

## Brood reduction and begging behaviour in the Swift *Apus apus*; no evidence that large nestlings restrict parental choice

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Brood reduction in birds is generally viewed as an adaptive process by which parents can maximize reproductive success in the face of an unpredictable environment. However, brood reduction may not be adaptive for the parents if the reduction is instead caused by large nestlings that block the nest entrance, thereby restricting parental choice. To determine the degree of difficulty faced by the parents in obtaining access to their smallest nestlings, a simple experiment was conducted in the Swift *Apus apus*. By inserting a human hand blindly into Swift nesting holes, nestlings were stimulated to beg and to grasp the approaching fingers. The results show that the smallest nestlings in the nest were the first to encounter the approaching fingers. Small nestlings were also just as likely to be found with at least some food in their crops as were medium and large nestlings, but gained mass at a significantly slower rate. I suggest that parent Swifts can easily access small nestlings, but prefer either to allocate more food to larger nestlings or to allow sibling competition in order to facilitate brood reduction.

Brood reduction in birds has been studied extensively from both theoretical and empirical perspectives (reviewed in Magrath 1990). Following Lack (1947), many researchers have suggested that, to maximize reproductive success in the face of an unpredictable environment, parents may start with broods which are larger than they can normally afford and allow the process of brood reduction to fit the brood size to current circumstances (Mock & Forbes 1995). However, the potential for parent–offspring conflict (Trivers 1974) raises the possibility that brood reduction may not always be adaptive for the parents. Food allocation in the nest may deviate from parental optimum if, for example, large nestlings can restrict parental choice by blocking the nest entrance (Stamps *et al.* 1985, Parker *et al.* 1989, Kacelnik *et al.* 1995), by killing their younger sibs (O'Connor 1978, Mock 1984, Godfray & Harper 1990) or even by merely threatening to kill their younger sibs (Rodríguez-Girones 1996).

Several studies have shown that sibling competition for a position close to the nest entrance (in hole nesters) or at the centre of the nest (in cup shaped nests) has a strong effect on a chick's probability of being fed (Ryden & Bengtsson 1980, Gottlander 1987, Bryant & Tatner 1990, McRae *et al.* 1993, Malacarne *et al.* 1994, Kacelnik *et al.* 1995, Kilner 1995). However, it is not clear whether parents were forced to accept the outcome of sibling competition or whether they could easily approach the nestlings at the back but chose not to do so. On the basis of observations only, it is often difficult to determine the degree of difficulty faced by the parents in obtaining access to their smallest nestlings.

Here I describe a simple experiment which attempts to

provide a better assessment of this problem in the Swift *Apus apus*. In this experiment, I inserted my hand blindly into Swift nesting holes to simulate a parental visit to the nest, thus eliciting nestling begging and grasping response toward my approaching fingers. Surprisingly, I was much more likely to first encounter the smallest chick in the brood rather than the largest one. I suggest that parent Swifts can easily reach small nestlings but prefer to feed the largest nestlings, or allow sibling competition, in order to facilitate brood reduction.

### METHODS

During April and May 1995, I studied a Swift colony located in a large deserted building 2 km northwest of Tel-Aviv University. The Swifts built their nests in holes in the concrete ceiling of the building, and the nests were easily accessible with a ladder. The holes were just wide enough to insert a hand into the nest and to reach its contents. Swifts are known to have hatching asynchrony, which often leads to marked differences in size between siblings and, occasionally, to brood reduction (Lack & Lack 1951, Perrins 1964, Martin & Wright 1993). As in other hole nesters, the entrance to the nest is physically restricted, and sibling competition for a favourable position may be expected.

Experiments were conducted on 63 nests containing nestlings aged 3–15 days. Each experiment was based on two consecutive tests, conducted 1 h apart, during which the Swift parents could visit the nest and feed one or more of the nestlings. In each test, I inserted my hand into the nest

to simulate a parental visit, thus eliciting nestling begging and grasping response toward my approaching fingers. This procedure was not necessarily an accurate imitation of a real parent, which may use a feeding call (J. Wright, pers. comm.) or may approach the nestling which begs the most. Rather, it was a simulation of a simple behaviour of entering a nest which could easily be performed by a parent Swift that makes no parental choice. The logic behind this experiment was that if, by using such a simple way of entering a nest, the chances of encountering small nestlings were no lower than those of encountering larger ones, then there is no evidence that large nestlings restrict parental access to small nestlings.

As soon as the first nestling grasped my finger or only touched it while attempting to do so, it was removed from the nest. The other nestlings were also taken out of the nest and all nestlings were weighed to the nearest 0.1 g with Ohus electronic portable balances CT 305 and checked to see if there was food in their crops. The described experimental procedure can be regarded as a "blind test" and could not be biased by my expectations because I was not able to see the nestlings or to feel their relative size before the test was completed.

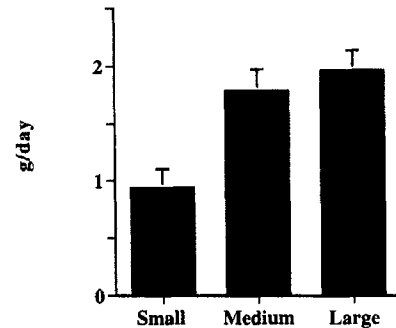
Most nests ( $n = 43$ ) were used for two experiments with an interval of 1 ( $n = 11$ ), 2 ( $n = 9$ ), 3 ( $n = 9$ ), 4 ( $n = 10$ ), 6 ( $n = 3$ ) or 7 ( $n = 1$ ) days between them. Some of the nests used for the first experiment were not used for the second experiment because the nestlings were older than 15 days, an age at which nestling recognition of their parents and the possible fear of a human hand may bias the results. The possibility that fear or parental recognition affected nestlings younger than 15 days, and therefore biased the results, will be discussed later.

To simplify the analysis presented here, I have included only broods of three nestlings (the commonest brood size) and only test results in which all three nestlings were still alive during the test. In each brood of three nestlings, a small, a medium and a large nestling could easily be distinguished by the marked differences in body size. The average masses (g,  $\pm$ s.d.) of small, medium and large nestlings were  $10.7 \pm 7.6$ ,  $16.9 \pm 9.8$  and  $21.0 \pm 11.4$  in the first experiment ( $n = 41$ ) and  $11.0 \pm 6.2$ ,  $19.1 \pm 8.9$  and  $23.4 \pm 9.4$  in the second experiment ( $n = 28$ ).

## RESULTS

### Brood reduction and nestlings' growth

Brood reduction occurred in 5 of 43 nests (all brood sizes included) that were inspected during various periods of time (average, 3.8 days; range, 2–8 days). All five cases of brood reduction occurred in broods of three nestlings (in three of them, the smallest nestling was found dead in the nest, and in the other two, the smallest nestling disappeared). To assess if the rest of the nests used for this study featured conditions that could lead to brood reduction, a mean daily mass gain was calculated for each nestling based on the



**Figure 1.** Daily mass gain (average  $\pm$  s.e.) of small, medium and large Swift nestlings in 28 broods of three nestlings each (see text for more details).

difference in mass between the first and second visits. Because nestlings were not individually marked, I used their relative size as an identity marker, assuming that fast changes in relative rank are rare (in 23 other nests in which nestlings were marked individually and were followed to the age of 15 days, changes in rank occurred only twice and only between medium and large nestlings; A. Lotem, unpubl.). The results (Fig. 1) indicate that the daily mass gain of small nestlings was only about half that of medium or large nestlings (two-way ANOVA without replications; differences within a nest:  $F_{2,80} = 9.8$ ,  $P < 0.001$ ; differences between nests:  $F_{1,80} = 0.038$ , n.s.). Such differences are too large to be explained as normal age differences in growth rate between small and large nestlings because under good conditions, daily mass gain of Swift nestlings is nearly constant during the first 10 days, and small nestlings can grow as fast as their larger brood mates (Lack & Lack 1951). Moreover, if age rather than rank was the source of the differences, daily mass gain should have been higher for older nestlings. The data given here show no increase in daily mass gain (measured between experiments) as a function of mass in the first experiment ( $r = 0.12$ ,  $n = 84$ , n.s.), suggesting that rank rather than age was the source of the differences described by Figure 1. Accordingly, the lower daily mass gain of small nestlings reflects asymmetric food allocation, typical to brood reduction conditions.

### Nestlings' response and the presence of food in the crop

Table 1 summarizes the number of cases in which small, medium or large nestlings were the first to grasp approaching fingers. Overall, the probability of being the first was highest for small nestlings (0.58), intermediate for medium nestlings (0.24) and lowest for large nestling (0.10). This trend was highly significant in three of the four tests (Table 1). These results are the opposite of what would be predicted by the hypothesis that large nestlings block the nest entrance and prevent the parents from feeding their small nestlings.

Table 2 shows that small nestlings were just as likely to

**Table 1.** Number of cases in which small, medium, or large Swift nestlings were the first to grasp the approaching hand (only data of broods containing three nestlings are included)

	Nestling size			Number of nests tested	$G_2$	P
	Small	Medium	Large			
First experiment						
Test 1	24	12	6	41 <sup>a</sup>	18.6	<0.001
Test 2 <sup>b</sup>	21	7	2	40 <sup>a</sup>	26.6	<0.001
Second experiment						
Test 1	21	7	0	28	43.9	<0.001
Test 2 <sup>c</sup>	13	6	6	27	5.5	n.s.
Total	79	32	14	136 <sup>d</sup>		

<sup>a</sup> Includes one case in which small and medium nestlings grasped approaching hand simultaneously.

<sup>b</sup> One nest used in test 1 was not used in test 2 because the small nestling fell during handling after test 1.

<sup>c</sup> One nest used in test 1 was not used in test 2 because the small nestling, already in poor condition, died before test 2.

<sup>d</sup> No result was obtained in 12 cases.

be found with food in their crop as were medium and large nestlings. This could indicate that they were fed by their parents at the same frequency as their older sibs (with at least some food) or that they were being fed at a lower frequency but kept food in their crops for longer periods. If small nestlings kept food in the crop for longer periods than medium and large nestlings, cases in which there was food in the crop in both the first and the second test but no increase in mass between tests should have been more frequent among small nestlings (i.e. cases in which food in the crop in the second test had already been in the crop during the first test). However, the data show that nestlings rarely kept food in their crops for 1 h and that the frequency of such cases was similar for small (2/17), medium (0/18) and large (2/17) nestlings (pooled data for first and second experiments). Accordingly, the results presented in Table 2 suggest that parents were able to reach and feed small nestlings (with at least some food) as frequently as medium and large nestlings.

Because, in general, begging behaviour increases with hunger and decreases with satiation (see Kilner & Jonstone 1997 for a review), it is possible that the results presented in Table 1 were partly a result of the fact that large nestlings with food in their crops had no incentive to compete for food and thus to block the nest entrance. To test this possibility, I conducted another analysis using only the cases in which all brood mates had an empty crop during the test. The results gave the same pattern as in Table 1, with highly significant differences in the first three tests ( $G_2 = 16.3$ , 16.3, 21.6;  $n = 27$ , 21, 13, respectively;  $P < 0.001$  in all cases) and with a similar but nonsignificant trend in the fourth test ( $G_2 = 1.76$ , n.s.,  $n = 15$ ). Hence, even when

**Table 2.** Number of cases in which small, medium, or large Swift nestlings had food in the crop when tested (only data of broods containing three nestlings are included)

	Nestling size			Number of nests tested	$G_2$	P
	Small	Medium	Large			
First experiment						
Test 1	6	7	5	41	0.392	n.s.
Test 2	12	8	5	40	3.775	n.s.
Second experiment						
Test 1	3	9	4	28	4.602	n.s.
Test 2	6	4	6	27	0.647	n.s.
Total	27	28	20	136		

large nestlings had an empty crop, they showed no tendency to block parental access to small nestlings. The relationship between having an empty crop and being the first to grasp an approaching hand (Table 3) was relatively weak and reached statistical significance in only one test.

### Possible biases of using a human stimulus

A critical problem to consider in this study is whether the experimental results could be an artifact of using a human hand to simulate a parental visit. The first possibility is that large nestlings, which were older and more developed, recognized that the stimulus was not a real parent and therefore did not try to compete for it with their smaller brood mates. An age effect of this kind also requires that, within

**Table 3.** Number of cases in which Swift nestlings had food in the crop in relation to whether they were the first to grasp the approaching hand (only data of broods containing three nestlings are included)

	First to grasp hand		Not first to grasp hand		$G_{adj}^a$ (d.f. = 1)	P
	Food in crop	No food in crop	Food in crop	No food in crop		
First experiment						
Test 1	3	39	15	66	3.072	n.s.
Test 2	3	27	22	68	3.111	n.s.
Second experiment						
Test 1	2	26	14	42	4.248	<0.05
Test 2	4	21	12	44	0.318	n.s.
Total	12	113	63	220		

<sup>a</sup> Williams' correction was applied, critical G-value for  $P < 0.05$ , d.f. = 1 is 3.841.

**Table 4.** Number of cases in which small, medium or large Swift nestlings were the first to grasp the approaching hand in nests where the largest nestlings weighed less than 20 g during the first experiment<sup>a</sup>

	Nestling size			Number of nests tested	$G_{nd}$ (d.f. = 1) <sup>b</sup>	P
	Small	Medium	Large			
First experiment						
Test 1	10	5	4	19	4.51	<0.05
Test 2	12	4	0	19	16.43	<0.001
Second experiment						
Test 1	11	6	0	17	10.73	<0.01
Test 2	10	4	3	16	7.31	<0.01
Total	43	19	7	71		

<sup>a</sup> Average masses ( $\pm$ s.d.) of large nestlings in the first and the second experiments were  $10.36 \pm 3.89$  g and  $17.06 \pm 4.97$  g, respectively.

<sup>b</sup> Because of smaller sample size in the new analysis, differences were tested between a pooled category of large and medium nestlings and the small nestling category (Williams' correction was applied).

the large nestling category, age would affect the probability of being the first to grasp the stimulus (i.e. that this probability would decrease with age). However, Spearman rank correlations between a large nestling mass (as indication of its age and developmental stage) and the nestling's response in a test ("1" v "0" for "was" or "was not" the first, respectively) gave no indication for an age effect. I was able to test for such correlations in three of the four tests (the first test of the second experiment was not informative because the large nestlings were never the first to respond). Despite a wide range of size differences within the large nestling category (4.7–45.8 g in the first experiment and 8.6–38.3 g in the second), none of the correlations was significant, and in only one of the three was the trend negative as would have been expected if there was an age effect ( $r = -0.17$ ,  $n = 41$ ;  $r = 0.20$ ,  $n = 40$ ;  $r = 0.09$ ;  $n = 27$ ).

To investigate further a possible age bias, I repeated the analysis presented in Table 1 but included only nests in which the largest nestling weighed less than 20 g during the first experiment. Swift nestlings below 20 g are usually less than 10 days old (Lack & Lack 1951) and are still blind (A. Lotem, pers. obs., based on a study of 75 other nestlings from the same colony). At this stage, differences in recognition ability are likely to be small, and the suspected age bias should therefore be less pronounced. The results of this new analysis (Table 4) did not differ from those presented in Table 1, and the greater likelihood of encountering small nestlings was significant in each test, giving no evidence of an age effect.

A second possible bias of using a human stimulus is that it caused some level of fear among all nestlings, but that

lower ranked nestlings, which were hungrier, were willing to take a greater risk in approaching a suspected parent. This possibility cannot be ruled out on the basis of the data and can therefore provide an alternative explanation for the results presented in Table 1. However, at least among the young nestlings used for the analysis in Table 4, there was no indications of fear behaviour (i.e. immobility and crouched position, as was frequent in nestlings older than 15 days).

## DISCUSSION

A greater begging effort by small brood mates has been reported and discussed in previous works on nestling begging (Bengtsson & Ryden 1983, McGillivray & Levenson 1986, Godfray 1995, Price *et al.* 1996). However, the success of small nestlings in reaching a potential parent was unexpected. Even if the experimental results were biased by the use of a human stimulus, the presence of food in the crop (Table 2) suggests that parents could and regularly did reach the small nestlings, and there is no evidence that large nestling blocked their way.

If parents could readily reach small nestlings, what did cause brood reduction conditions in the nests studied? A comparison of the results presented in Tables 1 and 2 suggests that although, in most cases, small nestlings may be the first to reach the parents, they are not fed more frequently than their brood mates (they were as likely to be found with food in their crops as their larger brood mates). Accordingly, parents do not feed small nestlings every time they are first to beg. Moreover, the quantity and quality of the food were not measured in this study but could have played a major role in preferential food allocation to large chicks and in the resulting brood reduction. Lack (1956) reported that when Swift nestlings were in their first week, the parent produced only part of the meal at a time and occasionally took the food back into its mouth and produced it again. By doing so, parent Swifts can divide the food between the chicks and produce meals of different sizes for different chicks. Martin and Wright (1993) suggested that parent Swifts may selectively feed heavier chicks and may feed the smallest chicks with a bolus of lower quality. These observations, together with the data presented above, suggest that parents make some active decisions regarding food allocation rather than feeding nestlings on the basis of "first come, first served".

The experimental results do not imply that sibling competition among Swift nestlings has no role in the process of brood reduction. They can only suggest that if sibling competition was maladaptive for the parents, parents could easily circumvent it by approaching small nestlings in the same way that I did. However, parents may behave differently because accepting the outcome of sibling competition may be adaptive for the parent when chick dominance is correlated with parental marginal gains (Mock & Forbes 1992, Kacelnik *et al.* 1995).

It is interesting to compare the results of this study with a recent study on food allocation in the congeneric Pallid Swift *Apus pallidus*. Malacarne *et al.* (1994) have shown that food allocation was affected by chick position at the nest. However, the preferred position was not necessarily at the immediate entrance, where nestlings could restrict parental movements, but in an "activity centre" that was formed within the nest cavity in the area where parents were most likely to visit (see Malacarne *et al.* 1994:fig. 1). Accordingly, I suggest that the parental tendency to visit a particular site may have developed to create activity centres where sibling competition takes place, allowing parents to allocate food in relation to nestling dominance.

Brood reduction in the Swift may be a result of both direct and indirect parental preference of larger nestlings. It is probably not a result of large nestlings monopolising the nest entrance.

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