

Differences in begging behaviour between barn swallow, *Hirundo rustica*, nestlings

ARNON LOTEM

Department of Zoology, Faculty of Life Sciences, Tel-Aviv University

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Abstract. Recent models of parent–offspring communication suggest that nestling begging reliably reflects food requirements, and therefore should increase with nestling need. Need may be affected by short-term variations in hunger, as well as by long-term factors such as relative size, growth rate and body condition. In the present study, the brood sizes of barn swallows were manipulated to create differences in nestling growth rate and body condition. The extent to which begging behaviour reflects these differences was tested. I measured begging behaviour by removing nestlings from the nest for three laboratory tests in which temporal variations in hunger were controlled, and four target nestlings (small and large, from small and large broods) were tested simultaneously. Small nestlings and nestlings from large broods had lower growth rates and poorer body condition than large nestlings and nestlings from small broods, respectively. Begging was positively correlated with both short- and long-term determinants of need. However, when nestlings grew older (second test), the trend was mixed, mainly because begging levels dropped in the neediest nestling category (small nestlings from large broods). After nestlings had been exchanged between broods for 24 h, small nestlings from large broods improved their growth rate and body condition, but still begged less than expected from their long-term need. The results suggest that nestling begging strategies vary with brood size and with nestling rank. However, these variations may reflect not only long-term need, but also nestling response to past experience or to variations in the cost and effectiveness of their begging efforts.

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The offspring of birds and mammals solicit food from their parents by a combination of movements and vocalizations which appear costly. This behaviour was once suggested to be a mechanism by which offspring manipulate their parents (Trivers 1974) and outcompete siblings (Harper 1986). Recently, however, there has been an increasing tendency among researchers to view it as an honest signal of need (Godfray 1991, 1995a, b; Redondo & Castro 1992; Kacelnik et al. 1995; Kilner 1995; Cotton et al. 1996; Kilner & Johnston 1997). This development is based on theoretical studies of the handicap principle (Zahavi 1975, 1987) for both signalling of quality (Grafen 1990) and signalling of need (Maynard Smith 1991). Using this framework, Godfray (1991, 1995b) has shown that the level of solicitation should be a true reflection of the offspring's

need (defined as the benefit to the nestling from obtaining extra resources) as long as solicitation is costly to produce and the benefit from obtaining more resources increases with diminishing returns. A general prediction of Godfray's models is that, everything else being equal, solicitation for food should increase with the offspring's need. However, this relationship may be confounded by additional factors, such as the offspring's past experience (Stamps et al. 1989), variations in the effectiveness and cost of solicitation (Parker et al. 1989; Godfray 1995b), and sibling competition (Smith & Montgomerie 1991; Price et al. 1996).

Another difficulty in testing the relationship between solicitation and need is that need, as defined by Godfray (i.e. the marginal benefit to the offspring from obtaining extra resources), is likely to be affected by short-term variations in hunger, as well as by long-term factors, such as relative size, growth rate and body condition (reviewed by Price et al. 1996). In birds, begging clearly increases with the degree of food

Correspondence: A. Lotem, Department of Zoology, Faculty of Life Sciences, Tel-Aviv University, Ramat Aviv, Tel-Aviv 69978, Israel (email: lotem@post.tau.ac.il).

deprivation (von Haartman 1953; Bengtsson & Ryden 1983; Stamps et al. 1989; Smith & Montgomerie 1991; Redondo & Castro 1992; Kacelnik et al. 1995; Kilner 1995; Price & Ydenberg 1995); however, the relationship between begging and long-term determinants of need is less clear. Stamps et al. (1989) did not find a correlation between food requirements, as indicated by nestling weight at a given age, and begging intensity in the following period. Redondo & Castro (1992) showed that daily growth during the preceding day, as well as average cumulative food intake by the brood during the preceding 24 h, did not influence begging intensity. Other evidence for the effect of long-term need is inconclusive because variations in hunger were not controlled. For example, small nestlings have typically been reported to beg more than their larger brood-mates (Bengtsson & Ryden 1983; McGillivray & Levenson 1986; Stamps et al. 1989), but this could simply be a consequence of their higher hunger levels during the period they were observed (because they are usually last to be fed). Similarly, the finding that nestling begging increases with brood size (Stamps et al. 1989; Kacelnik et al. 1995; Cotton et al. 1996) may also be explained by longer time intervals between feedings, rather than by differences in long-term determinants of need between small and large broods. To show that variations in long-term determinants of need affect begging behaviour, it is therefore crucial to control for short-term variations. Recently, Price et al. (1996) conducted such a set of controlled experiments. They showed that in the yellow-headed blackbird, *Xanthocephalus xanthocephalus*, male chicks and chicks in poor condition begged more than female chicks and chicks in good condition, respectively, and that chicks begged more when paired with larger rather than smaller nestmates. These results suggest that begging can carry information about long-term determinants of need.

In the present study I manipulated broods of barn swallow nestlings to generate differences in their long-term determinants of need (i.e. growth rate and body condition) and tested the extent to which begging behaviour reflects these differences. I measured begging behaviour by removing nestlings from the nest for a laboratory test in which I measured begging response to an artificial stimulus over a wide range of hunger states. This method controlled for short-term variations in

hunger levels and allowed me to compare the begging behaviour of nestlings from small and large broods which differed in their long-term determinants of need.

METHODS

Study Animal

During June–July 1994, I studied barn swallow nestlings from 38 nests at the University of British Columbia, Vancouver, Canada. The majority of nests were in a large colony in the Fraser parking building. The nests were built over light covers and were easily accessible with a small ladder. To determine the exact hatching date, I inspected nests regularly during egg laying and hatching. To minimize human disturbance during this stage, I inspected them from the ground using a mirror attached to an aluminium pole, and a flashlight to light the nest interior. The temporary removal of two nestlings from each nest for a laboratory behavioural test (see below) did not cause nest desertion, and parents continued to care for nestlings after they were returned to the nest. The legal authority under which the work was carried out was the Animal Care Committee of the University of British Columbia. Access to swallow nests was permitted by the Canadian Wildlife Service.

Brood Manipulation

I manipulated brood size to create nestlings growing under poor conditions (low-ranked nestlings in enlarged broods) and good conditions (in small broods). Nests were assigned to one of the two treatments in pairs based on hatching date (11 pairs with the same dates, seven pairs with a 1-day difference, and one pair with a 2-day difference). During the first day after hatching, I transferred one or two nestlings from one nest (randomly determined) to the other, creating small (three nestlings) and large (five to seven nestlings) broods. Natural brood sizes (before manipulation) were of three ($N=1$), four ($N=14$) and five ($N=23$) nestlings. Nestlings were not rejected after being transferred to a new nest. Because it was difficult to mark nestlings at the age of 1 day, I could not monitor the introduced nestlings. Swallows have no individual nestling recognition at this early stage of the nesting period (Burt

1977) and I assume therefore that parents treated the introduced nestlings as their own. Total nest failures during the study period (from hatching to day 10) occurred in two enlarged broods and in five small broods. Brood reduction also occurred, in which one ($N=6$), two ($N=1$), three ($N=1$), or four ($N=1$) chicks disappeared from nine of the large broods of five ($N=2$), six ($N=6$) and seven ($N=1$) nestlings but not in any of the small broods. It is possible that the frequency of brood reduction in enlarged broods (9/17) was especially high because of heavy rainfall during June 1994 (70.5 mm versus an average of 45.7 mm for June; Environment Canada, monthly meteorological summary for Vancouver International Airport). It is also possible that the daily disturbance in the nesting colony caused some reduction in parental activity thus making brood reduction more likely than in an undisturbed situation.

Experimental Procedure

At the age of 3–6 days, two nestlings from each brood were designated the 'target' nestlings and were marked individually with a non-toxic acrylic paint on one wing. Target nestlings were usually the two smallest nestlings from small broods (ranked second and third based on body mass) and two small nestlings (usually, ranked fourth and fifth based on body mass) from large broods. Nestlings ranked sixth or seventh in large broods were not selected as target chicks because of the high risk of brood reduction. Target nestlings from large broods were likely to grow under poorer conditions than those from small broods as a result of brood-size effects (lower per individual food provisioning) and/or their lower rank in the brood (fourth and fifth versus second and third). Small target nestlings were likely to grow under poorer conditions than large target nestlings taken from the same brood.

I transferred the four target nestlings of a pair of nests (large and small from a small brood, and large and small from a large brood) together to the laboratory for up to 2 h to test their begging behaviour under controlled conditions (see detailed methodology below). The target nestlings were first tested at the age of 3–6 days. Second and third tests were conducted 3 and 4 days after the first test at the same time of day. Immediately after the second test, I exchanged the small target nestlings of each brood between the nests for the

24 h between tests 2 and 3 (i.e. the small nestling from the small brood was transferred to the large brood, and the small nestling from the large brood was transferred to the small brood). The rationale behind this nestling exchange was to see whether nestlings changed their begging strategy when introduced to an environment different from that in which they were reared.

Measuring Growth Rate and Body Condition

I weighed target nestlings, using a pocket scale, to 0.5 g precision and measured their right wing length to the nearest 0.1 mm, prior to the first (3–6 days old), the second (3 days later) and the third (4 days later) tests of begging behaviour. To determine the rank of target chicks within their broods (based on body mass), I weighed all other brood-mates near the nest just before the target chicks were taken to the laboratory tests. To quantify long-term determinants of nestling need, I calculated three indices based on a step-wise polynomial regression (Sokal & Rohlf 1981). A 'body condition index' (see Hochachka & Smith 1991) was calculated as the residual from a cubic regression line of $\ln(\text{mass})$ over $\ln(\text{wing length})$ fitted through the data for all three measurements (in tests 1, 2 and 3) of large target nestlings from large broods that survived to the third measurement ($\ln \text{mass} = 13.557 (\ln \text{wing}) - 4.355 (\ln \text{wing})^2 + 0.492 (\ln \text{wing})^3 - 12.561$; $r = 0.929$, $N = 39$). I chose to fit the regression through the data of only one nestling category in order to minimize the effect of unequal distribution of nestling categories around the lower and upper extremes of body masses (I obtained similar results when I calculated body condition based on all nestling categories, or on a separate regression line for each test).

A 'relative growth index', reflecting the extent to which a nestling is small or large relative to its age, was calculated as the residual from a regression line of mass (g) over age (days) fitted through the data for all three measurements of the 60 target nestlings that survived to the third measurement ($\text{mass} = 1.493 (\text{age}) - 0.817$; $r = 0.794$, $N = 180$). This index was necessary to compare nestlings from small and large broods whose hatching dates differed by 1 or 2 days (see above).

I applied a 'mass gain index' to compare the mass gained by nestlings of different initial size (at time A) during a certain time interval (between

times A and B). This index expresses the mass gained by each nestling in relation to the expected mass gain of an average nestling of the same initial size during a similar time interval. The expected mass gain of a nestling for each time interval (between tests 1 and 2 and between tests 2 and 3) was obtained by regressing mass at test 2 against mass at test 1, and mass at test 3 against mass at test 2. A mass gain index was then taken as the residuals from these regression equations ($(\text{mass}_2) = 1.455 (\text{mass}_1) + 2.203$, $r = 0.811$, $N = 64$; $(\text{mass}_3) = 0.860 (\text{mass}_2) + 2.303$; $r = 0.911$, $N = 63$).

The mass gain index differs from the relative growth index as it represents a shorter, more recent growth interval, which is clearly defined, and controls for initial size. In contrast to the mass gain index, differences in the relative growth index may originate not only from differences in growth rate per se but also from differences in initial egg size and hatching time during the day. Note also that the data used for the relative growth index (mass over age) had a linear fit during days 3–10, although nestling growth is not typically linear (Ricklefs 1967). The mass gain index, on the other hand, appears to have a greater sensitivity to small variations in growth rate and it indicates that nestling growth was indeed not linear. The different coefficients found for calculating the mass gain index for the different time intervals (see above) suggest that during the period between tests 1 and 2, large nestlings were expected to gain more mass relative to small ones, and that the opposite was expected between tests 2 and 3. This trend is expected in a typical growth curve because at an early stage large brood-mates are the first to accelerate growth, while at a later stage they are the first to approach the asymptotic phase of the growth curve.

Behavioural Measurement of Begging Strategy

For each test, I transferred the four nestlings from their original nests to an artificial nest which was placed in a controlled temperature room (26°C) and its floor heated to 35°C. Barn swallow nestlings at this age (3–10 days) have little fear of approaching objects and tend to beg towards them. I stimulated nestlings to beg by momentarily shading them, waving a piece of cardboard over their heads and simultaneously making a high-pitched sound mimicking a parent swallow's call. The nestlings begged vigorously in response

to these stimuli. Each begging trial was recorded by a video-camera. I conducted the first trial (trial 0) 10 min after the nestlings were introduced into the artificial nest. Shortly afterwards I fed each nestling with a semi-liquid mixture of cat food and strained baby food until it stopped begging completely and refused to eat any more. Food was given from a syringe, allowing me to measure how much each nestling received (no significant differences were found, Friedman tests: $df = 3$, $P > 0.5$ for all behavioural tests). After feeding, the nestlings were stimulated to beg at 10-min intervals for nine consecutive begging trials during which they were not fed (trials 1–9). I returned the nestlings to their nests after trial 9. This procedure was designed to reduce momentary variations in hunger between the nestlings, allowing a comparison between their begging strategies (the reaction norm of begging for increasing level of food deprivation). Because variations in hunger were reduced, most differences in need between nestlings were likely to reflect long-term factors (i.e. size, growth rate and body condition), and these could be tested in relation to begging behaviour.

Video Analysis

I analysed the first 10 s of each begging trial from the video-recordings. This reflects the normal length of time available for nestlings to attract their parents' attention at the nest. Using movie-editing computer software (Adobe Premier 4.0, for Power Macintosh), the video-recording of each begging trial was sampled on a computer monitor at a rate of two frames/s (20 frames for a 10-s begging trial). A preliminary analysis with a full video-frame rate (30 frames/s) showed that a begging bout always exceeded 0.5 s. A sampling rate of two frames/s is therefore sufficiently informative for analysing nestling body postures during a begging trial. I ranked nestling posture from 0 to 3: 0, no gaping; 1, gaping; 2, gaping with neck stretched; 3, gaping with neck stretched, standing up (see Redondo & Castro 1992; Kacelnik et al. 1995; Kilner 1995, for similar methodology). This ranking method assumes that body posture while begging represents an escalation in extension and orientation of the body towards the food source and that it is therefore one of the major aspects of begging intensity. The coding of body postures to 0, 1, 2 and 3 implies that these values are arbitrary points

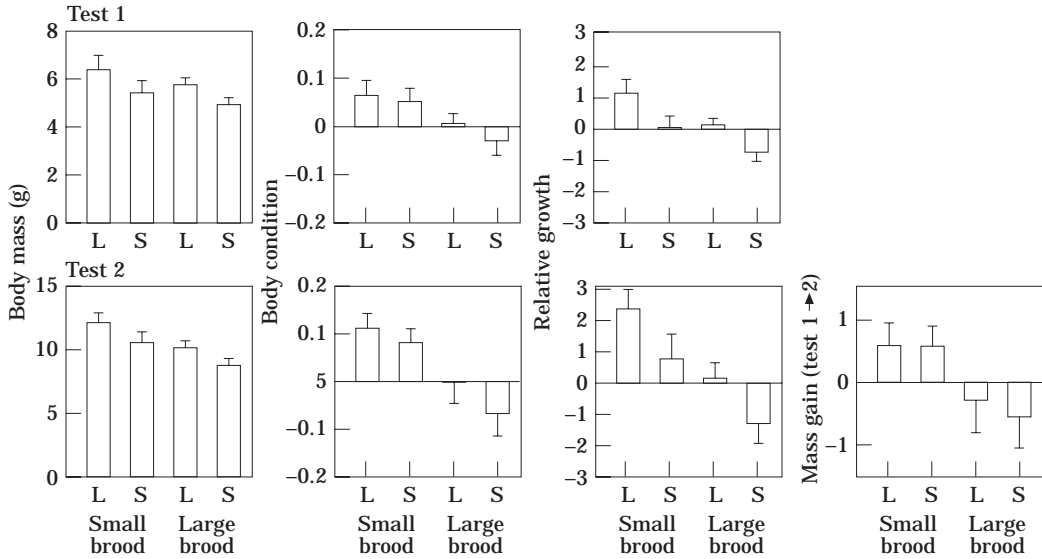


Figure 1. Long-term determinants of need of large (L) and small (S) nestlings from small and large broods in tests 1 (at 3–6 days of age) and 2 (3 days later). ($\bar{X} \pm \text{SE}$; $N=12$, for each nestling category.) See text for details of how body condition, relative growth and mass gain were calculated.

along a continuum of begging postures, which represent increasing ranks of begging intensities (see Sokal & Rohlf 1981, pp. 12–13). Previous studies that used this method (see references above) suggest that its assumptions were valid because body posture was correlated with hunger level, with parental response to begging, and with other begging parameters (the same results were also found in this study population; unpublished data). To score begging postures from the video-screen in an unbiased manner, a student (M. Strauss) assigned scores for each of the four nestlings in each of the 20 frames of a begging trial. The student could not tell which nestlings on the screen were from large or small broods (matching between colour marks and nestling identity was done at a later stage of the analysis). A nestling ‘begging intensity’ score in each begging trial was determined as the average of the begging posture scores recorded in the 20 sampled frames.

Data Analysis

Because the experimental design was focused on finding relative differences within test groups, it was crucial that all nestlings in a test group survive throughout the experiments. As a result of nest failures and cases of brood reduction, only 12

test groups could be used for the analysis of tests 1 and 2, and only 10 test groups could be used for the analysis of test 3. I used two-way ANOVA without replications blocked by ‘test group’ for analysing parameters of need, and non-parametric statistics for testing differences in begging behaviour. All statistical tests are two-tailed.

RESULTS

Long-term Determinants of Need

The experimental brood manipulation created significant differences in growth rate and body condition among nestling categories (Fig. 1, Table I). As expected, small nestlings and nestlings in experimentally enlarged broods had lower body condition scores, and lower relative growth scores, in comparison with their larger brood-mates and with the nestlings from the small broods. These differences became even more pronounced in test 2, suggesting that they continued to increase as nestlings grew. The differences in the mass gain index calculated for the time between tests 1 and 2 also suggest that nestlings in enlarged broods grew at a slower rate relative to those in the reduced broods (Fig. 1, Table I). The 12 pairs of small and large broods used for the analysis included 12

Table I. Results of ANOVA models for data on long-term determinants of nestling need in tests 1 and 2 (see Fig. 1)

Measurement	Differences between groups		Differences between nestling categories (within a group)	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Body mass				
Test 1	8.934	<0.001	5.260	0.002
Test 2	14.810	<0.001	14.190	<0.001
Body condition				
Test 1	9.736	<0.001	6.009	0.002
Test 2	3.980	0.001	8.068	<0.001
Relative growth				
Test 1	3.270	0.004	8.359	<0.001
Test 2	5.891	<0.001	12.801	<0.001
Mass gain index (Test 1 – test 2)	3.940	0.001	3.105	0.040

All models are two-way ANOVA without replication, testing for differences between groups ($df=11$) and between nestling categories within a group ($df=3$) over the error term of the model ($df=33$). The data include 12 test groups of four nestlings each ($N=48$).

small broods of three nestlings each, and 12 large broods of five ($N=4$), six ($N=7$) and seven ($N=1$) nestlings each. The average ranks (body mass rank within the brood) of the four different categories of target nestlings, large and small of a small brood, and large and small of a large brood, were 1.92, 2.92, 3.42 and 4.67, respectively.

Differences in Begging Behaviour

Figure 2 shows the average begging intensity of the four categories of target nestlings in each begging trial in tests 1 and 2. Begging intensity before feeding (trial 0) did not differ significantly between nestling categories (Friedman tests: test 1, $\chi^2_3=2.125$, $P=0.55$; test 2, $\chi^2_3=4.575$, $P=0.21$). Begging intensity data of all after-feeding trials (trials 1–9) were first analysed to test for differences between the nine repeated measurements of begging ($N=48$ nestlings). These differences were highly significant in both tests 1 and 2 (Friedman tests: test 1, $\chi^2_8=62.2$, $P<0.001$; test 2, $\chi^2_8=68.5$, $P<0.001$). The sum ranks of the different begging trials was positively and significantly correlated with the chronological order of begging trials (Spearman correlation coefficient: test 1, $r=0.950$, $P<0.001$; test 2, $r=0.967$, $P<0.001$), suggesting that begging increases with time after feeding (Fig. 2). There was also a significant agreement

among nestling categories in the rank order of begging trials according to begging intensity (Kendall coefficient of concordance between the sum ranks of the four nestling categories: test 1, $W=0.67$, $\chi^2_8=21.5$, $P=0.006$; test 2, $W=0.84$, $\chi^2_8=26.9$, $P=0.001$).

To analyse differences between nestling categories (within test groups), I ranked nestling begging intensity in each begging trial from 1 (lowest) to 4 (highest), and calculated the average rank of the nine after-feeding trials (trials 1–9) for each nestling. This parameter characterizes the begging strategy of a nestling over a wide range of states of hunger. Figure 3 shows average begging ranks of the four nestling categories in tests 1 and 2. The data on long-term determinants of need (Fig. 1, Table I) suggest that nestling need increases from the left end category in the figure, to the right one (i.e. large nestlings from small brood < small nestlings from small brood < large nestlings from large brood < small nestlings from large brood). The hypothesis that begging increases with long-term need therefore predicts that begging levels will follow this order and increase from left to right. As expected, the average begging ranks were positively correlated with this order, indicating an overall increase in begging with long-term need (Spearman correlation coefficient: test 1, $r=0.296$, $N=48$, $P<0.05$; test 2, $r=0.3$, $N=48$, $P<0.05$).

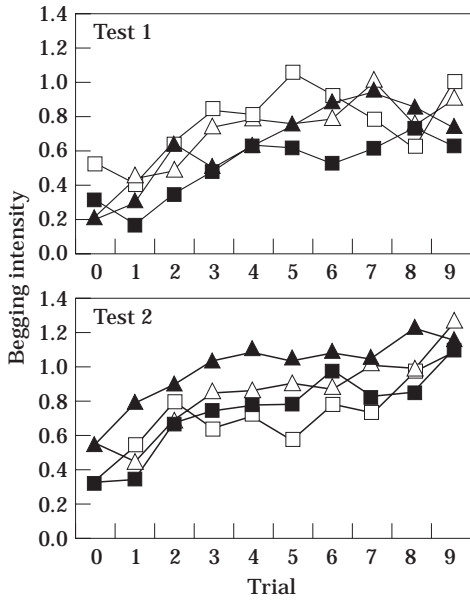


Figure 2. Average begging intensity of four nestling categories in 10 consecutive begging trials of tests 1 and 2 (■: large nestling from small brood; □: small nestling from small brood; ▲: large nestling from large brood; △: small nestling from large brood. $N=12$ for each nestling category).

In test 2, however, differences in average begging ranks within broods were inconsistent with the overall trend, and this weakened the correlation between begging and long-term need. A matched-pair test of nestlings from different broods (small from small broods versus small from large broods, and large from small broods versus large from large broods) indicated a marked increase in begging with need (Fig. 3; Wilcoxon signed-ranks test: $Z=2.679$, $N=24$, $P=0.007$). On the other hand, a similar test between small and large nestlings within broods indicates the opposite trend (Fig. 3; Wilcoxon signed-ranks test: $Z=2.115$, $N=24$, $P=0.034$). This latter effect was mainly because small nestlings from large broods (the neediest nestling category) begged less than their larger brood-mates in most cases (10 out of 12).

Effect of Nestling Exchange Between Broods

Figure 4 and Table II summarize the data of long-term determinants of nestling need and of their average begging rank in test 3 (i.e. after the

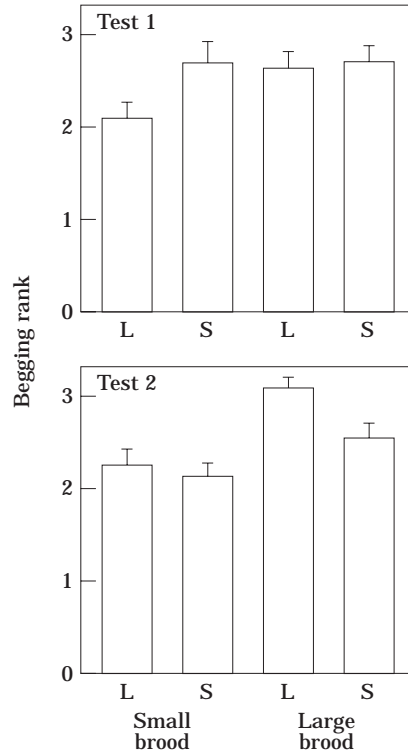


Figure 3. Average begging ranks of large (L) and small (S) nestlings from small and large broods in tests 1 and 2 ($\bar{X} \pm SE$; $N=12$, for each nestling category).

nestling exchange). The data suggest that small nestlings from large broods that were introduced for 24 h into small broods were able to enjoy the favourable conditions in the small broods. They had a similar mass gain index to that of the large target nestlings of those broods, and a higher mass gain index than that of the nestlings that were in large broods during the same period (Fig. 4, Table II). The body condition of small nestlings from large broods appeared to improve compared with their original nestmates which remained in the large broods (compare Figs 1 and 4). However, their long-term need remained relatively high as indicated by both body condition and relative growth. The begging behaviour of the exchanged nestlings appeared to be affected by the new environment. The average begging ranks of small nestlings from small broods increased relative to that of small nestlings from large broods, although not significantly so (compare Figs 3 and 4; the average begging rank of the former was

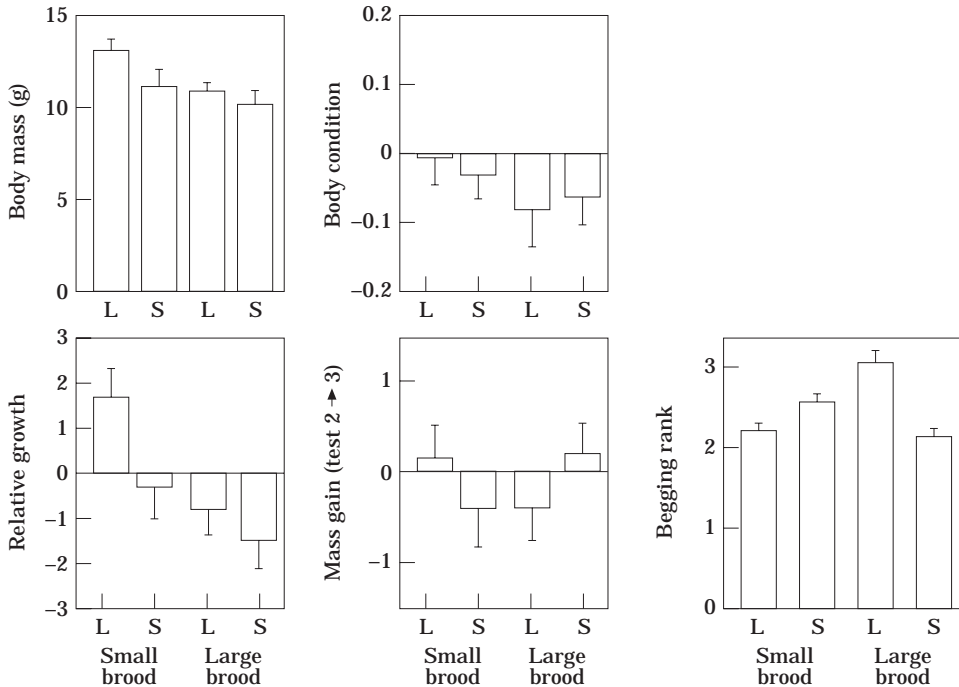


Figure 4. Long-term determinants of need, and average begging ranks, of large (L) and small (S) nestlings from small and large broods in test 3, after small nestlings from small broods were transferred to large broods and small nestlings from large broods were transferred to small broods for 24 h. Nestlings are shown in the broods they were in before the nestling exchange (as in Figs 1 and 3). ($\bar{X} \pm \text{SE}$; $N=10$ for each nestling category.)

greater than that of the latter in 3 out of 10 in test 2, versus 7 out of 10 in test 3; $G_{\text{adi},1}=3.06$, $P<0.1$). As before the nestling exchange, small nestlings from large broods still begged less than their original larger brood-mates from the larger broods, although not significantly so (Fig. 4; Wilcoxon signed-ranks test: $Z=1.837$, $N=10$, $P=0.066$).

DISCUSSION

The results of this study suggest that nestling begging increases with both short- and long-term need. However, the relationship between begging and long-term need does not appear to be simple. As in previous studies, begging intensity was strongly affected by short-term variations in nestling need (i.e. begging increased with time after feeding). I tested the effect of long-term need by using the average begging rank of a nestling in nine after-feeding trials in the laboratory, thus

controlling for short-term variations in hunger. This analysis suggests that begging increases with long-term need, as suggested by Price et al. (1996). However, the correlation was not very strong. One explanation is that given the sample size used, and the magnitude of the differences in long-term need, random variations in begging behaviour can easily weaken the correlation. Alternatively, some of the variations in begging behaviour that were not correlated with long-term need were not random, but were related to other factors. This latter possibility may provide a better explanation of the results of test 2, where, despite marked differences in long-term need, begging behaviour within broods differed significantly in the opposite direction.

As mentioned earlier, the lower begging levels of small nestlings in test 2 were mainly because small nestlings from large broods (the neediest nestling category) begged less than their larger brood-mates (Fig. 3). These differences were also indicated in test 3 (Fig. 4) and, in my opinion,

Table II. Results of ANOVA models for data on long-term determinants of nestling need in test 3 (after nestling exchange, see Fig. 4)

Measurement	Differences between groups		Differences between nestling categories (within a group)	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Body mass	12.185	<0.001	9.724	<0.001
Body condition	4.883	0.001	1.211	0.325
Relative growth	4.510	0.001	8.314	<0.001
Mass gain index (test 2 – test 3)	10.688	<0.001	2.425	0.087

All models are two-way ANOVA without replication, testing for differences between groups ($df=9$) and between nestling categories within a group ($df=3$) over the error term of the model ($df=27$). The data include 10 test groups of four nestlings each ($N=40$).

should not be dismissed as a random deviation from the general trend. Alternatively, there are several possible reasons why begging levels dropped in the neediest nestling category.

(1) Differences in the cost of begging. Despite being in greater need, small nestlings may beg less than their larger brood-mates if begging is more costly for them (Parker et al. 1989; Godfray 1991, 1995b). One simple version of this idea is that small nestlings from large broods are too weak, or do not have the energy to beg strongly. This possibility is not supported, however, by the results of test 3. After the nestling exchange, small nestlings from large broods improved their body condition and mass gain (Fig. 4), and should have been physiologically stronger. However, they did not increase begging despite still being undersized relative to the other nestlings. Instead, they appeared to decrease begging as if their recovery reduced their needs. It is possible, though, that these nestlings were able to beg more strongly but did not do so because it was more important for them to conserve their energy for faster growth. In this respect, it can be suggested that they beg less than their larger brood-mates because begging is more costly for them.

(2) Differences in the effectiveness of begging. In theory, nestlings are expected to adjust their begging strategies not only according to their need, but also according to the effectiveness of their begging (Parker et al. 1989; Godfray 1995b). Several studies suggest that for an equal level of begging, large nestlings are more likely to gain food than small nestlings (Kacelnik et al. 1995; Kilner 1995; Price & Ydenberg 1995). Accordingly, a small nestling in great need may beg less

than its larger brood-mates if it is constantly being pushed aside, and thus gains nothing by begging at higher intensities. Such a nestling may be better off by begging only at moderate levels (possibly to encourage the parents to make more feeding trips) and by waiting for those occasional parental visits when its larger brood-mates are satiated.

(3) Learning. At the proximate level, learning mechanisms in begging behaviour (Stamps et al. 1989) may cause small nestlings in great need to stop, or to reduce begging if they receive very little reward for their begging efforts. The experimental results can thus be explained by a situation in which large nestlings from large broods learned that intensive begging helps them to get food, while their smaller brood-mates, on the other hand, failed to compete for food despite their begging, and were not encouraged to increase begging.

(4) Undersized nestlings may not be in the greatest need. The long-term determinants of need measured in this study may not represent correctly the term 'need' as described by Godfray (1991, 1995b); that is, the marginal benefit from obtaining extra food (i.e. 'need' sensu Godfray) may not always be higher for undersized nestlings or for nestlings in poor body condition. Although such nestlings must grow faster in order to reach a target mass by the end of the nesting period (Price et al. 1996), their ability to use the food for faster growth may be limited. Furthermore, if their chances of survival become very small, they may gain higher inclusive fitness by reducing begging in favour of their larger siblings.

Considering the possible role of the factors discussed above, the observed correlation between

begging and long-term need should be viewed with some caution. One cannot exclude the possibility that differences in begging between nestling categories were caused, in whole or in part, by factors that coincide with long-term need, rather than by long-term need per se. In theory, differences in the effectiveness of begging can cause small nestlings to beg more than their larger brood-mates (Parker et al. 1989), and small nestlings may simply learn to beg more in order to be fed.

In conclusion, my results suggest that although nestling begging strategies vary with brood size and with nestling rank, the observed relationship may reflect a combination of several factors. The hypothesis that nestling begging is an honest signal of need is therefore not easy to test (see also Kilner & Johnstone 1997). If nestlings adjust their costly begging efforts in relation to several factors, begging will not be correlated with each of them separately but with a combination of all of them. The extent to which this combination is the message conveyed by begging, and the information sought by the parents, is yet to be studied.

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