

The role of feeding regularity and nestling digestive efficiency in parent–offspring communication: an experimental test

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Summary

1. Current theory suggests that by responding to offspring food solicitation, or begging, parents improve the efficiency by which they convert parental investment into offspring fitness. However, the proximate mechanisms of this conversion are not entirely clear. One potential function of responding to begging is to maintain feeding regularity. Feeding at regular time intervals may improve offspring fitness through increasing digestive efficiency, securing food receptivity, and reducing excessive begging displays.

2. To examine the adaptive value of parental responsiveness to begging, we simulated either responsive or non-responsive mutant parents while hand-raising nestling house sparrows (*Passer domesticus*). In a previous study we tested parental responsiveness *per se*, without changing feeding regularity. Here, we tested the impact of the very likely possibility that non-responsive parents also cause greater variability in the intervals between visits and feedings than do responsive parents, by experimentally scheduling either extremely variable or regular time intervals between visits and/or feedings in a two-way design.

3. Our results show that nestling growth, digestive efficiency and begging intensity were not affected by the level of feeding or visit regularity. However, within the regular feeding treatments (but not within the variable feeding treatments), digestive efficiency was positively correlated with nestling begging levels, and negatively correlated with how persistent the experimenter had to be to induce chicks to accept food.

4. These results suggest that nestlings are quite resilient to variable feeding schedules and that parents have therefore little to gain from regular feeding as long as they provide an adequate daily amount of food. Nestlings that are regularly fed even when they are satiated, however, may exhibit some reduction in digestive efficiency.

5. These data imply that digestive efficiency decreases only when the digestive system is very close to being full. Thus, when mediated by a reduction in begging displays near satiation, increased digestive efficiency imparts a previously unappreciated physiological benefit to signalling offspring and their responsive parents.

Key-words: nestling growth, offspring nutrition, parental care, parent–offspring conflict, signalling

Introduction

Offspring solicitation, or begging, is directed at acquiring resources from provisioning adults (usually the parents). Theoretical studies suggest that begging may be a reliable

signal of offspring ‘need’ for resources (Godfray 1991, 1995; Rodríguez-Gironés *et al.* 1996; Godfray & Johnstone 2000; Johnstone 2004). This hypothesis is supported by evidence that begging intensity of dependent young increases with food-deprivation, and that parents adjust their food delivery rates in response to begging intensity (reviewed in Kilner & Johnstone 1997; Budden & Wright 2001; Wells 2003; Kilner & Hinde 2008; see also Leonard & Horn 2005; Smiseth & Moore 2008; but see Royle *et al.* 2002). Theoretically, parents

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should respond to begging when allocating resources because this would lead to better translation of their resources into offspring fitness. However, the biological mechanisms underlying the adaptive value of such parental responsiveness to begging remain unclear. The term 'offspring need' is assumed to be a function of internal state, which determines fitness gains from receiving extra resources (see Godfray 1991, 1995; Cotton *et al.* 1999; Godfray & Johnstone 2000; Parker *et al.* 2002). However, beyond the reasonable assumption that food-deprived (i.e. hungry) young have more to gain from receiving extra food, very little is known about the physiological factors that make it adaptive for the parents to respond to begging (see e.g. Karasov & Wright 2002).

In a recent study of avian begging and parental provisioning behaviours (Grodzinski & Lotem 2007), we suggested that the adaptive value of parental responsiveness to begging may be explained by two, non-mutually exclusive, proximate mechanisms: the efficiency-based model, and the fuel-gauge model. The efficiency-based model assumes that because of some physiological constraint on offspring digestion, young whose digestive system is emptier will digest a given amount of food more efficiently, leading parents who respond more to increased begging displays to make better use of their investment. The fuel-gauge model, in contrast, does not require that digestive efficiency will be a function of how much food has already been provided. Instead, parental responsiveness may be adaptive because it improves parental time-budget by wasting less time trying to feed full, non-receptive, offspring, on the one hand, and by reducing the risk that one of the offspring will inadvertently be overlooked, on the other. Begging may thus serve as a fuel-gauge that indicates how close each offspring is to being either full or empty, enabling the responsive parent to avoid these potentially costly events (Grodzinski & Lotem 2007).

A different and relatively unexplored aspect of parental responsiveness to begging is related to feeding regularity. Responding to begging may not necessarily result in regular feeding, but it can potentially reduce the variation in inter-feeding intervals (because it leads to preferential feeding of hungrier offspring and to a faster return to hungry broods). Parental responsiveness may therefore bring the feeding regime closer to regularity, which has been suggested to be advantageous (Ricklefs 1979; Montgomerie & Weatherhead 1988; Redondo 1989; Rands *et al.* 2003; Royle *et al.* 2006). Regular visits at the nest may also reduce nestling begging, possibly due to nestlings being less uncertain of the time until the next parental visit (Ricklefs 1979; Clark 2002; Royle *et al.* 2006). It is important to note that reducing feeding variability may be adaptive under both the efficiency-based and the fuel-gauge models: regular feedings may improve digestive efficiency while also securing food receptivity by offspring (i.e. less food-refusals by chicks) and minimizing the risk of repeatedly neglecting an offspring by chance. In addition, feeding regularity may even reduce excessive begging by offspring experiencing long feeding intervals, which could be energetically costly (Kilner 2001) or increase predation risk (Haskell 1994; Dearborn 1999). None of these possible

benefits, however, has been tested experimentally, and very little work has been done in general on the relations between parental feeding patterns, begging, and chick digestion (Clark 2002; Karasov & Wright 2002; Budden & Wright 2008).

In a previous attempt to identify the adaptive value of parental responsiveness to begging (Grodzinski & Lotem 2007) we tested the effect of parental responsiveness *per se*, without changing feeding regularity. Using hand-raising of house sparrow (*Passer domesticus*, Fig. 1) nestlings, we simulated both parents that are responsive to begging and hypothetical mutant parents that offer similar food amounts at similar time intervals, but in a non-responsive manner (i.e. distributed randomly throughout the day, irrespective of nestling begging). The results were consistent with the fuel-gauge model and identified an adaptive value of parental responsiveness, in terms of chick growth, that was independent of the level of feeding regularity (which was similar in both treatments). Here we describe a complementary experiment, designed to test the effect of feeding regularity on nestling fitness. Specifically, we examined whether hypothetical non-responsive parents that generate highly variable visit and feeding schedules may be selected against because their nestlings suffer from lower digestive efficiency, slower growth rate (which affects post-fledging fitness; e.g. Magrath 1991; Kilner 2001; Schwagmeyer & Mock 2008) and higher begging intensities than nestlings raised under regular visit and feeding intervals (assumed to be generated by responsive parents).

Methods

SUBJECTS AND GENERAL METHODS

The 80 house sparrow nestlings used for the experiment were taken from 62 different broods in captive and free-living colonies in the I. Meier Segals Garden for Zoological Research of Tel-Aviv University during the spring of 2006 (see Dor & Lotem 2009, for more information). Nestlings weighing between 6.0 and 9.0 g were taken from their nests at 06 : 25 h on day 4 post-hatching (hatching = day 0) and returned on the morning of day 6 post-hatching. At this age house sparrow nestlings are in the middle of the linear phase of their growth curve (Lepczyk & Karasov 2000). Their inability to compensate for low mass gain by subsequently increasing their growth rate (Lepczyk & Karasov 2000) suggests that this stage is especially crucial for eventually reaching adequate fledging mass. Each nestling was individually kept for 48 h in a custom-made incubator (D.M.P. Engineering Ltd. based on the Lory10 model) set to 37 °C at 50–70% RH. At different times throughout each of the two experimental days, from 07 : 30 to 19 : 00 h (but not during a mid-day break for the experimenter between 13 : 30 and 14 : 30), we simulated 65 parental visits. At the onset of each visit we stimulated the nestling to beg by turning the incubator light switch off for 1 s, and then let the nestling beg for 4 s with no intervention. On 23 of the 65 daily visits, the nestling was offered a meal after these 4 s, which consisted of chopped fly larvae given through a syringe. Meal sizes were 0.25 mL on the first experimental day and 0.3 mL on the second, totalling 5.75 and 6.9 mL per day, respectively (adequate for normal growth, see Lepczyk *et al.* 1998; Lepczyk & Karasov 2000). The exact times of simulated parental visits, their subsequent distribution and whether they included a meal or not, were determined according to the four treatments detailed below.

Table 1. A schematic description of the four experimental treatments

Treatment	Feeding	Visits	Pattern
1	Regular	Regular *
2	Variable	Regular *
3	Regular	Variable *
4	Variable	Variable *

Feeding visit = '|'; Non-feeding visit = '.'; Mid-day break = '*'

In all treatments, when a nestling was to be fed according to the feeding protocol but had its beak closed, another light-out stimulus was given to stimulate gaping. If this was not enough, we applied up to five light touches to the beak with the syringe (1 s apart). If the beak still remained closed, the meal was not given and was noted as 'untaken food' (this happened in only $1.61 \pm 2.34\%$ of feeding visits). The reason we persisted in stimulating refusing nestlings (five touches to the beak compared to only one used by Grodzinski & Lotem 2007) was our aim to minimize the possible effect of such refusals on the degree of feeding variability implemented for each treatment group (see below). Furthermore, this persistency also resulted in a more powerful test of the efficiency-based model because it generated cases in which nestlings had to digest extra meals at a time when their digestive system was nearly or already as full as it could be (without artificially force feeding).

EXPERIMENTAL TREATMENT GROUPS

To test the effect of regularity in visit and feeding rate we created four different treatment groups ($n = 20$ nestlings each) with either regular or variable protocols in respect to their visit and feeding intervals. All treatments included 23 feedings out of 65 daily visits, and a standard mid-day break from 13:30 to 14:30 that was started and ended with a feeding visit (but contained no visits in between). A schematic description of the four treatments is illustrated in Table 1.

Treatment 1-regular visits, regular feedings

Daily protocols consisted of a visit every 10 min from 07:30 to 19:00 h, with a feeding offered every 30 min (excluding the standard mid-day break).

Treatment 2-regular visits, variable feedings

Daily protocols consisted of a visit every 10 min (as in treatment 1), with the feedings distributed among these visits such that the intervals between them were highly variable. To achieve this, we generated on a computer 500 protocols with 21 feedings randomly distributed among the visits (in addition to the fixed 13:30 and 14:30 feeding visits). For each daily protocol, the standard deviation of the interval between feedings was calculated, and out of the 100 (i.e. 20%) with the highest standard deviation, 40 daily protocols were randomly picked to be used in the experiment (2 daily protocols for each of the 20 nestlings). Note that by selecting the protocols for this treatment (as well as for treatments 3 and 4, Table 1) from the most variable protocols generated randomly, we designed a powerful test for the possible consequences of irregular feeding (those that may occur in only 20% of a random feeding schedule), while also avoiding pseudoreplication.

Treatment 3-variable visits, regular feedings

Daily protocols consisted of a feeding visit every 30 min (as in treatment 1), but the remaining 42 non-feeding visits were distributed throughout the day in such a way that the intervals between visits were variable. To achieve this, we generated on a computer 500 protocols in which the 42 non-feeding visits were randomly distributed between all possible visit times at 5 min intervals between the feeding visits (for example, 07:35, 07:40, 07:45, 07:50 and 07:55 are possible visit times between the first two feeding-visits of the day). For each daily protocol, the standard deviation of the interval between visits was calculated (both feeding and non-feeding visits counted as visits for this calculation), and out of the 20% with the highest standard deviation, 40 daily protocols were randomly selected and used.

Treatment 4-variable visits, variable feedings

In this treatment group, the intervals between visits (feeding and non-feeding visits alike) and the intervals between feedings were variable. To achieve this, we generated on a computer 500 protocols in which 21 feeding visits and 42 non-feeding visits were randomly distributed among the possible 5 min time intervals (07:30, 07:35, ..., 18:55, 19:00), (except between the 13:30 and 14:30 fixed feedings). For each daily protocol, we calculated the standard deviation of visits, and the standard deviation of feedings. To select our daily protocols from the most variable protocols both in visit and feeding intervals, we first selected the 224 most variable protocols (out of 500) in their visit schedule (based on visit-interval SD), and from those the 100 most variable in their feeding schedule (based on feeding-interval SD). Initially selecting 224 protocols ensured that the further selected 100 would represent the 20% most variable (in visit and feeding intervals) of the randomly generated protocols ($100/224 \approx 224/500 \approx$ square root of 20%). 40 of these 100 protocols were randomly chosen and used (2 for each of the 20 nestlings).

MEASURING NESTLING GROWTH AND DIGESTIVE EFFICIENCY

Nestling mass, wing and tarsus length were measured each morning (to the nearest 0.1 g, 0.1 mm, respectively) and used to compare the mass gained over the experiment (i.e. from morning of day 4 to morning of day 6 post hatching), as well as the growth rates of wing and tarsus, between treatment groups. In addition, further survival data were available for 78 out of the 80 nestlings used, which were checked at their nests on day 9 post-hatching and weighed.

To measure digestive efficiency (See Afik & Karasov 1995; Grodzinski & Lotem 2007), all faecal sacs from each nestling were collected soon after excretion during the experiment. Faeces were frozen at -20°C , dried at 60°C and weighed (to the nearest 0.0001 g). Food samples from each batch of chopped fly larvae were weighed both before and after drying. Thus, using the exact amounts of food ingested by each nestling, we were able to assess the apparent assimilation mass coefficient, or AMC* (hereby AMC), calculated as (dry mass ingested – dry mass excreted)/(dry mass ingested) (see Guglielmo & Karasov 1993; Afik & Karasov 1995). The energy content of excreta and food samples was measured using a ballistic bomb calorimeter (Gallenkamp cb-370, with a benzoic acid standard), enabling the calculation of another index of digestive efficiency, the apparent metabolizable energy coefficient, or MEC* (hereby MEC), calculated as (energy ingested – energy excreted)/(energy ingested) (see Guglielmo & Karasov 1993; Afik & Karasov 1995).



Fig. 1. A male house sparrow. Photo credit: E. Katsnelson.

MEASURING BEGGING INTENSITY

Nestling begging in all of the visits was video-recorded (using a digital Sony DCR-TRV355E camera) and begging postures were later analyzed, blind to treatment group, on a computer screen (using Adobe Premier 6.5). We scored nestling begging postures during one frame (1/25 s) from each of the 4 s of uninterrupted begging on a 0–3 scale (0, no begging; and 1–3 representing increasing body positions while gaping; see Kilner 1995; Dor *et al.* 2007; Grodzinski *et al.* 2008 for similar methodology). A mean begging posture was then calculated for each chick for each visit.

DATA ANALYSIS

The distribution of all variables used for parametric statistical tests was found not to differ from normal (using Kolmogorov–Smirnov's test). Statistical tests for our proportional data (AMC and MEC) were performed on transformed data (arsine of their square root), while our figures depict the raw indices for convenience.

To test the effect of visit and feeding regularity and the interaction between them, we performed two-way factorial-ANOVAs on the variables in accordance with the two-way design of the four experimental groups (see Table 1). For variables that were not normally distributed (i.e. the proportion of untaken food and the binomial survival data), we used nonparametric tests for each of those factors separately. To facilitate the assessment of non-significant results we provide effect sizes, for which confidence intervals were calculated (Nakagawa & Cuthill 2007).

Since our data consist of 80 nestlings from only 62 different broods, they might not be entirely independent. However, measurements for siblings were correlated in their mass on day 9 post-hatching (Pearson's $r_p = 0.78$, $P = 0.013$), after siblings had stayed together in the same nest for 4 days after the experiment, while there were no significant correlations between any of the response variables measured during or immediately following the experiment (tarsus growth $r_p = 0.48$, $P = 0.061$, all other $r_p < 0.31$, $P > 0.24$). Therefore, familial dependency probably had little effect on our results. In addition, although no siblings were subjected to the same treatment and we equally distributed the sibling-pairs among treatment groups, we conservatively performed all of the analyses again for a subset of our data containing only one randomly selected nestling from each brood ($n = 62$ nestlings). The results were indistinguishable from our main analyses presented.

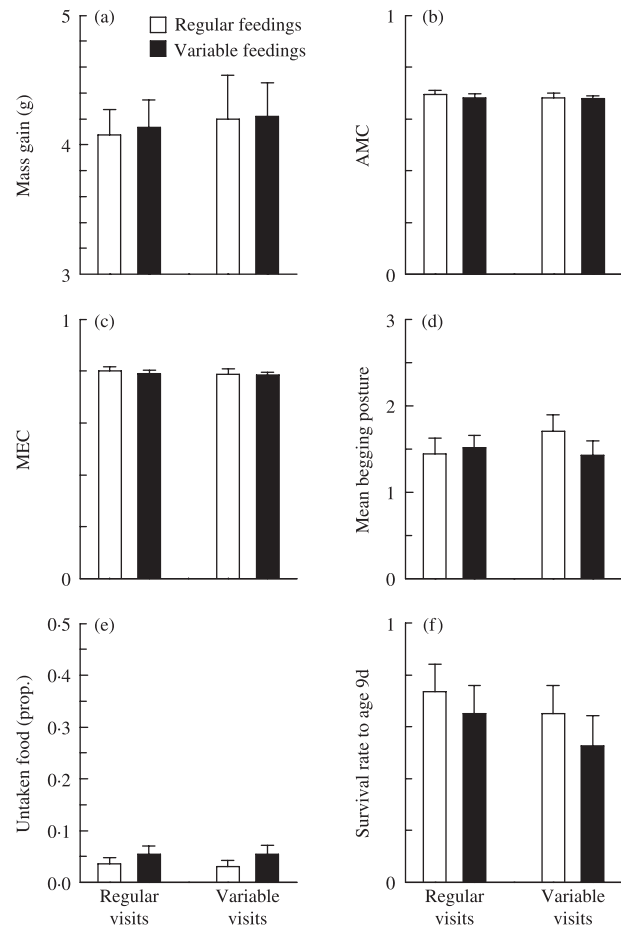


Fig. 2. Experimental response variables (means \pm SE) for regular feeding treatments (white bars) and variable feeding treatments (black bars) and for regular visit treatments (left two bars in each graph) and variable visit treatments (right two bars in each graph). (a) mass gain, (b) assimilation mass coefficient (apparent AMC), (c) metabolizable energy coefficient (apparent MEC), (d) mean begging posture, (e) the percentage of untaken food and (f) the survival rate from the end of the experiment until day 9 post-hatch. $N = 20$ for all bars (excluding the far left and far right bars in (f), for which $N = 19$).

Results

DIFFERENCES AMONG EXPERIMENTAL GROUPS

We first verified that the treatment groups were not initially different with respect to nestling origin (free or captive colonies; $\chi^2 = 1.07$, $P = 0.785$), date of hatching, rank or brood size (all Kruskal–Wallis $H_3 < 2.6$, $N = 80$, $P > 0.45$), nestling mass, wing length or tarsus length (all one-way ANOVA $F_{3,76} < 0.96$, $P > 0.41$).

Regarding the different treatments, our analysis showed that for all of our response variables tested with ANOVAs there was no significant effect of feeding regularity (all $F_{1,76} < 0.6$, $P > 0.44$), visit regularity (all $F_{1,76} < 0.41$, $P > 0.52$) or the interaction between them (all $F_{1,76} < 1.07$, $P > 0.3$). This was the case for mass gain (Fig. 2a), wing or tarsus growth, both indices of digestive efficiency (AMC and MEC; Fig. 2b,c), and for mean begging posture (Fig. 2d). While visit regularity

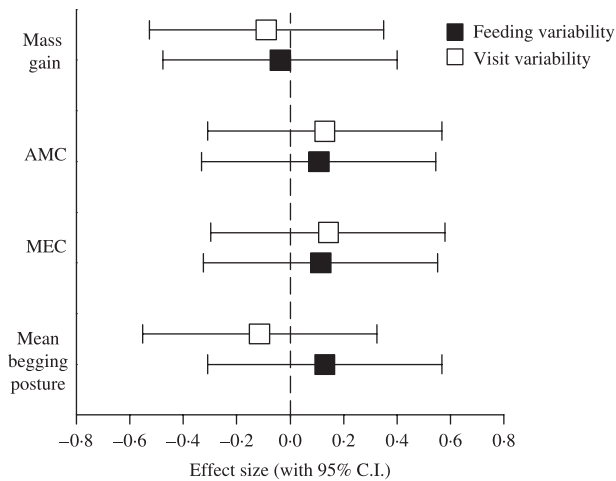


Fig. 3. The feeding regularity (black squares) and visit regularity (white squares) effect sizes (with 95% confidence intervals) regarding the response variables: mass gain, digestive efficiency indices (transformed AMC and MEC) and mean begging posture.

had no effect on the proportion of untaken food (Fig. 2e; Mann–Whitney $U = 755$, $N_1 = N_2 = 40$, $P = 0.66$), with respect to feeding regularity there was a trend toward higher proportions in the variable feedings treatment groups, as could be expected. Owing to our persistence of feeding initially refusing nestlings (see Methods), this effect of feeding-regularity on the proportion of untaken food was non-significant (Mann–Whitney $U = 695$, $N_1 = N_2 = 40$, $P = 0.31$) and did not cause a difference in the total amount of food ingested by nestlings from the different groups (food-intake: all $F_{1,76} < 2$, $P > 0.16$ for both effects and the interaction between them). Finally, for 78 out of 80 nestlings we had additional data showing that neither visit regularity nor feeding regularity had any lasting effect on nestling survival from the end of the experiment to day 9 post-hatching (Fig. 2f; Fisher exact $P = 0.48$, $N = 78$, for each of these factors), or on their mass at that age (19.3 ± 3.3 , 20.1 ± 2.9 , 21.1 ± 3.5 and 20.1 ± 2.8 g for treatments 1–4 respectively; all $F_{1,45} < 1.05$, $P > 0.31$). Given the potential effect of nestling sex on development (e.g. Tonra *et al.* 2008) and begging behaviour (Hauber & Ramsey 2003), we analysed the data from nestlings of known sex (12 males and 9 females), and found no statistical support for an effect of sex on any of the variables in Fig. 2a–e (all $t < 1.69$, $P > 0.1$, Mann–Whitney $U = 51$, $N_1 = N_2 = 40$, $P = 0.81$). However, our small sample sizes regarding sex did not allow us to draw strong conclusions or to control for a possible effect of sex in our statistical analysis.

The robustness of the null results illustrated by Fig. 2 (confirmed by our statistical analysis) is further supported from analysis of the effect sizes of separate t -tests between unified experimental groups of variable versus regular visits or variable versus regular feedings (Fig. 3; $N = 40$ nestlings in each unified group; all $t < 1.09$, $P > 0.28$). As illustrated by Fig. 3, the effects of regularity level in both feeding and visit rates are very close to zero, inconsistent in their direction and their confidence intervals are distributed quite evenly around

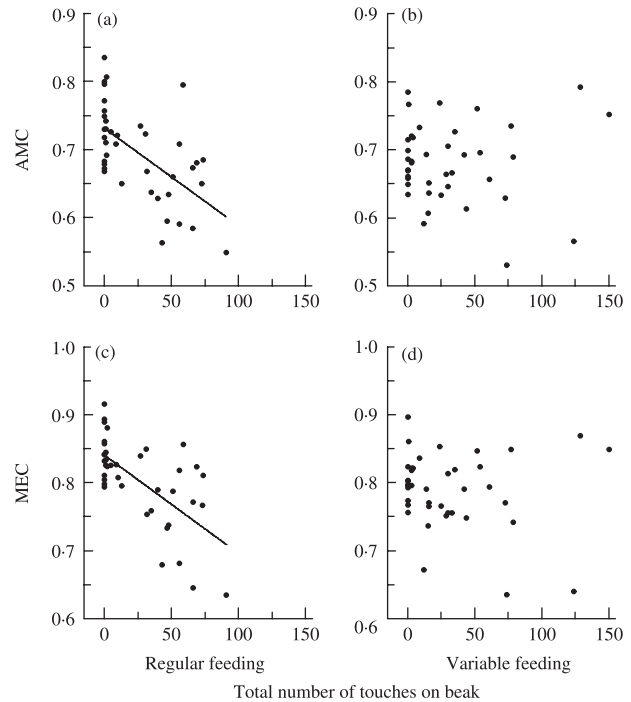


Fig. 4. The relationship between nestling digestive efficiency indices (AMC: a and b and MEC: c and d) and the total required number of touches to the beak. Data for regular-feeding groups (left panels; a and c) and variable-feeding groups (right panels; b and d) are shown separately.

zero. Finally, these results remain unchanged when we exclude one nestling (from treatment 3) which lost considerable weight over the experiment (all other 79 nestlings gained weight) and had exceptionally low digestive efficiency (approximately 4 SD less than the mean, for both indices used). The data for this nestling were excluded from our further analyses (see below), although including them does not change the results.

DIFFERENCES WITHIN EXPERIMENTAL GROUPS

While digestive efficiency was unaffected by the variability or regularity of feeding (see above), an analysis of variation in digestive efficiency within the unified variable and regular feeding groups (Fig. 4) showed a reduction in digestive efficiency for nestlings that required extra stimuli to be fed (i.e. elicited a higher total number of events where we had to touch their beak to feed them, during the two experimental days). This correlation was detected only for the regular-feeding treatments ($r_s = -0.58$, $N = 39$, $P = 0.0001$ and $r_s = -0.61$, $N = 39$, $P < 0.0001$ for the transformed AMC and MEC, respectively; Fig. 4a,c), and not in the variable-feeding treatments ($r_s = -0.02$, $N = 40$, $P = 0.91$ and $r_s = -0.12$, $N = 40$, $P = 0.46$ for the transformed AMC and MEC, respectively; Fig. 4b,d). These results held also when each of the unified regular and variable feeding treatment groups was subdivided according to the original regular and variable visit (within feeding) groups (treatments 1 and 3: $r_s < -0.5$, $P < 0.024$, treatments 2 and 4: $r_s > -0.19$, $P > 0.43$).

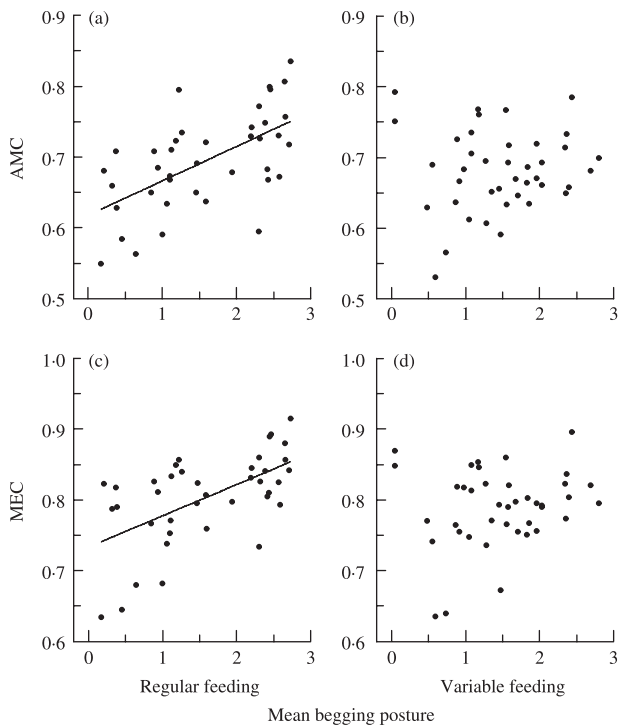


Fig. 5. The relationship between nestling digestive efficiency indices (AMC: a and b and MEC: c and d) and their mean begging posture. Data for regular-feeding groups (left panels; a and c) and variable-feeding groups (right panels; b and d) are shown separately.

Consistent with the above results (relating digestive efficiency to nestling motivation to eat), we also found that digestive efficiency was positively correlated with nestling mean begging posture for the regular-feeding treatments ($r_p = 0.59$, $N = 39$, $P < 0.0001$ and $r_p = 0.58$, $N = 39$, $P < 0.0001$ for the transformed AMC and MEC, respectively; Fig. 5a,c), but not for the variable-feeding treatments ($r_p = 0.06$, $N = 40$, $P = 0.72$ and $r_p = 0.16$, $N = 40$, $P = 0.33$ for the transformed AMC and MEC, respectively; Fig. 5b,d). Again, these patterns held when subdividing according to each of the original treatment groups (treatments 1 and 3: $r_p > 0.55$, $P < 0.011$, treatments 2 and 4: $r_p < 0.17$, $P > 0.47$).

Finally, since mass gain is expected to be affected by both food intake and digestive efficiency, we tested for these relationships in the entire data set using a multiple regression (Table 2). We also explored the data separately for each treatment group to check that the positive correlation between

digestive efficiency (transformed AMC and MEC) and mass gain was similar under all combinations of visit and feeding regularity (r was positive in all cases, and weaker correlations were consistent with small variation in the independent variable) (Table 2).

Discussion

We investigated whether some of the benefits in parental responsiveness to nestling begging may be derived from maintaining relatively regular time-intervals between parental visits at the nest and between feedings. In particular, we were interested to test the effect of feeding regularity on nestling digestion and begging behaviour. To that end, we subjected hand-raised nestlings to either regular or highly variable simulated parental visit and feeding schedules. A detailed statistical comparison among treatment groups shows that there is no evidence for an effect of feeding or visit regularity on nestling digestive efficiency, mass gain, average begging intensity, or survival. These results suggest that parents and offspring have little to gain from regular feeding or visit schedules, as long as the total daily required amount of food is provided to the nestlings.

Regarding the likelihood of our treatment design to detect an effect of regularity (if it were to exist), it is important to note several points. First, the protocols used for our variable treatments represent the 20% most variable protocols from those that may be generated randomly by a non-responsive parent (see Methods), so that the nestlings tested under our variable treatments represent those subjected to the most extreme possible consequences of a random schedule. Therefore, the degree of variability generated by a random, non-responsive parent would have caused overall even less of an effect compared to our variable treatments. Consequently, even if regularity has some small effect that was not detected with our sample size, or because of the experiment lasted for only 2 days, the relative importance of this effect is probably small. Second, feeding regularity appeared especially unimportant in comparison with the previously demonstrated critical role of parental responsiveness *per se*, which had been detected with a sample size of only 40 (pairs of nestlings) when feeding and visit regularity were kept the same and over a similar period of 2 days of experimentation (Grodzinski & Lotem 2007).

It should be noted that we tested nestlings individually to avoid the possibility that nestling behaviour will be affected on the short term by cues from their siblings' behaviour and/

Variable	Beta	t_{75}	P	r_p – independent correlation	P
Food intake	0.53	5.98	< 0.0001	0.62	< 0.0001
Assimilation mass coefficient (transformed)	-0.87	-3.65	< 0.0005	0.25	0.027
Metabolizable energy coefficient (transformed)	1.01	4.13	< 0.0001	0.39	< 0.0005

Table 2. A multiple regression of variables affecting mass gain. The overall model ($F_{3,75} = 25.13$, $P < 0.0001$, $R^2 = 0.50$) showed that mass gain in the course of the experiment was a function of food intake and the two indices of digestive efficiency (transformed AMC and transformed MEC). Independent correlation values between each of the variables and mass gain are also shown

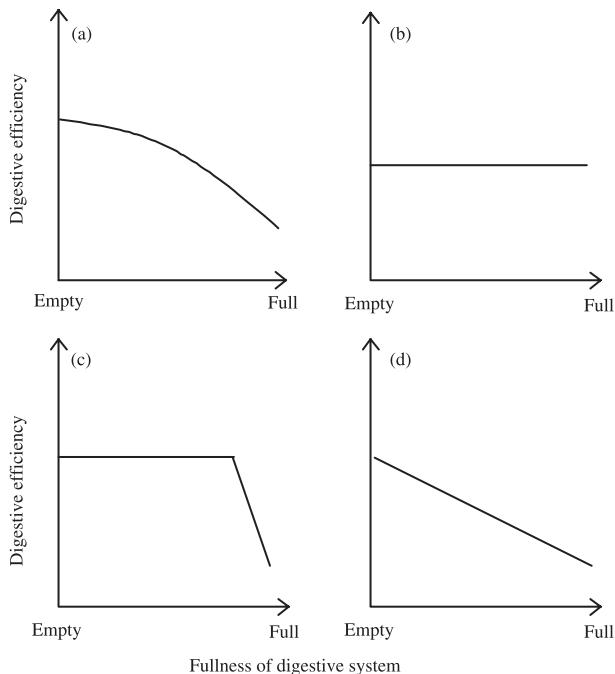


Fig. 6. Examples for alternative conceptual models of how the fullness of a nestling's digestive system (empty to full) may affect digestive efficiency. Digestive efficiency may: (a) decrease as a convex function of digestive system fullness, (b) be independent of digestive system fullness, (c) stay constant over most of the scale and reduce only when the digestive system is close to being full or (d) decrease linearly as the digestive system fills.

or their siblings' feeding schedule (e.g. Price *et al.* 1996; Leonard & Horn 1998; Bell 2007). The natural situation in the nest, however, includes sibling competition and sibling negotiation (Roulin *et al.* 2000). Therefore, our study does not address the possibility that some effect of feeding regularity is mediated by sibling competition and communication. While this seems unlikely for our physiological parameters (e.g. that digestive efficiency per se would be altered in the presence of siblings), it is quite possible that variable feeding schedule influences begging when nestlings are raised together. This may generate a benefit for regular feeding that was not tested in this study and should be explored in future work.

Considering the lack of any detected statistical difference among treatment groups, it appears somewhat perplexing that within the regular feeding groups (but not within the variable feeding groups), offspring digestive efficiency was correlated both with food receptivity and begging intensity (Figs 4 and 5). We use a graphical model (Fig. 6) to explain how this result may be consistent with our main results, and what can be learned from this regarding the relationship between feeding patterns, digestive efficiency and parent-offspring communication. Earlier we described the efficiency-based and the fuel-gauge models. Our graphic model (Fig. 6) clarifies the implied assumptions of each model with respect to the relationship between digestive efficiency and the fullness of the nestling digestive system: the efficiency-based model predicts better digestive efficiency with regular rather than

variable feeding if digestive efficiency is a decreasing convex function of fullness (Fig. 6a). This is because the reduction in digestive efficiency caused by occasionally feeding too much would not be fully compensated by the increase in efficiency when feeding too little (note that, for similar reasons, any other monotonic nonlinear function, whether decreasing or even increasing, would predict some effect for feeding regularity). The fuel-gauge model, in contrast, does not require such a relation (i.e., digestive efficiency may be constant; Fig. 6b), and does not predict that regular feeding would be better than variable feeding as long as the level of fullness does not reach zero or one. Our null results regarding the effect of feeding regularity on digestive efficiency are inconsistent with the efficiency-based model of the type illustrated by Fig. 6a, but may be consistent with the fuel-gauge model (Fig. 6b). The constant digestive efficiency of Fig. 6b cannot, however, explain the correlations between digestive efficiency and begging or food receptivity that were found for regularly fed nestlings (Figs 4a,c and 5a,c).

A novel, alternative model that explains both sets of results is the one illustrated by Fig. 6c. In this model digestive efficiency does not decrease until the system is very close to being full. Physiological causes for such a decrease include a combination of a shorter retention time and a limited spare enzymatic and transport capacity, known to affect digestive efficiency and to limit nestling growth-rate plasticity (Karasov 1996; Konarzewski *et al.* 1996; Lepczyk *et al.* 1998). With such a function, no differences will be seen in digestive efficiency between variable and regular feeding schedules, but nestlings that are regularly (and over 2 days) fed when they are close to being full may exhibit some reduction in their digestive efficiency. In our sample, such nestlings were probably those for which the daily food amount we provided was a little higher than required. When fed regularly, such nestlings were usually close to being full, not motivated to beg and occasionally not receptive. This can explain the correlations within the regular treatment group (Figs 4a,c and 5a,c) and their absence from the variable feeding group (Figs 4b,d and 5b,d). In the latter case, all nestlings experienced both short and long time intervals between feedings. The short time intervals may cause even nestlings which would otherwise remain in the high efficiency zone to experience occasional episodes of being full and with a low digestive efficiency (right end of Fig. 6c). The complementary long time intervals might have allowed nestlings that would otherwise be consistently full to experience occasional periods of emptier digestive systems and higher digestive efficiency. These effects should weaken the relationship between mean begging, reflecting the average state of fullness, and digestive efficiency, which drops only when very close to being full (according to Fig. 6c). Moreover, the different, specific feeding-protocol to which each nestling in the variable groups was subjected (see Methods), introduced additional variation to the data, thus obscuring the relation between digestive efficiency, begging and food receptivity in these groups even further.

Another possibility that appears consistent with our data is that digestive efficiency decreases linearly when the digestive

system is filled (Fig. 6d). This function predicts no treatment effect, because reduced efficiency due to transient periods of overfeeding (in the variable-feeding treatments) would be compensated in full by improved efficiency during the complementary periods of underfeeding. However, it remains unclear what physiological mechanisms might produce such a linear relationship. In addition, explaining why the within-group correlations emerged only in the regular feeding group, given this linear hypothesis, would require additional assumptions, including that (i) food refusals and reduced begging occur when the crop and stomach are full, and (ii) digestive efficiency is determined by the fullness of the intestines. In such a scenario we would expect a correlation between digestive efficiency and refusals or begging only in the regular-feeding treatments, where crop, stomach and intestine fullness are more likely to be correlated, while in the variably-fed treatments a transient fullness of the crop/stomach may occur without affecting digestive efficiency in the intestine.

Taken together, our results can be best explained under the view that nestling digestive efficiency drops when the digestive system is nearly full (but not before that; Fig. 6c). This combination of the fuel-gauge model and, at near satiation, the efficiency-based model, can explain why nestlings seem to be quite resilient to variable feeding schedules, and yet exhibit reduced digestive efficiency if repeatedly fed when satiated. It is also consistent with evidence that increased food intake may cause lower digestive efficiency in house sparrow (Lepczyk *et al.* 1998) and song thrush (Konarzewski *et al.* 1996) nestlings. These results suggest that parental response to begging has little to do with maintaining feeding regularity. Moreover, the results show for the first time that a reduction in begging when nestlings are nearly full can signal to the parent a state of low digestive efficiency. This is an important addition to our earlier study, where we showed that responsive parents can save the time that would have been wasted when trying to feed non-receptive nestlings (Grodzinski & Lotem 2007). We conclude that trying to feed such nestlings is not only time consuming but may also result in poor chick digestive efficiency.

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