

# Baby birds do not always tell the truth

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A parent bird carries prey to its nest and is met by chicks opening their colorful mouths, stretching their necks and bodies upward, and vocalizing enthusiastically (Fig. 1). At first glance, these active and noisy displays seem remarkably inconsistent with expectations that dependent nestlings ought to divert their energy to growth and do their best to avoid the attention of would-be predators (1). What, then, is all this fuss about? One possibility is that offspring solicitations (collectively termed “begging”) contain information that parents use to decide when and how much to feed their offspring (1–3). How accurate this information might be, however, has been a matter of some debate (1–3). As is the case in any sexually reproducing organism, there is only a coin flip’s chance that a nestling and its parent share any particular gene. This incomplete overlap in relatedness results in an incomplete overlap in desired food allocation, setting the stage for a selfish nestling to benefit from deception (4). In PNAS, Caro et al. (5) shed light on several factors that shape how honest offspring signals are.

One popular hypothesis for the evolution of information-rich begging suggests a particularly cooperative function for this display. According to the signal of need hypothesis, offspring in the lowest condition (highest need) produce the most intense signals, allowing parents to correct any deficits and maximize the survival of all family members (1, 6, 7). Central to signal of need is the requirement that high-condition individuals refrain from producing high-intensity signals (6, 7), an inversion of the predictions usually made about signal evolution and expression (8, 9). How could such deference evolve? By allowing nutrients to be directed to needier siblings (current or future), a modest signaler can improve its own inclusive fitness via the survival of these brothers and sisters, and, eventually, the existence of nieces and nephews (3–7). Because the benefits of this modesty are paid in the currency of genetic relatives, it stands to reason that honest signals of need should be more common when the relatives in question are more closely related. It is this prediction that Caro et al. (5) test, alongside the related prediction that competition



**Fig. 1. A parent robin (*Turdus migratorius*) delivers food to its nestlings. During a reproductive cycle, an avian parent may deliver thousands of individual food items to a brood of growing nestlings, each time deciding which of its young to feed. The begging displays of chicks have been hypothesized to function as honest signals of information valuable to choosy parents. In PNAS, Caro et al. (5) demonstrate that offspring signals are less honest when competition with siblings is high and unstable parental partnerships result in low genetic relatedness within families. Image courtesy of Arch Baker.**

with siblings always reduces the incentives for honesty because a chick cannot control what happens to food it passes up (2, 7, 10).

Nestling birds are not the only animals that solicit feedings from parents using complex displays (1, 3), but they are by far the most studied, allowing Caro et al. (5) to perform a metaanalysis in this group. The authors operationally define an honest signal of need as one for which signal intensity is positively and highly correlated with need, itself defined by a suite of proxies including low body condition or within-brood rank. They first limit their analysis to volitional components of begging (e.g., stretching, vocalizations), which are most likely to function as signals of need (11). Overall, they found that, as they predicted, nestling begging signals need more honestly when competition is relaxed and the beneficiaries of restraint are close kin

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(5). A chick raised alone is more honest about its needs than one reared with nest mates, and the magnitude of dishonesty increases with brood size. Competition with future siblings drives a similar pattern: when parents have the capacity to breed again, begging intensity less honestly reveals need. Supporting the prediction that high relatedness with competitors favors some restraint, Caro et al. (5) find that low adult mortality and low parental divorce (both of which increase a focal chick's relatedness to future siblings) are associated with more honest signals of need. The same, however, was not true with respect to concurrent siblings: low within-brood relatedness, caused by frequent extrapair mating by parents, was not associated with a decline in honesty.

An extremely "dishonest" signal of need, one produced most intensely by low-need (high-condition) nestlings, can be handily retermed an honest signal of quality (9). If only high-condition individuals are able to produce the most intense signals of quality, evolved restraint on their part should shrink differences between the begging of high- and low-quality chicks. Thus, cooperation manifests in this case as less honest signaling (of quality). Caro et al. (5) retested these predicted effects of competition and relatedness, this time using morphological components of offspring displays (e.g., nestling mouth coloration), the best candidates to reveal high quality in birds (3, 8, 11). They found no evidence that competition and/or relatedness shape the honesty of these signals, although a relative paucity of empirical work highlights the value of more studies on morphological components of offspring displays.

The demonstration by Caro et al. (5) that honesty can evolve along a continuum raises questions about how dishonesty evolves and how signals might remain reliable despite the incentives for nestlings to be deceitful. Comparisons of species in which nestlings express different relationships between begging (particularly its voluntary components) and need promise insights into the mechanisms linking internal physiological state to signal production, and the proximate routes by which these links might break down (12). Offspring that are dishonest about their needs might beg when they are not feeling particularly needy (lying to their parents), or they might feel needy even when they are not (accurately conveying the message of a body that is lying to itself). The factors that link condition proxies to begging shape the phenotypic space in which honesty can evolve and the extent to which honesty is plastic during the development of a single individual (12). Discovering and exploring the diversity of these mechanisms in animals will be particularly important to incorporating nonavian systems into future synthetic reviews and metaanalyses, as these constraints might differ substantially among taxonomic groups (13). More intense competition and conflict can lead not only to dishonesty but also to the evolution of ever more elaborate traits. Chicks in the avian family Rallidae (coots and rails), for example, are sometimes ornamented with colorful skin and plumage. The evolution of this elaborate ornamentation, just like dishonesty, is associated with large clutch size and the lack of stable pair bonds between parents (14). This elaboration of signals can enforce honesty by leaving only a subset of signalers (or signalers in a subset of conditions) able to afford efforts to attract parental attention (8, 9).

With a result that should not escape notice, Caro et al.'s authoritative summary of the avian begging literature highlights the vulnerability of signal of need as a general, much less universal, explanation for traits currently lumped under the implicitly biased label of begging. Even in the sample of offspring behaviors that the authors preselected as likely candidates to signal need, a relationship between need and signal intensity was often absent or

even negative (i.e., these signals functioned instead as signals of quality). In birds for which brood size is larger than one (the overwhelming majority of birds), the estimated mean correlation between begging and need overlapped zero, a statistical effect indicating that begging does not, on average, signal need. Mean effects across a large number of species should not be mistaken for biological rules, but this compelling result will no doubt generate even more empirical and theoretical interest in alternative hypotheses for the evolution and function of offspring solicitations (2, 3, 11).

Offspring displays have most likely evolved in concert with life history pressures shaping the optimal distribution of resources within families, sometimes signaling need, sometimes signaling quality, sometimes signaling hunger (3, 5, 11), and sometimes

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functioning in ways other than honest signaling to parents (2). Integrating the fields of life history and begging will require information about what each component of an offspring display means, how and when parents respond, and, critically, how offspring-parent interactions shape each party's total fitness, including any stake in the reproductive success of kin. The benefits of resource diversion to (signal of need) or away (signal of quality) from needy offspring will always depend on the nature of the trade-off between offspring quantity and quality (13, 15). Even signal information content and parental responses that match the predictions of signal of need or signal of quality support these evolutionary hypotheses only if fitness effects also match predictions.

Caro et al. (5)'s approach of studying the strength of relationships, rather than just their statistical presence or absence, is one that can be fruitfully applied to similar questions central to the study of signal evolution. In addition to the inclusive fitness costs that escalated (successful) begging can generate, the energetic costs of this vigorous display are often hypothesized to prevent exaggeration by chicks that do not need the food (2, 7). Empirical demonstrations that a behavior requiring muscle contraction has nonzero physiological costs is an unsatisfying test of the hypothesis that these costs are sufficient to maintain honesty (9). A demonstration that parents require more costly signals from offspring with whom they have relatively high levels of conflict (14), however, could provide more convincing evidence for a role of energetic costs in shaping honesty within families. As Caro et al. (5) note, signals and their honesty will coevolve with parental responses, and studies of reaction norms across players, timescales, and contexts will all be valuable.

When a parent bird visits its nestlings, a cacophony of colors, sounds, and motion illustrates an evolutionary story about why caring parents make the decisions they do, minute to minute, throughout a reproductive cycle, and across a lifetime. Although they may seem helpless to the casual observer, nest-bound chicks are far from passive players on this stage. As Caro et al. (5) demonstrate, an offspring's tendency to cooperate with parents by honestly revealing information depends on the extent to which its evolutionary interests align with those of other family members.

An understanding of begging as a phenomenon unto itself and as a piece of a larger story will stem from continued efforts to address two seemingly contradictory questions: Why do dependent young engage in conspicuous and costly displays at all? Why do strong

offspring not display more often and more intensely than they do? Caro et al. (5, 11) have confirmed the importance of competition and relatedness within families to answering both questions, moving an already rich and complex literature in new directions.

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