

THE ENERGETIC COST OF BEGGING IN NESTLING PASSERINES

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ABSTRACT.—A critical assumption of many of the current discussions of parent-offspring conflict and sibling competition is that the begging behavior of nestling birds is costly, either in terms of energetics or increased risk of predation. I measured the energetic expenditures associated with the begging of nestling birds using closed-chamber respirometry and found this cost to be surprisingly low. Active metabolic rate (AMR) while begging was 1.05 times the resting metabolic rate (RMR) in European Starlings (*Sturnus vulgaris*) and 1.27 times the resting metabolic rate in Tree Swallows (*Tachycineta bicolor*). The cost of 1 s of begging was 0.001 J/g in European Starlings and 0.008 J/g in Tree Swallows; this cost increased with age for all nestlings. Results of measurements on five other species are consistent with these values. The ratio of AMR:RMR did not change with ambient temperature for either Tree Swallows or European Starlings, but data for all seven species pooled did show a significant decrease in energetic costs with temperature. The amount of time spent begging had a negligible effect on cost for both Tree Swallows and European Starlings. Likewise, the intensity of the begging display had no effect on the AMR:RMR ratio in either species alone, but was positively correlated for the seven species pooled. Compared to the energy requirements for other avian behaviors, the cost of begging is low. Most discussions of the evolution of begging behavior in nestling birds have assumed that begging is costly. Based on my results, the assumption that begging is energetically costly needs to be reexamined and, until then, conclusions of models dependent on this assumption should be considered tentative. Received 6 September 1994, accepted 25 April 1995.

BEGGING FOR FOOD is an extremely important part of the biology of nestling birds, especially those with altricial development like passerines. Begging influences both the amount of food parents deliver to the brood (Haartman 1953, Bengtsson and Rydén 1983, Harris 1983, Litovich and Power 1992) and the proportion of the food received by individuals within the brood (Stamps et al. 1985, Gottlander 1987, Smith and Montgomerie 1991, Litovich and Power 1992, Teather 1992). Theoretical work on begging behavior has focused on its evolution as a method for offspring to communicate their needs to parents (Harper 1986, Hussell 1988, Motro 1989, Godfray 1991), as well as on the role begging plays in sibling competition (Macnair and Parker 1979, Godfray and Parker 1992) and parent-offspring conflict (Eshel and Feldman 1991, Mock and Forbes 1992). Models addressing these questions often rely on the assumption that begging is a costly display (*sensu* Zahavi 1975, Grafen 1990). This cost may be in

the form of either increased energetic expenditures or increased predation rates due to begging.

Little evidence is available with which to evaluate the validity of the assumption that begging is costly (but see Haskell 1994). While some behavioral displays in birds are energetically expensive (Vehrencamp et al. 1989, Eberhardt 1994) and the mating displays of frogs and insects are among the most energetically demanding behaviors known (Ryan 1988, Prestwich 1994), no measurements of the energetic costs associated with begging have been published. Given the interest in models incorporating estimates of the cost of begging, it is important to have empirical support for the assumption that begging is costly. In this paper, I present data on the energetics of begging in several species of passerine nestlings and discuss the importance of begging as a potential drain on the energy budget of these nestlings.

METHODS

The rates of oxygen consumption of begging nestling birds were measured in June and July of 1991 and 1992. Nests were located at the Cornell University

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Experimental Ponds Facility, Ithaca, New York. Species measured were Tree Swallows (*Tachycineta bicolor*), House Wrens (*Troglodytes aedon*), Black-capped Chickadees (*Parus atricapillus*), Eastern Bluebirds (*Sialia sialis*), European Starlings (*Sturnus vulgaris*), Red-winged Blackbirds (*Agelaius phoeniceus*), and House Finches (*Carpodacus mexicanus*). Nests with eggs were monitored to determine the date of hatching and subsequent age of nestlings.

Measurements of metabolic rate.—The energetic cost of begging was determined by measuring the oxygen consumption (VO_2) of begging nestlings using closed-chamber respirometry (Bennett 1986, Vleck 1987). For each nestling, I conducted one trial consisting of a measurement of nonbegging (or resting) VO_2 followed by a begging (or active) measurement of VO_2 (Bucher et al. 1982, Taigen and Wells 1985). Nestlings to be tested were removed from the nest and were held in a covered box until they were transferred to the metabolic chamber. In all cases I left at least two nestlings in the nest so that the parents would not abandon the brood.

Measurements of nestling metabolism began 30 to 90 min after nestlings were removed from their nest. Nestlings were placed in a glass metabolic chamber (volume of 900 or 2,900 ml) for 5 to 10 min before beginning a trial. Nestlings willing to beg in response to artificial stimuli were too young to exhibit a visible fear response and immediately settled down in the chamber (pers. obs.). To minimize the amount of time nestlings were away from the nest, the acclimation period was limited to 10 min. A series of trials of two consecutive measurements of resting metabolic rate showed no change in metabolic rate with longer acclimation periods ($n = 19$, paired t -test, $t = 1.16$, $P = 0.263$); thus, a 10-min period is sufficient. Metabolic chambers were at the same temperature as the box in which the nestlings were transported, so a longer acclimation period was not required for the nestlings to adjust to the chamber temperature. Chamber temperatures and nestling body temperatures were measured using Type-I thermocouples and an Omega HH-25 Digital Thermometer (Omega Engineering, Inc., Stamford, Connecticut).

Trials were done at a chamber temperature between 23° and 28°C. After the acclimation period, the chamber was sealed and an initial air sample taken with a syringe. The chamber was left sealed for 10 or 15 min, depending on the mass of the chicks and chamber volume (with length of the trial increasing with chamber volume and decreasing with nestling mass). The duration of any begging behavior during this period was recorded to the nearest 1 s. Any nonbegging measurements where the percentage of time spent begging was greater than 10% were eliminated. After 10 to 15 min, a second air sample was taken and the chamber ventilated. After 5 to 10 min the chamber was sealed again, and an initial air sample was taken. During this second period, I stimulated begging in

the chicks by tapping, moving, and/or shading the chamber. The duration of begging behavior was recorded to the nearest 1 s and the percentage of time spent begging was calculated.

If any begging occurred during the nonbegging trial, an adjustment of the percentage of time spent begging was made by subtracting the percentage of the first measurement spent begging from the percentage spent begging during the second measurement. Only trials where the adjusted percentage of time spent begging was greater than 10% were included. "Begging intensity" was measured as the mean length of begging bouts during the begging measurement, where a "begging bout" was defined as a period of display of 2 s or more, bracketed by nondisplaying periods of at least 2 s. The duration of begging bouts is correlated to other qualitative and quantitative measures of begging intensity (Smith and Montgomerie 1991, Redondo and Castro 1992). After 5 to 15 min, a second air sample was taken, and the chamber was ventilated. Nestlings were returned to their nests after testing. Nestlings were absent from the nest for 1 to 3 h, and no mortality was observed to be associated with this procedure.

The percent oxygen in each sample was measured using an Amatek N-22 Oxygen Sensor (Amatek, Inc., Pittsburgh, Pennsylvania) and either an Amatek S-3A/1 Oxygen Analyzer (1991) or an Applied Electrochemistry, S-3A Oxygen Analyzer (1992; Applied Electrochemistry Inc., Sunnyvale, California). Constant flow rate through the sensor was maintained using a Harvard Apparatus Infusion Pump (1991) or a Razel Scientific Syringe Pump (1992). In all cases, the decrease in oxygen concentration was held to less than 1%. VO_2 was calculated using equations from Vleck (1987) and converted to joules using a value of 20.08 J/ml O_2 (Williams and Prints 1986).

Calculation of the energetic cost of begging.—A trial consisted of two consecutive measurements on the same nestling. The initial nonbegging measurement in each trial represents the resting metabolic rate (RMR; $\text{J} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$). During the second measurement in each trial, the nestlings were stimulated to beg, giving the begging or active metabolic rate (AMR; $\text{J} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$).

Cost of begging was calculated in two ways: (1) as the scope of activity, which is the AMR:RMR ratio (Bennett 1986, Goldstein 1988, Ryan 1988); and (2) as a percentage of the total energy budget (Bennett 1986). The percentage of the total energy budget that can be attributed to begging was calculated for Tree Swallows based on the measures of metabolic rate presented here, and values for other variables taken from the literature or from McCarty (1995). These calculations are presented in the Discussion. Resting metabolic rate, rather than basal or standard metabolic rate, is used because RMR includes energetic costs of thermoregulation, specific dynamic action, being alert, and other factors that increase RMR over basal met-

TABLE 1. Energetics of begging behavior in nestling birds ($\bar{x} \pm SE$). Resting metabolic rate (RMR) and metabolic rate during active or begging measurement (AMR). Scope is the ratio of AMR:RMR.

Species	<i>n</i>	Age (days)	Percent time begging	RMR ($J \cdot g^{-1} \cdot h^{-1}$)	AMR ($J \cdot g^{-1} \cdot h^{-1}$)	Scope
Tree Swallow	13	9.6 \pm 1.0	45 \pm 3	68.5 \pm 6.8	83.5 \pm 8.6	1.27 \pm 0.14
European Starling	7	4.1 \pm 0.3	23 \pm 5	44.9 \pm 2.4	47.0 \pm 3.5	1.05 \pm 0.06
House Wren	3	12.0 \pm 0.0	33 \pm 4	89.3 \pm 1.4	89.4 \pm 6.1	1.00 \pm 0.08
House Finch	2	4.5 \pm 0.5	38 \pm 24	48.3 \pm 7.7	46.1 \pm 2.2	0.99 \pm 0.20
Black-capped Chickadee	1	7	24	110.4	133.8	1.21
Eastern Bluebird	1	5	54	87.9	87.2	0.99
Red-winged Blackbird	1	5	40	54.9	49.2	0.90

abolic rate (Gessaman 1987). All of these factors are included in the AMR, resulting in an inflated measure of energetic cost if calculations are based on basal metabolic rate. There also may be problems in defining basal metabolic rate for nestling passerines, which are growing rapidly and are not normally in a postabsorptive state.

The energetic cost of begging for nestlings with different begging rates can be determined by multiplying the rate of begging, in seconds begging per hour, by the incremental cost of begging, I ($J \cdot g^{-1} \cdot s^{-1}$). The incremental cost of begging is defined as:

$$I = (AMR - RMR)/B, \quad (1)$$

where B is the rate of begging expressed as seconds of begging per hour, and AMR and RMR are as defined above. This value (I) also can be converted into a ratio reflecting the instantaneous cost of begging, C_i , by using:

$$C_i = (RMR_s + I)/RMR_s, \quad (2)$$

where RMR_s (in seconds) is resting metabolic rate expressed on a per second basis ($J \cdot g^{-1} \cdot s^{-1}$). The instantaneous cost provides an index of the degree to which nestlings are exerting themselves while actually performing a begging display. Costs of other avian activities were taken from published sources giving active and resting metabolic rates, or the ratio of AMR:RMR. Due to small sample sizes, nonparametric tests were used (Wilcoxon signed ranks, Mann-Whitney U -test, and Spearman's Rank correlations). Except where noted, all P -values refer to two-tailed tests.

RESULTS

Energetic cost of begging.—For seven passerines, little difference among species was found in the mean resting metabolic rate, active metabolic rate, scope, and percentage of time spent begging (Table 1). Since five of the species are represented by measurements on three or fewer individuals, much of the following discussion will focus on the Tree Swallow ($n = 13$) and the

European Starling ($n = 7$), or on pooled data from all seven species ($n = 28$). Begging metabolic rates were significantly higher than resting metabolic rates for Tree Swallows (Wilcoxon signed ranks test, $Z = 1.99$, one-tailed, $P = 0.023$) but not for European Starlings ($Z = 0.845$, one-tailed, $P = 0.199$). When all species in Table 1 are pooled, begging metabolic rates are higher than resting metabolism ($n = 28$, $Z = 1.80$, one-tailed, $P = 0.036$).

The means of AMR:RMR ratios for Tree Swallows ($\bar{x} = 1.27 \pm SE$ of 0.14) and European Starlings ($\bar{x} = 1.05 \pm 0.06$) do not differ significantly (Mann-Whitney U -test, $U = 33.0$, $Z = 0.99$, $P = 0.322$). The estimates of begging energetics for the five species with small sample sizes all fall within the range of values for the Tree Swallow and European Starling (Table 1), indicating that there are no large differences among species in the cost of begging. In several cases the RMR was higher than the AMR, resulting in ratios of less than one; that is, I was unable to detect any increase in the metabolic rate associated with begging. The error associated with the methods I used is sufficiently high to account for this result, given a very small energetic cost of begging.

The incremental cost of begging was calculated for Tree Swallows and European Starlings using equation 1. For swallows, the cost of 1 s of begging is $0.008 \pm 0.003 J/g$, and for starlings the cost is $0.001 \pm 0.002 J/g$ for each second of begging. The difference is not significant (Mann-Whitney U -test, $U = 31.5$, $Z = 1.11$, $P = 0.267$). Using these values and equation 2, the instantaneous cost, C_i , gives a ratio of 1.42 for Tree Swallows and 1.08 for European Starlings. Nestling behavior typically includes periods of begging interspersed with nonbegging periods. The ratio of AMR:RMR is used in the current dis-

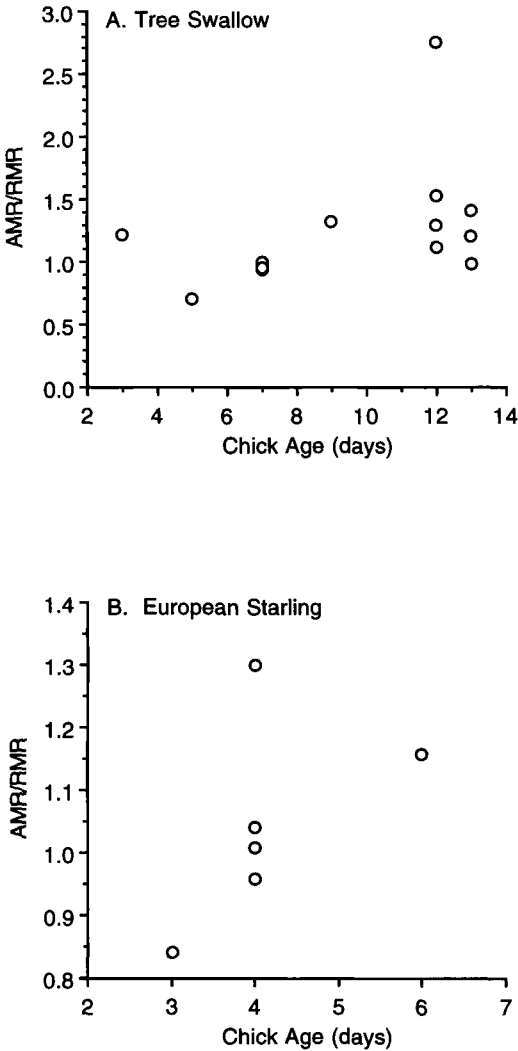


Fig. 1. Effect of nestling age on cost of begging. Increases seen in cost of begging with age are not significant in either: (A) Tree Swallows (Spearman's rank correlation, $\rho = 0.434$, $Z = 1.50$, $P = 0.133$); or (B) European Starlings ($\rho = 0.668$, $Z = 1.64$, $P = 0.102$).

cussion of the energetic cost of begging, since it includes such periods of begging and non-begging typical of natural displays. The AMR:RMR ratio is by definition smaller than the instantaneous cost, C_i ; however, the use of C_i would not change any of the conclusions drawn since it still suggests that the energetic cost of begging is relatively low.

Effects of nestling age and ambient temperature.— The age of nestlings measured ranged from 3 to 13 days ($\bar{x} = 7.5$ days). No significant rela-

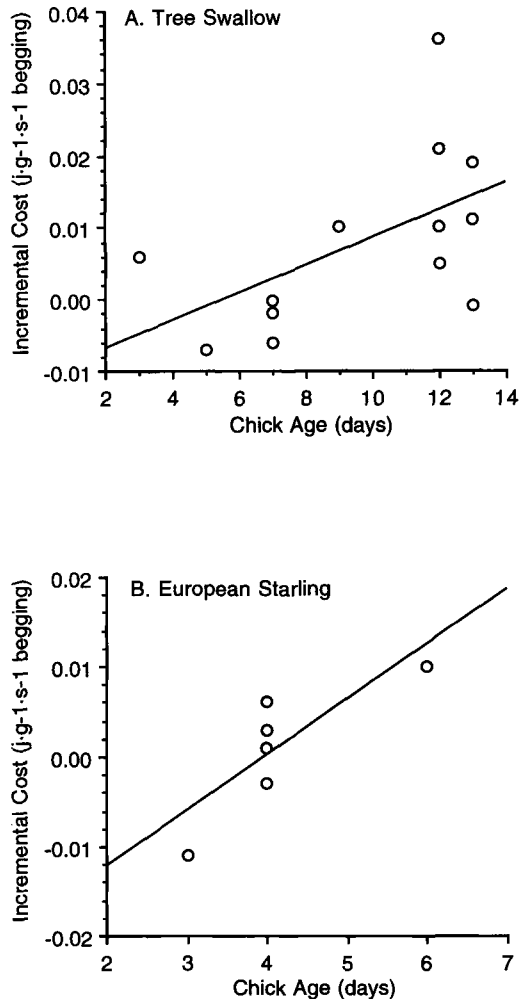


Fig. 2. Increase in incremental cost of begging with age. Incremental cost of 1 s of begging increases with age in: (A) Tree Swallows (Spearman's rank correlation, $\rho = 0.557$, $Z = 1.93$, $P = 0.054$); and (B) European Starlings ($\rho = 0.809$, $Z = 1.98$, $P = 0.048$). Lines fitted using least-squares technique.

tionship was found between age and AMR:RMR ratio for Tree Swallows or European Starlings (Fig. 1). The incremental cost of begging, I , increased with age in Tree Swallows and European Starlings (Fig. 2).

The percent time spent begging during each trial did not change with age in Tree Swallows (Fig. 3A), but the intensity of begging did increase with age (Fig. 3B). There were no significant associations between age and percent time begging ($\rho = 0.535$, $Z = 1.31$, $P = 0.190$), or between age and intensity of begging ($\rho =$

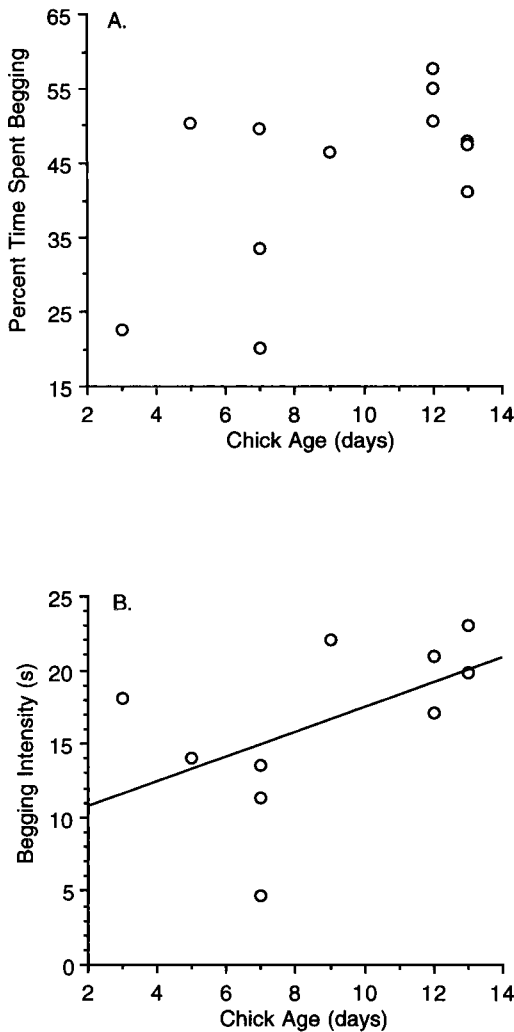


Fig. 3. Change in begging behavior with age. Tree Swallows show (A) no significant increase in percent time spent begging (Spearman's rank correlation, $\rho = 0.316$, $Z = 1.10$, $P = 0.274$), but (B) do show a significant increase in intensity of begging with age ($\rho = 0.600$, $Z = 2.08$, $P = 0.038$). Line fitted using least-squares technique.

-0.267 , $Z = -0.66$, $P = 0.513$) in European Starlings. The differences in the importance of nestling age in part may be due to the smaller range of ages (3 days) measured in starlings versus the range measured in swallows (10 days).

Temperature of the metabolic chamber did not differ between nonbegging and begging measures for each trial. For Tree Swallows the mean difference between chamber temperature

during the begging and nonbegging measurement was 0.3°C (Wilcoxon signed ranks test, $n = 13$, with 11 ties, $Z = 0.45$, $P = 0.654$). In starlings, this difference was 0.2°C ($n = 7$, with 5 ties, $Z = 0.45$, $P = 0.654$), while for all species pooled the difference was 0.2°C ($n = 28$, with 22 ties, $Z = 1.26$, $P = 0.207$).

Although chamber temperature did not vary between measures on an individual, chamber temperature was not standardized between trials on different birds. Measurements were made at chamber temperatures between 23° and 28°C . There are no significant effects of temperature on the AMR:RMR ratio for Tree Swallows (Spearman's rank correlation, $\rho = -0.353$, $Z = -1.22$, $P = 0.221$) or European Starlings ($\rho = 0.019$, $Z = 0.05$, $P = 0.963$). The incremental cost of begging, I , shows that same pattern for swallows and starlings ($\rho = -0.319$, $Z = -1.11$, $P = 0.269$, and $\rho = 0.113$, $Z = 0.28$, $P = 0.781$, respectively). When data for all species in Table 1 are pooled, the cost of begging shows a significant decrease with temperature (Fig. 4).

A negative effect of temperature on the percentage of time spent begging in Tree Swallows was found (Fig. 5A). Begging intensity in Tree Swallows, as measured by the mean duration of each begging bout, did not decrease significantly with temperature (Fig. 5B). In starlings, temperature had no effect on the percentage of time spent begging during each trial ($\rho = 0.449$, $Z = 1.10$, $P = 0.271$) or on the intensity of begging ($\rho = 0.056$, $Z = 0.14$, $P = 0.891$).

Variation in begging behavior and cost of begging.—The percent time spent begging did not have a significant effect on the cost of begging in Tree Swallows (Spearman's rank correlation, $\rho = 0.410$, $Z = 1.42$, $P = 0.156$) or European Starlings ($\rho = 0.679$, $Z = 1.66$, $P = 0.097$). Begging intensity also had no effect on the AMR:RMR ratio in swallows ($\rho = 0.364$, $Z = 1.26$, $P = 0.207$) or in starlings ($\rho = 0.357$, $Z = 0.88$, $P = 0.382$). There was no significant correlation between percent time begging and begging intensity for either species (swallows, $\rho = 0.246$, $Z = 0.852$, $P = 0.394$; starlings, $\rho = 0.036$, $Z = 0.087$, $P = 0.930$). The lack of an effect of begging behavior may be in part due to the small sample sizes. When data are pooled for all seven species, increasing the sample size to 28, there are significant increases with the percent time spent begging in both the AMR:RMR ratio (Fig. 6) and I ($\rho = 0.428$, $Z = 2.23$, $P = 0.026$). Begging intensity is also significantly correlated with

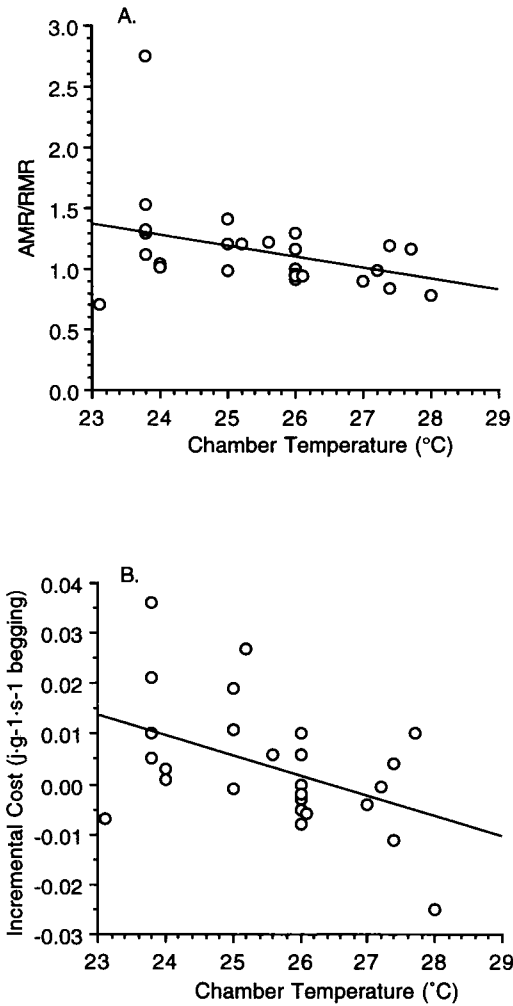


Fig. 4. Relationship between metabolic-chamber temperature and cost of begging in nestling birds. The AMR:RMR ratio decreases significantly with temperature for all species pooled (A; Spearman's rank correlation, $n = 28$, $\rho = -0.459$, $Z = -2.383$, $P = 0.017$). The relationship remains significant after removing the extreme value at AMR:RMR = 2.75 ($\rho = -0.418$, $Z = -2.13$, $P = 0.033$). There is also a significant decrease in I with temperature (B; $n = 28$, $\rho = -0.458$, $Z = -2.380$, $P = 0.017$). Lines fitted using least-squares technique.

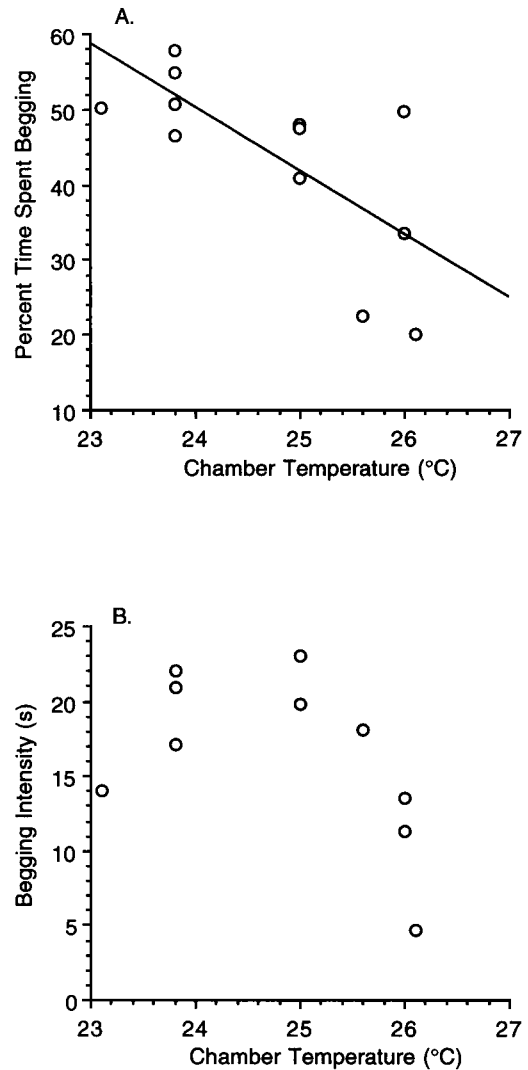


Fig. 5. Relationship between metabolic-chamber temperature and begging behavior in Tree Swallows. Percent time spent begging and chamber temperature are negatively related (A; Spearman's Rank correlation, $\rho = -0.733$, $Z = -2.54$, $P = 0.011$), while chamber temperature and begging intensity are not significantly related (B; $\rho = -0.437$, $Z = -1.52$, $P = 0.130$). Line fitted using least-squares technique.

AMR:RMR (Fig. 6) and, while not statistically significant, the relationship with I ($\rho = 0.348$, $Z = 1.81$, $P = 0.070$) is suggestive.

The ratios of AMR:RMR for begging in nestling European Starlings and Tree Swallows are well below those of most other avian activities (Table 2). Of those activity costs that have been

studied, the only activity costs as low as the begging costs are crowing in Red Junglefowl (*Gallus gallus*; Chappell et al. 1995), and standing and walking in Black Ducks (*Anas rubripes*; Wooley and Owen 1978). For passerines, the activity with the lowest cost is foraging in European Starlings (Westerterp and Drent 1985).

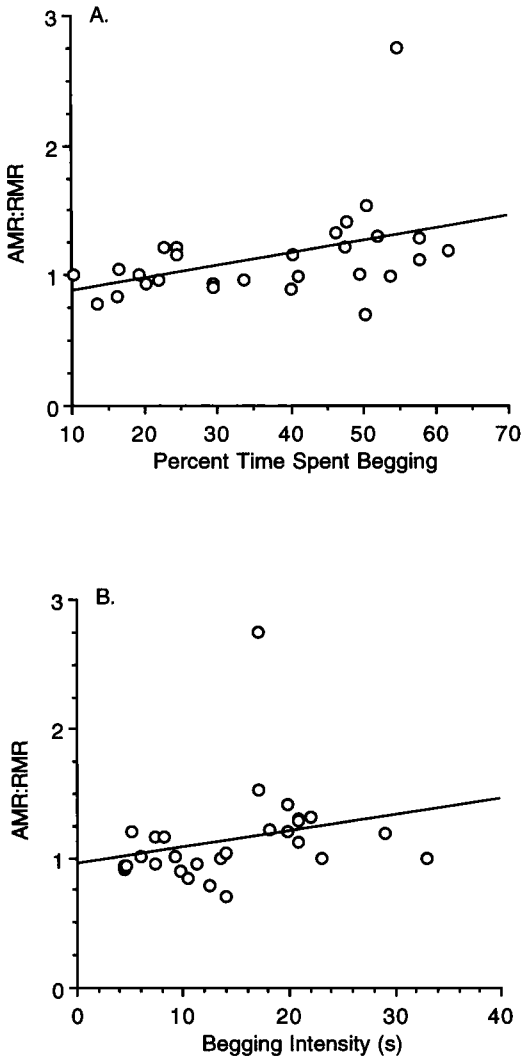


Fig. 6. Influence of percent time spent begging and begging intensity on the cost of begging. The increase in AMR:RMR with percent time begging is significant (A; Spearman's rank correlation, $n = 28$, $\rho = 0.459$, $Z = 2.39$, $P = 0.017$). AMR:RMR is also significantly correlated with begging intensity (B; $n = 28$, $\rho = 0.453$, $Z = 2.36$, $P = 0.019$). Lines fitted using least-squares technique.

DISCUSSION

The energetic cost of begging in nestling passerines is surprisingly low. High metabolic rates, such as those associated with behavioral displays in frogs, insects (Ryan 1988, Prestwich 1994), and some birds (Vehrencamp et al. 1989), were not found; indeed, it was often difficult to find any difference in metabolic rates be-

tween resting and begging birds. More sensitive methods of determining metabolic rate may be able to overcome some of the difficulties associated with obtaining precise measures of the cost of begging. Error associated with nonbegging factors that change metabolic rate (e.g. stretching and shuffling) will be difficult to eliminate (Chappell et al. 1995). While the existence of such error prevents the precise determination of the energetics of begging, the conclusion that begging is not energetically expensive is not dependent on obtaining such a measurement. If activities such as stretching and shuffling overwhelm the cost of begging, begging is not energetically costly.

The energetics of begging were consistently low for all species measured. Those in Table 1 represent seven different passerine families (AOU 1983) that differ in many aspects of nestling biology. Differences among species cannot be evaluated using statistical tests because of the small sample sizes available for several species. Some differences may be found among species with subsequent work; however, the overlap found suggests that such differences will not change the general conclusion that begging is not a costly trait. My analysis includes species that differ in many aspects of their biology and includes both cavity and cup-nesting species (Table 1). Begging of cavity-nesting and non-cavity-nesting species may vary in several characteristics, such as frequency and volume of calls produced (D. G. Haskell pers. comm., Redondo and Arias de Reyna 1988), yet the similarity in the energy costs for the two groups suggests that neither nest type nor a difference in calls is associated with large differences in begging energetics.

Given the dramatic changes passerine nestlings undergo in the first 10 days after hatching, the lack of a significant relationship between nestling age and AMR:RMR ratio is surprising. The incremental cost of begging, I , did increase significantly with age for both Tree Swallows and European Starlings. Since I is mass specific, this change represents an increase in cost with age that may be associated with a switch to a more demanding form of begging (pers. obs.).

The lack of a significant correlation between the percentage of each trial spent begging and the AMR:RMR in swallows and starlings likely is due to small sample sizes; when species are pooled, the effect of the amount of begging is significant (Fig. 6). There were dramatic differ-

TABLE 2. Energetic cost of activity in birds. Scope is measure of cost of activity equal to ratio of AMR:RMR, where RMR is resting metabolic rate (except where noted below) and AMR is active metabolic rate. Scope is the ratio of AMR:RMR.

Activity	Species	RMR ($J \cdot g^{-1} \cdot h^{-1}$)	AMR ($J \cdot g^{-1} \cdot h^{-1}$)	Scope	Source
Crowing	<i>Gallus gallus</i>	20.4	20.4	<1.03	Chappell et al. 1995 ^a
Begging	<i>Sturnus vulgaris</i>	44.9	47.0	1.05	Present study
Standing	<i>Anas rubripes</i>	17.2	19.3	1.12	Wooley and Owen 1978 ^b
Walk	<i>A. rubripes</i>	19.7	24.7	1.25	Wooley and Owen 1978 ^b
Begging	<i>Tachycineta bicolor</i>	68.5	83.5	1.27	Present study
Foraging	<i>S. vulgaris</i>	72.5	100.8	1.39	Westerterp and Drent 1985
Preening	<i>A. rubripes</i>	15.9	22.2	1.40	Wooley and Owen 1978 ^b
Hopping	<i>Erithacus rubecula</i>	85.7	120.4	1.40	Tatner and Bryant 1986
Hopping	<i>Zonotrichia leucophrys</i>	72.3	107.4	1.49	Paladino and King 1984 ^c
Swimming	<i>A. rubripes</i>	17.2	28.9	1.68	Wooley and Owen 1978 ^b
Calling	<i>A. rubripes</i>	19.7	41.4	2.10	Wooley and Owen 1978 ^b
Preening	<i>Lanius ludovicianus</i>	36.8	79.6	2.16	Weathers et al. 1984 ^d
Preening	<i>Melospittacus undulatus</i>	34.2	75.4	2.20	Buttemer et al. 1986 ^d
Hopping	<i>L. ludovicianus</i>	36.8	83.3	2.26	Weathers et al. 1984 ^d
Shuffling	<i>M. undulatus</i>	34.2	79.5	2.32	Buttemer et al. 1986 ^d
Flight	<i>Sterna fuscata</i>	31.2	92.1	2.95	Flint and Nagy 1984
Mound tending	<i>Leipoa ocellata</i>	13.4	41.9	3.13	Weathers et al. 1993 ^e
Flight	<i>Delichon urbica</i>	61.1	202.9	3.32	Hails 1979
Diving	<i>Aythya affinis</i>	29.0	105.4	3.64	Stephenson 1994 ^f
Singing	<i>Thryothorus ludovicianus</i>	66.5	258.2	3.9	Eberhardt 1994 ^g
Flight	<i>Hirundo rustica</i>	59.0	246.9	4.18	Hails 1979
Flight	<i>S. vulgaris</i>	72.5	488-584	6.7-8.1	Westerterp and Drent 1985 ^h
Flight	<i>Falco tinnunculus</i>	22.7	246.8	10.87	Masman and Klaassen 1987
Display	<i>Centrocerus urophasianus</i>	10.5	163.5	15.57	Vehrencamp et al. 1989 ⁱ
Flight	<i>Erithacus rubecula</i>	85.5	1,376.3	16.10	Tatner and Bryant 1986

^a Mean of three individuals estimated from Chappell et al. (1995: fig. 1) using 20.08 J/ml O₂ and a mass of 1.4 kg.

^b Calculated assuming mass of bird to be 1,000 g (Masman and Klaassen 1987).

^c Calculated from Paladino and King (1984: table 3) for a 28-g bird using T_a of 25°C, velocity of 0.46 km/h, and 20.08 J/ml O₂.

^d Basal metabolic rate used instead of RMR.

^e Based on oxygen consumption while running, using 20.08 J/ml O₂.

^f Assumes mass = 591 g, and 20.08 J/ml O₂.

^g Mean of four individuals from Eberhardt (1994: table 1) using BMR of 3.31 ml O₂ · g⁻¹ · h⁻¹ and 20.08 J/ml O₂.

^h Includes both long-distance flight after displacement from nest and flights while feeding young.

ⁱ Basal metabolic rate used instead of RMR, assuming mass of 2,500 g.

ences in the apparent intensity of begging among trials. Begging intensity, as measured by the average duration of begging bouts was significantly correlated with AMR:RMR ratio when all species were pooled (Fig. 6). I found no significant relationship between begging intensity and either AMR:RMR ratio or the incremental cost of begging for Tree Swallows and European Starlings analyzed alone. Although my statement about small sample sizes again is relevant, this lack of a relationship for Tree Swallows and European Starlings is unexpected. One explanation may lie in my characterization of begging intensity as the average duration of each begging bout. It is certain that, although this measure captures some of the variation in the intensity of begging, much of the variation in display type is not captured by this simple in-

dex. The combination of both visual and acoustic components form a wide range of intensities in begging. The visual component of the display ranges from virtually no movement to vigorous and precisely directed gaping. Similarly, the acoustic component ranges from no sound production to loud calls that can be heard far from the nest. Since begging behavior changed with age, variation in the nature of the begging display also may explain the relationship of nestling age to the cost of begging. Further empirical work on the importance of variability in the begging display and the relation to nestling age should be productive.

If heat produced by begging activity is substituted for heat otherwise produced by shivering thermogenesis, it is possible that my measurements of cost underestimate how strenuous

begging is (Hart 1960, Ketterson and King 1977, Walsberg 1983, Paladino and King 1984, Webster and Weathers 1990, Bevan and Butler 1992). The measurements I made were at temperatures well within the range of those normally experienced by nestlings (Withers 1977, Olson 1991, McCarty 1995), and were low enough that some of the older Tree Swallow nestlings may have been expending energy for thermoregulation. If begging replaced shivering in the begging trials, my methods would make begging appear to involve less work than it actually does; however, when ambient temperatures are below the thermoneutral zone, the realized cost of begging would still be quite low. Since ambient temperatures are usually below the thermoneutral zone of nestlings and since tree swallow nestlings older than five days are seldom brooded, the conditions used in these measurements are frequently encountered, at least in Tree Swallows (McCarty 1995). At ambient temperatures colder than those used here, the realized cost of begging would be reduced even further (Bevan and Butler 1992).

The relevance of these measures to discussions of the evolution of begging behavior can be addressed in two ways: (1) by comparing the cost of this behavior to that of other avian behaviors; or (2) by considering the cost of the behavior as a percentage of the daily energy budget of the nestlings (Bennett 1986). Clearly, the AMR:RMR ratio for begging is low compared to the costs of most other activities (Table 2), being similar to activities such as foraging, walking, or preening in adult birds. Thus, begging is an energetically inexpensive form of communication. Begging's energy cost is especially low when compared to the truly costly behavioral displays, such as singing in Carolina Wrens (*Thryothorus ludovicianus*; Eberhardt 1994) and mating displays in Sage Grouse (*Centrocercus urophasianus*; Vehrencamp et al. 1989). The costs of these avian displays are similar to the those associated with mating calls in anuran amphibians (AMR:RMR ratio = 6–21; Taigen and Wells 1985, Prestwich 1994) and insects (AMR:RMR ratio = 7–30; Ryan, 1988). The surprisingly low energetic cost of crowing in Red Junglefowl (Chappell et al. 1995, see also Horn et al. in press), together with the low cost for begging, demonstrates that it is not safe to assume that all behavioral displays are energetically expensive.

A second way to evaluate the energetic cost

of begging is to look at how much of a nestling's daily energy demands is due to begging. In the case of Tree Swallows up to 15 h/day could be spent begging (the maximum time available for foraging at Ithaca, New York), in which case the increase in daily energy expenditure must be less than the 22% increase in metabolic rate found for Tree Swallows. For example, if a 20-g Tree Swallow nestling has a daily energy expenditure of 32.9 kJ without begging (this study), and if it begs at the rate I measured for the entire 15 h, it will add 4.5 kJ or 12% to its daily energy budget. Actual rates of begging are usually much lower than those measured so these calculations probably overestimate the importance of begging.

This increase can be balanced by the energetic benefits of begging: increased feeding by parents. Tree Swallows feed nestlings at a rate of about 23 feeds per hour divided among an average of five nestlings, and each of these visits delivers approximately 545 J of food (McCarty 1995). Assuming that nestlings can assimilate 70% of this energy (Bryant and Bryant 1988), the begging cost can be met by receiving nine extra feedings per day or 0.6 visits per hour. Lower, more realistic rates of begging would be more easily compensated for. Studies of the response of parents to begging calls indicate that the increased feeding rate of parents easily would compensate if this additional energy were spent begging (Haartman 1953, Bengtsson and Rydén 1983, Harris 1983, Hussell 1988). Both of these approaches lead to the conclusion that begging is energetically inexpensive. The cost accrued by nestlings may be even lower when the benefits associated with begging, in the form of increased feeding rates to broods (Haartman 1953, Bengtsson and Rydén 1983, Harris 1983) and to individuals that beg most vigorously (Stamps et al. 1985, Gottlander 1987, Smith and Montgomerie 1991, Teather 1992) are taken into account.

Based on my results, the reliability of conclusions from models incorporating a cost of begging depend on the existence of an increased risk of predation due to begging. Conclusions from models that predict different results based on whether the cost of begging is due to energy expenditure or to predation (e.g. Macnair and Parker 1979, Harper 1986, Motro 1989, Godfray and Parker 1992) should be reconsidered based on the low magnitude of the energy cost presented here. Correlational studies provide weak

support for the existence of a predation cost associated with begging (e.g. Perrins 1965, Redondo and Castro 1992), while the only experimental evidence available suggests that the existence of such a cost may be limited to species that nest on the ground (Haskell 1994).

The unexpectedly low energy cost of begging described here further emphasizes the difficulty in predicting the energetic costs of displays in birds. Assumptions cannot be made based on measurements of other displays (e.g. Vehrencamp et al. 1989) or even of similar displays in different species (e.g. compare Eberhardt 1994 and Chappell et al. 1995). Until further empirical evidence is available on the energetics of begging, conclusions from models dependent on the assumption of a high cost to begging, particularly a large energetic cost, should be viewed with caution.

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