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Begging and digestive responses to differences in long-term and short-term need in nestling pied flycatchers

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Offspring begging provides parents with an honest signal of short-term nutritional need (i.e. hunger). However, offspring that have experienced contrasting levels of long-term food intake may beg differently for a given level of short-term need, perhaps as a result of developmental differences in behaviour and/or physiology. We tested for the effects of both short- and long-term need on begging and digestion by manipulating food intake rates of the junior and senior nestlings from broods of pied flycatchers, *Ficedula hypoleuca*. Artificial food intake at natural levels created stable and normal levels of begging in both senior and junior nestlings, over 10 h of hand-feeding individuals in isolation. In both classes of nestling, higher than natural levels of food intake led to similar progressive linear declines in begging effort, while lower than natural levels of food intake led to similar progressive increases in begging. However, there were no corresponding changes in digestive efficiency (assimilable mass coefficient). Consistent with previous studies, junior nestlings begged at consistently higher rates throughout compared with senior nestlings. There was also evidence that digestion by junior nestlings was slightly more efficient, but individual variation in begging effort (and change in begging effort) did not correspond to differences in digestive efficiency. These results show that begging does not reflect digestive efficiency across a range of natural food intake rates, and suggest that the honesty of offspring solicitation signals, such as the differences in begging between junior and senior nestlings, are not maintained by contrasting digestive development or function.

Begging signals are known to serve as the mechanism through which parents obtain information about the nutritional needs of individual offspring and adjust their behaviour to provision them accordingly (see Kilner & Johnstone 1997; Budden & Wright 2001; Wright & Leonard 2002). A central issue in parent–offspring conflict theory and the evolution of honest solicitation signals between offspring and their parents is the definition of offspring 'need' (Royle et al. 2002). This is normally assumed to take the form of nutritional need, with food (e.g. energy) intake producing marginal increases in offspring fitness, with some form of diminishing returns (e.g. Godfray 1991, 1995). However, to understand the evolution of begging behaviour in natural systems, we need to know precisely how different schedules of nestling food intake are converted into fitness-enhancing growth and development. While gut distension is hypothesized as the most obvious mechanism to regulate begging, comparatively little is known about additional psychological and physiological mechanisms that might allow nestling birds to respond adaptively to different feeding schedules (Clarke 2002; Karasov & Wright 2002). Given that there is natural variation in food intake rates, both within and between individual offspring, we need to understand the behavioural and physiological adjustments offspring may make to changes in rates of food intake over different timescales.

One piece of information we do have is that from the begging of junior nestlings it appears that they get hungrier more quickly following a given level of food intake or satiation, compared to their senior nestmates (Lotem 1998a; Cotton et al. 1999). One interpretation of this finding is that begging signals reflect not only recent feeding history or 'short-term' need (i.e. current gut contents), but also 'long-term' requirements in terms of the stage of nestling

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growth attained and thus the total amount of food required prior to independence (Price et al. 1996; but see Lotem 1998a, b). However, to qualify what we mean by 'honest' begging, it is vital to know whether such behavioural differences are confounded by strategic differences in gut capacity and/or digestive efficiencies between senior and junior nestlings, or whether they genuinely reflect contrasting nutritional requirements (see Wright et al. 2002). Kilner (1996) hypothesized that smaller, last-hatched junior nestlings could be making the best of their poor success in competition for food within the brood by more thoroughly digesting the scant resources that they do obtain. Conversely, higher begging in these junior nestlings might reflect the fact that they need to beg more to acquire the same amount of nutritional gain as their senior nestmates, and one reason for this might be that digestive efficiency per food reward (the proportion of ingested energy not eliminated in excreta but assimilated into the body) appears to be lower for younger nestlings (Karasov 1990). Either way, variation in how different offspring respond behaviourally to the same level of parental provisioning requires a more sophisticated conceptualization of 'honesty' in begging signals that incorporates individual variation in feeding experience and/or digestive development (Budden & Wright 2001; Karasov & Wright 2002; Wright et al. 2002). We therefore need to know more about how nestlings differing in long-term and short-term need assimilate resources for the purposes of growth, and whether such variation in digestive efficiency is associated with matching adaptive variation in begging signals.

Despite its obvious links to nutritional need, studies of offspring begging behaviour have typically ignored the substantial literature concerning digestive physiology, which demonstrates the considerable developmental plasticity and temporal flexibility of these parameters (reviewed in Karasov & Wright 2002; but for recent exceptions see Wright et al. 2002; Grodzinski & Lotem 2007; Budden & Wright 2008; Grodzinski et al. 2009). For example, high feeding rates can lead to reductions in mean gut retention times (MRT) of digesta in birds (Karasov 1996). This could be one reason why high parental provisioning of already satiated nestlings may produce diminishing fitness returns. However, since digestive efficiency is also modulated by variation in hydrolysis and absorption rate (Karasov 1990), to avoid a completely proportional loss of digestive efficiency there may well be compensation for reduced MRT via increased production of digestive enzymes (Klasing 1998; Karasov & Wright 2002). In hand-feeding trials on nestling house sparrows, *Passer domesticus* (Lepczyk et al. 1998) and song thrushes, *Turdus philomelos* (Konarzewski et al. 1996), increased food intake resulted in both reduced retention time and decreased efficiency of digestion. This would suggest that short-term flexibility does not involve too many compensatory changes in digestive enzymes, but this might differ according to an individual's long-term nutritional experience, such as that of junior versus senior nestlings within a brood.

Hand-feeding studies of nestling begging behaviour make it possible to control the schedule of food delivery and measure any effects of variation in nestling digestive efficiency. One such recent study by Budden & Wright (2008) on southern grey shrikes, *Lanius meridionalis*, demonstrated that nestlings fed small food items at frequent intervals begged more than siblings fed large food items infrequently, despite the two experimental groups experiencing identical numbers of regular begging events and exactly the same volume of food being received per hour. Nestlings fed more frequently had greater levels of undigested protein present in their faeces, suggesting lower digestive efficiencies on such feeding schedules. However, a possible additional effect of learning could not be ruled out, because the frequent feeding schedule necessarily meant that those nestlings had also been rewarded more consistently (i.e. every time, rather than just one time in four) for their begging effort. Such a learning effect of the profitability of begging has been shown to increase begging in house sparrows (Kedar et al. 2000), although this effect only seems to apply when nestlings are receiving more than adequate food and are begging at relatively low intensities (Grodzinski et al. 2008). Another recent hand-feeding study on house sparrows also demonstrated a negative association between begging effort and digestive efficiency, but like the effects of learning in this system it occurred only at relatively high feeding rates when nestlings were approaching satiation (Grodzinski et al. 2009). The suggestion here (and in Grodzinski & Lotem 2007) is that although nestling digestive efficiency remains largely unchanged over a wide range of natural rates of food intake, severely reduced digestive function close to satiation might still be important in ensuring begging honesty in nestlings adapted to avoid such digestive costs, which then allows parents to avoid wasteful provisioning of nestlings as they approach satiation.

In the present study we used experimental hand feeding of same-aged junior and senior nestlings from broods of pied flycatchers, *Ficedula hypoleuca*, to determine whether long-term differences in food intake (according to position in the competitive brood hierarchy) are important in affecting begging behaviour and digestive function. We also varied short-term need by adjusting food intake rates for different pairs of junior and senior siblings to assess their ability to compensate for the kind of variation in parental provisioning rates per nestling expected from differences in clutch size and daily effects of weather on prey availability (see Lundberg & Alatalo 1992). We asked whether differences in long-term need represented by contrasting nestling positions in the brood hierarchy influence assimilation efficiency (proportion of ingested food mass or energy not excreted). The different feeding rates over 10 h hand-feeding trials created a wide range of digestive flow and body mass gain for both junior and senior nestlings. Our specific predictions were that begging effort would be significantly higher in junior nestlings (i.e. those experiencing greater long-term need). However, there are contrasting predictions for digestive efficiency, and perhaps for any subsequent effects on begging effort. Lower assimilation efficiencies might be expected in the potentially less well-developed junior nestlings, especially when faced with high rates of food intake in the short term. Alternatively, adaptive trade-offs in nestling development may allow the junior nestlings to assimilate what little food they do receive more efficiently at all feeding levels.

METHODS

The Study Population

The study was carried out at Abergwyngregyn National Nature Reserve in North Wales (4°00.3′W, 53°13.7′N) between late May and early June 2001 and 2002. The habitat is a mixture of semi-natural deciduous woodland and conifer plantations in a steep-sided valley. Up to 40% of the 100 boxes have been occupied by pied flycatchers for the last 20 years.

Hand-feeding Protocols

Thirty broods (14 in 2001, 16 in 2002) were used in the study. Nestlings were weighed at the nest site (using a spring balance to the nearest 0.2 g) and individually marked on the head with small amounts of nontoxic acrylic paint (which is known to have no adverse effects on the behaviour of nestlings, their nestmates or parents). The senior and junior nestlings from each brood were temporarily removed from nests when they were each 7 days old