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# Can hungry nestlings be trained to reduce their begging?

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Nestling begging behavior is usually characterized by a behavioral response of increasing begging levels with an increase in nestling need or hunger. Recent evidence for the possible effect of learning on begging intensity raises the question of how learning can shape this response rule. In particular, it is not clear whether hungry nestlings can learn to reduce their begging when it is not successful or, rather, whether they must first acquire positive experiences with low begging levels in order to do so. To explore this question, we conducted 3 hand-feeding experiments with pairs of house sparrow (*Passer domesticus*) nestlings. In the first 2 experiments, the nestlings targeted to lower their begging were rewarded mainly or only for low begging postures. However, despite the high expected reward for low begging, these nestlings did not lower their begging. Controlled by their behavioral response function, hungry nestlings were "stuck" at high postures without being able to experience the potential success of low postures. In the third experiment, nestlings targeted to lower their begging levels were rewarded for any begging posture, ensuring that satiation would provide their initial "positive experience" with low begging postures. Begging postures were reduced by this treatment. In light of these results, we suggest that parents are unlikely to reduce offspring begging levels by simply ignoring them. However, they might be able to do so by attending to the begging as soon as possible, thereby allowing their offspring to explore low begging and learn that it is sufficiently effective. *[Behav Ecol 19:116–125 (2008)]*

Offspring solicitation of resources from their parents is a widespread phenomenon that has received considerable attention (Kilner and Johnstone 1997; Royle et al. 2002; Wright and Leonard 2002; Wells 2003). Much of the recent empirical work on parent–offspring communication has been aimed at testing whether begging is an honest signal of need (reviewed in Kilner and Johnstone 1997; Royle et al. 2002), as predicted by various game theory models (Godfray 1991, 1995; Johnstone and Godfray 2002; Johnstone 2004; but see Parker et al. 2002). A general feature of current models is that nestlings increase their level of begging in relation to need, according to their (presumably innate) response function, but this function itself is not allowed to change dynamically over time. This lack of nest dynamics in the models may be necessary for analytical tractability (Godfray 1995) and has been acknowledged before (Cotton et al. 1999; Godfray and Johnstone 2000; Johnstone and Godfray 2002). However, under natural conditions, flexible adjustments of the behavioral response function (e.g., changing its slope or asymptotic level) may be necessary for offspring in order to cope with phenotypic changes in the expected costs and benefits of begging (Cotton et al. 1999; Kedar et al. 2000; Lotem and Winkler 2004). For example, it has been shown that relative rank and competitive ability affect begging effectiveness (Kacelnik et al. 1995; Kilner 1995) and possibly also its cost (Kilner 2001) and may therefore explain phenotypic differences in begging strategies (Price et al. 1996; Lotem 1998a, 1998b; Cotton et al. 1999; for a theoretical discussion, also see Johnstone 2004). In other words, nestlings seem to change their begging response function over developmental or behavioral timescales.

Learning is an obvious candidate as a mechanism by which nestlings can adjust their begging response function to different conditions. Intuitively, by exploring the relative success of different begging functions (or different begging levels), nestlings may be able to be reinforced and eventually prefer (or develop) the most adaptive begging response given the circumstances. It has been previously suggested that learning can affect nestling begging and may therefore provide an explanation of observed variation in begging levels between chicks that had experienced different conditions (Stamps et al. 1985, 1989; Kacelnik et al. 1995; Lotem 1998a; Cotton et al. 1999; Wright et al. 2002). Another indication that learning may influence the nestling's begging function comes from a study of great tits, in which rearing conditions influenced the degree to which hunger increased begging (Kölliker et al. 2000, Table 1). More direct evidence for the effect of learning on the nestlings' begging function was provided by recent experiments with hand-raised nestlings (Kedar et al. 2000; Rodríguez-Gironés et al. 2002). Additional studies suggest that learning can influence other aspects of nestling behavior rather than their begging intensity. For example, nestlings may learn to position themselves in the location that was previously more profitable (Kölliker and Richner 2004; Budden and Wright 2005), or, in cuckoo nestlings, they can even learn to gradually mimic the host race–specific begging call structure (Madden and Davies 2006). However, although the possible role of learning in nestling begging is now widely recognized (Clark 2002; Wright and Leonard 2002; Royle et al. 2004), it is not at all clear what kind of learning mechanism is likely to operate in each case. This is especially crucial for the type of learning considered in this paper, where learning can presumably change the begging response function to nestling need. As we explain below, in this case, different learning mechanisms can have different consequences.

In contrast to the well-studied examples where a newly acquired behavior, such as pressing a lever, can be increased or decreased through operant conditioning (reviewed by Williams 1983), learning to increase or decrease begging levels is complicated by the fact that begging is an instinctive behavior with an innate tendency to increase with need. Training

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**Table 1**
**Parameters of nestling needs in experiment 3**

| | AB-HBO chicks | HBO-AB chicks | *t* | *P* |
|---|---|---|---|---|
| Initial body mass (g) | 7.13 ± 0.3 | 7.03 ± 0.34 | 0.6 | 0.55 |
| Experiment 3a (first session) | | | | |
| Food intake (ml) | 2.86 ± 0.12 | 2.67 ± 0.12 | 3.88 | <0.01 |
| Average meal size (ml) | 0.12 ± 0.00 | 0.16 ± 0.01 | −5.69 | <0.01 |
| Average time from last meal (min) | 14.54 ± 0.64 | 20.61 ± 1.09 | −5.46 | <0.01 |
| Mass gain (g) | 1.42 ± 0.09 | 1.39 ± 0.09 | 0.65 | 0.52 |
| Experiment 3b (second session) | | | | |
| Food intake (ml) | 1.87 ± 0.125 | 2.01 ± 0.11 | −1.64 | 0.11 |
| Average meal size (ml) | 0.13 ± 0.005 | 0.10 ± 0.005 | 4.63 | <0.01 |
| Average time from last meal (min) | 29.05 ± 2.80 | 23.43 ± 2.93 | $Z = 3.02$ | <0.01 |
| Mass gain (g) | 0.80 ± 0.43 | 0.94 ± 0.41 | −1.95 | 0.064 |

Treatment group means ± standard errors are shown. Results of *t*-test for dependent samples are given, except for the difference between average time between meals in the second training session, where a nonparametric Wilcoxon test for dependent samples was applied. $N = 28$ pairs for the first training session, and $N = 24$ pairs for the second session (see Methods). AB-HBO: rewarded for "any begging" in the first session and for high begging only in the second. HBO-AB: likewise but in the reverse order.

nestlings to reduce their begging may therefore resemble attempts to train animals to behave against their instincts, which is known to be complicated and frequently unsuccessful (See e.g., Breland K and Breland M 1961). However, under natural conditions, parental response, combined with sibling competition, may create some reinforcement regimes that allow such learning to take place. Studies of nestlings begging that indicate learning as a possible explanation of their results have implicitly suggested a certain learning mechanism. Parental feeding is usually viewed as providing the nestling with a positive experience that can potentially lead to high levels of begging (Stamps et al. 1985, 1989; Lotem 1998a; Wright et al. 2002), whereas when begging has been unsuccessful (or has not been related to feeding, Stamps et al. 1985, 1989), it was suggested that nestlings should learn to reduce their begging levels. In some cases, this would mean that learning should work in the opposite direction to that of food deprivation, causing nestlings that were fed less to beg less intensely, rather than more intensely (Lotem 1998a; Wright et al. 2002; but see Cotton et al. 1999). This mechanism of "learning to reduce begging when it is unsuccessful" is the first we set out to test (see below), but it is not the only possibility.

Another option is that nestlings need to acquire positive experience with low begging intensities before they reduce begging levels (as suggested by Lotem and Winkler 2004 for human infants) and that they will not reduce them when high begging levels are "unsuccessful." In other words, nestlings might be programmed to adjust their begging levels to the least demanding begging efforts that are positively reinforced and to escalate begging in the absence of positive reinforcement. This possibility is supported by laboratory experiments where nestlings that ultimately begged at lower levels were those that had been fed for all begging levels (Kedar et al. 2000) or those that had to spend only a little time begging before being fed (Rodríguez-Gironés et al. 2002). It would appear that, in these cases, the nestlings that applied low begging levels may have done so after gaining positive experience with low begging rather than by learning the ineffectiveness of high begging levels.

To study which of the above learning mechanisms may shape nestling begging, we conducted 3 hand-feeding experiments with pairs of house sparrow (*Passer domesticus*) nestlings and tested the possible consequences of different parental responses to nestling begging. In the first 2 experiments, designed to test the mechanism of learning to reduce begging when unsuccessful, one of the nestlings was rewarded with a low probability (0.2 or 0 in the first and second experiment, respectively) for "erect" begging postures and with a high probability (0.8 and 1.0) for "not-erect" begging postures. The other nestling in the pair was subjected to the opposite reinforcement regime. If nestlings can learn to reduce begging when begging intensely is unsuccessful (Stamps et al. 1985, 1989; Lotem 1998a; Wright et al. 2002), this straightforward protocol should result in lower begging by the first nestling. On the other hand, if nestlings require positive experience with low begging intensities before they can learn to reduce begging (the second mechanism proposed), unsuccessful nestlings of the first group may become hungry and therefore "stuck" at a high begging posture without being able to learn to reduce their begging. In this case, however, a different training procedure might work, which is consistent with the second learning mechanism suggested. To test this second possibility, a third experiment was carried out during which the nestling targeted to reduce its begging was rewarded for any begging posture. This ensured that the target nestling would apply low begging postures (initially, at least, due to satiation), could acquire positive experience with low begging postures, and thus learn that they are sufficiently effective.

## METHODS

### Subjects and general methods

Most of the nestlings studied in the experiments described here (53 out of 58 pairs of nestlings) were taken from different broods in a large captive house sparrow breeding colony at the I. Meier Segals Garden for Zoological Research at Tel-Aviv University. In this colony, 12–13 breeding pairs are kept in each of 5 large (5 × 4 × 3 m) outdoor aviaries with shelter, branches and at least 14 sheltered nest boxes. Water and food were provided ad lib. The additional 5 pairs that were used (for experiment 2) were taken from 5 different wild house sparrow nests located in the garden. We carried out most of the experiments during the breeding season of 2004, with experiment 2 being completed in 2005. Three 1-day experiments were conducted using pairs of 4-day-old nestlings ($n = 15$, $n = 15$, $n = 28$ pairs for experiments 1, 2, and 3, respectively, with 11/15 of the sample size for experiment 2 conducted in 2005), with each pair originating from the same nest (chosen as the 2 siblings closest in weight within the nest). The nestlings were taken from the nest at 0630 h and kept in a custom-made incubator (D.M.P Engineering Ltd., Israel, based on the Lory10 model) that was lit only brightly enough for video recording and set to 37 °C at 50–70% relative humidity. In experiments 1 and 2, each nestling was kept in a separate incubator, whereas in experiment 3, they were kept together, after being marked with nontoxic acrylic paint to enable individual recognition by the experimenter. The reason for separating the nestlings in experiments 1 and 2 (but not in experiment 3) was that in these experiments the experimenter had to quickly assess and respond to the nestling begging posture (see below) in a way that cannot be performed simultaneously with 2 nestlings. Begging trials were carried out at different times during the experimental day according to the relevant experimental procedure (see below). At the onset of each trial, we stimulated the nestlings to beg by turning the incubator light switch off and on (thereby also causing a sound stimulus). This stimulus was used because it mimics the sound-and-darkening stimulus that the nestlings experience when a parent arrives at the nest (for use of a similar stimulus to elicit begging behavior, see Kedar et al. 2000). A few seconds into the trial and only when appropriate according to the reinforcement regime of each experimental group, the nestlings were fed freshly chopped fly larvae through a 1-ml syringe (measured to the nearest 0.01 ml). Mass measurements were taken to the nearest 0.1 g before and after each experiment, as well as between phases "a" and "b" of experiment 3 (see below). No mortality or apparent stress was recorded during the experiments, and all nestlings were fed to satiation at the end of the experiment and returned to their original nests (not later than 1930 h).

## Experimental procedures

*Design and rationale*

It is inherently difficult to design controlled experiments in which nestlings are trained to beg at different levels. Although nestling use of begging activity to obtain food resembles an operant conditioning setup, begging activity cannot be controlled by the experimenter, unlike lever pressing or key pecking, which can be blocked to the animal. Nestlings can always beg and can only be fed when they beg; thus, if they are capable of learning, they are likely to learn something from their experience even if they were merely designated as a control group to determine the effect of other factors rather than learning. The begging levels of such "control nestlings" can therefore reflect a combination of their physiological state and the effect of learning and as such cannot be treated as free from learned effects. To get around this problem, we designed experiments based on differential training regimes that predict different learning outcomes while trying to minimize variation in physiological need between treatments or to control for them statistically as far as possible (see below).

The rationale for the choice of experiments was based on their biological relevance and feasibility and on their ability to distinguish between different learning mechanisms (see in the Introduction). We considered what types of parental response a nestling might experience at the nest and what would be a feasible parental response strategy to reduce the begging levels of offspring. Considering that parents are unable to recognize their nestlings individually, there are 2 main response rules possible for the parents: (a) rewarding low begging more than high begging and (b) rewarding any begging level equally, which makes low begging more profitable. In each experiment, we applied one of these options to the nestling targeted to reduce begging, whereas its sibling was subjected to a complementary regime (see below). Experiments 1 and 2 were used to test rule (a) (rewarding low begging more than high begging), whereas experiment 3 was conducted to test rule (b) (rewarding any begging).

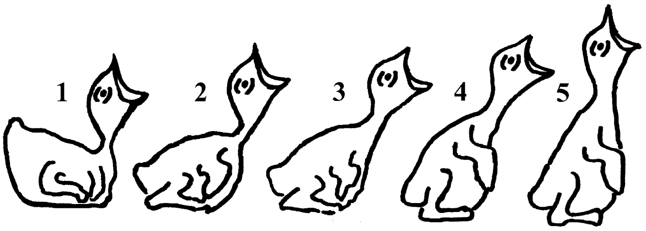

**Figure 1**
Begging behavior was measured by matching the begging postures to images along a graphic scale of increasingly erect begging postures from 1 to 5 (5 represents the most erect begging posture). During the experiments, begging postures exceeding "3" were classed as erect body postures and postures of "1–3" were classified as not erect (see Methods).

*Experiments 1 and 2*

At the onset of the experiment, 20 min after being put in their (separate) incubators, the nestlings were stimulated and fed twice to accustom them to the new conditions. A standard test (ST: 4 trials 5 min apart with no feeding) was then conducted to record initial begging levels (hereafter ST1) followed by 3 trials (5 min apart) in which the experimenter encouraged the nestlings to beg in an erect body position by touching the beak lightly with the syringe. This was done to ensure that all nestlings were healthy and able to beg in an erect body posture when highly stimulated. Up to this point, the experimenter was blind to the subsequent reinforcement regime for each nestling (see below), which was applied during the training session that started immediately afterward. The training session consisted of 4 subsessions (20 min apart) of 10 trials, one trial every 5 min (40 trials altogether, mimicking the high rate of parental visits at the nest). At the end of the training session, a second ST was performed (hereafter ST2), and the nestlings were fed to satiation and returned to their nest (by 1300 h).

In experiment 1, we investigated whether nestlings can be trained to beg at different levels when the probabilities of being fed during training depend on begging posture. To this end, we used the following reinforcement regimes: In each trial, we classified the body posture used by each begging nestling in the 3 s after a stimulus was given, based on a visual graphic scale of 1–5 (Figure 1), as either "erect" (a high begging posture, 4–5 on our scale, henceforth "H") or "not-erect" (a low begging posture, 1–3 on our scale, henceforth "L"). One of the nestlings in this experiment was to be fed in 80% of its low begging (not erect) trials and only 20% of its high begging (erect) trials. Such nestlings are termed here "LBM chicks" (low begging mostly) because they were reinforced in most of the cases in which they had used low begging postures and for high begging postures only rarely. The other nestling was subjected to the exact opposite reinforcement regime and fed in 20% of its low begging trials and 80% of its high begging trials (termed "HBM chick," rewarded for high begging mostly). In all feedings, meal size was a fixed amount of 0.1 ml. To generate the appropriate feeding probabilities for each begging category, a feeding chart for each nestling was prepared in advance, consisting of random blocks of 5 trials. For LBM chicks, for example, this meant that they were randomly fed on 4 out of 5 low begging trials. Note that such simple differential reinforcement, which is a common procedure in animal learning experiments (Keasar et al. 2002; Budden and Wright 2005), ignores a possible interaction with the tendency to increase begging when hungry and assumes that nestlings that fail to succeed in erect postures will eventually try the option of low postures.

Experiment 2 was an extreme version of experiment 1. It was based on an identical schedule, but the probabilities of being rewarded for using erect or not-erect postures were set to either 0 or 1 (instead of 0.2 and 0.8). Here, one of the nestlings was to be fed for low begging intensity only (LBO chicks) and the other for high begging intensity only (HBO chicks). Although this reinforcement regime may be less realistic, this extreme version of the experiment eliminates the variability of reward that was present in experiment 1 and could possibly impair nestling learning (Myers et al. 1965). Thus, if nestling learning is impaired by variability of reward, as known from other studies of learning (e.g., Keasar et al. 2002; Erev and Barron 2005), it could only impair learning in experiment 1 but not in experiment 2.

*Experiment 3*

The aim of this experiment was to first train one randomly assigned nestling in each pair to beg at a higher level than its pair mate (hereafter experiment 3a) and then to reverse the treatment and train this nestling to suppress its elevated begging (hereafter experiment 3b). In contrast with experiments 1 and 2, our method of trying to reduce begging was based on rewarding the nestling for any begging posture (an "AB" treatment), assuming that after satiation the nestling would use low begging postures and be able to learn that these are sufficiently effective. This "feed first" approach may mimic parental preference for dominant chicks that, under good conditions, may allow them to learn to reduce their begging (see Lotem 1998a; Cotton et al. 1999). Our method of causing one pair mate to beg at higher levels was similar to that used in experiment 2, namely, to feed it only if it used an erect body posture (i.e., an HBO, "high begging only" treatment). Because the training procedure was reversed during the second part of the experiment, each nestling was designated either as an "AB-HBO" chick (rewarded for any begging in the first part of the experiment and for high begging only in the second) or as an "HBO-AB" chick (likewise but in the reverse order).

The reinforcement procedure was as follows: In the trials of the first training session (experiment 3a), the nestling designated as an "AB-HBO chick" was subjected to an AB treatment, whereas the "HBO-AB chick" was subjected to an HBO treatment. In the AB (any begging) treatment, the nestling was always fed if it begged and was fed quickly after the beginning of the trial. In contrast, the second nestling (subjected to the high begging only treatment) was only fed when it used an erect body posture, and if both chicks begged, it was fed only after the first (AB) chick. Following the above procedure, the HBO chick was then to be reinforced for higher begging postures than was the AB chick. These reinforcement regimes were basically the same as those used by Kedar et al. (2000), with only slight differences in the exact timing of the trials. The 4-h training session was divided into 7 subsessions, 25 min apart, each consisting of 4 trials, one every 5 min (28 trials in total). In order to keep hunger levels as similar as possible throughout the experiment, the experimenter tried to ensure that each nestling had been fed a certain amount of food by the end of each subsession while always adhering to the reinforcement regimes described above (i.e., an HBO chick that applied high begging as required would eventually receive the same amount of food as an AB chick). Following the methods used by Kedar et al. (2000), subsession food amounts were set to 0.25, 0.33, 0.4, 0.45, 0.5, 0.55, and 0.6 ml for nestlings of initial mass of less than 4.4, 4.5–6.4, 6.5–8.4, 8.5–10.4, 10.5–11.4, 11.5–12.4, and above 12.4 g, respectively (food amounts were those shown to enable normal growth in the laboratory; Kedar 2003). In order to determine whether a learned begging strategy can be reversed, we applied the same protocol in the second half of the day but with the treatments switched between the nestlings (see above). This part of the experiment (3b) was carried out during the afternoon, soon after the first part (3a), with 24 of the 28 pairs.

To compare the begging behavior of the 2 nestlings under a similar level of "short-term need" (e.g., time since the last meal and size of last meal), STs were conducted before and after each training session (hereafter ST1, ST2, and ST3, where ST1 and ST3 were conducted at the beginning and at the end of the day, respectively, and ST2 between the training sessions). No food was supplied during the STs, which consisted of trials given 25, 30, 55, and 60 min after both nestlings had been fed with a full subsession amount of food (see above) to reduce their hunger. The feeding of the first ST(ST1) started 20 min after the nestlings were placed in the incubator. The feedings of the other 2 STs (ST2 and ST3) were given in the last 2 trials of the preceding training session that had been modified to that aim (i.e., the nestlings were no longer fed according to their reinforcement regime in these 2 trials). Because there is some controversy as to whether STs of the kind described above (as well as in experiments 1 and 2) can really control for variation in hunger (Wright et al. 2002), we used a complementary method to control for "need variables" statistically by including them as covariates in a statistical model (see below). The detailed data for such an analysis were available because we closely monitored the time and the exact size of each meal provided to the nestlings in all experiments.

## Measuring begging posture

Nestling begging postures were used to assess begging intensities throughout all the experiments and to analyze begging behavior after their completion. Begging posture has been used to measure the level of begging in several previous studies (e.g., Redondo and Castro 1992; Kacelnik et al. 1995; Kilner 1995; Leonard et al. 2003) and was found most suitable for our study both because it is relatively easy to assess quickly and because among the wild population of house sparrows from which our captive colonies are derived it has been shown to correlate positively with the probability of being fed and with food deprivation time (Yedvab 1999; Kedar 2003). The nestlings' behavior in all trials of the above experiments was video recorded using a Digital Sony video camera (DCR-TRV355E). Video recordings were transferred to a computer (using Adobe Premier 6.5), and begging postures were analyzed blind to the different nestling treatments. Begging behavior was measured by matching the begging postures to images along a graphic scale of increasingly erect begging postures starting from 0 (no begging) through 1–5 (5 represents the most erect begging posture) (Figure 1). This scale is based on graphic scales used in previous studies (Redondo and Castro 1992; Lotem 1998a; Kedar et al. 2000) and can be read as class marks along a continuum of begging postures. During the experiments, estimated begging scores of 1–3 were classified as "not-erect trials" and scores of 4–5 as "erect trials." During video analysis, the appropriate score was given to each nestling for a sample of 1 video frame from every second of the first 3 s after the stimulus or until the feeding syringe entered the frame, whichever came first. The analyzed begging posture was therefore only affected by the nestling's state or past experience and could not be biased by the experimenter's effect on begging in the analyzed trial. The mean posture used by a nestling in each trial was calculated from the sample of 1-frame scores. For the ST trials, in which no feeding syringe interfered, begging postures were similarly analyzed for each of the first 10 s after the stimulus, and a mean posture for each nestling was then calculated.

### Statistical analysis

*Controlling for need variables*

Nestling begging postures during the various training sessions can be confounded by temporal variation in short-term need variables such as time since (and size of) the last meal. One way to control for such variation statistically is to include need variables as covariates in a statistical model (e.g., Kedar et al. 2000; Rodríguez-Gironés et al. 2002; Dor et al. 2007). In our data set of experiment 3, however, we found that a simple application of this approach was unsuitable because adding these need variables to the model only increased significance levels, even though it was expected to confound them. The reason for this was that the effect of the hunger covariates among pairs was the opposite of their expected effect within a pair (i.e., in experiment 3, pairs that begged more ate more during the experiment, creating an inverse relationship between hunger and begging). The possibility that 2 opposing trends affect begging within and between pairs violates the assumptions of analysis of covariance (ANCOVA) (that a covariate should have the same effect in all cells, see Sokal and Rohlf 1981, p. 522) and precluded its application in this case. Nevertheless, there is a relatively straightforward method (albeit uncommon) to control for hunger covariates while avoiding the artifacts described above. This can be done by producing, separately for each pair of nestlings, an adjusted begging posture value that is free of the covariate effects within the pair. To that end, we carried out a separate ANCOVA on the raw data for each pair, using the begging postures of the training session trials as the dependent variable (one data point per chick per trial), the treatment group as the categorical factor, and with time from and size of the last meal as covariates (in experiments 1 and 2 only time from the last meal was used as a covariate because meal size was constant). Thus, for each nestling and for each training session, a mean begging posture, adjusted for hunger covariates, was obtained (hereafter adjusted begging posture), which was then taken as the independent data point for the comparison between treatment groups. This method ensures that detected differences in adjusted begging posture within a pair cannot be attributed to differences in the above need covariates.

*General statistical methods*

The SAS system for mixed models (version 8.2, SAS institute, inc., Cary, NC) was used to analyze training session begging postures, with mean adjusted begging posture as the dependent variable, treatment as a fixed effect, nestling pair as a random effect, and with the begging score for the ST preceding the training session as a possible covariate. When *t*-tests were conducted (using STATISTICA 7.0 by StatSoft, Inc.), they were 2-tailed tests for dependent variables, as a paired design was used in all experiments. Distributions of all variables used for parametric tests were first found not to differ significantly from normality using the Kolmogorov–Smirnov test. Means + standard errors are presented.

## RESULTS

### Experiments 1 and 2

As experiment 2 constitutes an extreme version of experiment 1, their results are presented together. There were no initial differences between the treatment groups in nestling mass, rank at the nest (according to mass relative to siblings), or average begging score in ST1 (the ST of begging before training) either in experiment 1 ($t_{14} = 0.48$, $P = 0.64$; Wilcoxon matched pair test $Z = 0.22$, $N = 15$, $P = 0.83$; $t_{14} = 0.14$, $P = 0.89$, respectively) or in experiment 2 ($t_{14} = 1.12$, $P = 0.28$; $Z = 0.94$, $N = 15$, $P = 0.35$; $t_{14} = 0.11$, $P = 0.91$, respectively).

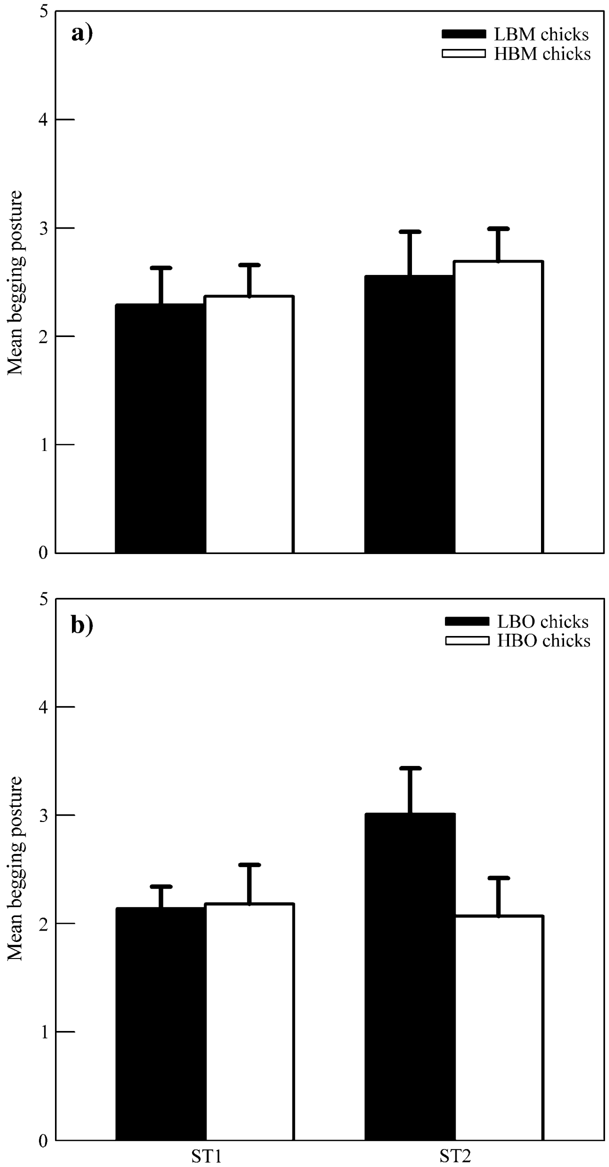

**Figure 2**
Means + standard error values of nestling begging postures in the STs before and after the training sessions of experiments 1 (a) and 2 (b). LBM, rewarded for low begging mostly; HBM, rewarded for high begging mostly; LBO, rewarded for low begging only; HBO, rewarded for high begging only.

Figure 2 shows the begging posture scores of the 2 treatment groups in experiments 1 and 2 before and after the training sessions (ST1 and ST2, respectively). In experiment 1 (Figure 2a), there was no difference in the mean begging scores of the 2 treatment groups after the training session (ST2; $t_{14} = 0.21$, $P = 0.83$) or in the change (arithmetic difference) between ST1 and ST2 ($t_{14} = 0.17$, $P = 0.91$). In experiment 2 (Figure 2b), there was a significant difference at ST2 ($t_{14} = 2.3$, $P = 0.037$), but it was in the opposite direction to that predicted by the treatments (the LBO chicks used more erect body postures). There was no significant difference in the change in begging between ST1 and ST2 ($t_{14} = 1.68$, $P = 0.11$). There was also no difference in the begging postures applied by the 2 treatment groups during the training sessions of the 2 experiments (the data of the 40 trials adjusted for variation in the time interval between meals; see Methods),

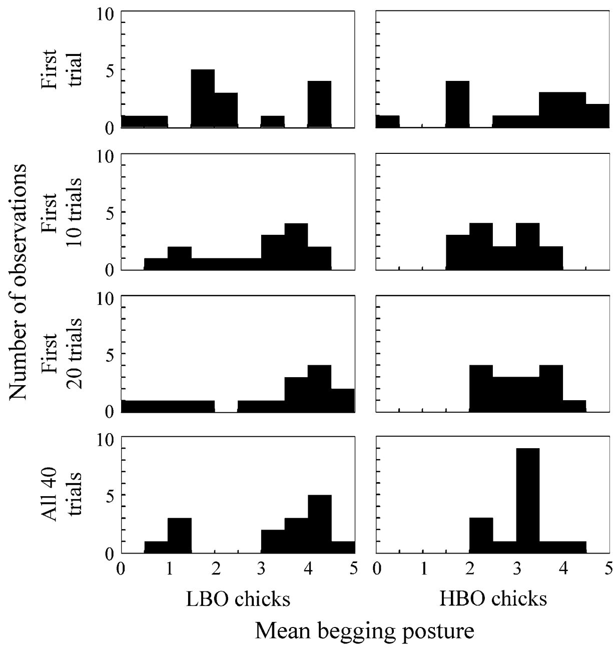

**Figure 3**
Histograms showing mean begging scores of the nestlings in the first 1, 10, 20, or all 40 trials of the training session for the LBO (rewarded for low begging only; left panel) and HBO (rewarded for high begging only; right panel) chicks of experiment 2.

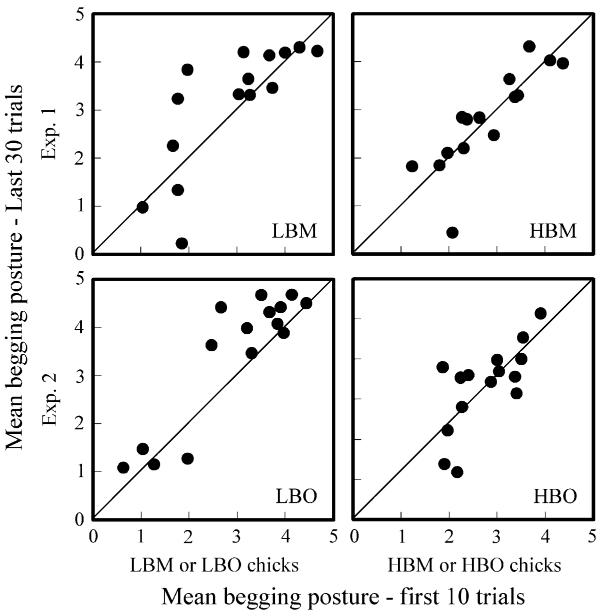

**Figure 4**
Mean begging postures used in the last 30 trials plotted against mean begging postures used in the first 10 trials of the training session for experiments 1 (top panels) and 2 (bottom panels). (Each data point represents a specific nestling.) LBM, rewarded for low begging mostly; HBM, rewarded for high begging mostly; LBO, rewarded for low begging only; HBO: rewarded for high begging only.

with or without the begging posture at ST1 as a covariate ($F_{1,13/14} < 0.6$, $P > 0.4$ for the treatment effect in all models). Altogether, there was no evidence that reinforcing either erect or not-erect begging postures with high probabilities of being fed can create differences in begging behavior.

Analysis of the distribution of begging postures during the training sessions might explain the above results. The analysis of these 40 trials shows an interesting trend that was especially pronounced in the more extreme case of experiment 2 and is illustrated in Figure 3. While the distribution of begging postures in the first trial of the training session was similar for both treatment groups, as the session progressed, this distribution became bimodal in the case of the LBO chicks but not in the case of the HBO chicks (compare the bottom panels of the 2 treatment groups in Figure 3). This different distribution can be characterized by the nonhomogeneous variances of the LBO and HBO groups (Levene's test: $F_{1,28} = 12.08$, $P = 0.0016$) and suggests that a simple comparison of group means (i.e., Figure 2) may overlook the real experimental effect. The bimodal distribution of the mean begging postures used by different LBO chicks suggests that those LBO chicks whose begging average lies within the high posture score range did not explore the not-erect postures. Moreover, because they were never fed for their usually erect begging postures, they presumably became hungrier, continuing to apply erect begging postures as expected by their increasing begging response function to need. On the other hand, those LBO nestlings whose begging average lies within the not-erect range might simply have fortuitously started the training session with low begging postures that guaranteed food reward and therefore kept using low postures only either because they had become satiate or because, in addition, they had learned that low postures were highly successful. The lower number of such LBO chicks in comparison to the LBO chicks using high begging posture (see Figure 3, bottom left panel) could explain the slightly higher mean of LBO chicks' begging at ST2 (Figure 2b).

To further explore these possibilities, we plotted for each nestling the average begging posture applied during its last 30 trials of the training session against that of its first 10 trials. This plot (Figure 4) shows that when LBM chicks, and especially LBO chicks, had happened to start the training session using erect postures (right hand side of each plot), they continued to use high postures later on (in most cases even higher postures than before, with data points above the equality line). On the other hand, the only nestlings in the LBM or LBO treatments that were able to end the experiment with low begging postures were those that had started the training session with low postures (left hand side of each plot). Note that no such partitioning of the data was observed for the HBM or HBO chick groups, in which there was no conflict between the postures rewarded by the experimenter and those favored by hungry nestlings based on their innate behavioral response function.

## Experiment 3

At the beginning of the experiment, there were no significant differences between the 2 treatment groups in nestling mass (see Table 1), relative rank in the brood (Wilcoxon matched pair test $Z = 0.17$, $N = 28$, $P = 0.86$), or in the average begging score in ST1 (the ST before training: Figure 5a, $t_{27} = 0.56$, $P = 0.58$). Although the latter difference was not significant (see Figure 5a, ST1), we later cautiously included this initial begging level as a possible confounding variable when testing differences in begging during the training session (see below). After the first training session, the begging postures showed a trend in the expected direction (Figure 5a; after they had experienced the HBO treatment, HBO-AB chicks used more erect postures in ST2 than in ST1, whereas AB-HBO chicks used lower postures in ST2 than in ST1). However, this trend, as measured by the arithmetical difference between ST1 and ST2 posture scores, was not significantly

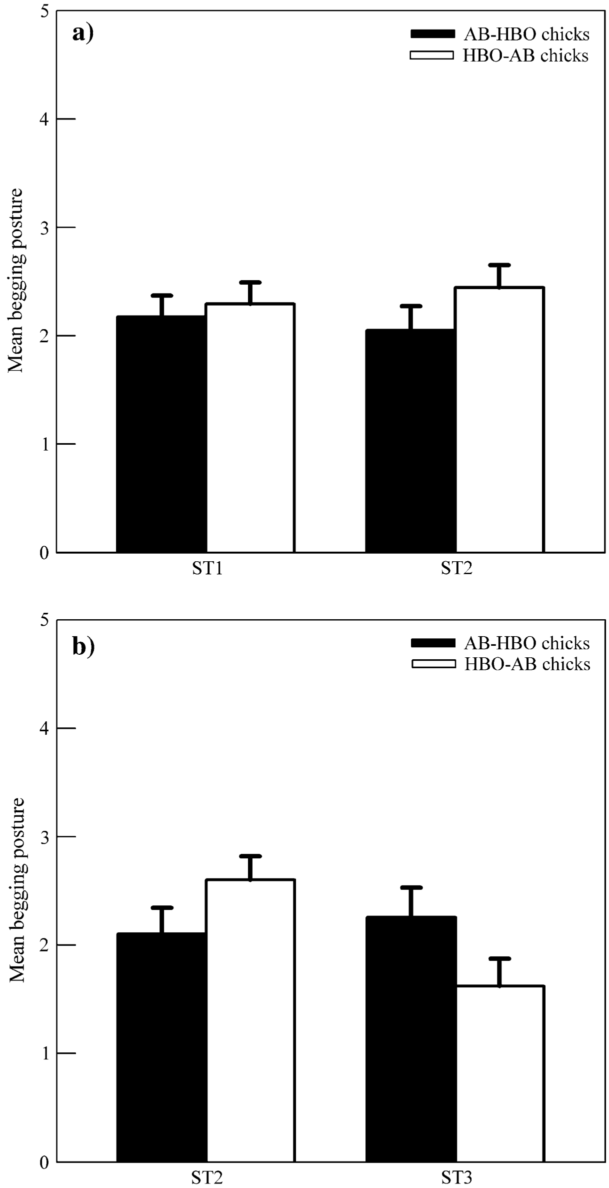

**Figure 5**
Means + standard error values of nestling begging postures in the STs before and after the first (a) and second (b) training sessions of experiment 3. AB-HBO: rewarded for "any begging" in the first session and for "high begging only" in the second. HBO-AB: likewise but in the reverse order.

different between treatment groups ($t_{27} = 1.64$, $P = 0.11$). In the second half of the day, (Figure 5b) this trend was reversed, as expected from the treatments being switched between nestlings. This time, the change in mean begging posture from the second to the third STs differed significantly between the experimental groups ($t_{23} = 2.4$, $P = 0.025$).

In addition to the above results, which were based on begging behavior during the 3 STs, we also had detailed measurements of the begging postures used during the 28 begging trials of each training session. Before analyzing these data, we first verified that the 2 experimental groups had similar distributions of mean begging postures (as opposed to experiment 2 results), by confirming the homogeneity of their variances (session 3a: Levene's $F_{1,54} = 0.04$, $P = 0.84$; session 3b: Levene's $F_{1,46} = 0.64$, $P = 0.43$). We then calculated, for each nestling, a mean adjusted begging posture for each training session. The adjusted begging posture was calculated to statistically control for differences in short-term need variables (see statistical methods) that emerged during the experiment (see Table 1).

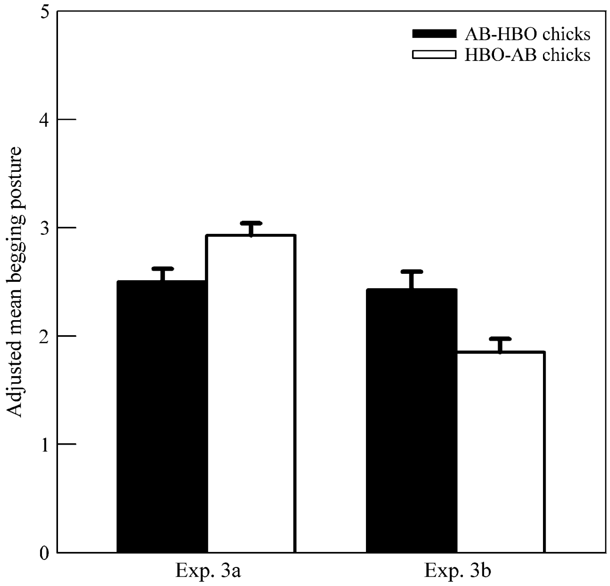

**Figure 6**
Means + standard error values of nestling adjusted begging postures in the first (experiment 3a) and second (experiment 3b) training sessions of experiment 3. AB-HBO: rewarded for "any begging" in the first session and for "high begging only" in the second. HBO-AB: likewise but in the reverse order.

The adjusted begging postures of the 2 treatment groups in the first and second training sessions of experiment 3 are depicted in Figure 6. In the first training session, HBO-AB chicks (rewarded only for high begging intensity in this session) exhibited higher begging postures than AB-HBO chicks (rewarded for any begging) ($F_{1,27} = 8.88$, $P = 0.006$). In the second training session, when these treatments were switched, HBO-AB chicks began to use less erect body postures than AB-HBO chicks (Figure 6; experiment 3b; $F_{1,23} = 7.65$, $P = 0.011$). These differences were even more significant when the initial begging scores (in the ST before the relevant training session) were included as an additional covariate in the model (session 3a: $F_{1,26} = 9.56$, $P = 0.0047$; session 3b: $F_{1,22} = 16.01$, $P = 0.0006$). Finally, we note that neither training session resulted in remarkable differences in the nestlings' mass gain during the half-day sessions (Table 1).

## DISCUSSION

In light of accumulating evidence for the possible role of learning in nestling begging (Kedar et al. 2000; Rodríguez-Gironés et al. 2002; Kölliker and Richner 2004; Budden and Wright 2005), we carried out 3 experiments to explore how different reinforcement regimes affect begging levels. We focused on the question of whether hungry nestlings can learn to reduce their begging when high begging is less successful or, rather, whether they must first acquire positive experiences with low begging levels in order to do so. We should first clarify that while we believe that our experiments shed light on the above question, we acknowledge that their results alone cannot be used as proof that learning was indeed involved in these cases. This is because in experiments 1 and 2, the simple training regime was unsuccessful in reducing begging levels, and in experiment 3, where it was apparently successful, we cannot completely rule out (despite the statistical control) the possibility that group differences were caused in whole or in part by differences in hunger or need. As we discuss below, the behavioral response of increasing begging when hungry makes it very difficult to train nestlings to beg at different levels without the risk of somehow affecting their level of need. Bearing this in mind, we discuss learning rules as possible explanations of our data rather than as a proven fact (for a similar approach, see Erev and Roth 1998 on human decision making and Luttbeg and Langen 2004 on animal foraging behavior).

### Can nestlings be trained to reduce begging?

The results of this study suggest that if learning is involved in shaping nestling begging, it must be strongly affected by the nestlings' instinctive tendency to increase begging with hunger. Although the method used in experiment 3 (and also by Kedar et al. 2000) was successful in creating differences in begging levels, the seemingly more simple reinforcement regimes of the first 2 experiments failed. The reinforcement regime of LBM and LBO chicks was intended to lower begging levels by rewarding mostly (LBM, experiment 1) or only (LBO, experiment 2) low begging postures. However, our results suggest that this caused nestlings that happened to start the experiment with high begging postures to become hungrier and therefore to be "stuck" in the high posture zone without being able to explore lower postures and learn that these could have been highly successful (Figures 3 and 4). Their tendency to increase begging when hungry (Kilner and Johnstone 1997 and references therein) thus appears to have impaired their ability to explore and thereby learn the high profitability of low begging postures. These findings imply that nestlings are unlikely to be able to learn to use less intensive begging when begging has proved unsuccessful (as suggested by Stamps et al. 1985, 1989; Lotem 1998a; and Wright et al. 2002); but, rather, they require positive experience with less intensive begging in order to do so (as suggested by Lotem and Winkler 2004, for human infants). It is possible that if we had continued the LBM or LBO treatments for an extended period of time the high beggars among those nestlings would eventually have become exhausted. Such fatigue might have led to a reduction in begging intensity, which would then have allowed them to learn the success of these less erect postures. This possibility should be explored further but would appear quite costly as a potential method for the parents to reduce begging.

An alternative strategy for lowering begging levels (a feed-first strategy) is suggested by the apparent success of the method used in experiment 3. Accordingly, attending to a nestling's needs as soon as possible could enable it to beg less intensely and to learn that low begging postures are sufficiently effective. The results of the second training session of experiment 3 show that by switching the feed-first treatment between groups, the emerging differences of the first session can be reversed (see Figures 5 and 6). An alternative explanation for this reversal is that nestlings that begged more intensely in the first half of the day (HBO-AB chicks) were simply tired by the second half of the day. However, this seems unlikely given that nestlings of the same species and similar age that were under an HBO treatment throughout the day showed no reduction in their begging levels ("chick 2" in Kedar et al. 2000). The results of both sessions suggest, therefore, that if nestlings can be trained to reduce their begging, the feed first method is probably the way by which it can be done. It is interesting to note that a similar strategy of attending to offspring needs as soon as possible was applied with some success to reduce crying in human babies, where simply ignoring colicky crying was apparently unsuccessful (Taubman 1984; see also Wells 2003; Lotem and Winkler 2004).

### Can learned effects be distinguished from need?

Because the treatment groups in experiment 3 were subjected to different regimes, it can be claimed that even after carefully controlling for the measured need variables (see Methods), there may still be some "remaining variation in need" that has not been measured and could be responsible for the different begging intensities. For example, we cannot be certain that the higher begging postures of chicks under HBO treatment did not entail some higher begging costs that created differences in some hidden aspects of nestling need (Kacelnik A, personal communication). In fact, the difficulty in refuting this argument stems directly from the broad definition of "need" as the expected fitness gain from receiving extra resources (Godfray 1991, 1995; see also Godfray and Johnstone 2000; Parker et al. 2002; Grodzinski and Lotem 2007), which makes it very hard to control (experimentally or statistically) for all imaginable factors that could potentially influence this need. This problem of remaining variation in need is also likely to arise when trying to assess how much of the natural variation in begging can be explained by learning, as well as by other factors such as relative rank and competition levels (i.e., by their direct effect on begging levels and not their need-mediated effects). Unfortunately, there seems to be no easy solution to this problem. In contrast to cases where nestlings learn the more profitable location at the nest (Kölliker and Richner 2004; Budden and Wright 2005), learning the more profitable begging intensity can always be confounded by some cryptic variation in need. However, although we cannot really prove that learning was involved, it may not be productive to ignore its possible role just because such proof is inherently difficult to obtain. We believe that the most productive way would be to carefully consider learning mechanisms as possible explanations of begging data without ruling out alternative explanations. Future work may eventually reveal whether learning models have better explanatory power than nonlearning ones.

### Learning and parent–offspring relationship

Although providing unequivocal evidence for learning effects on begging levels may continue to be difficult, our results clearly suggest the type of learning mechanism that should be considered if learning is indeed involved in this species. The success of the feed first method (AB treatment) in reducing begging levels, as opposed to the failure of the method of experiments 1 and 2 (LBM and LBO treatments, respectively), suggests that if house sparrow nestlings can learn to reduce begging, this can happen only through positive experience with low begging intensities and will not follow negative experience with high begging intensities. It is interesting to note that learning of this type can help nestlings and parents to reduce begging and minimize begging costs only under good conditions. Under such conditions (or when parents are good providers), nestlings are likely to be fed before they become hungry and escalate their begging level, which allows them to be rewarded for low begging and learn that a moderate begging strategy is sufficiently effective. Under poor conditions, on the other hand, this type of learning (as opposed to learning to reduce begging when it is unsuccessful, see above) may lead to an inefficient escalation in begging because hungry nestlings will not learn to reduce their high begging even when it is unsuccessful. Simply said, learning can potentially make the "rich" richer, by minimizing the cost of begging, and the “poor” poorer, by leading to inefficient escalation in begging (a prediction supported so far by a computer simulation of learning rules in begging behavior; Biran 2004). At the population level, such learning dynamics may result in a negative correlation between parental provisioning and offspring begging, which can potentially interact with the genetically based positive or negative correlation between these traits that was suggested by several recent studies (Kölliker et al. 2000; Agrawal et al. 2001; Lock et al. 2004).

The learning type suggested by our study may be adaptive for the nestling for 2 reasons: First, by applying low begging levels that are sufficiently effective in eliciting parental provisioning under good environmental conditions (or in the absence of strong competition), nestlings can save begging costs (as suggested by Cotton et al. 1999, for “senior” nestlings, which can occupy preferable positions in the nest). It is not yet clear whether begging costs are high enough to make this worthwhile, as the growth costs of begging were found to be substantial in some studies (Rodríguez-Gironés et al. 2001, for magpies; Kilner 2001) but not in others (Kedar et al. 2000; Rodríguez-Gironés et al. 2001, for ring doves; Leonard et al. 2003). Second, when the level of food supply is low, this type of learning can still generate competitive begging levels (which may be better on the average than a tendency to reduce begging when unsuccessful). It is still not clear how learning affects begging “honesty” and the stability of parent–offspring communication. The effect of learning on begging intensity implies that begging reflects more than just the nestling’s expected gain from receiving extra resources (or need; see Godfray and Johnstone 2000; Parker et al. 2002). Affected by past experience, begging can also reflect differences in begging effectiveness between nestlings raised under different environmental conditions or with different competitive abilities (Cotton et al.1999; Kedar et al. 2000; Rodríguez-Gironés et al. 2002; Wright et al. 2002). In other words, asymmetry in begging costs or effectiveness among nestlings can create some level of “dishonesty” in nestling begging (as suggested by Johnstone and Grafen 1993 and Lotem 1993 for some sexual signals). Despite this asymmetry, parent–offspring communication may remain stable if begging is still honest “on average” (Johnstone and Grafen 1993). This is likely to be the case at least for food allocation within the brood because learned differences in begging should still be correlated with differences in need: needy nestlings learn to escalate their begging, whereas less needy nestlings learn to reduce it. On the other hand, the overall intensity of brood demands can potentially be inflated (or attenuated) by learning and may therefore require some parental strategy to cope with such deviations. Although our results suggest that begging levels cannot be reduced by simply ignoring high begging, parents may nevertheless be able to lower their provisioning response to begging in order to correct for the newly inflated levels of begging. It will be interesting to explore the mutual adjustments by both parents and offspring that learning suggests in light of recent consideration of behavioral adjustments in evolutionary game theory modeling (negotiation Evolutionarily Stable Strategy models regarding sexual conflict over care: McNamara et al. 1999; Johnstone and Hinde 2006; and parent–offspring conflict: Johnstone RA, unpublished data). For example, future theoretical exploration of parent–offspring communication may benefit from including explicit learning rules (that modify the begging response function to changes in need) as part of the model’s evolving strategy set.

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