ORIGINAL ARTICLE

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Does begging affect growth in nestling tree swallows, *Tachycineta bicolor*?

Abstract Much of the theoretical work on the evolution of begging assumes this elaborate display is costly. The evidence for an energetic cost to begging has, however, been equivocal. Metabolic studies on nestling birds suggest that begging requires minimal energy, but some growth studies have shown that excess begging reduces growth rates. One difficulty in interpreting these results is that metabolic and growth studies have each been performed on different species. Here, we test whether high begging frequencies depress growth in nestling tree swallows, *Tachycineta bicolor*, a species in which the metabolic cost of begging has been measured. When we compared the growth of nestlings stimulated to beg at either high or low frequencies, we found no significant differences in their mass gained, wing growth or portion of ingested energy devoted to begging either during the experimental period or in the 24 h following the end of the experiment. We also found no significant relationship between begging intensity and growth measurements. The results of our study are consistent with previous metabolic studies on this species suggesting that the energetic cost of begging is relatively low. More generally, evidence for a fitness cost of begging via decreased growth is equivocal.

Keywords Begging · Costs · Energy · Growth · Tree swallows

Introduction

The conspicuous begging of young birds has become a model for understanding the evolution of extravagant animal signals. Much of the theoretical development in this area has focussed on the costs of producing this elaborate display. Early work suggested that conflicts of interest amongst siblings and between parents and young would select for exaggerated begging, as offspring attempted to gain more than their fair share of resources (e.g. Parker and Macnair 1979). At equilibrium, costly begging prevented escalation of competition and resolved conflict between parents and young. Later models showed that begging could honestly signal cryptic aspects of offspring need, and thus could be used by parents to allocate resources at the parental optimum (Godfray 1991, 1995). These handicap models also required that the signal be costly, but here costs were needed to maintain honesty in the face of parent-offspring conflict (Godfray 1991). More recently, models showing that cost-free signals can be stable, despite conflict, have been proposed (Bergstrom and Lachmann 1998). Thus, begging costs or the lack thereof have featured in the development of a variety of models related to the evolution of begging (Johnstone and Godfray 2002).

Increased energy expenditure is assumed to be one of the main costs of begging. However, the empirical evidence for this cost is mixed. Metabolic studies on several species, including house wrens, *Troglodytes aedon*, starlings, *Sturnus vulgaris*, and tree swallows, *Tachycineta bicolor*, have found that the energy expended during begging was relatively low and comprised only a very small proportion of a nestling's total daily energy budget (reviewed in Chappell and Bachman 2002). These results suggested that the energy required for begging would probably not be diverted from nestling growth, the component of the daily energy budget most likely to influence fitness (Bachman and Chappell 1998). The results of these metabolic studies suggested that the energetic cost of begging was probably lower than predicted by handicap theory (Chappell and Bachmann 2002; Johnstone and Godfray 2002).

More recently, however, the link between begging and nestling growth has been examined directly. Studies designed to investigate the growth cost of begging in

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nestling canaries, *Serinus canaria*, and magpies, *Pica pica*, found that nestlings stimulated to beg at higher intensities suffered reduced growth compared to those that begged at lower intensities (Kilner 2001; Rodríguez-Gironés et al. 2001). This pattern was not, however, supported in a similar experiment using ring doves, *Streptopelia risoria*, (Rodríguez-Gironés et al. 2001) or in a study designed to determine the effects of learning on begging intensity in house sparrows, *Passer domesticus*, (Kedar et al. 2000). So, although the metabolic studies consistently showed a low energetic cost to begging, the growth studies suggested that, at least in some species, begging could negatively impact growth.

One difficulty in interpreting these results is that the metabolic and growth studies have each been performed on different species. Discrepancies between results based on the two approaches may be due to variation in the cost of begging across species or in the methodology used to estimate the costs. Measurement of metabolic and growth costs on single species would help to explain these discrepancies.

Here, we adopt the approach of recent growth studies (Kilner 2001; Rodríguez-Gironés et al. 2001) to examine whether there is a growth cost to begging in nestling tree swallows, a species for which metabolic measurements of begging exist. Specifically, we compare the growth of nestlings stimulated to beg at high and low frequencies, and examine how variation in begging intensity relates to differences in growth. We discuss the results of this experiment in light of earlier metabolic studies showing that begging raised metabolic rate about 1.28 times above resting (Leech and Leonard 1996; McCarty 1996) and accounted for less than 1% of the total daily energy budget of a nestling begging at typical rates (Leonard and Horn 2001).

Methods

Study species

Tree swallows are aerial insectivores that breed in tree cavities produced by other species. Their nestlings produce a loud, conspicuous begging display that intensifies with hunger, and is used by parents to allocate food to individuals within broods and to the brood as a whole (reviewed in Horn and Leonard 2002). Nestlings reach their asymptotic body mass between 10 and 12 days post-hatch, with peak mass accumulation between days 5 and 7 (Teather 1996; McCarty 2001; Kilpatrick 2002). Wing length, which represents both skeletal and feather growth, reaches asymptotic values after nestlings fledge (McCarty 2001). However, the skeletal component of this character (i.e. the manus) reaches the asymptotic length by 10 days post-hatch, with peak growth between days 5 and 6 (McCarty 2001). Both nestling mass and wing length influence fledgling return rates, with heavier, longer-winged nestlings more likely to return to the breeding site following migration (McCarty 2001). Thus, both mass gain and wing growth during the nestling period have potential fitness consequences.

Experimental protocol

This study was conducted between 1 May and 15 July 2002 in the Gaspereau Valley of Nova Scotia, Canada. Tree swallows at our study sites breed in wooden nestboxes. The study sites and nestboxes are described in detail in Leonard and Horn (1996). First egg and hatching dates were determined by checking boxes every second day until 2 days before the predicted hatching date, after which they were checked daily.

When broods were 6 days old, we weighed each nestling in the field and removed the two nestlings closest in weight (mean ± SE difference in mass: 0.03±0.166 g) from each of 25 broods. We placed the nestlings in a container with a hot water bottle and transported them to the laboratory. Once in the laboratory, we re-weighed the nestlings to the nearest 0.001 g using a Mettler H10 W electronic balance and measured the length of the flattened right wing to the nearest 0.01 mm. Measurements were highly repeatable for weight, but not for wing length, so for wing length we took three measurements and used the average value in the analyses. Because feathers typically emerge on day 7 in tree swallows, the wing length measurement reflects mostly skeletal growth.

We put each nestling in an artificial nest cup and placed both nest cups side by side in a heated chamber maintained at 37°C (mean temperature in the centre of a group of nestlings in natural broods at this age: 38.4°C, n=16 broods). We placed high and low begging nestlings in one chamber, so that they had the same environment and exposure to potential stressors, such as the sounds and movement associated with our presence. On the first trial, we randomly assigned the nest cup on the right or left side of the chamber to the high or low begging treatment. After this point, we alternated whether the high or low begging nestling was placed in the left or right cup. Nestlings were always assigned to treatment at random. We also placed a Panasonic PV-900-K VHS videocamera on a tripod facing the front of the chamber, so that we could videotape nestling begging behaviour during the experiment.

After 15 min and every 15 min thereafter for 6 h, we stimulated the nestlings to beg (see Kilner 2001 for similar protocol) by playing recordings of parental contact calls. This call stimulates begging in natural situations (Leonard et al. 1997) and reliably produces begging in the laboratory. Nestlings in the low begging treatment were fed after begging to the first contact call of a sequence of six by placing mealworm(s) (0.01±0.003 g/feeding) in the open gape with forceps. Nestlings in the high begging treatment were fed the equivalent weight of mealworm (mean difference in total weight fed to high and low begging nestlings: 0.00±0.002 g) after having begged to each of the six contact calls (see below for description of begging). Calls were given every 5 s, so high and low begging nestlings were fed approximately 30 s apart. Thus, for the same amount of food, nestlings in the low begging treatment had to beg once, while nestlings in the high begging treatment had to beg 6 times. In the wild, tree swallow nestlings have short begging bouts (range: 1–7 s/beg) and often beg multiple times per feeding visit (range for 6-day-old nestlings: 1–8 begs/visit; Leonard and Horn, unpublished data), so our experimental protocol was within the natural range of begging frequencies. Similarly, the feeding rate used in the experiment was within the natural range for nestlings of this age (2–5 feedings/h). The quantity of mealworms that each nestling received during a feeding period provided approximately the energy equivalent of a parental food bolus for nestlings of this age (McCarty 1995).

We weighed faecal sacs as they were produced because begging could affect growth rates through its impact on digestion, as well as energy expenditure (Kilner 2001). After the last feeding of the trial, we weighed and measured nestlings as above, and returned them to their home nestbox. To determine whether effects of the treatment persisted beyond the experimental period, we also weighed and measured nestlings, as described above, 24 h after the end of the experiment. Comparing mass changes in the following 24 h would also allow us to control for the effect of water loss on mass change during the trial (Kilner 2001). With the exception of one brood that was depredated, all the nestlings used in this experiment fledged successfully.

Video and statistical analyses

At each feeding (i.e. the interval during which we stimulated begging and fed the nestlings) we recorded the number of times that each nestling begged and measured the duration of each begging response. We also scored each begging response based on the following scale of increasing intensity: (1) head down, gaping, sitting on tarsi; (2) head up, gaping, sitting; (3) same as (2) plus neck stretched upward; (4) same as (3) but body lifted off tarsi; and (5) same as (4) plus wings waving. This scale produces raw scores that are discontinuous, but ordinal, because they represent points along a continuum of begging intensity. The distribution of raw scores and their tight correlation with continuous variables, such as nestling height (Leonard and Horn, unpublished data) suggest that they represent a linear increase in begging intensity. By averaging the scores across the experimental period for each nestling, we convert the scale into a continuous variable that is normally distributed. We multiplied the average begging score for each nestling by the average duration to calculate a measure of begging intensity for each nestling.

Although nestlings in the high begging treatment typically begged at the frequencies intended by our protocol (i.e. 6 times/ feeding), nestlings in the low begging treatment sometimes begged more than once. This reduced the difference in begging frequency between treatments, and so ultimately reduced the potential to detect differences in growth, if they existed. To increase our ability to detect differences between the two treatments, we excluded trials (n=9) in which the average number of begging responses/feeding for the low begging nestling exceeded the minimum value for nestlings in the high begging treatment (i.e. 4 times/feeding).

Histograms, normal quartile plots and Shapiro-Wilk W tests of the data in each analysis showed approximately symmetric, normal distributions, so we used parametric tests throughout. Means are presented ±SE and statistical tests yielding $P<0.05$ are considered statistically significant.

We used a paired t-test to compare differences in ingested mass that might be attributable to energy expenditure by high and low begging nestlings during the experimental period. In order to allow a direct comparison of our results with those of Kilner (2001), we followed that study in defining mass lost to energy expenditure (M_{EE}) as follows. First, we assume that the mass of food ingested (M_I) by nestlings during the experimental period can be spent on growth [mass at the end of the trial minus mass at the start of the trial (M_G)], lost as waste (M_W), or expended as energy (M_{EE}) to fuel metabolic activities, such as begging:

$$M_I = M_G + M_W + M_{EE}$$

Rearrangement of this equation provides a measure of the mass of ingested food that is lost to energy expenditure:

$$M_{EE} = M_I - M_W - M_G$$

The difference in M_{EE} for nestlings in the high and low treatments yields the portion of the ingested mass (M_I) that nestlings in the high treatment lost in begging over that of nestlings in the low treatment, given nestlings do not differ in M_I or M_W, and metabolic costs other than begging are identical (e.g. costs of thermoregulation or digestion). The difference also reflects the mass that nestlings in the high treatment might otherwise have devoted to growth. If, however, M_I or M_W differ between treatments, then the difference in M_{EE} could be biased. For example, a slightly lower, but statistically non-significant, M_I and slightly higher, but statistically non-significant, M_W in the high treatment could combine to yield a statistically significant difference in M_{EE}. In addition, the mass of food, faeces and nestlings will also include the mass of unmeasured quantities of water that cannot be directly related to energy gain and loss. In this case, the simple difference in mass gained or wing growth from the beginning to the end of the experimental period may be a better estimate of the growth cost of begging. We therefore also used paired t-tests to compare differences in mass gained and wing growth for high and low begging nestlings during the experimental period and in the following 24 h. The minimum effect sizes that we could detect with

Table 1 Mean (±SE) differences in M_{EE}, mass gained and wing growth for tree swallow, *Tachycineta bicolor*, nestlings in the high and low begging treatment during the experiment and in mass gained, wing growth, and total mass and wing length after 24 h. High and low begging nestlings were compared using paired t-tests

	Difference	t	df	P
During				
M_{EE} (g)	0.02±0.021	0.90	15	0.39
Mass gained (g)	−0.08±0.065	1.19	15	0.25
Wing length (mm)	−0.2±0.11	1.62	15	0.13
After 24 h				
Mass gained (g)	0.03±0.129	0.25	15	0.81
Wing length (mm)	0.0±0.17	−0.08	14	0.93
Total mass (g)	−0.08±0.186	0.42	15	0.68
Total wing length (mm)	−0.4±0.26	1.35	14	0.20

a power of 0.90 and a significance level of $P<0.05$, were 0.07 g for M_{EE}, 0.21 g and 0.3 mm for mass gained and wing growth, respectively, during the experiment and 0.42 g and 0.5 mm for mass gained and wing growth in the following 24 h.

We used simple linear regressions to test whether differences in M_{EE}, mass gained or wing growth varied with differences in the begging intensity of nestlings in each treatment.

The starting mass of nestlings in each treatment was not significantly related to their mass gain or wing growth during either the experimental period (mass: $F_{1,14}$=3.00, P=0.11; wing: $F_{1,14}$=0.72, P=0.41) or in the 24 h following the trial (mass: $F_{1,15}$=0.16, P=0.70; wing: $F_{1,13}$=2.34, P=0.15).

Results

Effect of treatment on begging behaviour

Over the 6-h experimental period, nestlings in the high begging treatment begged significantly more often (high: 144±3.8, low: 54±5.4; t_{15}=12.35, $P<0.0001$) and spent significantly more time begging (high: 504±33.4 s, low: 152±16.6 s; t_{15}=11.18, $P<0.0001$) than nestlings in the low begging treatment. The average begging scores of nestlings in the two treatments did not, however, differ significantly (high: 2.7±0.15, low: 2.6±0.80; t_{15}=0.91, P=0.38).

Effect of treatment on M_{EE} and growth

Nestlings in the high and low begging treatments showed no significant difference in M_{EE} (i.e. mass they lost to energy expenditure), mass gained or wing growth over the experimental period or in the 24 h following the experiment (Table 1). Similarly, high and low begging nestlings showed no significant difference in their total mass or wing length 24 h after the experiment (Table 1).

Effect of begging intensity on M_{EE} and growth

The difference between high and low begging nestlings in M_{EE}, mass gained and wing growth did not vary

significantly with the difference in their begging intensity during the experimental period (M_{EE}: $F_{1,14}=0.04$, $P=0.85$; mass gained: $F_{1,14}=1.72$, $P=0.21$; wing growth: $F_{1,14}=1.06$, $P=0.32$) or in the 24 h following the experiment (mass gained: $F_{1,14}=1.48$, $P=0.24$; wing growth: $F_{1,13}=1.80$, $P=0.20$).

Effect of treatment on the production of faecal material

The number, total mass and mean mass of faecal sacs produced during the experiment by high and low begging nestlings did not differ significantly (number: high: 3.8 ± 0.37, low: 3.4 ± 0.26, $t_{15}=1.31$, $P=0.21$; total mass: high: 0.95 ± 0.080 g, low: 0.88 ± 0.069 g, $t_{15}=1.21$, $P=0.25$; mass/sac: high: 0.27 ± 0.022 g, low: 0.27 ± 0.025 g, $t_{15}=-0.18$, $P=0.86$).

Discussion

The results of our study suggest that begging in nestling tree swallows has relatively little impact on growth. The growth of nestlings stimulated to beg at higher frequencies during a 6-h period did not differ significantly from that of nestlings stimulated to beg at lower frequencies, whether growth was measured in terms of mass gained, wing growth or energy expended on begging. Furthermore, 24 h after the experiment ended, nestlings in the two treatment groups showed no significant difference in their average mass or wing length.

To put our results into perspective, the difference in total mass and wing length between high and low begging nestlings 24 h after the experiment is equivalent to 0.50% and 0.05% of fledging mass and wing length, respectively. Thus, begging appears to have a relatively small impact on the growth of 6-day-old tree swallow nestlings.

Two methodological issues must be addressed before concluding that begging does not depress growth in tree swallows. First, nestlings may not have begged at sufficiently high levels to affect growth. This seems unlikely because nestlings in our high treatment begged at over double the average rates for nestlings at this age (i.e. 24 versus 10 begs/h; Leonard and Horn, unpublished data). In addition, we conducted the study when begging was most likely to impact growth, that is when growth rates, particularly mass gain, were highest (see Kilner 2001). A second possibility is that our high and low treatments did not differ enough to detect an effect. Again, this seems unlikely because high begging nestlings begged at over 2.5 times the rate and 3 times the duration of low begging nestlings. Furthermore, irrespective of treatment, there was no relationship between begging intensity and any of our measures of growth. Thus, both the absolute level of begging in the high treatment, and its relative increase over the low treatment should have been sufficient to reveal a growth effect, if it existed.

The results of our study are consistent with those of earlier metabolic studies on this species showing that begging contributes little to a nestling's daily energy expenditures (McCarty 1996). A metabolic study on the tree swallow population used in the current study (Leech and Leonard 1996) suggested that begging accounted for 12.9% of a nestling's daily energy budget. Based on this value, the authors hypothesised that this energy expenditure might affect growth in poor feeding conditions. These calculations were, however, based on the rather high rates of begging that were stimulated in the lab and not on natural begging rates. When the values were recalculated based on natural rates, begging accounted for less than 1% of a nestling's daily energy budget (Leonard and Horn 2001).

Previous metabolic measures can be used to examine how much energy was consumed by tree swallow nestlings in the high and low begging treatments. Using the energetic cost of 1 s of begging for 5-day-old tree swallow nestlings (Leech and Leonard 1996), we determined that nestlings in the high begging treatment spent 0.038 kJ of energy on begging during the trial while low begging nestlings spent 0.011 kJ. If nestlings begged at these rates all day (i.e. 14 h), then high begging nestlings would spend 0.088 kJ/day and low begging nestlings 0.026 kJ/day. Adjusting the resting metabolic rate calculated in the earlier study (Leech and Leonard 1996) for the 6-day-old nestlings used in this study, we found that the energy spent daily on begging at our high and low rates would account for 1.2% and 0.3%, respectively, of the daily energy budget. In comparison, over 30% of the daily energy budget of a 6-day-old house wren is deposited in new tissue (Bachman and Chappell 1998) and over 14% of the daily energy budget of a 6-day-old tree swallow is used for thermoregulation (McCarty 1996). Our calculations suggest, therefore, that slightly more than 1% of the daily energy budget of a 6-day-old tree swallow nestling would be spent on begging, even at rates over double those typically found in nature.

The results of our study are in contrast to recent studies showing a negative relationship between begging and growth in domestic canaries (Kilner 2001) and magpies (Rodríguez-Gironés et al. 2001). Our results are most directly comparable to the study on canaries, which compared M_{EE} in high and low begging treatments over a 6-h experimental period. In canary nestlings, the difference in M_{EE} between high and low begging treatments, at the age at which begging had its greatest impact on growth (i.e. when daily mass gain was highest), was 0.42 g (Kilner 2001), a difference that we could easily have detected, given the power of our analyses (see Methods). In comparison, the difference in M_{EE} for high and low begging tree swallow nestlings at the same stage was 0.02 g, or at least 20 times less than the difference in canaries. Although the effect of begging on growth is small for both species, the magnitude of the effect is certainly smaller for tree swallows.

It is not clear why some species appear to bear a growth cost to begging while others do not. One possibility is that measurement error may obscure differences in growth between treatments for small species, like

tree swallows, as compared to larger species such as magpies. However, our power to detect differences in mass for tree swallows was at least as good as the canary study (see above) which found significant growth effects. Differences in nestling energetics may also offer explanations for species differences in the cost of begging. For example, species vary in their growth rates and peak energy demands (Weathers 1992). Detecting growth effects of begging may be relatively difficult in slower growing species that allocate smaller amounts of their daily energy budgets to new tissue.

Interest in the energetic cost of begging stems from how this cost might work to reduce sibling competition or maintain the honesty of begging signals (Johnstone and Godfray 2002). To date, the reported effects of begging on metabolism and growth have been very small. Growth studies might provide a more direct link between begging and fitness than metabolic studies, because growth is related to fitness, at least in some species (e.g. Rodríguez-Gironés et al. 2001). Nonetheless, there is no direct evidence that the growth effects of begging have fitness consequences in the species tested. Until this critical link is made, the question of whether begging has an energetic cost will remain unanswered.

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