
Sibling competition stabilizes signalling resolution models of parent–offspring conflict

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Young of altricial birds use conspicuous displays to solicit food from their parents. There is experimental evidence that the intensity of these displays is correlated with the level of food deprivation of young, and that parents respond to increased levels of solicitation by increasing the rate of food delivery to the nest. Game-theoretical models based on the handicap principle show that, when solicitation is costly, there is a signalling equilibrium at which there is a one-to-one correspondence between the condition of the young and the intensity of their display. Parents use this information to adjust their levels of investment on the current offspring. However, the models also have a non-signalling equilibrium, and computer simulations show that only the non-signalling equilibrium is stable. Here I show that when direct sibling competition is introduced into the model, in such a way that parents have control on the amount of food provided to the nest, but not on the way the food is allocated among siblings, the non-signalling equilibrium disappears and the signalling equilibrium becomes stable.

Keywords: begging; signalling of need; sibling competition

1. INTRODUCTION

In most avian species, parents arriving to their nest are received by a handful of wide-open, screaming beaks. A number of non-mutually exclusive hypotheses have been proposed to explain this common observation. Realizing that family harmony is undermined by a genetic conflict of interests between parents and their offspring, Trivers (1974) suggested that begging displays were psychological weapons aimed to increase parental investment beyond the level that would maximize parental fitness. It was later proposed that begging was the result of sibling competition (Macnair & Parker 1979): begging chicks might be attempting to out-compete their siblings in a scramble for limited resources. Today, it is commonly believed that begging is a signal of need (Harper 1986; Hussell 1988; Godfray 1991, 1995), whereby offspring inform their parents about their internal condition. Although recent models (Godfray 1991, 1995), based on the handicap principle (Zahavi 1977; Grafen 1990a), seem to receive confirmation from the observation that begging intensity increases with food deprivation and that parental provisioning increases with begging intensity (reviewed by Kilner & Johnstone 1997), the validity of such models has been questioned by further analysis showing that the signalling equilibrium is not evolutionarily stable (Rodríguez-Gironés *et al.* 1998).

Godfray's model of signalling of need (Godfray 1991) leaves two questions open: how does begging evolve and how is it maintained. The model has two equilibria: a signalling and a non-signalling one (Grafen 1990b; Rodríguez-Gironés *et al.* 1996; Bergstrom & Lachmann 1997)—plus a large number of equilibria with non-continuous strategies that have received little attention (Rodríguez-Gironés *et al.* 1998; Lachmann & Bergstrom

1998): throughout this paper, 'the signalling equilibrium' will refer to the equilibrium in continuous strategies derived by Godfray (1991). Assuming that non-signalling was the ancestral condition, a mechanism must be devised to explain how populations shifted to the signalling equilibrium. A number of possible mechanisms have been suggested, such as the existence of parental biases or the action of sibling competition (Rodríguez-Gironés *et al.* 1996). In fact, the stability of the non-signalling equilibrium depends on the hypothesized shape of the fitness functions, and there are plausible fitness functions for which non-signalling would be unstable (Payne & Rodríguez-Gironés 1998). Unfortunately, the instability of the non-signalling equilibrium does not imply that signalling should be stable, and computer simulations have shown that when a population is initialized at the signalling equilibrium, it quickly departs from it (Rodríguez-Gironés *et al.* 1998).

2. THE MODEL

The goal of the present model was to explore the possibility that sibling competition might play an important role in the evolution and stabilization of signalling of need. To do this, I consider a brood of two chicks tended by a single parent. The fitness of chick i ($f(y_i, x_i, c_i)$, $i=1$ or 2) is a function of its internal condition (c_i), the level at which it begs (x_i) and the amount of food it consumes (y_i). The internal condition of chick i is known to itself, but unknown to its sibling and parent. Chicks are assumed to follow a strategy such that begging intensity is affected by their internal condition, but not by the begging intensity of their nest mates. Parents perceive the begging intensities of the two chicks and respond by delivering to the nest a certain amount of food ($y_{\text{tot}}(x_1, x_2)$). The expected

future reproductive success of the parent ($g(y_{\text{tot}})$) decreases as a result of investing in the present brood.

In order to introduce direct sibling competition, I assume that parents do not have control over food allocation among siblings: parents can determine how much food to deliver, but not how this food is allocated among offspring. Siblings may interfere with parental decisions in a number of different ways, such as monopolizing nest positions closer to the feeding parent, intercepting feeds directed to their nest-mates or physically punishing their nest-mates when they beg for food (Mock & Parker 1997). As a result of sibling competition, I will assume that the amount of food consumed by each chick follows the relationship (Parker *et al.* 1989):

$$y_i = \frac{x_i}{x_1 + x_2} \times y_{\text{tot}}. \quad (1)$$

This model differs from Godfray's (1995) in three respects. First and foremost, parental investment per brood is a fixed amount in Godfray's model, while in this model parents can adjust their total level of food provisioning according to the begging level of the chicks. Furthermore, I am assuming that the begging intensity of a chick is not affected by the condition of its nest-mate. This assumption is supported by data from starlings (*Sturnus vulgaris*), where it has been shown that the begging intensity of a target chick is not affected by the level of food deprivation of its nest-mates (Cotton *et al.* 1996). The last difference lies in my assumption that parents have no control over food allocation: food allocation is assumed to follow equation (1), regardless of whether this allocation does or does not optimize expected parental fitness. Although it has been found that food allocation is partly determined by the behaviour of the chicks (Kacelnik *et al.* 1995), our assumption is most likely a simplification of the real situation. Other than these points, the model is identical to the one analysed by Godfray (1995).

We are interested in the Nash equilibria of the model. A Nash equilibrium (Gibbons 1992) is a set of strategies $\{x_1^*(c_1), x_2^*(c_2), y_{\text{tot}}^*(x_1, x_2)\}$ such that none of the players can increase their expected inclusive fitness by a unilateral modification of their behaviour, a condition that must clearly be satisfied at the evolutionary equilibrium (Maynard Smith 1982). Inclusive fitness functions are given by

$$\left. \begin{aligned} F_1 &= f(y_1, x_1, c_1) + r_s \times f(y_2, x_2, c_2) + r_p \times g(y_{\text{tot}}) \\ F_2 &= r_s \times f(y_1, x_1, c_1) + f(y_2, x_2, c_2) + r_p \times g(y_{\text{tot}}) \\ F_p &= f(y_1, x_1, c_1) + f(y_2, x_2, c_2) + g(y_{\text{tot}}) \end{aligned} \right\}. \quad (2)$$

where r_s and r_p are the coefficients of relatedness of a chick with its nest-mates and with future offspring of the caring parent, respectively. To proceed further, we must specify the shape of the fitness functions. I will assume (Godfray 1991, 1995) that $f(y, x, c) = 1 - e^{-cy} - x$, $g(y) = 1 - 0.08 \times y$ and that $r_s = r_p \equiv r$. Godfray (1991, 1995) provides extensive discussion of these fitness functions. Basically, the fitness of a chick increases asymptotically with the amount of food received, and the rate of approach to the asymptote depends on the condition of the chick. Furthermore, chick fitness decreases linearly with their begging intensity and parental fitness decreases

with food provisioning. With these functions, it is easy to verify that the strategies

$$\left. \begin{aligned} x_i &= \frac{0.08 \times (1-r)}{c_i} \times \log\left(\frac{c_i}{0.08}\right) \\ y_{\text{tot}} &= \frac{1}{0.08 \times (1-r)} \times \sum_{j=1}^2 x_j \end{aligned} \right\}, \quad (3)$$

constitute a Nash equilibrium of the model. Notice that, at evolutionary equilibrium, food intake per offspring is the same as in the single-chick model of Godfray (1991). The begging strategy differs from the one proposed by Godfray (1991) by a constant. The similarity between the equilibrium strategies of the single- and two-chick models is due to the presence of a linear cost of provisioning in the parental fitness function and does not generalize to other scenarios.

3. STABILITY OF THE SIGNALLING EQUILIBRIUM

I used computer simulations to study the stability of this Nash equilibrium. The simulations were conducted as follows. At the beginning of the t th generation, the strategies of the first and second chick, and of the parent, were given by functions $x_1(t, c_1)$, $x_2(t, c_2)$ and $y_{\text{tot}}(t, x_1, x_2)$, respectively. The average inclusive fitness of a parent using $y_{\text{tot}}(t, x_1, x_2)$ and 100 random mutations (derived from it as explained below) was calculated (assuming that c_1 and c_2 were evenly distributed on a square grid, taking values between one and three, with nodes separated by 0.2 units), and the function achieving the highest inclusive fitness was selected to become $y_{\text{tot}}(t+1, x_1, x_2)$. The same procedure was used for the strategies of each offspring, and the algorithm was iterated until convergence. Begging strategies were codified as second-order polynomials, and parental strategies had the form $y_{\text{tot}}(x_1, x_2) = a + b \times x_1 + c \times x_2 + d \times x_1 \times x_2$. In all cases, mutants were obtained by randomly selecting a subset of coefficients and adding to them a normal deviate, with zero mean and a standard deviation of 0.001. (Increasing the order of the polynomials by one led to a change of less than 1% in the equilibrium functions.) Notice that this technique aims at testing the evolutionary stability of behavioural strategies, but it does not in the least pretend to mimic the evolutionary dynamics of a system.

In the absence of direct competition (i.e. when food allocation among siblings is under parental control) the signalling equilibrium of the two-chick model was unstable, in agreement with the results obtained for the single-chick model (Rodríguez-Gironés *et al.* 1998). However, the introduction of direct sibling competition stabilized the signalling solution. Regardless of whether the simulations started at a signalling or non-signalling state, the simulations converged to equation (3) (figures 1 and 2).

4. DISCUSSION

Since not all possible initial conditions can be tested with computer simulations, we cannot claim that the signalling equilibrium constitutes a global attractor of the model. Nevertheless, it is clear from the results that, when direct sibling competition is introduced into signalling

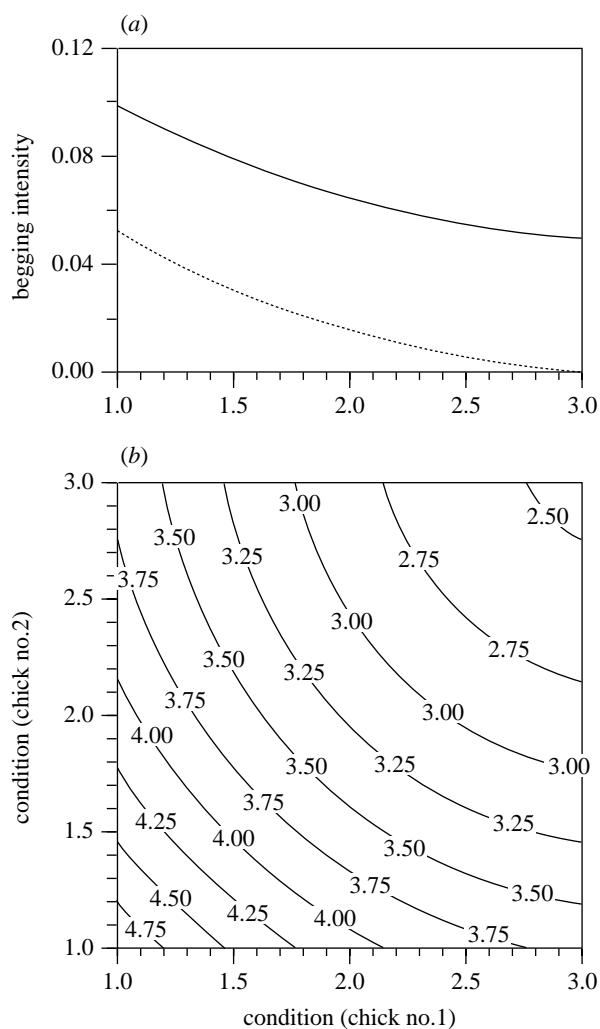


Figure 1. Equilibrium strategies. (a) Begging intensity as a function of condition, and (b) parental provisioning as a function of the condition of both chicks at the signalling equilibrium. The begging intensity of a chick according to Godfray's (1991) model is given in (a) as a dotted line for comparison.

models, (i) the non-signalling equilibrium becomes unstable, and (ii) the signalling equilibrium becomes both stable and evolutionarily robust: in the long term, random modifications of the equilibrium strategies will have no effect on the signalling strategies.

The results of the simulations can be explained as follows. Let us first assume that parents deliver a fixed amount of food to the brood, irrespective of the behaviour of the offspring, and that chicks do not beg, so that the food is shared equally between them. An infinitesimal increase in begging intensity will allow a mutant chick to capture any share of the food it desires (equation (1)) at basically no cost, and therefore non-signalling is not a Nash equilibrium (Macnair & Parker 1979; Parker *et al.* 1989). When the amount of food delivered to the brood is fixed, offspring will fight (beg) in order to increase their share, and a level of escalation will be reached where the marginal benefits and costs of begging exactly balance. This equilibrium is evolutionarily stable (Macnair & Parker 1979; Parker *et al.* 1989). Moreover, at equilibrium, the begging intensity of a chick reflects its internal condition and, therefore, parents can acquire information

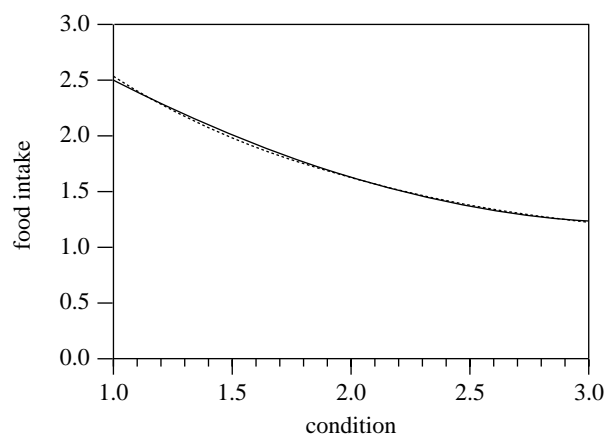


Figure 2. Food intake at equilibrium. At equilibrium, the food intake (solid line) of a chick is almost independent of the condition of its nest-mate (the ratio between the standard deviation and the mean food intake of a chick when the condition of its sib changes is smaller than 0.04%), and almost identical to the food intake predicted by Godfray's (1991) single-chick model (dashed line).

concerning the condition of their young by monitoring the level of sibling competition (Rodríguez-Gironés 1996). Selection will now favour parents who use begging intensity in order to adjust the amount of food delivered to the brood: in this way sibling competition becomes a signal (Lotem *et al.* 1999).

It would be futile to argue whether it is the handicap principle or sibling competition that stabilizes the signalling system. In a broad sense, the handicap principle implies that signalling systems will only be reliable if the balance between the costs and benefits of signalling is condition dependent (Grafen 1990a; Getty 1998). This is still the case in the present model: sibling competition will be unable to stabilize the signalling system in the absence of signalling costs (Macnair & Parker 1979; Bergstrom & Lachmann 1997). Hence, according to this model, it is the combination of a signalling cost (with condition-dependent trade-offs between the costs and benefits of signalling) and the presence of direct sibling competition that enables the evolution and stability of the signalling system, in agreement with previous suggestions (Rodríguez-Gironés *et al.* 1996).

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