Begging for control: when are offspring solicitation behaviours honest?

Nick J. Royle, Ian R. Hartley and Geoff A. Parker

There is burgeoning interest in the idea that conspicuous begging displays, when parents are provisioning dependent young, advertise offspring need honestly to parents. Many empirical studies claim to support the theory of honest signalling of need, where parents control resource allocation. The evidence, however, also fits the predictions of recent models for the evolution of costly begging where offspring control allocation. These models incorporate variation in offspring condition and show that the three main predictions of honest signalling models are also found with models of sibling scramble competition. Consequently, it is difficult to discriminate between the two different modelling approaches from their predictions, despite their having been the focus of much empirical work. In particular, the evidence indicates that the prediction that begging intensity signals offspring need honesty is strongly context dependent. Begging might be ‘honest’ only when the potential for conflict is low and food is not limiting.

Published online: 11 July 2002

Ever since Trivers [1] showed that parents and their offspring could be in conflict over the amount of parental investment, the evolution and maintenance of begging behaviour has been an area of increasing interest to evolutionary biologists. Trivers considered the relationship from the point of view of the offspring, and saw begging as a form of psychological manipulation by the offspring to obtain a higher amount of parental investment than the parents were selected ideally to give. Subsequent theoretical treatments of begging have tended to model the allocation of parental provisioning to dependent young in terms either of the outcome of scramble competition among siblings (i.e. offspring control parental investment allocation [2–5]), or, more recently, in terms of honest signals [6] of offspring ‘need’ (i.e. parents control parental investment allocation [7,8]). So, are family dynamics regarding provisioning controlled primarily by parents or by their offspring?

Since Kilner and Johnstone [9] reviewed the evidence for honest signalling, more recent work has cast some doubt on the stability of the honest-signalling solution [10,11] (but see [12]). Nevertheless, increasing numbers of recent empirical studies claim to support honest signalling [13–16]. Here, we re-evaluate critically the application of honest signalling to the evolution of costly begging displays in the light of recent models of sibling scramble competition [17,18], which show that the primary predictions generated by honest-signalling models and scramble models are not mutually exclusive (Box 1).

Key predictions of honest-signalling theory

When delivering food to dependent young, parents often face a barrage of extravagant begging calls and postures. If the brood size is greater than one, the parent has to make a decision as to which of its young to feed and, if the current load is divisible, how much to feed each offspring. Information received by parents during feeding bouts might also influence future feeding episodes and affect overall provisioning rate [12]. Consequently, the decision-making processes surrounding the feeding of dependent young by parents are a dynamic, and potentially complex, series of interactions.

Models of offspring solicitation are based on key simplifying assumptions (Box 1). Kilner and Johnstone [9] reviewed the evidence for begging as an honest signal of need based on three main predictions of honest-signalling models: (1) begging intensity should reflect offspring need, (2) parents should provision young in relation to begging intensity and (3) begging should be costly. However, as Kilner and Johnstone acknowledge, neither prediction 2 nor 3 is unique to honest signalling. In both scramble and honest-signalling models, an offspring that begs more receives more food, and both models require a cost of begging. Kilner and Johnstone found little firm support for predictions 2 and 3 – possibly owing to the simplicity of these predictions in relation to the complexity of the behaviour – but they concluded that the empirical data provided good support for the first prediction, which is

References

Box 1. Mechanisms of food allocation and begging ‘honesty’

The terms ‘scramble’ and ‘honest signalling’ relate primarily to the mechanism of food allocation (passive and active, respectively) and to the underlying causes of the begging behaviour. In models of scramble competition, the parent is viewed as being essentially passive, giving food to offspring in proportion to the relative stimulus intensity that each offspring presents [a]. In honest signalling models, the parent is omnipotent, measuring begging levels precisely and then allocating food actively in accordance with the message that the signal prescribes. A historic parallel here relates to sexual advertisement by males in leks or in choruses. The need to distinguish active choice (where females differentiate between costly signals of male quality) from passive attraction (where females simply move towards the strongest stimulus in sexual advertisement scrambles) was stressed two decades ago, because the observed patterns of mating could be very similar in each case [b,c].

Confusingly, begging can be regarded as ‘honest’ under both mechanisms of resource allocation because in both cases the benefits of increased begging are balanced by the costs. In addition, both mechanisms can be considered to be signals, in that the behaviour of the parent(s) is/are influenced by the behaviour of the offspring. A crucial difference between the two mechanisms rests in the precision of this communication. In honest signalling, any effect of offspring’s competitive abilities on the strength of their begging signals should be discounted by parents, so that food allocation relates only to need. In begging scrambles, competitive abilities are not discounted since parents respond passively to the signal strength. A common assumption is that the probability of receiving a given food item is proportional to the signal strength of the offspring relative to the average for the brood [d]. Here, begging does not relate directly to need unless offspring are competitively equal [e]. Using this stricter definition of ‘honesty’, although begging under scramble can sometimes be honest, only begging under honest signalling is always honest. Consequently, in spite of the two modelling approaches representing different ends on a biological continuum, there is considerable overlap in the predictions generated by each approach.

What is need?

For present purposes, we can define ‘need’ as a measure of the increase in an offspring’s personal fitness resulting from receipt of a unit of food. In honest-signalling models, begging is seen as a communication of need from offspring to their parents [7], with the intensity of begging reflecting an individual’s true need (Box 2). Consequently, empirical demonstrations that hungrier offspring are fed more food are posited as support for honest signalling of need (prediction 1 as reviewed by Kilner and Johnstone [9]). However, qualitatively equivalent results are obtained if offspring condition is included into models of scramble competition (Box 3). Begging levels correlate with true need because the costs that can be ‘afforded’ by the offspring increase with the potential gains. We therefore see no way to discriminate empirically between scramble competition and honest signalling from the three predictions listed by Kilner and Johnstone [9].

The main difference between approaches will be in the exact quantitative relation between true need (condition) and the begging level of the evolutionarily stable strategy (ESS), which depends on the mechanism of resource allocation (Box 3). In practice, it will often be impossible to discriminate between scramble and honest-signal mechanisms of food allocation in unmanipulated, observational situations.

Thus, scramble models predict that food allocation and begging costs are influenced strongly by competitive asymmetries (Box 3), but under honest signalling parents should compensate for asymmetries and allocate food in relation to need. There is an explicit assumption that enough food is available to allow all the brood to survive. If, as is often the case [19], food resources for provisioning parents are more limited, honest signalling might be an unstable strategy. For example, assume that parents supply food preferentially to offspring that are in poorer condition [8]. If a parent has two offspring to feed but the total food is insufficient to allow both to survive, how should it be allocated? With honest signalling, the parent feeds the offspring in poorest condition each time, which results in underinvestment in both offspring. However, under scramble competition (Box 3), a unit of begging by the stronger offspring is more effective at obtaining food than is a unit from the weaker offspring. So if offspring are unequal and food is limiting, parents pay out more often to the stronger offspring, which then has an increased chance of survival. Parents might then be more likely to raise offspring successfully when the latter scramble for food [18], although the best strategy would be to feed the stronger offspring exclusively [19,20].

Given that the scramble models of Rodríguez-Gironés et al. [17] and Parker et al. [18] produce the same qualitative results as those of the signalling model of Godfray [8] (Box 3), it is appropriate to ask how the two approaches can be distinguished empirically. To demonstrate honest signalling in begging systems requires evidence that parents assess need, rather than simply allocate passively to the strongest source of stimulus. Active assessment of begging signals is implied if parents inspect each offspring’s begging level in turn, and then return to feed a given offspring. Convincing confirmatory evidence would be that parents discount amplification of begging stimuli due to an offspring’s age or competitive strength, and allocate food only in relation to each offspring’s true need or condition. Occasionally, increased food supplied to nestlings has been found to amplify, rather than reduce chick begging [19]; for these cases, begging cannot reflect true need. Additional clues to distinguishing between the two approaches relate to the biological context in which begging is enacted.

Context dependency

Although signalling and scramble models have been criticised for ignoring much of the dynamics involved in parent–offspring communication [21], they are

References


thought to be unique to honest-signalling models. So, does begging intensity reflect offspring need honestly?
Box 2. The concept of ‘need’ in honest-signalling models

Offspring have different levels of need or condition, which reflect the value of extra parental investment to them [a]; offspring in poorer condition or with a greater need benefit more from receiving extra food than would offspring in better condition. This variation in the level of need is assumed to be cryptic, such that the parent cannot monitor it directly [b]. Honesty is maintained by the costly nature of the signal [c,d]: an offspring that signals at a higher level than the ESS level for its true need gains more resources but suffers higher costs, which more than offset its extra gains. At the ESS level, costs counterbalance exactly the benefits of escalating the level of begging, and signal strength is assumed to correspond to offspring need on a one-to-one basis [a]. Consequently, the intensity of begging reflects an offspring’s true need.

Godfray developed a second model [e] in which two offspring competed for the fixed food allocation to the brood (intrabrood competition [f]). The fitness benefit, $f$, of y units of food to each chick were assumed to be (Eqn I)

$$f = B(1 - e^{-c})$$

where $B$ is the asymptotic or maximum benefit, and $c$ is a constant defining the rate at which fitness to $B$. The effects of variation in need or condition of chicks can be simulated by giving different values of $c$, whilst keeping $B$, the asymptotic maximum benefit, fixed [c,d] (Fig. I). The fitness costs of begging to level $x$ are assumed to be linear, rising as $Ex$, where $E$ is the energetic cost of each unit of begging. Thus the personal fitness of chick A is (Eqn II)

$$W_A = B(1 - e^{-cA}) - Ex_A$$

Fig. I. Relation between the ‘fitness benefit’, $f$, of a chick and its food uptake, $y$, from a given meal (from Eqn I). This formulation of benefits has been used in honest-signalling models [b,e], and in the scramble-competition models discussed in Box 3. As the shape constant, $c$, in Eqn I increases, the rate of approach of the curve to the asymptote increases. This means that if we compare two curves (one for each of two chicks, A and B, competing in a nest), the curve with the higher $c$-value has the higher gradient (or marginal gains) initially for a given amount of food, $y$. But as $y$ increases, the situation reverses, so that the curve with the lower $c$ has the higher marginal gains. Thus, whether the need (i.e. a measure of the relative fitness benefit of one small unit of food) is directly or inversely proportional to $c$ depends on the total food available to be divided between A and B.

Consequently, the intensity of begging reflects an offspring’s true need.

Fig. II. Begging levels of the focal chick A in Godfray’s [e] model of intrabrood signal begging for two chicks in relation to $c_A$. (A’s condition; see Eqn II). The condition of the nonfocal chick B ($c_B$) is held constant at 7.0 throughout and the maximum for $c_A = 10.0$. The asymptotic food benefit is $B = 1.0$ and the total food available is $Y = 1.0$ (see Eqns I-IV). As begging decreases as its condition increases to the maximum, at which point it ceases to beg. The continuous curves are for the case where A and B are full sibs ($r = 0.5$) at different levels of cost $E$ (see Eqn II) for each unit of begging ($E = 0.08, 0.1$ or $0.13$), and the broken curve is for the case where A and B are half sibs ($r = 0.25$) with $E = 0.1$. Adapted, with permission, from [e].

Consider a brood of two chicks, A and B. The food gained by each chick sums to $Y$, such that the total food input to the nest (Eqn III):

$$Y = y_A + y_B$$

The inclusive fitness of the chick A is (Eqn IV)

$$W_{incl} = W_A + rW_B$$

where $r$ is the relatedness between the sibs (0.5 for full sibs, 0.25 for half sibs).

Keeping the condition of chick B as $c_B = 7.0$, Godfray [e] showed that the signalling level of chick A decreased to zero when it reached the maximum possible condition, $c_A = 10.0$ (Fig. II). The same qualitative relationship between begging level and condition remains even if the costs of begging are altered, but begging decreases when the costs of begging are relatively high and increases when costs of begging are low; begging also increases if the chicks are half rather than full sibs (Fig. II).

References

Box 3. The concept of ‘need’ in scramble competition models

Two recent models of begging scramble competition [a, b], derived from an earlier model of Parker et al. [c] have incorporated variation in offspring need. Parker et al. [b] examined pure intrabrood sibling competition in a similar way to Godfray’s two-chick model [d] for signalling; the two chicks A and B receive a total food input of Y food units from their parents, where A gets \( y_A \) and B gets \( y_B \) (see Fig. I and Eqsns I–IV in Box 2). Following Parker et al. [c], it was assumed that chicks A and B had competitive abilities a and b, respectively, so that their perceived begging levels were \( ax_A \) and \( bx_B \). Their food gains were therefore (Eqn Ia)

\[
y_A = Y(ax_A)/(ax_A + bx_B) \text{ for } A \quad \text{[Eqn Ia]}
\]

\[
y_B = Y(bx_B)/(ax_A + bx_B) \text{ for } B \quad \text{[Eqn Ib]}
\]

This pure scramble model gives remarkably similar results to Godfray’s analogous honest-signalling model. For exact comparison with Godfray’s results [d] in Box 2, the condition of chick B was held as \( c_B = 7.0 \). The begging costs paid by chick A always decreased with its condition, but were also dependent on its competitive ability (Fig. I). Across a wide range of differences in competitive ability between the chicks (a/b between 0.5 and 2.0), scramble solutions gave much higher ESS begging costs than honest signalling for the range of values used in Godfray’s model [d], suggesting that honest signalling might be a less costly food allocation mechanism than scramble competition under certain circumstances. Parker et al. [c] also showed the need for caution when using c as a measure of chick need, because this will depend strictly on the magnitude of c relative to total food, Y [b] (see Fig. I in Box 2).

Another recent set of sibling competition models generates similar conclusions, although a direct comparison with signalling is more difficult. Rodríguez-Gironés et al. [a] use the term ‘signalling’ synonymously with begging, which they distinguish from other components of ('non-signalling') foraging effort. Under our definitions, all their models would be forms of sibling scramble competition because they use modifications of the scramble equations to deduce how chick foraging effort converts into food allocation. Their simplest model [d] used exactly the same explicit assumptions as those in Eqsns Ia and Ib, and Eqsns I–IV of Box 2 (Fig. II). The begging costs of each chick decreases with condition as for Godfray [d] and Parker et al. [b], and those of the stronger chick are lower than that of the weaker chick. Only the total food input to the nest evolves (see also [e]), and a fixed parental mechanism operates (Eqsns la and lb) to determine food allocations. This is quite different from the evolution of begging signals sensu Godfray [f].

References

a Rodríguez-Gironés, M. A. et al. (2001) Role of begging and sibling competition in foraging strategies of nestlings. 
Am. Behav. 61, 733–745
Ecol. Lett. 5, 206–215
c Parker, G.A. et al. (1989) How selfish should stronger sibs be? 
Am. Nat. 133, 846–868
Am. Nat. 146, 1–24
Anim. Behav. 27, 1210–1235
**The power continuum**

Honest-signalling outcomes can occur only if there is parental control of resource allocation, and scramble outcomes can occur only when offspring control allocation. This power continuum has important implications for the mechanism of resource allocation; it is not the determinant of the parental investment level that the offspring obtain per se [19].

In the context of parental feeding of dependent young, honest signalling is perhaps more likely to occur under uniparental care, when offspring are produced singly or when the ability of parents to provide resources to offspring is high and/or the costs of doing so are low. However, if offspring are produced in large broods, and especially if there are two parents caring for them, offspring are in a much better position to reduce the degree of parental control over allocation of parental investment, and a scramble outcome becomes more plausible.

Biology allows for all possibilities in the power continuum [19]. When parents mass provision larvae by abandoning their clutch within a food resource, only scramble is possible because no parent is available during resource consumption. In mammals, it is unlikely that the mother could effect selective control of milk supply to different offspring because the most competitive young usually control access to the best teats [22]. If the more active sucklers gain most milk, it will be very hard to determine whether this results from scramble or honest signalling. With birds, there is a greater opportunity for parents to control food allocation.

Perhaps the best current evidence for honest signalling of need comes from studies of gape colour in nestling birds. Kilner [23] showed that the gapes of canary *Serinus canaria* nestlings flushed a redder colour when they were deprived of food. Parents fed chicks with redder mouths preferentially, suggesting that they responded to honest signals of offspring need. Recent data presented by Saino et al. [15], however, indicate a different reason for an association between gape colour intensity and feeding preference of nestlings by parent barn swallows *Hirundo rustica*. Brighter gape colour in swallow nestlings is carotenoid-mediated, indicating a higher level of immunocompetence. Chicks challenged with a novel antigen had less brightly coloured gapes, and so parents were found to invest preferentially in chicks with a higher reproductive value. Gape colour intensity was apparently an honest indicator of health, but not necessarily of chick need.

Thus, it is not possible to rule out a scramble rather than an honest-signalling mechanism, because chicks in better health can ‘afford’ to pay the costs of increasing the stimulus to which the food-allocating parent responds. It should be noted that Kilner’s study [23], relating mouth colour to chick hunger, used canary nestlings that were 2–4 days old, at which age vocalization ability is rudimentary or absent, and the parental effort needed to sustain the whole brood is likely to be much lower than for parent swallows feeding 10-day-old nestlings. In the early stages of nestling development, the communication system is likely to be less complex, possibly because conflict will be low owing to the relative ease with which parents can meet the full needs of their brood. This is also likely to apply to parent–offspring communication in other taxa. For example, Agrawal et al. [16] have presented evidence recently that maternal provisioning of food in burrower bugs *Sehirus cinctus* is responsive to variation in offspring condition. This was interpreted as evidence for honest signalling in this species. A predictable ad-lib. food source was available throughout the experiment, so the mother bugs could afford to attend fully to offspring need. However, given that mothers do not allocate food actively to their offspring [16], a scramble-allocation mechanism would seem more appropriate, especially if, as is probable under natural conditions, food availability is neither predictable nor superabundant.

**The shifting power balance during ontogeny**

Although all points of the power continuum are plausible biologically, the power balance is likely to shift during offspring development. In large clutches of nearly fully-grown offspring, scramble competition might primarily determine resource allocation during parental feeding; however, parents are likely to have a high degree of control over offspring in early stages of their development and possibly even total control before they are born or hatch. In real systems, resource availability tends to vary in its predictability, and for many species with dependent young, parents influence the rearing environment routinely before offspring hatch, hedging their bets against uncertain resource availability [24]. In birds, for example, parents can vary the clutch size, the degree of hatching asynchrony [19], and the testosterone [25] and antioxidant [26] concentrations of individual eggs. Consequently, there are often distinct competitive asymmetries among chicks within a brood.

A chick’s competitive ability will often correlate positively with its reproductive value to the parent. Hatching asynchrony favours earlier-hatched young, especially when food is in short supply [19]. In such circumstances, passive feeding, by allowing young to scramble, might be a cheap (if slightly inaccurate) mechanism by which parents can load investment towards offspring of high reproductive value [27,28], even if there is a risk that, if food availability improves, this strategy might reduce parental fitness by some offspring taking more food than the parents would ideally ‘prefer’. At this point, active allocation is likely to be better for parental fitness. However, if parents allocate food actively, there might be a confounding effect of competitive asymmetries if the cost of signalling varies for chicks with identical need. If only the begging signal can be monitored, then honesty can be corrupted [29] because stronger chicks...
Box 4. Information exchange

The accuracy, reliability and meaning of the information exchanged between offspring and parents is also likely to be strongly context dependent. With begging, the simplest scenario is a single parent feeding a single offspring. Here, there is just one avenue of parent-offspring communication. With a single parent feeding two offspring, there might be three communication routes if siblings can also communicate with each other [a]. The situation becomes increasingly complex when two or more providers (parents and/or helpers) are involved because each provider might also have a different response to begging.

Offspring might have little information about the ability of parents to provide food: the offspring does not know the constraints operating on the parent and hence the context in which the signal will be judged. Extreme begging of one offspring relative to the others within a brood might indicate its high true need. If the parent can afford to attend to this need, both parent and offspring will benefit, but if the parent is unable to provision this need fully, it might do better to direct food to other offspring that would give a better return from its limited investment. So, although the signaler might be advertising only one message — ‘I’m very hungry’ — the receiver might read the message in more than one way, depending on food supply in this case, about which the signaler has little or no information. The signaler might be able to gain information if there is more than one provider of the resource, and so modify its signal accordingly. This sort of effect would compromise the accuracy and reliability of the information exchanged between signalers and receivers. In great tits, for example, only mothers responded to a greater intensity of begging by bringing more food [b]. Consequently, honest signalling becomes more unlikely as the number of potential routes of communication increases, particularly when the potential for conflict is high. It would be interesting to see the results of more research into the differences between providers in their response to particular begging behaviours.

References


are likely to be more able to bear the costs associated with begging [20]. This point is well illustrated by Kübler [30], who presented evidence that the cost of begging is traded off against growth in canaries. She suggests that older chicks can afford to beg harder than their younger siblings because they have been freed from the costs of devoting energy to growth. Consequently, the meaning of the signal has changed during ontogeny. Such ‘begging apparency’ [18] can present a problem for parents in the accurate reading of signals when there are asymmetries of age and size among chicks within a brood. In these circumstances, assuming the parent can assess competitive ability directly but not true need, an ESS for honest signalling is possible only if the parent can calibrate the signal against the offspring’s competitive ability.

Once competitive asymmetries have been established, the amount of sibling competition itself could become a signal [11,31], and parents might adjust their overall level of provisioning to the brood accordingly. If ostensibly non-signalling behaviour, such as the level of jostling by siblings, can be used as a signal by the parent, then the scramble and honest-signalling approaches converge and parents might allocate parental investment based on signal strength of individual offspring and/or the brood as a whole. For example, parents might use the total amount of direct competition among offspring to adjust the total parental investment supplied to the brood, and the relative amount of jostling (discounting competitive ability) as an indicator of the amount of parental investment to supply to individual offspring.

Cues of size and vigour are probably more reliable than are begging signals correlating with true need. Dishonesty can be difficult to detect [32], and the potential costs of determining the honesty of signalling chicks (i.e. mechanisms of discounting competitive asymmetry) might also lead to a corruption of honesty [33] (Box 4). Time and energetic constraints might limit the amount of food that can be delivered to the young, so the costs of determining the honesty of signals are likely to be highest when food is in short supply. Recent work on great tits *Parus major* by Oddie [34] provides good evidence for offspring control of food allocation under such circumstances [35]. Contrary to theoretical expectations, the sex ratio of great tits at fledging is often male-biased when food is scarce [34] because male chicks are larger than their female sibs and secure most of the food delivered to the nest. Given that the secondary sex ratios of the great tit broods appear to be maladaptive from the parental point of view [35], the way in which food is distributed is costly to parents. Offspring have apparently the upper hand in control over allocation of food in this situation.

Conclusions and prospects

Recent studies have shown that parents do not always respond to signals of chick need [21,36], and that begging is much more plastic than realised previously [37]. Moreover, as we illustrate in this review, empirical results demonstrating that hungry chicks get more parental investment do not necessarily provide support for honest signalling of need, especially as sibling scramble competition can explain the same result [18]. Rather, empirical work indicates that begging is a complex process involving multiple signalling components [21,38]. In most bird species, and under most circumstances, the largest (senior) chick receives most food, even though their begging rates might be less than those of junior siblings [21]. This allocation pattern could be a consequence of either parental control or offspring control of resources, depending upon the context. Less frequently, the smallest, and presumably most needy, chick receives most food [13,39]. Although this would appear to be further evidence of honest signalling, even this behaviour is consistent with scramble under certain conditions [18] (Box 3). Empirical determination of the underlying mechanism involved in begging behaviour requires experiments that establish that parents or offspring benefit at the expense of the other. This might be particularly hard to establish if, as this review suggests, the honesty of the begging signal varies depending upon the context. The crux of the problem in this form of parent-offspring communication is in the power dynamics [17]. Unless one or other party can gain and maintain control, power will fluctuate back and forth along the continuum [40].
Recent theoretical work suggests that honest signalling might have evolved via sibling conflict [11, 12]. Honest signalling is consequently more probable when the potential for parent–offspring conflict is low, so that neither party gains much by dishonesty; for example, in communication between offspring and parents over optimal temperature for warmth [41]. Under this scenario, begging as an honest signal can be viewed as fine tuning to the main stimulus or signal; that is, as a secondary signal (or ‘back-up’) [42], although this implies that the primary signal has somehow failed) because, under certain circumstances, it has lower costs than does scramble competition [18]. Such facultative switching between signal and scramble competition remains to be modelled. The relative prevalence of passive or active allocation mechanisms might depend on the tradeoff between benefits of mechanistic simplicity [10, 43] (passive allocation of resources) and the cost to parents of failing to feed the neediest offspring when begging is amplified by competitive asymmetries. Incorporation of uncertainty in both resource availability (Box 4) and signal/receiver error [12] into future models could help to establish the relative importance of honest signalling and scramble competition in the evolution and maintenance of costly begging displays.

The evidence presented here suggests that empirical studies of begging would be better served by focusing on variation in begging signals in relation to the social and environmental context in which they are operating [37], rather than assuming per se that begging intensity is an honest signal of need. In this way, it might be possible to establish which attributes of power determine the outcome of the struggle for control of parental investment [40]. Most begging models ignore such dynamic aspects of offspring feeding, and it has been suggested that real progress on a theoretical front might not be forthcoming until this degree of complexity can be incorporated [12]. However, we are faced with a tradeoff because increased realism through the incorporation of power dynamics in model building is technically more complex and harder to interpret, making predictions very difficult to test empirically [40]. Recognizing and incorporating the complexities of parent–offspring communication is an achievable challenge for future work on begging.

References

17 Rodríguez-Gironés, M.A. et al. (2001) Role of begging and sibling competition in foraging strategies of nestlings. Anim. Behav. 61, 733–745
41 Evans, R.M. (1994) Cold-induced calling and shivering in young American white pelicans: honest signalling of offspring need for warmth in a functionally integrated thermoregulatory system. Behav. Ecol. 12, 14–24