



Role of begging and sibling competition in foraging strategies of nestlings

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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 nonsignalling behaviours that are not perceived by the parents. We explore different ways in which signalling, nonsignalling behaviours and competitive asymmetries might interact to determine food allocation. In Model 0 only signalling affects food allocation. More competitive chicks beg less and obtain a greater share of the food than their smaller siblings. In Model 1, a linear combination of signalling and nonsignalling behaviours determines food allocation. When nonsignalling behaviours are the main determinant of food allocation, chicks do not signal and parents deliver a fixed amount of food. 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 nonsignalling behaviours. In Model 2, the product of signalling and nonsignalling intensities determines food allocation. Larger chicks invest more in signalling and less in nonsignalling behaviours. Larger chicks get more food than their siblings. Overall 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.

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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. Rodríguez-Gironés (1999) has shown that introducing direct sibling competition stabilizes the signalling equilibrium; we refer to this model as the sibling

competition model. The possibility that other factors, as yet ignored, may also stabilize the signalling equilibrium deserves further study.

The sibling competition model works in the following way. 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 in Appendix 1.) This begging effort is a function of the condition of the chick, c_i . The parent observes the begging effort of each chick and gets information about 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 maximizing the expected fitness of the parent. Following Parker et al.

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(1989), the model assumes that the amount of food allocated to chick i , y_i , is given by:

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

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

(1) It assumes that the parent cannot influence the allocation of food between the two chicks but in the majority of species the parent does have some control over food allocation.

(2) It assumes that the parent observes all efforts made by the chicks to get food, and makes 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 cannot be perceived (or 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 their behaviour.

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 and those that have an effect on food allocation but do not affect food provisioning. We refer to the set of behaviours that have an effect on food intake 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. We refer to these behaviours as the signalling component of the foraging strategy. Behaviours that affect food allocation but cannot be perceived by the parent we refer to as the nonsignalling component of the chick's foraging strategy. Clearly, nonsignalling behaviours cannot affect parental food provisioning. Signalling behaviours, on the other hand, may affect both parental food provisioning and food allocation between siblings (as in the sibling competition model).

The food intake of a nestling is known to be determined by a number of factors. The models developed here should help us understand 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 consider 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/s), pitch and intensity of the calls can contain information about 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.) Similarly, chicks with stretched body postures receive more food than prostrate chicks. Posture, then, is a component of the foraging strategy of nestlings. It is unclear whether posture affects the amount of food that parents deliver to the nest: it may be a nonsignalling 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 nestmates. (When the chicks are close to fledging, one of the nestlings can block the nest entrance and monopolize 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 nonsignalling 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 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', 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, h_i (for hidden). Thus, the total foraging effort of a chick is the sum

$$x_i = s_i + h_i. \quad (2)$$

In the context of this two-component model of parent-offspring interactions, we avoid the use of the term 'begging'. Behaviours belonging to the signalling component of the foraging strategy can unambiguously be termed begging behaviours. But it is not so clear whether the nonsignalling component of the chick's foraging strategy can be classified as begging. 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 simply talk of the

foraging strategy and its signalling and nonsignalling components.

Within this framework, we consider three different models, corresponding to different ways in which signalling and nonsignalling foraging behaviours can interact to determine the pattern of food allocation. Model 0 is a simple extension of the sibling competition model: the nonsignalling 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 play a key role in subsequent models. In Model 1, food allocation is determined by a linear combination of the signalling and nonsignalling 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 nonsignalling components of foraging (or in both), but in Model 2 chicks must invest in signalling and nonsignalling 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 nonsignalling component is to modulate, or 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. (Note, though, that in some situations gaping may be a signalling behaviour, [Kilner et al. 1999](#).) In both models, we consider the effect of competitive asymmetries between the chicks.

None of the models that we consider, however, applies to situations where sibling competition results in escalated fighting that can lead to physical damage of the chicks. If older chicks peck their younger siblings 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 2 for details).

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

$$W_{\text{ch}} = 1 - e^{-c_i y_i} - x_i, \quad (3)$$

where the total effort x_i is the sum specified in equation 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 equation 5. 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 \(1991, 1995\)](#) gave the rationale behind this fitness function. The residual fitness of the parent (expected fitness from future broods) is modelled by

$$W_p = 1 - \gamma \times Y_{\text{tot}}^2. \quad (4)$$

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](#)), residual fitness was assumed to decrease linearly with investment in the current brood. Although this assumption has no special implications when modelling the behaviour of single chicks, in multichick 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 nonsignalling component of foraging, h_i . We 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):

$$y_i = Y_{\text{tot}} \frac{z_i}{z_A + z_B}. \quad (5)$$

Our aim is to find functions $s_i = s_i(c_i; a)$, $h_i = h_i(c_i; a)$ and $Y_{\text{tot}} = Y(s_A, s_B; a)$ 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

$$\left. \begin{aligned} F_A &= W_{\text{ch},A} + r_s \times W_{\text{ch},B} + r_p \times W_p \\ F_B &= r_s \times W_{\text{ch},A} + W_{\text{ch},B} + r_p \times W_p \\ F_p &= W_{\text{ch},A} + W_{\text{ch},B} + W_p \end{aligned} \right\} \quad (6)$$

where r_s and r_p represent the coefficients of relatedness between a chick and its sibling and parent, respectively. (Note 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 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

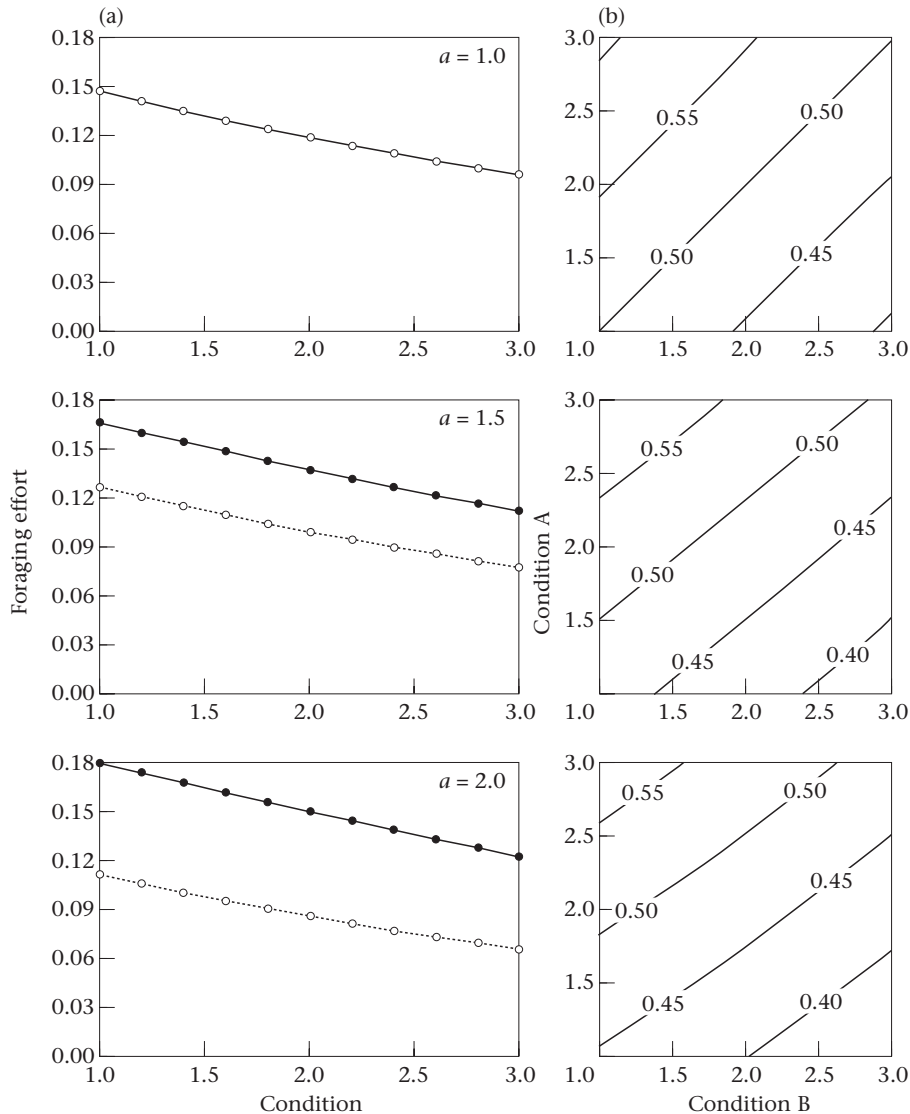


Figure 1. Evolutionarily stable strategies resulting from Model 0. (a) Foraging effort (signalling intensity) of chicks A (○) and B (●) as a function of their condition and (b) proportion of the parentally provided food allocated to chick B as a function of the condition of both chicks. The relative competitive ability of chick A is $a=1$, $a=1.5$ and $a=2$. For $a=1$ both chicks use the same strategy (○).

(or behaviour) of its sibling. 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). Furthermore, 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 nonsignalling component of foraging and let the foraging score be

$$z_i = a_i \times s_i, \quad (7)$$

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 sibling.

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 nonsignalling component of the foraging strategy: behaviours that affect food allocation but not food provisioning. In Model 1, we assume that the signalling and nonsignalling components interact additively to produce the foraging score. This can be done in a number of ways.

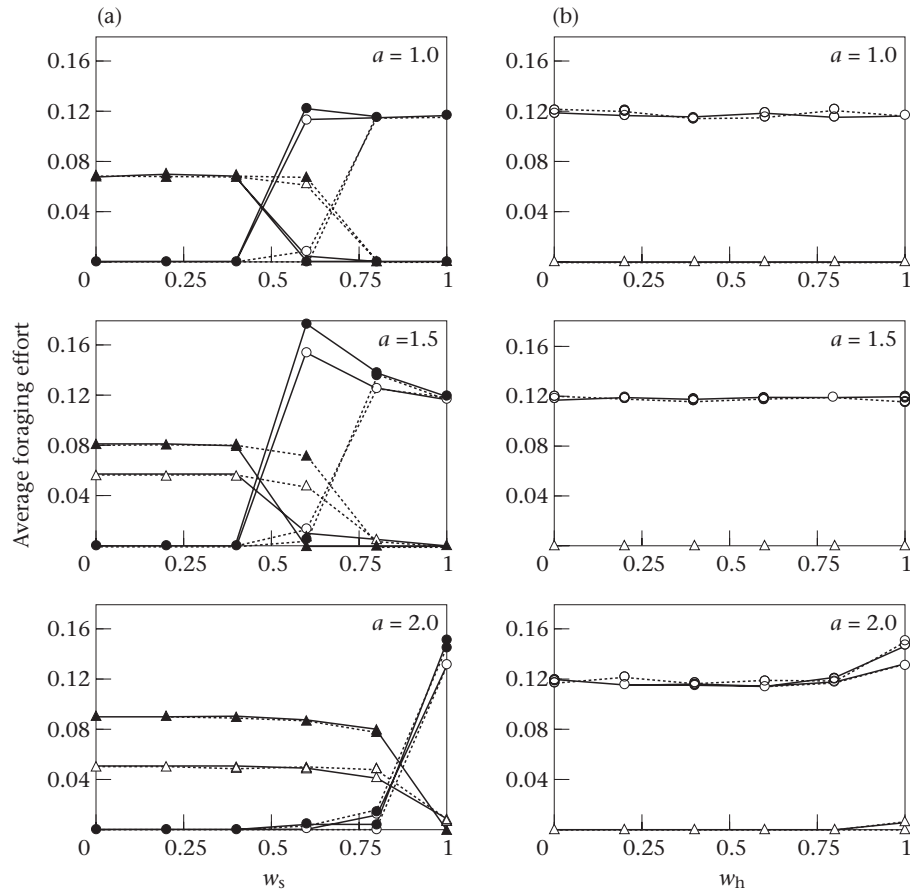


Figure 2. Average foraging effort of chicks A and B as a function of the linear weight of the signalling component of the foraging score, w_s , when the linear weight of the nonsignalling component of the foraging score was $w_h=1$ (a) and as a function of w_h when $w_s=1$ (b). The relative competitive ability of chick A is $a=1$, $a=1.5$ and $a=2$. \circ , \triangle : Chick A; \bullet , \blacktriangle : chick B. \circ , \bullet : Investment in signalling behaviours; \triangle , \blacktriangle : investment in nonsignalling behaviours. The solid line connects points in the ascending series (w goes from 0 to 1) and the dashed line connects points in the descending series (w goes from 1 to 0). Note that, when both chicks use the same strategy, this strategy appears as open symbols.

In particular, we consider the following expressions for the foraging score:

$$z_i = a_i \times h_i \quad (8a)$$

and

$$z_i = s_i + a_i \times h_i. \quad (8b)$$

These two expressions are particular cases of the more general model

$$z_i = w_s \times s_i + w_h \times a_i \times h_i, \quad (8c)$$

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 nonsignalling intensities, respectively, of the foraging strategy of chick i . When $w_s=0$ (equation 8a), the signalling component determines food provisioning and the nonsignalling component determines food allocation. When $w_s=w_h$ (equation 8b) food allocation is equally determined by the signalling and nonsignalling 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 a starting point, we increase w_h by 0.2 . With this solution as a starting point, we increase w_h to 0.4 , and so on until $w_h=1$ (equation 8b). From here we decrease w_s in steps of 0.2 (with $w_h=1$ all the time) until we reach $w_s=0$ (equation 8a). We now proceed backwards, first increasing w_s to 1 and then decreasing 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 .

For most conditions investigated, chicks invest only 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 nonsignalling 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 nonsignalling behaviours increases with the asymmetry in competitive ability (Fig. 2). Between these two regions, there is a narrow transition zone where chicks invest

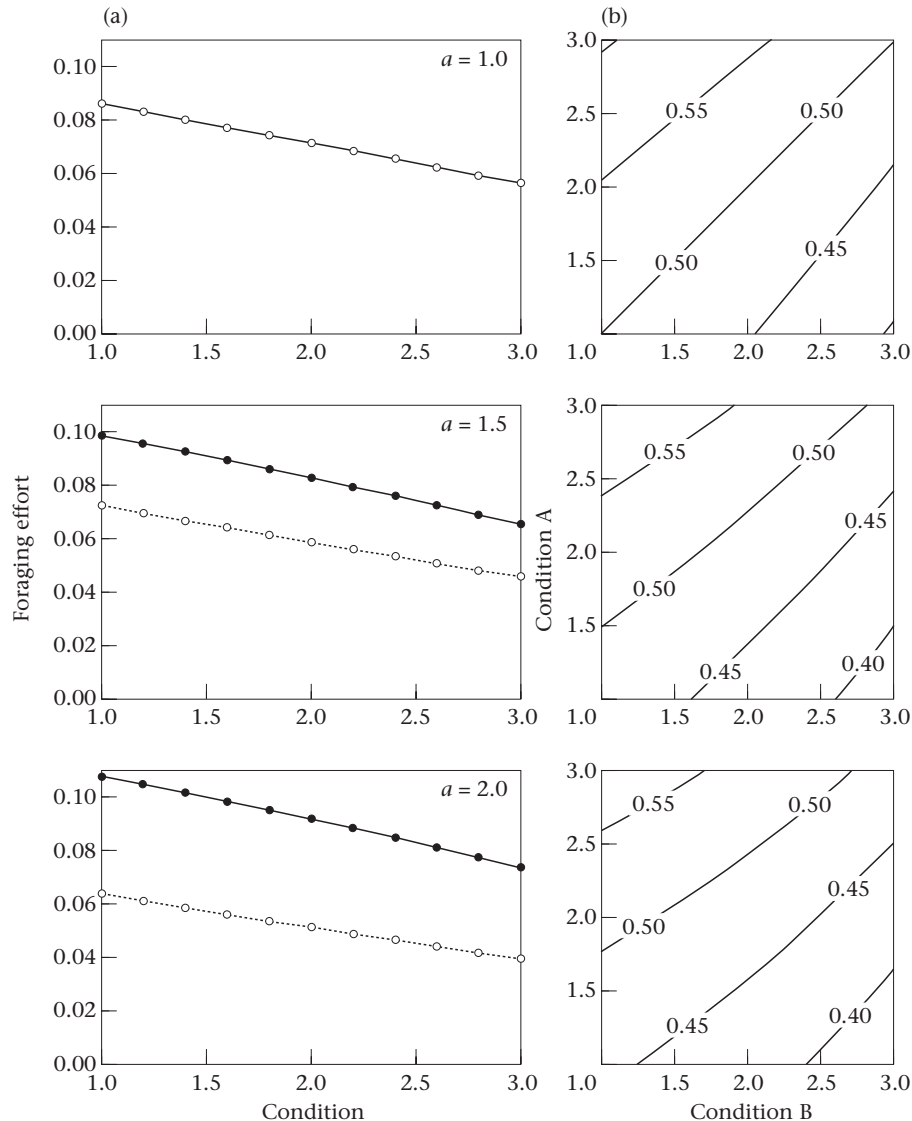


Figure 3. Evolutionarily stable strategies resulting from Model 1 when the linear weight of the signalling component of the foraging score is $w_s=0$ and the linear weight of the nonsignalling component of the foraging score is $w_h=1$. (a) Foraging effort (nonsignalling) of chicks A (\circ) and B (\bullet) as a function of their condition and (b) proportion of the parentally provided food allocated to chick B as a function of the condition of both chicks. The relative competitive ability of chick A is $a=1$, $a=1.5$ and $a=2$. For $a=1$ both chicks use the same strategy (\circ).

mainly in signalling, but there is also some investment in nonsignalling foraging behaviours. This transition zone is associated with an overall increase in foraging effort. Chick A invests slightly more than chick B in nonsignalling 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 found only 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. 1a) except when $a=2.0$ (Fig. 4).

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 1 million generations). In fact, we have already noted (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 nonsignalling 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.

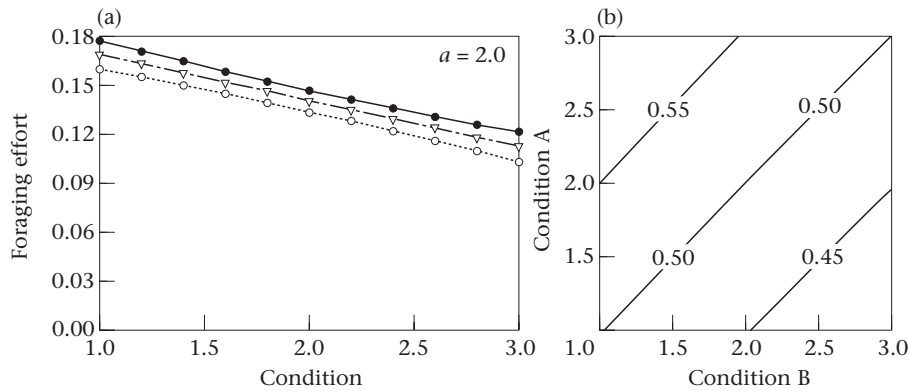


Figure 4. Evolutionarily stable strategies resulting from Model 1 when the linear weights of the signalling and nonsignalling components of the foraging score are $w_s = w_h = 1$ and the relative competitive ability of chick A is $a = 2$. (a) Foraging effort of chicks A and B as a function of their condition and (b) proportion of the parentally provided food allocated to chick B as a function of the condition of both chicks. Chick B (●) invests only in signalling, and chick A invests in signalling and nonsignalling behaviours (○: signalling; ▽: sum of signalling and nonsignalling behaviours).

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. 5b). Similarly, 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. 5c). For intermediate competitive asymmetries ($a = 2.2, 2.4 \dots$) the algorithm does not converge either (in 500 000 generations): chick A uses a mixture of signalling and nonsignalling behaviours, and the relative intensity of nonsignalling increases with the level of asymmetry.

It is possible to derive an analytical condition for the stability of the nonsignalling 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 maximize its expected fitness by minimizing its total foraging effort, x_i . Investing solely in nonsignalling behaviours will minimize foraging cost if $a_i w_h \geq w_s$. Inspection of Fig. 2 shows that the nonsignalling equilibrium always satisfies this condition. However, there are regions of the parameter space where this condition is satisfied and our algorithm does not converge to the nonsignalling equilibrium. It is not difficult to understand why. First, the stability of the nonsignalling equilibrium does not imply that there is no stable signalling equilibrium. Second, 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 nonsignalling equilibrium becomes more stringent.

MODEL 2

In Model 2 we consider the possibility that the product of the signalling and nonsignalling efforts determines the

foraging score. (Arnon Lotem suggested this possibility.) Both components, signalling and nonsignalling, 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

$$z_i = a_i \times s_i \times h_i. \quad (9)$$

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 is invested in signalling and one-third in other behaviours that are not detected by the parent. In asymmetric broods ($a > 1$) chick A invests less in nonsignalling behaviours and slightly more in signalling than its sibling.

DISCUSSION

Model 0 extends the sibling competition model by introducing asymmetries in competitive abilities between the siblings. 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) assumed that the condition of the chicks is fixed in an evolutionary time scale and that parental provisioning is fixed. They looked for the begging effort that maximizes the expected fitness of a chick, using chick condition as a parameter. Here, however, we looked 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 sibling, 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

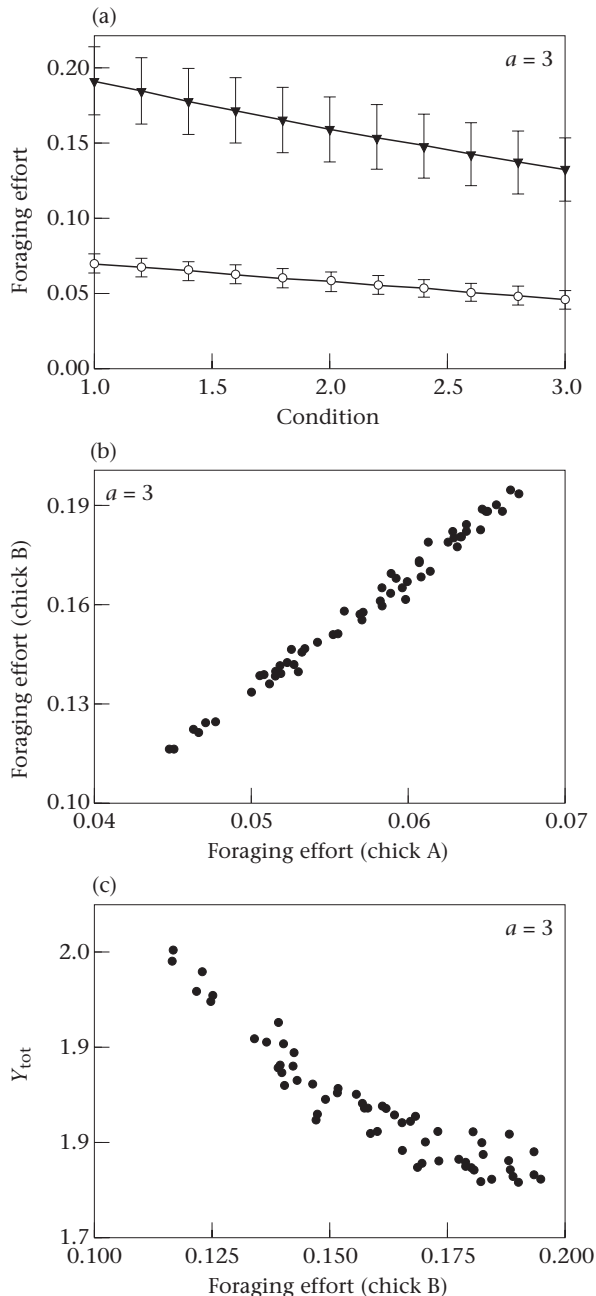


Figure 5. Behavioural strategies resulting from Model 1 when the linear weights of the signalling and nonsignalling components of the foraging score are $w_s = w_n = 1$ and the relative competitive ability of chick A is $a = 3$. (a) The foraging effort ($\bar{x} \pm SD$) of chicks A (non-signalling; \circ) and B (signalling; \blacktriangledown) as a function of their condition. The averages were calculated over 25 points at 5000-generation intervals, 10 points at 500-generation intervals and 25 points at 10-generation intervals. (b) The average investment in foraging by chicks B (signalling) versus investment by chick A (nonsignalling). (c) The average parental investment, Y_{tot} , versus average investment in signalling by chick B. In (b) and (c) each dot is one point of the time series.

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 (equation 8a) invest only in maximizing 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 nestmates will share the benefits of this effort, while only one of them is paying the costs. Since every chick benefits from letting its nestmate 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) reported that nestlings of the European cuckoo, *Cuculus canorus*, mimic the begging calls of an entire brood of their hosts, the reed warbler, *Acrocephalus scirpaceus*. Lotem (1998b) claimed 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 reared in broods of five chicks. Hence, Lotem (1998b) argued, reed warbler chicks will benefit little from unilateral increases in their begging intensity: a chick that begs more than its broodmates will have to share the benefits of the increased brood provisioning with its siblings, 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 which sibling competition could stabilize 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 opportunity 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

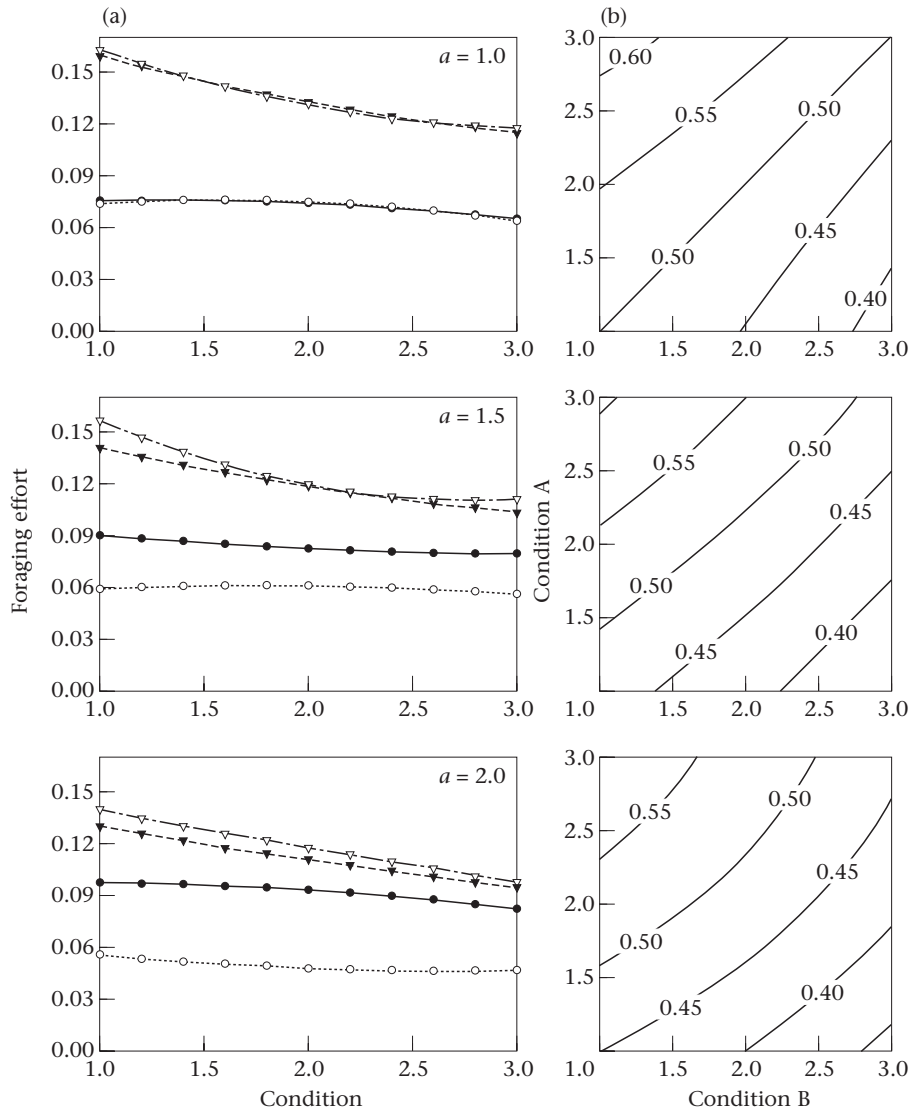


Figure 6. Evolutionarily stable strategies resulting from Model 2. (a) Foraging effort of chicks A and B as a function of their condition and (b) proportion of the parentally provided food allocated to chick B as a function of the condition of both chicks. The relative competitive ability of chick A is $a=1$, $a=1.5$ and $a=2$. ○, ∇: Chick A; ●, ▼: chick B. ○, ●: Investment in nonsignalling behaviours; ∇, ▼: investment in signalling foraging behaviours.

start crying. In the absence of signalling, then, parents will bring to the nest the amount of food that maximizes their expected fitness. It is true, however, that in most species chicks beg when their parents arrive at 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 $w_s > 0$ and Model 2 provide more plausible descriptions of the parent–offspring interaction.

When equation 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 nonsignalling component ($a_B=1$). 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 $a > 1$, however, 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 nonsignalling behaviours only. For low competitive asymmetries, the optimal strategy of chick A is to invest exclusively in signalling. It is only for $a=2$ that chick A starts investing in the nonsignalling component of foraging. For larger asymmetries, chick A invests only in nonsignalling behaviours.

The results of Model 1 with $w_s=w_h=1$ and $a > 2$ 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. (By 'the signalling equilibrium', we mean 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 the chick's condition and signalling effort. Nevertheless, 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 $w_s > 0$ (e.g. equation 8b and Fig. 4). The difference is that, in Model 2, chicks must invest in both the signalling and nonsignalling components of foraging if they want to obtain any food. Under these conditions, chicks invest more in signalling than in nonsignalling 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. With one-chick broods, expected fitness is higher in the absence than in the presence of begging (Rodríguez-Gironés et al. 1996). 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 equation 8a, which leads to the evolution of nonsignalling 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 gaining access to 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 siblings, 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 to obtain those resources (Parker et al. 1989). The hierarchical models assume that older chicks can dispose of their younger siblings 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) argued 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 better describes the biology of these species.

Note 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 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. (1) The information can be redundant. (2) It can be costly to get the information (for instance, parents might need to inspect their offspring for some time, and it may be better to spend that time foraging). (3) 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. Similarly, 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 . ($a_A \equiv a_B = 1$.)

c_i : condition of chick i .

F_i : inclusive fitness of chick i .

F_P : inclusive fitness of parent.

h_i : intensity of the nonsignalling component of i 's foraging strategy.

$h_{i,n}$ ($n=0-2$): coefficients of the polynomial relationship between condition and intensity of the nonsignalling 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 siblings.

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_n : linear weight of the nonsignalling 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 are truncated between 0.001 and 1:

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

The parental investment strategy is encoded as the coefficients p_n ($n=0 \dots 5$) of the function:

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

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 equations 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 $n=0 \dots 2$) and the coefficients of the parental strategy (p_n , $n=0 \dots 5$), 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 \dots 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 5000 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 maximization procedure. (If we imagine a maximization 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 ε , which we initialize to $\varepsilon=1$ 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 ε . 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, 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 equation 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 this strategy back 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).