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Is Begging Cheap?

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Avian nestlings beg to obtain food (von Haartman 1953), and begging is used increasingly as a model to study game-theoretic problems, the evolution of signaling, and parent-offspring conflict (Godfray 1991, Cotton et al. 1996). A fundamental assumption in these studies is that begging is costly (Godfray 1991). McCarty (1996) recently provided the first estimates of the costs of begging. These estimates were obtained by monitoring oxygen consumption of nestlings induced to beg in metabolic chambers. The metabolic rate during begging was increased by 8% in European Starlings (*Sturnus vulgaris*) and by 42% in Tree Swallows (*Tachycineta bicolor*). From these data (in combination with some tentative extrapolations to a nestling's daily energy demands), McCarty concluded that "the energetic cost of begging is surprisingly low" and that "conclusions from models dependent on the assumption of a high cost to begging should be viewed with caution."

However, McCarty expressed costs in energetic terms, whereas the relevant currency in an evolutionary sense reflects the fitness consequences of variations in begging rate. To translate the energetic costs of begging to fitness costs, one needs to know how energy allocation to begging affects growth, as well as the relationship between growth and reproductive prospects of the chick. We believe that such a calculation may lead to a very different conclusion. Among developing birds, only 13–28% of the total metabolized energy is allocated to growth, the remainder being spent largely on maintenance and thermoregulation (Weathers 1992). Thus, a chick spending an extra 10% of its total energy budget on begging may thereby reduce the amount of energy available for growth by 50%. In theory, this problem could be solved by increasing the energy budget (if extra food is obtained with begging), but at some point the energy budget will be constrained by the digestive capacity of the chick (Weiner 1992), or by other factors (Konarzewski et al. 1996). Thus, a small increase in energy expenditure for begging may result in a disproportionate decrease in reproductive prospects of the chick, and it is only this decrease that may yield a relevant estimate of the costs of begging.

Nevertheless, studies of energetics may be critical to bridge the gap between behavior and fitness. In birds, fitness consequences of variation in growth rate are relatively well known (Tinbergen and Boerlijst 1990), and as McCarty (1996) demonstrated, the energetic costs of begging can readily be measured in the laboratory. This makes it feasible to obtain estimates of the link between behavior and fitness, via the energetics of begging and growth, which is rarely possible in free-living animals. Such knowledge in turn will make it possible to develop parameterized models of begging behavior that are sufficiently detailed to be tested against reality.

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