the brood, an additional series of observations was made. Broods of nine nestlings each were created, composed of nestlings from five nests containing approximately 1-week-old young. Age variation within the artificial broods was 3–4 days, corresponding to a degree of hatching asynchrony characteristic for broods raised late in the hatching season (Neub 1979). The experimental condi-

tions used in the preceding series of observations were applied, but only three nestlings were fed or deprived of food. In each experimental condition, small and large nestlings were equally represented.

Effects on Parental Feeding Rate of Removing Larger vs Smaller Nestlings from the Brood. To estimate the relative influence on parental feeding rate of nestlings' occupying different positions in the weight hierarchy, an experiment was carried out where part of the brood was temporarily removed from the nest and the number of feeding visits to the remaining nestlings recorded. All broods studied were natural ones of nine nestlings each where either the three heaviest or the three lightest nestlings were removed for an observation period of 1 h. Each brood was monitored on two separate occasions on the same day, involving different experimental conditions. Which nestlings were to be removed during the first observation period was determined by a balanced sequence. A total of 12 matched observations was obtained from 8 broods. The observations were spread over the first two-thirds of the nestling period, the oldest nestling being 12 and the youngest nestlings 2 days of age. Weight spread within the broods on observation days ranged from 0.80 g to 3.41 g ($\bar{X}=1.86$; SD = 0.80; $N=12$).

Weight Development in Broods with Large vs Small Weight Spread. To compare the weight development in broods that differed in weight spread, pairs of broods inhabitating nestboxes near each other in the same habitat and containing nestlings of similar age were formed. All nestlings were individually marked. The nestlings in each pair of broods were rearranged so that the broods thus formed were identical in size and very close to each other in total weight. However, weight spread among the nestlings was maximized in one brood and minimized in the other. Initial data on the eight pairs are found in Table 1. In pairs 7 and 8, one brood suffered severe losses from predation during the experiment. Data from the intact brood in these pairs will be presented only in connection with the question of the development of weight spread within the broods. The broods were weighed at a similar time every third day during the remaining nestling period, yielding data from four occasions (including the one when the pair was established).

Table 1. Initial weight data for pairs of broods in the experiment on weight development in pairs of artificial broods with small and large weight spread

Pair no.	Broad-range broods		Narrow-range broods		Brood size
	Mean weight (g)	Standard deviation	Mean weight (g)	Standard deviation	
1	6.76	2.71	7.27	0.74	10
2	5.18	1.48	5.45	0.55	11
3	5.15	0.90	4.98	0.21	11
4	3.56	0.84	3.56	0.20	9
5	6.48	1.02	6.54	0.31	9
6	4.18	1.74	4.21	0.54	8
7	[a]		5.27	0.22	13
8	5.55	1.17	[a]		12

[a] Brood lost through predation

Results

Effects of Replayed Begging Calls on Parental Feeding Rate and Distribution of Food

In Fig. 1 and Table 2, the summed results for experimental and control days, pooled for broods 1 and 2, are compared with those for brood 3. In brood 3, only nestlings that survived during the entire observation period are included. Changes in weight refer to average values obtained from the smallest (S) and largest (L) nestlings in each brood. Weight change is expressed as percentage increase in weight from 10.00 a.m. to 3.00 p.m. in relation to weight at 10.00 a.m.

Parental feeding rate showed a significant increase on experimental as compared with control days in broods 1 and 2 only. This finding demonstrates the validity of the experimental procedure and supports the idea that the adult birds usually feed the brood at a rate below their maximum working capacity. It corroborates similar results published by Khayutin and Dmitrieva (1979). In addition, the lack of experimental effect in brood 3 suggests that these parents were already feeding at maximum capacity.

In broods 1 and 2 the smallest young show a greater increase in weight on experimental than

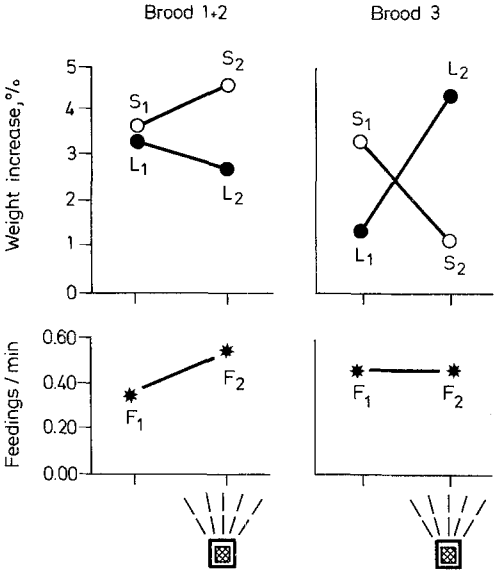

Fig. 1. Average weight increase and parental feeding rate (F) during a 5-h period on days when taped begging calls were played through a loudspeaker, as compared with control days. S and L denote average values for small and large nestlings, respectively, on control (S_1, L_1) and experimental (S_2, L_2) days. Broods 1 and 2 were raised under favourable, brood 3 under strained conditions

Table 2. Effects of playing taped begging calls at parental visits to the nest on parental feeding rate (*F*) and on weight increase of small (*S*) and large (*L*) nestlings in three great tit broods raised under favourable (1 and 2) and strained (3) conditions. The suffixes 1 and 2 denote the control and experimental conditions, respectively

Comparison	P^a	*N*
Brood 1+2, S_1–S_2	NS	15+14
Brood 1+2, L_1–L_2	NS	16+12
Brood 1+2, F_1–F_2	<0.001	5+ 9
Brood 1+2, S_1–S_2/L_1–L_2	0.05	15+13
Brood 3 S_1–S_2	NS	8+ 8
Brood 3 L_1–L_2	NS	13+10
Brood 3 F_1–F_2	NS	6+ 6
Brood 3 S_1–S_2/L_1–L_2	<0.05	8+10
Brood 1+2, L_1–L_2/		
Brood 3 L_1–L_2	<0.05	13+10
Brood 1+2, S_1–S_2/		
Brood 3, S_1–S_2	NS	15+18

[a] Two-tailed *t*-tests

on control days; the largest young show the opposite change. Neither difference is by itself significant (Table 2). A comparison of the two differences, however, reveals that playing the begging calls favoured the growth of the smallest young.

Brood 3 shows a reverse trend, i.e. the largest young gain more weight and the smallest young less weight on experimental compared with control days. Although neither trend is significant, the difference between them is.

Finally, the difference is significant between the smaller weight increase during experimental as compared with control days for the largest young in broods 1 and 2 and the reverse change in brood 3.

Under the experimental conditions the adult birds were exposed to auditory stimulation from a brood in which all the nestlings were begging during the entire 3-h period of observation. The results indicate that, compared with the larger young, the smaller young received a greater proportion of prey during the experimental as compared with the control condition. Since large young tend generally to be favoured when food is distributed (Rydén and Bengtsson 1980; Bengtsson and Rydén 1981), we conclude that in the experimental condition the largest young became relatively satiated and competed less intensively for food whereas the adult birds continued to feed the brood at a high rate since the auditory stimulation did not change. These results suggest that under normal conditions the smallest young would be able to consume more food than they are allotted. They also demonstrate the importance of auditory stimulation in the regulation of the parental feeding rate.

The results obtained from brood 3 indicate an additional parental option when feeding rate has reached an adaptive maximum: namely, increasing the proportion of food available to the largest nestlings. As shown earlier (Rydén and Bengtsson 1980; Bengtsson and Rydén 1981) this can be achieved by restricting the distribution of prey to a smaller area of the nest or, in older broods, by delivering food from a position at the nest entrance.

Parental Feeding Rate as Related to Brood Size and Degree of Food Deprivation of the Young

Food deprivation resulted in intense begging of the nestlings during the entire subsequent hour of observation. After artificial feeding, the nestlings usually resumed begging only at the end of the observation period and then only sparsely.

Suddenly encountering an intensely begging brood, the adult birds, after an initial reaction of alarm and hesitancy, typically increased their feeding rate sharply. We often noticed that the prey items brought to the brood tended to be smaller when the feeding rate increased; on some occasions the adult birds visited the nest with no apparent prey.

The opposite situation, encountering a brood which had been silenced through artificial feeding, elicited temporary alarm in most adult birds. At first, they visited the nest several times in succession and thereafter left the area for a few minutes; this behaviour was repeated several times, after which they disappeared for a longer period, sometimes during the rest of the observation session.

A summary of the results is given in Fig. 2. Clearly, the parental feeding rate changes with changes in the begging intensity of the brood independent of its size. This finding is direct evidence that the parents adjust their feeding rate to the nutritional needs of the nestlings as expressed by the intensity of their begging calls. Feeding rate was not related to brood size in any of the conditions of satiety. The short period of observation used here is not long enough for significant differences in hunger level in small and large broods to develop. When longer observation sessions are used, large differences appear in average feeding rate to small and large broods (e.g. Royama 1966).

Effects on Parental Feeding Rate of Changes in Begging Intensity in Part of the Brood

The results are shown in Fig. 3. There is no significant overall difference between the three condi-

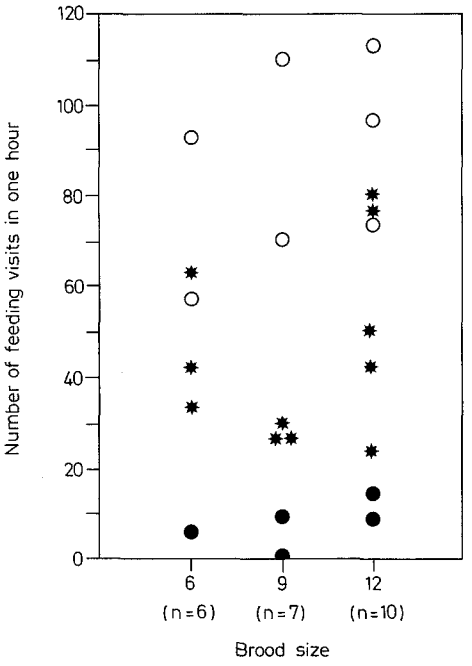

Fig. 2. Number of feeding visits during 1 h for artificially composed great tit broods containing 6 ($N=6$), 9 ($N=7$), and 12 ($N=10$) nestlings respectively in one of three conditions of satiation: 4 h of food deprivation (*open circles*), after artificial feeding (*filled circles*), and (control condition) without intervention (*asterisks*). *Comparisons.* Between: conditions of satiation for brood sizes 6, 9 and 12 ($H=3.09$, $P>0.05$; $H=4.77$, $P<0.05$; and $H=6.45$, $P<0.05$, respectively); brood sizes for artificially fed, food deprived, and control broods ($H=5.20$, $P\sim 0.05$; $H=1.10$, $P>0.05$; and $H=3.02$, $P>0.05$, respectively). Kruskal-Wallis one-way analysis of variance, two-tailed, in each case

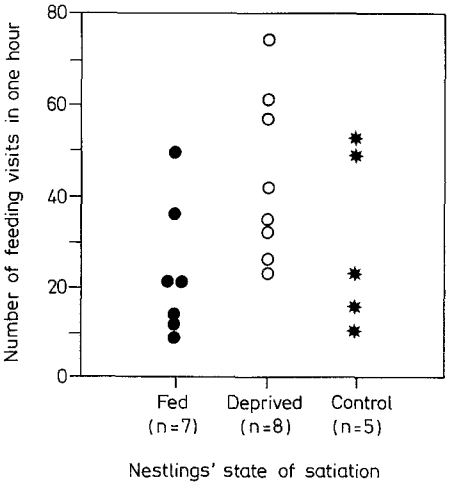

Fig. 3. Number of feeding visits during 1 h at artificially composed great tit broods containing nine nestlings. In the experimental conditions, three nestlings have been either artificially fed or deprived of food before observation of parental feeding rate. *Comparison.* Between all three conditions of satiation: $H=5.23$, $P>0.05$ (Kruskal-Wallis one-way analysis of variation); fed vs food deprived nestlings, $P=0.014$ (Mann-Whitney U-test, one-tailed)

tions. A comparison of the Fed/Control conditions, i.e. when six as compared with nine nestlings are begging at a normal (unmanipulated) intensity, shows no marked difference in feeding rate. This agrees with the finding in the preceding experiment where no difference was found in feeding rate in nests containing six versus nine unmanipulated nestlings. A greater difference, although not statistically significant ($P=0.09$), is found between the Deprived vs the Control conditions, where nine nestlings are begging in both conditions, three of them intensely in the Deprived condition. Finally, feeding rate is significantly higher in the Deprived than in the Fed condition, where in the latter case six of the nestlings are begging at normal intensity.

In conclusion, the present data corroborate the finding of the preceding experiment that the parental feeding rate is less influenced by changes in the number of nestlings than by changes in the intensity of their begging behaviour.

Effects on Parental Feeding Rate of Removing Larger vs Smaller Nestlings from the Brood

During the first 30 min of the observation period the number of feeding visits was lower when the lightest as compared with the heaviest nestlings had been removed from the nest ($\bar{X}_A=4.33$, $\bar{X}_B=7.75$; A/B, $T=11.0$, $N=11$; $P=0.05$, Wilcoxon matched-pairs signed ranks test, two-tailed). This finding suggests that in broods with a weight spread the lightest nestlings stimulate the parents to feed more than the heavier nestlings do. Again this points to the importance of the nestlings' hunger level in the regulation of parental feeding effort. In broods with a weight hierarchy, heavier nestlings are favoured in the competition for a feeding offer. Lighter nestlings beg on a larger number of feeding visits and their average hunger level is probably higher (Rydén and Bengtsson 1980).

During the last 30 min of the observation period the difference in the number of feeding visits had disappeared (lightest nestlings removed $\bar{X}=9.17$, heaviest nestlings removed $\bar{X}=7.08$; NS). This result is not surprising if one considers that the hunger level in the two experimental groups has presumably been affected by the difference in the number of feeding visits during the first half of the observation period.

The demonstrated ability of the lightest nestlings to stimulate the parents to feed the brood makes it less probable that the weight development of the smallest nestling is limited by a lower paren-

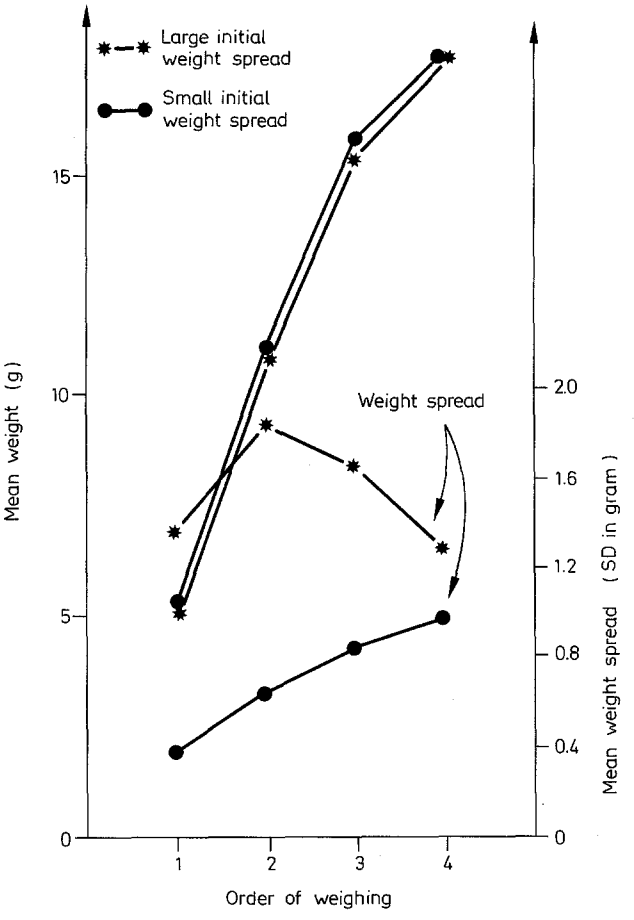

Fig. 4. Weight development in broods with small and large initial weight spread. Weight spread of broods was established on the first weighing as either narrow-ranged or broad-ranged. Weighings were made every third day following this

tal feeding rate under conditions of large hatching asynchrony (cf. Werschkul 1979). To subject this conclusion to a further test, we compared, in the final experiment, the weight development in broods with different initial weight spreads.

Weight Development in Broods with Large vs Small Weight Spread

In both broad-range and narrow-range broods weight spread increased during the first 3 days of the observation period (Fig. 4). During the remaining period, ranges continued to increase in the narrow-range broods, whereas the trend was reversed in the broad-range broods. In natural broods a decrease in weight spread is normally seen after the first 10 days of the nestling period (Gibb 1950; Neub 1979). This is due mainly to the fact that the growth curve is sigmoid in shape and that the heavier (older) nestlings start to level off at a point in time when the lightest nestlings are still growing with a linear increase in weight. The broods in the narrow-range group deviated from this normal pattern, the differences between the nestlings continuing to increase so that on the last two weighings a significant difference in weight spread between the pairs emerged only in 3 cases out of 12. On the first two weighings the difference was significant in 11 cases out of 12.

The growth rates exhibited by the broods in the two experimental groups are also shown in Fig. 4. The two groups are very similar in their development; at no point do they differ significantly from each other. There is a tendency for the young of narrow-range broods to gain more weight between the first and the third weighings than do the young of the broad-range broods, (in five cases out of six) but the difference is not statistically significant.

The results appear to indicate, therefore, that the amount of food fed to both types of broods was approximately equal.

Discussion

Three main factors are conceivable as playing a part in the proximate regulation of parental feeding effort. These are the working capacity of the parents, the hunger level of the nestlings, and environmental conditions such as temperature and food abundance. Changes in environmental conditions influence the other two factors directly; if the temperature decreases or food conditions deteriorate, the nestlings' hunger level increases. Similarly, the parent's working capacity varies with the density of food in the habitat.

An interpretation of the proximate regulation of the parental feeding effort must also consider more ultimate factors, however. For example, the optimal working capacity (Royama 1966) is lower than the maximum physical output which the parents can achieve for a short period. Time must also be devoted to activities other than feeding the young, and the parents must avoid risks such as predation and physical exhaustion that reduce their total reproductive output. Of particular interest are conflicts of interest between parents and offspring and between individual offspring with respect to the allocation of parental investment, conflicts that may affect parent-offspring and inter-sibling interaction (Trivers 1974; O'Connor 1978).

Importance of the Begging Call as a Stimulus Variable for Parental Feeding

The results of the first two experiments show that variations in the intensity of the begging calls are accompanied by congruent changes in parental feeding rate. An increased foraging intensity was elicited when food-deprived young were introduced into the nest. It was also elicited through artificial stimulation – taped begging calls – which were not modified by increased parental feeding. In the latter case, the smaller nestlings were fed to a greater extent, presumably because competition from their larger siblings became successively less intense. These results, taken together, indicate that it is the intensity of the brood's begging calls – rather than the number of nestlings per se or the non-vocal components of the begging response (stretching and gaping) – which affects the parental feeding rate. In broods with a weight spread, small young beg more intensely than large (Löhrl 1968; Rydén and Bengtsson 1980). Accordingly, they seem on average to provide greater stimulation for parental feeding than do the larger young, as the third experiment indicates.

The behaviour of the hungriest nestling, particularly in broods containing a runt, does not reliably reflect the average hunger level of the brood. Consequently, the parents must in some way estimate the hunger level from the behaviour of all nestlings as a whole. Our data suggest that they are able to do this. Despite initially large differences between the weight spreads in the paired broods in the last experiment, these broods showed strikingly similar weight developments. We conclude that the effective stimulation of the youngs' begging behaviour that governs the parental feeding rate is the average intensity of their begging calls, each nestling contributing to the net effect on parental feeding rate, but to a degree dependent on its size (reflected in the amplitude of the begging call) and level of hunger.

Begging Intensity in Small vs Large Nestlings in Relation to Sibling Competition

In species with multiple broods containing multiple offspring, parent-young and inter-sibling interaction can be expected to be influenced by conflicting interests regarding the allocation of parental investment (Trivers 1974; Dawkins 1976; O'Connor 1978). Each brood competes with future broods for a larger investment of parental investment than what is optimal for the parents. Within each brood, inter-sibling competition can be expected to give rise to dominance interactions as shown, e.g. for the western grebe (*Aechmophorus occidentalis*) (Nuechterlein 1981) where larger nestlings suppress the begging response of their smaller siblings by pecking them until a dominance hierarchy is established. Given these conflicting interests, it seems possible, following Dawkins and Krebs (1978), that the nestlings' begging behaviour does not veridically indicate their nutritional state but has been selected in the evolutionary process for its effects on the parents.

Larger nestlings in great tit broods have an interest in maintaining a weight spread within the brood if food supplies deteriorate and competition becomes keener. Domination by physical attacks is hardly an available option in altricial nestlings; it is conceivable, however, that the begging intensity of the larger young represents a balance between their interest in maximizing parental feeding effort, on the one hand, and in preserving a weight hierarchy within the brood, on the other. In support of this reasoning, our data indicate that it is often the smaller nestlings that would benefit the most from an increase in the parental feeding rate. Further, since larger nestlings compete more effectively than their smaller siblings when food is distributed, they can obtain some prey that is brought to the nest mainly through the 'efforts' of the smaller nestlings.

Antecedent Conditions of the Development of a Weight Hierarchy Within the Brood

Both the average hunger level of the nestlings and differences between them in begging intensity are determined to some extent by preadaptations such as clutch size and asynchronous hatching. The most widely accepted functional interpretation of hatching asynchrony in passerine birds is that it allows the parents to starve selectively the last-hatched (smallest) young if sufficient food is not available to raise the entire brood (Lack 1956; 1968; Howe 1976, 1978). This interpretation identifies hatching asynchrony as a mechanism to produce a weight hierarchy within the brood. In a critical review, Clark and Wilson (1981), however, refute the brood reduction hypothesis, indicating for example that a much smaller degree of hatching asynchrony than that observed in many species is sufficient for selective starvation. In support of their inference, our data show that in the great tit a weight spread within the brood will develop even out of a very small initial range of weights.

An alternative function of hatching asynchrony may be that it speeds up hatching of the first-laid eggs in species dependent on peaked or declining food resources (Clark and Wilson 1981). In this view, large differences in body size between the nestlings in a brood are likely to be a cost rather than a benefit. This agrees with the observation that asynchrony is greater late in the season – when food resources are declining; it is also compatible with the fact that in second clutches egg-weight increases with position in the laying sequence (providing late-hatched young with extra yolk reserves). Both these features are also possible to reconcile, however, with the brood-reduction hypothesis (see Howe 1978; Rydén 1978). The ability of late-hatched young to grow faster than early-hatched young and reach similar weight at fledging (Neub 1979) may then have evolved as a co-adaptation to hatching asynchrony.

Within a brood, smaller nestlings beg more frequently and more intensively than larger nestlings (Löhrl 1968; Rydén and Bengtsson 1980; Khayutin and Dmitrieva 1977; Bengtsson and Rydén 1981) and are disfavoured compared with larger nestlings even when food conditions are adequate (Lack 1956; Hussell 1972; Schifferli 1973; Balph 1975; O'Connor 1975; Bryant 1978; Khayutin and Dmitrieva 1978; Werschkul 1979); in the great tit, late-hatched nestlings may develop into runts (Gibb 1950; Löhrl 1968). In view of this, one may ask what factors besides food availability limit the growth of late-hatched nestlings? One such factor might be the brood's ability to induce the parents to feed. Under equal food conditions, the mean nestling weight of House Martins (*Delichon urbica*) on the 10th nestling day was depressed when the difference in hatching weight within the brood was large (Bryant 1978). This suggests that a brood with smaller weight spread stimulates the parents to feed at a higher rate. However, the generality of Bryant's finding is questioned by our results showing no differences between the total weights of broad-range and narrow-range broods.

Clearly, the suggestion put forward by Clark and Wilson that hatching asynchrony primarily serves to speed up hatching in some species, including the great tit, does not contradict the idea that a weight hierarchy within the brood is established to make possible selective starvation of the smaller young. Other effects of hatching asynchrony may also be adaptive. Hatching asynchrony spreads out the peak demands for food of individual offspring, as Hussell (1972) has indicated. We would add that the extended period of hatching may facilitate the transition from incubating to feeding behaviour, since at hatching the feeding procedure is slow and inefficient due to the immature state of the nestlings (Bengtsson and Rydén 1981). In addition, the nestlings are initially fed exclusively by the female with prey delivered by the male. Obviously, differentiating the various functions and other effects of hatching asynchrony in the great tit requires additional study.

Why did a successively greater weight spread develop with initially even-sized nestlings in our broods even though the nestlings presumably were equally competitive when the broods were established? We would suggest that three factors gave rise to this development. First, food is unevenly distributed in the nest because the parents tend to feed from specific positions, favouring nestlings close to this position (Rydén and Bengtsson 1980). Second, larger nestlings tend to be favoured independent of their positions in the nest (Bengtsson and Rydén 1981). Third, the relatively large number of nestlings augments the effects of the previous factors (cf. Best 1977). Further, as argued above, once a weight hierarchy has been established, additional factors may contribute to its maintenance.

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