

The energetic cost of begging behaviour in nestling house wrens

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(Received 15 August 1997; initial acceptance 20 September 1997;
final acceptance 20 September 1997; MS. number: A7828R)

Abstract. This study presents data relevant to the hypothesis that the energy expenditure associated with begging influences the signalling of need by nestling birds. We used open-circuit respirometry to measure the energy costs of resting, begging and non-begging activities in nestling house wrens, *Troglodytes aedon*, ranging in age from 1 to 11 days post-hatching. Across all ages, begging caused a 27% increase in metabolism above resting rates. The metabolic rate during begging was not related to begging vigour. However, more vigorous begs were longer and so required a greater total energy expenditure. We analysed videotapes of broods for nestling behavioural time budgets which were combined with the metabolic data and data on growth at different ages to generate daily energy budgets. Over a 24-h period, the cumulative energy allocated to begging was slight, ranging from 0.02% of the energy budget in younger nestlings (3 days old) to 0.22% in older ones (10 days old). In contrast, non-begging movements accounted for 2 and 9% of the daily energy budget of younger and older nestlings, respectively. Relative to daily growth, the energy allocated to begging was equivalent to 0.05% (younger nestlings) and 2.3% (older nestlings) of the energy sequestered in new tissue, whereas the values for non-begging activities were 5.1 and 96.8%, respectively. These results suggest that the energetic cost of begging is not likely to have a substantial role in influencing communication of need by nestlings.

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Solicitation of food by begging is a conspicuous component of the behaviour of nestling birds. Begging may promote provisioning of the brood as a whole (Stamps *et al.* 1985) and within a brood, nestlings that beg more are provisioned more (reviewed in Leonard & Horn 1996), although a number of other factors may also affect which chick is fed. Begging has been shown to vary with a nestling's need for food. For example, increased begging activity has been associated with increased hunger (reviewed by Price & Ydenberg 1995; Leonard & Horn 1996) and reduced body condition (Price *et al.* 1996).

If parents rely on nestlings to indicate need, a conflict of interest may arise because a chick may benefit from more food than is optimal for a parent to deliver, and within broods, siblings may disagree with each other and with their parents over how food should be allocated among them (Godfray & Parker 1992). In theory, evolutionarily stable communication of need by a nestling to

a parent (i.e. honest signalling) can occur when two conditions are satisfied: (1) the benefit of feeding to a chick increases with its need; and (2) begging reduces fitness (Godfray 1991, 1995; Johnstone & Grafen 1992). The evolutionary benefit of honest signalling should result in begging performance which varies with need and is costly (see review by Kilner & Johnstone 1997). Competition among siblings may also result in additional selection to elevate begging costs (Parker & Macnair 1978).

Despite theoretical predictions that begging should be costly (i.e. reduce fitness), there are few empirical data on such costs. Begging might reduce the fitness of a chick directly as well as indirectly through effects on siblings or parents. Two of the more obvious ways in which begging can reduce nestling fitness is by attracting predators (Haskell 1994) and increasing energy expenditures. If begging requires a substantial energy expenditure, then it can potentially divert critical energy from growth, development or maintenance which could affect post-fledging survival. Recent studies (Leech & Leonard 1996; McCarty 1996)

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suggest that begging has a small energy cost, but these studies were limited in scope and used measurement techniques with poor temporal resolution.

Here we present laboratory measurements of metabolic expenditures during rest and activity, especially begging, in nestling house wrens, *Troglodytes aedon* through the majority of the nestling growth period. To put these data into an ecological context, we constructed daily energy budgets for nestlings using time budgets generated from video records of broods and measurements of metabolism in the laboratory and in the field. These data allowed us to evaluate the potential impact of begging costs on a nestling's energy requirements for maintenance and growth.

METHODS

Study Site and Animals

We studied house wrens nesting on the grounds of the Sierra Nevada Aquatic Research Laboratory (SNARL), a University of California reserve at 2160 m elevation on the eastern slope of the Sierra Nevada (Mono County, California, U.S.A.). House wrens migrate to SNARL in May and set up territories in riparian vegetation (primarily aspen, *Populus tremuloides*, and willow trees, *Salix* spp.). Nestboxes (10 × 10 × 18.5 cm internal dimensions) were attached to trees and bushes at a height of 1.5–2 m and were readily occupied by the wrens. During our study (1995 and 1996), egg laying began in June.

As they hatched, we marked nestlings (ventrally) with paint for individual recognition. Median brood size was six (10 of 28 nests under observation), with fledging of entire broods being completed at an average age of 18 days. To avoid inducing premature fledging we did not disturb nests beyond the 11th day post-hatching (day 0 = day of hatching).

We measured temperatures ($\pm 0.5^\circ\text{C}$) in 25 occupied nestboxes with a Bailey BAT-12 thermocouple thermometer. Measurements were taken over 9 consecutive days at times ranging from 0800 to 1730 hours (mean = 1100 hours). Most boxes were in partial or light shade for most of the day. Air temperatures taken just inside the box entrance averaged 20°C (range = $11^\circ\text{--}30^\circ\text{C}$). Temperatures measured in the centre of the

brood mass were higher (range = $24^\circ\text{--}38^\circ\text{C}$). Average brood temperatures were used for metabolic studies (below).

Laboratory Metabolic Studies

We used 54 nestlings from 11 nests for the laboratory studies. Nestlings used for the day's metabolic measurements were removed from nestboxes, brought into the laboratory, and placed in a temperature-controlled environment within 5 min. Chicks were fasted for at least 1.5 h prior to testing to avoid the post-prandial elevation of metabolism (heat increment of feeding; Chappell et al. 1997) and to encourage begging. Following measurements for that day, we fed each chick and returned it to its nest.

We used open-circuit respirometry to measure the O_2 consumption and CO_2 production of single nestlings and groups of chicks. Metabolism chambers were acrylic plastic boxes fitted with ports for air flow and an artificial padded nest cup. We used chambers ranging in volume from 340 to 850 ml depending on the size and number of chicks being studied. An environmental cabinet maintained chamber temperature at 30°C (large chicks) to 34°C (small chicks). Dry, CO_2 -free air was pumped through mass flow controllers (Tylan) at flow rates of 210–2000 ml/min (standard temperature and pressure; STP), depending on the size and number of nestlings being measured. The mass flow controllers were calibrated against a Singer dry volume meter to an accuracy of $\pm 2\%$ at the flow rates used.

Approximately 100 ml/min of chamber excurrent air was dried (magnesium perchlorate), directed through an Anarad AR-50 CO_2 analyser, scrubbed of CO_2 (Ascarite), redried and passed through the sensor of an Applied Electrochemistry S-3A/II O_2 analyser. The CO_2 analyser was calibrated daily by zeroing with CO_2 -free air and spanning precision calibration gases (0.250 or 0.501% CO_2 in air); the O_2 analyser was calibrated against ambient air (20.95% O_2). Both analysers were referenced by sampling ambient air before and after each set of measurements. Instrument outputs were sampled every 1.5–2 s by a Macintosh computer equipped with a National Instruments analog-to-digital converter and custom software. Multiple readings (30–60 depending on sample rate) were averaged for each recorded sample point. With signal averaging, resolution

was $\pm 0.0015\%$ for O_2 and $\pm 0.001\%$ or better for CO_2 . We calculated oxygen consumption ($\dot{V}O_2$; ml/min) following Withers (1977):

$$\dot{V}O_2 = \dot{V}(F_iO_2 - F_eO_2)/(1 - F_iO_2)$$

where \dot{V} is flow rate (STP, in ml/min) and F_iO_2 and F_eO_2 are the fractional concentrations of O_2 in incurrent and excurrent air, respectively (F_iO_2 was 0.2095 and F_eO_2 was always >0.2045). Carbon dioxide production ($\dot{V}CO_2$; ml/min) was calculated as:

$$\dot{V}CO_2 = \dot{V}(F_eCO_2 - F_iCO_2)$$

where F_iCO_2 and F_eCO_2 are the fractional concentrations of CO_2 in incurrent and excurrent air (F_eCO_2 was always <0.0045). Maximum cumulative error for calculations of $\dot{V}O_2$ and $\dot{V}CO_2$ was less than 5% based on the estimated calibration errors and resolution of the gas analysers and the mass flow controllers.

We computed resting metabolic rates as the lowest 2-min continuous average during periods when no activity occurred and nestlings had been at constant temperature for more than 30 min. We elicited begging by hand clapping, fluctuating light intensity, tapping the chamber, or using playbacks of male house wren song. Begging events were brief, and the respirometry system did not reach steady-state conditions during begs. We could not use the 'instantaneous' method (Bartholomew et al. 1981) to correct for this because of mixing problems. The chicks' rapid and occasionally extensive head movements relative to the input and output ports created transient rarifactions and enrichments in gas concentration (Berrigan & Lighton 1993) that invalidated the use of instantaneous conversion (which assumes a temporally variable but spatially fixed source of gas exchange). Therefore, we determined energy expenditure during individual begs (as ml O_2) by subtracting 'baseline' resting metabolism from the metabolic rate during a beg, and then integrating the remainder over time (Fig. 1a). We calculated average metabolic rates during begs (ml O_2 /min or J/min; 0.0498 ml O_2 /J) by dividing energy expenditure by beg duration as determined from videotape records (below).

To avoid the confounding effects of non-begging activity, we report data from groups

for two conditions only: (1) all chicks begged nearly simultaneously (between-chick differences of <1 s for initiation or cessation of begging), or (2) a subset of chicks begged simultaneously while all others appeared immobile throughout the event.

To measure the resting metabolism of nestlings in natural conditions, we attached plastic tubing to the bottoms of the 1.85-litre nestboxes and used a vacuum pump to pull air through them at rates of 7–9 litres/min STP (measured at ambient humidity with a mass flow controller; 9–12 litres/min at the ambient pressure of about 580 torr). The nestbox entrance hole (2-cm diameter) remained open but all other openings were sealed with modelling clay. Nestlings were approximately 5 cm below the nest entrance, approximately a third of the distance between the entrance and the bottom of the box. With these flow rates we assumed the box functioned as a mask (Withers 1977) capturing exhaled CO_2 . About 150 ml/min of excurrent air was diverted through a Viasala humidity sensor, dried, and sent through a LiCor LI6251 CO_2 analyser (resolution $\pm 0.0001\%$) connected to a Macintosh computer. Data were recorded every 10 s and each recorded point was an average of 50 samples. The LiCor LI6251 CO_2 analyser was calibrated as described above for the Anarad AR-50. Reference air was automatically sampled (to determine F_iCO_2) for 2 min every 2 h. Chicks were weighed at the conclusion of measurements. We made an average of 2.4 all-day measurements of each of eight nestboxes; successive measurements were made at least 3 days apart.

We computed $\dot{V}CO_2$ as described above, after correcting the recorded STP flow rate for the fraction of air occupied by water vapour. These records included parental metabolism as well as chick metabolism. Observations showed that the presence of a parent resulted in clear peaks and plateaus in $\dot{V}CO_2$ (Fig. 1b). Accordingly, we computed the $\dot{V}CO_2$ produced by the brood by interpolating between peaks and plateaus, and calculated the average metabolic rate of individuals by dividing the result by the number of chicks. Because nestlings were brooded at night, we obtained nestling $\dot{V}CO_2$ from periods between 0530 and 1930 hours. To convert $\dot{V}CO_2$ to $\dot{V}O_2$, we used a respiratory quotient ($\dot{V}CO_2/\dot{V}O_2$) of 0.806 which was obtained from our laboratory studies of resting metabolic rates.

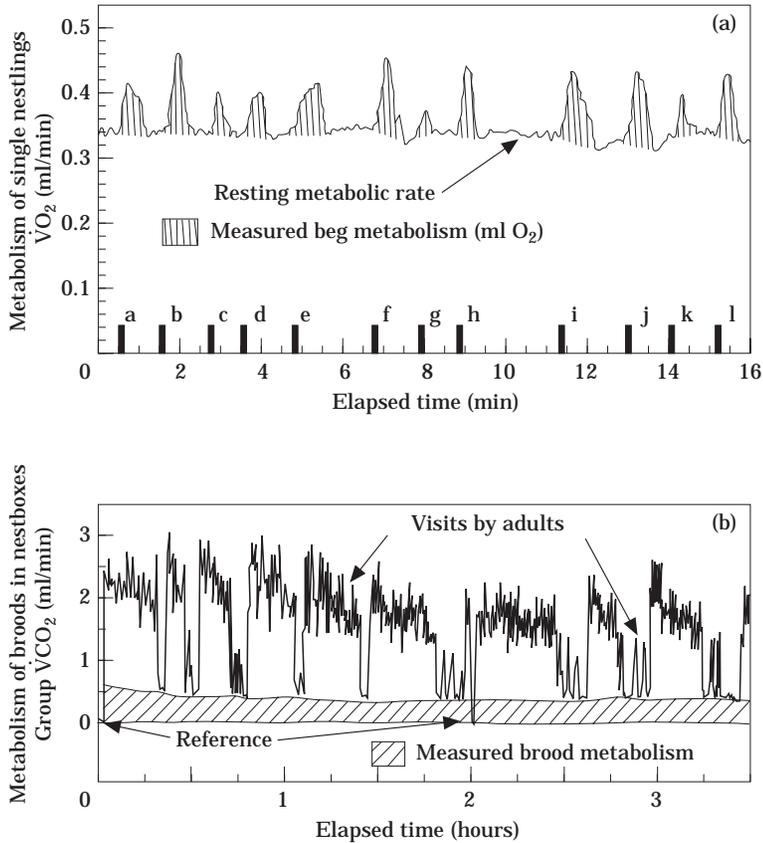


Figure 1. Examples of metabolic data. (a) Laboratory metabolic data. Begging (and other activities) produced peaks of O₂ consumption which were tagged with event markers and synchronized to a video recording. (b) Field metabolic data measured on an entire brood. Increases in whole-nest CO₂ production associated with parental visits were removed prior to estimating nestling field metabolism.

Behaviour

We studied nestling behaviour in natural conditions in broods that were not used for metabolic work. We fitted video cameras to replacement nestbox lids which maintained a complete cover over the brood. Parents were allowed to habituate to the set-up prior to taping. Each taping lasted 2 h and took place between 0800 and 1600 hours. Some feeding visits occurred earlier and later than this, but we restricted our schedule to minimize disturbance during possibly critical brooding periods (mornings and evenings were much cooler) and to allow sufficient light for the camera without having to open the box for additional light. We taped three nestling age categories (day 1–4, day 5–8 and day 9–11) in each of 20 nest-

boxes, for a total of 120 h of data. Nest 'age' was the median chick age as there was slight hatching asynchrony.

We timed the duration of behavioural events to the nearest second from a digital clock readout in the video frame. We defined the duration of a beg as the duration of gaping. We scored begging vigour on a four-point scale (Table I). We scored non-begging activity as individual events; bouts of twitching or shivering, vocalizations not associated with gaping, weak head movements, sitting alert, and three categories of movement distinguished by whole body displacements to less than one body width, greater than one body width, or two or more body widths from its starting location. We also recorded posture (resting on sternum, on tarsi or standing).

Table I. Begging vigour of all nestlings was ranked from lowest (rank 1) to highest (rank 4) based on the following criteria

Behaviour	Rank 1	Rank 2	Rank 3	Rank 4
Bill gaping	Weak	Strong	Strong	Strong
Neck extension	Weak	Stretched	Stretched	Stretched
Head movement (horizontal)	None	<One head width	>One head width	>One head width
Standing	No	No	On tarsi	On feet
Lungeing	No	No	No	Yes

We also videotaped behaviour during laboratory metabolic studies and scored each behaviour using the same criteria. In the metabolic study, if the chick crawled or moved immediately after begging, we discarded the record because it could not be classified as a discrete event. We also limited analyses of non-begging activity to discrete events. Microphones on the cameras and in the chambers, together with electronic markers in data files, allowed us to match episodes of activity to segments of recorded metabolic data.

Analysis

Typically we obtained numerous measurements of metabolic rate during begging from each chick in the laboratory. Of the 54 nestlings sampled, 20 were measured individually on 1 day only, 26 were measured on 2 different days and eight were measured on 3 different days. Usable data included 620 begs, and 178 other (non-begging) activities. We avoided pseudoreplication by basing our analyses on the mean values for each individual for each day it was used. For groups of nestlings ($N=117$ individual measures on eight groups) we used an average for each group.

RESULTS

Nestling Growth and Resting Metabolism

The body mass of house wren nestlings appeared to plateau by day 11 (Fig. 2). There were no consistent differences in mass between nestlings used for metabolism studies and those used for behavioural observations.

The resting metabolic rate (RMR) of single nestlings increased with mass (Fig. 3a). RMR appeared to plateau at day 9, approximately when nestlings achieve the ability to thermoregulate

independently (Kendeigh & Baldwin 1928; Dunn 1976).

The RMR of a nestling measured under laboratory conditions may not fully reflect the energetic expenditures of a quiescent nestling in the field because the laboratory measurements did not include the costs of digestion (Chappell et al. 1997) or thermoregulation. Nevertheless, our measurements of field metabolism from nestboxes were similar to the laboratory RMR values (Fig. 3b).

Energy Expenditures for Begging and Other Activities

Begging resulted in clearly identifiable increases in oxygen consumption. The increment in metabolic rate during begging increased with nestling mass ($\dot{V}O_2$ ml/min = 0.003 mass(g)^{1.82}, $r^2=0.79$, $N=54$, $P<0.0001$; Fig. 4a). Using the mean cost per age, the begging energy expenditures as

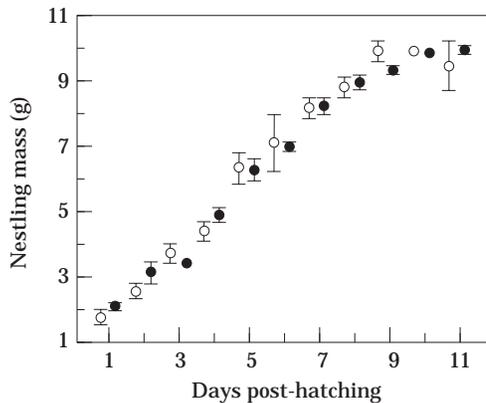


Figure 2. Mean mass of nestlings (up to day 11 post-hatching) used in metabolism studies (○: $N=54$, 11 nests) and studied for time budget data (●: $N=116$, 20 nests). Bars indicate \pm 95% confidence interval.

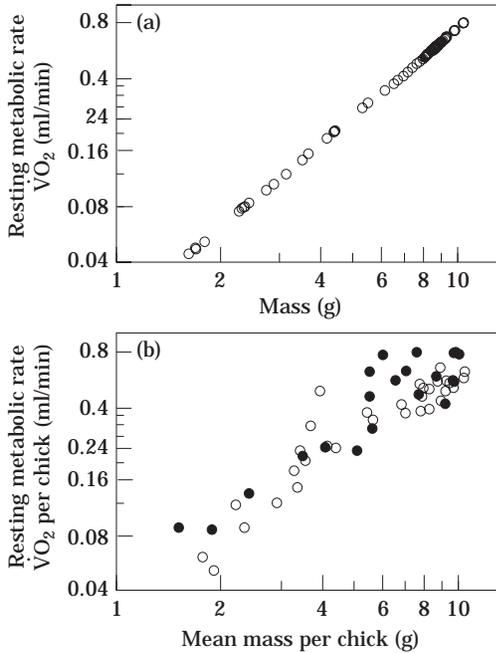


Figure 3. (a) Resting metabolic rates for nestlings measured as single chicks in the laboratory. Each nestling is represented once ($N=54$), selecting among repeated measurements for that chick across different ages. $\text{RMR}_{\text{single}} \text{ ml O}_2/\text{min}=0.02(\text{mass, g})^{1.57}$, $r^2=1.0$, $P<0.0001$. The relationship between RMR and nestling age is described by: $\text{RMR ml O}_2/\text{min}=0.039 - 0.020(\text{day}) + 0.023(\text{day})^2 - 0.001(\text{day})^3$, $r^2=0.99$, $N=11$, $P<0.0001$. (b) Resting metabolic rates for nestlings in groups measured in the laboratory (\circ), in nestboxes in the field (\bullet). $\text{RMR}_{\text{groups}} \text{ ml O}_2/\text{min}=0.052(\text{mass, g})^{1.07}$, $r^2=0.84$, $N=33$, $P<0.0001$; $\text{RMR}_{\text{nests}} \text{ ml O}_2/\text{min}=0.05(\text{mass, g})^{1.2}$, $r^2=0.83$, $N=19$, $P<0.0001$.

a function of age is described by ($\dot{V}\text{O}_2 \text{ ml/min} = -0.007 + 0.019 \text{ age}$ ($r^2=0.8$, $N=11$, $P<0.0001$)). The metabolic scope for begging (=metabolic rate while begging/RMR) did not vary with either age ($P=0.12$) or mass ($P=0.30$; Fig. 4b). For nestlings of all ages tested, the metabolic scope averaged 1.27 times RMR.

Per capita metabolic rates of groups of nestlings begging simultaneously were not significantly different from those measured for single chicks at any age (paired $t_7=1.09$, $P=0.31$; Table II). When a subset of nestlings in a group begged, however, their estimated per capita metabolic rates were significantly greater than for single chicks ($t_7=4.60$, $P=0.003$) or for per capita costs in

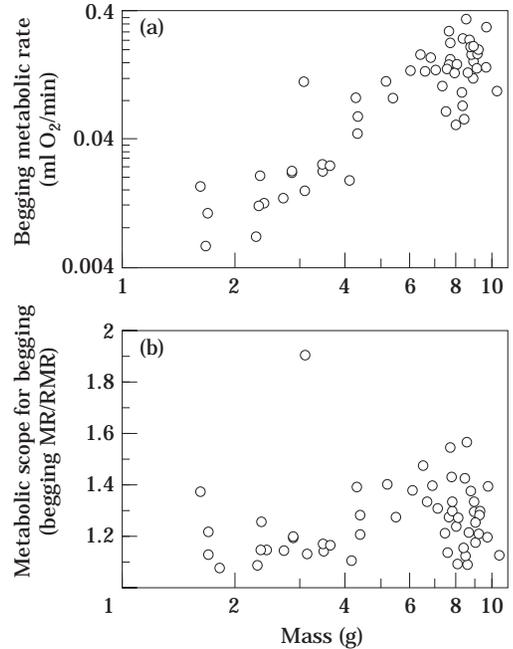


Figure 4. Begging metabolism versus mass. Each nestling measured is represented once ($N=54$). (a) Energy expenditure due to begging versus nestling mass. These values are metabolic rates above resting ($\log \dot{V}\text{O}_2(\text{ml/min}) = -2.52 + 1.82 \log(\text{mass, g})$, $r^2=0.79$, $P<0.0001$). (b) Metabolic scope for begging versus nestling mass. The scope is calculated as the ratio of total metabolic rate while begging (baseline or resting metabolism+begging metabolism) over the RMR for a nestling of a given mass.

simultaneous group begs ($t_8=3.94$, $P=0.004$). This suggests that metabolic rates of non-begging chicks (even apparently inactive ones) may increase when nestmates beg, possibly because of increased muscle tension or postural adjustments.

Metabolic rates while begging did not increase with the behavioural 'intensity' or vigour of begging after controlling for body mass and beg duration. For each age from 1 to 11 days, we obtained rank correlations between beg metabolic rate and vigour to describe the direction of the relationship. The correlations were positive for only four of the 11 age classes (sign test: $P=0.58$). We did not test individual coefficients because sample sizes were inflated by multiple representations of most nestlings.

In videotaped field observations, the duration of begging increased with begging vigour (Fig. 5).

Table II. Average metabolic rate while begging (ml O₂/[g · min]) for chicks begging singly and in groups

Age	Group								
	Single*			Group					
	Mean	(SD)	N	All begging†			Subset begging‡		
			Mean	(SD)	N	Mean	(SD)	N	
1	0.005	(0.005)	5	0.022		1	0.028	(0.007)	2
2	0.007	(0.003)	14	0.013		1	0.03		1
3	0.009	(0.006)	14	0.011	(0.002)	4	0.049		1
4	0.018	(0.013)	4	0.024	(0.01)	3	0.058		1
5	0.022	(0.005)	8						
6	0.013	(0.006)	6	0.015	(0.009)	3	0.071		1
7	0.021	(0.01)	5	0.023	(0.007)	4	0.023		1
8	0.016	(0.008)	8	0.016	(0.011)	4	0.036	(0.025)	2
9	0.013	(0.006)	7	0.013	(0.009)	3	0.031	(0.035)	3
10	0.017	(0.007)	12	0.006					
11	0.025	(0.012)	12						
12				0.028		1	0.043		1

*N=number of chicks.

†N=number of groups contributing average values of metabolic rate during begging episodes when all individuals begged simultaneously.

‡N=number of groups contributing average values of metabolic rate during begging episodes when only a subset of the individuals begged, and others appeared to be unresponsive.

Within each of three age categories, begging duration differed across the three most commonly occurring vigour ranks (ranks 1-3; Friedman two-

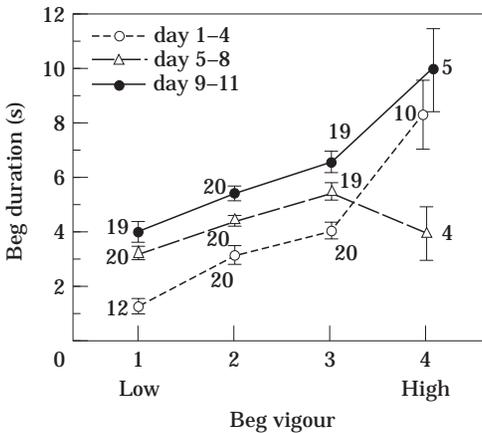


Figure 5. Begging vigour in relation to beg duration. The duration of unrewarded begs of 116 chicks in 20 nests was measured along with the behavioural vigour. The mean duration of each beg rank was obtained for each chick, and values were then averaged within each nest to give a mean duration for a given beg intensity for each nest. The mean for each nest was then averaged across nests so the maximum sample size is 20. This mean ± SE and sample size are shown. See text for statistics.

way ANOVA: day 1-4 chicks: $\chi^2=19.5$, $N=12$ nests, $P<0.0001$; day 5-8 chicks: $\chi^2=23.4$, $N=19$ nests, $P<0.0001$; day 9-11: $\chi^2=26.8$, $N=18$ nests, $P<0.0001$). For the 1-4 day and 9-11 day chicks, begging duration differed across all four vigour ranks (Friedman two-way ANOVA: day 1-4 chicks: $\chi^2=11.2$, $N=5$ nests, $P<0.01$; day 9-11: $\chi^2=8.76$, $N=5$ nests, $P<0.03$). The positive relationship between begging vigour and duration applies to unrewarded begs in the field; rewarded begs were shorter because they terminated when chicks were fed.

We were able to determine the metabolic expenditures associated with specific activities other than begging in 46 nestlings at the youngest and oldest ages studied. Begging and other activities increased metabolism above resting rates (Fig. 6). ANOVAs comparing behaviour classified as low activity (twitching, vocalization and weak head movements), high activity (sitting alert and substantial movement) and begging were significant for the oldest and youngest nestlings (day 1-4, $F_{2,64}=3.832$, $P=0.03$; day 9-11, $F_{2,60}=3.266$, $P=0.05$). In the oldest chicks, the mean metabolic rate during begging exceeded both activity levels, and was significantly greater than low-activity behaviour. In the youngest nestlings, the behaviour in the low- and high-activity

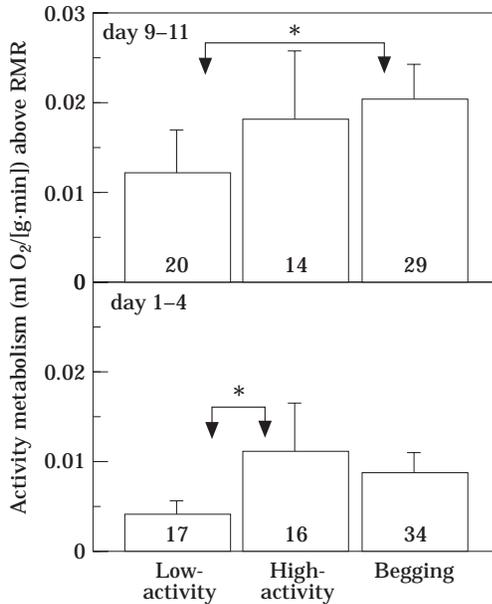


Figure 6. Activity metabolism above resting for nestlings in two age groups. Each bar represents the mean energy cost for begging, and low- and high-activity behaviour (N displayed in each bar, with 95% confidence intervals). A single nestling is represented no more than once per activity level. Low-activity behaviour included shivering, vocalizations and weakly lifting the head. High-activity behaviour included sitting upright, and movement or displacement of the whole body. Asterisks signify differences between groups based on Bonferroni-adjusted tests of significance. The confidence intervals indicate that each activity group increased metabolic rate above resting levels.

groups were significantly different, but begging was intermediate and was not distinguishable from either activity level. Thus for older nestlings, begging was clearly among the more costly activities.

Nestling Energy Budgets and Food Intake

Adult house wrens typically brought a single food item on each visit to the nest. The prey included a variety of spiders, small lepidoptera (adults and larvae), and other insects associated with riparian habitat (e.g. mayflies). Depending on age, each nestling was fed an average of 2.3–4.0 prey items per hour, but the maximum observed feeding rates to individual chicks were at least two times higher (G. Bachman, unpublished data).

Average prey size increased with the age of the brood (unpublished data).

We estimated daily energy expenditures of 3-, 6-, and 10-day-old nestlings for the median brood size of six, using a combination of growth rate data, time budgets from field videotapes, and laboratory and field measurements of metabolism. Daily energy budgets (DEB) were calculated as

$$\text{DEB} = \text{energy in new tissue} + \text{maintenance metabolism} + \text{activity metabolism.}$$

Energy deposited in new tissue was computed from age-specific mass gain rates (g/day; Fig. 2) and tissue energy density (Robbins 1993). Maintenance metabolism over a 24-h period was calculated assuming 14 h of field metabolism and 10 h of resting metabolism as measured in the laboratory (Fig. 3b). Field estimates of maintenance metabolism were slightly greater than laboratory estimates of RMR; the latter assumes that nestlings are fasted and in thermo-neutral conditions while brooded overnight. We assumed that digestive costs over a 24-h period were adequately accounted for in the combined estimates.

We obtained time budgets for activities (including begging) from videotapes of nestboxes. The time spent in each non-begging activity was multiplied by the energy costs obtained from laboratory measurements of individual activities described previously. The totals are shown in Table III. To calculate begging costs, we assumed all begs had a vigour rank of 3 and a duration typical of unrewarded begs; therefore our begging cost values probably overestimate actual costs.

This method of producing an energy budget can underestimate actual energy expenditures (Weathers 1991). The daily energy budget we obtained for a 10-day-old nestling (9.8 g), however, was similar to the 24-h field metabolic rate for house wrens of similar mass measured by Dykstra & Karasov (1993) using the doubly-labelled water technique (27.7 kJ/day for 9.8 g nestlings). These data indicate that our energy budget model provides reasonable approximations of real values (see also Williams & Prints 1986).

For all three age categories, maximal estimated begging expenditures comprised less than 1% of

Table III. Daily energy budgets (DEB) for house wren nestlings in three age classes

	Chick age (days post-hatching)		
	3	6	10
Mass (g)	3.4	6.9	9.8
Growth rate (kJ/day) (g/day)	4.7 (0.9 g)	6.5 (1.0 g)	2.6 (0.3 g)
Resting metabolism (kJ/day)	5.3	13.5	21.6
Activity other than begging (kJ/day)	0.2	0.4	2.5
Begging (kJ/day)			
Average	0.002	0.03	0.06
Maximum	0.01	0.08	0.2
Total DEB (kJ/day)	10.3	20.4	26.7

Energy expenditures during begging were calculated from metabolic rates during begging (Fig. 4a) and time spent begging (Table IV). Costs for activities other than begging were obtained from metabolic measurements (Fig. 6) and time budgets from video records of nestboxes. The total daily energy budget was calculated assuming average begging frequencies.

the daily energy budget, and ranged from 0.2 to 7.7% of the energy deposited in new tissues each day (Table III). Mean values of begging costs were smaller.

DISCUSSION

Our goal in this study was to evaluate the extent to which energy expenditures associated with begging might impact fitness, and therefore influence the signalling of need by nestling birds. We first discuss the impact of begging on the nestling's daily energy budgets and then evaluate the potential role of these energy costs in the evolution of begging behaviour.

Energy Cost of Begging

We found that begging requires an increased rate of energy expenditure that is significantly greater than RMR, and is equal to or greater than the effort required for weak levels of activity. Begging increased metabolic rates by an average of 27% above resting levels across all ages tested, which is well below the maximum metabolic rates measured for house wren nestlings, although occasional begs can reach this limit (unpublished data). Our estimates of begging costs are greater than estimates for starlings, *Sturnus vulgaris* (5% above RMR, McCarty 1996), but are similar to data for tree swallow nestlings, *Tachycineta*

bicolor (28% above RMR, Leech & Leonard 1996; 27% above RMR, McCarty 1996), even though the method used by these studies (closed-system respirometry) is not readily applicable to measuring the cost of brief events like begging.

We found no association between metabolic rate while begging and begging vigour in our laboratory studies. In the field, however, the total energy cost of begging increases with vigour because of the positive correlation between vigour and beg duration (Fig. 5). Leech & Leonard (1996) also report a positive relationship between metabolic rate and a measure of begging intensity that included both vigour and duration for older nestling tree swallows. Positive correlations between variables reflecting the vigour and duration of begging have been found in other species (e.g. Smith & Montgomerie 1991; Redondo & Castro 1992).

To date, all studies of begging energetics, including this one, have determined only the aerobic component of the energy cost of begging. This might underestimate total costs if begging is partially based on anaerobic metabolism (Weathers et al. 1997). While we have no direct measurements of anaerobic metabolism (e.g. whole body lactate concentrations), our results are not consistent with substantial anaerobic costs. Our methods would include any short-term or immediate repayment of an 'oxygen debt' incurred by anaerobic metabolism. There was no indication of an

Table IV. Activity time budgets and food intake estimates for house wren nestlings in three age classes

	Age (days post hatching)		
	3	6	10
Mean begs/h	4.3	10.6	10
Maximum begs/h	16	32	34
Beg duration (s)	4.0	5.3	6.5
Cumulative begging, mean min/day	4.0	13.1	15.2
Cumulative begging, maximum min/day	14.9	39.6	51.7
Non-begging activity (min/day)	29.6	18.7	55.1
Feedings per day (mean)	32.2	56	43.4

Data were obtained from video records of nestboxes ($N=20$ nestboxes in each age class). Begging frequency data are shown for mean and maximum values obtained at each age.

elevated resting oxygen consumption following begs (Fig. 1a).

Impact of Begging on Energy Budgets and Growth

Although metabolic rates increased markedly during begging, the cumulative energy cost of begging was a very small fraction of the daily energy budget (DEB) of house wren nestlings (Table III). Our estimates of begging costs averaged from 0.02% to less than 0.25% of DEB, depending on nestling age. In contrast, non-begging movements on average accounted for 2% to over 9% of the DEB, and the energy used for digesting and utilizing food approached 9% (assuming DEB equals metabolizable energy intake; Chappell et al. 1997). More importantly for fitness (e.g. Verhulst & Wiersma 1997), costs were also a small fraction of the energy deposited in new tissue, averaging from 0.05 to 2.3% of growth (Table III). In contrast, the energy allocated to non-begging movement constituted a much greater fraction of the energy deposited in new tissue, ranging from 5.1% in young nestlings to 96.8% in the oldest nestlings.

The minimal impact of begging costs on energy budgets and growth is primarily a function of the small amount of time that chicks are actually begging: chicks beg only a few times per hour and each beg lasts for only a few seconds, even though parents visit more often (Table IV). Low overall costs may also reflect the rapidity with which parents reach a decision about which chick to feed (1–2 s, G. Bachman, unpublished data).

How would the impact of begging change if frequencies and durations were to increase? We explore this question by simply adding additional beg costs to the existing DEB (Table III). If begging frequencies were increased to the maximum observed values (Table IV) the time spent begging would increase by 27% (youngest nestlings) and 33% (oldest nestlings). This scenario would increase begging to 0.08, 0.40 and 0.75% of DEB in each of the three age groups studied (from youngest to oldest), and is equivalent to 0.18, 1.2 and 7.7% of the energy diverted to tissue growth. If beg duration were doubled (retaining maximum beg frequencies) the impact of begging on DEB and growth would also double. However, older nestlings in particular are growing very little so the reduction of available energy even in an extreme scenario may have an insignificant effect on growth rate.

Honest Signalling and the Low Energetic Cost of Begging

Studies in a variety of species (including house wrens; G. Bachman, unpublished data) indicate that begging behaviour indicates need (see Introduction). Our data and other studies (Leech & Leonard 1996; McCarty 1996), however, suggest that the energy cost of begging is unlikely to have a significant impact on the nestling energy budget and thus probably does not constitute a cost sufficient to maintain begging honesty. For example, if a 10-day-old house wren nestling were to escalate begging dishonestly to twice the mean frequencies observed (from 10 to 20 begs/h), the

increased energy expenditure would be equivalent to a decrease of 0.007 g, or 2.3% of growth. Using estimates of prey size, if the nestling received only a single additional feed per day for the increased effort, the energy remaining after digestive expenditures would supply 0.06 g of growth, or an increase of 18.2% if no other aspects of the daily energy budget changed (G. Bachman, unpublished data). For younger nestlings, the relative benefit of a single feed despite a doubling of average beg costs would be even greater. More detailed analysis of the trade-offs associated with escalation requires an understanding of parental feeding rules, but it appears that escalation would provide a net energetic benefit to the nestling.

If the direct cost of energy expenditure is slight, it is possible that the honesty of begging could be maintained through the cost of increased predation risk. Haskell (1994) has demonstrated that predators may be attracted by nestling calls and, if begging causes parents to visit nests more frequently, parental activity itself may attract predators. Honest begging might also be enforced without direct costs if begging is rewarded by feeds that reduce the food allocation to siblings, thereby lowering the inclusive fitness of the begging chick (Godfray 1995).

ACKNOWLEDGMENTS

We would like to thank J. Odell and R. Gibson for their talented and cheerful assistance during data collection. We also thank the staff of the Sierra Nevada Aquatic Research Laboratory, Mammoth Lakes, California for allowing us to work there. R. Gibson and 2 referees provided useful discussion and comment on an early draft of this paper. This project was carried out under the provisions of animal care and use permits from the University of California (Riverside and Santa Barbara campuses). Funding was provided by a UC Riverside Intramural Award to M.A.C. During analysis and writing G.C.B. was supported by NSF-GIR2813 and hosted by the Department of Zoology, University of Oklahoma.

REFERENCES

- Bartholomew, G. A., Vleck, D. & Vleck, C. M. 1981. Instantaneous measurements of oxygen consumption during pre-flight warm-up and post-flight cooling in sphingid and saturniid moths. *J. exp. Biol.*, **90**, 17-32.
- Berrigan, D. & Lighton, J. R. B. 1993. Bioenergetic and kinematic consequences of limbllessness in larval Diptera. *J. exp. Biol.*, **179**, 245-259.
- Chappell, M. A., Bachman, G. C. & Hammond, K. A. 1997. The heat increment of feeding in house wren chicks: magnitude, duration, and substitution for thermostatic costs. *J. comp. Physiol. B.* **167**, 313-318.
- Dunn, E. H. 1976. The relationship between brood size and age of effective homeothermy in nestling house wrens. *Wilson Bull.*, **88**, 478-482.
- Dykstra, C. R. & Karasov, W. H. 1993. Daily energy expenditure by nestling house wrens. *Condor*, **95**, 1028-1030.
- Godfray, H. C. J. 1991. Signalling of need by offspring to their parents. *Nature, Lond.*, **352**, 328-330.
- Godfray, H. C. J. 1995. Signaling of need between parents and young parent-offspring conflict and sibling rivalry. *Am. Nat.*, **146**, 1-24.
- Godfray, H. C. J. & Parker, G. A. 1992. Sibling competition, parent-offspring conflict and clutch size. *Anim. Behav.*, **43**, 473-490.
- Haskell, D. 1994. Experimental evidence that nestling begging behaviour incurs a cost due to nest predation. *Proc. R. Soc. Lond. Ser. B*, **257**, 161-164.
- Johnstone, R. A. & Grafen, A. 1992. The continuous Sir Philip Sidney game: a simple model of biological signalling. *J. theor. Biol.*, **156**, 215-234.
- Kendeigh, S. C. & Baldwin, S. P. 1928. Development of temperature control in nestling house wrens. *Am. Nat.*, **62**, 249-278.
- Kilner, R. & Johnstone, R. A. 1977. Begging the question: are offspring solicitation behaviours signals of need? *Trends Ecol. Evol.*, **12**, 11-15.
- Leech, S. M. & Leonard, M. L. 1996. Is there an energetic cost to begging in nestling tree swallows *Tachycineta bicolor*. *Proc. R. Soc. Lond. Ser. B*, **263**, 983-987.
- Leonard, M. & Horn, A. 1996. Provisioning rules in tree swallows. *Behav. Ecol. Sociobiol.*, **38**, 341-347.
- McCarty, J. P. 1996. The energetic cost of begging in nestling passerines. *Auk*, **113**, 178-188.
- Parker, G. A. & Macnair, M. R. 1978. Models of parent-offspring conflict. I. Monogamy. *Anim. Behav.*, **26**, 97-110.
- Price, K. & Ydenberg, R. 1995. Begging and provisioning in broods of asynchronously hatched yellow-headed blackbirds. *Behav. Ecol. Sociobiol.*, **37**, 201-208.
- Price, K., Harvey, H. & Ydenberg, R. 1996. Begging tactics of nestling yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, in relation to need. *Anim. Behav.*, **51**, 421-435.
- Redondo, T. & Castro, F. 1992. Signalling of nutritional need by magpie nestlings. *Ethology*, **92**, 1193-1204.
- Robbins, C. T. 1993. *Wildlife Feeding and Nutrition*. 2nd edn. San Diego: Academic Press.
- Smith, H. G. & Montgomerie, R. 1991. Nestling American robins compete with siblings by begging. *Behav. Ecol. Sociobiol.*, **29**, 307-312.
- Stamps, J., Clark, A., Arrowood, P. & Kus, B. 1985. Parent-offspring conflict in budgerigars. *Behaviour*, **94**, 1-40.

- Verhulst, S. & Wiersma, P. 1997. Is begging cheap? *Auk*, **114**, 134.
- Weathers, W. W. 1991. Scaling nestling energy requirements. *Ibis*, **134**, 142–153.
- Weathers, W. W., Hodum, P. J. & Anderson, D. J. 1997. Is the energy cost of begging by nestling passerines surprisingly low? *Auk*, **114**, 133.
- Williams, J. B. & Prints, A. 1986. Energetics of growth in nestling Savannah sparrows: a comparison of doubly labeled water and laboratory estimates. *Condor*, **88**, 74–83.
- Withers, P. C. 1977. Measurement of $\dot{V}O_2$, $\dot{V}CO_2$, and evaporative water loss with a flow-through mask. *J. appl. Physiol.*, **42**, 120–123.