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Experimental evidence for offspring learning in parent–offspring communication

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The offspring of birds and mammals solicit food from their parents by a combination of movements and vocalizations that have come to be known collectively as 'begging'. Recently, begging has most often been viewed as an honest signal of offspring need. Yet, if offspring learn to adjust their begging efforts to the level that rewards them most, begging intensities may also reflect offsprings' past experience rather than their precise current needs. Here we show that bird nestlings with equal levels of need can learn to beg at remarkably different levels. These experiments with hand-raised house sparrows (*Passer domesticus*) indicated that chicks learn to modify begging levels within a few hours. Moreover, we found that the begging postures of hungry chicks in natural nests are correlated with the average postures that had previously yielded them parental feedings. Such learning challenges parental ability to assess offspring needs and may require that, in response, parents somehow filter out learned differences in offspring signals.

Keywords: parent–offspring conflict; nestling begging; learning; signalling

1. INTRODUCTION

The study of the evolution of communication has gone through some major changes during the last decade. Animal signalling behaviour, which was once viewed as manipulative and deceptive (Krebs & Dawkins 1984), is nowadays interpreted as honest communication enforced by the handicap principle (Zahavi 1975, 1987; Grafen 1990; Johnstone 1997). Communication between parents and offspring has been central to these developments. Offspring begging was initially suggested to be a mechanism by which offspring manipulate their parents (Trivers 1974) or through which they outcompete siblings (Harper 1986). However, recent signalling theory suggests a stable resolution for such conflicts in which offspring honestly beg for food according to their needs and parents respond with food provisioning in proportion to begging intensity (Godfray 1995*a*; Kilner & Johnstone 1997). This resolution can be stable against cheating if begging is costly and the benefit to the offspring from obtaining extra resources increases with diminishing returns (Godfray 1991, 1995*b*). In accordance with these predictions, studies of bird nestlings have shown that nestlings' begging increases with their level of food deprivation and stimulates increased parental provisioning (Bengtsson & Ryden 1983; Redondo & Castro 1992; Kacelnik *et al.* 1995; Price & Ydenberg 1995; Cotton *et al.* 1996; Leonard & Horn 1996; Kilner & Johnstone 1997; Davies *et al.* 1998). However, the relationships between begging and its various predictors, such as nestlings' relative size in the brood (Price *et al.* 1996), body condition or mass gain in the previous day, have been less clear or more complex (Stamps *et al.* 1989; Redondo & Castro 1992; Lotem 1998*a*; Cotton *et al.* 1999).

Begging models implicitly assume that offspring are selected to beg at adaptive levels. Yet, it is not clear how well and by which mechanism nestlings adjust their begging in relation to competitive dynamics in the nest (Parker *et al.* 1989; Smith & Montgomerie 1991; Kacelnik *et al.* 1995) and variations in the cost and the effectiveness of their begging (Parker *et al.* 1989; Godfray 1995*b*; Lotem 1998*a*,*b*). It has been suggested that nestlings may learn to adjust their begging efforts to levels that have rewarded them most effectively in the past (Stamps *et al.* 1989; Kacelnik *et al.* 1995; Lotem 1998*a*; Cotton *et al.* 1999). Learning was suggested as an explanation for higher begging levels in budgerigar nestlings fed by responsive fathers (Stamps *et al.* 1989) and variations in begging strategies among brood mates in starlings (Cotton *et al.* 1999) and swallows (Lotem 1998*a*,*b*). However, such learning could create situations in which begging intensities may reflect more the past experience of offspring rather than their precise current needs. Interestingly, the idea that learning shapes offspring signalling of need has also been considered in recent discussions on human infant crying (Messer *et al.* 1993; Acebo & Thoman 1995) and even implied in some therapeutic treatments of excessive baby crying (Wolke 1993). However, experimental evidence that learning can modify begging levels in any organism is still lacking.

In this study we tested the effect of learning on nestling begging experimentally. We hand raised house sparrow nestlings in the laboratory and tested whether nestlings with equal levels of need can be trained to beg at different levels as a result of experiencing different reinforcement programmes. We predicted that begging intensities of nestlings that have been rewarded with food only for intensive begging would be higher than those of nestlings that were fed as soon as they started to beg. To find out whether the learning process studied in the laboratory also occurs in nature, we monitored nestling begging and parent–offspring interactions in wild house sparrows'

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nests. We predicted that, if nestlings learn to beg at the most effective levels, begging postures of hungry chicks in natural nests would be correlated with the postures that had previously yielded them parental feedings.

2. METHODS

(a) *Hand-raising nestlings*

We hand raised 20 pairs of house sparrow nestlings in the laboratory which had been taken from a captive breeding colony in Tel-Aviv University Zoo during the springs of 1997 and 1998. Pairs of nestlings, similar in mass and of an average age of two days, were taken from the nest in the evening and were hand raised in the laboratory for three and a half days (until 10.00 of the fourth morning after their removal). During the night, they were held in an incubator at 36 °C and during the day (07.00–20.00) they were placed in a temperature-controlled box that allowed us to stimulate them to beg, to feed them and to record their behaviour with video cameras. Throughout the experiments the nestlings experienced similar conditions to those in natural nests. We stimulated them to beg by momentarily darkening the box as if a visiting parent were blocking the nest entrance and we fed them in response to their begging. To mimic the frequent parental visits in natural house sparrow nests (Yedvab 1999) we conducted our parental visit trials 67 times during a day, clustered in an 'early morning session' of three begging trials separated by 30 min each and 16 'daily sessions' 25 min apart, each consisting of four trials, one every 5 min. The experiment was conducted in accordance with animal care institutional guidelines and under a permit from the animal care committee of Tel-Aviv University. At the end of the experiment the nestlings were returned to their nests in the breeding colony ($n = 14$ pairs) or euthanized when a successful reintroduction was not possible ($n = 6$ pairs).

(b) *Experimental procedure*

The aim of our experiment was to train nestlings that were in similar physiological conditions to beg at different levels. To that end, we randomly assigned different reinforcement programmes for each of the two nestlings in a pair. One nestling (hereafter chick 1) was always fed immediately after it started to beg, even if it begged very weakly. The second nestling (hereafter chick 2) was fed only when it begged intensively in an erect body posture and always after the first nestling had been fed if they both begged. Hence, on average, chick 1 was rewarded with food for lower begging postures than was chick 2. These two reward treatments may reflect what a dominant chick and its smaller brood mate would experience in natural nests (Parker *et al.* 1989; Kacelnik *et al.* 1995). In order to control for differences in physiological need, we fed both chicks with equal amounts of food (by the end of each trial) and monitored their growth. Food (chopped fly larvae) was given from a syringe and was measured to the nearest 0.05 ml. We took daily measurements of wing length and mass to the nearest 0.1 mm and 0.1 g, respectively. A body condition index was calculated as the residual from a polynomial regression line of mass over wing length (Hochachka & Smith 1991; Lotem 1998*a*).

(c) *Measuring begging behaviour*

In order to measure begging behaviour when nestlings were equally hungry, we video recorded their responses in the three begging trials of the early morning session (when hungry from not eating during the night and 30 and 60 min after both nestlings were fed to satiation). We also monitored begging behaviour by video recording a random sample of six daily sessions (i.e. 24 begging trials). Because chick 2 (which was fed with second priority to chick 1) could beg at higher levels during the daily sessions simply because it was hungrier more often, we included the time since their last meal and the size of the last meal as covariates in the statistical analysis. Begging was measured by analysing begging postures from the videos on a computer screen using a graphic scale of 0 (no begging) and postures 1, 2 and 3, representing an increasing extension of the mouth towards the food source (see the illustrations in figures 1 and 2 and Lotem (1998*a*) for a detailed description of this method). Begging body postures have been found to be related to nestlings' level of hunger and to parental response in both previous studies (Redondo & Castro 1992; Kacelnik *et al.* 1995; Kilner 1995) and in our natural population of house sparrows (Yedvab 1999). We measured the average begging posture in each begging trial during the first 10 s after stimulating the nestlings or until one of them was fed, whichever came first. Hence, the begging measured each time had not yet been affected by the different reinforcement in current feeding but only by the differences in previous feedings.

(d) *Field experiment*

In order to study nestling begging in relation to past experience in natural nests, we placed video cameras in 14 nest-boxes located on the Tel-Aviv University campus (the nests contained four ($n = 8$) or three ($n = 6$) nestlings). The cameras were used to monitor parent–offspring interactions during the third day after chick hatching for 90–180 min. Soon after that, we brought the nestlings into the laboratory, fed all of them to satiation and then deprived them of food for 1.5 h. (The nestlings were first kept in the laboratory for 1 h (during which other nestlings were introduced to their nest to prevent desertion by the parents) and were returned to their nest for another 30 min during which the nest entrance was blocked by a screen.) When we finally allowed the parents to feed the nestlings, we were able to video nestling begging behaviour under natural conditions in the nest when all the chicks were equally hungry. We analysed their begging postures as described in § 2(c) and tested for a statistical correlation between the average begging posture applied by each nestling when hungry and the begging postures that had yielded it parental feedings during the preceding period in the nest.

(e) *Statistical analysis*

We analysed begging behaviour during the laboratory experiment while controlling for physiological parameters that were likely to affect nestlings' need (i.e. body mass, food intake and body condition) with the SAS system for mixed models (Littell *et al.* 1996) (using SAS software v. 7.0). This statistical method allowed us to construct the appropriate mixed models with treatment (chick 1 versus chick 2) as a fixed effect, pair of nestlings as a random effect, days of the experiment as repeated measurements and physiological parameters of nestling need as possible covariates.

In order to test the relationship between nestling begging postures when hungry and the begging postures that had yielded them parental feedings during the preceding period in the nest, we calculated the partial correlation between these parameters after removing the variation between nests and reducing the degrees of freedom as required (Sokal & Rohlf 1995, § 16.4). This method allowed us to use each nestling's data independently of the nest in which it was reared.

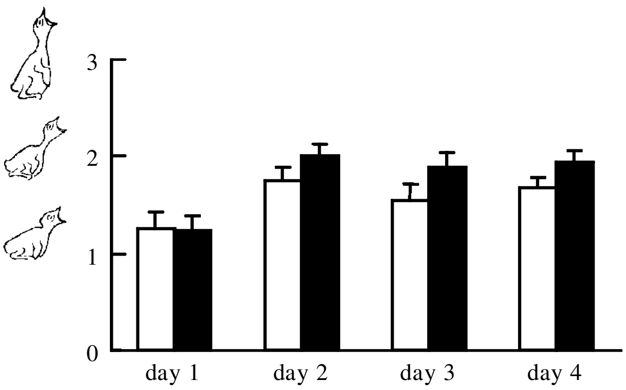

Figure 1. A day's first begging posture (mean ± s.e) of chick 1 (open bars) and chick 2 (shaded bars) based on each nestling's average posture during the first three begging trials of each morning (before the first feeding and 30 and 60 min after both nestlings in a pair were fed to satiation with no difference in begging reward) ($n = 20$ pairs).

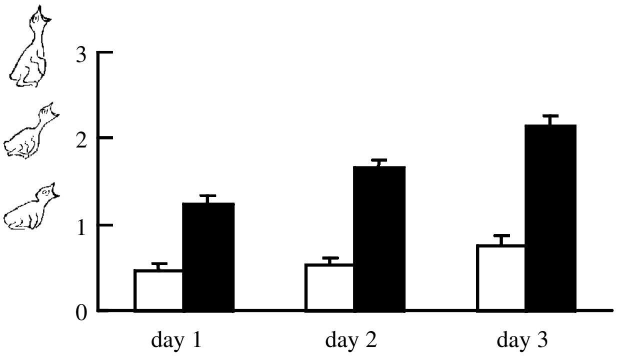

Figure 2. Daily begging posture (mean ± s.e) of chick 1 (open bars) and chick 2 (shaded bars) statistically adjusted for hunger and body condition (only the 16 pairs with data for a complete feeding schedule were included in this analysis; see §3).

3. RESULTS

Despite the different reinforcement programmes, the nestlings of the two experimental groups did not differ significantly in the amounts of food they received, nor in most other physiological parameters that were likely to affect their need (table 1). A small difference in body condition index was the only exception and was already apparent in the first morning of the experiment before the differential reinforcement was applied (means ± s.e. 0.119 ± 0.22 versus -0.120 ± 0.23 for chicks 1 and 2, respectively). However, in order to control for the possible effects of differences in body condition or in any of the other need parameters in table 1 (some of which indicate a slight trend towards a higher need of chick 2), we tested their effects as covariates in the statistical analysis of begging behaviour (see below).

Table 1. *Physiological parameters of nestling needs*

(The values for chicks 1 and 2 are the cell means (± s.e.) of each chick group during the three days of the experiment (adjusted for the repeated measurements of each). The F-values are the statistical results of mixed models with repeated measurements (Littell *et al.* 1996) (pair and treatment group as random and fixed effects, respectively) ($n = 20$ pairs and d.f. = 1,95 for all tests). The body condition index was calculated as the residual from a polynomial regression line of mass over wing length (Hochachka & Smith 1991; Lotem 1998*a*).)

	chick 1	chick 2	F	p
body mass (g)	8.57 ± 0.39	8.47 ± 0.39	0.05	0.82
daily food intake (ml)	6.99 ± 0.26	6.74 ± 0.26	1.45	0.24
number of meals per day	25.13 ± 1.08	23.77 ± 1.08	1.92	0.19
average meal size (ml)	0.29 ± 0.02	0.29 ± 0.02	0.00	0.95
daily mass gain (g)	2.08 ± 0.14	2.04 ± 0.14	0.09	0.76
body condition index	0.13 ± 0.17	− 0.13 ± 0.17	3.98	0.05

The analysis of begging behaviour showed that the different reinforcement programmes had a significant effect on the begging behaviour of the two chicks. Initially, on the first morning, before the nestlings experienced any differential treatment, there were no differences in their begging behaviours (figure 1) (paired $t_{19} = 0.047$ and $p = 0.96$). However, during the following three mornings chick 2 begged at a significantly higher level than did chick 1 (figure 1) ($F_{1,92} = 6.31$ and $p = 0.014$) (mixed model with repeated measurements (Littell *et al.* 1996), pairs and treatment as random and fixed effects, respectively, and body condition index, body mass and food intake during the previous day as covariates). We tested the possible effects of all need parameters from table 1 on the model's results and removed non-significant covariates and interaction terms, but conservatively kept body condition index in the model, as it differed between treatment groups (see table 1). The differences in begging between chicks remained significant under all inclusions or exclusions of need parameters as covariates.

The difference in begging between chicks 2 and 1 was even greater during the daily sessions (figure 2). In order to control for a possible higher level of hunger of chick 2 during these daily sessions (see §2) we applied a similar mixed model with repeated measurements (Littell *et al.* 1996) (pairs and treatment as random and fixed effects, respectively) and tested the effect of hunger and need parameters as covariates. The begging data for each chick were based on its average begging posture as sampled in 24 begging trials in the six sessions sampled for each chick during the day. Hunger covariates were taken as the daily average time since their last meal and size of the last meal measured for the begging trials that were analysed. The final model includes these hunger covariates and their interactions with day and body condition (all of which were significant). The difference between chicks 1 and 2 was highly significant (figure 2) ($F_{1,64} = 154.5$ and $p < 0.0001$) and increased with age (a significant treatment by day interaction) ($F_{2,64} = 15.43$ and $p < 0.0001$). The differences between chicks in their begging remained highly significant under all inclusions or exclusions of need parameters as covariates. A detailed plot of all begging data in relation to hunger covariates (available upon request from the authors) showed that differences between chicks were consistent under all hunger levels and that our analysis, which was based on individual daily averages, was not confounded by nonlinear effects or biased distributions of hunger states.

In order to assess how rapidly learning occurred, we analysed the begging trials sampled during the first half day of the experiment separately (from the beginning of the differential treatment until 13.00). The difference between the chicks was highly significant even at this early stage, showing that learning modified begging within less than a few hours. (Mixed model with pairs and treatment as random and fixed effects, respectively and conservatively including time since last meal, size of last meal, body condition and initial begging levels as covariates, $F = 31.05$ and $p = 0.0003$ and adjusted means (± s.e.), 0.41 ± 0.11 versus 1.27 ± 0.11 for chicks 1 and 2, respectively). This rapid change through the morning makes it even less likely that our results were confounded by physiological differences between the chicks.

Our fieldwork on house sparrow nestlings indicated that a nestling's average begging posture after food deprivation was positively correlated with the mean value of begging postures that had previously rewarded it with parental feedings (figure 3) (partial correlation after controlling for nest effect, $r = 0.44$, $n = 44$, d.f. = 28 and $p < 0.05$). However, a nestling's average begging posture when hungry was not related to its relative rank in the brood (Yedvab 1999), nor to its average body posture (including unsuccessful begs) measured at the nest before it was removed ($r = 0.152$, $n = 44$ and $p > 0.3$).

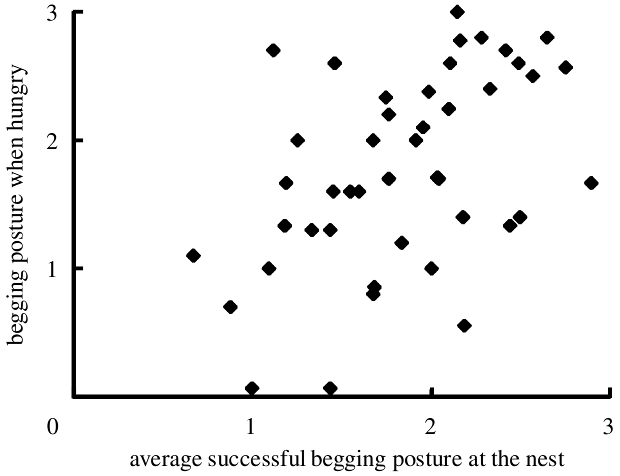

Figure 3. The relationship between average body posture of food-deprived house sparrow nestlings at the nest and the mean value of begging postures that had previously rewarded them with parental feedings.

4. DISCUSSION

To the authors' knowledge, this study provides the first experimental evidence that learning modifies offspring signalling of need to their parents. Nestlings that have been rewarded with food only for begging in erect body postures developed a tendency to apply these postures much more frequently than nestlings that have been rewarded with food as soon as they open their bill to beg. The different reinforcement programmes yielded substantial differences in begging intensity (figure 2) that were comparable to those observed between hungry and satiated chicks in other studies (e.g. Redondo & Castro 1992; Kacelnik *et al.* 1995; Kilner 1995; Lotem 1998*a*). Our field experiment suggested that the learning process discovered in the laboratory also occurs in nature because begging postures of hungry chicks were correlated with the average successful postures (and were not simply correlated with their average postures including unsuccessful begging). Hence, nestlings seem to learn the begging postures that are most rewarding in the nest and to use them more frequently when hungry.

The effect of learning on begging was much more pronounced during the day (figure 2) than in the first begging trials of the following morning (figure 1). This can either suggest that nestlings 'forget' some of what they had learned the day before during the night or that higher hunger levels early in the morning obscured some of the learning effect. The difference in begging during the day also increased with chick age (figure 2). However, we could not determine whether this increase was the result of an additive learning effect from day to day or an age-related increase in learning ability or begging intensity.

The indistinguishable growth rates of nestlings that begged at different levels (table 1 versus figure 2) is further evidence that the metabolic cost of begging is relatively low (McCarty 1996), though the lack of persistent begging at maximal levels suggests that there may be other costs.

The finding that nestlings in a similar physiological state can learn to beg at remarkably different levels presents a challenge to the concept of begging as an honest signal of need (Godfray 1991; Kilner & Johnstone 1997; Kilner *et al.* 1999). If, as a result of different experiences, nestlings in a similar physiological state can beg so differently, the relationship between begging and need may be much weaker than the 'one-to-one' relationships predicted by perfect honesty. On the one hand, learning might be viewed as the mechanism that allows offspring to adjust their investment in begging precisely as required by honest signalling theory. However, on the other hand, the adjustment of begging efforts in relation to past experience may cause begging intensities to reflect not only current physiological needs but also the degree to which begging postures were effective in the past. This depends on the outcomes of a dynamic sibling competition and parent–offspring interaction. When begging reflects a combination of all these factors, its absolute levels may no longer be correlated with the kind of information about offspring need that is of interest to the parents. For example, a medium chick in a large brood that had to beg intensively in order to be fed may learn to beg at higher levels than a needier smaller brood mate that fails to compete for food and, therefore, was never reinforced to increase begging (Lotem 1998*a*). In a similar manner, nestlings raised by responsive parents during a good breeding season may learn to beg at low intensities (like chick 1 in our experiment), but their food requirements can still be high. In such a case, the low begging levels were caused by the fact that food was easy to obtain but should not signal to the parents to reduce their provisioning rate.

A dynamic adjustment of signalling behaviour based on learning is not necessarily incompatible with the concept of honest signalling. However, such learning by signallers may require that receivers will also be able to adjust their behaviour dynamically and modify their rules of response accordingly. Hence, it seems that, for parent–offspring communication through begging to be reliable, parents must be able to somehow filter out the effect of nestlings' past experience in assessing offsprings' needs. Parents may do so by continuously learning the typical begging levels of their offspring, either individually or as a brood and responding to relative deviations from this level. Alternatively, parents could counteract confusion from learned begging differences indirectly by feeding chicks on the basis of their begging intensity relative to their size or position in the nest. This mechanism could work, for example, in systems where nestlings of different size may learn to beg at different levels (Stamps *et al.* 1989; Lotem 1998*a*; Cotton *et al.* 1999). If small chicks learn to average stronger begging for a given need than do their larger nest-mates, parents might use chick size as a basis for filtering out the effects of chick learning. Regardless of how parents might decode learned differences in offspring signals, the extent to which they can do so may determine the degree of reliability in parent–offspring communication.

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