



LETTER TO THE EDITOR

The Origins of Parent–Offspring Signalling

The solicitation of food by young from their parents is a widespread phenomenon in species with parental care. This solicitation is often interpreted as being an honest signal of need, maintained by a costly “handicap” (Kilner & Johnstone, 1997). Here we address the question of how such handicap signals can originate. We identify a threshold that must first be surpassed, and suggest a method by which observation of contemporary parental behaviour can be used to investigate this ancestral threshold. The existence of such a threshold would indicate a role for processes such as sensory bias. Thus it is argued that to understand the evolutionary origins of begging requires experiments to focus not on parental responses to typically sized signals, but on parental responses to minimally sized signals.

Background and Model

When parents provide their young with resources, the act is often associated with conspicuous begging behaviour on the part of the recipients. The question of why such behaviour should be so common—given that parental provisioning is expected even in the absence of begging—has stimulated a number of theoretical models (Parker & McNair, 1979a,b; McNair & Parker, 1979; Eshel & Feldman, 1991; Yamamura & Higashi, 1992; Godfray, 1991, 1995). The signalling “resolution” models of Godfray (“resolution” of parent–offspring “conflict”) are based on the theory of so-called handicap or strategic signalling (Zahavi, 1975), in which “honesty” is predicted to be maintained in the system provided the form of the costs incurred by the solicitants fulfil certain criteria. Godfray applied handicap principles to the scenario of parent–offspring begging and

showed, using a mathematical model, that it is possible for costly solicitation to be stable to simple mutations (Godfray, 1991, 1995).

Recent work has, however, thrown doubts on the evolutionary accessibility of begging between relatives. Rodríguez-Gironés *et al.* (1996) pointed out, for Godfray’s (1991) model, that the situation in which no young signal is also an equilibrium, and numerically calculated that this equilibrium can have a higher overall fitness than does the signalling equilibrium. Moreover, Rodríguez-Gironés *et al.* (1998) described computer simulations of the same model, in which the non-signalling state was not invaded. That is, when the parent–chick system was started with no begging in the population, begging behaviour did not spread, despite the fact that the signalling equilibrium (i.e. one in which all chicks beg) was predicted according to Godfray’s equations to be stable. Comparable objections have been raised by Bergstrom & Lachmann (1997) with respect to the Sir Philip Sydney game played between relatives (Maynard Smith, 1991; Johnstone & Grafen, 1992).

Godfray’s aim was to demonstrate the handicap theory to be a viable explanation of offspring begging behaviour, and so he only examined the signalling equilibrium. The stability of the non-signalling equilibrium was not considered. Here we examine the stability of the non-signalling equilibrium for the general case, in order to determine a necessary condition for signalling behaviour to arise in the first place. From the analyses it is shown why a pre-existing bias in the parental response can be, but is not necessarily required for the evolutionary initiation of signalling behaviour. This then allows us to delineate those circumstances under which there is a need for pre-existing receiver

responsiveness in the ancestral state, as hypothesised by Rodríguez-Gironés *et al.* (1996). The receiver responsiveness could exist for a number of reasons, for example as a result of a sensory bias (Ryan, 1990; Arak & Enquist, 1993), or as a pre-adaptation in response to inter-young aggression.

Here we are concerned only with that component of solicitation that might constitute a handicap signal. This does not preclude the possibility that other components of begging reflect other factors, such as age, interchick conflict, or merely that the offspring is awake. In places we draw on the language of avian begging (that being the area in which the majority of studies have appeared) but this should not be taken to imply any restriction to the avian. The formulation used is more general than that of Godfray (1991) in order that the invasion behaviour can be properly investigated.

Suppose that at each feeding event an offspring with quality q begs at level $x(q)$, and the parent that perceives the begging responds with provisioning amount $y(x)$. Let the increment in payoff to the offspring following each event be some function $f(q, x, y)$; and the decrement to the parental fitness (that is, parental fitness excluding that attributable to the current focal offspring) be $-j(y)$. We let the expected overall parental fitness in the absence of the current offspring be G_0 . By definition begging is costly, so $f_x \leq 0$, and provisioning is beneficial to the young, so $f_y \geq 0$ (subscripts denote partial differentials). We assume, without loss of generality, that q is defined such that $f_q \geq 0$. The decrement in parental fitness exclusive of the focal offspring, is greater under increased provisioning supplied to the focal offspring so that $j_y \geq 0$. Over a number of such encounters, the inclusive fitness for the parent is

$$U[y(x)] = r_p \left\{ \int p(q) f(q, x, y) dq + G_0 - \int p(q) j(y) dq \right\} \quad (1)$$

and for an offspring is

$$W[x(h)] = \int p(q) f(q, x, y) dq + r_s [G_0 - \int p(q) j(y) dq] \quad (2)$$

where r_p is the relatedness of parent to chicks, r_s is the relatedness between sibling chicks, and the

function $p(q)$ is the normalised probability density function of offspring qualities. For the offspring the aim is to optimise the begging function $x(q)$ so as to maximise W for given $y(x)$. For the parent the aim is to optimise the provisioning function $y(x)$ so as to maximise U for given $x(q)$.

For the time being let us assume that at the full-signalling equilibrium $x(q)$ is monotonic decreasing (in fact this simplification is not necessary, but it prevents us from becoming submerged in excessively long equations). This permits (1) to be rewritten as an integral over x . Thus

$$U[y(x)] = r_p \left\{ \int P(q(x)) [f(q(x), x, y) + G_0 - j(y)] dx \right\} \quad (3)$$

For convenience we define $g(y) = G_0 - j(y)$. To find optimal $x(q)$ and $y(x)$ one can use basic calculus of variations methods. For the current system this simply requires solution of

$$f_y + g_y = 0 \text{ for all } q \quad (4)$$

$$f_x + \frac{dy}{dx} [f_y + r_s g_y] = 0 \text{ for } x > 0 \quad (5)$$

These last two equations are similar to those in Godfray (1991). This does not, however, mean that the two systems are equivalent. As soon as one considers a situation in which some subset of the population does not beg, the integral present in eqn (1) must be taken into explicit consideration. This is the basis of the following section.

Notice that we have referred to the young as having a ‘‘quality’’, rather than the more conventional term ‘‘need’’. To call begging a signal of need implies that the signal increases for young of intrinsically lower fitness (i.e. $dx/dq \leq 0$). But this is an unnecessary restriction. Handicap signals can equally well evolve if the signal is of some condition correlated with higher intrinsic fitness (i.e. if $dx/dq \geq 0$), such as, for example, a signal of immunocompetence, or of ‘‘good genes’’ *per se*.

When can Begging Invade?

We assume the ancestral state to involve no active offspring begging. Thus, to examine a

necessary condition for signalling to arise, the stability properties of a non-signalling state need to be determined. Assuming that $x(q) = 0$ for all q , and that $y(0) = y_0$, then eqn (3) at $x = 0$ is

$$\int_{q_{\min}}^{q_{\max}} p(q)[f_y(q, 0, y_0) + g_y(y_0)] dq = 0 \quad (6)$$

and is undefined for $x > 0$. For the young we need to examine the sign of $\partial w(q, x = 0, y = y_0)/\partial x$, for given $y(x)$ (and hereafter we will refer to r_s simply as r). Substituting from (4), we find that

$$\partial w/\partial x = f_x(q, 0, y_0) + k\phi \quad (7)$$

where $k = dy(x = 0)/dx$, and $\phi = f_y(q, 0, y_0) - r \int p(q)f_y(q, 0, y_0) dq$. In order to demonstrate the possibility that signalling behaviour can invade, we only have to show that $\partial w/\partial x$ is positive for at least some value of q . From the definition of ϕ , it is clear that there will always be a range of values of q for which ϕ is positive. Recall that, by definition, $f_x \leq 0$. Thus the first term on the right-hand side of (7) is negative (or zero), whereas the second term on the right-hand side can be positive when $k > 0$. This allows us to describe two ways in which signalling can evolve.

(a) Without receiver bias:

signalling can evolve without the aid of ancestral receiver bias, provided the slope of the cost of signalling tends to zero as the signal tends to zero. Note that the parameter k is the slope of the parental response to small signals. If this is large we identify the parent (receiver) as having a pre-existing bias. (For this label to not be trivial, “large” must be defined relative to the typical phenotypic variance of mutant receivers—i.e. to be considered a bias, k must be large enough that it could not be obtained as a mutation of $k = 0$, or vice versa.) Thus, to examine a putative ancestral state with no bias, we investigate the stability of a non-signalling equilibrium subject to perturbations restricted to k close to zero. But if k is close to zero (hence $k\phi$ likewise) then the only way to permit the possibility of $\partial w/\partial x$ being positive is if $f_x(q, 0, y_0)$ is also small. Put formally, if k is perturbed in the neighbourhood of zero, then $\partial w/\partial x > 0$ can only be attained if $f_x(x \rightarrow 0) \rightarrow 0$.

(b) When receiver bias is required:

if the shape of the cost of signalling is always negative, even for small signals, then signalling can only evolve if there is sufficient ancestral receiver bias. If $f_x(x = 0) < 0$ then it is only possible for $\partial w/\partial x$ to be positive if $k\phi$ exceeds the threshold value $k\phi > -f_x(x = 0)$. This is not possible if k is being perturbed about zero. The initial value of k needs to be positive, and the more so the more negative $f_x(x = 0)$. In other words, having $f_x(x = 0) < 0$ presents an adaptive barrier which can only be surmounted if the parental responsiveness or bias in the ancestral state exceeds some threshold.

Figure 1(a) illustrates the situation under the explicit functional forms used by Godfray (1991) and by Rogríguez-Gironés *et al.* (1996) and (1998). Invasion of the signalling behaviour is only possible in regions where $\partial w/\partial x > 0$. The plot shows how, when $k = 0$ there are no values of q for which this is possible (because $f_x = -V$ is negative). In this case, signalling can only evolve if there is enough bias in the receiver that $k > 0.72$ (approx.). In contrast, consider Fig. 1(b), which uses the same equations with only one small change (see figure caption), such that $f_x = -2Vx$ is zero when $x = 0$. In this case no receiver bias is required, since $\partial w/\partial x$ is positive for at least some values of q even for very small k .

A METHOD FOR IDENTIFYING THE ANCESTRAL THRESHOLD

An unexpected advantage of our model is that it can, in principle, be combined with observation of a contemporary equilibrium to provide evidence on whether a threshold criterion pertained for the ancestral state.

As we have just seen, the slope of signal cost for small signals, $f_x(x = 0)$, is critical in determining the presence of the required threshold in the ancestral receiver bias. When $f_x(x = 0)$ is zero, so is the threshold. The critical value of $dx(0)/dx$ that must be exceeded for invasion to occur is $dy(0)/dx_{\text{threshold}}$, which is obtained from eqn (7):

$$\frac{dy(0)}{dx}_{\text{threshold}} = -f_x(q_{\min}, 0, y_0)/\phi \quad (8)$$

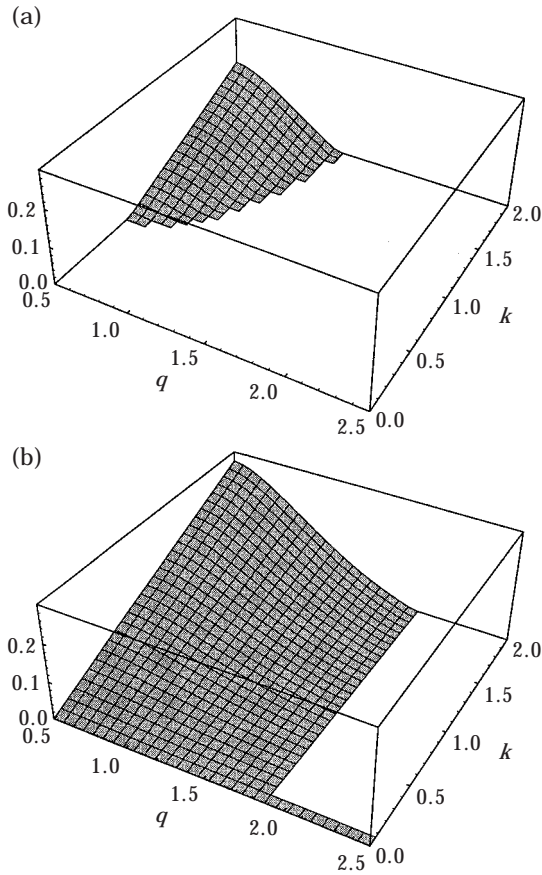


FIG. 1. Stability of a non-signalling ancestral state. The vertical axis gives $\partial w/\partial x(x=0)$ calculated for an equilibrium in which no young signal using (6) and (7). The parameter $k = dy(x=0)/dx$ is the selectively neutral receiver response (at non-signalling equilibrium), which may be positive either from drift or from sensory bias, say. For any value of q for which $\partial w/\partial x > 0$, the non-signalling state is unstable and signalling behaviour can invade: (a) explicit forms, following Godfray (1991): $f(q, x, y) = 1 - e^{-qy} - 0.1x$, $g(y) = 1 - 0.08y$. The probability density function of young qualities, $p(q)$, was taken to be uniform over the range $0.5 < q < 2.5$. Here $\partial w/\partial x > 0$ only for $k > 0.72$. Thus in this case some sort of receiver bias is required for signalling to invade; (b) as for (a), except $f(q, x, y) = 1 - e^{-qy} - 0.1x^2$. Here $\partial w/\partial x > 0$ for all values of q , even for very small k . Thus in this case signalling will always invade, even without receiver bias.

Compare this to the value of $dy(0)/dx$ apparent at a full signalling equilibrium, $dy(0)/dx_{ESS}$ which is obtained from solving eqns (4) and (5) simultaneously at $x = 0$. That is,

$$\frac{dy(0)}{dx}_{ESS} = f_x(q_{max}, 0, y(0)) / [(1-r)g_y(y(0))] \quad (9)$$

But for the explicit fitness functions used by Godfray (1991), f_x is independent of q and y , and

so $f_x(q_{max}, 0, y(0)) = f_x(q_{min}, 0, y_0) = f_x(x=0)$. This allows us to combine (8) and (9) to get

$$\frac{dy(0)}{dx}_{threshold} = \frac{dy(0)}{dx}_{ESS} (1-r)g_y(y(0))/\phi$$

The point here is that this is simply of the form

$$\frac{dy(0)}{dx}_{threshold} = \frac{dy(0)}{dx}_{ESS} \times \text{constant} \quad (10)$$

Because there is a direct linear correlation between $dy(0)/dx_{ESS}$ and $dy(0)/dx_{threshold}$ this gives a method for deducing ancestral constraints based on contemporary behaviour. Naturally, in a real experimental situation, one would not know the value of the constant of proportionality. But nonetheless, if for example one were to observe the slope of parental response for small $(dy(0)/dx_{ESS})$ to be zero (e.g. solid line of Fig. 2), then the ancestral threshold $(dy(0)/dx_{threshold})$ must also have been zero. That is, we deduce that in such a case no initial parental bias was needed to originate the evolution of begging. Contrastingly, if the observed slope is positive (e.g. dashed line in Fig. 2) then the threshold must have been positive, and in this case one would deduce that some sort of sensory bias or other exaptation must have been needed to initiate the

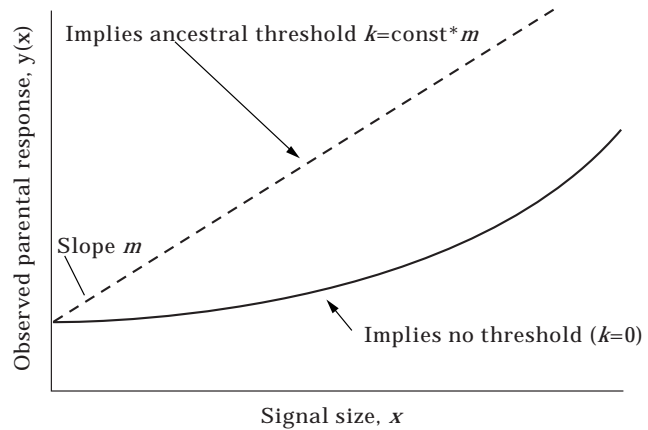


FIG. 2. An experimental approach to investigating the preference threshold. We predict that the ancestral preference threshold is proportional to the currently observed parental behaviour [equation (10)]. Here two fictional examples are shown. For the example represented by (---) (which has positive slope m for small signals) the threshold is deduced to be positive. For the example represented by (—) the response curve is flat for small signals, implying a zero threshold. In this latter case sensory bias would be unnecessary in the evolution of handicap begging signals.

spread of begging behaviour. This inference assumes only that the form of the costs to chick fitness $f(q, x, y)$ has not changed.

Godfray (1991) determined the behaviours that under his model gave both young and parents the best response against each other, but it was not demonstrated whether the equilibrium could be invaded by simultaneous mutations in chick and parent. Rodríguez-Gironés *et al.* (1998) examined this problem using computer simulations. They found that under some circumstances the signalling equilibrium was not stable. They found, furthermore, that this stability depended on whether the signalling interaction was considered as a single-encounter game (for which the full-signalling equilibrium was unstable) or as an iterated game (for which the full-signalling equilibrium was unstable). Both in the simulations of Rodríguez-Gironés *et al.* (1998) and in the current work, the presence of the integral in eqn (1) appears to be critical. We suggest that a proper examination of the stability of signalling systems will require study of the role of partial-signalling equilibria (part signalling, part non-signalling). This depends on considering an integral over a subset of q in a similar manner to that in the analysis presented here (although in a less straightforward way). It appears therefore that a full understanding of begging behaviour must address factors such as to what extent the game is iterated (i.e. what exactly the integral represents), and whether signal mutations typically affect the behaviour for one quality or for a range thereof (phenotypic extent of mutations).

Discussion

Recent concerns over the evolutionary pathways for signalling between relatives (Yachi, 1995; Rodríguez-Gironés *et al.*, 1996, 1998; Bergstrom & Lachman, 1997) have helped bring attention to the neglected question of how handicap begging arises in the first place. The simulations of Rodríguez-Gironés *et al.* (1998) found that, even when signalling was predicted to be stable, begging did not invade an initially non-signalling state. This was suggested to be a challenge not just to the theory of parent-offspring begging, but to the theory of handicap

signals in general. Our results partially resolve this problem by exposing the role of thresholds in the evolution of “handicap” begging. A parallel result obtains in relation to handicap theories of sexual selection (Payne & Pagel, manuscript). We have shown that for signalling behaviour to be evolutionarily accessible, from a non-signalling ancestral state, requires either that the slope of the signalling costs tends to zero for very small signals [$f_x(x=0) = 0$], or that there is a sizeable pre-existing receiver responsiveness [$dy(0)/dx > \text{threshold}$]. For the simulations of Rodríguez-Gironés *et al.* (1998) the functions and parameter values used, following Godfray (1991), were such that a threshold did exist—and the initial perturbations were not sufficient to overcome this threshold.

The adaptive barrier presented by the threshold needs to be overcome for begging to evolve. Rodríguez-Gironés *et al.* (1996) posited that exploitation of sensory biases could provoke signal evolution. As Rodríguez-Gironés *et al.* pointed out—at the non-signalling equilibrium the receiver response to signals is selectively neutral [$y(x)$ is undefined for $x > 0$], and so a bias could evolve by neutral drift. Alternatively, the parent might have been previously adapted to respond to competitive behaviour between chicks in a multi-chick brood. In this case, the signalling of need (or quality) would be considered an exaptation derived from the adaptation for direct resource competition. The results of the present work suggest this route is not a prerequisite in the evolution of offspring begging.

Although our work explains the apparently paradoxical invasion behaviour found by Rodríguez-Gironés *et al.* (1998), it does not explain the other problematic feature of their simulations—that stability of the signalling equilibrium depends on the number of iterations of the begging game carried out within each breeding season. We suggest that this is because analysing stability of a full-signalling equilibrium requires consideration of the behaviour of nearby partial-signalling equilibria; and this in turn will depend explicitly on the nature of integration of the distribution of offspring qualities over a population, and thus also on the nature of the possible mutations or

recombination, and of the behavioural “encoding” involved. Experimental evidence concerning these aspects must in future be examined more closely and modelled more carefully.

There are many studies of avian solicitation that have indicated begging intensity to be correlated with food deprivation, for example in pigeons (Mondloch, 1995), magpies (Redondo & Castro, 1992) and yellow-headed blackbirds (Price & Ydenberg, 1995); vocalisation can also be correlated with temperature, as has been noted in pipped eggs of white pelican (Evans, 1990) and ring-billed gulls (Evans *et al.*, 1994). Such experiments are looking at an intrinsically dynamic situation. Once the resource is supplied the need is satiated (or at least alleviated); after feeding, need gradually increases again. In this respect, current models need careful interpretation when being applied to signals of need. Suppose that the fluctuation of need is mimicked by allowing q to be a dynamical variable: q is augmented by some amount every time the offspring is fed, then $q = q(t)$ declines monotonically with time, until the parent returns with more food. Thus $p(q)$ can be viewed as synonymous with the probability distribution of parental return times. But in what way might such short-term dynamics of need interact with any longer-term level of “base-rate” quality—especially in light of the observation that iterated (e.g. when signals are short-term) games and one-off (e.g. when signals are long-term) games are liable to yield different behaviours? The results of Price *et al.* (1996) support the notion that solicitation magnitude can be comprised of both a dynamic short time-scale signal of need and a more consistent longer time-scale signal of intrinsic quality. Understanding whether begging is a cost-maintained handicap signal would seem to require the two to be teased apart.

An interesting contrast is the mammalian foetus–mother interaction, in which there is a comparable genetic conflict over resources (Haig & Graham, 1991; Haig, 1993). In these, the biochemical exchanges are continuous (as opposed to the discrete packages of food delivered by parent birds) and so the dichotomy of need/quality time-scales should be much less apparent, and thus temporal fluctuations less of an issue. Moreover, the mother, presumably,

cannot use alternative, non-signalling traits as cues. The same arguments apply to the chemical signals used to mobilise maternal resource allocation to seeds in angiosperms (Ravishankar *et al.*, 1995). These aspects may make biochemical mother–offspring signalling systems more open than avian systems to testing of the handicap principle.

The arguments presented here point to a number of aspects of begging that require greater experimental focus. We have already indicated the usefulness of measuring the slope of parental response to low intensity signals, and the need to determine the way in which payoffs for different qualities/needs are integrated into fitness for a single individual. It is worth noting that apart from the threshold in slope of parental response, there could also be thresholds in absolute response—and so the two need to be experimentally distinguished. There is an important dichotomy here. The slope threshold arises from the form (i.e. constraint) of the chick fitness costs, whereas an absolute threshold depends on a constraint on the parent. Putative absolute thresholds could arise for a number of reasons—not just from physiological constraints, such as minimum resolution levels, but also adaptively, for example to cope with noise in the system such as from perceptual error (Johnstone, 1994). We would therefore additionally encourage studies to investigate whether the parent only responds to begging above a certain magnitude. Moreover, does the begging of chicks involve a discontinuous jump in magnitude between non-signalling and signalling (resolving this will need both more detailed time series, and paying attention not just to average but to individual chick behaviour)? And if so, parents need to be tested by somehow being presented with a signal within the range of that jump.

Given the ubiquitous presence of begging in animals with parental care, one might argue that the invasion threshold must always be zero. This can be investigated experimentally using the method that we have outlined. If measurements of the parental response to begging of minimal magnitude show a curve that becomes flat as the signal tends to zero, then we have reason to believe that no ancestral threshold had to be overcome for begging to arise. The principle here

is that observation of contemporary minimal signals can point to the form of the cost functions involved, and those cost functions then tell us whether evolution of costly begging required the helping hand of a pre-existing receiver response. We therefore recommend that measurements of parental responses to minimal levels of offspring signalling (rather than to more average sized signals) must be made if the evolutionary origins of offspring–parent signals are to be understood.

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