

HIGHER LEVELS OF BEGGING BEHAVIOR BY SMALL NESTLINGS: A CASE OF A NEGATIVELY CORRELATED HANDICAP

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ABSTRACT

Recent theoretical models of parent–offspring conflict suggest that costly solicitation by offspring reflects offspring need in a reliable manner, and that parents are, therefore, selected to increase parental effort in response to offspring solicitation. However, theory and experiments suggest that parents pay attention not only to their nestlings' needs, but also to their relative quality as reflected by size and competitive ability. A study on barn swallow nestlings, described here, investigates how such complex feeding rules affect nestling begging strategies, and how different begging strategies affect the nestlings' relative success. Begging strategies were compared for large and small brood mates, assumed to represent high and low nestling qualities, respectively. The results indicate that small nestlings tend to beg at greater intensities than large nestlings for a similar level of food deprivation. A higher intensity of begging does not, however, guarantee greater success for smaller nestlings because mass gain by nestlings is affected by both size and begging differences among the competing nestlings. I suggest that higher levels of begging by small nestlings are caused by differences in the expected benefit for a given level of begging, and create a negative correlation between the optimal level of signaling and the signaler's quality. This contrasts with the typical handicap case discussed in the literature, in which differences among individuals in the cost of signaling create a positive correlation between the optimal level of signaling and the signaler's quality. This study suggests that "negatively correlated handicaps" may emerge whenever receivers integrate cryptic information about the signaler's momentary need or motivation, based on one signal, and non-cryptic information about the signaler's quality based on other cues.

INTRODUCTION

The begging behavior of bird nestlings provides an excellent model for studying parent–offspring conflict and communication (Mock and Forbes, 1992; Godfray, 1995a; Kilner and Johnstone, 1997). Parent–offspring conflict theory (Trivers, 1974) suggests that

nestlings can be selected to demand more food than parents are selected to provide. Intensive begging activity has, therefore, been regarded as a "psychological manipulation" aimed at shifting the parents' behavior from the parental optimum of food allocation toward the offspring optimum. An alternative resolution for parent-offspring conflict has emerged recently from new advances in the theory of biological signaling. Models of the handicap principle for the evolution of signals predict that, at equilibrium, signals will be honest because the cost of the signal to a potential cheater will be greater than to an honest signaler, to an extent that makes cheating maladaptive (Zahavi, 1975; 1987; Nur and Hasson, 1984; Grafen, 1990). Using this approach, Godfray (1991, 1995b) has shown that the level of offspring solicitation should be a true reflection of offspring need (defined as the benefit to the nestling from obtaining extra resources) as long as solicitation is costly to produce, and that the benefit from obtaining more resources increases with diminishing returns. Under these conditions, parents will be selected, rather than manipulated, to provide more food in response to higher degrees of begging.

Godfray's prediction that begging intensity reflects the nestlings' true need is generally supported by an observed positive correlation between begging intensity and the length of time of food deprivation (Haartman, 1953; Behgsson and Ryden, 1983; Smith and Montgomerie, 1991; Redondo and Castro, 1992; Cotton et al., 1996). However, several lines of evidence suggest that begging behavior may be much more complicated than a simple signal of need [see also Godfray's (1995b) model of two nestlings that differ in more than one respect]. Although begging stimulates parents to increase the rate of food delivery, or to prefer one nestling over the other (Muller and Smith, 1978; Bengtsson and Ryden, 1983; Stamps et al., 1989; Smith and Montgomerie, 1991; Redondo and Castro, 1992; Kacelnik et al., 1995), intense begging does not always guarantee parental attention. A nestling's probability of being fed is also affected by its ability to compete for a favorable position in the nest (Ryden and Bengtsson, 1980; Gottlander, 1987; McRae et al., 1993; Kacelnik et al., 1995; Kilner, 1995), and as a general rule, parents seem to prefer large nestlings over small ones (Kilner, 1995; Price and Ydenberg, 1995). This preference makes adaptive sense because under a wide range of conditions larger nestlings promise a greater marginal return for the parents' investment (Lack, 1954; O'Connor, 1978; Parker et al., 1989). Hence, parents appear to take into account not only cryptic information on nestling "need", conveyed by nestling begging, but also information on nestling "quality" as reflected by size and competitive ability.

The term "quality" will be used here to describe non-cryptic variations in the parents' marginal return from feeding nestlings with a different asymptotic fitness (Haig, 1990). Because parental fitness is a function of offspring fitness, the term quality can also be described as the non-cryptic variations in nestling condition (Godfray, 1995b) multiplied by the coefficient of relatedness between parent and offspring.¹ In short, given a

¹ The term "quality" in signaling models is defined from the perspective of how the response to the signal affects the fitness of the signal's receiver (i.e., the parent, or a female in a sexual

choice between two nestlings at the same level of cryptic condition (i.e., at the same level of "need", which usually means at the same degree of food deprivation²), parents are expected to prefer the one perceived as the higher quality one (the larger, the older, the healthier—or other attribute indicating higher chances of survival). Recent studies suggest that parents may, in fact, integrate both nestling need, (expressed as begging) and quality (expressed by size or competitive ability) in their feeding decision rules (Kacelnik et al., 1995; Kilner, 1995; Price and Ydenberg, 1995). However, it is not clear how such feeding rules affect the nestlings' begging strategy.

In the present study, begging strategies of barn swallow, *Hirundo rustica*, nestlings were compared for large and small brood mates, assumed to represent, respectively, high and low qualities (from the parents' perspective). Begging strategies were determined by removing a pair of nestlings from the nest for a laboratory behavioral test in which begging response to an artificial stimulus was measured over a wide range of hunger states. The relative growth and body condition of the two nestlings were measured over time intervals between and after the behavioral tests to assess the effect of size and begging strategy on the nestlings' relative success.

METHODS

THE STUDY ANIMAL

During June and July 1993, barn swallow nestlings were studied from 11 nests located in the south campus of the University of British Columbia, Vancouver, Canada. The nests contained five ($n = 6$), four ($n = 3$), three ($n = 1$), and two ($n = 1$) nestlings. Brood reduction during the study period occurred in two nests (of 5 and 4 nestlings) in which the smallest chick disappeared. The temporary removal of nestlings from their nests for periods of up to 2.5 h did not cause nest desertion, and parents continued to care for returned nestlings. Nestlings were marked on one wing with nontoxic acrylic paint.

BEHAVIORAL TESTS

Begging strategies were compared between small and large brood mates by a paired design behavioral test in the laboratory. Brood mates were assigned to pairs randomly,

selection model). The term "need", on the other hand, is defined from the perspective of how the response to the signal affects the fitness of the signaler (i.e., the nestling). Parent-offspring communication presents a special case where the receiver's fitness is a function of the signaler's fitness, and therefore need and quality are interrelated. I choose to describe non-cryptic variations in nestling condition (size and competitive ability) from the parent's perspective (i.e., by the term "quality", as in Haig [1990]) because these variations are perceived directly by the parents. I use the term "need" to describe cryptic variations in condition (as in Godfray, 1991) as these are signaled by the nestling based on their effect on the nestling fitness.

² I do not deal here with the concept of "long-term" need (Price et al., 1996), which presents an alternative theoretical framework that will be considered in the discussion.

and were classified as "small" or "large" based on their initial mass differences (mean mass difference \pm standard deviation within a pair in the first test was $2.026 \text{ g} \pm 1.342 \text{ g}$). Each pair of nestlings was first tested at the age of 3–5 days ($n = 20$ pairs), and a second test was conducted three days later at the same time of day ($n = 18$ pairs; 2 pairs were lost as a result of brood reduction—see above). Barn swallow nestlings at this age (3–8 days) have little fear of approaching objects and tend to beg toward them. For each test, the two nestlings were transferred from the nest to an artificial nest which was placed in a controlled-temperature room (26°C). The nest was divided into two sections to control nestling position and jostling, and its floor was heated to 35°C . Nestlings were stimulated to beg by momentarily shading them—waving a piece of cardboard over their heads—and simultaneously producing a human high-pitched sound mimicking a parent swallow call. Nestlings begged vigorously in response to these stimuli, as they normally do toward an approaching parent. Each begging trial was recorded by a video camera. The first trial (trial 0) was conducted 10 minutes after the nestlings were introduced into the artificial nest. Shortly afterwards each nestling was fed with a semiliquid 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 measurement of the amount of food received by each nestling. After feeding, the nestlings were stimulated to beg at 10-minute intervals for nine consecutive begging trials during which they were not fed (trials 1–9). Nestlings were returned to their nests after the ninth begging trial. This procedure was designed to reduce momentary variations in need between the two nestlings, allowing a comparison between their begging strategies (the reaction norm of begging for increasing level of need). A nestling at satiation is assumed here to reflect a momentary state of "no need", not because it does not require more food, but because it cannot utilize extra resources due to the limitations of its digestive system. This method does not control for differences in long-term need (Price et al., 1996) which may be determined by relative size and body condition. The extent to which long-term need might have affected the results of these experiments will be discussed later in this paper.

MEASURING BEGGING BEHAVIOR

The first 10 seconds of each begging trial were analyzed from the video recordings. This length of time reflects the normal length of time available for nestlings to attract their parents' attention at the nest. Nestling posture was ranked from 0 to 3; 0, no gaping; 1, gaping; 2, gaping with neck stretched; 3, gaping with neck stretched standing up (see Redondo and Castro, 1992; Kacelnik et al., 1995; Kilner, 1995, for a similar methodology). This ranking method assumes that these different begging postures represent an escalation in extension and orientation of the body toward the food source, and that they therefore constitute a major criterion for determining begging intensity. The coding of body postures from 0 to 3 implies that these values are arbitrary points along a continuum of begging postures representing increasing ranks of begging intensities (see Sokal and Rohlf, 1981: 12–13). Previous studies that used this method suggest that its assumptions are valid because body posture was correlated with the level of food deprivation, with parental response to begging, and with other begging parameters.

Each nestling was measured for (1) *begging posture*: average posture while begging (i.e., when posture > 0), (2) *duration*: time spent begging during the trial, (3) *use of voice*: proportion of begging duration accompanied by vocalization, and (4) *latency*: time to first begging response. Because begging behavior is a combination of postures and vocalizations displayed over time, nestlings could apply different combinations of begging parameters to obtain similar levels of overall begging intensity. In such a case, a composed index of begging behavior may provide a better approximation of begging behavior than each of the begging parameters alone. Two begging indices (a priori designed) were therefore calculated and analyzed. The first index, overall posture, was calculated as: *begging posture* \times *duration*, thus adding a time dimension to begging posture. This index is mathematically equivalent to the average posture during the first 10 seconds of a trial, including posture 0. The second index was of *overall intensity* and was given by: *begging posture* \times *duration* + *use of voice* \times *duration*. In this index, posture and use of voice were weighted subjectively, giving 75% weight to posture and 25% to use of voice, because the maximum possible score of posture and use of voice was 30 and 10, respectively. There is no guarantee that these indices reflect the way parents integrate posture, duration, and vocalization when responding to nestling begging. However, the use of both indices in testing the effect of begging on nestling success gave significant results, suggesting that they are biologically meaningful. I also examined the data by using the factor scores of begging which resulted from a principal component analysis of the average posture, duration, and use of voice of a nestling in the nine after-feeding trials of tests 1 and 2. These factor scores may be considered more objective because the relative weight of each begging parameter is derived from the data itself (although it does not imply that such a "black box" index is more correct). The factor scores of begging were correlated with the overall intensity index, more than with any begging parameter alone ($r = 0.967$ versus $r = 0.887, 0.852, 0.798, -0.857$ for posture, duration, use of voice, and latency, respectively; $N = 72, p < 0.001$ in all cases), and the analysis gave similar results.

MEASURING NESTLING RELATIVE SUCCESS

The number of feedings received by each nestling can demonstrate the effect of begging on nestling success (e.g., Smith and Montgomerie, 1991; Kacelnik et al., 1995). However, this parameter could be biased if load sizes given to small and large nestlings differ (a problem difficult to solve in swallows because their load size is hard to observe). A second problem with using the number of feedings as the benefit currency for begging strategies is that although a strategy of intense begging may increase the feeding rate, it may not result in a greater net benefit if begging itself is very costly. In the present study therefore measurements of mass gain and nestling condition were employed, both known to be correlated with nestling survival in other altricial birds (Hochachka and Smith, 1991; Magrath, 1991), and are likely to reflect the net results of the overall begging activity of a nestling.

Nestlings were weighed, using a pocket scale to 0.5 g precision, and their right wing length was measured to the nearest 0.1 mm. Measurements were taken prior to the first

and second test, and 24 h after the second test (two repeated measurements were taken each time and their average value was used as a single data point). Gain in mass over time is perhaps the most important measurement of nestling success. However, comparing the mass gain (g per day) of small versus large nestlings is complicated by the fact that the growth curve of nestlings is not linear and therefore at some stages the two types of nestlings are expected to grow at different rates. To overcome this problem, the actual mass gain of each nestling should be expressed relative to the expected mass gain of a nestling of that size. The expected mass gain of a nestling of a certain size for each time interval (between tests 1 and 2, and during the 24 h after test 2) was obtained by regressing the mass at test 2 over the mass at test 1, and the mass 24 h after test 2 over the mass at test 2 (using stepwise polynomial regression). A mass gain index was then taken as the residuals from these equation lines [(mass 2) = 1.826 (mass 1) - 0.048 (mass 1)² + 2.818, $r = 0.912$, $n = 38$; (mass 3) = 0.958 (mass 2) + 2.444, $r = 0.968$, $n = 35$]. Note that this method controls for differences in mass gain due to differences in initial size. These are likely to originate from age differences as well as from differences in the nestlings' past history. The mass gain index was based on initial size rather than on age per se because even when precise hatching dates were known, initial size at time A was a much better predictor of mass at time B than nestling age ($r = 0.811$, $n = 64$ versus $r = 0.448$, $n = 64$, respectively). A condition index (Hochachka and Smith, 1991) was calculated as the residual from a quadratic regression line of $\ln(\text{mass})$ over $\ln(\text{wing length})$ fitted through the data points of all three measurements (tests 1 and 2, and 24 h after test 2) of the smaller nestling in a pair [$\ln(\text{mass}) = 2.906 (\ln \text{wing length}) - 3.382$; $r = 0.976$; $n = 38$].

STATISTICS

Data were analyzed using parametric or nonparametric statistics when the underlying distribution was normal or not normal, respectively. All statistical tests are two-tailed. Curve fits for condition and mass gain indexes (see above) were based on a stepwise polynomial regression. Although nine of the nests under study provided two pairs of nestlings each, all pairs were treated as independent. This assumption of independence seems valid because only within-pair differences were tested, and these were not correlated between two pairs taken from the same nests.

RESULTS

BEGGING STRATEGIES

Figure 1 shows the average begging measurement of small and large pair mates in each begging trial of test 1 and 2. Before nestlings were fed (trial 0), small nestlings begged at higher levels than large nestlings and had shorter latency to begging (Wilcoxon sign rank tests: $p < 0.05$, for all begging measurements except for use of voice in test 1). Small nestlings were also fed more than their larger pair mates in order to reach satiation (amount of food in ml, mean \pm sd: 0.092 ± 0.104 versus 0.057 ± 0.075

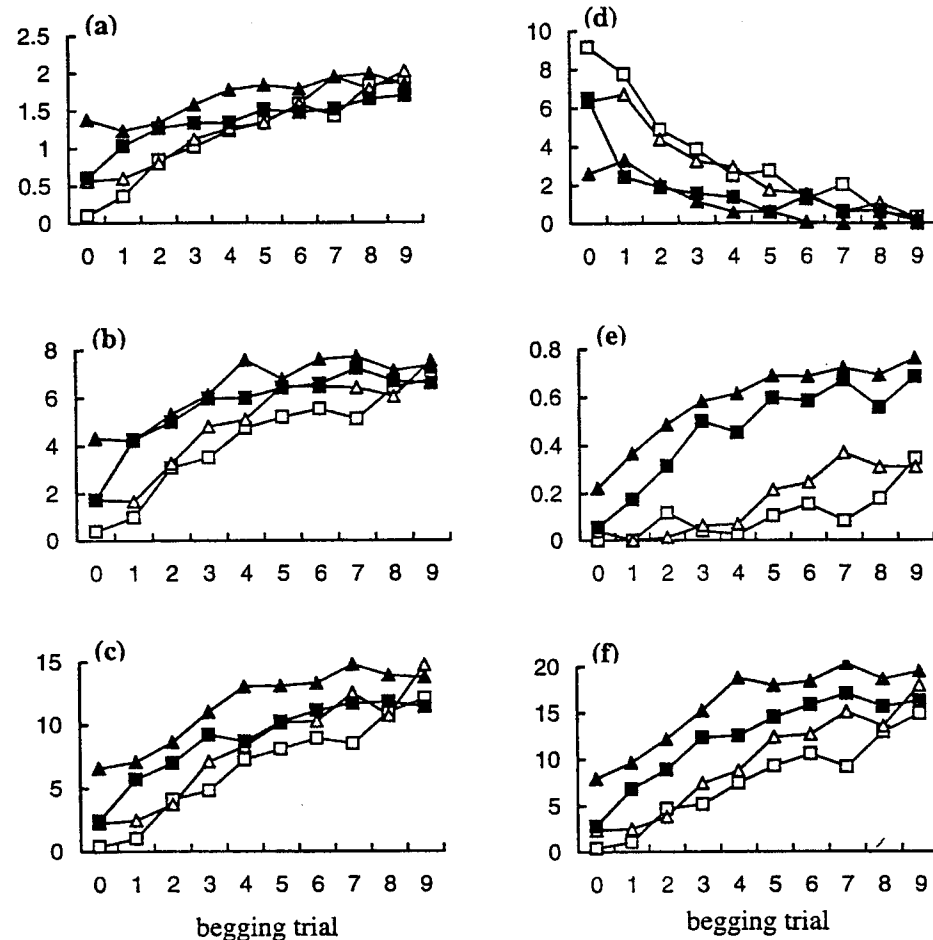


Fig. 1. The average begging measurements of small (triangles) and large (squares) pair mates in each begging trial of test 1 (open symbols, $n = 20$ pairs) and test 2 (filled symbols, $n = 18$ pairs). (a) begging posture; (b) duration; (c) overall posture; (d) latency; (e) use of voice; (f) overall intensity.

in test 1, and 0.286 ± 0.257 versus 0.169 ± 0.211 in test 2; Wilcoxon sign rank tests: $p < 0.05$ in both tests). As time passed after feeding (trials 1-9), latency to begging decreased and all other begging measurements increased (Fig. 1, Spearman rank correlations on the average values of each trial: $r > 0.7$, $p < 0.05$, $n = 9$, for all cases, negative correlation in the case of latency). The rate of increase in begging appears similar for small and large nestlings, suggesting that there is no difference in the slope of their reaction norms of begging for increasing levels of need (differences in begging measurements between large and small nestlings did not increase or decrease significantly with the sequence of begging trials: $r < 0.7$, $p > 0.05$ for all cases). However, on the average,

small nestlings begged more than large nestlings for each level of need (see Fig. 1). Because the suspected differences in begging strategies are not due to differences in slopes, for each begging measurement, the average value of all after-feeding trials (trials 1–9) can be used to characterize the begging strategy of a nestling. These average values of the six different begging measurements were calculated for each nestling and are referred to as measurements of typical begging.

The analysis of the different measurements of typical begging is summarized in Table 1. The results suggest that small nestlings tend to beg at higher levels than their larger pair mates also after they are fed to satiation. The difference between small and large nestlings was significant in begging posture, and nearly significant in overall posture, overall intensity, and use of voice in test 2. Although other differences were not significant, they showed the same trend (small nestlings had higher begging measurements in 11 of the 12 comparisons presented in Table 1). An additional analysis of typical begging was based on the factor scores of begging resulting from a principal component analysis of begging measurements (see Methods). This analysis also suggests that small nestlings beg more than large ones (repeated measures ANOVA: begging factor scores in tests 1 and 2 = constant + pair + size, $F_{1,17} = 4.146$, $p = 0.058$, for differences between small and large nestlings within a pair). Two additional pairs in which brood reduction took place could not be included in any of the ANOVA models above, but in both of them the small nestling begged more than the large one. Including these two pairs, and comparing the average overall intensity of all after-feeding trials (average of 18 trials in 18 pairs, and of 9 trials in the two additional pairs), the difference in overall intensity is clearly significant (paired $t = 2.43$, $n = 20$, $p = 0.025$). All measurements of begging, presented in Table 1, showed highly significant differences between the first and second test, suggesting that begging intensity increases as nestlings grow. Therefore, small nestlings which beg slightly more than their larger brood mates, may in fact beg much more relative to their age and size.

To assess whether differences in begging behavior within a pair tended to be consistent over time, nestlings' begging measurements of overall intensity were compared in each pair, for all begging trials conducted after feeding (trials 1–9) in both behavioral tests (18 begging trials total). In 14 of the 18 pairs available for this analysis, begging differences were consistent over time (Wilcoxon sign rank tests, $p < 0.05$). However, although in 10 of these cases the small nestling begged at higher intensities (in accordance with the results presented above), in four cases it was the large nestling that displayed higher begging intensities.

NESTLING RELATIVE SUCCESS

The mass gain index, measured between test 1 and 2, was somewhat lower (but not significantly) for small nestlings than for their larger pair mates (paired $t = 1.963$, $n = 18$, $p = 0.066$), and the mass gain index, measured between test 2 and 24 h later, did not differ for small and large nestlings (paired $t = 0.994$, $n = 18$, $p = 0.334$). Small nestlings may not gain more mass, despite their intensive begging, if the effect of begging behavior is confounded by parents' preference of large nestlings. To analyze the

Table 1
Measurements of "typical begging" (average \pm standard error) of small and large pair mates in the first and second tests, and statistical differences between tests (test 1 and test 2) and between small and large nestlings within a pair (S and L)

Begging measurement	test 1 *			test 2			test 1 – test 2		S – L	
	small	large		small	large		F^b	P	F^b	P
Begging posture	1.327 \pm 0.095	1.201 \pm 0.1		1.699 \pm 0.188	1.427 \pm 0.107		20.42	<0.001	5.46	0.032
Duration	5.103 \pm 0.547	4.526 \pm 0.568		6.625 \pm 0.416	6.092 \pm 0.504		42.31	<0.001	1.48	0.240
Overall posture	7.467 \pm 1.101	6.007 \pm 0.898		11.56 \pm 1.166	9.389 \pm 0.969		28.68	<0.001	3.27	0.088
Overall intensity	9.528 \pm 1.115	7.857 \pm 1.071		16.71 \pm 1.562	13.39 \pm 1.403		57.69	<0.001	3.87	0.065
Use of voice	0.126 \pm 0.039	0.099 \pm 0.044		0.622 \pm 0.079	0.507 \pm 0.074		3.62	<0.001	0.78	0.435
Latency	2.676 \pm 0.55	3.109 \pm 0.618		1.167 \pm 0.512	0.881 \pm 0.319		3.38	0.001	1.87	0.062
							2.50	0.012	0.86	0.388
							2.53	0.011	1.16	0.245

* Data of two additional pairs that were not tested in the second experiment (due to brood reduction) are not included. In both of these cases, small nestlings begged at higher intensity than the large ones.

^b Results of repeated measures ANOVA (begging in test 1 and 2 = constant + pair + size) for each begging measurement, 18 pairs (df = 17), two tests (df = 1).

^c Results of Wilcoxon sign rank tests (data are not normally distributed): Differences between tests were tested separately for large and small nestlings, and differences between small and large nestlings were tested separately for the first and the second tests (df = 17).

combined effects of size and begging on mass gain differences, the differential mass gain index of a pair (small–large) was plotted in a regression model against the mass differences within a pair (small–large) and the begging differences within a pair (measurement of typical begging of small – measurement of typical begging of large). The results (Table 2) suggest that both size and begging differences in test 2 had a strong effect on the differences in mass gain during the following 24 h, but that size and begging differences in test 1 had no significant effect on the mass gain differences measured between test 1 and test 2.

In all the three measurements (test 1, test 2, and 24 h after test 2), the smaller nestlings tended to have a lower condition index than their larger pair mates. However, these differences did not reach statistical significance (mean condition index \pm sd: 0.004 \pm 0.118 versus 0.053 (0.070; 0.002 \pm 0.124 versus 0.034 \pm 0.091; -0.015 ± 0.130 versus 0.085 \pm 0.282; paired *t*-tests: $p = 0.084, 0.157, 0.109, n = 20, 18, 17$, respectively). The tendency of small nestlings to beg at higher levels (Table 1) is probably not a direct result of their poorer condition because when pairs were divided into high and low level “beggars” (based on overall intensity), high level beggars did not differ in their condition index from low level beggars (test 1: 0.027 \pm 0.120 versus 0.031 \pm 0.075, $n = 20, p = 0.940$; test 2: 0.014 \pm 0.101 versus 0.022 \pm 0.118; $n = 18, p = 0.721$; paired *t*-tests). Note also that small nestlings did not improve their condition index, as they developed, or

Table 2

The effect of differences in mass and begging on nestlings' mass gain. Regression model: mass gain index difference = constant + mass difference + begging difference; $N = 18$

Begging measurement	Effect of differences in mass and begging in test 1 on the mass gain differences measured between tests 1 and 2					Effect of differences in mass and begging in test 2 on differences in mass gain during the following 24 h						
	mass differences ^a		begging differences ^b		model	mass differences ^a		begging differences ^b		model		
	T	p	T	p	R	T	p	T	p	R	p	
Begging posture	0.945	0.360	0.569	0.578	0.265	0.578	2.632	0.019	2.205	0.043	0.624	0.025
Duration	0.777	0.449	0.301	0.767	0.237	0.649	2.078	0.055	3.217	0.006	0.722	0.004
Overall posture	0.811	0.430	0.446	0.662	0.251	0.615	2.504	0.024	2.779	0.014	0.682	0.009
Overall intensity	0.747	0.467	0.718	0.484	0.286	0.527	2.694	0.017	3.290	0.005	0.728	0.003
Use of voice	0.698	0.496	0.520	0.611	0.259	0.594	1.950	0.070	2.010	0.063	0.602	0.034
Latency	0.900	0.382	0.275	0.787	0.235	0.654	1.422	0.175	-1.015	0.326	0.493	0.124

T—“t statistic”; R—correlation coefficient.

^aIn all cases, mass difference is measured in g (small – large).

^bDifferent measurements of begging were used in each analysis (begging measurement of small – begging measurement of large).

close the gap in condition with their larger pair mates (see above data). There are no indications, therefore, that benefit gained by small nestlings went towards reserves (expressed by condition) rather than for overall growth (expressed by mass gain). Mass gain index was therefore a good measure of differences in benefit between small and large nestlings.

DISCUSSION

The results presented here suggest that a combination of begging behavior and body size determines the relative success of competing nestlings. These relationships were clearly established during the second time interval but not during the first one (see Table 1). A possible explanation for the different results is that when nestlings are young, food demand is relatively low, and parents are able to feed all nestlings so as to meet all their demands. The combined effect of begging and size is consistent with other recent studies (Kacelnik et al., 1995; Kilner, 1995; Price and Ydenberg, 1995) and suggests that large nestlings are likely to receive more resources than their smaller brood mates for the same level of begging.

The results of nestling begging strategies indicate that small nestlings tended to beg at a slightly higher level than their larger sibs in each begging trial. This tendency was most pronounced and significant before the nestlings were fed, suggesting that the higher begging intensity of small nestlings observed in natural nests (e.g., Bengtsson and Ryden, 1983; McGillivray and Levenson, 1986) may be in part due to their being hungrier most of the time. However, the fact that most of the small nestlings continued to beg at higher levels after they were fed (with even larger amounts of food) suggests that they also typically use higher levels of begging for a given level of food deprivation. Because the slopes of increase in begging with time are similar for small and large nestlings (Fig. 1), it is unlikely that small nestlings begged at a higher level simply because they became hungrier more quickly. In such a case, we would expect small nestlings to beg less than the large ones at first (e.g., during trials 1–3) and more than them later.

Although the results reported in this study are statistically not very strong, a tendency of small brood mates to beg at higher intensities has been found in a second study of this swallow population (Lotem, 1998) and in other studies. Recent experiments conducted by Price et al. (1996) also indicate that small nestlings beg more than their larger brood mates for the same level of food deprivation, and a similar trend has been observed in starlings (P. Cotton, personal communication).

Why should small nestling beg more than their larger brood mates when at the same level of need? Signaling models of two chicks that differ in non-cryptic condition (Godfray, 1995b) predict that higher begging levels will be exhibited by the nestling for whom: (1) the cost of begging is lower, (2) the asymptotic fitness is higher, and (3) the maximum attainable condition is higher. All these predictions are more likely to fit the larger nestling in the brood rather than the smaller one.

THE CONCEPT OF LONG-TERM NEED

Price et al. (1996) suggest that even when hunger level is controlled, small nestlings are still in greater need than their larger brood mates because they require a greater amount of food to reach fledging (i.e., they are in greater long-term need). Although this explanation cannot be ruled out, it involves some problems. Theoretically, it is not clear why small nestlings should signal differences in need that are related to size differences if parents can judge size directly and adjust food provisioning accordingly (i.e., why signaling non-cryptic variations). Note that the above-mentioned evidence that parents prefer large nestlings for the same level of begging suggests that parents are able to judge size independent of begging (also see Table 1). It is hard to understand, therefore, how costly begging that signals variations in size already known to the parents can benefit the parents, and why it should have evolved (M. Rodriguez-Girones, personal communication). At the empirical level, it is not clear that nestlings in great long-term need always beg more. In this study, nestlings that begged more than their pair mates were not in poorer body condition (see Results) and, as mentioned earlier, in four cases it was the larger nestling of a pair that begged at a consistently higher level than its sibling. Such cases of the opposite trend featured frequently in another study (Lotem, 1998) when small nestlings in experimentally enlarged broods begged less than their larger brood mates (see Lotem 1998, for discussion).

DIFFERENTIAL BENEFIT CURVES AND NEGATIVELY CORRELATED HANDICAPS

Current ESS signaling models fail to predict higher levels of begging by small nestlings possibly because they do not account for complexities such as dynamic interaction in parent-offspring communication. Until more realistic ESS models are available, I will try to use a simpler approach which hopefully can lead to further advances.

Our aim is to investigate how non-cryptic variations in nestling quality (i.e., size and competitive ability) affect the level of begging for a given level of need. Most handicap-type models are based on the idea that individuals of different quality differ in the cost of signaling (Zahavi, 1975; Nur and Hasson, 1984; Grafen, 1990). Accordingly, high-quality nestlings will beg at higher intensities for a given level of need because begging is less costly for them to produce. This "differential cost" factor creates the positive correlation between signaler quality and signaling intensity, typical for most handicap models. However, individuals of different quality may also differ in the benefit they gain by signaling as a result of differences in their degree of attractiveness, which can be perceived directly by the receiver (Reynolds, 1993). In such a case, Reynolds (1993) has shown that the optimal level of courtship display might be lower for the more attractive (large) individuals, thus creating a negative correlation between signaler quality and signaling intensity. Applying Reynolds' idea to nestling begging behavior may suggest that larger nestlings, which are more attractive to their parents, should beg less than their smaller brood mates. In such a case, begging intensity will be negatively correlated with a nestling's quality (hereafter: "negatively correlated handicaps" as opposed to "positively correlated handicaps"). It should be noted that the idea that greater begging

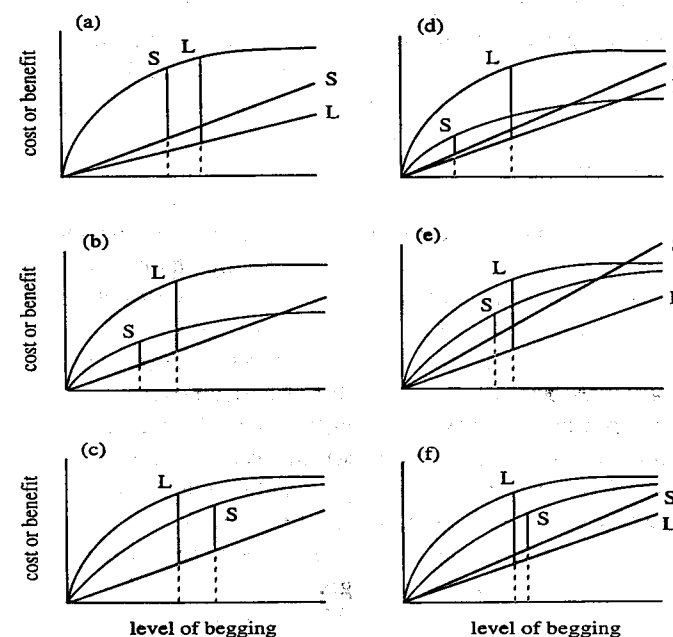


Fig. 2. Optimal levels of begging for large (L) and small (S) nestlings obtained by maximizing the vertical distance between the benefit and the cost curves of signaling behavior (i.e., maximizing the net benefit of signaling in a simple additive model). All benefit curves are convex, assuming diminishing return, and all cost curves are illustrated as linear: (a) differential cost and equal benefit (a traditional handicap model): large individuals can "afford" to beg at higher levels because begging is less costly for them; (b) differential benefit and equal cost: large nestlings benefit more than small nestlings for a given level of begging; (c) similar to "b" but in this case the benefit curves of the two nestlings reach an asymptote at about the same benefit level, creating a "negatively correlated handicap"; (d) begging is more costly and also less beneficial for small nestlings causing their optimal level of begging to be much lower than that of large nestlings; (e) differential benefit and similar benefit asymptotes (as in Fig. 1c) push toward lower begging levels of large nestlings but the differential cost effect which is much stronger keeps the begging levels of small nestlings lower than that of large nestlings; (f) similar to "e" but in this case the differential benefit effect is stronger, creating a negatively correlated handicap (see text for more details).

effectiveness may cause large nestlings to beg less than their smaller sibs has been suggested independently, and even before handicap type models were applied to the study of parent-offspring communication (see Parker et al., 1989).

A simple graphic model (Fig. 2) is used to illustrate how begging strategies of small and large brood mates may be affected by the differential cost and benefit of their begging behavior (an important simplification is that benefit curves are given as a constraint, rather than as a result of the evolving parental response in an ESS model).

Each figure (a–f) represents the optimal begging level for small and large nestlings at an equal level of need. Only a single state of need is illustrated, but the same picture should recur at different levels of need, whether the optimal begging level of both nestlings is lower (if need is low) or higher (if need is high). A second simplification in the model is that an overall cost of begging is illustrated without making a distinction between the direct and the indirect component of the cost of begging (see Godfray, 1991). Because nestlings are genetically related, differences in the benefit of begging and in nestling quality may lead to differences in the indirect cost of begging, and therefore in the overall cost of begging. However, this interaction would not change the qualitative predictions described here, which merely summarize the range of possible outcomes of facing different combinations of cost and benefit curves.

The traditional handicap model (Fig. 2a) predicts that large (high quality) nestlings will beg at higher levels because they pay a lower cost for a begging effort (see also Lotem, 1993, and Johnstone, 1997, for a similar graphic illustration). The differential benefit model (Figs. 2b, 2c) is based on the idea that because parents prefer (directly or indirectly) large nestlings over small ones, large nestlings will gain more resources for a given level of begging. Depending on the shape of the benefit curves and on the degree to which they tend to converge toward the asymptote, large nestlings will beg at greater intensities (Fig. 2b) or at lower intensities (Fig. 2c) than their smaller brood mates. It is quite likely that large and small nestlings would vary in both the cost and the benefit of begging behavior. This may lead to a case in which both the differential cost and the differential benefit effect act in the same direction to produce a positively correlated handicap (Fig. 2d) or to cases where the two act in opposite directions and their relative strength determines whether begging intensity will be positively (Fig. 2e) or negatively (Fig. 2f) correlated with nestling size.

As can be seen from Fig. 2, negatively correlated handicaps emerged only when the benefit curves of small and large nestlings tended to converge toward the asymptote. This may occur if parent preference for large chicks decreases when begging is strong (a situation which I find less likely) or, alternatively, it can be a result of the dynamic interaction between parents and competing nestlings. For example, if parents prefer large nestlings and therefore feed them first, small nestlings will have to wait longer to be fed, and by then will become hungrier and beg more. At this point, however, a small nestling may be more likely to be fed than before because its larger brood mates have already been fed (and stopped begging). Intensive begging may therefore coincide with periods in which, on the average, small nestlings are faced with less competition. In such a case, the benefit curves of begging for large and small nestlings may become closer (as in Fig. 2c) and negatively correlated handicaps can emerge. Unfortunately, a dynamic model of costly begging is not yet available, and almost nothing is known about the exact shapes of the cost and benefit curves of begging behavior. The graphic models presented here only illustrate that in theory, when both differential cost and benefit are considered, a range of different possible outcomes can be predicted.

Negatively correlated handicaps can be predicted by differential benefit alone (Fig. 2c) or by a combination of differential cost and benefit (Fig. 2f). I suggest that the latter

is the more realistic and better fits the results of this study because: (a) begging level increases with age, suggesting that smaller nestlings have to put relatively more effort into producing the same level of begging as their larger brood mates; (b) small nestlings were already in poorer body condition and lagging behind in growth, making any energy expenditure relatively more costly; and (c) the indirect component of the cost of begging should also be higher for small nestlings because they are of a lower quality relative to their larger sibs (i.e., considering inclusive fitness, they should care about their larger sibs more than their larger sibs should care about them). The higher begging cost for small nestlings pushes the optimal begging level to the left and may explain why small nestlings begged only slightly more than the large ones (compare Fig. 2f with 2c).

As mentioned earlier in four cases in this study, and in experimentally enlarged broods in another study (Lotem, 1998), small nestlings begged less than their larger brood mates. The complexity of these results may be explained when both the differential cost and benefit of begging are considered. Cases in which large nestlings beg more than small ones may occur when the cost of begging is much higher for small nestlings, or when the benefit curve of the small nestlings has a much lower asymptote than that of the large one (Figs. 2b, 2d, and 2e). A lower benefit asymptote is expected when a small nestling is constantly being pushed aside by many larger sibs and thus gains nothing by continuing to increase its begging.

Further experimental work is needed to determine under what circumstances nestlings develop different begging strategies, and by which mechanism. Some studies have suggested that this process may involve learning (Stamps et al., 1989) and a response of nestlings to the size and behavior of their brood mates (Smith and Montgomerie, 1991; Price et al., 1996; but see Cotton et al., 1996). Interestingly, in this study, higher begging levels by small nestlings were indicated already in test 1 (Fig. 1), before the differential benefit effect could be detected (Table 1: mass differences had no effect on mass gain differences between test 1 and 2). This could have been a result of the fact that although at this stage small nestlings received an equal share of food, they already had to wait longer to be fed and consequently learned to correlate intensive begging with higher success. Alternatively, small nestlings responded to the presence of their larger sibs. The extent to which nestlings manage to optimize their begging effort is still an open question.

In conclusion, higher begging levels by small nestlings may provide the first example of a case in which differential benefit of signaling creates a negative correlation between signaler quality and signaling intensity, as predicted by Reynolds (1993); see also Parker et al., 1989). The case of nestling begging discussed here suggests that negatively correlated handicaps have the potential to emerge whenever receivers integrate cryptic information about the signaler's momentary need or motivation (Godfray, 1991; Enquist, 1985), and non-cryptic information about the signaler's quality. A small individual may have to use high levels of aggressive display to deter rivals, whereas larger individuals have to add very little display to a body size that already deters rivals. A low quality, poorly ornamented male may use a very intensive courtship display to signal its motivation and strong interest in the courted female, whereas a well orna-

mented male may be sufficiently attractive without it. Such cases, if they occur, are not inconsistent with the handicap principle, but suggest that the evolution of signaling behavior through the handicap mechanism could be far more complicated than previously thought.

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