The Role of Begging and Sibling Competition in Foraging Strategies of Nestlings

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Role of begging and sibling competition in foraging strategies of nestlings

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ABSTRACT

In this paper we assume that parents use the signalling intensity of their young to determine how much food they bring to the nest, and that the pattern of food allocation is determined by the signalling intensity and by the intensity of other non-signalling behaviours that are not perceived by the parents and have no effect on total food provisioning. We explore the consequences of assuming different ways in which signalling and non-signalling behaviours, as well as competitive asymmetries, might interact to determine food allocation. In Model 0 only signalling affects food allocation. For the same level of need, larger (more competitive) chicks beg less and obtain a greater share of the food than their smaller sibs. In Model 1, food allocation is determined by a linear combination of the signalling and the non-signalling behaviours. When non-signalling behaviours are the main determinant of food allocation, chicks don't signal and parents bring a fixed amount of food to the nest. Larger chicks receive a greater share of this food. When both types of behaviour are equally weighted, the pattern of investment depends on competitive asymmetry. For low asymmetry levels, both chicks invest in signalling. For large asymmetries, the less competitive chick invests in signalling and the more competitive chick invests in non-signalling behaviours. In Model 2, food allocation is determined by the product of the signalling and non-signalling intensities. Larger chicks invest more in signalling and less in non-signalling behaviours. Larger chicks get more food than their siblings. A comparison of the different models shows that the chicks waste more resources when signalling evolves. Hence, if natural selection could act on the mechanism of food distribution, we would expect signalling to play a minor role in the actual pattern of allocation of resources.

Food solicitations are almost ubiquitous in species with parental care. To explain their evolution, Godfray (1991, 1995) proposed game-theoretical models based on the handicap principle (Zahavi 1987; Grafen 1990) and showed that a signalling equilibrium exists between a parent and its young if signalling is costly. The signalling equilibrium derived by Godfray (1991), however, was shown to be unstable in computer simulations (Rodríguez-Gironés et al. 1998). These simulations questioned the validity of the model's assumptions and forced us to reconsider the evolution and stability of food solicitations. Recently, it has been shown that introducing direct sibling competition leads to the stabilisation of the signalling equilibrium (Rodríguez-Gironés 1999 –in what follows, this model will be referred to as the sibling-competition model). The possibility that other factors, as yet ignored, may also stabilise the signalling equilibrium deserves further study.

The sibling-competition model works in the following way. Let us assume that, in a two-chick brood, chick i (i = A, B) invests a certain effort into procuring food, x_i. (All the symbols used in this paper are listed at the beginning of appendix 1.) This begging effort is a function of the condition of the chick, c_i. The caring parent observes the begging effort of each chick and gets information concerning the condition of its offspring. The parent uses this information to determine the level of investment in the current brood, Y_{tot}. So far, the assumptions correspond to those of other begging models. But the sibling-competition model departs from signalling models in a key assumption. It assumes that the parent has no control over food allocation between chicks. According to the sibling-competition model, the amounts of food consumed by chicks are determined by their relative begging efforts, regardless of whether this allocation pattern corresponds to the one maximising the expected fitness of the parent. Following Parker et al. (1989), the model assumed that the amount of food allocated to chick i, y_i, was given by:

$$y_i = Y_{tot} \frac{x_i}{x_A + x_B}. \qquad (1)$$

The sibling-competition model does show that the introduction of direct sibling competition can stabilise the signalling equilibrium, but it is unrealistic in two important aspects.

1. – It assumed that the parent could not influence the allocation of food between the two chicks. In most species the parent does have some control over food allocation.

2. – It assumed that the parent observed all efforts made by the chicks in order to get food, and the model made no distinction between signalling and other behaviours that may influence the pattern of food allocation, such as jockeying for favourable positions. This is unrealistic because some of the behaviours that lead to a bias in the pattern of food allocation can not be perceived (nor inferred) by parents, and therefore cannot be used by parents to determine how much to invest in the current brood. For instance, chicks may compete for some "hot spots" (such as the nest entrance in cavity nests) while the parents are foraging. If parents are not present at the time when the competition takes place, they cannot assess the chick's efforts, and hence this effort can have no influence on the behaviour of the parents.

In this paper, we focus on the second problem of the sibling-competition model: the explicit distinction between those behaviours that lead to an increase in parental food provisioning from those behaviours that have an effect on food allocation but do not affect food provisioning. The set of behaviours that have an effect on food intake will be referred to as the foraging strategy of a chick. Some of these behaviours can be perceived by the parent and may, in principle, have an effect on parental provisioning. In what follows, these behaviours will be referred to as the signalling component of the foraging strategy. Behaviours that affect food allocation but cannot be perceived by the parent will be referred to as the non-signalling component of the chick's foraging strategy. Clearly, non-signalling behaviours cannot affect parental food provisioning. Signalling behaviours, on the other hand, may affect both parental food provisioning and food allocation between sibs (as was the case in the sibling-competition model).

It has long been known that the food intake of a nestling is determined by a number of different factors. The models developed here should help us understand what is the optimal foraging strategy of nestlings as a function of their social context and the mechanism of food allocation. They should help us understand how chicks should partition their resources between increasing the amount of food delivered to the nest and increasing their own share of that food. Before introducing the formal models in the next section, we will consider here some behaviours that are likely to affect food allocation and food provisioning. When analysing the begging behaviour of chicks we often distinguish between begging calls and body posture (Redondo & Castro 1992; Lotem 1998a). The rate (number of calls per second) pitch and intensity of the calls can contain information concerning the condition of the chicks. Begging calls affect parental investment in the brood and belong to the signalling component of the foraging strategy. Chick posture influences the pattern of food allocation between chicks. Chicks that gape towards the parents receive more food than chicks gaping away from the parents. (Gaping away from the parents is observed mainly in small, blind chicks.) Likewise, chicks with stretched body postures receive more food than lying chicks. Posture is, then, a component of the foraging strategy of nestlings. It is unclear whether posture affects the amount of food that parents deliver to the nest: posture may be a non-signalling component of the foraging strategy of nestlings. Position in the nest affects food allocation, particularly in cavity nesters. In these species, chicks closer to the nest entrance receive relatively more food than their nest mates. (When the chicks are close to fledging, one of the nestlings can block the nest entrance and monopolise food temporarily, Litovitch & Power 1992.) The relative position of nestlings is determined through a jostling competition that takes place, by and large, in the absence of the parents. The effort put into this competition affects food allocation but cannot affect food availability. This effort is therefore part of the non-signalling component of the foraging strategy.

GENERAL MODEL

The foraging strategies of chicks are multidimensional. Chicks must determine the pitch, rate and intensity of their begging calls, the effort they put into fighting for a position close to the nest entrance, their posture, etc. For simplicity, however, we will consider chicks that must determine how much effort to invest in two sorts of behaviours, thus lumping all the behavioural dimensions into two variables. We call the intensity of the “*signalling component*”, $\underline{s_i}$, of a chick’s foraging strategy the effort that the chick puts into all those behaviours that are perceived by the parents. And we refer to the effort put into all other behaviours that can influence food allocation but are not perceived by parents as the intensity of the "*non-signalling component*" of the foraging strategy, $\underline{h_i}$ (for hidden). Thus, the total *foraging effort* of a chick is the sum

$$x_i = s_i + h_i \,. \tag{2}$$

In the context of this two-component model of parent-offspring interactions, we will avoid the use of the term "begging". Behaviours belonging to the signalling component of the foraging strategy can unambiguously be termed as begging behaviours. But it is not so clear whether the non-signalling component of the chick's foraging strategy classifies as begging or not. Some investigators may consider jostling for favourable positions as part of the chick's begging strategy, but others may identify begging with the purely signalling component. To avoid confusion, therefore, we will simply talk of the foraging strategy and its signalling and non-signalling components.

Within this framework, we consider three different models, corresponding to different ways in which signalling and non-signalling foraging behaviours can interact to determine the pattern of food allocation. Model 0 is a simple extension of the sibling-competition model: the non-signalling component is not included, but we consider the effect of introducing *competitive asymmetries* between the chicks. We do this for the sake of comparison, since competitive asymmetries will play a key role in subsequent models. In Model 1, food allocation is determined by a linear combination of the signalling and non-signalling components of the foraging strategy. In Model 2, the product of the two components determines food allocation. In Model 1 chicks can opt between investing in the signalling or non-signalling components of foraging (or in both), but in Model 2 chicks must invest in signalling and non-signalling components in order to obtain food. Model 1 applies if, for instance, the advantage of being close to the nest entrance (or the advantage of stretching the neck) is independent of the intensity with which a chick produces begging calls. In Model 2 the effect of the non-signalling component is to modulate, to potentiate, the effectiveness of the signalling component. For instance, a calling chick may receive more food in the front than in the back of the nest, but being well placed and gaping may not be enough to get food. (Notice, though, that in some situations gaping may be a signalling behaviour, Kilner et al. 1999.) In both models, we will consider the effect of competitive asymmetries between the chicks.

None of the models that we will consider, however, apply to situations where sibling competition results in escalated fighting that can lead to physical damage of the chicks. If older chicks peck their younger sibs to death, or if they force them to submissive postures with their repeated blows (Mock & Parker 1997), the assumptions of our model do not hold.

Although parents cannot interfere with the pattern of food allocation, and they cannot benefit one chick over another, parents perceive size differences and can respond to them: parents can respond differentially to the two young (see appendix 1 for details).

We use the following fitness functions. For the chicks, fitness will be

$$W_{ch} = 1 - e^{-c_i y_i} - x_i \,, \tag{3}$$

where the total effort x_i is the sum specified in Eq. 2, c_i is the condition of the chick and y_i its food intake, determined from the amount of food provided to the nest according to Eq. 1. Fitness increases with the condition of chicks and with the amount of food they receive, but is a decreasing function of foraging effort. The marginal benefit of food is a decreasing function of the amount of food received and of the condition of the chick. Godfray (1991, 1995) gives the rationale behind this fitness function. The residual fitness of the parent (expected fitness from future broods) will be modelled by

$$W_p = 1 - \gamma \cdot Y_{tot}{}^2 \,. \tag{4}$$

That is, investment in the current brood, Y_{tot}, has a negative effect on expected future reproductive success, and the decrease in expected fitness is quadratic. All our results are based on $\gamma = 0.08$. In previous models (Godfray 1991; Rodríguez-Gironés 1999) it has been assumed that residual fitness decreases linearly with investment in the current brood. Although this assumption has no special implications when modelling the behaviour of single chicks, in multi-chick broods chick behaviour and parental investment per offspring are unaffected by brood size if parental fitness is linear (Rodríguez-Gironés 1999). In natural nests, however, parental investment per chick decreases as brood size increases. This implies that the relationship between residual parental fitness and current investment must be convex. Hence our choice of a quadratic function.

Let chick i (i = A, B) invest some effort into the signalling component of foraging, s_i, and some effort into the non-signalling component of foraging, h_i. We will assume that the relative competitive ability of A is $a_A = a \geq 1$, and the relative competitive ability of B is $a_B = 1$. The foraging efforts and relative competitive abilities combine to produce "*foraging scores*" $z_i = z(s_i,h_i,a_i)$. It is these foraging scores that determine the pattern of food allocation, according to a simple extension of (1):

$$y_i = Y_{tot} \frac{z_i}{z_A + z_B}. \tag{5}$$

Our aim is to find functions $s_i = s_i(c_i;a)$, $h_i = h_i(c_i;a)$ and $Y_{tot} = Y(s_A,s_B;a)$ that constitute a Nash equilibrium for a fixed value of a. In other words, we look for behavioural strategies such that none of the players (chick A, chick B and parent) can increase its expected inclusive fitness with a unilateral modification of behaviour. Inclusive fitness functions for the chicks, F_i, and for the parent, F_p, are given by

$$\left.\begin{aligned} F_A &= W_{ch,A} + r_s \cdot W_{ch,B} + r_p \cdot W_p \\ F_B &= r_s \cdot W_{ch,A} + W_{ch,B} + r_p \cdot W_p \\ F_p &= W_{ch,A} + W_{ch,B} + W_p \end{aligned}\right\}, \tag{6}$$

where r_s and r_p represent the coefficients of relatedness between a chick and its sib and parent, respectively. (Notice that these fitness functions make implicit assumptions about the ecological circumstances and breeding system. For further discussion, see Rodríguez-Gironés et al. 1998; Lessells & Parker 1999.) Throughout this paper, we will assume that $r_s = r_p = 0.5$.

An analytical derivation of the Nash equilibria of the models is beyond our mathematical skills. We have therefore used the same algorithm implemented to study the stability of the solution of the sibling-competition model (Rodríguez-Gironés 1999) to find the Nash equilibria numerically. The implementation of the algorithm is explained in appendix 2. We restrict our search to strategies such that the begging intensity of a chick depends on its own condition, but is independent of the condition (or behaviour) of its sib. This assumption is made to simplify the analysis. It fits the observed behaviours in some species (Cotton et al. 1996), but by no means in all (Price et al. 1996). It should also be noticed that our algorithm searches only continuous Nash equilibria, although a large number of discontinuous equilibria also exist (Lachmann & Bergstrom 1998; Rodríguez-Gironés et al. 1998).

MODEL 0

For the time being, we ignore the non-signalling component of foraging and let the foraging score be

$$z_i = a_i \cdot s_i , \tag{7}$$

where a_i is the competitive ability and s_i the signalling intensity of chick i.

Figure 1 shows the foraging effort (signalling component) for each chick and the pattern of food allocation as a function of chick condition for a = 1.0, 1.5 and 2.0. When a > 1, chick A invests less in foraging and obtains more food than its sib.

Figure 1 here.

MODEL 1

In the sibling-competition model, the same behaviour determines how much food is provided to the brood and how food is shared between the chicks. Here we introduce the non-signalling component of the foraging strategy: behaviours that affect food allocation but not food provisioning. In Model 1, we assume that the signalling and non-signalling components interact additively to produce the foraging score. This can be done in a number of ways. In particular, we will consider the following expressions for the foraging score:

$$z_i = a_i \cdot h_i \tag{8a}$$

and

$$z_i = s_i + a_i \cdot h_i. \tag{8b}$$

These two expressions are particular cases of the more general model.

$$z_i = w_s \cdot s_i + w_h \cdot a_i \cdot h_i, \tag{8c}$$

where the weight factors w_s and w_h are positive (possibly equal to zero), a_i is the competitive ability and s_i and h_i are the signalling and non-signalling intensities, respectively, of chick's i foraging strategy. When $w_s = 0$ (Eq. 8a), the signalling component determines food provisioning and the non-signalling component determines food allocation. When $w_s = w_h$ (Eq. 8b) food allocation is equally determined by the signalling and non-signalling components, the latter weighted by the competitive-asymmetry coefficient.

To study the behaviour of this model, we proceed as follows. For each level of competitive-asymmetry (a = 1.0, 1.5 and 2.0), we find the solution for $w_s = 1$, $w_h = 0$. With the solution for these parameters as starting point, we increase w_h by 0.2. With this solution as starting point, we increase w_h to 0.4, and so on until $w_h = 1$ (Eq. 8b). From here we decrease w_s in steps of 0.2 (with $w_h = 1$ all the time) until we reach $w_s = 0$ (Eq. 8a). We now proceed backwards, increasing first w_s to 1 and decreasing then

w_h to 0. This procedure allows us to see whether the signalling equilibrium for a set of parameter values is unique, or whether it depends on the evolutionary history of the system. Figure 2 shows the average foraging effort as a function of w_s and w_h.

Figure 2 here.

For most conditions investigated chicks only invest in signalling and both siblings use the same strategy (Fig. 2). For small values of w_s and with $w_h = 1$, on the other hand, both chicks invest in the non-signalling component of the foraging strategy. In this case, chick A invests less than chick B. The range of w_s values for which chicks invest in non-signalling behaviours increases with the asymmetry in competitive ability (Fig. 2). Between these two regions, there is a narrow transition zone where chicks invest mainly in signalling, but there is also some investment in non-signalling foraging behaviours. This transition zone is associated with an overall increase in foraging effort. Chick A invests slightly more than chick B in non-signalling behaviours and somewhat less in signalling behaviours. In this transition zone, the equilibrium reached depends on the evolutionary history of the system, but for other regions we have only found a single equilibrium (Fig. 2).

The foraging strategies and pattern of food sharing are depicted in Fig. 3 for $w_s = 0$ and $w_h = 1$. For $w_s = 1$ and $w_h = 1$, the foraging strategies are identical to those of the symmetrical version of Model 0 (Fig. 1, top) except when $a = 2.0$ (Fig. 4).

Figures 3 and 4 here.

For most of the models that we have examined, increasing the value of a has a quantitative effect, but it does not introduce qualitative differences. Model 1 with w_h and w_s strictly positive is an exception. As we have seen in Figs. 2 and 4, when $a = 2.0$ the solution is qualitatively different from $a = 1.0, 1.5$. What happens if the competitive asymmetry increases further? For $a = 3.0$, the algorithm fails to converge (in one million generations). In fact, we have already noticed (Fig. 2) that with $w_h = 1$ and $w_s > 0$ the algorithm may converge to different equilibria depending on the initial conditions. (For Models 0 and 2 there seems to be a unique equilibrium.) When $w_h =$

$w_s = 1$ and $a \leq 2.0$, we find only one equilibrium, but convergence is very slow for some initial conditions. For larger competitive asymmetries ($a = 3$), the problem is different. After an initial phase, chick A invests only in non-signalling behaviours and chick B in signalling. But once this situation is established, the strategies fail to converge. Rather, they chase each other for hundreds of thousands of generations.

Despite the lack of an evolutionary equilibrium, however, clear patterns do emerge. If we look at two points in time, the strategy of a chick differs (roughly) by a vertical displacement. At any time, the average investment of chick A is proportional to the average investment of chick B (Fig. 5). Likewise, there is a strong, negative relationship between the average investment of chick B in signalling and the amount of food brought to the nest by the parent (Fig. 5). For intermediate competitive asymmetries ($a = 2.2, 2.4\ldots$) the algorithm does not converge either (in 500,000 generations): chick A uses a mixture of signalling and non-signalling behaviours, and the relative intensity of non-signalling increases with the level of asymmetry.

Figure 5 here.

It is possible to derive an analytical condition for the stability of the non-signalling equilibrium in this model, on the assumption that parents do not respond to signalling ($dY_{tot} / ds_i = 0$). In this case, Y_{tot} is independent of the behaviour of the chicks. For a given foraging score z_i, the i-th chick will maximise its expected fitness by minimising its total foraging effort, x_i. Investing solely in non-signalling behaviours will minimise foraging cost if $a_i\ w_h >= w_s$. Inspection of Fig. 2 shows that the non-signalling equilibrium always satisfies this condition. However, there are regions of the parameter space where this condition is satisfied and our algorithm did not converge to the non-signalling equilibrium. It is not difficult to understand why. First of all, the stability of the non-signalling equilibrium does not imply that there is no stable signalling equilibrium. Besides, the stability condition assumes that parents do not respond to offspring solicitation by increasing food provisioning. Our algorithm introduces random mutations in the parental strategy at a high rate, and at any time, it is likely that $dY_{tot} / ds_i > 0$. When this is the case, the stability condition for the non-signalling equilibrium becomes more stringent.

MODEL 2

In model 2 we consider the possibility that the product of the signalling and non-signalling efforts determines the foraging score. (Arnon Lotem suggested this possibility.) Both components, signalling and non-signalling, have some effect on food allocation. Moreover, the foraging score of a chick equals zero unless the chick invests in both components. Specifically, we assume that

$$z_i = a_i \cdot s_i \cdot h_i . \tag{9}$$

Figure 6 shows the foraging strategies and the pattern of food allocation for this model. Total foraging effort is maximal (and efficiency minimal) for this model. Roughly two-thirds of the foraging effort are invested in signalling and one third in other behaviours that are not detected by the parent. In asymmetric broods ($\underline{a} > 1$) chick A invests less in non-signalling behaviours and slightly more in signalling than its sib does.

Figure 6 here.

DISCUSSION

Model 0 extends the sibling-competition model by introducing asymmetries in competitive abilities between the sibs. The result is straightforward, and agrees with the findings of Parker et al. (1989). The main difference between Model 0 and the model developed by Parker et al. (1989) is that the latter is not a signalling model. Parker et al. (1989) assume that the condition of the chicks is fixed in an evolutionary time scale and that parental provisioning is fixed. They look for the begging effort that maximises the expected fitness of a chick using chick condition as a parameter. Here, however, we look for signalling and parental investment strategies: rules that determine how much effort chicks will invest in signalling as a function of their condition, and how much food the parents will deliver as a function of the signalling intensity of the chicks. Despite these differences, the two models give similar results:

asymmetries in the competitive ability of the chicks lead to a bias in the food allocation. The more competitive A chick receives a larger share of the food than its sib, although the A chick invests less in signalling (Fig. 1). This pattern reappears in most of the models and is in agreement with the pattern of begging and food distribution in asynchronous broods (Kilner 1995, Price & Ydenberg 1995, Price et al. 1996, Lotem 1998a, Cotton et al. 1999).

When given a choice between investing in two different components of food acquisition, chicks opt to invest in the one yielding the highest payoff. This can lead to somewhat counterintuitive results. Chicks that must allocate their effort between increasing brood provisioning and increasing their share of the food provided (Eq. 8a) invest only in maximising their share of available food. They do not attempt to increase the total amount of food available by displaying to their parent. The reason for this is as follows. If a chick invests in signalling, the two nest mates will share the benefits of this effort, while only one of them is paying the costs. Since every chick benefits from letting its nest mate invest in signalling rather than spending some resources in the enterprise itself, signalling eventually disappears. This is another instance of the "tragedy of the commons".

Davies et al. (1998) report that nestlings from the European cuckoo, Cuculus canorus, mimic in their begging calls the begging calls of an entire brood of their hosts, the reed warbler, Acrocephalus scirpaceus. Lotem (1998b) claims that the difference in begging between reed warbler and cuckoo chicks may arise through a mechanism similar to Model 1. Cuckoo chicks, after ejecting the eggs and newly hatched offspring of their foster parents, remain alone in the nest. They are the only recipients of any food brought to the nest by the parents and they profit from increasing begging intensity because any extra food brought to the nest as a result of their effort will be delivered to them. Reed warbler chicks, on the other hand, are normally raised in broods of five chicks. Hence, Lotem (1998b) argues, reed warbler chicks will benefit little from unilateral increases in their begging intensity: a chick that begs more than its brood mates will have to share the benefits of the increased brood provisioning with its sibs, while paying the costs of the extra effort individually. The results of model 1 (Fig. 3) strengthen the plausibility of Lotem's argument. This argument is related to game-theoretical models of cooperation, which show that cooperation is most likely between two players, and becomes increasingly difficult as the number of players increases (Boyd & Richerson 1988).

The results in Fig. 3 would seem to contradict those of the sibling-competition model. In the sibling-competition model, it was argued that sibling competition could stabilise a signalling system (Rodríguez-Gironés 1999). Here we have shown that if different behaviours determine parental food provisioning and food allocation, chicks will invest only in increasing their share of resources and no signalling will be observed. This result shows once more that a stable signalling system is not necessarily the outcome of parent-offspring conflict: stable communication appears only when we make specific additional assumptions.

In the absence of signalling, the amount of food delivered to the nest must be independent of chick condition, because parents have no possibility to infer the condition of their offspring. As a result, parents adjust their provisioning to the average condition of the chicks. It could be claimed that parents would not bring any food to their chicks in the absence of signalling. This is, clearly, not a logical necessity. It is not, either, a biological necessity: many mothers feed their babies before they start crying. In the absence of signalling, then, parents will bring to the nest the amount of food that maximises their expected fitness. It is true, however, that in most species chicks beg when their parents arrive to the nest. What this tells us is that the assumptions behind Fig. 3 are probably unrealistic. Indeed, it is unlikely that the signalling component of foraging has no effect whatsoever on food allocation. In this respect, Model 1 with $\underline{w}_s > 0$ and Model 2 provide more plausible descriptions of the parent-offspring interaction.

When Eq. 8b applies, the signalling component affects both food provisioning and food allocation. For chick B, increasing its foraging effort has the same effect on its food share regardless of whether the chick increases its investment in the signalling or non-signalling component ($\underline{a}_B = 1$). Since an increase in the signalling component is associated with an increase in food availability, the decision is easy: chick B will invest only in signalling. The same applies to chick A when there are no competitive asymmetries. For $\underline{a} > 1$, however, things need not be so. In this case, chick A faces a delicate trade off: increases in its signalling intensity will increase its share of available food and the amount of food available. But its share of food will increase even more if the same effort is put into non-signalling behaviours only. For low competitive asymmetries, the optimal strategy of chick A is to invest exclusively in signalling. It is only for $\underline{a} = 2$ that chick A starts investing in the non-signalling component of foraging. For larger asymmetries, chick A invests only in non-signalling behaviours.

The results of Model 1 with $\underline{w_s} = \underline{w_h} = 1$ and $\underline{a} > 2$ are similar to those of Rodríguez-Gironés et al. (1998). When Godfray's (1991) model for the evolution of signalling of need in single-chick broods was simulated in a computer, we found that, under some conditions, the signalling Nash equilibrium of the model was unstable. (With "the signalling equilibrium" we refer to the Nash equilibrium in continuously derivable strategies where the behaviour of the chick is condition dependent.) Signalling strategies changed with time, and there was no one-to-one relationship between chick's condition and signalling effort. All the same, at any point in time the signalling strategy of a chick transferred information to the parent, who could adjust its level of investment in an almost-optimal way. These results suggest that we should pay as much attention to the dynamic properties of evolving systems as to their equilibrium points. Models of the evolution of signalling based on neural networks reach similar conclusions (Arak & Enquist 1995; Krakauer & Johnstone 1995). In practice, however, models become very difficult to test if they incorporate the dynamics of the evolutionary process (Frank 1998).

In Model 2 the signalling component affects the amount of food delivered to the brood and the pattern of food allocation. This is similar to Model 1 with $\underline{w_s} > 0$ (e.g. Eq. 8b and Fig. 4). The difference is that, in Model 2, chicks must invest in the signalling and non-signalling components of foraging if they want to obtain any food. Under these conditions, chicks invest more in signalling than in non-signalling behaviours, the difference being greater for chick A. The total foraging effort of chick A is lower than the effort of chick B, and its share of food is greater.

Different assumptions about the mechanism of food allocation lead to different levels of investment in begging behaviours. Rodríguez-Gironés et al. (1996) have shown that, with one-chick broods, expected fitness is higher in the absence than in the presence of begging. This might seem paradoxical, because begging leads to a more efficient distribution (between parent and offspring) of resources. The reason why fitness is lower in the presence of begging is that the cost of begging more than offsets its benefit. It would seem, then, that parents would benefit from decreasing begging costs even if this reduction is associated with a less efficient pattern of food distribution. With the assumptions of the current models, the absence of foraging costs is not evolutionarily stable (Rodríguez-Gironés 1999). But comparison of Figs. 1, 3, 4 and 6 shows that foraging costs are lowest when chicks do not invest in signalling at all (Fig. 3). This suggests that, if parents could determine the mechanism of food allocation, they should favour one similar to Eq. 8a, which leads to the evolution of non-signalling foraging behaviours. In practice, however, we know that the behaviour of nestlings contains information and that parents adjust their effort to the begging level of their brood (reviewed in Kilner & Johnstone 1997). The reason for this discrepancy may be as follows. Parents are better off at an evolutionary equilibrium without signalling than at a signalling equilibrium. Nevertheless, if chicks behave in such a way that they confer information to the parents, neglecting that information is not evolutionarily stable. (A rather different modelling approach suggests that the signalling equilibrium might be efficient for large broods, Johnstone 1999.)

In a number of species, particularly when hatching asynchrony is large and chicks have powerful beaks, older chicks can prevent their siblings from accessing food (for discussion and references, see Mock & Parker 1997). This situation has been modelled by assuming that the oldest chick can determine how much food it takes and how much food it leaves for the rest of the brood. The second oldest takes a share from this food and leaves the rest for its younger sibs, and so on down the dominance hierarchy (Parker et al. 1989; Forbes 1993; Rodríguez-Gironés 1996). These hierarchical models differ in a number of important aspects from the ones developed here. Dominant chicks are assumed to enforce their optimal pattern of food allocation without cost. In our models, chicks must spend some effort in order to obtain their share of resources. More competitive chicks (normally larger chicks) will be able to obtain a certain share with lower investment, but they do need to invest some effort in order to obtain those resources (Parker et al. 1989). The hierarchical models assume that older chicks can dispose of their younger sibs without cost (Forbes 1993;

Rodríguez-Gironés 1996) and that the threat of brood reduction can act as an evolutionary blackmail, leading to a parental investment greater than the one favoured by parents (Rodríguez-Gironés 1996). Rodríguez-Gironés (1996) argues that, in an uncertain world, parents can use the level of aggression within the brood to infer the condition of the brood and to modulate their rate of food provisioning. But none of the hierarchical models incorporates this possibility. In fact, the hierarchical models assume that the condition of the chicks is fixed, so that signalling is irrelevant. To study the interaction between signalling and aggressive behaviour in species with clear brood hierarchies, one would have to proceed as we have done here, but implementing a mechanism of food allocation that describes better the biology of these species.

It should be pointed out that the models considered here are purely functional. Because of this, if certain behaviour of the chicks is correlated with their body condition, and if parents can perceive this behaviour, we have assumed that parents will use the information contained in this behaviour in order to modulate their pattern of investment in the brood. In practice, this need not be so. There are a number of reasons why parents may ignore information contained in the behaviour of their offspring. (i) The information can be redundant. (ii) It can be costly to access the information (for instance, parents might need to inspect their offspring for some time, and it may be better to spend that time foraging). (iii) Or parental behaviour may not be optimal. The development of optimality models does not imply that we believe that functional considerations completely determine the outcome of evolutionary processes. (Indeed, recent findings show that ontogeny plays an important role in the observed begging strategies; Kedar et al. 2000.) Rather, we believe that the results of functional models can be used to develop new research questions. Likewise, it is not because something conveys information that it is a signal. The presence of a prey conveys information to the predator, but it is unlikely to be a signal to the predator advertising the availability of food. For continuous characters (the only ones considered in this paper), however, the level of expression of the character will most often become a signal if a receiver derives information from it, even if the character evolved for a different purpose (for further discussion, see Lotem et al. 1999).

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APPENDIX 1

The following symbols are used in this paper:

a_i: relative competitive ability of chick i. ($a_A \equiv a \geq a_B = 1$.)

c_i: condition of chick i.

F_i: inclusive fitness of chick i.

F_p: inclusive fitness of parent.

h_i: intensity of the non-signalling component of i's foraging strategy.

$h_{i,n}$ ($n = 0 – 2$): coefficients of the polynomial relationship between condition and intensity of the non-signalling component for chick i.

p_n ($n = 0 – 5$): coefficients of the relationship between signalling intensity of young and total parental provisioning.

r_p: coefficient of relatedness between a chick and its parent.

r_s: coefficient of relatedness between sibs.

s_i: intensity of the signalling component of i's foraging strategy.

$s_{i,n}$ ($n = 0 – 2$): coefficients of the polynomial relationship between condition and intensity of the signalling component for chick i.

w_h: linear weight of the non-signalling component of the foraging score (Model 1).

w_s: linear weight of the signalling component of the foraging score (Model 1).

$W_{ch,i}$: fitness of chick i.

W_p: residual parental fitness.

x_i: foraging effort of chick i.

y_i: amount of food received by chick i.

Y_{tot}: total amount of resources brought to the nest by the parent.

$z_i = f(s_i, h_i, a_i)$: foraging score of chick i.

ε: noise parameter (temperature) in the simulated annealing algorithm.

γ: coefficient that determines the rate of decrease of residual parental fitness as investment increases.

APPENDIX 2

To search for a Nash equilibrium, we encode the chick strategies, $s_i(c_i,a)$and $h_i(c_i,a)$, as the coefficients of second-order polynomials in c_i. The polynomials were truncated between 0.001 and 1:

$$\left.\begin{aligned} s_i(c_i;a) &= \min\left(1, \max\left(0.001, s_{i,0}(a) + s_{i,1}(a)\cdot c_i + s_{i,2}(a)\cdot c_i^{\,2}\right)\right) \\ h_i(c_i;a) &= \min\left(1, \max\left(0.001, h_{i,0}(a) + h_{i,1}(a)\cdot c_i + h_{i,2}(a)\cdot c_i^{\,2}\right)\right) \end{aligned}\right\} \quad i = A, B. \qquad \text{(A1)}$$

The parental-investment strategy is encoded as the coefficients p_n (n = 0… 5) of the function:

$$Y_{tot}(s_1, s_2) = \sqrt{\max\left(0, p_0 + p_1 s_1 + p_2 s_2 + p_3 s_1^{\,2} + p_4 s_2^{\,2} + p_5 s_1 s_2\right)}\,. \qquad \text{(A2)}$$

Notice that there is no reason to believe that the Nash equilibrium of the problem is a second-order polynomial: we are, in effect, searching for polynomial approximations to the solution. In the sibling-competition model, where the analytical solution can be derived, this method has proved very useful. Although the begging strategy depends logarithmically on the condition of the chicks, the polynomial approximation calculated by the algorithm is very accurate (Rodríguez-Gironés 1999). We use a square root for the parental strategy because, in the one-chick problem without sibling competition, parental investment increases as the square root of signalling intensity if the fitness functions given in Eqs. 3 and 4 are assumed. The dependency of behaviour on competitive asymmetries is introduced by calculating a different set of coefficients for each level of asymmetry that we investigate.

Given a set of strategies, represented by the coefficients of the foraging strategies ($s_{i,n}$, $h_{i,n}$, i = A, B and n = 0… 2) and the coefficients of the parental strategy (p_n, n = 0… 5), we can calculate the expected fitness of any player (equation 6) as a function of c_A and c_B: first we calculate the foraging efforts according to A1, then total parental provisioning according to A2 and we use (5) and (6) to calculate food allocation and inclusive fitness. This allows us to calculate the expected fitness of a strategy (in this paper, we assume that c_i can take values 1.0, 1.2… 3.0 with equal probability). Starting from an arbitrary set of strategies, we calculate the expected fitness of the parent. We then try 25 random mutations and calculate their average fitness. (In a mutant strategy, a random term, normally distributed with mean 0 and standard deviation 0.01 is added to each coefficient with probability 0.25.) If one of these strategies has an average fitness higher than the initial strategy, the mutant strategy substitutes the old one. The same process is repeated for the strategies of the chicks, and the entire cycle iterated until the algorithm converges. (Operationally, we say that the algorithm converges if, in 5,000 iterations, the foraging strategies have changed, on average, less than 0.1%.) At this point none of the players can increase its fitness by a unilateral modification of its behaviour: we have found a (local) Nash equilibrium.

As explained so far, the algorithm implements a hill-climbing maximisation procedure. (If we imagine a maximisation problem as the search for a mountain top in a multidimensional landscape, a hill climbing algorithm is one that only moves upwards in the landscape.) Hill climbing leads to a local maximum that, in a multidimensional space, is unlikely to represent the global maximum of the function. (In a complex landscape, going uphill will eventually take us to the top of the mountain where we started, but only by chance will this be the highest mountain in the area.) To improve the performance of the algorithm we implement some sort of simulated annealing. In this approach, mutations leading to a decrease in expected fitness (downhill steps) are accepted with some (small) probability. The probability decreases with the difference in expected fitness between the two strategies and with the number of iterations. In particular, we define a noise parameter $\underline{\varepsilon}$, which we initialise to $\underline{\varepsilon} = 1$ and we multiply by 0.999 after each iteration. If the fitness of a mutant strategy is greater than the fitness of the original strategy, the mutation is accepted. If it is smaller, we compare the fitness difference with a random variable, exponentially distributed with mean $\underline{\varepsilon}$. The mutation is accepted if the fitness difference is smaller than the random variable. Hence, we start our search accepting downhill steps with a relatively large probability: these downhill steps are required in order to get away from local maxima and approach the absolute maximum of the function. After some iterations (when, presumably, we are close to the global maximum) downhill steps become less and less likely, until the algorithm becomes essentially a hill-climbing one. Simulated annealing can work well provided that the pattern of “cooling” (changes in the probability of accepting downhill steps as the algorithm proceeds) is properly chosen, but there is no guarantee that it will converge to the global maximum. (In a multidimensional space, no algorithm –other than point by point sampling of the entire space-- guarantees convergence to the global maximum of a general function. For further discussion, see Press et al. 1992.)

In the sibling-competition model, there was a single Nash equilibrium with continuous strategies, and that equilibrium was a global attractor (Rodríguez-Gironés 1999). For some versions of the model explored in this paper (Model 1), however, things are otherwise: it sometimes happens that begging effort goes on increasing until expected fitness is negative. Although the possibility of such runaway evolutionary processes is intriguing, we want to concentrate on equilibrium points. Hence, if the foraging strategy of chick i was such that s_i (c_i) = 1 (or h_i (c_i) = 1) for all c_i, the strategy was converted into s_i (c_i) = 0.001 (or h_i (c_i) = 0.001) for all c_i. If the signalling component was altered, the parental strategy was adjusted so that food provisioning did not change. At other times, either the signalling or hidden component was equal to its lowest value for all conditions. Because of the truncation in Eq. A1, there are infinitely many sets of coefficients that code for this strategy, and there is no selection pressure to maintain one set of coefficients rather than another. The coefficients can, in principle, change by drift. But some coefficients make it virtually impossible for the foraging effort to become positive again. (Imagine that $s_{A,0} = s_{A,1} = s_{A,2} = -10$. No small mutation can bring back this strategy into the positive domain.) To avoid this problem, if a mutant strategy had foraging effort below the minimum threshold (0.001, equation A1) for all conditions, the coefficients were set to $b_{i,0} = 0.001$, $b_{i,1} = b_{i,2} = 0$ (where b stands for either s or h).

FIGURE LEGENDS

Figure 1. Evolutionarily stable strategies resulting from Model 0. Foraging effort (signalling intensity) of chicks A and B as a function of their condition (left) and proportion of the parentally provided food allocated to chick B as a function of the condition of both chicks (right) for $\underline{a} = 1$ (top), $\underline{a} = 1.5$ (middle) and $\underline{a} = 2$ (bottom). For $\underline{a} = 1$ (top left) both chicks use the same strategy, and this strategy appears with empty symbols.

Figure 2. Average foraging effort of chicks A and B as a function of $\underline{w_s}$ when $\underline{w_h} = 1$ (left) and as a function of $\underline{w_h}$ when $\underline{w_s} = 1$ (right) for $\underline{a} = 1$ (top), $\underline{a} = 1.5$ (middle) and $\underline{a} = 2$ (bottom). Empty symbols represent chick A, filled symbols chick B. Circles represent investment in signalling behaviours and diamonds in non-signalling behaviours. The solid line connects points in the ascending series ($\underline{w}$ goes from 0 to 1) and the dashed line connects points in the descending series ($\underline{w}$ goes from 1 to 0). Notice that, when both chicks use the same strategy, this strategy appears with empty symbols.

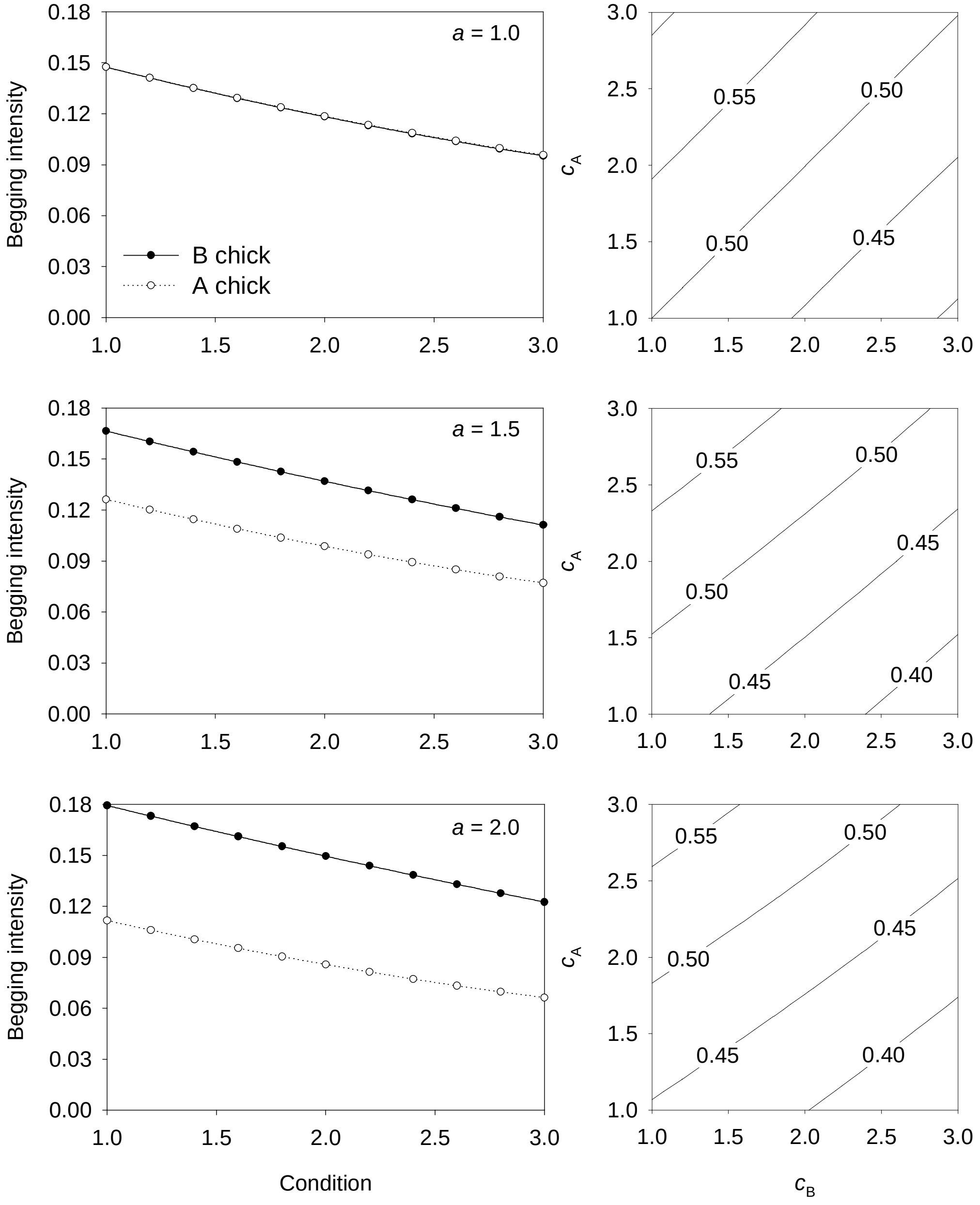
Figure 3. Evolutionarily stable strategies resulting from Model 1 with $\underline{w_s} = 0$ and $\underline{w_h} = 1$. Foraging effort (non-signalling) of chicks A and B as a function of their condition (left) and proportion of the parentally provided food allocated to chick B as a function of the condition of both chicks (right) for $\underline{a} = 1$ (top), $\underline{a} = 1.5$ (middle) and $\underline{a} = 2$ (bottom). For $\underline{a} = 1$ (top left) both chicks use the same strategy, and this strategy appears with empty symbols.

Figure 4. Evolutionarily stable strategies resulting from Model 1 with $\underline{w_s} = \underline{w_h} = 1$ and $\underline{a} = 2$. Foraging effort of chicks A and B as a function of their condition (left) and proportion of the parentally provided food allocated to chick B as a function of the condition of both chicks (right). Chick B (filled circles) invests only in signalling, and chick A invests in signalling (empty circles) and non-signalling (empty triangles) behaviours.

Figure 5. Behavioural strategies resulting from Model 1 with $\underline{w_s} = \underline{w_h} = 1$ and $\underline{a} = 3$. The top panel represents the average (± SD) foraging effort of chicks A (non-

signalling, empty circles) and B (signalling, black triangles) as a function of their condition. The averages were calculated over 25 points at 5,000 generation intervals, 10 points at 500 generation intervals and 25 points at 10 generation intervals. The middle panel plots average investment in foraging by chicks B (signalling) vs. investment by chick A (non-signalling), and the bottom panel plots average parental investment vs. average investment in signalling by chick B. In the two lower panels, each dot is one point of the time series.

Figure 6. Evolutionarily stable strategies resulting from Model 2. Foraging effort of chicks A and B as a function of their condition (left) and proportion of the parentally provided food allocated to chick B as a function of the condition of both chicks (right) for $\underline{a} = 1$ (top), $\underline{a} = 1.5$ (middle) and $\underline{a} = 2$ (bottom). Empty and filled symbols represent chicks A and B, respectively. Circles represent investment in non-signalling behaviours and triangles investment in signalling foraging behaviours.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a = 1.5
a = 2.0
Begging intensity
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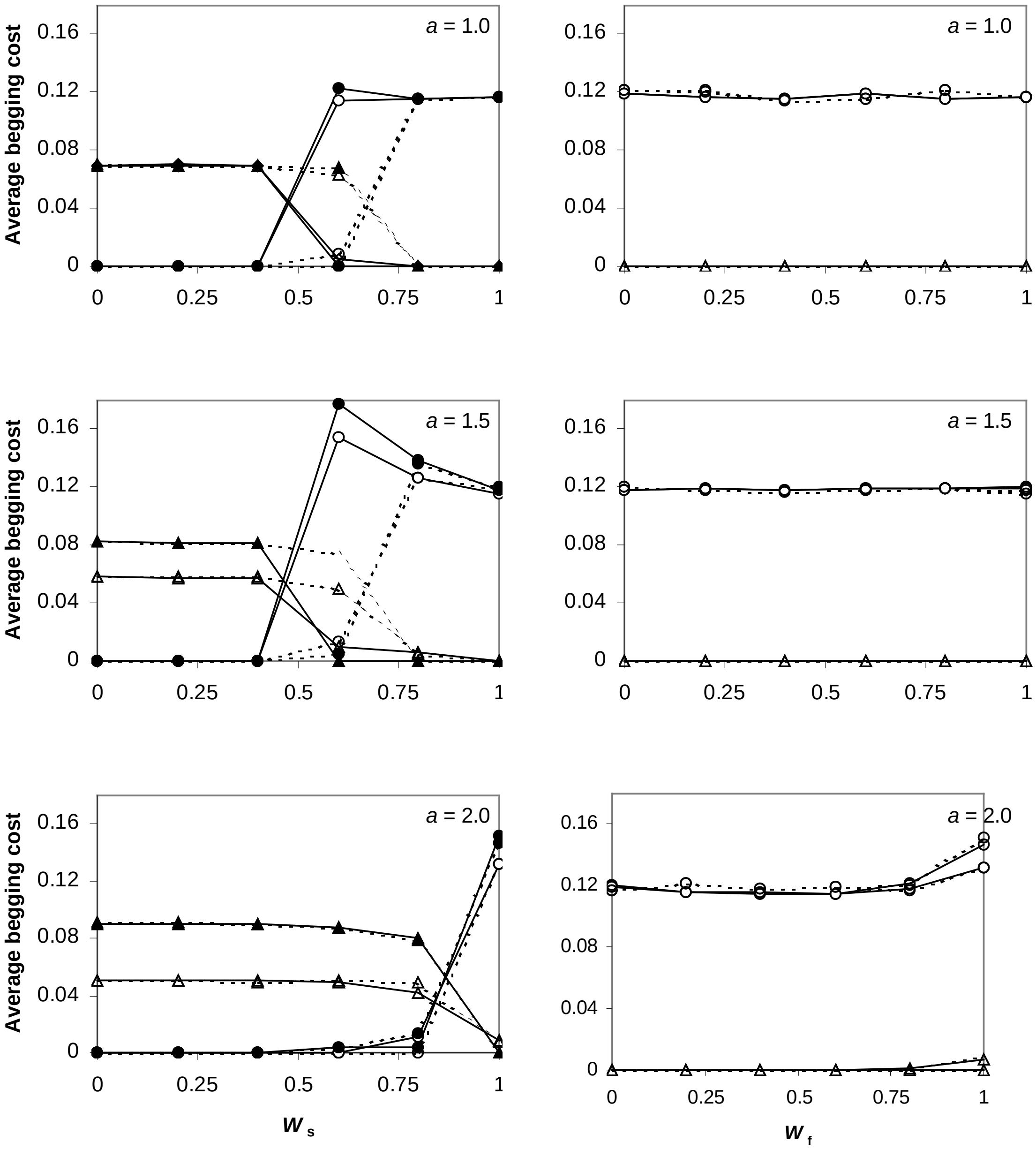
0.15
0.12
0.09
0.06
0.03
0.00
B chick
A chick
Condition
1.0
1.5
2.0
2.5
3.0
c_A
c_B
0.55
0.50
0.45
0.40


a = 1.0
a = 1.0
a = 1.5
a = 1.5
a = 2.0
a = 2.0
Average begging cost
Average begging cost
Average begging cost
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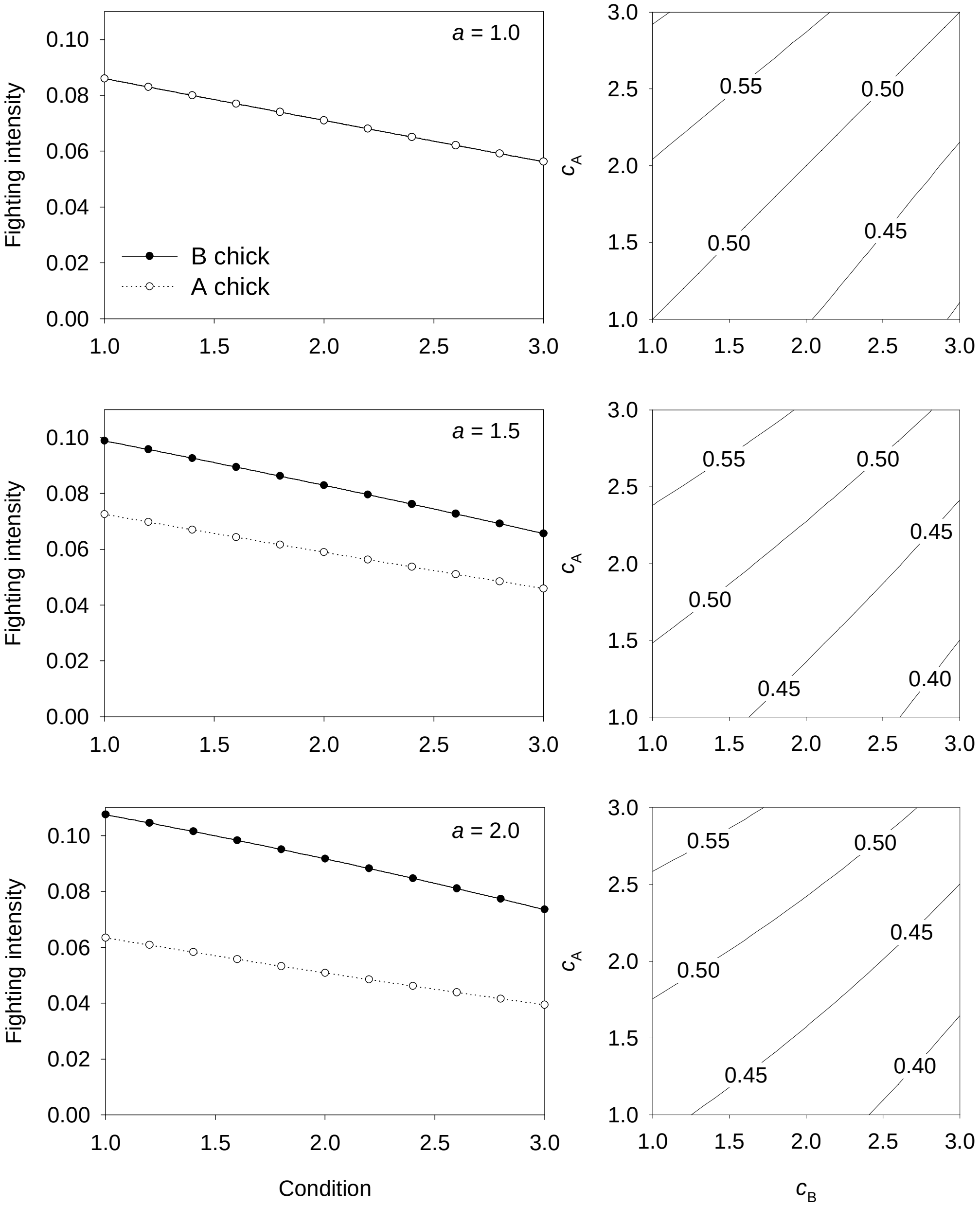
0.04
0.08
0.12
0.16
0
0.25
0.5
0.75
1
W s
W f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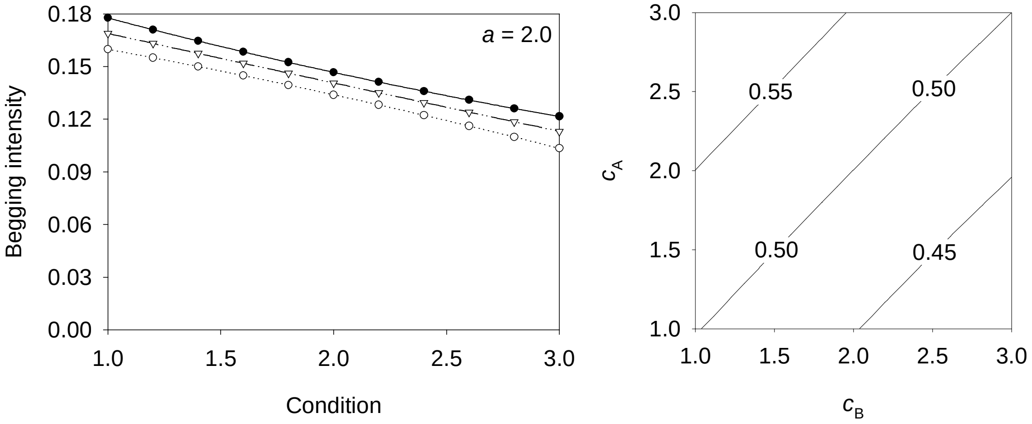
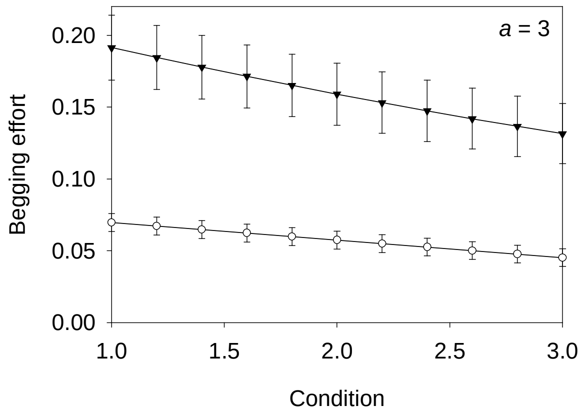
a = 2.0
Fighting intensity
0.00
0.02
0.04
0.06
0.08
0.10
B chick
A chick
Condition
1.0
1.5
2.0
2.5
3.0
c_A
c_B
0.55
0.50
0.45
0.40


Begging intensity
0.18
0.15
0.12
0.09
0.06
0.03
0.00
1.0
1.5
2.0
2.5
3.0
Condition
a = 2.0
c_A
3.0
2.5
2.0
1.5
1.0
0.55
0.50
0.50
0.45
1.0
1.5
2.0
2.5
3.0
c_B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Begging effort
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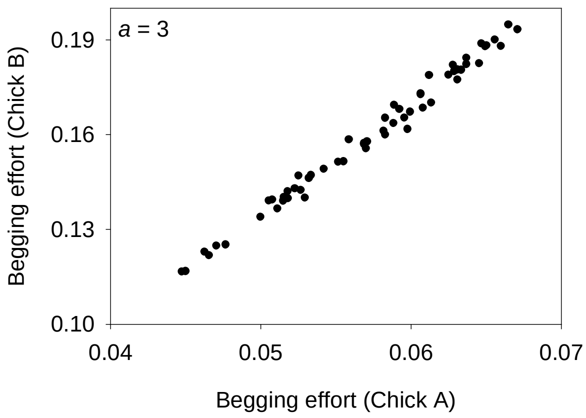
0.15
0.10
0.05
0.00
1.0
1.5
2.0
2.5
3.0
Condition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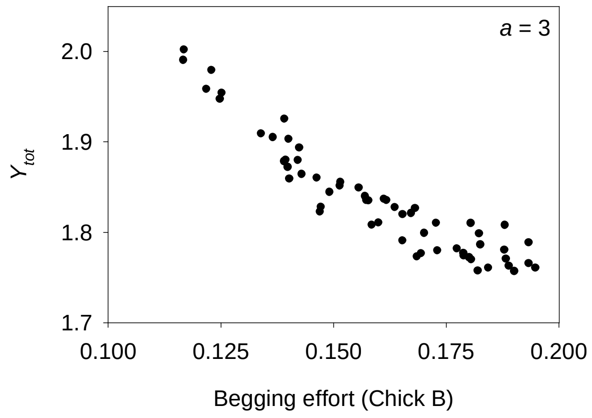
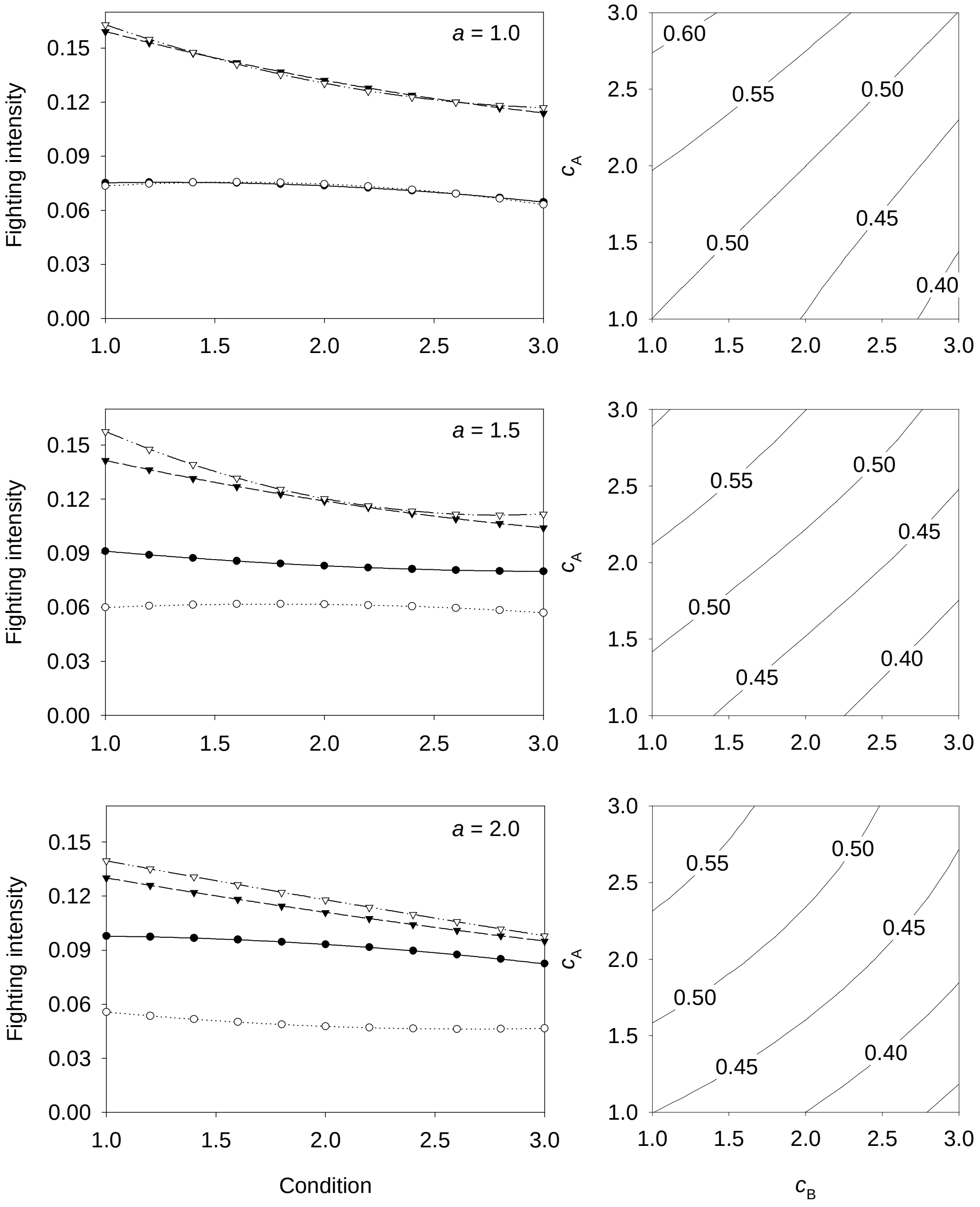
Begging effort (Chick B)
0.19
0.16
0.13
0.10
0.04
0.05
0.06
0.07
Begging effort (Chick A)


a = 3
Y_{tot}
2.0
1.9
1.8
1.7
0.100
0.125
0.150
0.175
0.200
Begging effort (Chick B)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a = 1.5
a = 2.0
Fighting intensity
0.00
0.03
0.06
0.09
0.12
0.15
1.0
1.5
2.0
2.5
3.0
Condition
c_A
c_B
0.60
0.55
0.50
0.45
0.40