

Effects of begging on growth rates of nestling chicks

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We investigated whether an increase in begging levels delays growth of chicks. In experiment 1, we hand-reared nine pairs of ring dove squabs, divided into a control and a begging group. All squabs received similar amounts of food, but those in the begging group had to beg for a prolonged period in order to be fed, while squabs in the control group received food without begging. Squabs stopped responding to the treatment after 10 days and, at that time, there was no effect of induced begging on their body mass. In experiment 2, we hand-reared 27 pairs of magpie chicks for 3 days. The design of experiment 2 was similar to that of experiment 1. Daily food intake and begging affected growth rates. On average, chicks in the begging group grew 0.8 g/day less than control chicks, which represents a decrease of 8.15% in growth rate. Because growth is usually positively associated with expected fitness, this demonstrates that begging is a costly behavior, an assumption routinely made in models of begging behavior. *Key words*: cost of signaling, handicap principle, magpies, *Pica pica*, ring doves, signaling of need, *Streptopelia risoria*. [*Behav Ecol* 12:269–274 (2001)]

In species with parental care, young normally solicit food and other resources from their parents. These solicitations, often conspicuous, have attracted the attention of biologists for decades and have been interpreted in different ways. The research in food solicitation behavior has centered mainly on birds, where it has been suggested that begging is the result of parent–offspring conflict (Trivers, 1974; see also Eshel and Feldman, 1991; Mock and Forbes, 1992), that begging influences the outcome of sibling competition (Macnair and Parker, 1979; Rodríguez-Gironés, 1999), and that it provides parents with reliable information regarding the internal state of the chicks (Godfray, 1991, 1995; Harper, 1986; Hussell, 1988; Rodríguez-Gironés, 1999). In these three contexts (which are not mutually exclusive), begging is the visible outcome of an underlying tension, be it a conflict between siblings or between parents and their offspring, which endows the begging young with an advantage. If young are going to have stable solicitation strategies, if we require that begging does not escalate ad infinitum, it would seem that we must add a negative cost term to the equation such that, at evolutionary equilibrium, the marginal cost of increasing begging exactly balances its marginal benefit, thus stabilizing the begging strategy. The presence of this cost term has been made explicit in most discussions of begging, and several models seem to confirm the intuitive idea that no evolutionarily stable begging strategy will exist unless begging is costly (i.e., Godfray, 1991, 1995; Harper, 1986; Macnair and Parker, 1979).

In agreement with some of these models (Godfray, 1991, 1995; Harper, 1986; Rodríguez-Gironés, 1999), a number of experimental studies have shown that begging intensity is correlated with levels of food deprivation and that parents increase provisioning rates in response to increased levels of begging (reviewed by Kilner and Johnstone, 1997). Furthermore, our understanding of biological signaling systems in general is by and large conditional to signals being costly. Our

main theoretical framework for analyzing the evolution and stability of signaling systems is the handicap principle, which states that reliable signals must be costly (Grafen, 1990; Zahavi, 1977). Although, strictly speaking, signaling systems can be at equilibrium in the absence of any cost (e.g., Enquist et al., 1998; Lachmann and Bergstrom, 1998), the amount of information that can be conveyed with cost-free signals is very small if there is conflict of interests between sender and receiver. On the other hand, recent findings suggest that the cost of begging required to stabilize begging may be very small under some conditions (Johnstone, 1999).

Considering that, according to existing models, the assumption that begging is costly is absolutely critical for the stability of the begging strategies, relatively little effort has been dedicated to carefully examining this hypothesis. Discussions on the cost of begging have focused on two alternative mechanisms that might make begging costly: by attracting predators and through a direct energetic cost. The predation cost and other possible alternatives are discussed below, and for the time being we will concentrate on the energetic cost. McCarty (1996) measured the energetic cost of begging in seven passerine species using closed-chamber respirometry and found that the active metabolic rate while begging was of the same order of magnitude as the resting metabolic rate. The highest energetic cost he measured was in tree swallows, *Tachycineta bicolor*, where the active metabolic rate while begging was 1.27 times the resting metabolic rate. Leech and Leonard (1996) and Bachman and Chappell (1998) found similar ratios (1.28 and 1.27) in tree swallows and house wrens, *Troglodytes aedon*, respectively. This relatively low metabolic cost led McCarty (1996) and Bachman and Chappell (1998) to suggest that the hypothesis that begging is energetically costly might have to be rejected.

It is important to clarify, however, that when the models refer to begging being costly, what is meant is that an increase in begging intensity is associated with a decrease in expected fitness. In principle, a relatively low increase in the resting metabolic rate can be associated with a high begging cost. Indeed, most of the energy ingested by growing chicks is spent in thermoregulation and maintenance (Weathers, 1992, 1996). Therefore, a modest increase in energy expenditure can substantially reduce the amount of energy available for

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growth, and this energy increase can be associated with a meaningful decrease in growth (Leech and Leonard, 1996; Verhulst and Wiersma, 1997). For this reason, short-term measurements of metabolic rate are insufficient to investigate the energetic costs of begging. Bachman and Chappell (1998) have measured metabolic rates in the field and in the laboratory for chicks of different ages engaged in different activities. Their data suggest that the energy spent in begging daily accounts for less than 1% of the daily energy budget, well below 7.7% of the energy deposited in new tissues each day. Their measurements probably incorporate short-term repayments of anaerobic metabolism, but they cannot address the possibility of energy reallocations during begging episodes.

The purpose of this study was to investigate the effect of begging on growth. In the experiments reported, we hand-reared two groups of ring dove (*Streptopelia risoria*) squabs and two groups of magpie (*Pica pica*) chicks. For each species, we fed both groups the same amounts of food, and we kept subjects in identical conditions, except that the squabs/chicks in one group were required to beg for their food. The comparison of the growth rates between both groups gives an indication of the cost of begging in terms of body size, a parameter known to influence survival probability and expected reproductive success (e.g., carrion crow, *Corvus corone corone*; Richner, 1989, 1992; collared flycatcher, *Ficedula albicollis*; Lindén et al., 1992; blue tit, *Parus caeruleus*; Merilä and Svensson, 1997; great tit, *Parus major*; Haywood and Perrins, 1992; Verhulst et al., 1997; zebra finches, *Taeniopygia guttata*; Haywood and Perrins, 1992; for a recent review, see Lindström, 1999).

METHODS

This work was conducted after approval by the ethical committee of animal experimentation (CEEA) and following the Animal Behavior Society/Association for the Study of Animal Behavior (ABS/ASAB) guidelines for ethical treatment of animals.

Experiment 1

Experimental subjects

We kept six pairs of adult ring doves in breeding cages (80 × 90 × 100 cm) from January to May 1998. Cages had a nesting bowl and nest material and birds were provided with grit, water, and food (mixed seed) ad libitum. The nine two-squab broods that they produced were used for the experiment. (All pairs produced second clutches. In three cases only one squab hatched, and we left singletons with their parents until independence.) We removed the squabs from their nests on the evening of day 3 (hatching = day 0) and hand-reared them to independence.

Mortality

All four chicks in broods one and two died within 24 h. They were aged between 5 and 9 days, shared an incubator, and showed signs of respiratory distress, suggesting that they died from some contagious disease. The control chick of the eighth pair died on day 15 (weight 88 g).

Housing of squabs

We raised the squabs following the procedure developed by Balsam (see Balsam et al., 1992). We kept young squabs in straw-lined bowls in an incubator at 32°C, one squab per bowl. (The two squabs of a brood were always kept in the same incubator, and therefore an incubator always had the same number of begging and control squabs.) Bowls were 15 cm deep, and therefore squabs were in visual isolation. After day

Table 1
Food composition by age of squabs

Age (days)	Soya milk (cm ³) ^a	Soja FLT (g) ^b	Nutrilon Soya Plus (g) ^c	Seeds (g) ^d
4–8	17	5.6	0	0
9–14	20	5.6	4.6	0
15–end	20	5.6	4.6	5.5

^a With added calcium.

^b DieMilk.

^c Nutricia.

^d Ground adult seed mixture.

10, we placed the squabs, still in their bowls, in cardboard boxes in a room at 26°C, one pair of siblings per box. All squabs older than 21 days and unable to feed on their own were kept together in a large aviary at 26°C. Independent young were kept in breeding cages with ad libitum food and water.

Feeding of squabs

Since there are, to our knowledge, no published data concerning the daily energy intake of growing ring dove squabs in the wild (nor in the laboratory), we estimated their requirements from published values and allometric equations derived from a number of species (Weathers, 1996). From these data, we can infer that the daily energy intake of squabs must be in the range $4.8 \cdot M^{0.845} - 6.24 \cdot M^{0.845}$ kJ, where M is the mass (g) of the squab. This is a rather wide range, and the amounts provided in the experiment (see below) correspond to the lower portion of the spectrum. This choice ensured that squabs were slightly food deprived; with a very abundant food supply, both groups might be growing at the maximum rates, the limit to growth being dictated by physiological constraints other than energy intake.

Food composition as a function of squab age is given in Table 1 (some drops of a liquid multivitamin compound were added to this mixture). This diet mimics the composition of crop milk in white Carneaux pigeons, *Columbia livia*, and the diet of older squabs (Griminger, 1983; Leash et al., 1971). Based on the energetic requirements of squabs and the composition of food, we decided to feed squabs up to (and including) 8 days an amount (cm³) that was equal to half their morning weight (g). We fed older birds according to their age: squabs 9 and 15 days old were fed 24 cm³ of their corresponding diet, and 1 cm³ was added each day to the last daily consumption, up to and including 30 cm³. Squabs up to and including 12 days old were fed five times per day (0800, 1030, 1300, 1530 and 1800 h), while older squabs were fed only three times per day (0800, 1300 and 1800 h). Squabs older than 21 days were weaned progressively. We fed them decreasing amounts twice per day (0800 and 1800 h) until they were able to feed independently.

Treatments

Squabs in the begging group were stimulated by touching their bills and crops for 2 min before feeding. Each meal was divided in seven small morsels, so that squabs in the begging group were stimulated to beg for approximately 14 min during each meal, or some 70 min per day. Squabs in the control group were fed as soon as possible after removal from the incubator. Squabs eagerly accepted their meal in one or at most two portions, and feeding of control chicks normally took less than 1 min.

Because feeding took place outside the incubator, and to

control for the possibility that thermoregulation while out of the incubator was costly, control squabs remained outside the incubator while their siblings were being fed.

In the first brood produced by the breeding pairs, squabs were allocated randomly to the begging and control groups. Thereafter, we allocated the first-hatched squab of each new brood to the begging and control groups in alternation to make sure that both groups had the same proportion of first- and second-hatched squabs. With second clutches, the allocation of squabs (first- and second-hatched) to experimental groups (begging and control) was the reverse of the allocation in the first clutch of the same breeding pair. For statistical analysis, we looked at within-brood differences between begging and control chicks.

Experiment 2

Experimental subjects

We collected magpie chicks in Santa Fe (Granada, Spain) during April 1999. Details of the study area can be found elsewhere (Zúñiga and Redondo, 1992). We collected 54 magpie chicks, with body mass in the range of 20–100 g, from their nests on the evening before the experiment (day 0). We hand-reared chicks in the laboratory for 3 days and returned them to their original nests on the evening of day 3. The chicks were used for an experiment investigating the plasticity of begging strategies, and only the experimental details relevant for the study of begging costs are reported here.

Housing and feeding of chicks

We kept artificial broods of two chicks in straw-lined bowls (hereafter referred to as nests) at temperatures ranging between 27°C and 36°C, according to the age of chicks. We fed them a mixture of 1 kg raw cow heart, six boiled eggs, and 100 g of carrots, to which we added a multivitamin complex. The morning weight of a chick determined the amount of food that it would receive during the day. We calculated the relationship between body mass and food intake of chicks from allometric relationships (Weathers, 1996), calibrated with the ad libitum food intake of 1-week-old chicks raised on the same diet (Redondo, 1993). The daily ratio of a chick was $0.98 \cdot M^{0.814}$ g, where M is the mass (g) of the chick. Chicks received their daily food ratio in 14 equal, hourly portions. Half of the artificial broods received a “fasting” diet, in which daily intake was decreased by 5%.

Treatments

Each nest contained a chick from the begging and a chick from the control (nonbegging) group. We fed chicks with one meal per hour. During a meal, we visited each nest a random number of times, in 3- to 5-min intervals. The number of visits per meal took values 1–4 and there were, each day, 4, 4, 3, and 3 meals with 1, 2, 3, and 4 visits, respectively. We stimulated chicks to beg (by saying “toma” close to their nest) in every visit. Chicks in the control group received most of their portion in the first visit of each meal (we held back a small amount to feed them in subsequent visits if they begged again), while chicks in the begging group received their entire portion in the last visit, after prolonged begging. We videotaped the begging intensity of each chick every day, at three levels of food deprivation (30, 60, and 150 min). Regular meals were videotaped when time permitted.

Analysis

We scored from the videotapes the amounts of time that chicks spent begging during a random subset of meals and all behavioral tests. The meals analyzed corresponded to 13 broods, although several meals were analyzed for each brood.

For the analysis, we calculated the time that each chick spent begging per meal.

In experiment 1, siblings had similar sizes at the beginning of the experiment, and therefore growth differences could be assessed by comparing the size of siblings at the end of the experiment. In experiment 2, initial size differences between chicks were pronounced. Due to the nonlinearities of the functions relating growth and food requirements of chicks to their weight, we cannot compare the growth rate of a 20-g chick with that of a 100-g chick. To study whether food intake and growth rates differed between control and experimental magpie chicks, we performed regression analysis of the variable of interest on the controlling variables and compared the residuals of control and experimental chicks. Thus, for the food intake, a second-order polynomial regression of food intake on initial weight was performed. The residuals of this regression give us an idea of whether the total food intake of a chick was greater or smaller than expected from its initial mass. These residuals were analyzed with a repeated-measures ANOVA with begging level as the within-subject comparison and diet as the between-subject factor. (In this analysis, brood was the independent unit.) For the analysis of growth, we included total food intake and its square as independent variables in a stepwise regression before calculating the residuals. All statistical tests are two-tailed. Results are reported as means \pm SE unless otherwise noted.

RESULTS

Experiment 1

Begging

Tactile stimulation of the bill and crop succeeded in inducing strong begging in young squabs of the begging group. Young squabs stretched their legs and body and flapped their wings vigorously for the duration of the meals. As squabs grew, tactile stimulation became less and less effective in inducing begging, and the squabs eventually stopped responding (median age 13, range 12–14 days).

Food intake

Daily food intake for 4- to 8-day-old squabs was weight dependent and hence variable. Food intake during these days for the control (114.6 ± 3.7 cm³, $n = 7$), and experimental (113.6 ± 4.2 cm³, $n = 7$) squabs did not differ significantly (paired t test: $t_6 = -0.31$). From 9 to 15 days of age, the only variability was due to some squabs occasionally refusing to eat their entire share. Total food intake during these days did not differ between control (195.7 ± 7.0 cm³, $n = 6$) and experimental (195.5 ± 6.6 cm³, $n = 6$) squabs (paired t test: $t_5 = 0.25$). From 16 days onward, all squabs ate their full share every day, and there were no differences between groups.

Growth

For the analysis of growth rates, only the pairs in which both chicks survived to day 13 were used. Figure 1 shows the growth of the begging and control groups. At the end of the experimental period (day 13, when most squabs stopped begging), the body mass of control (87.20 ± 1.65 g, $n = 7$) and experimental (87.86 ± 1.80 g, $n = 7$) squabs did not differ significantly (paired t test: $t_6 = -0.14$, $p = .74$).

Experiment 2

Begging

There was a significant difference between the time that chicks in the experimental and control groups spent begging per meal (paired t test: $t_{12} = 10.36$, $p < .0001$). Chicks in the

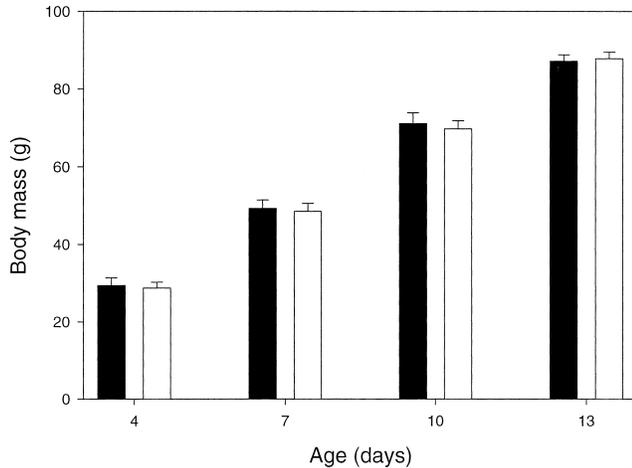


Figure 1
Average body mass (g) of the control (filled bars) and begging (open bars) squabs as a function of age (days). Error bars are SEs.

begging group begged for longer periods (103.8 ± 11.2 s/meal, $n = 13$) than chicks in the control group (29.6 ± 4.9 s/meal, $n = 13$). The difference resulted from the combination of two factors. For a given level of food deprivation, chicks in the begging group begged for longer periods than chicks in the control group (Rodríguez-Gironés et al., in preparation). Furthermore, during most of the feeding events, chicks in the begging group were hungrier than their foster siblings because chicks in the control group were always fed in the first nest visit of a meal, while their siblings were not. Hungrier chicks begged longer and at higher intensities than satiated chicks (Rodríguez-Gironés et al., in preparation).

Food intake

Initial weight of chicks had a significant effect on their food consumption during the experiment ($F_{2, 51} = 157.71$, $p < .0001$; $R^2 = .866$). The analysis of the residuals from the regression of food intake on initial weight of chicks showed that diet did not have a significant effect on food intake ($F_{1, 25} = 3.928$, $p = .059$), and both begging level ($F_{1, 25} = 0.557$, $p = .462$) and the interaction between diet and begging level ($F_{1, 25} = 0.380$, $p = .543$) were clearly nonsignificant. Diet had no significant effect on food intake because chicks in the high intake rate groups left part of their food uneaten more often than chicks in the low diet groups.

Growth

The average growth rate of chicks during the experiment was 9.8 ± 0.4 g/day ($n = 54$). The stepwise regression (overall: $F_{3, 50} = 691.98$, $p < .0001$; $R^2 = .977$) showed that the final weight of chicks was a function of initial weight ($t_{50} = 8.105$, $p < .0001$), food intake ($t_{50} = 5.516$, $p < .0001$) and the square of initial weight ($t_{50} = -3.028$, $p = .003$). The regression equation was:

$$W_3 = 0.548976 + 1.163558W_1 + 0.387830FI - 0.003260W_1^2,$$

where W_3 represents the weight (g) at the beginning of day 3, W_1 the weight (g) at the beginning of day 1, and FI the amount of food consumed (g) during days 1 and 2.

The repeated-measures ANOVA on the residuals showed that diet had no significant effect on growth ($F_{1, 25} = 0.040$, $p = .843$), but begging significantly retarded growth of chicks ($F_{1, 25} = 4.791$, $p = .038$). The interaction was not significant ($F_{1, 25} = 0.113$, $p = .739$). On average, induced begging delayed growth by 0.8 g/day (Table 2).

Table 2

Residuals of final mass on initial mass and total food intake for the different groups of magpie chicks

Begging	Diet	Average (g)	SE (g)	n
High	Rich	-0.775	0.824	14
High	Poor	-0.857	1.187	13
Low	Rich	0.518	0.866	14
Low	Poor	1.077	0.804	13

DISCUSSION

Current explanations of the evolution of biological signaling systems in general, and of begging in particular, rely on the assumption that signaling (begging) is costly—costly in the sense that an increase in signaling intensity must be associated with a decrease in expected fitness (Godfray, 1991, 1995; Grafen, 1990; Harper, 1986; Macnair and Parker, 1979; Zahavi, 1977). In the case of begging, two potential sources of a signaling cost have been discussed: begging may attract predators and hence increase the probability of predation, or it may have a direct effect on expected survival and lifetime reproductive success.

At least two experiments have tried to evaluate the predatory cost of begging (Haskell, 1994; Leech and Leonard, 1997). Haskell (1994) played tapes of begging calls from artificial nests baited with quail (*Coturnix coturnix*) eggs and found that the begging calls increased predation rates in ground, but not in tree nests. Leech and Leonard (1997) used a similar approach and found that begging tapes increased predation both on the ground and in nest-boxes. These results suggest that begging is indeed costly, as hypothesized by the models, and that the models can therefore be used with confidence. There are, however, a number of reasons that the results of Haskell (1994) and Leech and Leonard (1997) must be interpreted with care. For instance, the playback experiments may not provide an accurate representation of the natural situation: in Haskell's (1994) experiments, about 60% ($n = 24$) of the control tree nests, and about 70% ($n = 45$) of the ground nests with high rates of begging calls were predated within 5 days. Leech and Leonard (1997) obtained predation rates of more than 30% ($n = 88$) within 2 days in control nests. Clearly, predation rates in both experiments (even in the control nests, and thus in the absence of begging calls) are much higher than in natural nests: during a 2-week period, predation would be very close to 100% at this rate. We must conclude that the experimental setup has introduced a factor that increases predation rate, and it is in principle possible that the predatory cost of begging only exists in the presence of this experimental factor. Leech and Leonard (1997) acknowledged that predators probably followed their scent to the vicinity of the nests, and once there located the experimental nest before the control one because of the begging calls.

Briskie et al. (1999) have shown that, in a forest community, the begging calls of species with higher predation risks are more difficult to detect by predators. The authors interpret this finding as evidence that begging increases the probability of predation. However, it seems clear that the higher predation risk cannot be the consequence of having less conspicuous begging calls. It may, of course, be that predation risk imposes a selection pressure leading to the evolution of less conspicuous calls. But this does not necessarily imply that, in their present form, begging calls increase predation risk.

Let us now assume that the predatory cost of begging has been shown beyond doubt. Can this cost stabilize begging?

The answer is probably not, other than in species that rear one young per brood. In multichick broods, if begging is going to be stabilized by its cost, this cost must be higher for the chick that begs than for its siblings (Godfray, 1995). This premise is almost certainly false in the case of a predatory cost, since any predator that follows the begging calls all the way to the nest will most likely eat all the chicks. So begging may have a predation cost, but this predation cost is not the one hypothesized by the models. To apply the models to species with multichick broods, we must be able to show that begging has a direct cost—that the chick that begs incurs a higher cost than its nest mates do.

Begging can also reduce fitness if the energy allocated to begging interferes with other activities or growth. In terms of total energy expenditure, begging has a very modest cost (Bachman and Chappell, 1998; Leech and Leonard, 1996; McCarty, 1996; Soler et al., 1999). The question remains whether this low cost had a large enough effect on growth and development to have deleterious consequences for expected fitness. To answer this question we need to know how big a difference in mass must be present to affect expected fitness. In a population of great tits living in a patchy environment, a mass increase of 3 g in the mass of a fledging chick (15% body mass) more than doubled (0.3 to 0.75) the probability that the bird obtained a breeding territory in the rich habitat the following year (Verhulst et al., 1997). In the zebra finch, a difference of 1 g in the mass of young birds (45 days) was equivalent to a difference of 0.3 eggs in the expected clutch size (Haywood and Perrins, 1992). And in carrion crows, a 12% difference in the body mass of a fledging shifted its probability of being large enough to breed from 25% to 64% (Richner, 1989, 1992). From these data, it seems clear that mass differences of approximately 10% are sufficient to have a significant effect on fitness. In experiment 1, begging had no effect on growth and (in all likelihood) expected fitness of the ring doves. Begging had, on the other hand, an effect on the growth rates of magpie chicks that was both statistically significant and biologically meaningful.

It is difficult to interpret the results of the ring dove experiment for a number of reasons. Although it could be argued that a larger sample size might reveal a difference in growth rates between the begging and control groups, a power analysis suggests that this is not the case. A difference of 2.6 g (3%) on day 13 was associated with a power of 90%, and we may therefore assume that control squabs were not more than 2.6 g heavier than their sibs were. (A 10% weight difference was associated with a power of 0.9996.) On the other hand, it is difficult to compare the begging levels of the squabs during the experiment with those of squabs growing under natural circumstances. Although young squabs begged with high intensity, as they grew older it became more and more difficult to keep squabs begging, and begging intensity decreased with age. (Squabs do not open their beaks when begging. They had to be held by hand in order to insert the syringe used for feeding them in their crop. It is possible that older squabs associated begging with a being held in the hand of the experimenter and therefore refrained from begging.) Indeed, on day 9 size differences between begging (62.3 ± 2.1 g, $n = 8$) and control (63.8 ± 2.8 g, $n = 8$) squabs reached their largest difference, although this difference was still nonsignificant (two-tailed paired t test: $t_7 = 1.168$, $p = .28$).

Experiment 2 produced clearer results. Despite large inter-individual variability, begging significantly retarded growth of magpie chicks. After 2 days of treatment, control chicks were, on average, 1.6 g heavier than chicks in the begging group with the same diet. Hence, intensive begging resulted in a growth rate 0.8 g/day (or 8.15%) lower than what chicks could achieve in the absence of begging. A note of caution is

required here. It should be noted that the treatment had two effects: control chicks had to beg less than their nest mates, but they also had more time to rest. After being fed (in the first visit of a meal), control chicks could simply go to sleep. Chicks in the begging group might stay alert while waiting for future visits. Because we did not record the behavior of the chicks between visits, we cannot quantify the time spent sleeping by chicks of the two groups. In principle, it is possible that control chicks slept more and that this difference in time spent sleeping is responsible for the different growth patterns.

Although it is possible that the difference between the outcomes of experiments 1 and 2 was due to methodological problems, it might also reflect species differences. In an experiment almost identical to experiment 2, Kedar et al. (2000) did not find an effect of begging on the growth rates of house sparrow (*Passer domesticus*) nestlings. Because this experiment induced clear and systematic differences on begging intensities, and because chicks were stimulated to beg more than 70 times per day, the lack of effect of begging on growth cannot be ascribed to a methodological problem. It seems, therefore, that begging may retard growth in some circumstances, but not always. In this respect, the effect of begging may be species specific, but it may also be related to growing conditions, such as ambient temperature and feeding regime. At any rate, the results presented in this paper show that begging can have a cost of the sort that is normally assumed by theoretical models of signaling of need. With respect to the controversy concerning the importance of the low metabolic rate measured in begging chicks, our results also confirm the suggestion that short-term studies of oxygen consumption during begging are insufficient to study the fitness consequences of begging (Verhulst and Wiersma, 1997). To be sure, energy consumption is an important component and deserves to be studied. But the measurements obtained must be integrated in the general framework of chick physiology and development if we are to understand the pathways through which begging exerts its cost.

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REFERENCES

- Bachman GC, Chappell MA, 1998. The energetic cost of begging behaviour in nestling house wrens. *Anim Behav* 55:1607–1618.
- Balsam PD, Graf JS, Silver R, 1992. Operant and Pavlovian contributions to the ontogeny of pecking in ring doves. *Dev Psychobiol* 25:389–410.
- Briskie JV, Martin PR, Martin TE, 1999. Nest predation and the evolution of nestling begging calls. *Proc R Soc Lond B* 266:2153–2159.
- Enquist M, Ghirlanda S, Hurd PL, 1998. Discrete conventional signalling of a continuous variable. *Anim Behav* 56:749–754.
- Eshel I, Feldman MW, 1991. The handicap principle in parent-offspring conflict: comparison of optimality and population-genetic analyses. *Am Nat* 137:167–185.
- Godfray HCJ, 1991. Signalling of need by offspring to their parents. *Nature* 352:328–330.
- Godfray HCJ, 1995. Signaling of need between parents and young: parent-offspring conflict and sibling rivalry. *Am Nat* 146:1–24.
- Grafen A, 1990. Biological signals as handicaps. *J Theor Biol* 144:517–546.

- Griminger P, 1983. Digestive system and nutrition. In: Physiology and behaviour of the pigeon (Abs M, ed). London: Academic Press; 19–39.
- Harper AB, 1986. The evolution of begging: sibling competition and parent-offspring conflict. *Am Nat* 128:99–114.
- Haskell D, 1994. Experimental evidence that nestling begging behaviour incurs a cost due to predation. *Proc R Soc Lond B* 257:161–164.
- Haywood S, Perrins CM, 1992. Is clutch size affected by environmental conditions during growth? *Proc R Soc Lond B* 249:195–197.
- Hussell DJT, 1988. Supply and demand in tree swallow broods: a model of parent-offspring food-provisioning interactions in birds. *Am Nat* 131:175–202.
- Johnstone RA, 1999. Signaling of need, sibling competition, and the cost of honesty. *Proc Natl Acad Sci USA* 96:12644–12649.
- Kedar H, Rodríguez-Gironés MA, Yedwab S, Winkler DW, Lotem A, 2000. Learning modifies offspring signalling of need to their parents. *Proc R Soc Lond B* 267:1723–1727.
- Kilner R, Johnstone RA, 1997. Begging the question: are offspring solicitation behaviours signals of need? *Trends Ecol Evol* 12:11–15.
- Lachmann M, Bergstrom CT, 1998. Signalling among relatives. II. Beyond the tower of Babel. *Theor Popul Biol* 54:146–160.
- Leash AM, Liebman J, Taylor A, Limbert R, 1971. An analysis of the crop contents of white Carneaux pigeons (*Columbia livia*), days one through twenty-seven. *Lab Anim Sci* 21:86–90.
- Leech SM, Leonard ML, 1996. Is there an energetic cost to begging in nestling tree swallows (*Tachycineta bicolor*)? *Proc R Soc Lond B* 263:983–987.
- Leech SM, Leonard ML, 1997. Begging and the risk of predation in nestling birds. *Behav Ecol* 8:644–646.
- Lindén M, Gustafsson L, Pärt T, 1992. Selection on fledging mass in the collared flycatcher and the great tit. *Ecology* 73:336–343.
- Lindström J, 1999. Early development and fitness in birds and mammals. *Trends Ecol Evol* 14:343–348.
- Macnair MR, Parker GA, 1979. Models of parent-offspring conflict. III. Intra-brood conflict. *Anim Behav* 27:1202–1209.
- McCarty JP, 1996. The energetic cost of begging in nestling passerines. *Auk* 113:178–188.
- Merilä J, Svensson E, 1997. Are fat reserves in migratory birds affected by condition in early life? *J Av Biol* 28:279–286.
- Mock DW, Forbes LS, 1992. Parent-offspring conflict: a case of arrested development? *Trends Ecol Evol* 7:409–413.
- Redondo T, 1993. Exploitation of host mechanisms for parental care by avian brood parasites. *Etología* 3:235–297.
- Richner H, 1989. Habitat-specific growth and fitness in the Carrion Crows (*Corvus corone corone*). *J Anim Ecol* 58:427–440.
- Richner H, 1992. The effect of extra food on fitness in breeding carrion crows. *Ecology* 73:330–335.
- Rodríguez-Gironés MA, 1999. Sibling competition stabilizes signalling resolution models of parent-offspring conflict. *Proc R Soc Lond B* 266:2399–2402.
- Soler M, Soler JJ, Martínez JG, Moreno J, 1999. Begging behaviour and its energetic cost in great spotted cuckoo and magpie host chicks. *Can J Zool* 77:1794–1800.
- Trivers RL, 1974. Parent-offspring conflict. *Am Zool* 14:249–264.
- Verhulst S, Perrins CM, Riddington R, 1997. Natal dispersal of great tits in a patchy environment. *Ecology* 78:864–872.
- Verhulst S, Wiersma P, 1997. Is begging cheap? *Auk* 114:134.
- Weathers WW, 1992. Scaling nestling energy requirements. *Ibis* 134:142–153.
- Weathers WW, 1996. Energetics of postnatal growth. In: Avian energetics and nutritional ecology (Carey C, ed). New York: Chapman & Hall; 461–496.
- Zahavi A, 1977. Reliability in communication systems and the evolution of altruism. In: Evolutionary ecology (Stonehouse B, Perrins CM, eds). London: Macmillan; 253–259.
- Zúñiga JM, Redondo T, 1992. No evidence for variable duration of sympathy between the great spotted cuckoo and its magpie host. *Nature* 359:410–411.