

Feeding experience and relative size modify the begging strategies of nestlings

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The offspring of birds and mammals use a combination of movements and vocalizations, known as begging, to solicit food from their parents. A widespread interpretation of begging is that it constitutes an honest signal of offspring need. But we know that in the house sparrow (*Passer domesticus*) the intensity of begging calls reflects the past experience of offspring in addition to their need. Here we show that this result generalizes to other species. An experiment with hand-reared magpies (*Pica pica*) and great spotted cuckoos (*Clamator glandarius*) indicates that the begging strategies depend on the past experience of chicks and the composition of their brood. In asynchronous two-magpie broods, both chicks begged at the same intensity when the large chick obtained food more easily than its sibling, but the large chick begged at higher intensity when it was easier for the smaller chick to obtain food. Cuckoo chicks begged at higher intensity than magpies. *Key words*: begging, communication, handicap principle, hatching asynchrony, learning, signaling of need. [*Behav Ecol* 13:782–785 (2002)]

In most avian species studied, food deprivation and the begging intensity of chicks are positively correlated. Likewise, food provisioning by parents increases with the brood's demands (Kilner and Johnstone, 1997). Begging has thus become one of the main paradigms for the study of animal communication. It has inspired the development of game-theoretical models suggesting that parents use the begging intensity of their offspring to decide how much food to provide (Godfray, 1991) and how to allocate it among siblings (Godfray, 1995). These models, however, present theoretical and experimental problems. Computer simulations show that the signaling equilibrium derived is sometimes unstable (Rodríguez-Gironés et al., 1998), and the observation that smaller chicks beg at higher intensity and receive less food than their nest mates (Cotton et al., 1999; Kilner, 1995; Lotem, 1998; Price and Ydenberg, 1995; Price et al., 1996) seems difficult to reconcile with the models. These problems can be solved if we assume that parents can control how much food to deliver to the brood, but not how this food is allocated among siblings (Rodríguez-Gironés, 1999). Under this assumption, the begging intensity of a chick, at evolutionary equilibrium, reflects its internal state and conveys information to its parent. The parent uses this information to decide how much food it should bring to the brood, but it cannot decide how the food is allocated between its young.

A recent experiment (Kedar et al., 2000) challenges the idea that begging intensity reflects the internal state of chicks. Kedar et al. hand-reared house sparrows (*Passer domesticus*) under two different conditions: all chicks received the same amount of food per day, but while one group was fed when chicks begged at low intensity, the other chicks were only fed when they begged at high intensity and for prolonged periods. Chicks in both groups grew at the same rate, and body

condition (the residual of a regression between body mass and tarsus length) did not differ between groups, indicating that the internal state of all chicks was the same. And yet, the chicks in the second group begged at higher intensity during standard tests, when the internal state was the same for all chicks. Clearly, then, the begging intensity of the experimental chicks did not reflect in an unequivocal way their internal state.

The results obtained by Kedar et al. (2000) can be interpreted in at least two ways. First, it may be that, in natural broods, begging intensity is not a signal of need. That is, it may be that parents cannot deduce the nutritional requirements of their young from their begging behavior. This interpretation would force us to reconsider our present understanding of begging. An alternative possibility is that, in natural nests, begging intensity does indeed act as a signal that allows parents to infer how much food they must provide to the nest. Begging behavior is clearly plastic (Kedar et al., 2000). There must be a mechanism that determines the begging strategy of young as a function of their experience. If the combination of the learning mechanism and the natural rearing conditions results, by and large, in begging strategies that allow parents to infer the need of their offspring, the plasticity of these strategies is not evidence against our current interpretation of begging. In this case, we would have to interpret the results of Kedar et al. as an experimental artifact: the difference in begging intensity between chicks having the same internal state would be due to the fact that these chicks have been reared in unnatural conditions.

The experimental set-up of Kedar et al. (2000) tried to mimic rearing conditions in nests with hatching asynchrony, where (for reasons that are not altogether clear) older chicks normally get more food than their siblings for a given begging intensity (Cotton et al., 1999; Kilner, 1995; Lotem, 1998; Price and Ydenberg, 1995; Price et al., 1996). In these nests, however, parents can use both begging level and relative size to determine food provisioning. In principle, then, parents could infer the internal state of their young even if different chicks use different strategies. (For this to be so, the rearing conditions of small chicks should be comparable across nests, and the same should apply for large chicks.)

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Because of the potential implications of the experiment presented by Kedar et al. (2000), we believe that it is important to replicate the results using different species. We therefore ran a new experiment with the aim of validating the original results and extend our understanding of the mechanisms responsible for the development of the begging strategies. The main difference between our experiment and the one of Kedar et al. is that we introduced size asymmetries in our design.

METHODS

Subjects

Fifty-two magpie (*Pica pica*) and 12 great spotted cuckoo (*Clamator glandarius*) chicks, in the ranges of 20–100 g and 18–60 g, respectively, were used for the experiment. We brought chicks to the laboratory in the evening before the experiment started and housed them at temperatures ranging between 27° and 34°C, according to size. All magpie chicks came from unparasitized broods, and we never used the smallest chicks of a brood. Chicks were placed in artificial nests, two chicks per nest. (We call “brood” a pair of nest mates.) Broods consisted of a “large” and a “small” conspecific chicks, large chicks being, on average, 23 g (SD 10 g) heavier than their nest mates. Within each brood, one chick was allocated to treatment A and the other one to treatment B (see below the definition of treatments). For every two consecutive broods (of the same species), the large chick was allocated to treatment A in a randomly selected brood and to treatment B in the other one. Thus, we had two types of nests for each species: nests where the large chick received treatment A and nests where the large chick received treatment B. Notice that chicks of intermediate size could be either large or small chicks, depending on the size of their foster sibling. Hence, large and small are relative, not absolute, attributes.

Chicks were marked with nontoxic acrylic paint for individual identification. We fed chicks a mixture of boiled carrots, boiled eggs, and raw cow heart (Redondo, 1993). The relationship between body mass and food intake of chicks was calculated from allometric relationships (Weathers, 1996), calibrated with the ad libitum food intake of 1-week-old chicks raised on the same diet (Redondo, 1993). For details about housing and feeding conditions, see Rodríguez-Gironés et al. (2001).

Treatments

Let F be the amount of food that a chick should receive in a day. This amount was divided in 14 equal portions. We fed chicks one portion per hour, starting at 0700 h. Within an hour, a nest was visited M times in 3- to 5-min intervals. The number of visits per day with M equal 1–4 was 4, 4, 3, and 3, respectively. Chicks were stimulated every visit. Chicks in treatment A received most of their portion in their first visit (a small bit was kept in case that they would still beg in subsequent visits), while chicks in treatment B received their share in the last (M th) visit of each hour. This way, all chicks receive the same amount of food per day, but chicks in treatment A were fed (almost) every time they begged, while chicks in treatment B had to beg several times before being fed. If a chick did not consume its entire portion in one hour, the leftovers were added to its portion for the following hour. At the end of the day all the food was normally consumed, and the statistical analysis controlled for the variability in ingested food.

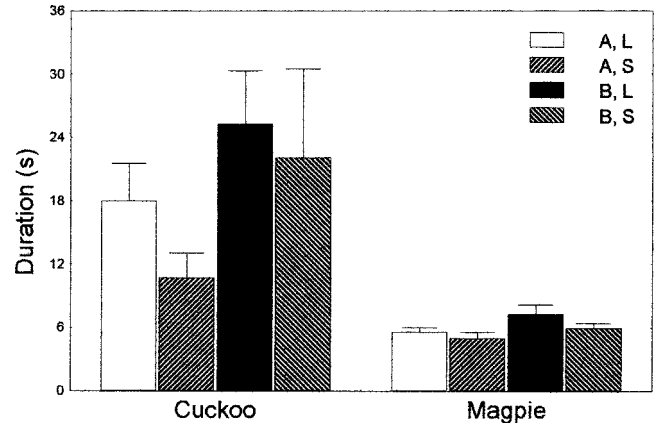


Figure 1

Average duration (in seconds) of the begging bouts for large (L) and small (S) magpie and cuckoo chicks as a function of the treatment they experienced (A and B, see text for details). Error bars are SE.

Behavioral tests

Chicks were kept for 3 days in the laboratory. They were fed at 1700 h (all chicks in the first visit, $M = 1$) and stimulated 30, 60, and 150 min following this visit. Chicks received no food during this period, and their behavior following each stimulation was recorded with a video camera. Normal feeding was reinstated at 1930 h and continued till 2130 h. The amount of time that a chick spent begging at each intensity was scored for each visit. A begging bout was considered finished if the chick spent more than 2 s without begging. Because the begging strategies of chicks adapt to new feeding conditions within a few hours (Kedar et al., 2000), we averaged the time that each chick spent begging in each posture over the 3 days.

Statistical analysis

For this analysis, we used the duration of the begging bouts of chicks, averaged over the 3 days and the three levels of food deprivation. These averages were log transformed for the analysis. The data were analyzed independently for each species as a split-plot design (main block: pair of broods, subplot: brood). In a first analysis we controlled for average size of the chick throughout the experiment, food intake, and condition. Condition was defined as the residual of a second-order polynomial regression of final body mass on initial body mass and food intake (Rodríguez-Gironés et al., 2001). We controlled for these variables because the variability in initial size of chicks and the associated differences in food intake could, in principle, affect the duration of begging bouts. Furthermore, the treatment affected growth of magpie chicks (Rodríguez-Gironés et al., 2001), and slow-growing chicks might have begged at higher intensities than fast-growing chicks. Because none of the covariates was significant ($R^2 = .042$ for the full model, $p > .39$ for all three covariates), we removed them from the analysis. Only the results of this second analysis are presented in the article. The cuckoo data were analyzed in the same way, but due to the small sample size the validity of a parametric analysis can be questioned and the results should be taken as merely indicative.

RESULTS

Figure 1 shows the average duration of the begging bouts for magpie and cuckoo chicks. Cuckoos begged for longer peri-

ods than magpies. Otherwise, the relative differences between groups were similar in both species. For magpie chicks, both treatment ($F_{1,24} = 11.064$, $p < .003$) and its interaction with type of nest ($F_{1,24} = 6.335$, $p < .02$) had significant effects on the duration of begging bouts, but the effect of type of nest was not significant ($F_{1,12} = 0.109$, $p > .7$). The same result was obtained for cuckoos: treatment ($F_{1,4} = 20.234$, $p < .02$) and its interaction with type of nest ($F_{1,4} = 11.944$, $p < .03$) had significant effects on the duration of begging bouts, but the effect of type of nest was not significant ($F_{1,2} = 0.140$, $p > .7$).

DISCUSSION

The results of our experiment confirm the basic findings of Kedar et al. (2000): The begging strategies of chicks are plastic, and they do not reflect precisely their internal condition. This is the case in sparrow (Kedar et al., 2000), magpie, and great-spotted cuckoo chicks. These results do not, however, tell us to what extent parents can extract information from the begging intensity of their offspring. Field experiments will be required to elucidate this question.

In two-chick sparrow broods, the chick that must beg more often and at higher intensity in order to be fed (B chick) learns to beg more than its sibling (A chick) when they both have the same internal state. Our experiment shows that the difference in begging intensity decreases if the B chick is smaller than the A chick, and it increases if the B chick is larger than the A chick. Hence, the mechanism responsible for the development of the begging strategies is sensitive to the social context of a chick.

Our results seem to contradict field observations of younger chicks begging more and receiving less food than their larger siblings (Cotton et al., 1999; Kilner, 1995; Lotem, 1998; Price and Ydenberg, 1995; Price et al., 1996). The natural situation seems equivalent to the nests where B chicks were smaller than A chicks. In these nests, there were no differences between the begging levels of A and B chicks. There is, however, a fundamental difference between the natural situation and our experimental broods. In our experiment, B chicks got the same amount of food as A chicks of the same size, whereas in natural nests small chicks are often underfed relative to their larger siblings (but see Stamps et al., 1985, 1989, for an exception). This difference in feeding regime might, in principle, account for the development of different strategies.

In an experiment with yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, Price et al. (1996) showed that the begging strategy of chicks is actually context dependent. It is not just that small and large chicks have different begging strategies. A chick switches its begging strategy when it is transferred from a nest where it is the largest chick to a nest where it is the smallest (or vice versa), and this behavioral switch occurs within an hour. It seems unlikely that such fast behavioral switches can be attributed to a modification of the internal state of the chicks. The differences between the results obtained by Price et al. (1996) in the field and the results presented here might be species specific. Yellow-headed blackbirds modulate their begging intensity in response to an increase or decrease in the begging intensity of their siblings (Price et al., 1996). This effect, which is not present in all species (see, e.g., Cotton et al., 1996) might be responsible for the behavioral switch. Indeed, the transfer of a chick from a brood where it is the largest to another where it is the smallest implies transferring the chick from a younger to an older brood, and the overall begging intensity of the brood increases with its age (Price et al., 1996).

Cuckoo chicks beg at higher intensity than magpie chicks. This finding is consistent with other studies of begging in brood parasites (Davies et al., 1998; Dearborn, 1998; Kilner et

al., 1999; Lichtenstein and Sealy, 1998; Redondo, 1993) and suggests that much of the cost of begging is indirect. Magpie chicks incur two types of costs by begging. The direct cost is a reduction of expected fitness due to predation (Redondo and Castro, 1992) and retarded growth (Rodríguez-Gironés et al., 2001). The indirect cost is a decrease in their inclusive fitness due to the fact that the food a chick consumes cannot be ingested by its siblings and that parents might pay a cost to increase the rate of food provisioning to the nest. Because brood parasites are never related to the birds that feed them and they are often not related to any of the chicks with which they share the nest, the indirect cost of begging is either absent or largely reduced for brood parasites. In the great-spotted cuckoo, a female may lay several eggs in the same nest. The indirect cost of begging is, therefore, not completely absent.

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