

## The Role of Energetic Costs in the Evolution of Begging Behavior of Nestling Passerines

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Dramatic advances have been made in our understanding of how elaborate traits and signals, such as the begging behavior of nestling passerines, might evolve. Some of the most fruitful theoretical advances have involved the assumption that such traits must carry a high cost. One of the clearest statements of the importance of this assumption is by Harper (1986), who assumes that begging is costly either in terms of increased predation risk or increased energy expenditures. Most models of begging share the assumption that begging is costly.

In an earlier paper (McCarty 1996), I presented results of measurements of the metabolic rates of begging nestlings and found the scope of activity to be 1.05 times resting metabolic rate (RMR) in European Starlings (*Sturnus vulgaris*) and 1.27 times RMR in Tree Swallows (*Tachycineta bicolor*). As begging generally has been thought to result in a large increase in energy consumption (e.g.  $3.5 \times$  RMR, Beauchamp et al. 1991; or comparable to calling in frogs and insects [ $6$  to  $30 \times$  RMR], Redondo and Castro 1992), and because other avian displays have been found to involve increases in metabolic rate as high as  $3.9$  to  $15 \times$  RMR (Vehrencamp et al. 1989, Eberhardt 1994), I concluded that the cost of begging was "surprisingly low" compared with costs of other activities, and that the assumption that begging was an energetically extravagant trait was not supported.

The commentaries by Verhulst and Wiersma (1997) and by Weathers et al. (1997) question my conclusions and make several interesting suggestions for future research. Weathers et al. propose the intriguing hypothesis that energetic costs accrued through anaerobic metabolism may actually make begging an expensive display. Anaerobic metabolism is thought to be most important in terrestrial birds after work rates exceed the ability of aerobic metabolism to sustain activity (estimated to be  $>5 \times$  BMR in adult birds; Weathers and Sullivan 1989), but the aerobic capacity of nestling passerines is virtually unknown. Although it will be interesting to learn about the use of anaerobic metabolism by nestling passerines in general, I think it is unlikely that its role in fueling begging will be found to change my conclusions. Accumulation of lactic acid in tissues during anaerobic

metabolism results in extreme fatigue and discomfort, limiting the possible duration of activity before an extended period of rest is needed (Guyton and Hall 1996). If begging were always confined to short bursts of activity separated by long rest periods when lactic acid could be metabolized, nestlings could use anaerobic metabolism to fuel begging. However, begging rates often are quite high and separated by only short periods of rest. For example, Tree Swallows typically visit the nest every 2 to 3 min, and nestlings beg vigorously during each visit; visitation frequency may be even higher under some conditions (McCarty 1995). Under more extreme conditions, nestlings of both Tree Swallows and European Starlings may beg continually for extended periods of time when parents are absent (pers. obs.), allowing no time for the rest periods needed to aerobically metabolize lactic acid. Furthermore, if the recovery time of nestlings is fast enough to metabolize lactic acid during the rest periods that are typically available, measurements using my closed-chamber technique would have included the increase in oxygen consumption as lactic acid was metabolized.

Although I believe the nature of the behavior makes it unlikely that anaerobic metabolism is an important source of energy for begging, it is possible that future work could find that such pathways are important for nestlings. What if nestlings are expending extra energy on begging using anaerobic metabolism: At what point do these expenditures become great enough to prevent the prediction that "the intensity of begging will escalate and increase beyond all bounds" (Motro 1989)? In addition to involving the expenditure of energy, begging results in an energy intake, as parents feed nestlings that beg. This combination of costs and benefits makes the quantitative assessment of how costly is too costly difficult in the context of current analytic models. The commentary of Verhulst and Wiersma (1997) suggests additional empirical data that may be needed to solve this problem.

Verhulst and Wiersma correctly point out that I expressed cost in energetic terms. Because the assumption I was testing had to do with energetic costs, I maintain that my approach was appropriate. Verhulst and Wiersma also raise the more interesting point that ultimately, what is required to understand the evolutionary implications of this cost is to somehow translate energetics to fitness (see also Godfray 1995).

Verhulst and Wiersma also suggest several pieces of additional information that may be useful in the

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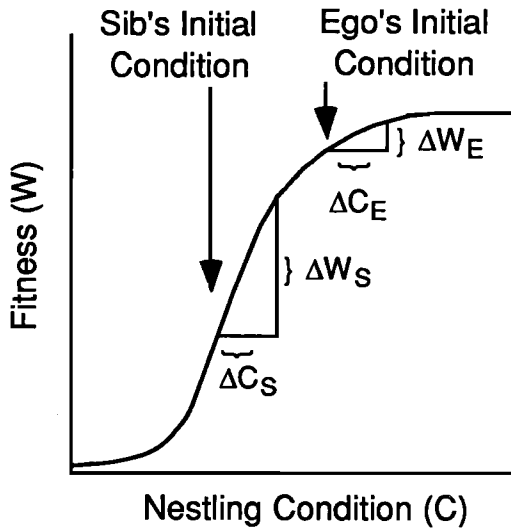


Fig. 1. An example of how the begging strategies of siblings might depend on the nature of the relationship between nutritional condition and fitness. If the relationship between a change in condition and the subsequent change in fitness is as shown (perhaps due to constraints on nestling digestive capacity decreasing the benefits associated with multiple feedings), then the total inclusive fitness of the sibling in better condition (Ego) may be maximized by reducing its begging intensity and allowing its weaker sibling (Sib) to be fed (using Hamilton's Rule)

development of subsequent models of begging. I agree that incorporating the points raised by Verhulst and Wiersma (and others) will augment our understanding about the evolution of begging. Indeed, incorporating additional information about how energetic and nutritional conditions relate to fitness may make the existence of a direct cost of begging unnecessary for restraining the intensity of begging or for making it an honest signal. For example, it may be possible to slightly modify existing models (such as Godfray 1995) in such a way as to eliminate the need for a direct energetic or predation cost of begging, relying only on the adverse effects on siblings to prevent cheating. Consider begging by two full siblings (Ego and Sib) that differ in their nutritional condition (C) and where nutritional condition in turn plays a role in determining fitness (W). If both siblings gain an equivalent increase in condition from a feeding ( $\Delta C$ ; Fig. 1), then the increase in fitness to each sibling will depend on the nature of the relationship between energetics and fitness. Under these conditions, it may be in the best interest of the stronger sibling (Ego) to forgo begging for food as long as the increase in fitness gained by its weaker sibling (Sib) is more than twice the gain Ego would experience. The likelihood of such an occurrence would depend on the (un-

known) shape of the relationship between nutritional condition and fitness (shown to be sigmoidal in Fig. 1), but this suggests an approach to developing detailed, parameterized models that may avoid the difficulties of defining how large of a direct energetic cost is sufficient to constrain the evolution of begging. The possible importance of adverse effects on kin in constraining begging is supported by the observed relationship between the intensity of begging and average relatedness within broods (Briskie et al. 1994).

Although both Weathers et al. and Verhulst and Wiersma raise interesting points, the main conclusion of my paper was that behavioral ecologists should not assume that begging is energetically costly until data supporting this assumption are obtained; such support is still lacking. My original paper did not suggest that previous models should be rejected. Indeed, I recognize that there may be other costs associated with begging (e.g. Haskell 1994), and future theoretical or empirical work might find even small energetic costs to be significant. Models are only as sound as their assumptions, and the available evidence supports my conclusion that "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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## Double Jeopardy and the Parameterization of Brood Reduction Models: A Comment on Mock and Forbes (1994)

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Hatching asynchrony in birds has puzzled ornithologists for years because it presents a paradox: Parental behavior appears to produce a hatching pattern that frequently results in the death of the last-hatched offspring (Magrath 1990). Lack (1947, 1954) proposed that asynchrony allows parents to reduce brood size to track unpredictable variations in food supply (the Brood Reduction Hypothesis). However, experimental tests of this hypothesis generally have found that fledging success of artificially synchronized broods was equal to or greater than that of asynchronous broods (32 of 34 tests; Stoleson and Beissinger 1995).

Mock and Forbes (1994) recently argued that effects on long-term fitness should be considered in studies of hatching asynchrony. They pointed out that, by using fledging success as the sole criterion for evaluating different hatching strategies, most authors have failed to recognize or assess possible differences in reproductive costs. Mock and Forbes suggested that in the absence of a mechanism to reduce brood size to available resources, parents at experimental synchronous nests may invest an imprudent level of effort in raising all their young, with a consequent reduction in future survival. Thus, asynchronous hatching may be favored over synchronous hatching if any long-term gain in adult survival compensates for any short-term losses in reproduction.

The tradeoff of fecundity and survivorship (hence, future reproduction) is central to studies of life-history evolution (e.g. Williams 1966, Charnov and Krebs

1974, Reznik 1985) but has been neglected in studies of hatching asynchrony. As Mock and Forbes (1994) noted, the effect of hatching patterns on the future survival of parents is poorly known. Few studies have quantified parental effort as an approximation of reproductive costs. Of 34 field studies reviewed recently, only six measured parental provisioning effort directly (Stoleson and Beissinger 1995), and one used an indirect measure (Gibbons 1987). Thus, the approach of Mock and Forbes in identifying life-history consequences of hatching asynchrony is particularly relevant and valuable.

To illustrate their argument graphically, Mock and Forbes (1994) presented a simple model that compares the relative fitness (measured as expected lifetime reproductive success) of a "brood-survival" strategy (i.e. synchrony) with that of a "brood-reduction" strategy (i.e. asynchrony). Synchronous and asynchronous hatching are preferable terms for the two strategies because they do not presume an adaptive function, but for the sake of clarity I will follow the usage of Mock and Forbes. Their model is meant to illustrate the effects on lifetime reproductive success of two different hatching strategies in relation to the frequency of good and bad food years. They presented two basic conclusions from their model results. First, a brood-survival strategy is less likely to prevail when good years are rare. Second, long-lived species are especially sensitive to survival penalties for using the brood survival strategy in bad years.

These conclusions, however, are to some extent dependent on the values used to parameterize the model. Mock and Forbes set the reproductive success of

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