Behavioral Ecology Vol. 7 No. 2: 178–182

# Chick begging as a signal: are nestlings honest?

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Begging by dependent avian offspring is known to correlate with hunger level, and parents use this as a signal of brood demand to adjust their chick feeding behavior. While there is information on how each chick adjusts its begging to its own condition, little is known of how chicks adjust to the state of their nest mates. In two experiments we manipulated the competitive environment of individual European starling (*Sturnus vulgaris*) chicks by altering the state of nest mates while holding the state of target chicks constant. In the first experiment we placed the target chick's nest mates in neighboring nests with brood sizes of two, five, or eight chicks. Following the manipulation we returned them to their own nests and recorded begging behavior on videotape. In the second experiment we separated a target chick from its siblings and manipulated feeding level in the laboratory. The siblings were fed at one of three levels; meanwhile, all the target chicks were fed at the intermediate level. After the manipulation we placed the target chicks with their siblings and recorded their begging in response to an artificial stimulus. In neither experiment was the begging effort of the unmanipulated target chicks affected by the changes in begging behavior of their siblings. This result supports the view that begging is a reliable signal of individual chick state and does not involve responses to the effort of nest mates. *Key words:* begging, parent-offspring conflict, signaling, starling, *Sturnus vulgaris. [Behav Ecol 7:178–182 (1996)]*

The young of altricial birds are entirely dependent on their parents to feed them from hatching to fledging. Von Haartman (1953) first demonstrated that chick begging is a stimulus to parental feeding and that the begging level of the brood increases with deprivation. It seems clear that the begging behavior of the young acts as an important factor in the proximate control of parental feeding intensity, and this has been confirmed in both empirical (e.g., Bengtsson and Rydén, 1983; Henderson, 1975; Khayutin and Dmitreva, 1979) and theoretical studies (e.g., Godfray and Parker, 1992; Harper, 1986). This implies that chicks beg at a level dictated by their own need, but does not necessarily mean that they will act independently of the begging levels of their brood mates (Harper, 1986; Parker, 1985; Stamps et al., 1978). If chick begging functions as a signal to influence parental distribution of food within the brood, the begging strategy of individual chicks may be influenced by the begging of their siblings (Eshel and Feldman, 1991; Harper, 1986; Macnair and Parker, 1979). Behavioral strategies of chick begging may therefore arise from the selective pressures of sibling competition as well as nutritional requirements.

Sibling competition and parent-offspring conflict have been the subject of numerous theoretical studies concerning inter- and intrabrood relationships (Clark and Ydenberg, 1990a,b; Eshel and Feldman, 1991; Feldman and Eshel, 1982; Godfray, 1991; Godfray and Parker, 1992; Macnair and Parker, 1978, 1979; Parker, 1985; Parker and Macnair, 1978, 1979). In addition, recent theories concerning signal selection have provided a conceptual framework with which to consider the evolution of chick begging (Grafen, 1990; Johnstone and Grafen, 1992; Maynard Smith, 1991; Zahavi, 1987). Such a signaling system has to regulate both parental provisioning and the behavior of chicks so that modeling the evolutionary stability of possible behavioral strategies is a complex task (Godfray, 1995).

Because competition between chicks in a nest is likely to be between siblings, the evolution of begging strategies must be examined in the context of kin selection. This leads to potentially contradictory expectations. If the marginal benefit resulting from an extra unit of food to a sibling was twice that to a chick itself, then the chick might be expected to accrue a greater benefit by reducing its begging effort in response to an increase in begging by its sibling so that the food was directed to its hungrier sibling. However, if the nest mate's benefit is less than that, the intensity of competition in the nest might favor "selfish" competitors, and chicks may respond to the begging of other brood members by escalating their own begging rates (Harper, 1986; Stamps et al., 1978). An extreme outcome of such intense begging competition is the death of some of the chicks, and siblicide is a common occurrence when competition between nestlings is aggressive (Mock, 1984, 1987; Mock et al., 1990).

A complicating factor is that begging has, in addition to its effect on distribution of food among nestlings, the effect of increasing the overall provisioning effort of the parent (e.g., Bengtsson and Rydén, 1983), so that a chick's begging effort at one moment may be rewarded even if it leads to no immediate feeding.

Because actual fitness costs and benefits are hard to measure, few empirical investigations have been able to test predictions arising from theoretical models of begging and parent-offspring conflict, and most studies to date have concentrated on establishing basic relationships in these systems (Gottlander, 1987; Gowaty, 1983; McRae et al., 1993; Teather, 1992). Although it is often stated that chicks alter their begging behavior in response to factors other than their own nutritional state (e.g., McRae et al., 1993; Redondo and Castro, 1992), the evidence for this is scant and equivocal. Muller and Smith (1978) demonstrated that the frequency of chick begging and parental feeding was increased by playing recorded begging calls. However, they were unable to separate the effects of the calls on the parent and the chicks, and concluded that the playback affects both parents and offspring to initiate a feeding sequence. Smith and Montgomerie (1991) used a

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Received 8 March 1995; revised 13 June 1995; accepted 16 June 1995.

food deprivation experiment to examine the effects of hunger on begging intensity. They report a weak correlation between the time spent begging by control nestlings and their food-deprived siblings. However, their manipulation affected the state of both the control and experimental nestlings.

Kacelnik et al. (1995) manipulated European starling (*Sturnus vulgaris*) chicks by temporarily placing individual chicks in nest-boxes with varying brood sizes and then returning them to their original nest for observation, while controlling for the state of siblings. The chicks responded to being manipulated by changing their begging behavior according to the brood size during the displacement, but their unmanipulated siblings did not show any treatment effect. This suggests that chicks do not interact by adjusting their begging to the effort of their nest mates. This lack of adjustment is compatible with the possibility that chicks signal with intensity proportional only to their own needs (i.e., "honestly"), however, the experiment may have failed to show an effect because only one of five chicks was manipulated, and thus the treatment may not have produced a strong enough effect to influence the other brood mates.

In this study we used both field and laboratory experiments to examine the response of an individual chick's begging effort to changes in the behavior of its brood mates.

## METHODS

To assess the effects of changes in sibling condition on begging effort, we manipulated nest mates either by placing them in natural nests with a range of brood sizes or by feeding them at different levels in the laboratory.

The hunger or nutritional state of chicks can be manipulated by hand feeding (e.g., Litovitch and Power, 1992; Redondo and Castro, 1992). However, unless chicks experience the changes in provisioning rate as part of real broods, conditions of sibling competition are not maintained. In natural broods the number of parental feeding visits per chick, and weight gain per day by chicks, are negatively correlated to brood size (Wright and Cuthill, 1990a,b). As brood size increases, the begging noise level of the starling broods increases (Wright and Cuthill, 1990b) so that sibling competition is expected to be more intense in larger broods. Experience in larger broods therefore reduces feeding rates as well as increasing the intensity of begging stimuli perceived by the chick itself (see Kacelnik et al., 1995).

### Experiment 1

The study was conducted on a colony of European starlings at the University Farm, Wytham, Oxford, UK. Forty-eight of the nest-boxes on the farm are attached to sheds, allowing access to the rear of the boxes for filming. All pairs used in the present study were monogamous (i.e., both male and female directed their attentions exclusively to one nest, resulting in full-time biparental care).

Between 5 and 13 May 1994, the broods of ten "target" nests were standardized to contain five chicks of approximately equal weight and with a hatching interval of less than 24 h. The median weight chick of each target nest was selected as the "target" chick. In order to manipulate begging effort, on three successive days we placed each of the four siblings of each target chick in a "manipulation" nest with a total of two, five, or eight chicks. To control for the order of the treatments, the target nests experienced these manipulations in a random order. The chicks remained in the manipulation nests from 1500 until 0900 h on the following day. During this time other chicks of similar age and weight were placed into the target nest with the target chick, thereby maintaining "normal" five-chick parental feeding and chick begging rates during the other chicks' absence.

At 0900 h the manipulated chicks were returned to their nests and the substitute chicks removed. Video recordings of the target nest were then made from 0900 until 1200 h. Natural light levels within the boxes were sufficient for camera operation and the parent birds rapidly became habituated to the camera's presence. To allow identification on the video recordings, chicks were individually marked on their head with acrylic paint. From previous work this is known not to affect noticeably parental or chick behavior (Kacelnik et al., 1995).

Each videotape was numbered and the details of the tape were recorded separately. This provided a control against observer bias in the analysis of the tapes, with data being matched to treatment after all the videos had been analyzed and the data extracted. Behavioral data was collected from the video recordings for the first 25 parental feeding visits (approximately 1 h) to the target nests using the same protocol as Kacelnik et al. (1995). Chick begging effort during a parental visit was quantified into three categories: 0) no effort, 1) extended neck and gape, 2) full stretch (standing) and gape. Categories 1 and 2 were accompanied by loud begging calls. Target chick position was recorded on a scale of 1 (closest) to 5 (furthest), as a function of the target chick's position in the brood relative to the nest-box entrance. Because the effect of the manipulation is likely to be modified by cumulative parental visitation and feeding, only the first five visits were considered in the principal analysis. Analyses over all 25 visits gave qualitatively similar results.

All data presented here were recorded in the target nest following two-, five-, or eight-chick manipulations on the target chick's siblings. Each nest experienced all treatments, so the effects of manipulation were analyzed using repeated measures ANOVAs (with treatment as the repeated measure) on the mean values over 5 visits and over 25 visits.

### Experiment 2

When chicks were 3 days old, we manipulated broods of starlings nesting at the Wytham colony so that 10 nests contained four equal-sized and -aged chicks. From day 5, on three successive mornings, three chicks were removed from the nest and taken into the laboratory for 5 h. The median-sized chick from each nest was selected and its head marked with white acrylic paint. These target chicks were always placed with two other target chicks and were fed two food items every 30 min. On successive days the other two chicks from each brood received, in random order, either one, two, or three food items every 30 min. These manipulation chicks were also kept in "broods" of three, all of which received the same treatment. The food items used were a mixture of pastry and dried insects (Orlux®), in equal parts, with water added to make a soft consistency. The mixture was extruded through a syringe to form cylinders (5 mm in diameter) that were then cut into 10 mm lengths.

After 4 h, during which the chicks experienced one of the experimental feeding levels, they were placed with their original nest mates so that each target chick was accompanied by two chicks that had received one of the three treatment levels. The chicks were then stimulated to beg without being fed and their behavior recorded on videotape until there was a gap of 5 s without any begging. This test was repeated three times. The analysis of the videotapes was conducted blind regarding treatment. From each video we recorded the order in which chicks started begging (latency), the begging score (0, 1, or 2; as in Experiment 1), and the total amount of time each

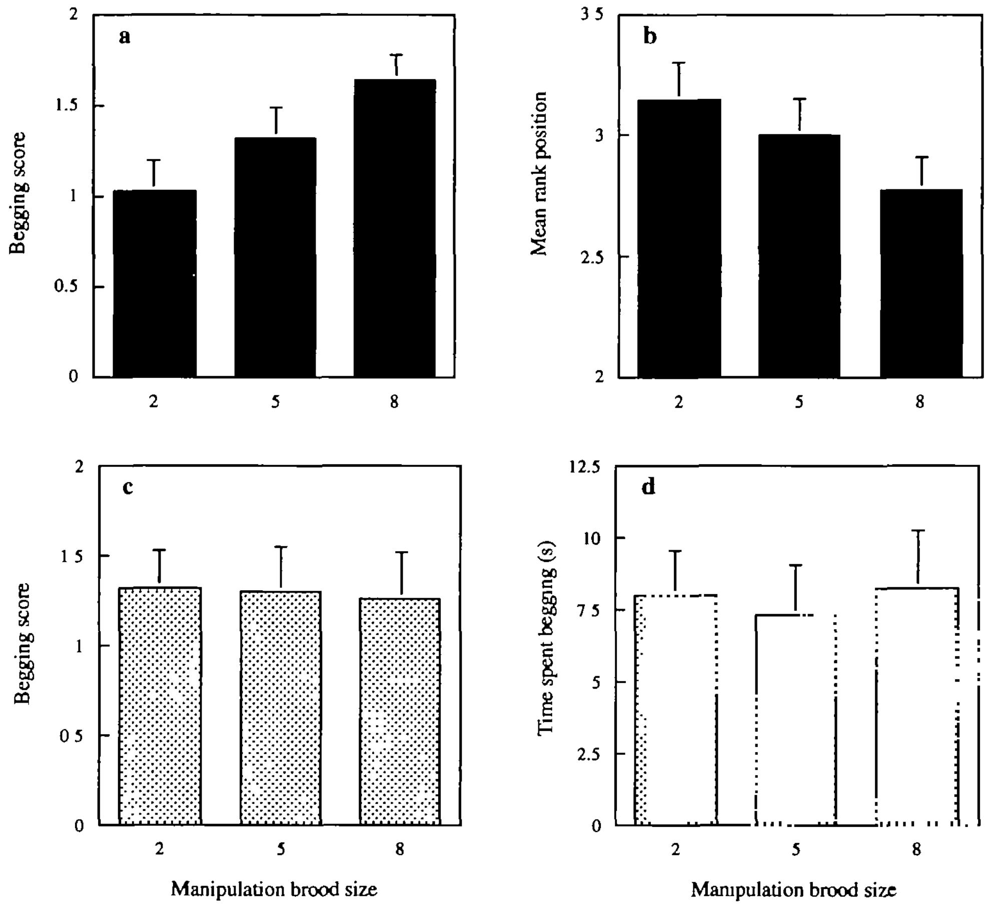

**Figure 1**
The effect of manipulation brood size on (a) the mean (+ SE) begging score of the manipulated chicks (0 = no begging, 1 = begging from sitting position, 2 = begging with fully stretched legs); (b) the mean (+ SE) rank position of the manipulated chicks (rank proximity to the nest entrance, 1 = closest); (c) the mean (+ SE) begging score of the target chick; and (d) the mean time (in seconds + SE) spent begging by the target chick; $n$ = 10 for all bars.

chick spent begging. All analysis was conducted using repeated measures ANOVA on the mean value for the three trials.

## RESULTS

### Experiment 1

The manipulation significantly affected the behavior of the manipulation chicks; their mean begging effort was significantly different between treatments ($F_{2,9}$ = 5.50, $p$ = .014; Figure 1a), with chicks from the eight-chick manipulation achieving the highest begging scores and those from the two-chick manipulation the lowest.

Treatment also significantly affected the nest positions occupied by the manipulated chicks ($F_{2,9}$ = 5.29, $p$ = .015; Figure 1b); this in turn influenced the rank position in the nest of the target chick, since the two are not independent. Following the eight-chick manipulation, chicks positioned themselves nearer to the entrance of the nest-box with respect to the target chick. After the two-chick manipulation the reverse was true, and the manipulated chicks tended to position themselves more to the rear of the nest than the target chick. Although their rank position in the nest was affected, target chicks did not alter their begging level in response to the behavior of their nest mates ($F_{2,9}$ = 0.01, $p$ = .994; Figure 1c), nor did they adjust the amount of time they spent begging ($F_{2,9}$ = 0.06, $p$ = .945; Figure 1d).

Analysis of the data over 25 visits gave qualitatively similar results, indicating that the effects of such manipulations are present for as long as 1 h, and that even given a longer period in which to adjust to the changes in sibling behavior, the target chicks did not respond by altering their own begging.

### Experiment 2

The manipulation had a significant effect on the manipulated chicks' latency to start begging ($F_{2,9}$ = 16.14, $p$ < .001; Figure 2a), their mean begging score ($F_{2,9}$ = 15.22, $p$ < .001; Figure 2b), and the amount of time which they spent begging ($F_{2,9}$ = 9.38, $p$ = .002; Figure 2c).

Chicks previously fed one pellet every 30 minutes were the first to start begging, begged the longest, and begged at constantly high levels. Those that had been fed three pellets every 30 min often showed only a weak begging response, sustained over a short period.

In spite of these changes in their siblings' behavior, the unmanipulated target chicks did not respond by significantly altering their begging. There was no significant effect of treatment on the mean begging score of the target chicks ($F_{2,9}$ = 1.87, $p$ = .183; Figure 2b) or the amount of time the target chicks spent begging ($F_{2,9}$ = 0.15, $p$ = .859; Figure 2c). Rank latency to beg was significantly affected ($F_{2,9}$ = 16.14, $p$ < .001; Figure 2a), but it is not independent of the behavior of the manipulated chicks.

## DISCUSSION

### The reliability of begging as a signal

In both experiments the treatments produced highly significant changes in the behavior of the manipulation chicks. In spite of this, target chicks showed no detectable adjustment in their begging behavior. Significant changes were found in the rank latency and position of unmanipulated target chicks, but these rank scores are not independent and probably re-

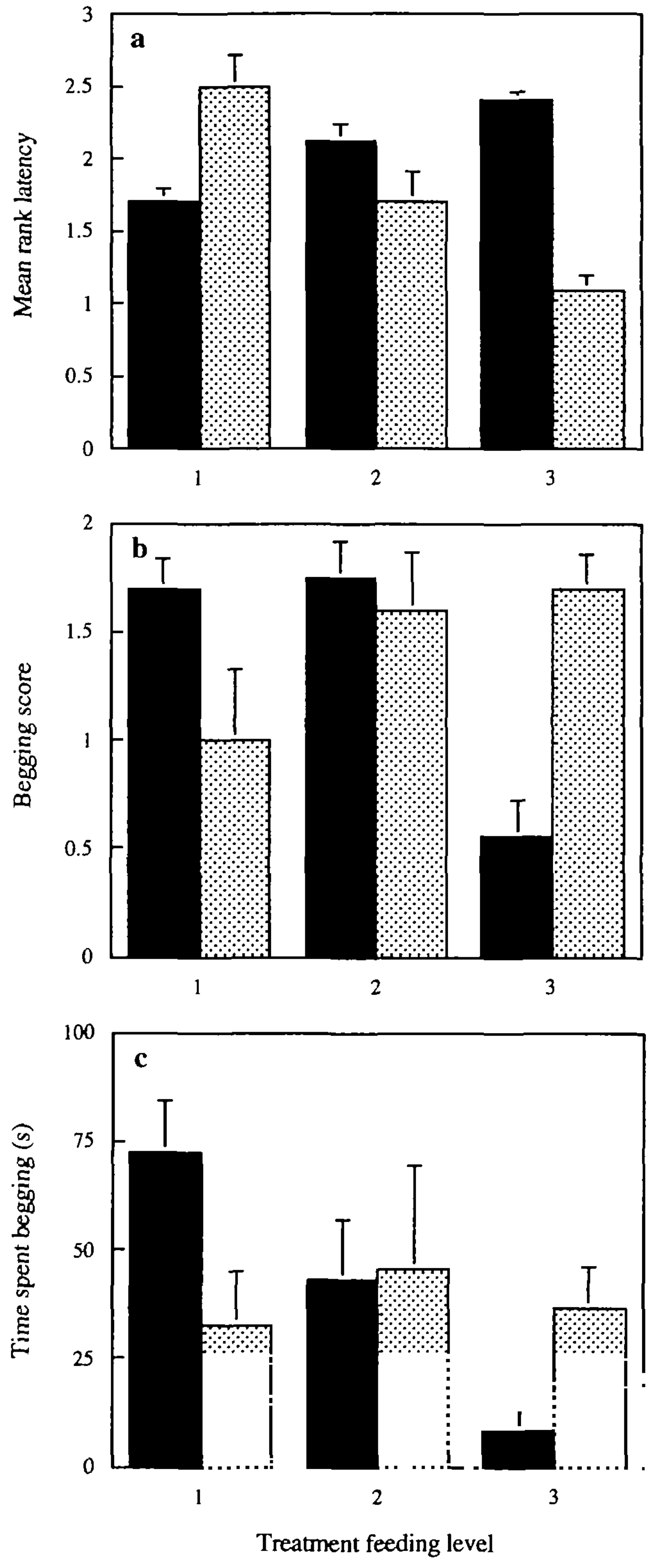

**Figure 2**
The effect of treatment feeding level (1 = lowest) on (a) the mean rank latency to beg by the manipulated chicks (■) and their unmanipulated target sibling (■); (b) the mean (+ SE) begging score (0 = no begging; 1 = begging from sitting position; 2 = begging with fully stretched legs); and (c) the mean (+ SE) time spent begging; *n* = 10 for all bars.

flect the behavioral changes of the manipulated chicks rather than an active response by the target chick.

These results support the view that chick begging is a relatively reliable indicator of short-term changes in chick state, and does not involve any changes in relation to the begging effort of brood mates. Recent theoretical treatments of chick begging as a signal consider the implications of such "honesty," and conclude that the relationship between a parent and a single offspring could be stable if the chick signals at a rate strictly determined by its condition and the parent allocates resources using this as an accurate indicator of chick condition (Godfray, 1991).

A number of empirical studies support the idea that parents allocate resources among members of each brood in proportion to chick begging behavior (e.g., Kacelnik et al., 1995; Litovitch and Power, 1992; McRae et al., 1993; Smith and Montgomerie, 1991). This study demonstrates clearly that, even when facing varying competition from siblings, chicks signal in relation to their own condition.

Although our conclusion hinges on the acceptance of the null hypothesis, we have made an effort in designing the experiment so as to maximize the chances of showing an effect if an effect were there. We cannot for the moment exclude the possibility that more discriminating measures of effort by the chicks might show an effect, but until that happens, the most parsimonious conclusion is the temporary acceptance of the absence of effects.

In his recent model of a single parent feeding two chicks, Godfray (1995) showed that the optimal level of solicitation of a chick is dependent primarily on its own condition and to a lesser extent on the condition of its nest mates. This comparatively small effect of sibling behavior on a chick's begging could be overlooked in natural data, but given the strength of our treatments one would expect to see such trends in the present data sets. Our observations of chick behavior show no sign of a trend in the direction predicted by Godfray's model.

In extending his model to consider the cost of reproduction, Godfray (1995) showed that the influence of the begging effort of nest mates is less strong if the costs of provisioning are borne by future broods rather than the current brood. However, we believe that the discrepancy arises through Godfray's assumption that, "the period of parental care can be divided into a series of episodes whose outcome has an independent effect on future lifetime fitness." If chick begging strategies are shaped by their effect on future visits as well as the present one, the evolutionary equilibrium could be different. This is because even if a chick is not fed, its begging effort may increase parental provisioning and hasten the next visit. Exerting control on future parental provisioning rate may at times be more beneficial than engaging in an escalatory contest for the present food item.

## Conclusions

By placing companion chicks in broods at the extremes of the natural range of sizes, we produced short-term effects on their begging behavior. The begging effort of the unmanipulated target chicks was, however, not influenced by changes in the begging effort of their manipulated siblings. The laboratory experiment revealed similar results; target chicks did not alter their behavior in response to changes in the behavior of their nest mates. Although it is impossible to demonstrate the validity of the null hypothesis, the absence of observable trends and the strength of our treatments suggest a lack of effect of treatment on the unmanipulated chicks. These two results, taken together with those of Kacelnik et al. (1995) indicate that begging effort is a reliable indicator of individual chick state which is not influenced by the competitive environment within the nest.

Richard Warren assisted with the field work and analysis of videotapes. This work was funded by a Natural Environment Research Council grant (GR3/9239) to A.K.; J.W. is funded by an NERC postdoctoral fellowship. We are grateful for comments made by Charles Godfray and an anonymous referee.

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