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REPORT

Begging scrambles with unequal chicks: interactions between need and competitive ability

Geoff A. Parker,[1]* Nick J. Royle[2] and Ian R. Hartley[2]
[1]*Population & Evolutionary Biology Research Group, Nicholson Building, School of Biological Sciences, University of Liverpool, Liverpool L69 3GS, U.K.*
[2]*School of Biological Sciences, Institute of Environmental and Natural Sciences, University of Lancaster, Lancaster LA1 4YQ, U.K.*
**Correspondence: E-mail: gap@liverpool.ac.uk*

Abstract

When offspring compete for the attentions of provisioning parents, empirical and theoretical work has generally concluded that chicks honestly signal their "need" for resources and that parents control allocation. Here, we develop models to show that when allocation of food resources is determined by competitive begging scrambles between sibs, the offspring's ESS begging levels, shares of food and personal fitness gained will be determined by an interaction between their competitive abilities and their true needs. Many of the predictions of this scramble competition model are qualitatively very similar to models of honest signalling of need, where parents, not offspring, control the allocation of food. Consequently it will be difficult to distinguish between the two mechanisms of food allocation based on empirical observations of the responses of chicks to feeding by parents.

Keywords

Begging, evolutionarily stable strategies, parent–offspring conflict, scramble, sib-competition.

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INTRODUCTION

Following the pioneering work of Trivers (1974), the first theoretical analyses saw begging or food solicitation by offspring to parents essentially as scramble competition among siblings (Stamps *et al.* 1978; Macnair & Parker 1979; Parker & Macnair 1979; Parker 1985; Godfray & Parker 1991). Food allocation by parents to offspring was seen as following a simple, fixed mechanism set by scramble competition. As such, parents passively fed the offspring presenting the greatest stimulus. More recent models have interpreted begging as honest biological signals (Grafen 1990) to parents of an offspring's true "need" (Godfray 1991, 1995; 1999; see also Harper 1986). In honest signalling models, parents are predicted to distribute resources following their assessment of the signals of different chicks.

The critical distinction between scramble and honest signalling models relates to the mechanism of food allocation by the parent. From each offspring's point of view, however, the different feeding mechanisms will affect the way in which they attempt to obtain food from the parent. With scramble, parents simply feed passively to the chick presenting the greatest stimulus. With honest signalling, parents actively choose between competing signals. Consequently, scramble competition is likely to apply when offspring control food allocation, and honest signalling when parents have control (Mock & Parker 1997; Royle *et al.* in prep.). The choice of the terms "scramble" and "honest signal" relate mainly to the passive and active mechanisms of food allocation, and to the underlying causes of increased begging. Under passive food allocation, sib-competition scrambles drive up begging levels, and chicks in greater "need" can afford to spend more in the scramble. Under active allocation, begging relates to need and, again, a chick in greater need can afford to beg more, but there is no escalation of begging due to sib-competition.

Under both mechanisms, chicks can increase their share of food by increasing their level of begging and, because any benefits of increasing begging are balanced by the costs, begging can be viewed as being "honest", regardless of whether food allocation is passive or active. A chick could "lie" about its level of need by begging more, but at the ESS it will not pay it to do so (hence the signal is "honest"). With active allocation, however, signal strength is assumed to correspond to need on a one-to-one basis so that the parent receives only "honest" information from the chicks, whereas under scramble models, the begging level may be modified by sib-competition and competitive ability, so that begging does not necessarily relate directly to need. For offspring in broods, some mix of scramble competition and

honest signalling often seems likely, depending on the balance of power between parents and offspring.

Perhaps as a consequence of the clearer link between mechanism (of food allocation) and function (of begging) inherent in honest signalling theory, recent empirical work has generally concluded that begging is an honest signal of "need" and that parents are in full control of resource allocation. A correlation between a chick's hunger state and its begging level, and hence food gain, is routinely taken as evidence for honest signalling (e.g. Kölliker *et al.* 1998; Rauter & Moore 1999; Saino *et al.* 2000). Here, we extend the sib-competition scramble model of Parker *et al.* (1989) and compare the results with Godfray's (1995) two-chick model of honest signalling to show that such evidence equally supports scramble theory. Recently, Rodríguez-Gironés *et al.* (2001), in a rather similar extension of the scramble model of Parker *et al.* (1989) to that developed here, use "signalling" synonymously with "begging". Whilst it can certainly be argued that begging is a signal, even under scramble conditions, we propose that to avoid confusion and to distinguish between mechanisms, "signalling" is used only for "honest signalling" (*sensu* Grafen 1990; Godfray 1991), i.e. where parents evolve precise responses to signals from individual offspring. As defined here, in a begging scramble, a parent's input to the nest may evolve but parents cannot, or do not, control the food shares of individual chicks.

We show here that although the mechanism of food allocation differs between honest signalling and scramble competition, the food gained in relation to an offspring's condition will be very similar, making interpretations of mechanism and function difficult for empiricists. However, under scramble, competitive asymmetries between chicks can dominate food gains – which is not predicted for honest signalling.

BEGGING AS A SCRAMBLE BETWEEN SIBS

Early scramble models assumed that offspring were equal in competitive ability, and sought ESS begging levels when parental food input to the nest was fixed (Stamps *et al.* 1978; Macnair & Parker 1979), or when the parental input was allowed to evolve (Parker & Macnair 1979; Parker 1985). Later models examined the ESS begging of two nestlings differing in competitive ability, with a fixed food input to the nest (Parker *et al.* 1989). We extend this model to include differences in "need" (defined as the value of the next unit of parental investment to personal fitness) between the two chicks to examine the interaction between competitive ability and need. The function used by Parker *et al.* (1989) to define chick success is termed the "one-component" fitness function (see below).

Godfray's (1995) honest signalling model examined ESS begging of two nestlings differing in need, with a fixed food input to the nest. However, he (and Rodríguez-Gironés *et al.* 2001) used a slightly different formulation of fitness, which we call the "two-component" fitness function (see below). This is incorporated into the model of Parker *et al.* (1989) so that scramble predictions can be compared with Godfray's honest signal predictions.

The two types of fitness model (one-component; two-component) generate similar results, particularly with regard to inclusive fitness and parental fitness. The one-component model is designed for cases where begging gains and losses are energetic, so that the net energy gain defines a chick's success. The two-component model is appropriate where there are two additive components of chick success, for example when benefits are food, and costs are, say, risk of predation or damage.

Both Parker *et al.* (1989) and Godfray (1995) considered the case of two chicks, A and B, which compete for the fixed input (a single feed or feeding bout worth Y food units) supplied to the nest by parent(s). An offspring's food gains, y, depend on its begging effort, x. Since $y_A + y_B = Y$, increased demand by one chick reduces the amount of food available for the other chick, but does not affect future broods produced by the same parent(s).

The one-component fitness function (Parker *et al.* 1989)

The direct (= personal) fitness benefit of m units of net energy gain by a chick is represented here by the single function $f(m)$. The energetic cost of begging effort x is $E(x)$, so that net energetic gains are $m_A = y_A(x_A) - E_A(x_A)$ to A and $m_B = y_B(x_B) - E_B(x_B)$ to B. By Hamilton's (1964) rule, if chicks A and B have a coefficient of relatedness of r, A's ESS begging level, x_A^*, should evolve to maximize its inclusive fitness $W_A^i = f_A + rf_B$, where $r = 0.5$ for full sibs and 0.25 for half sibs. Similarly, for B, x_B^* evolves to maximize $W_B^i = f_B + rf_A$, and an ESS can exist (x_A^*, x_B^*) which is a stable equilibrium in the sense that if either deviates unilaterally by playing $x \neq x^*$, its inclusive fitness is reduced. The ESS is found in the usual way by setting

$$\left.\frac{\partial W_A^i}{\partial x_A}\right|_{x_A = x_A^*} = 0; \quad \left.\frac{\partial W_B^i}{\partial x_B}\right|_{x_B = x_B^*} = 0 \qquad (1)$$

(Maynard Smith 1982).

Chick A differs in competitive ability from its full sib, B. If A begs to level x_A and B begs to level x_B, food gains are

$$y_A = Yax_A/(ax_A + bx_B) \text{ to A and}$$
$$y_B = Ybx_B/(ax_A + bx_B) \text{ to B}$$

(Parker *et al.* 1989), where a, b are positive constants, so that if $a > b$, A's begging is amplified relative to B's. Thus ax_A,

bx_B are the apparent begging stimuli presented by A and B to the parent. Net energy gains are

$$m_A = y_A - E_A(x_A) \text{ to A and}$$
$$m_A = y_A - E_A(x_A) \text{ to B.}$$

Using primes to denote differentials, applying eqn 1 gives

$$\frac{x_A^*[f_B'(m_B^*) - rf_A'(m_A^*)]}{f_B'(m_B^*)E_B'(x_B^*)} = \frac{x_B^*[f_A'(m_A^*) - rf_B'(m_B^*)]}{f_A'(m_A^*)E_A'(x_A^*)} = \frac{(ax_A^* + bx_B^*)^2}{Yab} \quad (2a)$$

where the ratio of begging levels is

$$\frac{x_A^*}{x_B^*} = \frac{f_B'(m_B^*)E_B'(x_B^*)[f_A'(m_A^*) - rf_B'(m_B^*)]}{f_A'(m_A^*)E_A'(x_A^*)[f_B'(m_B^*) - rf_A'(m_A^*)]}. \quad (2b)$$

The two-component fitness function (Godfray 1995)

Fitness is the sum of two components, benefits and costs. Modifying Godfray's original notation, the benefit to a chick of gaining y units of food is now $f(y)$, and the cost is $E(x)$. The net fitness benefit $= f(y) - E(x)$. Inclusive fitness for A becomes $W_A^i = f_A(y_A) - E_A(x_A) + r[f_B(y_B) - E_B(x_B)]$; for B, $W_B^i = f_B(y_B) - E_B(x_B) + r[f_A(y_A) - E_A(x_A)]$. Note that whereas in the one-component model, begging costs are the energetic costs of begging effort, in the two-component model, they are fitness costs (measured in the same units as the benefits due to feeding).

A scramble version of this model allows food gains, y_A, y_B, to depend on x_A, x_B exactly as above. The ESS (x_A^*, x_B^*) for scramble competition is again found from eqn 1 and has

$$\frac{x_A^*[f_B'(y_B^*) - rf_A'(y_A^*)]}{E_B'(x_B^*)} = \frac{x_B^*[f_A'(y_A^*) - rf_B'(y_B^*)]}{E_A'(x_A^*)} = \frac{(ax_A^* + bx_B^*)^2}{Yab}. \quad (3a)$$

The ratio of begging levels is

$$\frac{x_A^*}{x_B^*} = \frac{E_B'(x_B^*)[f_A'(y_A^*) - rf_B'(y_B^*)]}{E_A'(x_A^*)[f_B'(y_B^*) - rf_A'(y_A^*)]}. \quad (3b)$$

Note the similarity of eqns 2a, 2b, to 3a, 3b. Apart from the difference between y and m eqn 3a differs from 2a only in the absence of the gradient of f in the denominator.

Godfray (1995) calculated his signalling ESS differently; he assumed that each chick has direct information about its own need, but gains information about the need of its sib by monitoring that sib's begging level.

EXPLICIT FORMS

To investigate further we require explicit forms for $f(m)$, $f(y)$, and $E(x)$. The effects of differences in need were modelled by allowing the benefit function, $f(m)$ or $f(y)$, to differ for the two chicks. We assume that benefits follow exponentially diminishing returns, so that for a given chick I (A or B)

$$f_I(m_I) = B_I(1 - e^{-c_I m_I}); \quad (4a)$$
$$f_I(y_I) = B_I(1 - e^{-c_I y_I}); \quad (4b)$$

in which the constant c_I determines the rate at which the asymptotic maximum benefit (B_I) is approached. Differences in the need of chicks can be simulated by giving them different values for c_I (Parker *et al.* 1989; Godfray 1991, 1995), while holding B constant ($B_A = B_B = 1.0$) so that both chicks have ultimately the same potential maximum gains (Fig. 1). For simplicity, we take begging costs to be linear and equal for the two chicks, so that

$$E_A(x_A) = E_B(x_B) = jx \quad (5)$$

(see Parker *et al.* 1989). Thus if $a > b$, we have made each unit of begging for A more effective in gaining food resources, rather than cheaper in terms of energy.

With $j_A = j_B$, $B_A = B_B = 1.0$, substituting these forms into eqns 2a and 3a gives, for the one-component model,

$$x_A^*\left[1 - r(c_A/c_B)e^{(c_B m_B - c_A m_A)}\right] = x_B^*\left[1 - r(c_B/c_A)e^{(c_A m_A - c_B m_B)}\right] = \frac{j(ax_A^* + bx_B^*)^2}{Yab}, \quad (6a)$$

so that the ratio of begging levels is

$$\frac{x_A^*}{x_B^*} = \frac{1 - r(c_B/c_A)e^{(c_A m_A^* - c_B m_B^*)}}{1 - r(c_A/c_B)e^{(c_B m_B^* - c_A m_A^*)}} \quad (6b)$$

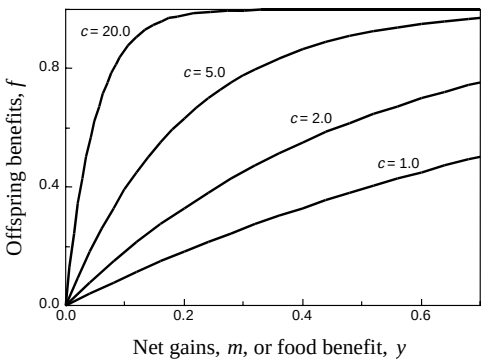

Figure 1 Relation between the direct (= personal) 'fitness' f of a chick and its net calorific intake, m (one-component fitness function of Parker *et al.* 1989), or total food benefit y (two-component fitness function of Godfray 1995) from a given meal (from eqn 4a or 4b with $B_I = 1.0$; see text). The parameter values are in the range used to generate the ESS solutions in the later figures. Note that as c increases, the rate of approach to the asymptote increases.

(cf. equation 12 of Parker *et al.* 1989). Calling $\alpha = a/b =$ the ratio of competitive abilities, equal begging levels ($x_A^* = x_B^*$) applies if

$$\ln\left(\frac{c_A}{c_B}\right) = Y\left(\frac{c_A\alpha - c_B}{\alpha + 1}\right) - xj(c_A\alpha - c_B). \qquad (6c)$$

Under the two-component model, the ESS has

$$x_A^*[c_Be^{-c_By_B} - rc_Ae^{-c_Ay_A}] = x_B^*[c_Ae^{-c_Ay_A} - rc_Be^{-c_By_B}] = \frac{j(ax_A^* + bx_B^*)^2}{Yab} \qquad (7a)$$

and

$$\frac{x_A^*}{x_B^*} = \frac{c_Ae^{-c_Ay_A} - rc_Be^{-c_By_B}}{c_Be^{-c_By_B} - rc_Ae^{-c_Ay_A}} \qquad (7b)$$

so that equal begging levels ($x_A^* = x_B^*$) apply if

$$\ln\left(\frac{c_A}{c_B}\right) = Y\left(\frac{c_A\alpha - c_B}{\alpha + 1}\right). \qquad (7c)$$

Note that both 6c and 7c are independent of the relatedness between chicks (r).

NUMERICAL RESULTS

Numerical solutions were iterated for x_A^*, x_B^* and the various fitness measures using the pairs of equations 6a, 6b or 7a, 7b. To do this, we take A as the focal chick, and increase its c_A above 1.0 whilst holding B's c_B constant at 1.0, increasing the difference in shape of two benefit functions (Fig. 1). Focal chick A may be stronger ($a > b$), equal to ($a = b$), or weaker ($a < b$) than chick B. Solutions depend only on the ratio, $\alpha = a/b$, not on the absolute values of a and b.

Equations 2 and 3 show that the ESS depends on the gradients of the benefit functions, $f(m)$ or $f(y)$. Consider two such functions (Fig. 1), one for chick A and the other for B. The gradients are steepest at lowest values of m or y, with the function with the higher c having the higher gradient. But at higher values of m or y the situation reverses: beyond a certain m or y, the function with the lower c has the higher gradient. Hence defining need in terms of c requires caution. Defining relative need in terms of which chick profits more from a marginal increase in food, c relates *directly* to need when food resources are low, and *inversely* to need when total food resources are high. Godfray (1995) focuses on high values of c in his signalling models, such that the marginal benefit of additional food decreases with c over the range considered.

Relative begging cost and apparency

Figure 2(a) shows the ratio of ESS begging costs, x_A^*/x_B^*, for the one- and two-component fitness models, in relation to the asymmetry in benefits, expressed as $\log_{10}(c_A/c_B)$, when A and B are full sibs ($r = 0.5$). The chicks are either competitively equal ($\alpha = 1$), or strongly unequal, so that a unit of begging cost by focal chick A has either twice ($\alpha = 2$) or half ($\alpha = 0.5$) the competitive weight of chick B. Solutions for x_A^*/x_B^* are consistently higher for the one-component model, though both models show qualitatively similar responses across the wide range of $\log_{10}(c_A/c_B)$.

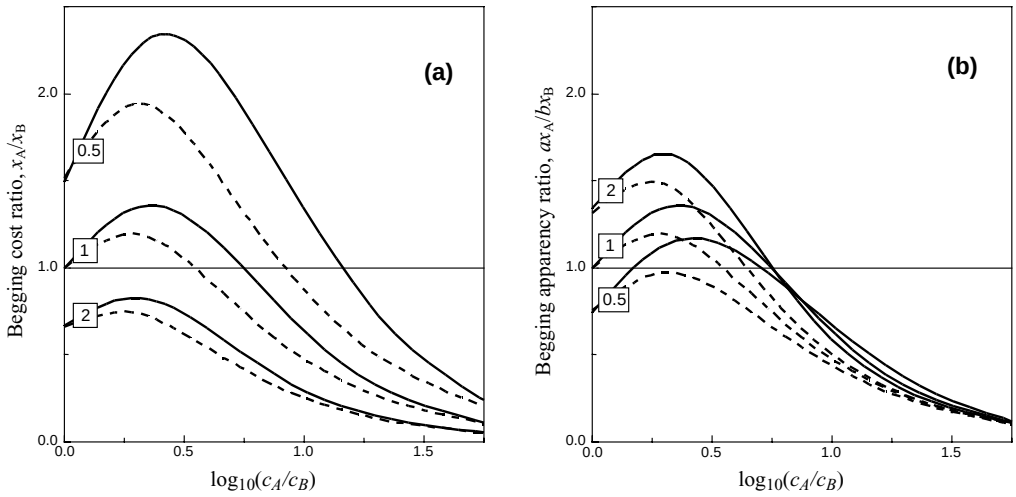

Figure 2 Ratio of ESS begging costs (A chick/B chick), x_A^*/x_B^*, in relation to the $\log_{10}$ of the ratio of the c-values (see Fig. 1) for the two chicks (zero when $c_A/c_B = 1.0$). For the focal chick A, c_A is increased above the fixed value for the B chick of $c_B = 1.0$, so as $\log_{10}(c_A/c_B)$ increases, chick A rises more quickly towards the asymptotic value of $f(m)$ or $f(y)$. Continuous curves = the one-component fitness model; broken curves = the two-component model. The three pairs of curves are for three ratios of chick competitive ability (α values shown between curves): $\alpha = 0.5$ (focal chick A is weaker), $\alpha = 1.0$ (chicks of identical competitive ability), $\alpha = 2.0$ (focal chick A is stronger). $Y = B = j = 1.0$.

The begging cost ratio does not change monotonically with c_A/c_B. Consider equal sibs ($\alpha = 1.0$, $c_A = c_B = 1$). Both show the same begging level, so that $x_A^*/x_B^* = 1$. Suppose that the food ($Y/2$) each gets is insufficient to raise benefits far up the f curve (Fig. 1). As c_A increases above c_B, chick A can increase its fitness f_A more by a unit increase in begging than can chick B, whose c_B remains at 1.0. Thus, chick A begs harder than chick B ($x_A^*/x_B^* > 1$). However, as c_A increases further, the benefits of begging for chick A decline faster, so that x_A^*/x_B^* peaks, and as x_A^*/x_B^* declines, a point is reached where the situation becomes reversed and B begs more than A ($x_A^*/x_B^* < 1$). At very high disparities in c, chick B shows far higher begging costs than the satiated A. Thus the chick with the higher c-value may beg more or less than its sibling, depending on the magnitude of the total food Y relative to the c-values. As c_A/c_B increases, begging is equal at two points; one where $c_A = c_B$, and the other (where $c_A > c_B$) defined by eqns 6c, 7c. Between these, the chick with the higher c begs most, and above the second point, the chick with the higher c begs increasingly less.

When sibs are unequal, similar effects occur if chick A is weaker ($\alpha = 0.5$), except that the cost ratio, x_A^*/x_B^*, is higher, and both models again show the initial zone where $x_A^* > x_B$. When chick A is stronger, cost x_A^* always exceeded x_B^* for the case examined ($\alpha = 2$) (see also Parker *et al.* 1989; Rodríguez-Gironés *et al.* 2001).

Note that x_A^*, x_B^* are begging costs, not the begging stimuli apparent to the parent, which are ax_A*, bx_B*. The ratio, ax_A^*/bx_B^*, gives the relative apparency of the begging stimuli (A/B) to the parent (Fig. 2b). These show the same

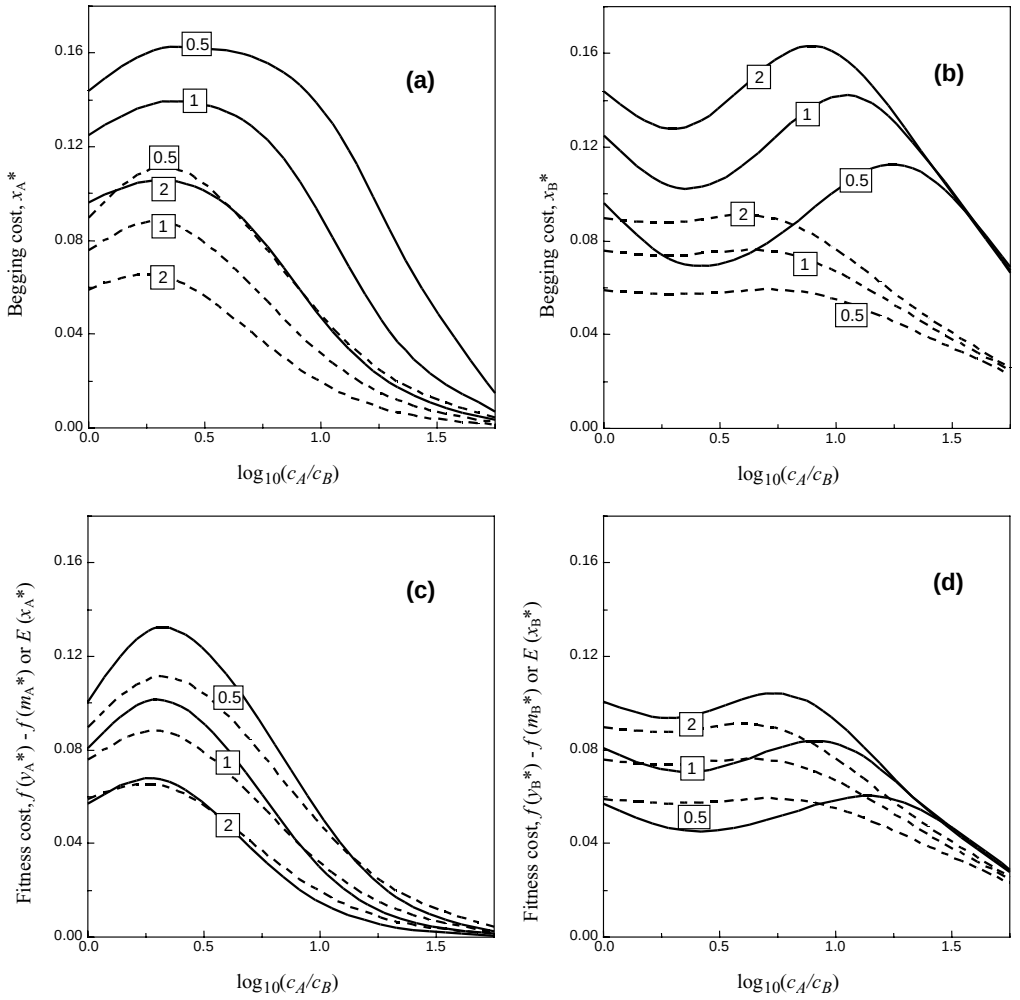

Figure 3 Absolute begging costs at the ESS, in relation to the $\log_{10}$ of the ratio of the c-values for the two chicks. (a) Costs x_A^* for the focal chick. (b) Costs x_B^* for the non-focal chick. (c) Fitness costs, $f(y_A^*) - f(m_A^*)$ or $E(x_A^*)$, for the focal chick. (d) Fitness costs, $f(y_B^*) - f(m_B^*)$ or $E(x_B^*)$, for the non-focal chick. Continuous curves = the one-component fitness model; broken curves = two-component model. The sets of curves are for the three ratios of chick competitive ability (α values shown on curves): $\alpha = 0.5$ (focal chick A is weaker), $\alpha = 1.0$ (chicks of identical competitive ability), $\alpha = 2.0$ (focal chick A is stronger). $Y = B = j = 1.0$.

forms as relative costs, but show (1) much less difference between A and B under the three conditions for relative chick strengths ($\alpha = 0.5, 1.0, 2.0$), and (2) reversed ordering, so that for very low c_A/c_B, the begging apparency of a stronger A is greater than that of the weaker B, and that of a weaker A is less than that of the stronger B (cf. Fig. 2a).

Begging costs and associated fitness costs

Figure 3(a,b) shows the ESS begging response across the range of c_A/c_B. Absolute begging costs are lower at a given competitive asymmetry (α) with the two-component fitness model, otherwise both models respond similarly. Chick A (Fig. 3a) shows an initial rise to a peak of begging as its c_A increases above the fixed $c_B = 1.0$ of B, after which it declines towards zero for huge c_A/c_B. A's begging costs are higher when it is weaker than B, decreasing as A's relative competitive ability increases.

Chick B's response to the increase in chick A's c_A value (Fig. 3b) first shows a decrease, then a rise to a peak, then a second decrease, this time towards zero. This effect is much weaker in the two-component fitness model. As expected, in both models at a given c_A/c_B ratio, chick B's begging costs decline as it becomes stronger relative to chick A.

Figure 3(c,d) shows the fitness costs of begging for the two chicks. For the two-component model, fitness costs of begging equal the begging costs, $E(x^*)$, but for the one-component model, they are the fitness that would be achieved from the energy in a given food share minus the fitness actually realized, given that begging reduces these energetic gains, i.e. $f(y^*) - f(m^*)$. The fitness costs of begging for A (Fig. 3c) and B (Fig. 3d) behave quantitatively similarly in relation to c_A/c_B as do the absolute costs (Fig. 3a,b), but show a marked dampening of differences between (1) the one- and two-component models, and (2) the effects of strength asymmetries between the chicks.

Food shares

The food share gained by focal chick A (y_A^*) across the c_A/c_B range is shown in Fig. 4(a) (B's share is $y_B^* = 1 - y_A^*$). When competitively stronger than B, A gains a greater share of food as c_A increases initially above c_B, despite paying lower begging costs (it has greater begging "apparency"). But with $\alpha = 0.5$ under the two-component fitness function, chick A always gained less than half the resources. In the other cases A's share peaked above 0.5 and then declined as c_A/c_B increased further. The peak y_A^* occurs at a lower c_A/c_B with the two-component function.

We can compare A's food share with that maximizing parental fitness in the absence of any sib-competition. The "ideal" parental food share for A, $\hat{y}_A$ occurs at equal marginal benefits for the two chicks:

$$f_A'(\hat{y}_A) = f_B'(\hat{y}_B)$$

(Temme 1986). Using eqn 4b gives

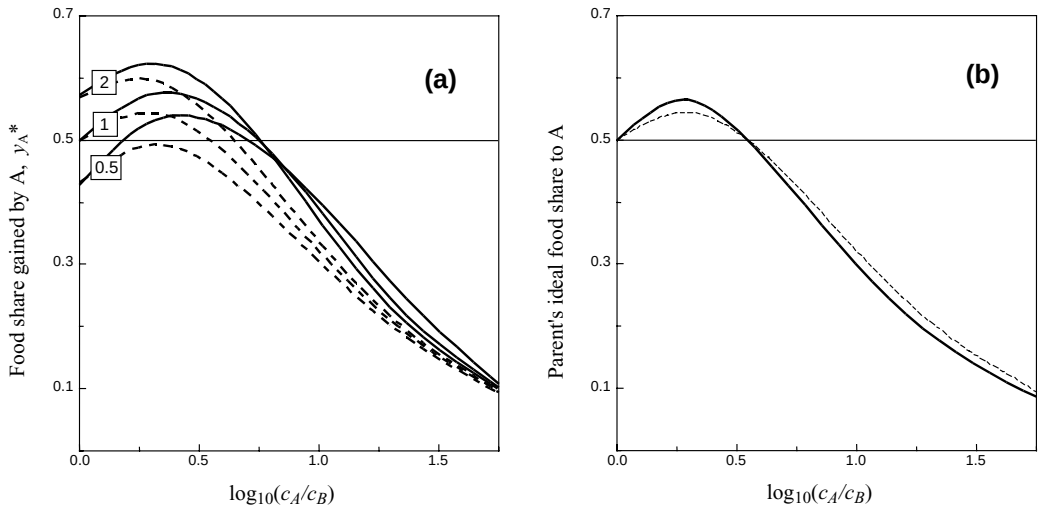

Figure 4 Food share (y_A^* = proportion of total food input) gained by focal chick A at the ESS, in relation to the $\log_{10}$ of the ratio of the c-values for the two chicks. (a) Continuous curves = the one-component fitness model; broken curves = two-component model. The three pairs of curves are for three ratios of chick competitive ability (α values shown on curves): $\alpha = 0.5$ (focal chick A is weaker), $\alpha = 1.0$ (chicks of identical competitive ability), $\alpha = 2.0$ (focal chick A is stronger). $Y = B = j = 1.0$. (b) Ideal food share for A from parent's perspective, $\hat{y}_A$ from eqn 8 under zero sib-competition (heavy curve). Thin broken curve shows, for comparison, the case for the two-component model when chicks have equal competitive ability ($\alpha = 1$), which is the ESS share under sib-competition (from (a)) that is closest to the parental ideal.

$$\hat{y}_A = \frac{\ln\left(\frac{c_A}{c_B}\right) + c_B}{(c_A + c_B)}. \quad (8)$$

Note that $\hat{y}_A$ (Fig. 4b) responds similarly to c_A/c_B as does y^*_A (Fig. 4a); quantitatively, $\hat{y}_A$ is most similar overall to y^*_A under the two-component model when chicks have equal competitive ability ($\alpha = 1$).

Personal, inclusive, and parental fitnesses

Both fitness models generate similar results for all fitness measures, with differences in personal fitness usually less than 10% (often much less), differences in inclusive fitness usually less than 2%, and parental fitnesses virtually identical. For this reason only the results of the one-component model are shown in Fig. 5.

Personal fitness ($f(m^*)$ for the one-component model) is shown in Fig. 5(a). The higher the c-value a chick has, the more favourable for its personal fitness. Each chick's personal fitness increases as its relative competitive ability increases. Whatever its competitive ability, the personal fitness of the focal chick A rises as its c_A increases. B's personal fitness first declines, and later increases as c_A for chick A increases. Note that in "contradictory" conditions, where the chick with the higher c has lower competitive ability ($\alpha = 0.5$), then the chick with the higher competitive ability can achieve higher fitness than the chick with the higher c for an initial range of c_A/c_B.

Inclusive fitness ($f_A(m^*_A) + 0.5\ f_B(m^*_B)$ for the one-component model) is shown in Fig. 5(b). The effect of competitive asymmetries is much dampened, and both chicks show increasing inclusive fitness as c_A increases.

As c_A increases, parental fitness ($f_A(m^*_A) + f_B(m^*_B)$ for the one-component model) increases because chick A makes increasingly better use of the food. Parental fitness is remarkably insensitive to the effects of competitive asymmetries between the chicks. In Fig. 5(a), the parental fitness curve

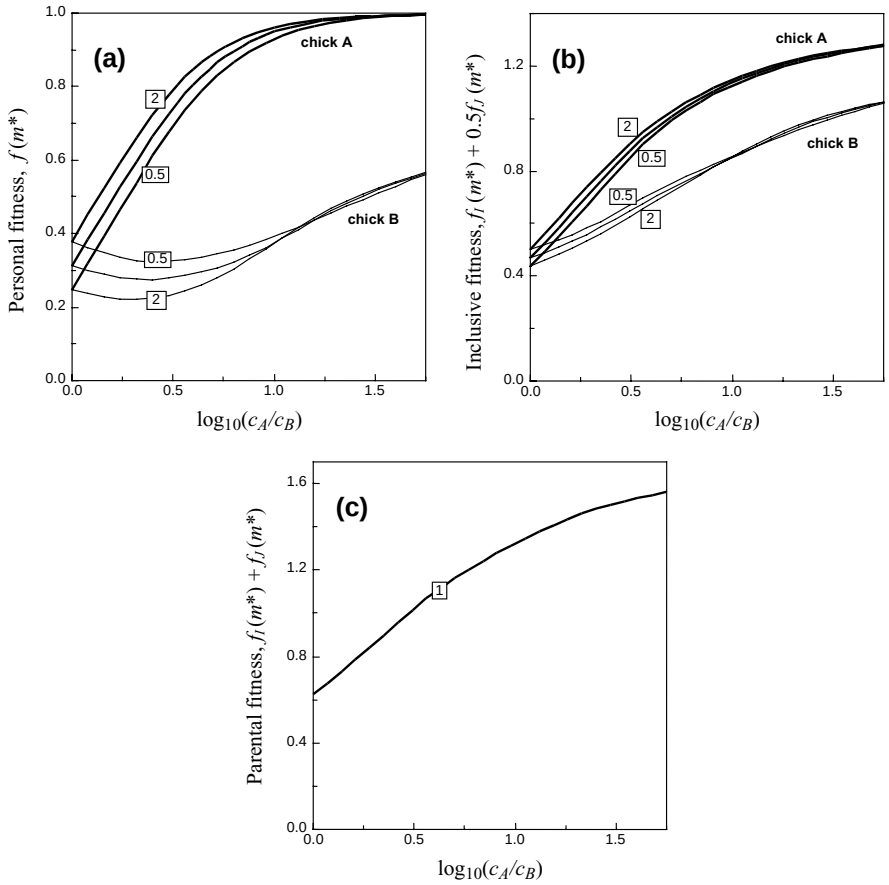

Figure 5 Fitness measures in relation to the $\log_{10}$ of the ratio of the c-values for the two chicks. Results are for the one-component fitness model. (a) Personal fitness. (b) Inclusive fitness. (c) Parental fitness. Each set of three curves are for three ratios of chick competitive ability: $\alpha = 0.5$ (focal chick A is weaker), $\alpha = 2.0$ (focal chick A is stronger); remaining curves are for $\alpha = 1.0$ (chicks of identical competitive ability). $Y = B = j = 1.0$.

for equal chicks is shown, because the other two conditions ($\alpha = 2$, $\alpha = 0.5$) generate such close values to $\alpha = 1$ (never deviating more than 1%; usually much less) as to be indistinguishable. Under this form of scramble competition, competitive asymmetries between sibs across this fourfold range have virtually no consequences for parental fitness.

Comparison of scramble with honest signalling

The two-component model was used to generate a direct comparison of ESS begging under scramble competition with the predictions of Godfray's (1995) honest signalling model. We iterated solutions for the three cases ($\alpha = 2$, 1, 0.5), varying c_A across the range 4.0–10.0 for the focal chick A, while holding c_B constant at 7.0 for chick B. These conditions (also with $Y = 1.0$, $B = 1.0$ and $j = 0.01$) were used for many of Godfray's honest signalling calculations, with the maximum condition of a chick fixed at $c = 10$. The comparison between the signal and scramble results is shown in Fig. 6.

The most obvious difference is that for these conditions, scramble suggests much higher begging costs; there is no overlap even when the focal chick has twice the competitive weight of its sib. This may be due to one or both of two effects.

1 *Maximum condition*. In general, the effort invested in begging by chicks with a given condition is independent of the maximum possible need in the scramble model, but not in the signal model. In Fig. 6, maximum condition was $c = 10$, at which begging is zero under the signalling model. Setting the maximum c to a greater value may increase the signalling begging costs across this range.

2 *Other chick's response*. The scramble model assumes that each chick is informed of its own condition and that of its sib, and requires that at the ESS, any unilateral change in begging for either chick, holding the behaviour of sib constant, reduces inclusive fitness (eqn 1). In contrast, in the signal model, although a chick "knows" its own condition, it must infer the condition of its sib from the latter's begging level. When deriving the ESS, a strategic increase in begging by a given chick provokes escalation in the begging level of the other, which is not held constant. This, rather than the scramble–signal dichotomy, may favour lower begging effort in the signalling case.

Thus further analyses will be required before true quantitative comparisons can be made. However, both scramble and signal solutions show a qualitatively similar decline in begging with need, demonstrating how difficult it will be to differentiate between them from measures of begging in relation to condition. Across the range shown in Fig. 6, true need decreases as c_A increases, relating to the declining part of the x_A curve in Fig. 3(a).

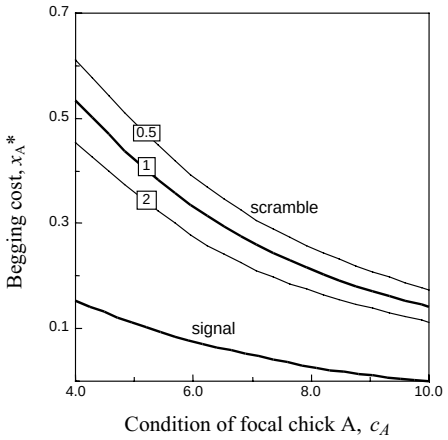

Figure 6 Comparison of ESS begging levels for scramble with those from Godfray's (1995) honest signalling model, in relation to changes in the condition (c_A) of the focal chick A. The top three curves (scramble) are for three ratios of chick competitive ability (α values shown on curves): $\alpha = 0.5$ (focal chick A is weaker), $\alpha = 1.0$ (chicks of identical competitive ability), $\alpha = 2.0$ (focal chick A is stronger). The condition (c_B) of the non-focal chick is held at 7.0 throughout. For other conditions see text.

DISCUSSION

There is little doubt that when offspring are begging for food their behaviour reflects the value of that food to their personal fitness. This has been termed the true "need" of offspring (reviewed in Kilner & Johnstone 1997). Unfortunately this term implies the information given by offspring begging behaviour is honest, i.e. that the strength of the begging signal corresponds directly to offspring need. However, this is not necessarily so. As this paper indicates, its adaptive interpretation must consider scramble competition as well as honest signalling.

Caution is required when interpreting terms used to represent "need" or "condition" in begging models. The relationship between need and condition is assumed to be negative, because a chick in good condition should need less food (Godfray 1991, 1995; Rodríguez-Gironés *et al.* 2001). However, the current analysis shows that this negative relationship only holds when the asymmetry of condition is large between chicks. When there is little difference in condition between chicks the marginal gains will be higher for feeding the strongest chick, and need relates directly to condition. Consequently empirical measurements of chick "condition" and "hunger" do not necessarily equate to need. Despite the confusing and loaded nature of the term "need" no suitably neutral replacement is currently available, so we retain its use for consistency.

The present models confirm that when offspring control food allocation through scramble competition, ESS begging levels and food shares will be strongly influenced by competitive asymmetries (Parker *et al.* 1989; Rodríguez-Gironés *et al.* 2001). Under honest signalling, the parent is expected to compensate for any amplification of begging signal due to a chick's strength, and to allocate food only in relation to true need. An exception may apply if competitive ability correlates with a chick's value to the parent. Parents are expected to feed higher value offspring preferentially, even at the expense of the condition of their weaker sibs. This assumes that competitive ability is fixed, and independent of food supply over the longer term. Studies on species with hatching asynchrony suggest that the primary determinant of competitive ability is relative age (Mock & Parker 1997). Parents appear not to compensate for relative competitive ability, so that the simplest version of the honest signalling model is unlikely to apply when chicks are unequal and food supply is limiting.

The current models also confirm the prediction that chicks with higher competitive ability typically experience reduced begging costs, but may achieve higher fitness (Parker *et al.* 1989; Rodríguez-Gironés *et al.* 2001). For example, when food is scarce and the asymmetry of need is small, the stronger chick can achieve greater fitness even though its weaker sibling has a greater need (Fig. 5a). Despite the fact that for a given asymmetry of need, increasing a chick's competitive ability reduces its begging costs, its "begging apparency" nevertheless increases. The stronger chick achieves a greater begging stimulus for relatively less cost than its weaker sib. The distinction between begging apparency and begging cost is an important one; in experiments, it will be easier to measure apparency than metabolic cost. The results presented here show that apparency typically correlates positively, and costs negatively, with relative competitive ability. Thus under scramble, if both are measured across a range of chicks differing in competitive ability, a negative relationship between cost and apparency will be generated. The relationship between costs and apparency remains to be investigated for honest signalling; a difference in response may offer a way of discriminating between signal and scramble systems.

Remarkably, parental fitness is hardly affected by the occurrence of competitive differences between offspring in begging scrambles (Fig. 5c). This result parallels that for cases where food allocation is settled by a strict power hierarchy between chicks, so that the strongest chick takes first share of the food input, followed by the second strongest, and so on down the hierarchy. Here, the parental fitness achieved at the ESS is very similar to the "ideal" parental allocation (Parker *et al.* 1989).

For two chicks at least, the relations between ESS begging and true need are qualitatively almost identical for signalling and scramble, though quantitatively scramble appears to generate higher overall begging costs (Fig. 6). Begging levels in scrambles correlate with true need because higher costs can be "afforded" as an offspring's potential marginal gains increase. This similarity poses problems for empiricists. In experiments that measure chick begging levels after manipulating their hunger levels, a positive correlation between hunger and begging support both approaches and cannot therefore be taken as support for just one (typically honest signalling; see Royle *et al.* in prep.). The present scramble model approach and the parallel honest signal model of Godfray (1995), are designed to apply to feeding allocations made over the short-term, i.e. a single feed, feeding bout or day. Both predict that food allocation will reflect chick need, so whether parents or offspring control food allocation, begging behaviour may be very similar. However, the applicability of these models across a broader time scale (e.g. the dependent life of the chicks) is questionable, because they assume implicitly that the total food is sufficient to ensure at least some prospect of survival for each chick. If the total food, allocated equally, is insufficient to allow both chicks to survive, parents and both chicks would do better if just one chick receives all the food, though chicks would "disagree" as to which should be favoured. Longer-term models typically assume zero fitness for chicks receiving low parental investment (e.g. Parker & Macnair 1978), but are primarily mechanistic rather than functional in approach, as they assume that chicks have an inflexible begging strategy over time.

The only difference between scramble and signal approaches will be in the quantitative relation between true "need" (condition) and the ESS begging level, which depends on the mechanism of resource allocation. To determine whether it is primarily parental or offspring's interests that are being served requires experiments that establish that one party benefits at the expense of the other. However, if similar outcomes are likely to be achieved by scramble and signal mechanisms, it may be in parental interests (coincident with offspring's interests) to allocate food passively, rather than to incur the costs of inspecting each chick's begging level and allocating food according to honest signalling (R. M. Kilner, in prep.). Under such circumstances it will be extremely difficult to infer empirically which party has ultimate control of resource allocation.

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