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Begging and bleating: the evolution of parent–offspring signalling

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The evolution of biological signalling in the face of evolutionary conflicts of interest is an active area of evolutionary ecology, and one to which Maynard Smith has made important contributions. We explore the major theoretical challenges in the field, concentrating largely on how offspring signal to their parents when there is the potential for parent–offspring conflict. Costly offspring solicitation (begging etc.) has been interpreted in terms of a Zahavi–Grafen honest handicap signal, but this has been challenged on the grounds of the costs of signalling. We review this controversy and also explore the issue of pooling versus separating signalling equilibrium. An alternative explanation for costly begging is that it is due to sibling competition, and we discuss the relationship between these ideas and signalling models in families with more than one offspring. Finally we consider signal uncertainty, how signalling models can be made dynamic, and briefly how they may be tested experimentally.

Keywords: parent–offspring conflict; sibling conflict; signalling; evolutionarily stable strategy; game theory

1. INTRODUCTION

The battle of Zutphen in 1586 had little impinged on the consciousness of evolutionary biologists until it was brought to their attention by Maynard Smith (1991). The battle was a relatively minor engagement in the long series of wars during which the emergent protestant United Provinces of what is now The Netherlands tried to shake off the yoke of catholic Spain. At that time, English policy to continental Europe was as confused and contradictory as it is today. The protestant Elizabeth I of England had sent an expeditionary force to the low countries, but had refused to finance it properly. However, this did not stop the romantic element of the younger aristocracy from volunteering for glory in the cause of their faith; and none came more romantic than the poet, soldier and paragon of renaissance chivalry, Sir Philip Sidney. At Zutphen he disdained upper-leg armour seeing that a colleague had forgone his, and sustained a serious wound to the thigh, from which he died 26 agonizing days later. He was only 31. Lying wounded on the battlefield, he was offered water, but gave it to another more severely injured soldier saying 'thy need is greater than mine'. Maynard Smith (who was not, as is widely believed, present himself on the battlefield) used this legendary example of altruism as the basis of a game theory model of the signalling of need between relatives. The 'Sir Philip Sidney game' seeks to explore how individuals with overlapping but not identical genetic interests can communicate information using costly signals in the face of potential within-family genetic conflict.

The idea that signal costs are critical to the evolutionary stability of signalling systems is due to Zahavi (1975, 1977*a*), although it was a pair of papers by Grafen (1990*a*,*b*) that established the theoretical framework upon which most recent analyses have been based. Grafen concentrated on signals of quality such as males displaying their prowess to potential mates, and attempted a general characterization of the signalling equilibrium, couched in coloratura mathematics. Maynard Smith (1991) introduced the Sir Philip Sidney game as a relatively straightforward model to investigate the evolution of signalling, in this case of need rather than quality, while Godfray (1991) used Grafen's ideas to investigate signalling of need between offspring and parent. The original Sir Philip Sidney game assumes the donor and recipients to have discrete levels of need, but Johnstone & Grafen (1992*a*) relaxed this assumption to create the continuous Sir Philip Sidney game, the basis of much subsequent work.

The aim of this paper is to explore and comment upon recent developments in signalling theory, concentrating on signals of need and, in particular, signals made by offspring to their parents. We begin by describing the biological motivation for this work, and review a basic model of offspring begging. We then critically discuss the suggestion that most evolutionarily stable strategy (ESS) signalling systems are less efficient than not signalling at all, and go on to derive pooling equilibria for begging models, in which there is no longer a unique relationship between signalling level and offspring state. We also discuss the issues of signal uncertainty, signalling in large families, and moving from a static to a dynamic theory of signalling. We finish by highlighting the areas where new work is needed, and how the theory may better serve the needs of experimental biologists.

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2. BEGGING FOR FOOD

(a) *Why is begging costly?*

Young chicks beg food from their parents in ways that seem extravagant in terms of the noise produced and the energy expended. Similarly, young mammals often demand resources from their parents by screaming, bleating or crying, and sometimes by direct tussling. Trivers (1974) pointed out that these behaviours seemed inconsistent with traditional notions of the family as a harmonious evolutionary unit, but could be explained by the kin selection theory that had recently been propounded by Hamilton (1964). Parents and young are obviously related but are not genetically identical, and hence there is the possibility that selection acts in subtly different ways on genes expressed in offspring and parents. Trivers suggested that genes in the former may cause the young to misrepresent their need, in effect to attempt psychologically to manipulate their parents into giving them extra food. At about the same time Zahavi (1977*b*) suggested that offspring may deliberately endanger themselves to force their parents to provide extra resources, a type of blackmail.

These potent verbal metaphors were given mathematical flesh in a series of papers by Parker & Macnair (1978, 1979; Macnair & Parker 1978, 1979; Parker 1985). They assumed that parents responded to higher levels of begging by providing more food, and that offspring begged less if fed more (these responses were fixed and themselves did not evolve). At evolutionary equilibrium, costly begging was observed, and the amount of resources obtained by the offspring was intermediate between the parental and offspring optima. Macnair & Parker (1979) also added sibling to parent–offspring conflict and showed that in families with more than one offspring, costly begging might arise if young competed amongst themselves with the parent more likely to feed the winner. All of the Parker & Macnair models were explicitly genetic, typically with two biallelic loci determining offspring and parent behaviour, but the same results can be obtained using a kin selection approach (Godfray & Parker 1992).

Prior to Trivers, most people had assumed begging was a means by which offspring communicated their resource requirements to their parents. But this idea was dropped in the face of the genetic conflicts of interest identified by Trivers (1974). The Parker & Macnair models, for example, assumed all offspring to have identical resource requirements. Signalling models resurrect the idea of begging as communication, and simultaneously explain why begging is evolutionarily stable in the face of conflicting genetic interests and also extravagant and costly. It is the costliness of the signal that prevents its misuse, as argued by Zahavi (1975, 1977*a*). In the simplest signalling model, young differ in a factor that has been called hunger, condition or need, but which might be better referred to as just state, that reflects the value of extra resources to them (Godfray 1991). Young with a low value of state benefit to a greater degree from additional resources than those with a high state value. It is assumed that the offspring's state cannot be directly perceived by the parent. At the ESS, young signal at a level that has a one-to-one correspondence with their state, and parents use this information to allocate an appropriate (from their point of view) amount of resources. The signalling system is stable because the advantages to an individual offspring in a certain state of misrepresenting its needs, and hence getting more food, is exactly balanced by two types of cost. First, the costs of signalling at a higher level, and second, the inclusive fitness of costs of depriving food from relatives (either nest-mates or future unborn siblings). It is the necessity for these costs and benefits to balance each other that determines the shape of the function relating signalling levels to need. Thus signalling models predict the parent wins the parent–offspring conflict in the sense that the amount of food an offspring receives is the parental optimum, but the parent wins at a price. The price is that for a communication system to be evolutionarily stable in the face of parent–offspring conflict it must be costly.

(b) *A formal framework*

Consider a species that produces a single offspring each breeding season and is reared by a single parent. We divide the season up into a series of feeding episodes that have independent effects on the final fitness of offspring and the parent at the end of the breeding season (in other words we 'assume away' the dynamic aspects of rearing a young). At the beginning of each episode, the young is in a cryptic state, c, that cannot be perceived directly by the parent. The benefits of extra food come with decreasing returns, and young with a high value of the parameter c gain relatively less from being given extra food than those with a low value. Providing more food to the present offspring is costly to the parent in terms of its future reproductive success (perhaps the weight of the parent at the end of the season reflects its cumulative effort in foraging for its offspring, and its weight determines its probability of surviving to breed again).

We now state a candidate ESS signalling system and then prove its stability. Let offspring in state c produce a costly signal $x^*(c)$ that uniquely reveals its state; and parents respond to a signal of intensity x by providing offspring with an amount of food $y^*(x)$. Because the offspring signal provides an unambiguous indication of state, we can write the parental response as $y^*(x^*(c)) = \tilde{y}(c)$.

Let $g(y)$ be the personal future fitness of a parent that feeds its young an amount y during the current feeding episode. The parent's residual fitness declines as it feeds the current young more (i.e. $g_y = g_y(y) < 0$, where here and throughout a subscripted function means the derivative with respect to the subscript, and the function arguments are often omitted where unambiguous). Offspring fitness is $f(x, y, c)$ where more food leads to increased fitness and higher levels of signalling to decreased fitness ($f_x < 0$, $f_y > 0$, $f_{cy} < 0$). Finally, let r be the coefficient of relatedness of the current offspring to its parent's future offspring. We can now write W_{P} and W_{O}, the inclusive fitness of the parent and offspring:

$$W_{\mathrm{P}}(x, y, c) = f(x, y, c) + g(y),$$
$$W_{\mathrm{O}}(x, y, c) = f(x, y, c) + rg(y).$$

These equations show that the source of the parent–offspring conflict is the relative weighting that parents and offspring accord to current versus future young. The formal conditions for the Nash equilibrium that defines the ESS are then

$$W_{\mathrm{O}}(x^*(c), \tilde{y}(c), c) \geqslant W_{\mathrm{O}}(x, y^*(x), c) \text{ for all } c, x;$$
$$W_{\mathrm{P}}(x^*(c), \tilde{y}(c), c) \geqslant W_{\mathrm{P}}(x^*(c), y, c) \text{ for all } y.$$

In addition, a boundary condition is required. Young in the highest state (c_{h}) should not signal.

An assumption that considerably simplifies the mathematics is that the benefits of resources and the costs of signalling combine additively to determine fitness, say $f(x, y, c) = u(y, c) + v(x)$. In that case, the optimum resource distribution for the parent is implicitly given by the marginal value relationship $u_y + g_y = 0$. Were the young to have its way, its optimal resource distribution would be given by $u_y + rg_y = 0$, but it can only act through altering its level of signalling, and hence its optimum is governed by $(u_y + rg_y)(\mathrm{d}y/\mathrm{d}x) + v_x = 0$. The term $(\mathrm{d}y/\mathrm{d}x)$ in this expression represents the effectiveness of offspring begging in soliciting food. At the ESS we can substitute $u_y = -g_y$, separate variables and integrate to obtain

$$x^*(c) = K + (1-r)g(\tilde{y}(c)),$$

where K is a constant of integration. Because young in the highest state do not signal $x^*(c_{\mathrm{h}}) = 0$, we can solve for K to obtain

$$x^*(c) = (1-r)[g(\tilde{y}(c_{\mathrm{h}})) - g(\tilde{y}(c))] = (1-r)Z.$$

In this interpretation, due largely to Nöldeke & Samuelson (1999), the ESS level of signalling for an offspring in state c is such that the costs incurred through signalling ($x^*(c)$) are $(1-r)$ times the extra costs ($g(\cdot)$) incurred to the parent through feeding at the rate appropriate to a state c offspring ($\tilde{y}(c)$) compared to a c_{h} offspring in the highest possible state and hence requiring the least amount of food ($\tilde{y}(c_{\mathrm{h}})$). A concrete example of these results is given in figure 1.

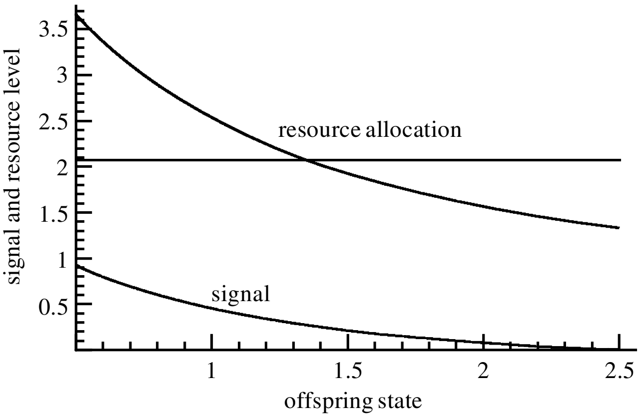

Figure 1. ESS levels of signalling and resource allocation for the basic signalling model with one offspring (separating equilibrium). The lower curve is the level of offspring signal, and the upper the optimum resource allocation for the parent. The horizontal line is the optimum resource allocation for the parent in the absence of any information about individual offspring state (and assuming a rectangular distribution of offspring states between 0.5 and 2.5). The ESS assumes $u(y, c) = 1 - \exp(-cy)$; $v(x) = vx$, and $g(y) = G - \gamma y$, with $v = -0.1$, $G = 1$, $\gamma = 0.08$ and $c_{\mathrm{h}} = 2.5$.

3. THE COST OF SIGNALLING

The early models of signalling between offspring and parent tacitly assumed that the fitness of the parent at the ESS would be higher than the situation when no signalling took place and the parent always gave its offspring the same amount of food (Godfray 1991). However, as pointed out for the chick model by Rodríguez-Gironés *et al.* (1996) and for the Sir Philip Sidney game by Bergstrom & Lachmann (1997), this need not be so. This observation does not mean that the signalling equilibrium is unstable—no single mutation in either the parent's or young's strategy can invade a population at the equilibrium—but it does call into question whether any population will evolve a signalling system that entails a reduction in overall fitness. Is costly signalling between parent and offspring akin to the 'paradoxical' ESSs observed in hawk–dove and similar discrete strategy games, technically stable but never likely to be seen in nature?

In fact the case against costly signalling is not as dire as first appears. First, we digress briefly to state how the costs of signalling and non-signalling are calculated. The costs of these different strategies are obviously influenced by the probability distribution of offspring states which do not actually come into the calculation of the optimal levels of signalling. If we say that offspring states lie in the range $c_{\mathrm{l}} \leqslant c \leqslant c_{\mathrm{h}}$ we can write this probability distribution $p(c)$. Using this probability distribution we can easily calculate $\bar{y}$, the optimum amount of food a parent should give its young in the absence of any information about its individual state (though with knowledge of $p(c)$). We can now compare expected parental fitness with no signalling,

$$\langle W_{\mathrm{P}} \rangle_0 = \int_{c_{\mathrm{l}}}^{c_{\mathrm{h}}} W_{\mathrm{P}}(x = 0, y = \bar{y}, c)p(c)\mathrm{d}c,$$

with expected parental fitness at the signalling equilibrium

$$\langle W_{\mathrm{P}} \rangle_{\mathrm{S}} = \int_{c_{\mathrm{l}}}^{c_{\mathrm{h}}} W_{\mathrm{P}}(x = x^*(c), y = \tilde{y}(c), c)p(c)\mathrm{d}c.$$

We follow Rodríguez-Gironés *et al.* (1996) and calculate a quantity ΔW_{P} which is the expected percentage increase in parental fitness if the population changed from signalling to non-signalling.

For the original equations and parameter values used by Godfray (1991; see legend to figure 1), and assuming that offspring in all states between $c_{\mathrm{l}} = 0.5$ and $c_{\mathrm{h}} = 2.5$ are equally likely to occur, $\Delta W_{\mathrm{P}} = 0.8$ (Rodríguez-Gironés *et al.* (1996) give a figure of 1.6, see legend to figure 2). Thus there is a *ca.* 1% fitness advantage in leaping from the signalling to the non-signalling equilibria. Although this is not a huge difference, it is nevertheless a significant tax and one sufficient to question the existence of costly signalling. The distribution of chick states influences the advantages of switching, if low-state chicks are more abundant signalling is more expensive (with $p(c)$ left triangular $\Delta W_{\mathrm{P}} = 1.8$), but it is less expensive if high-state chicks are commoner (with $p(c)$ right triangular $\Delta W_{\mathrm{P}} = 0.4$). The benefits of non-signalling also increase with higher costs of reproduction.

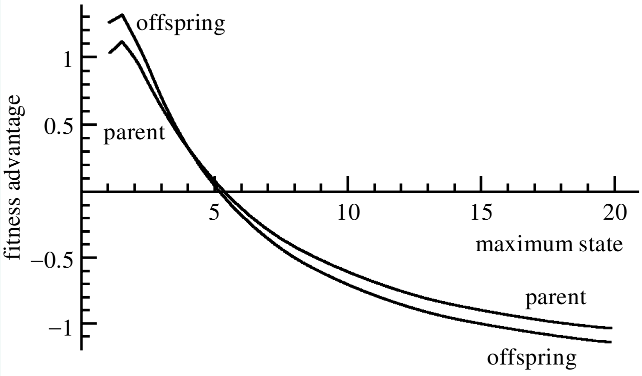

Figure 2. The percentage change in fitness that the parent or offspring would experience if a switch occurred in the type of signalling equilibrium shown in figure 1 to not signalling at all. Equations and parameters as in figure 1 with offspring state rectangularly distributed between 0.5 and the maximum state indicated on the horizontal axis. Below *ca*. 5, refraining from signalling is more efficient, above this figure signalling has higher fitness. (In comparison with Rodríguez-Gironés *et al*. (1996), our values for $c_h = 2.5$ are slightly lower and we believe that they assumed $G = 0$. The advantage of signalling for $c_h > ca.$ 5 is unaffected by the value of G.)

Rodríguez-Gironés *et al*. (1996) followed Godfray (1991) in assuming $c_l = 0.5$ and $c_h = 2.5$. However, these limits were chosen for convenience rather than for any biological reason and c_h in particular can be much larger and even approach infinity (this does not of course imply a super-fit chick, just one that gets no extra benefit from more than the absolutely smallest amount of food). Figure 2 shows how the benefit of switching from signalling to non-signalling changes as c_h varies in the range 1–20 (assuming a rectangular $p(c)$). As Rodríguez-Gironés *et al.* (1996) found, signalling is relatively expensive for low values of c_h but once c_h exceeds a value of about 5 the non-signalling equilibrium has a lower fitness.

Why does increasing the range of chick states reduce the relative cost of signalling? Compare figure 1 with $c_h = 2.5$ and figure 3 with $c_h = 20$. In both figures the amount of food that the parent would be selected to provide in the absence of signalling ($\bar{y}$) is plotted as a horizontal line. With greater variance in offspring state there is a larger average mismatch between this non-signalling value and the particular optimum for the individual offspring. The non-signalling parent provides excess food to many offspring that require very little food, and substantially underfeeds the offspring in the lowest state. The increased range of offspring states also leads to a greater variance in signalling levels, with the lowest-state chicks having to signal more, though this effect is relatively small and not enough to counter the advantages of signalling to more efficient resource distribution.

We conclude from this that there will be many situations where a signalling equilibrium will have a higher fitness than a non-signalling equilibrium. For the model based on the specific equations in Godfray (1991) this occurs simply when there is high variance in chick states, but we note that there are many other ways to model the value of parental care and so generalizations must be made with care. Rodríguez-Gironés *et al*. (1998; see also Payne & Rodríguez-Gironés 1998; Rodríguez-Gironés *et al*. 1996) conclude that lower signalling fitness is 'the norm rather than the exception' and that the seemingly ubiquitous presence of begging as a signal of need is thus a 'paradox'. These conclusions seem premature.

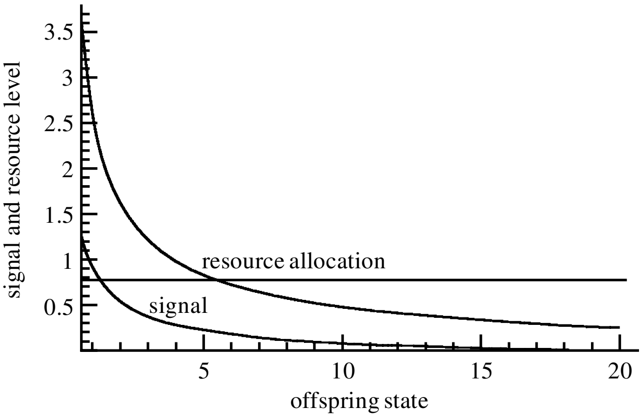

Figure 3. As in figure 1 but highest-state offspring $c_h = 20$.

Where signalling is more expensive than non-signalling should we expect no signalling to occur? As will be discussed in § 4, it is now clear that there is more than one signalling equilibrium, and so the costs of these other 'pooling' alternatives need to be considered. For broods of more than one offspring, costly begging may involve interactions between siblings in the nest, a possibility we also return to in § 6. But even in the simplest case where we are considering a single offspring and non-pooling strategies, the issue is very difficult to resolve as the answer requires a knowledge of the evolutionary dynamics as well as the evolutionary end-points. To model the dynamics, a very much larger number of assumptions have to be made than when end-points alone are considered, and for this reason it is something that is undertaken relatively rarely. Rodríguez-Gironés *et al.* (1998) explored this issue using some complex simulations in which parent and offspring strategies ($x(c)$ and $y(x)$) could mutate but remained essentially smooth. The results depended on population size but showed that when signalling was more expensive (they used the model described in § 2(b) with $c_h = 2.5$), the signalling equilibrium was unstable, though even after 10 000 iterations substantial signalling was observed for large population sizes. Their results also implied that non-signalling was a stable equilibrium, though this conclusion was subsequently modified by Payne & Rodríguez-Gironés (1998). This latter paper showed that if the costs of very low levels of signalling are small, and/or if there is a sensory bias in the receiver, signalling strategies will invade the non-signalling state. These studies are important attempts to move beyond static theories to a dynamic theory of the evolution of parent–offspring signalling, but a number of technical issues need to be resolved before they can speak clearly to experimentalists.

4. POOLING SOLUTIONS

Much of recent signalling theory has followed Grafen (1990*a*,*b*) in using calculus to derive an ESS signalling system (for example, with parent–offspring signalling (Godfray 1991) and in the continuous Sir Philip Sidney game (Johnstone & Grafen 1992*a*)). While calculus successfully discovers one signalling equilibrium, it misses other strategies that are discontinuous. The demonstration that an infinite number of other signalling solutions are possible in biological signalling games is due to Bergstrom & Lachmann (1997, 1998; Lachmann & Bergstrom 1998), though there are related results in the economics literature (Kreps & Sobel 1994). Working with the continuous Sir Philip Sidney game, Bergstrom & Lachmann showed that many partitions of the signaller's state into a series of intervals within which all individuals make the same signal could be an ESS for the appropriate choice of signal. They refer to these solutions as pooling equilibria and the original continuous signalling strategy as the separating equilibrium. However, as pointed out by Bergstrom & Lachmann, and illustrated below for the offspring begging model, the pooling equilibria often share qualitative features in common with the separating equilibrium so that both can be considered 'honest, handicap' signals, though cost-free signals can also be stable (Maynard Smith 1994; Bergstrom & Lachmann 1998; Lachmann & Bergstrom 1998).

To see how a pooling equilibrium can be calculated, consider the begging model described above and assume offspring state varies in the range $0.5 \leqslant c \leqslant 10.5$. Begin by arbitrarily dividing this range into two: $0.5 \leqslant c_2 \leqslant 5.5$ and $5.5 \leqslant c_1 \leqslant 10.5$. We ask now whether there is an evolutionarily stable signalling system $\{x_1, x_2\}$ such that no chick in either interval will be selected to use the other signal (we return to the issue of out-of-equilibrium signals—neither x_1 or x_2—below). At the ESS, the parent will obtain some information that will correctly tell her which interval the offspring is in. She will respond by giving an appropriate amount of food $\{\bar{y}_1, \bar{y}_2\}$ based on this limited information (and also her global information about $p(c)$). The optimal signal for the chicks in the highest state is clearly $x_1 = 0$; the parent will always know that the highest-state chicks will make the lowest signal. To derive the value of x_2 we should concentrate on chicks with state $c_{1l} = 5.5$, right on the boundary (we write c_{1l} for the lower limit of interval 1). These offspring should be indifferent to signalling at $x_1 = 0$ and receiving $\bar{y}_1$ or signalling at x_2 and receiving $\bar{y}_2$. More formally we can solve for x_2 from

$$W_O(x_1, \bar{y}_1, c_{1l}) = W_O(x_2, \bar{y}_2, c_{1l}).$$

Exactly the same procedure can be used to calculate iteratively optimal signalling levels for any partition of offspring state, $\{c_{1l}, c_{2l}, \ldots c_{nl}\}$, beginning with $x_1 = 0$.

Figure 4 shows examples of pooling signalling equilibria for the offspring model with $0.5 \leqslant c \leqslant 10.5$. The range of offspring states has been divided into n intervals of equal length where $n = \{2, 4, 8, 16, 32, \infty\}$ the last partition actually being the original separating equilibrium. Figure 4*b* shows how the parental strategy successively homes in on the separating equilibrium as the parent gets more and more accurate information about the state of its young. The offspring strategy also approaches the separating equilibrium as the number of partitions increases, but it approaches it from below suggesting that the cost of signalling may be reduced when there are a more limited number of pooling equilibria. In particular, the sum costs of signalling for a partition into two equal intervals is particularly low.

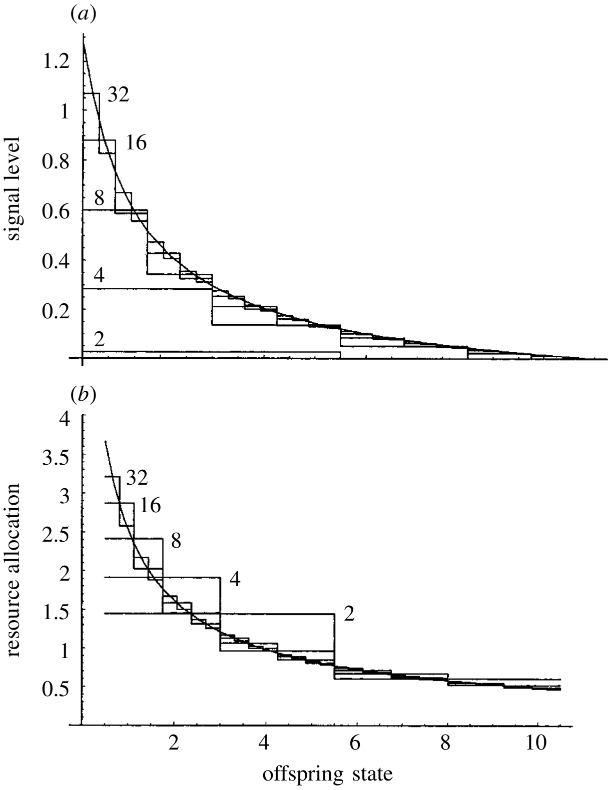

Figure 4. (*a*) Signal levels and (*b*) resource allocation for pooling signalling ESSs. The graph axes are the same as those of figures 1 and 3 but with maximum state $c_h = 10.5$. The continuous lines are the values for separating equilibrium while five pooling equilibrium (offspring state divided into 2, 4, 8, 16 or 32 equally sized intervals) are plotted on the same graph. Note that as the number of intervals increases, the signalling and resource ESSs converge on the separating equilibrium. However, while the resource allocation solution converges symmetrically, the signalling solution converges from below.

The costs of any particular pooling equilibria can be calculated by summing the piecewise integrals of parental or offspring fitness for each interval. We have assessed the costs for the same set of equal-length partitions described above, but have also explored other values of $c_h = \{2.5, 6.5, 10.5, 14.5, 18.5, 22.5\}$ keeping c_l constant at 0.5. The results are shown in figure 5 where each line represents the advantage of jumping to the non-signalling equilibrium as the number of partitions increase for a particular value of c_h. For $c_h = 2.5$ at the separating equilibrium, there is a 0.8% advantage to the switch, as calculated in §3. Reducing the number of partitions all the way to two decreases the disadvantages to signalling, but no signalling equilibrium ever has a higher fitness than non-signalling. As c_h increases beyond 5, the separating equilibrium attains a higher fitness than the non-signalling equilibrium (see also figure 2). However, in all cases the separating equilibrium has lower fitness than the pooling equilibria. For $c_h = \{6.5, 10.5\}$, the best (equally partitioned) pooling equilibrium has just two intervals, while for $c_h = \{14.5, 18.5, 22.5\}$ the best has four.

We can also explore which of a certain class of partition has the highest fitness. Consider the set of partitions

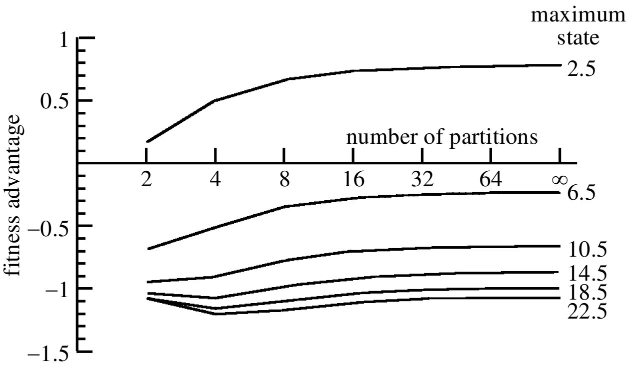

Figure 5. The percentage change in fitness that the parent would experience if a switch occurred from a pooling signalling equilibrium to no signalling at all. Seven different pooling equilibria are explored and plotted along the horizontal axis. On the left the spectrum of offspring states is equally divided into two pools and then, moving right, into 4, 8, 16, 32 and 64 equal pools. The final ∞ number of partitions is the same as the separating equilibrium. Throughout, minimum offspring state is taken to be 0.5 and curves are plotted for six values of the maximum offspring state listed on the right (the distribution of states is always rectangular).

where there are two categories of young, high and low state, with the boundary at c_{11}. We illustrate the effect of moving the boundary for the model described above where offspring state varies from 0.5 to 10.5. When the boundary is near the minimum, low-state offspring are selected to make a quite costly signal to distinguish themselves from the mass of high-state offspring. The signal is particularly costly as the young have a relatively large amount to gain. As the boundary is raised, more and more offspring are included in the low-state category and the difference in the amount of food received by the two types of young decreases. This leads to a reduction in signalling level until a point is reached (specifically when $c_{11} = 5.78$) when a cost-free signal is produced at the ESS. Overall parent and offspring fitness is maximized at this point.

Thus at least for a division into two partitions, maximum fitness is attained at a signalling equilibrium with a signal of minimum cost (see also Bergstrom & Lachmann (1998) and Lachmann & Bergstrom (1998) for similar results in the Sir Philip Sydney game). This system is more efficient than the non-signalling equilibrium. An unresolved question is whether there is a more efficient three-partition or n-partition, and if there were what signalling costs are implied.

5. UNCERTAINTY AND SIGNALLING

The chick begging model and the Sir Philip Sidney game both assume that signals are detected and assessed with perfect accuracy. Thus, at a separating equilibrium, communication eliminates all uncertainty regarding the state of the signaller. Pooling equilibria are less informative—at an ESS of this kind, the recipient of the signal knows in which interval the signaller's need lies, but not its precise level. However, this uncertainty is a consequence of the signalling strategy, not of any inaccuracy in assessment.

In reality, however, error is an inescapable feature of communication (Wiley 1983, 1994). By the time a signal reaches the recipient, it is likely to be attenuated, degraded and mixed with irrelevant background noise. Consequently, communication is unlikely to eliminate all uncertainty, even at a separating equilibrium. Signal intensity may uniquely reveal signaller state, but if it cannot be precisely assessed by the receiver, then some uncertainty will remain.

There is a large body of literature that deals with the impact of error and uncertainty on communication and signal design. Unfortunately, however, there has been little attempt to integrate this work with models of honest signalling (see Johnstone & Grafen 1992*b*; Wiley 1994). These models usually assume, for instance, that signal costs are required only for the maintenance of honesty, and ignore the possibility that more costly displays may evolve simply because they are easier to detect or to assess. Two exceptions are Lachmann & Bergstrom (1998) and Johnstone (1999), who examined the impact of error on pooling and on separating equilibria in the Sir Philip Sidney game.

Lachmann & Bergstrom (1998) allow for some probability that a signaller that gives one signal may be mistakenly perceived as giving another, and show that higher probabilities of error reduce the signal cost required to maintain honesty. The reason is simply that there is less to gain by deceptively signalling high need when the signal may not be detected. Johnstone (1998) examines in more detail the effects of error on separating equilibria, allowing for two further possibilities. First, receivers may trade off failures to respond to a signaller against inappropriate responses, so that the probabilities of these two types of error are not fixed, but can be adjusted in relation to the costs they incur. Second, signallers may reduce the expected level of error by employing more exaggerated, costly displays. In this model, increasing error generally favours more costly signals, because more effort must be expended to ensure accurate discrimination in the presence of noise. At the same time, though, signal cost will vary in relation to the distribution of signaller states. Earlier, we pointed out that in error-free signalling models, the presence of just a few high-state individuals may force the majority of individuals, in lower states, to adopt a costly display. When error is introduced, however, this problem is resolved. If high-state signallers are rare, selection will favour 'adaptive gullibility' on the part of the donor, so that low-state signallers need only pay a low cost to elicit a response.

Uncertainty and perceptual error also provide one possible explanation for the evolution of multi-component begging displays. Although empirical studies of parent–offspring communication have devoted much attention to vocal signals (see Kilner & Johnstone (1997) for a review), begging often involves a visual component as well. This can range from simple postural and positional cues to ornamental traits such as the bright mouth colours and plumage ornaments of some nestling birds (Lyon *et al.* 1994; Götmark & Ahlström 1997; Kilner 1997; Kilner & Davies 1998; Saino *et al.* 2000). There is growing evidence that parents integrate information from both visual and auditory sources in making feeding decisions. For instance, in a particularly elegant study, Kilner *et al.*

(1999) showed that reed warbler (*Acrocephalus scirpaceus*) parents adjust the rate at which they visit a brood of young in relation to both the gape area on display and the calling rate of the brood.

In the presence of noise, and given the risk of perceptual error, multi-component displays may evolve simply because they are easier to detect, or to assess (Johnstone 1996*a*; Rowe 1999). For instance, a comparative study by Kilner & Davies (1998) found that the fleshy white border of nestling mouths was wider in species from darker nests and also showed the greatest brightness contrast with the colour of the mouth interior. This aspect of visual display can thus be explained in terms of selection for efficient detection (with a larger, brighter mouth flange favoured when ambient light levels at the nest are low). Alternatively, visual signal elements may provide additional information about the same aspects of chick condition that influence vocal display (i.e. they may function as 'back-up' signals; Johnstone 1996*a*). Kilner (1997), for instance, found that small variations in the mouth colour of canary nestlings convey accurate information to parents about chick nutritional state. Finally, visual display features may also provide information about different aspects of chick condition that are not reflected in vocal begging (i.e. different components of begging may serve as 'multiple messages'; Johnstone 1996*a*). Saino *et al.* (2000), for example, suggest that the mouth coloration of nestling barn swallows (*Hirundo rustica*) reveals their health state to parents, since they found that nestlings challenged with a novel antigen (sheep red blood cells) had a less bright gape colour than control siblings.

Despite these empirical studies, existing theoretical analyses of parent–offspring communication focus only on simple displays, which vary along a single dimension of intensity. Given the increasing evidence that parents respond to both vocal and visual aspects of offspring display, and that these may vary independently in relation to chick condition, there is a clear need for future models of begging to allow for complex, multi-component signals.

6. SIGNALLING IN LARGE FAMILIES

It is much harder to analyse parent–offspring signalling ESSs when there is more than one offspring, though larger families are the norm in birds and mammals. The main difficulty is that with larger families interactions between offspring have to be considered, in addition to interactions with the parent. It is useful to consider two types of parental provisioning in larger families which represent the two ends of a continuum. First, situations where offspring interact amongst themselves to determine the probability of getting fed, the parent acting simply as a passive provider of food, and second, situations where individual young signal independently to the parent, though possibly modulating their signal in response to those produced by their siblings.

Macnair & Parker (1979) and Godfray & Parker (1992) studied the first situation in a model where they assumed young produced a costly begging signal and that the amount of food they received depended on relative begging levels. There is no difference in offspring state, so that at the ESS all young receive the same amount of food. The ESS is stable because any young that beg less (and so incur less signalling costs) suffer a reduction in fitness through reduced food intake. For the ESS to occur, it has to be explained why the parent acquiesces to the young determining who gets fed; why does it not ignore begging and give everyone the same amount of food (the strategy that maximizes fitness)? One possibility is that the parent cannot exercise choice. Consider a cavity-nesting bird where the parent can only physically feed the chick nearest the entrance hole (or where alternative provisioning strategies would be wasteful in time to implement). The Macnair & Parker model can then be reinterpreted in terms of costly sibling conflict for the prime feeding position. McRae *et al.* (1993) and Kacelnik *et al.* (1995) have argued for the importance of sibling conflict in determining food share and there is a large body of literature on how sibling conflict may influence brood reduction (Mock & Parker 1997). A very clear case where sibling conflict determines resource share is when the parent lays a clutch of eggs on a fixed amount of resource (perhaps a herbivorous insect laying a clutch of eggs on a plant, or a gregarious parasitoid ovipositing into a host). However, in these cases, as well as in hole-nesting birds, the parent can still influence the extent of conflict by altering clutch size (Godfray & Parker 1992).

Turning to the opposite end of the continuum described at the beginning of this section, Godfray (1995*a*) extended the honest begging model from a family containing one offspring to a family with two young. Initially he assumed a fixed pot of resources that the parent had to divide between the two young based on their obvious and cryptic state, that one offspring monitored the signal of another, and that the costs of signalling were experienced by the signaller alone and not its brood-mate. In these circumstances, an ESS separating equilibrium solution is possible, which qualitatively is very similar to the single-offspring solution. One difference is that the begging intensity of a focal sibling is influenced not only by its own state, but also by that of its sibling. Specifically, a chick with a low state value will signal at a relatively high intensity if its brood-mate is also in a low state value. If both chicks have great 'need' for the limiting resource there is a greater evolutionary temptation to cheat and hence a more costly signal is required for stability.

The dependence of signal intensity on the state of one's siblings suggests a test of the theory: feed or starve siblings and monitor the behaviour of a focal individual. This experiment has been performed three times with mixed results, two studies finding an effect (Smith & Montgomerie 1991; Price *et al.* 1996), and one not (Cotton *et al.* 1996). One problem with the test is that the predicted effects of sibling state are relatively small, at least compared with changes in the focal individual's state, and hence there is always the possibility that a negative result may just reflect a lack of resolving power. Alternatively, the absence of an effect may indicate that the parent responds to increased begging by increasing the amount of food available to its current offspring at the expense of its future reproductive success. When the costs of providing more food to the current brood are linear, offspring begging is unaffected by the state of its brood sibling (Godfray 1995*a*).

Extending models in which young are able to monitor each other's signals to larger broods is technically difficult. However, large-family models in which individuals signal simultaneously can be studied. Johnstone (1999) modified the continuous Sir Philip Sidney game so that the donor had an indivisible resource that it might give to one of a number of related signallers. He was able to show that an ESS signalling system was possible at which each potential recipient produced a signal that revealed its need, and the donor transferred the resource to the most needy recipient, provided it was not in its best interest to retain the resource itself. The costs of the signalling system decreased as the number of recipients increased. Moreover, with many recipients, the typical signalling costs were lower, except for the offspring in lowest state. The reason for this is that as the number of recipients goes up, the conflict shifts from donor–recipient to recipient–recipient, and as the resource is indivisible it is only the lowest-state recipients who have a realistic chance of getting it, and hence it is only these individuals that signal at high intensity. For the same reason, signal costs are influenced by both coefficients of relatedness with low numbers of signallers but largely by recipient–recipient relatedness when there are many signallers. It would be interesting to explore similar questions in a begging model with a divisible pool of resources.

Real systems are likely to be at neither end of the continuum identified at the beginning of this section, but somewhere in the middle. (Lotem *et al.* 1999) suggested that the extent of sibling conflict itself may be a signal, a possibility modelled by Rodríguez-Gironés (1999). The latter assumed, as did Macnair & Parker (1979), that a disproportionate share of the resource went to the chick that begged at the highest level, but now begging levels were influenced by state. The parent was able to use the information to assess offspring need and so adjust the total amount of food brought to the nest (though it had no control over resource share). Rodríguez-Gironés also explored the stability of the separating signalling system using a model of evolutionary dynamics (as in Rodríguez-Gironés *et al.* (1998) and see §3). Interestingly sibling conflict seemed to stabilize the ESS.

7. DYNAMIC SIGNALLING GAMES

The basic begging model we have described effectively ignores the dynamic aspects of rearing offspring. The period of dependency is divided up into a series of feeding episodes, and each of these is treated independently. This greatly simplifies the model, but it does so at the price of a loss of realism. Parent–offspring interactions in nature often extend over a considerable period of time, and each begging exchange takes place in the context of this larger process. The state of offspring and parents at any given time reflects the history of their interaction, and their current behaviour will not only influence immediate state, but also the future course of that interaction. Models that ignore the dynamic nature of parent–offspring communication may thus fail to capture important aspects of the process.

Johnstone (1996*b*) illustrates how dynamic considerations can modify the predictions of signalling models. He considers a simple extension of Godfray's (1991) begging model in which the parent may transfer resources prior to as well as immediately after begging. This is only a small step towards a full dynamic treatment of parent–offspring signalling, since it does not allow for repeated begging or for any change in offspring condition over time. Even such a simple extension of the basic model, however, has significant consequences. In Godfray's (1991) original model, as pointed out earlier, the parent wins the conflict over resource allocation, in the sense that the amount of food an offspring receives is the parental optimum (though this victory comes at the price of costly signalling). In Johnstone's (1996) extension, however, the threat of costly begging induces the parent to over-allocate resources, in order to reduce the subsequent level of solicitation by the young. This outcome bears some similarity to the predictions of 'pure conflict' or 'blackmail' models of begging (Zahavi 1977*b*; Parker & Macnair 1978, 1979; Macnair & Parker 1978, 1979; Parker 1985; Eshel & Feldman 1991), in that offspring solicitation leads parents to allocate more resources than would otherwise be optimal for them. However, solicitation still serves as a signal of offspring state (indicating that blackmail and signalling explanations of begging are not mutually exclusive).

More extensive dynamic analyses of parent–offspring communication have yet to be carried out. Such models would have to allow for repeated signalling, and for change in offspring (and possibly parental) state over time. This would probably also require a more complex characterization of 'state'. As numerous empiricists have pointed out, offspring may vary independently in their immediate level of satiation, reflecting the time since they were last fed, and in their longer-term need for resources, reflecting a more extensive feeding history (see Price *et al.* 1996; Iacovides & Evans 1998; Lotem 1998). A chronically undernourished offspring that is underweight for its age may have a marked long-term need for resources, even if, having been fed recently, its short-term need is low. This distinction between short- and long-term need raises questions about what aspects of offspring condition begging can be expected to advertise, and whether different components convey information about different aspects of state (i.e. whether they serve as 'multiple messages' rather than 'back-up signals' of a single facet of condition; see Johnstone 1996).

Just like offspring condition, parental state and feeding behaviour may vary over time. Greater feeding effort now may entail a decline in parental condition that reduces feeding ability later. Responsiveness to begging in the short term thus does not necessarily imply equivalent responsiveness in the long term, as parents might exhibit less flexibility in total feeding effort over prolonged periods than in immediate rates of visiting a brood (Stamps *et al.* 1989; Price 1998). Also, in light of variability in parental state, feeding behaviour will provide young with information about the consequences of begging as well as with resources. Dynamic models must permit offspring to adjust their begging behaviour in response to parental feeding rates, as well as allowing parents to modify feeding rates in response to offspring begging (see McNamara *et al.* 1999). In short, the dynamic nature of parent–offspring interaction raise a great many issues that have yet to be explored by current models of begging.

8. DISCUSSION

Grafen's (1990*a*,*b*) and Maynard Smith's (1991) important papers established a new framework for investigating the evolution of biological signalling in the presence of potential conflict of interests. These methods have proved particularly fruitful in the study of begging in birds and mammals, and other forms of parent–offspring communication (e.g. Rauter & Moore 1999). Yet we are still some way from a mature theory of parent–offspring signalling, and we now recognize a number of theoretical complexities that were not apparent in the analyses of the early models in this field. Some of these complexities have parallels in other areas of evolutionary biology, and in other fields such as economics where optimality and game theory arguments are also important. There is a real need for new mathematical ideas and tools to attack some of these outstanding problems. While the increased theoretical activity in this field has spurred a variety of fascinating experiments and comparative studies of begging and related topics (reviewed in Kilner & Johnstone 1997) we feel that experimentalists are still relatively ill-served by theory in this field, and sympathize with their frustration at the protean nature of many model predictions.

There are at least three possible explanations for costly begging in birds and mammals which are not mutually exclusive (Godfray 1995*b*). First, that it does not involve the communication of need but is a form of blackmail in the sense of Trivers, Parker and Macnair. Young produce a costly signal and the parents respond by providing more resources that cause the young to moderate their behaviour. The last two authors showed how such a system might be an ESS, though their models require fixed responses by parents and offspring and it is not clear whether the ESS remains when these traits are themselves allowed to evolve. Further exploration of this issue will almost certainly require a dynamic framework, and may link with other related ideas in the field such as Yamamura & Higashi's (1992) model of how conflicts are resolved when each party can modify the behaviour of the other, but at a cost; Eshel & Feldman's (1991) suggestion that the structural nature of the interaction (the form of the equations rather than the parameters) may evolve to reduce conflicts of interest; Clutton-Brock & Parker's (1995) exploration of punishment, the idea in this context that parents may impose fitness-reducing punishments for inappropriate offspring behaviour (see also Viljugrein 1997); as well as the main topic of this paper, parent–offspring signalling (Johnstone 1996*b*).

A second explanation is that costly begging is aimed not at the parent but is part of sibling conflict, tussles between brood-mates to determine who gets fed. While this cannot be the whole story—apparently costly begging occurs in broods of one—sibling conflict is certain to be important in larger families. Until recently, models had tended to concentrate on purely the amongst-sibling or parent–offspring aspects of conflict, but a recent realization that the level of sibling conflict itself may be a signal of offspring state (Lotem *et al.* 1999) suggests a means of merging these two classes of explanation (Rodríguez-Gironés 1999).

The last suggestion is that begging is an honest signal of need, the main focus of this paper. There have been two major challenges to this idea. The first is that although the separating equilibria identified by Godfray (1991) are evolutionarily stable, they are sufficiently expensive compared with non-signalling equilibria that they are unlikely to evolve, or only under special circumstances (Rodríguez-Gironés *et al.* 1996). The model with the particular parameters used by Godfray (1991) certainly does suffer from this problem, but it disappears when one parameter value is changed. Moreover, the precise equations used by Godfray and by most subsequent workers were chosen almost wholly for mathematical convenience, and there is a need to see whether signalling is expensive for a much broader range of functional forms. Possibly, honest signalling will only evolve under certain circumstances when it benefits receiver and signaller, or possibly it may arise even if less efficient through perception bias or via sibling conflict (Rodríguez-Gironés *et al.* 1998; Rodríguez-Gironés 1999).

The second major challenge is due to the work of Bergstrom & Lachmann (1997, 1998; Lachmann & Bergstrom 1998) who pointed out that there was not a unique signalling equilibrium as believed by Grafen (1990*a*,*b*) and Godfray (1991) but an infinite number. Grafen's techniques were based on calculus and could not identify the discontinuous, pooled equilibria described by Bergstrom & Lachmann. But although infinite in number, the pooling equilibrium are not arbitrary and share many features with the original separating equilibria. Comparing like with like, in both cases the level of signalling increases as state declines, but whereas in the separating equilibria the increase in signalling is smooth so that the receiver can at all times precisely determine signaller state, with pooling solutions signalling levels increase in discrete steps so that the receiver can only determine signaller state within certain bounds. Pooling solutions thus convey honest but not completely precise information, and as Bergstrom & Lachmann (1998) stress are in the spirit of Zahavi–Grafen signals, though often less expensive in terms of fitness costs. Pooling equilibria can also be cost free (Maynard Smith 1994; Bergstrom & Lachmann 1998), typically when one class of signallers wants to convey information such as 'there is no point in feeding me'.

Perhaps the greatest theoretical challenge at present is to develop the methodologies to determine which of the infinite number of signalling solutions (including making no signal at all) biological evolution will converge upon. To answer this would almost certainly involve getting to grips with evolutionary dynamics which, as we discuss in § 7, is going to be essential in making begging models more realistic. In addition, there are a number of technical problems to address (Lachmann & Bergstrom 1998). The stability of a pooling equilibrium at which offspring signal at a series of discrete levels depends upon how the parent responds to signals that are not included in this set, so-called out-of-equilibrium signals. Out-of-equilibrium problems also occur with separating ESSs (Grafen 1990*a*). Most models assume a fixed one-to-one relationship between signal and cost. What happens when a mutation arises that allows a certain signal to be made with a reduced cost, and how does the parent respond to a novel signal? Models that incorporate uncertainty may offer some hope of tackling this question, since perceptual error can give rise to a much greater range of perceived signals at equilibrium than the range of signals actually given, allowing one to determine evolutionarily stable responses to signals never employed at the ESS (Johnstone & Grafen 1992*b*). Alternatively, however, such responses may drift or fluctuate because they are rarely tested, opening up possibilities for exploitation of 'hidden preferences' that arise for novel signal traits (Grafen 1990*a*; Arak & Enquist 1993, 1995).

We conclude, however, by observing that theoretical debate over the stability and accessibility of different forms of signalling equilibria has distracted from the complexities revealed by empirical studies of begging. While modellers have argued over separating versus pooling equilibria, and the costs of honesty, field and laboratory studies have increasingly shown that basic signalling models such as the Philip Sydney game and the chick begging model overlook many significant aspects of parent–offspring interaction. Begging forms part of a long-term, dynamic exchange between parents and young (Stamps *et al.* 1989; Price *et al.* 1996; Iacovides & Evans 1998; Lotem 1998; Price 1998), and generally involves interaction and competition among many siblings (Smith & Montgomerie 1991; McRae *et al.* 1993; Kacelnik *et al.* 1995; Cotton *et al.* 1996; Price *et al.* 1996), who must often deal with two parents that may differ in their level of parental effort and response to begging (Kölliker *et al.* 1998). The resolution of family conflicts over resource allocation may involve communication among siblings as well as between parents and offspring (Roulin *et al.* 2000), and communication is itself a complex process that can involve many different signal components (Lyon *et al.* 1994; Götmark & Ahlström 1997; Kilner 1997; Kilner & Davies 1998; Kilner *et al.* 1999; Saino *et al.* 2000). As discussed above, theoreticians have only begun to incorporate some of these possibilities into models of begging. It may be that the solution to the theoretical puzzles they confront lies not only in the development of new mathematical tools and techniques, but also in their application to more realistic models that reflect the complexity of real parent–offspring interactions.

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