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Signalling of Nutritional Need by Magpie Nestlings

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Abstract

The relationship between begging behaviour, chick nutritional state, and parental distribution of food within broods was studied in 4- and 5-chick magpie *Pica pica* broods under natural conditions. Three components of the begging display (duration, latency, and posture) were highly correlated with each other and also with the emission and duration of begging calls. Begging performance was strongly influenced by the food intake of nestlings during the preceding 1-h interval, indicating that begging may reliably reflect the nutritional need of nestlings. Daily growth during the preceding day, as well as average cumulative food intake by the brood during the preceding 24 h, seemed not to affect begging in a similar way. Begging signals employed by hungrier nestlings involved a higher degree of muscular activity, thus supporting the prediction that nestlings in greater need should employ more costly signals. Overall, those nestlings who begged more tended to obtain more food, but the relationship between feeding success and begging behaviour was weak due to a high variation between broods in the way that parents seemed to respond to variations in begging behaviour. Possible causes for this variation, and its implications for the evolution of reliable begging displays, are discussed.

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Introduction

The conspicuous begging behaviour of many nestling birds was traditionally regarded as a signalling system for informing the parents about the nutritional requirements of chicks (WELTY 1975; RYDEN & BENGTSSON 1980). This interpretation is considered untenable from an adaptationist viewpoint because it fails to explain why begging seems to be so costly for its function (STAMPS et al. 1978, 1985; HARPER 1986; SMITH & MONTGOMERIE 1991). Begging can be both energetically expensive (KREBS & DAWKINS 1984; HARPER 1986) and attract predators to the nest (REDONDO & ARIAS DE REYNA 1988; REDONDO & CASTRO 1992), hence selection should favour less expensive signals to communicate the chick's hunger to its parents.

An alternative explanation for the evolution of conspicuous begging is offered by kin selection theory. Since parents and offspring are not genetically identical, the fraction of parental expenditure allocated to individual nestlings which maximizes inclusive fitness is always greater for the offspring than for the parent (TRIVERS 1974; LAZARUS & INGLIS 1986). This conflict of evolutionary interests provides a theoretically feasible scenario in which conspicuous begging can evolve (PARKER & MACNAIR 1978; STAMPS *et al.* 1978; MACNAIR & PARKER 1979; PARKER 1985; HARPER 1986; ESHEL & FELDMAN 1991; GODFRAY & PARKER 1991). Once parents rely on begging signals as a cue for detecting fluctuations in offspring need, and try to compensate for them by selectively feeding the nestling who begs most, selection favours more and more intense begging by nestlings (HARPER 1986). In this way, chicks can obtain a larger fraction of resources than their parents have been selected to give, the final amount of food transferred being a compromise between the parental and offspring optimum levels (PARKER 1985).

A problem central to the discussion of how begging signals evolve, and to the evolution of communicative signals in general, is that of honesty (ZAHAVI 1977). An honest signal is one which shows a necessary and reliable relationship with some quality of the sender that provides the receiver with an adequate estimate of such quality (DAWKINS & GUILFORD 1991). If the quality that must be advertised is deviating from a desired motivational state (e.g. hunger), then an honest signal must be gradual. Most theoretical models for the evolution of begging behaviour based on the Parent-Offspring Conflict Hypothesis have assumed that begging intensity covaries with chick hunger in a predictable way (STAMPS *et al.* 1978; PARKER 1985; HARPER 1986). However, it is unclear how such honest signals could be evolutionarily stable if parents allocate food in proportion to the begging level of a chick relative to that of its nestmates (GODFRAY 1991), because scramble competition among nestlings would result in the lowest begging levels falling into disuse. However, if begging carried an energetic cost, then any dilution of the benefits of extra begging would tend to limit the evolution of escalated begging among the offspring (STAMPS *et al.* 1978). Recent theoretical advances (GRAFEN 1990; GODFRAY 1991; MAYNARD SMITH 1991) show that the accurate communication of offspring need to their parents indeed requires that the signalling system is costly to be evolutionarily stable, this requirement being a direct consequence of the potential for parent-offspring conflict (GODFRAY 1991; MAYNARD SMITH 1991). This theoretical framework leads to a testable prediction concerning how nestlings should allocate their signalling effort. Under the assumptions that parents feed a nestling in direct proportion to its begging intensity, and that nestlings in greater need benefit more from a given amount of food, it is predicted that hungrier nestlings should employ more costly begging signals (GODFRAY 1991).

This model has not yet received strong empirical support from field data. For example, virtually all studies aimed at finding a relationship between hunger and begging intensity are based on food-deprivation experiments (HAARTMAN 1953; HENDERSON 1975; CONOVER & MILLER 1981; BENGTSSON & RYDEN 1983; DRUMMOND & GARCIA 1989; SMITH & MONTGOMERIE 1991). However, the appropriateness of this method requires that the resulting degree of nutritional

need falls within the range in which hunger normally fluctuates under natural conditions, a measure rarely (if ever) taken. This paper contributes evidence in support of the prediction that nestlings honestly signal their nutritional need to parents by analyzing the relationship between food requirements, begging behaviour, and food provisioning of magpie *Pica pica* nestlings under natural conditions. We manipulated chick hunger by selectively feeding (instead of depriving) some nestlings in the brood with the aim of testing one of the above assumptions (namely that parents feed more the nestlings who beg more) and the two main predictions from signalling models of begging (GODFRAY 1991; MAYNARD SMITH 1991):

1. Begging intensity should vary in a reliable way with the nutritional requirements of chicks.
2. Hungrier nestlings should employ more energetically costly signals.

Methods

Data were collected during April–June 1990 at Doñana Biological Reserve, Southern Spain. Details of the study area have been published elsewhere (REDONDO & CASTRO 1992). We selected 30 magpie broods containing 4 and 5 nestlings. Chicks were individually marked with non-toxic waterproof ink and plastic coloured rings. Nestling age was known with an accuracy of ca. 12 h. We tried to perform most tests (see below) when the eldest nestling in a brood was 6–8 d old. This gives a total maximum age range of 5–9 d for the whole sample of broods. Despite the existence of asynchronous hatching, age variations within a brood were low, with an average age range of $1.2 \text{ d} \pm 0.6 \text{ SE}$. Nests were visited in the early morning (8.00–11.00 h), when food provisioning by parents reaches a daily peak (BUISTRON 1988).

Measuring Begging Behaviour

Begging behaviour was recorded in the absence of parents. On arriving at a nest, we stimulated nestlings to beg by talking to them. Magpie parents give a “food call” to trigger chick begging which has a frequency distribution very similar to that of human voice (BIRKHEAD 1991). The same monosyllabic word was used to stimulate nestlings throughout the study. The following behavioural variables of the begging display were considered: (a) Level of postural intensity of the display, categorized into four levels: 1) fails to beg; 2) gapes resting on its belly; 3) gapes with the body elevated on tarsi; 4) same as 3) plus wing flapping. No nestling was observed to flutter its wings while begging in a resting posture; (b) whether the nestlings gave begging calls or not; (c) rank of latency to response (shortest latency, rank = 1); (d) the nestling who begged most persistently, defined as the one who held its begging display for the longest time. Begging calls were given with the higher levels of postural intensity (see Results). Hence, we combined both intensity scales into a single scale (begging intensity) categorized into 5 levels: 1) fails to beg; 2) gapes silently, tarsi flexed; 3) gapes calling, tarsi flexed; 4) gapes calling, tarsi extended; and 5) same as 4) plus wing flapping.

In addition, we recorded begging calls with a Uher 4200 Report Monitor stereo tape recorder through an AKG 568 EB condenser microphone. Each nestling was given a number code, so that individual calls were distinguished by recording the code of each nestling as it called. The duration of begging calls was measured in a FFT real time sound spectrograph Uniscan II (Multigon Ind.) by using the 300-Hz band-pass filter. We compared the duration of begging calls uttered by the nestling with the shortest latency time to respond with the average duration of the first calls given by its siblings during the same begging bout.

Measuring Nutritional Need

To investigate whether hungrier nestlings begged more intensively, we first equalized begging intensity by artificial feeding, and then measured the mass gain of the chicks during a 1-h period (as a measure of their hunger), and their begging behaviour at the end of the hour. We visited each brood

and determined the relative begging (judged from postural intensity and latency measurements) of each nestling. The nestlings begging most were fed 1 to 3 g of boiled egg, until the whole brood stopped begging or all nestlings begged with a similar degree of postural intensity. In more than 90 % of tests, a maximum of two chicks were fed. After that, all nestlings were weighed with a Pesola spring balance and put back in the nest in a random distribution. We revisited each nest one hour later, recorded the begging behaviour of each nestling and weighed them again. "Relative food intake" (RFI) was defined as the increment in mass expressed as a percentage of initial body mass. We assumed RFI to be a better measure of nutritional need than absolute intake, since it takes into account variations in energy requirement due to variations in body mass, but in fact absolute and relative food intake were highly correlated (Kendall's $r = 0.89$, $n = 145$, $p < 0.01$). Each brood was tested only once, and we discarded those broods in which parents apparently had not fed. This was assumed to occur when all nestlings in a brood showed negative or zero mass increments. Since adult provisioning rates at the age broods were tested are about 1 feeding visit to the nest per h (BUIRON 1988), most broods probably received a single feed. Magpie parents carry large amounts of food in a sublingual pouch (BIRKHEAD 1991), which ensures that several nestlings are fed during a single feeding visit.

We also examined whether begging performance was affected by long-term variations in nutritional need by looking for a relationship between begging behaviour and the amount of food ingested during the preceding 24 h. First, during six consecutive days (days 5 to 10 post-hatching), we obtained measures of RFI during a 1-h interval in the morning. In addition, before weighing the nestlings for the first time in a day, we recorded the number of nestlings begging in each postural category. We then looked for a correlation between the number of nestlings begging and the average food intake of the brood (the sum of mass increments divided up by the initial mass of the brood) during the preceding 24 h. Only those broods in which the average food intake reached positive values during at least four consecutive days were taken into account. Second, we determined whether begging intensity was correlated within broods with the mass gained by each nestling during the preceding 24 h. Daily mass gain was expressed as a percentage of initial body mass.

Measuring Parental Feeding

To investigate whether begging behaviour affected parental allocation of food within broods, we first enlarged within-brood differences in begging by artificial feeding, and then measured the mass gain of the chicks during the following 1-h period as a measure of their feeding success. In a morning different from that in which we tested whether hunger affected begging, we visited each brood and again determined the relative begging of each nestling. To enlarge the differences in hunger within a brood, we gave 1 g of boiled egg to the two nestlings begging least intensively, recorded their begging intensity again and weighed all of them. Nestlings were put back in the nest in a random distribution. On returning 1 h later, we determined the RFI of each nestling as above. Again, RFI values were highly correlated with absolute food intake (Kendall's $r = 0.86$, $n = 94$, $p < 0.001$). Each brood was tested only once and those broods in which all nestlings failed to gain any mass were excluded from the analysis. Deviations from the mean RFI of the brood were computed as a measure of the success of each nestling in obtaining food.

Data Analysis

To guarantee statistical independence between data points, we analyzed only mean values for each level of begging intensity for each nest. To determine the relationship between begging and food intake, we performed non-parametric statistical correlations (Kendall) for each brood separately. We then determined whether there was a significant trend in the correlation between each pair of variables by comparing the number of positive and negative correlation coefficients using a binomial test (ZAR 1984). All p values are two-tailed unless otherwise stated.

Results

Characteristics of the Begging Display

The different features considered for characterizing the begging display covaried with each other in a highly predictable way. Higher levels of postural

intensity were associated with the emission of begging calls, shorter latency times and longer begging persistence. Table 1 shows that nestlings were much more likely to call when in a posture involving extension of tarsi and wing flapping than when begging in a resting posture. The sequential order in which nestlings begged within a brood was also related to begging intensity. Virtually all broods showing variation in both begging intensity and latency time ($n = 19$) showed a negative correlation between order rank and begging intensity (8 of them significantly); that is the chicks that were first to beg in a brood begged more intensely. Nestlings with the highest persistence in maintaining the begging posture also scored higher in the rank of begging intensity (2.7 ± 0.17 SE) than the average for their less persistent broodmates (2.4 ± 0.14 SE) (Wilcoxon test, $Z = 2.45$, $n = 18$, $p < 0.05$).

Table 1: Number of begging displays involving emission of begging calls according to the level of postural intensity of the display. Each display corresponds to a different nestling

	Level of postural intensity		
	gaping	gaping on tarsi	gaping on tarsi plus wing flapping
Vocalization:			
yes	51	41	23
no	65	3	1
% Calling	43.9	93.2	95.8

$$\chi^2 = 46, df = 2, p < 0.001$$

A short latency time to respond was also associated with a high begging persistence and the emission and duration of begging calls. Those nestlings with the highest begging persistence also scored lower in the begging sequence (1.2 ± 0.12 SE) than their sibs (2.3 ± 0.17 SE) (Wilcoxon test, $Z = 3.5$, $n = 18$, $p < 0.001$), i.e. the most persistent chicks were among the first to beg. Those nestlings with the shortest latency time to respond were more likely to beg standing on their tarsi (14/16, 87.5 %) than their broodmates (20/90, 22.2 %) ($\chi^2 = 23.7$, $df = 1$, $p < 0.001$). Begging calls emitted by nestlings with the shortest latency were significantly longer ($431.9 \text{ ms} \pm 32.5$ SE) than the average duration of calls given by their broodmates ($384.9 \text{ ms} \pm 65.9$ SE) (Wilcoxon test, $Z = 1.87$, $n = 24$, $p < 0.05$).

The Relationship between Begging Behaviour and Nutritional Need

Fig. 1 shows that the RFI of each nestling during 1 h was a good predictor of its level of begging intensity at the end of that period. The relationship between a nestling's begging intensity and the deviation from the mean RFI of its brood was less clear (Kruskal-Wallis, $H = 5.74$, $n = 59$, ns), but still both variables showed a significant correlation (Kendall's $r = -0.18$, $p < 0.05$). Sequential begging order was also correlated with RFI, so that the first nestlings to beg had lower

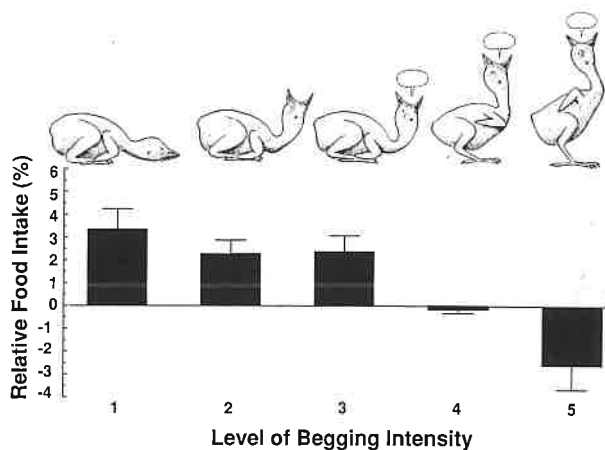


Fig. 1: The relationship between the level of begging intensity of the display and the hunger motivation of magpie nestlings, estimated as the relative food intake RFI (expressed as a percentage of body mass) during the preceding 1-h interval (Kruskal-Wallis $H = 13.7$, $n = 59$, $p < 0.01$; Kendall's $r = -0.31$, $p < 0.01$). Levels of begging intensity are: 1) fails to beg; 2) gapes silently, tarsi flexed; 3) gapes calling, tarsi flexed; 4) gapes calling, tarsi extended; 5) same as 4) plus wing flapping. Errors are SE around means

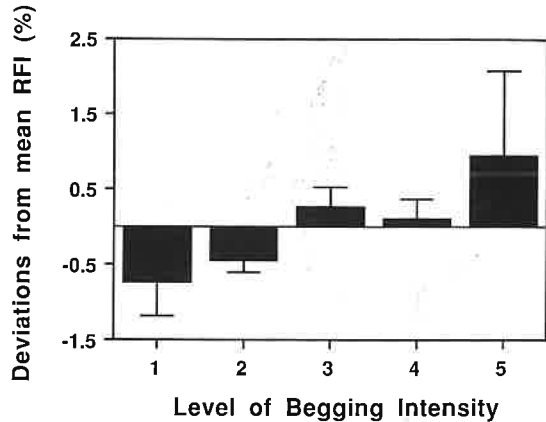
RFI during the preceding hour. Out of 30 broods, 24 showed a positive relationship (5 significant, one-tailed) and 6 a negative one (binomial test, $p < 0.01$). Nestlings which kept on begging for the longest time tended to have lower RFI ($1.3 \% \pm 0.75 \text{ SE}$) than the average for their less persistent broodmates ($2.5 \% \pm 0.63 \text{ SE}$), but the difference was not significant (Wilcoxon test, $Z = 1.7$, $n = 18$, $p = 0.089$). Analyses involving absolute food intake instead of RFI led to virtually the same results.

The above relationship between begging performance and RFI was partly a result of differences between egg-fed and unfed chicks. We failed to detect any significant effect of artificial feeding upon sequential begging order but egg-fed chicks showed higher levels of begging intensity 1 h later ($2.7 \pm 0.14 \text{ SE}$) than unfed chicks ($2.4 \pm 0.15 \text{ SE}$) (Wilcoxon test, $Z = 2.37$, $n = 30$, $p < 0.05$). This was probably a consequence of egg-fed chicks having a lower RFI during the following h ($1.39 \% \pm 0.47 \text{ SE}$) than their unfed broodmates ($2.33 \% \pm 0.36 \text{ SE}$) (Wilcoxon test, $Z = 1.97$, $p < 0.05$).

Contrasting with the predictable relationship observed within broods between begging performance and the amount of food received during the preceding h, there seemed not to be a comparable long-term effect of nutritional need over a 24-h period. We failed to detect a clear effect of the average food intake by the brood during the preceding 24 h upon the begging behaviour of chicks. Considering the total number of nestlings which begged, 12 broods showed a positive relationship (one significant) and 6 a negative one (binomial test, ns). Similarly, 5 broods showed a positive relationship between the number of nestlings giving begging calls and the average food intake of the brood during the preceding day, and 8 broods showed a negative relationship (binomial test, ns). The only observed trend approaching statistical significance was a reduction in the number of nestlings begging on their tarsi on the days following a high average food intake: out of 15 broods, 11 showed a negative trend (two significant) and 4 a positive one (binomial test, $p = 0.06$).

Begging intensity also showed no correlation with the percentage of mass gain of nestlings during the preceding 24 h. Out of 21 broods, 13 showed a negative correlation, and 8 a positive trend (binomial test, ns).

Fig. 2: Relationship between parental feeding (estimated as the deviation from the mean relative food intake RFI of the brood during 1-h intervals) and the level of begging intensity of the display recorded for each nestling at the beginning of the interval (Kruskal-Wallis $H = 4.3$, $n = 38$, ns; Kendall's $r = 0.22$, $p < 0.05$). Explan. as in Fig. 1



The Relationship between Parental Feeding and Begging Behaviour

Deviations from the mean RFI of the brood showed a significant correlation with levels of begging intensity at the beginning of the preceding h, suggesting that, on average, nestlings in greater need actually garnered more food (Fig. 2). However, the relationship was less clear than that existing between begging performance and hunger. One possibility is that parents respond to the begging intensity of a nestling relative to that of its nestmates, rather than to the absolute begging intensity (GODFRAY & PARKER 1992). If so, this would obscure the relationship between food provisioned and begging intensity when all broods are pooled together, as in Fig. 2. However, individual correlation analyses confirmed that the relationship between parental feeding and begging intensity was quite variable. 8 broods showed a positive relationship (two significant, one-tailed), while 6 showed a negative relationship (binomial test, ns). The lack of a clear relationship between parental feeding and begging performance is further suggested by the fact that neither begging order nor begging persistence adequately predicted RFI over the following h. RFI showed a positive correlation with sequential begging in 8 broods, and negative in 13 (3 significant, one-tailed) (binomial test, ns). Furthermore, those nestlings with the longest begging persistence showed higher deviations from the mean RFI of the brood ($0.07\% \pm 0.51\text{ SE}$) than their less persistent siblings ($-0.58\% \pm 0.53\text{ SE}$), but the difference was non-significant (Wilcoxon test, $Z = 0.63$, $n = 8$, ns). Considering absolute values of food intake instead of RFI led to the same result. The only significant effect detected was a correlation between deviations from the mean absolute food intake of the brood during a 1-h period and the level of begging intensity at the beginning of this period (Kendall's $r = 0.16$, $n = 38$, $p < 0.05$).

In this case, no significant differences were detected between the RFI of egg-fed ($1.51\% \pm 0.42\text{ SE}$) and unfed chicks ($2.13\% \pm 0.43\text{ SE}$) (Wilcoxon test, $Z = 1.21$, $n = 21$, ns).

Discussion

Our results are consistent with the hypothesis that begging behaviour is an honest communicative system by which parents could assess the nutritional state of nestlings. First, begging signals are redundant, i.e. different components of the display (e.g. latency, duration, posture, and the duration of begging calls) co-vary in a way that enriches the information content of the signal. Two other studies have also found a correlation between different components of the begging display (GOTTLANDER 1987; SMITH & MONTGOMERIE 1991). Second, begging performance was strongly and reliably affected by variations in the degree of food requirements within the range of hunger fluctuations which are likely to occur under natural conditions. Part of this relationship was, however, a consequence of our experimental procedure because egg-fed chicks had lower RFI during the following hour and showed higher levels of begging intensity at the end of this period. While this result stresses the view that RFI during the preceding hour influenced begging intensity, it also casts doubt on our assumption that the hunger of egg-fed and unfed chicks should increase by the same amount over the next hour. It is likely that feeding has no immediate effect upon begging behaviour but it takes some time for chicks to lower their begging intensity after food is ingested. Further work on the relationship between begging behaviour and food consumption should take into account this effect.

Formerly, HENDERSON (1975) and KHAYUTIN (1985) found a gradual relationship between calling rate and latency, respectively, and the extent of food deprivation. All this evidence suggests that begging behaviour may be a finer predictor of nutritional need than suspected from previous studies based on food-deprivation experiments (HAARTMAN 1953; BARRAUD 1961; CONOVER & MILLER 1981; RYDEN 1982; BENGTSSON & RYDEN 1983; DRUMMOND & GARCIA 1989; SMITH & MONTGOMERIE 1991).

The prediction that nestlings in greater need should employ more costly signals to solicit food also gains support from the data. Hungrier nestlings begged in postures which necessarily implied a greater energetic cost. The main postural elements of the begging display superseded each other, so that nestlings in greater need progressively added more features to the basic gaping display: vocalizations, vocalizations plus standing on tarsi, vocalizations plus standing on tarsi plus wing flapping. This cumulative sequence of separate locomotory elements requires an increasing degree of muscular activity. The existence of an excess energetic cost of higher begging levels is consistent with the finding that a decrease in body temperature exerts a stronger effect upon the motor performance of calling and posture compared with latency and gape width (CHOI & BAKKEN 1990). In addition, begging calls given in connection with intense begging postures by magpie nestlings lasted for longer. The available information on the energetic cost of vocalization in both endothermic and ectothermic vertebrates indicates that calling may be an extremely expensive activity (RYAN 1988; WELLS & TAIGEN 1989). It was previously found that, under laboratory conditions, magpie nestlings increase their calling rate in response to food deprivation (REDONDO 1991). Consequently, both calling duration and calling rate contribute to increase energetic cost.

Begging displays are not the only costly solicitation signals observed in birds. Many penguin chicks solicit food by vigorously running after their parents, and some studies have found a correlation between hunger and chasing effort (THOMPSON 1981; BUSTAMANTE *et al.* 1992). Another example is provided by the violent frantic convulsions of many cormorants, pelicans and sulids (DRUMMOND 1987). There is some evidence that convulsions varies according to the nutritional state of chicks. For instance, American white pelican chicks were less likely to engage in convulsions following those feedings in which the chick apparently approached satiation (CASH & EVANS 1987).

We found no clear relationship between begging intensity and two long-term measures of nutritional need: the average food intake by the brood and the relative mass gain of nestlings during the preceding day. This result parallels that previously obtained with budgerigars by STAMPS *et al.* (1989), who failed to show a relationship between begging, and chick body mass at the preceding developmental phase (an estimate of nutritional need). Instead of considering these apparently anomalous results as evidence that begging is not related to offspring need, we feel that they reflect that begging may be only sensitive to short-term variations in nestling food requirements (*i.e.* hunger motivation), and not to food deficits in the longer term (*e.g.* body condition). This seems a necessary prerequisite for a signalling system of this kind being capable of such fine gradations as those suggested by this study.

The hypothesis that begging signals are honest indicators of a chick nutritional need is however contradicted by the fact that nestlings can escalate their begging behaviour for the same degree of need in response to several factors. For example, nestling budgerigars are highly sensitive to changes in the potential rewards of begging, and show exaggerated solicitation rates when begging is positively reinforced by parental feeding (STAMPS *et al.* 1985). On the other hand, both zebra finch (MULLER & SMITH 1978) and American robin (SMITH & MONTGOMERIE 1991) nestlings increase their begging in response to begging by siblings. Even tiny nestlings may be capable of various types of simple learning processes by instrumental conditioning and observational learning (HUSSELL 1988; STAMPS *et al.* 1989). Although energetic costs of begging may help to maintain a reliable relationship between relative begging intensity and relative food requirements within a brood, it has been suggested that such processes (and, in particular, intra-brood scramble competition) could ultimately lead to an exaggeration of the absolute begging intensity if the lowest begging levels fall into disuse over evolutionary time (HARPER 1986).

GODFRAY's (1991) model did not account for intra-brood competition effects but, in fact, a two-chick model also predicts honest signalling (GODFRAY, *pers. comm.*). The extent to which sibling competition may contribute to an evolutionary runaway escalation of begging intensity depends on how much exaggerated begging helps a nestling to gain a competitive advantage for parental attention over its siblings. Only when the parental response to increased chick begging (*i.e.* give more food) is fixed and evolutionary invariable can exaggerated, dishonest begging evolve (GODFRAY 1991). Most previous parent-offspring conflict models for the evolution of begging have implicitly assumed a fixed response of this kind

on the part of the parent (PARKER & MACNAIR 1978; STAMPS et al. 1978; LAZARUS & INGLIS 1986) but there are grounds to suspect that such an assumption is unrealistic.

Overall, a positive relationship between parental feeding and begging intensity has been reported in most studies (HAARTMAN 1953; LOCKIE 1955; HENDERSON 1975; MULLER & SMITH 1978; RYDEN & BENGTTSSON 1980; BENGTTSSON & RYDEN 1981, 1983; HARRIS 1983; GOTTLANDER 1987; HUSSELL 1988; DRUMMOND & GARCIA 1989; STAMPS et al. 1989; SMITH & MONTGOMERIE 1991). However, evidence is accumulating that this parental rule is flexible according to several factors, suggesting that intense begging does not always guarantee parental attention, and that parents may ignore solicitation under certain circumstances. Three such factors have been identified:

1. Parental sex. Budgerigar fathers tended to feed the offspring who begged more while mothers allocated food according to offspring size (STAMPS et al. 1985).

2. Offspring size. Several studies have found that parental food allocation is affected by an interaction between nestling relative size and begging: lighter nestlings have to beg more for the same amount of food (BENGTTSSON & RYDEN 1981, 1983; MCGILLIVRAY & LEVENSON 1986; DRUMMOND & GARCIA 1989).

3. Other studies have described the existence of favoured nest positions from which parents preferentially feed nestlings (RYDEN & BENGTTSSON 1980; BENGTTSSON & RYDEN 1981; REED 1981; GOTTLANDER 1987; SMITH & MONTGOMERIE 1991). The proximity of a nestling to such favoured positions may be a powerful predictor of parental feeding, and there is some evidence that nestling position and begging intensity are not correlated with each other (RYDEN & BENGTTSSON 1980; BENGTTSSON & RYDEN 1983; SMITH & MONTGOMERIE 1991).

The interaction between such factors is likely to be complex. For example, GOTTLANDER (1987) found that pied flycatcher mothers tended to favour lighter nestlings but that the converse was true after the brood was subjected to a period of experimental food deprivation. Begging intensity positively affected parental feeding when the brood was not food-deprived. However, after food deprivation, nestling position was the only predictor of parental feeding. Such interactions would make the relationship between parental feeding and begging intensity vary from one brood to another. We found a great deal of such variability in magpies, as have previous studies in other species (HUSSELL 1988; STAMPS et al. 1989). Accordingly, the success of any mutation promoting exaggerated begging may depend upon brood characteristics which are largely determined by unpredictable factors like brood size, food abundance or the extent of hatching asynchrony. Behavioural flexibility on the part of the parents may thus help in maintaining the reliability of begging signals over evolutionary time.

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