

# Sibling negotiation

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Current discussions of offspring begging typically assume either that it is a signal directed at parents or that it represents a form of scramble competition to gain access to them. However, offspring might also display to inform nest mates that they will contest the next food item to be delivered; in other words, begging (possibly in the absence of parents) might serve purely as a form of negotiation among siblings. Here, we develop a game-theoretical model of this possibility. We assume that offspring vary in their need for food, which influences how intensely they compete for access to parents. Before parental arrival, however, young may exchange signals informing each other of their state, and these signals may influence their subsequent competitive behavior. We focus on the possibility that a costly display during the “negotiation” phase can serve to inform rivals of a chick’s need for resources and thereby deter them from competing intensely when the parent arrives. We show that this form of negotiation is more likely to prove stable when the food delivered by parents is indivisible, and when it is hard for one chick to monopolize access to resources. Investment in negotiation (as opposed to competition) is predicted to increase with nestling relatedness; in addition, all other things being equal, hungrier chicks are expected to invest relatively more effort in displaying to their rivals, whereas weaker or smaller chicks are expected to invest less. *Key words:* begging, handicap principle, parent-offspring conflict, sibling competition, sibling negotiation, signaling. [*Behav Ecol* 14:780–786 (2003)]

Offspring are commonly selected to demand more resources than parents are selected to provide (Godfray, 1995a; Lessells and Parker, 1999; Macnair and Parker, 1978; Mock and Parker, 1997; Parker, 1985; Parker and Macnair, 1978, 1979). Moreover, each individual in a brood of young is selected to demand a greater share of these resources than its siblings are selected to yield (Macnair and Parker, 1979; Mock and Parker, 1997). Family conflicts over resource provision and allocation find expression in the vigorous begging behavior of nestling birds, which includes loud calling, posturing, and jostling for position (Kilner and Johnstone, 1997; Mock and Parker, 1997).

Current discussions of begging tend to assume either that it is a signal directed at parents (Godfray, 1991, 1995b; Godfray and Johnstone, 2000; Kilner and Johnstone, 1997) or that it represents a form of scramble competition to gain access to them (Macnair and Parker, 1978, 1979; Mock and Parker, 1997; Parker and Macnair, 1978, 1979; for the possibility of begging behavior that combines these functions, see Rodriguez-Girones, 1999). However, although the arrival of parents does elicit intense activity on the part of the brood, begging may also occur in their absence (Budden and Wright, 2001; Clemmons, 1995; Leonard and Horn, 2001; Price and Ydenberg, 1996; Roulin et al., 2000). Roulin et al. (2000; see also Roulin, 2001a) suggest that offspring vocalize to inform nest mates that they will contest the next food item to be delivered; in other words, begging may serve as a signal directed at siblings, rather than (or in addition to) a form of scramble competition or a signal directed at parents (for an alternative explanation of begging in the absence of parents as an “error,” see Leonard and Horn, 2001; Roulin, 2001b).

The possibility of communication between nest mates has received little attention in formal models of begging (Roulin, 2001a; Roulin et al., 2000). For instance, models of sibling competition typically assume either that offspring do not vary in need, so that there is nothing for them to communicate to

one another (see Macnair and Parker, 1978, 1979; Parker and Macnair, 1978, 1979), or that if offspring do vary in need, they do not adjust their own begging in relation to the condition or behavior of competitors (see Johnstone, 1999; Rodriguez-Girones, 1999; Rodriguez-Girones et al., 2001). An exception is Godfray’s (1995b) influential model of competitive begging, in which offspring display in order to advertise to parents their need for food, but may also adjust their own behavior in response to that of a nest mate. This analysis does include an element of negotiation; however, no distinction is drawn between begging directed at parents and at nest mates.

Here, we develop a game-theoretical model of sibling negotiation, in which we treat these two aspects of begging separately (assuming that negotiation precedes competition). In our model, offspring vary in their need for food, which influences how intensely they compete for access to parents (who lack full control of food allocation). Before the arrival of the parents, however, young may exchange signals informing each other of their state, and these signals may influence their subsequent competitive behavior (note that we deal only with allocation of food among the chicks in a single brood; offspring cannot influence the total amount of food delivered by parents). We focus on the possibility that a costly display during the “negotiation” phase may serve to inform rivals of a chick’s need for resources and, thereby, deter them from competing intensely when the parent arrives.

## A model of sibling negotiation

We focus on negotiation and competition in a brood of two young, who are symmetrically related to one another with coefficient  $r$ . When a parent arrives bearing food, the two offspring compete to acquire it (the parent thus lacks full control of food allocation). We will write  $x_1$  and  $x_2$  for the levels of effort that both invest in this competition, where  $x_i$  denotes the additive fitness cost incurred by chick  $i$  (note that the cost of a given level of effort does not depend on the state of a chick). Initially, we assume that the food is indivisible, in which case the probability that a chick obtains it depends on its level of effort compared to that of its rival, and on the degree of competitive asymmetry between the two (reflecting differences in age and size, or in sex in dimorphic species).

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Received 21 December 2001; revised 18 September 2002; accepted 4 October 2002.

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Formally, the probability that chick 1 obtains the food, denoted  $p_1(x_1, x_2)$ , is given by

$$p_1(x_1, x_2) = \frac{x_1^k}{x_1^k + (bx_2)^k} \quad (1)$$

where  $k$  is a parameter that determines how easily a chick may monopolize access to the parent (a high value of  $k$  indicating that a chick's probability of obtaining food increases more rapidly as its effort,  $x$ , increases), and  $b$  denotes the competitive ability of the second chick relative to the first. In a subsequent extension of the model, we consider the possibility of divisible food. In this case, Equation 1 specifies the proportion of the food that a chick will obtain (as a function of its own effort and that of its rival), as opposed to the probability of obtaining the entire food item.

A high value of  $k$  implies that monopolization is easy, and a chick that gains a slight competitive edge over its rival is very likely to obtain the food (or will obtain a very large share if it is divisible)—this may be the case in hole-nesting species, in which a chick can prevent competitors from gaining access to the nest entrance. Conversely, a low value indicates that much greater investment relative to the rival (or a much larger competitive advantage) is required to be equally sure of obtaining the food item—this is more likely in open-nesting species, in which it is harder for a chick to monopolize feeding. A value of  $b = 1$  implies that both chicks are equal in competitive ability; conversely, a lower value of  $b$  implies that the second chick, referred to as the subordinate, is less competitively able than the first, referred to as the dominant (i.e., it must invest more effort to obtain the same chance of claiming a contested food item or the same share of a divisible food supply).

The value of an indivisible food item to each offspring, denoted  $v_1$  for the first chick and  $v_2$  for the second, in relation to its state (because the same item will be worth more to a hungrier chick). For simplicity, we will refer to the fitness benefit that a chick stands to gain from obtaining the item as its need. Both levels of need,  $v_1$  and  $v_2$ , are independently drawn from the same distribution, ranging between  $v_{\min}$  and  $v_{\max}$ ; for simplicity, we will assume an even distribution. We also assume that  $v_{\min} > rv_{\max}$ , so that there is always a conflict over acquisition of the resource (i.e., even a chick with the lowest need for food, competing with a rival with the greatest need, prefers not to yield the item).

In the case of divisible food, we assume that the fitness benefit that a chick stands to gain is an increasing but decelerating function of the share it obtains. Formally, the benefit to chick,  $i$ , from a share,  $p_i$  is given by

$$(1 - e^{-ap_i})v_i \quad (2)$$

where the parameter  $a$  determines how rapidly the benefits of additional food diminish.

Each chick is uninformed as to its competitor's need for food. However, before parental arrival the two young may advertise their state to each other by means of a costly display. We will write  $z_1$  and  $z_2$  for the intensity with which both display during this negotiation phase, where  $z_i$  denotes the additive fitness cost incurred by chick  $i$ .

### Solving the model

We focus here on the possibility of a stable solution featuring fully informative negotiation, i.e., one in which the equilibrium intensity with which each chick displays during the first stage of the game is a strictly increasing function of its need, denoted  $z_1(v_1)$  for the first chick and  $z_2(v_2)$  for the second. Under these circumstances, the intensity with which each chick then competes, denoted  $x_1(v_1, v_2)$  for the first chick and

$x_2(v_1, v_2)$  for the second, is a function of both its own state and that of its rival, because each is informed as to the other's state by the time the parent arrives. We do not consider the possibility of partially informative display during the negotiation phase (a pooling equilibrium; sensu Bergstrom and Lachmann, 1998).

To determine under what conditions fully informative equilibria of the kind described above can prove stable, and to characterize them, we proceed as follows: First, we calculate the levels of effort that both chicks would be expected to invest in competition during the second phase of the game, if they were fully informed as to each other's need. Based on these expected levels of effort, we can then derive the signaling intensities (costs) that we would expect to observe during the negotiation phase (we must begin by determining competitive effort during the second phase of the game, because the signal intensities expected during the first phase reflect what will happen in the second). If the signal intensities we derive in this way are a strictly increasing function of chick need, then we may conclude that fully informative negotiation is feasible, because a signaling strategy that provides nest mates with full information is stable, given the levels of competitive effort expected when individuals adopt that strategy. In some cases, however, the levels of competitive effort expected when chicks are fully informed may be such that fully informative display during the negotiation phase cannot, in fact, prove stable. Under these circumstances, the competitive strategy we have derived for the second phase of the game (based on the assumption of full information) will never actually be realized.

Below, we run through the above procedure in detail, for the case of indivisible food. This is followed by a shorter summary of the equivalent procedure when food is divisible, highlighting the differences between the two circumstances.

### Competitive effort

At equilibrium, assuming that the chicks are fully informed as to each other's need, the level of competitive effort adopted by each must be optimal given the behavior of the other. Formally, writing  $w_1(v_1, v_2, x_1, x_2)$  for the inclusive fitness payoff to chick 1 from the competitive phase of the game, and  $w_2(v_1, v_2, x_1, x_2)$  for the inclusive fitness payoff to chick 2, we have

$$w_1(v_1, v_2, x_1, x_2) = [p_1(x_1, x_2)v_1 - x_1] + r\{[1 - p_1(x_1, x_2)]v_2 - x_2\} \quad (3a)$$

$$w_2(v_1, v_2, x_1, x_2) = r[p_1(x_1, x_2)v_1 - x_1] + \{[1 - p_1(x_1, x_2)]v_2 - x_2\} \quad (3b)$$

(assuming that food is indivisible). In each case, the payoff is equal to the direct fitness of the focal individual (i.e., the probability of obtaining the resource times the gain from doing so, minus the cost of competition) plus  $r$  times that of its nest mate. At equilibrium we require that

$$\frac{\partial w_i[v_1, v_2, x_1(v_1, v_2), x_2(v_1, v_2)]}{\partial x_i} = 0 \quad \text{for } i = 1, 2. \quad (4)$$

Combining Equations 3 and 4, we obtain the following expressions for the equilibrium levels of competitive effort of the two chicks (assuming that they are fully informed as to each other's need),  $x_1(v_1, v_2)$  and  $x_2(v_1, v_2)$

$$x_1(v_1, v_2) = \frac{k(v_1 - rv_2)(bA)^k}{(A^k + b^k)^2} \quad (5a)$$

$$x_2(v_1, v_2) = \frac{k(v_2 - rv_1)(bA)^k}{(A^k + b^k)^2} \quad (5b)$$

where

$$A = \frac{v_1 - rv_2}{v_2 - rv_1} \tag{5c}$$

**Signaling intensity**

Having calculated the levels of competitive effort that would be expected at equilibrium if chicks are fully informed as to each other’s need, we can go on to derive the signaling intensities (costs) that we would expect to observe during the negotiation phase given this competitive strategy. Let  $u_1(v_1, v'_1)$  denote the expected total inclusive fitness payoff to chick  $i$  (from both stages of the game) if it is of true need  $v_i$ , but adopts the signaling behavior (during the negotiation phase) characteristic of an individual of need  $v'_i$ . We then have

$$u_1(v_1, v'_1) = \frac{1}{v_{\max} - v_{\min}} \times \int_{v_{\min}}^{v_{\max}} [p_1(x_1(v_1, v_2), x_2(v'_1, v_2))v_1 - z_1(v'_1) - x_1(v_1, v_2)] + r[(1 - p_1(x_1(v_1, v_2), x_2(v'_1, v_2)))v_2 - z_2(v_2) - x_2(v'_1, v_2)]dv_2 \tag{6a}$$

$$u_2(v_2, v'_2) = \frac{1}{v_{\max} - v_{\min}} \times \int_{v_{\min}}^{v_{\max}} r[p_1(x_1(v_1, v'_2), x_2(v_1, v_2))v_1 - z_1(v'_1) - x_1(v_1, v'_2)] + [(1 - p_1(x_1(v_1, v'_2), x_2(v_1, v_2)))v_2 - z_2(v'_2) - x_2(v_1, v_2)]dv_2 \tag{6b}$$

(assuming that a change in the display behavior of one chick will lead to a change in the competitive effort of the other during the subsequent competitive phase of the game). At equilibrium, we require that neither chick stands to gain by misrepresentation of its state, implying that

$$\frac{\partial u_i(v_i, v'_i)}{\partial v'_i} = 0 \text{ for } v'_i = v_i, \quad i = 1, 2. \tag{7}$$

Combining Equations 6 and 7, we find that

$$z'_1(v_1) = \frac{1}{(v_{\max} - v_{\min})} \times \int_{v_{\min}}^{v_{\max}} \left[ (v_1 - rv_2) \frac{\partial p_1(x_1(v_1, v_2), x_2(v_1, v_2))}{\partial x_2} - r \right] \times \frac{\partial x_2(v_1, v_2)}{\partial v_1} dv_2 \tag{8a}$$

$$z'_2(v_2) = \frac{1}{(v_{\max} - v_{\min})} \times \int_{v_{\min}}^{v_{\max}} \left[ -(v_2 - rv_1) \frac{\partial p_1(x_1(v_1, v_2), x_2(v_1, v_2))}{\partial x_1} - r \right] \times \frac{\partial x_1(v_1, v_2)}{\partial v_2} dv_1. \tag{8b}$$

Together, Equations 3, 4, and 8 then yield

$$z'_1(v_1) = -\frac{(1 - r^2)v_1}{(v_{\max} - v_{\min})} \int_{v_{\min}}^{v_{\max}} \frac{1}{(v_2 - rv_1)} \frac{\partial x_2(v_1, v_2)}{\partial v_1} dv_2 \tag{9a}$$

$$z'_2(v_2) = -\frac{(1 - r^2)v_2}{(v_{\max} - v_{\min})} \int_{v_{\min}}^{v_{\max}} \frac{1}{(v_1 - rv_2)} \frac{\partial x_1(v_1, v_2)}{\partial v_2} dv_1. \tag{9b}$$

These differential equations, together with the boundary condition  $z_1(v_{\min}) = z_2(v_{\min}) = 0$  (implying that a chick with the lowest level of need will not expend any effort on display; see Godfray, 1991, 1995b; Grafen, 1990), uniquely specify the equilibrium signal intensity of the offspring (although one must additionally confirm that the equilibrium is globally stable, i.e. that  $u_i(v_i, v_i) > u_i(v_i, v'_i)$  for all  $v'_i \neq v_i$ ).

If Equation 9 yields a globally stable solution at which signaling effort is a strictly increasing function of chick need, then (as stated above) we conclude that fully informative negotiation can prove stable, and that chick signaling and competitive behavior at this equilibrium will be described by Equations 9 and 5. If not, then no equilibrium is possible at which signaling during the negotiation phase provides full information about chick need (although we cannot rule out the possibility of partially informative pooling equilibria under these circumstances).

Unfortunately, we are unable to derive an analytical solution to Equation 9 and, therefore, cannot give an explicit condition for the existence of stable, fully informative negotiation or a general expression for the behavior expected under these circumstances. In the Results section, however, we present results based on numerical solution of the relevant equations. We focus first on conditions under which stable negotiation is possible, and we illustrate the patterns of signaling and competitive behavior expected under these circumstances. We then move on to consider what factors may threaten the stability of negotiation.

**Divisible food**

The solution procedure adopted when food is assumed to be divisible is very similar to that described above. In this case, however, the payoffs to the chicks from the competitive phase of the game,  $w_1(v_1, v_2, x_1, x_2)$  and  $w_2(v_1, v_2, x_1, x_2)$ , are given by

$$w_1(v_1, v_2, x_1, x_2) = [(1 - e^{-ap_1(x_1, x_2)})v_1 - x_1] + r[(1 - e^{-a(1-p_1(x_1, x_2))})v_2 - x_2] \tag{10a}$$

$$w_2(v_1, v_2, x_1, x_2) = r[(1 - e^{-ap_1(x_1, x_2)})v_1 - x_1] + [(1 - e^{-a(1-p_1(x_1, x_2))})v_2 - x_2] \tag{10b}$$

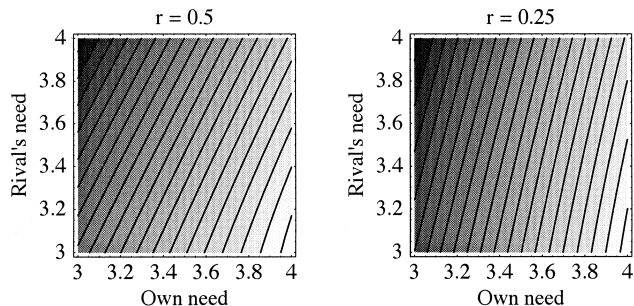
rather than by Equation 3. Combining Equations 10 and 4 yields different values for the equilibrium competitive efforts of the two chicks,  $x_1(v_1, v_2)$  and  $x_2(v_1, v_2)$ , than we obtained for the case of indivisible food. Unfortunately, we cannot derive analytical expressions for these values and must once again resort to numerical solution of the relevant equations.

As before, having calculated the levels of competitive effort that would be expected at equilibrium if chicks are fully informed as to each other’s need, we can go on to derive the signaling intensities (costs) that we would expect to observe during the negotiation phase given this competitive strategy. For the case of divisible food, however, this is generally unnecessary because (as detailed below) the pattern of competitive behavior derived in the first step clearly does not favor fully informative signaling during the negotiation phase. In other words, when food is divisible, informative negotiation is generally unstable.

**RESULTS**

**Stable negotiation**

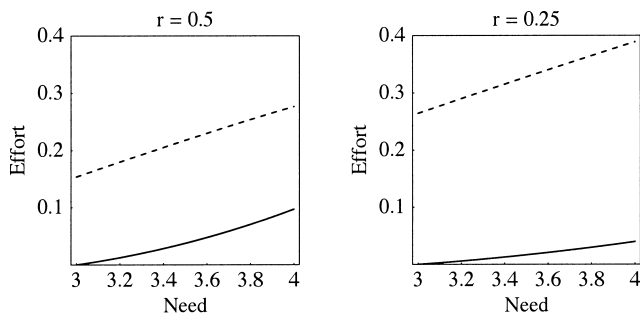
When food cannot be easily monopolized (i.e., when  $k$  is low), when offspring do not differ in competitive ability, and when



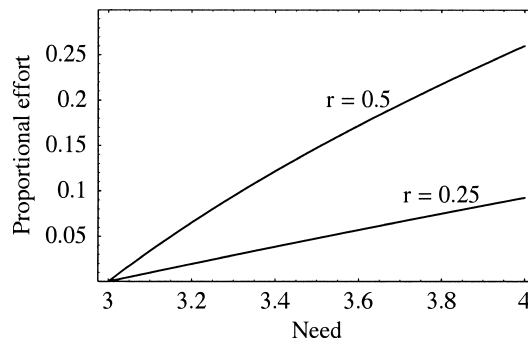
**Figure 1**  
Competitive effort after parental arrival, at equilibrium, as a function of an individual offspring's own need for food and the need of its rival, for  $r = .5$  (left-hand graph) and  $.25$  (right-hand graph). Dark shading indicates low effort; pale shading, high effort. Other parameter values are  $b = 1$ ,  $k = 0.5$ ,  $v_{\min} = 3$  and  $v_{\max} = 4$ .

they are fully informed as to each other's state, they can be expected to compete more intensely when their own need for food is greater (Figure 1). At the same time, they will reduce their efforts when paired with a needier rival, to a greater extent the more closely related the two are (Figure 1). Under these circumstances, an individual stands to gain by advertising its own need during the negotiation phase of the game, because this will induce its rival to compete less strongly when the parent arrives. The needier the focal chick, the greater the benefit to be gained; hence, as can be seen in Figure 2, a stable signaling equilibrium is possible at which hungrier chicks expend more effort on display during negotiation (as well as competing more intensely following delivery of food).

Although sib-sib communication is stable under these circumstances, however, chicks are expected to invest considerably more effort in competition once the parent has arrived than in negotiation beforehand. The less closely related they are, the greater this difference; thus, half-sibs are expected to invest less than full sibs in negotiation and more in competition (Figure 2). Similarly, the less hungry chicks are, the less effort they should invest in negotiation relative to competition (Figure 3). The reason for this trend is that although both negotiation and competitive effort increase with need, the former does so at a proportionately greater rate.



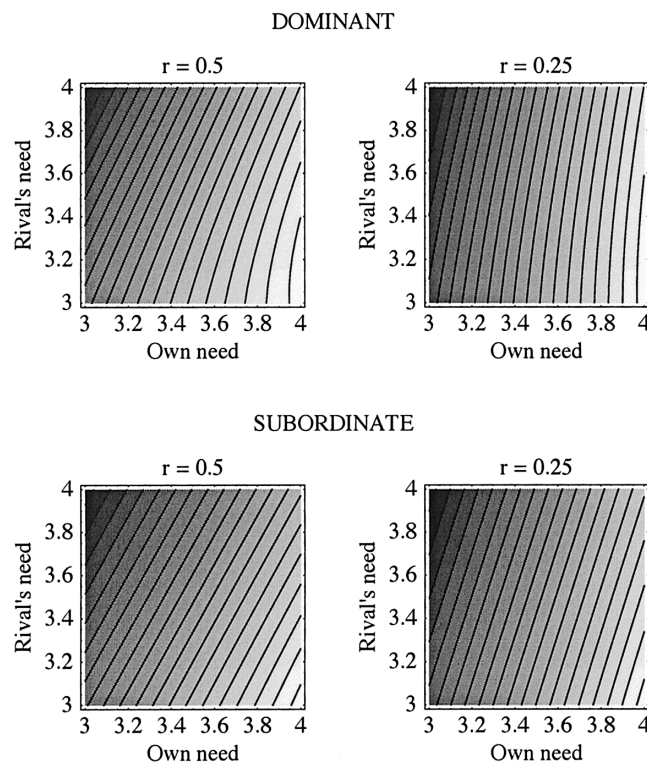
**Figure 2**  
Negotiation effort before parental arrival (solid lines) and mean begging effort after parental arrival (dashed lines), as a function of chick need, for  $r = .5$  (left graph) and  $.25$  (right graph). Other parameters are as in Figure 1.



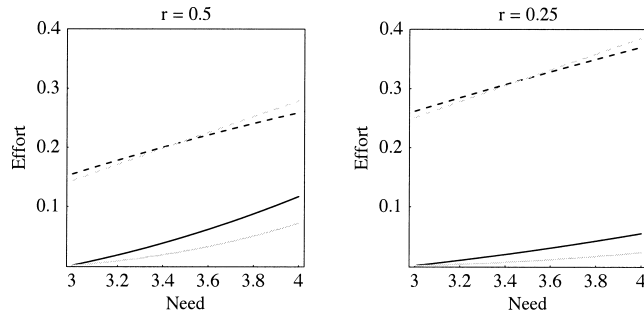
**Figure 3**  
Average proportion of total effort invested in negotiation (rather than competition), as a function of chick need, for  $r = .5$  and  $.25$ , as indicated on the graph. Other parameters are as in Figures 1 and 2.

**Consequences of competitive asymmetry**

When offspring differ in competitive ability, the dominant chick may be expected to adjust its competitive effort less in relation to the subordinate chick's need than vice versa (Figure 4). Under these circumstances, mean competitive effort is similar for both offspring, although the level of effort invested by the dominant varies less in relation to own need than does the effort invested by the subordinate (Figure 5). Negotiation effort, by contrast, differs between the two, with



**Figure 4**  
Competitive effort after parental arrival, at equilibrium, as a function of an individual offspring's own need for food and the need of its rival, for the dominant chick (top graphs) and the subordinate chick (bottom graphs), when  $r = .5$  (left graphs) and  $.25$  (right graphs). Dark shading indicates low effort; pale shading, high effort. Other parameter values are as in Figures 1–3, except that  $b = 0.5$  (implying that the second chick has only half the competitive ability of the first).



**Figure 5**  
Negotiation effort before parental arrival (solid lines) and mean competitive effort after parental arrival (dashed lines), as a function of chick need, for  $r = .5$  (left graph) and  $.25$  (right graph). Other parameters are as in Figure 4. In both graphs, dark lines show the effort invested by the dominant chick; pale lines, the effort invested by the subordinate chick.

the subordinate offspring investing less than the dominant (Figure 5). This reflects the finding referred to above, that the dominant responds less strongly to the subordinate's need than vice versa.

#### When negotiation breaks down

So far, we have focused on parameter values for which stable negotiation is possible. As  $k$  increases (i.e., as it becomes easier to monopolize access to food), however, negotiation may break down. Chicks (if they were fully informed about each other's state) would then be expected to reduce their competitive effort when facing a rival whose need is much less than their own (Figure 6, visible in the lower right-hand corner of each graph, where own need is high and rival's need is low). This occurs because the focal chick can be fairly sure of obtaining the contested food item (whereas when it is hard to monopolize access to food, the focal chick cannot afford to relax its competitive efforts in this way).

The above trend means that for sufficiently high values of  $k$ , it may no longer pay to invest in negotiation. Under these circumstances, it is better for a chick to refrain from displaying to its nest mate, because such display would have the counterproductive effect of stimulating the latter to compete more strongly. For  $k = 1.5$ , the rival's expected

competitive effort is no longer a uniformly decreasing function of the focal chick's need (Figure 7). This implies that an equilibrium at which negotiation effort is a uniformly increasing function of need is not possible (because, in the region of the graph where rival's effort decreases with the focal chick's need, the latter does better to refrain from advertising its state). Consequently, the pattern of competition illustrated in Figure 7 (for  $k = 1.5$ ) will never actually be realized.

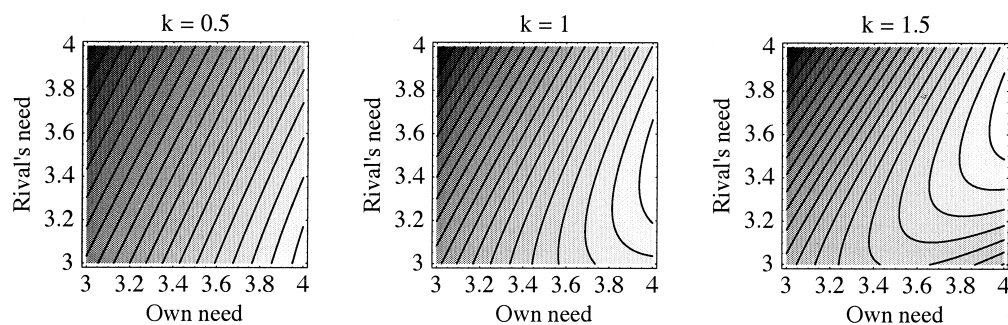
#### Divisible resources

When the resources delivered by the parent are divisible, negotiation is once again feasible only if resources cannot be too easily monopolized (i.e., only for low values of  $k$ ), but the threshold value of  $k$  below which it proves stable is much lower. In other words, negotiation is less likely when resources are divisible. For  $k = 0.125$ , competitive effort decreases with a rival's need, favoring negotiation (Figure 8). As  $k$  increases, however, this pattern quickly reverses; for  $k = 0.5$  (a value that was compatible with negotiation for the case of indivisible resources), the competitive effort that would be expected if offspring were fully informed as to each other's state is an increasing function of rival's need. Under these circumstances, advertising one's own need is not advantageous, because it will induce a rival to compete more strongly.

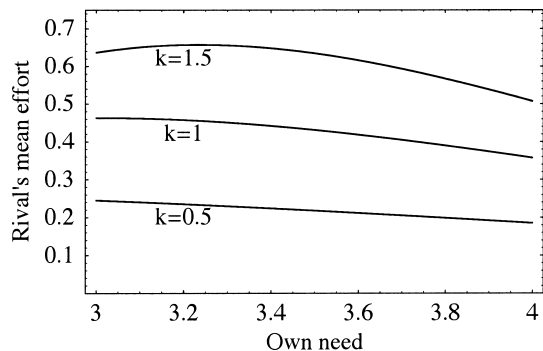
#### DISCUSSION

The model we have presented demonstrates that (under some conditions) sibling negotiation can prove evolutionarily stable. Offspring may gain by advertising their need to one another (in the absence of parents) with costly displays because this deters competitors from competing intensely when a parent arrives.

Our model suggests that negotiation is most likely when the resources that the parent provides cannot be shared. Why should the divisibility of resources have such an important influence? When food can be divided among the young, an individual competing with a hungrier rival is likely to obtain a smaller share (because the rival will compete more strongly). Given that offspring enjoy diminishing fitness returns from additional resources, the marginal fitness gain for the focal individual from competing with a hungrier nest mate will thus be greater (an increase in its expected share of food from, say, 20–25%, bringing greater benefits than an



**Figure 6**  
The competitive effort that would be expected after parental arrival, at equilibrium, if chicks were fully informed as to each other's state, as a function of an individual offspring's own need for food and the need of its rival, for  $k = 0.5, 1$  and  $1.5$ . Dark shading indicates low effort; pale shading, high effort. Other parameter values are as in Figure 1, with  $r = .5$ . Note that for  $k = 0.5$  or  $1$ ; fully informative negotiation proves stable, so that the corresponding graphs describe the actual pattern of behavior expected at equilibrium. For  $k = 1.5$ , by contrast, fully informative negotiation is unstable, and hence, the pattern of behavior expected given full information (illustrated in the graph) will never, in fact, be realized.



**Figure 7**  
The mean competitive effort that a rival would be expected to invest after parental arrival, at equilibrium, if chicks were fully informed as to each other's state, as a function of the focal offspring's need for food, for  $k = 0.5, 1,$  and  $1.5$  (as indicated on the graph). Other parameter values are as in Figure 6. Note that for  $k = 0.5$  or  $1$ , fully informative negotiation proves stable, so that the corresponding graphs describe the actual pattern of behavior expected at equilibrium. For  $k = 1.5$ , by contrast, fully informative negotiation is unstable, and hence, the pattern of behavior expected given full information (illustrated in the graph) will never, in fact, be realized.

increase from 75–80%). This favors escalation on the part of the focal chick; it should beg more strongly when competing with a hungry rival (see Godfray, 1995b). Under these circumstances, it does not pay for a hungry chick to advertise its need to a less hungry competitor, as this will induce the latter to beg more strongly rather than less.

By contrast, when food is indivisible, a chick's marginal fitness gain from competitive effort does not depend on its expected success. An increase in its probability of obtaining food from 20–25% yields exactly the same fitness gain as an increase from 75–80%. Under these circumstances, a chick will tend to beg less strongly when competing with a hungrier rival, because it is less likely to obtain food and hence any extra effort in competition is unlikely to be rewarded. Negotiation may therefore pay, because advertising one's need to a competitor will induce the latter to beg less intensely.

The above situation will, however, break down when food can be too easily monopolized (i.e., when the value of  $k$  is sufficiently large). Under these circumstances, offspring begin to reduce their competitive effort when paired with a rival whose need is much less than their own, in anticipation of an

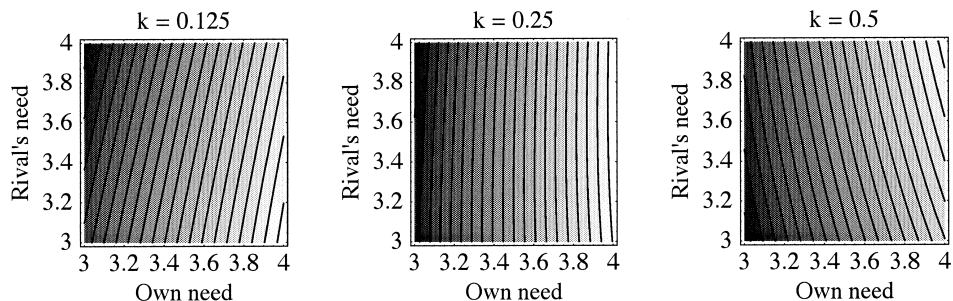
easy victory (because the rival is expected to compete only weakly for resources). Negotiation then becomes unstable, because an individual that refrains from displaying to its nest mate may actually benefit from a reduction in the latter's competitive effort (although, conversely, an individual that does display to its nest mate may actually cause it to compete more strongly).

To sum up, we predict that sibling negotiation is most likely to occur when food is indivisible and individual offspring cannot easily monopolize access to parents. Too few comparative data are available to test these predictions at present; however, it can at least be observed that in the barn owl (*Tyto alba*), the study species that prompted the development of the sibling negotiation hypothesis (Roulin, 2001a, 2002; Roulin et al., 2000), both conditions are met.

More data are available regarding the model's prediction that hungrier offspring should invest relatively more effort in negotiation compared to competition. Roulin (2001a) manipulated the food supply of barn owl broods by adding or removing prey items, and found that in the absence of parents, food-added broods vocalized less than food-removed ones, whereas after parental arrival, vocalization was not significantly affected by food manipulation. In other words, as predicted by the model, hunger affected sibling negotiation to a larger extent than sibling competition (although overall, offspring called more vigorously in the presence of parents, also as predicted).

Clearly, however, more data on a wider range of species are needed to assess the scope of the sibling negotiation hypothesis. There is also considerable room for more theoretical work. The present model extends most previous analyses by dividing begging into two sequential phases: intrabrood communication, followed by parent-offspring communication (for an earlier two-step model, see Johnstone, 1996). However, it still deals with only a single feeding episode. Roulin (2002), by contrast, argues that the dynamics of competition are of particular importance for sibling negotiation, because a chick is more likely to relinquish a food item during the current visit if it is then more likely to obtain food at the next. In other words, models of sibling interaction need to consider behavior over a number of successive visits. The model we have presented here represents only a first step towards a full, dynamic treatment of sibling interaction.

A.R. was supported by a grant from the Swiss Science Foundation (no. 823A-064710).



**Figure 8**  
Predictions of the model when resources are divisible. The graphs show the competitive effort that would be expected after parental arrival, at equilibrium, if chicks were fully informed as to each other's state, as a function of an individual offspring's own need for food and the need of its rival, for  $k = 0.125, 0.25,$  and  $0.5$ . Dark shading indicates low effort; pale shading, high effort. Other parameter values are as in Figure 6. Note that for  $k = 0.125$  or  $0.25$ , fully informative negotiation proves stable, so that the corresponding graphs describe the actual pattern of behavior expected at equilibrium. For  $k = 0.5$ , by contrast, fully informative negotiation is unstable, and hence, the pattern of behavior expected given full information (illustrated in the graph) will never, in fact, be realized.

## REFERENCES

- Bergstrom CT, Lachmann M, 1998 Signaling among relatives, III: talk is cheap. *Proc Natl Acad Sci USA* 95:5100–5105.
- Budden AE, Wright J, 2001. Falling on deaf ears: the adaptive significance of begging in the absence of a parent. *Behav Ecol Sociobiol* 49:474–481.
- Clemmons JR, 1995. Vocalizations and other stimuli that elicit gaping in nestling black-capped chickadees (*Parus atricapillus*). *Auk* 112: 603–612.
- Godfray HCJ, 1991. Signalling of need by offspring to their parents. *Nature* 342:328–330.
- Godfray HCJ, 1995a. Evolutionary theory of parent-offspring conflict. *Nature* 376:133–138.
- Godfray HCJ, 1995b. Signaling of need between parents and young: parent-offspring conflict and sibling rivalry. *Am Nat* 146:1–24.
- Godfray HCJ, Johnstone RA, 2000. Begging and bleating: the evolution of parent-offspring signalling. *Phil Trans R Soc Lond B* 355:1581–1591.
- Grafen A, 1990. Biological signals as handicaps. *J Theor Biol* 144: 517–546.
- Johnstone RA, 1996. Begging signals and parent-offspring conflict: do parents always win? *Proc R Soc Lond B* 263:1677–1681.
- Johnstone RA, 1999. Signalling of need, sibling competition and the cost of honesty. *Proc Natl Acad Sci USA* 96:12644–12649.
- Kilner R, Johnstone RA, 1997. Begging the question: are offspring solicitation behaviours signals of need? *Trends Ecol Evol* 12: 11–15.
- Leonard ML, Horn AG, 2001. Begging in the absence of parents by nestling tree swallows. *Behav Ecol* 12:501–505.
- Lessells CM, Parker GA, 1999. Parent-offspring conflict: the full-sib-half-sib fallacy. *Proc R Soc Lond B* 266:1637–1643.
- Macnair MR, Parker GA, 1978. Models of parent-offspring conflict, II: promiscuity. *Anim Behav* 26:111–122.
- Macnair MR, Parker GA, 1979. Models of parent-offspring conflict, III: intra-brood conflict. *Anim Behav* 27:1202–1209.
- Mock DW, Parker GA, 1997. *The evolution of sibling rivalry*. Oxford: Oxford University Press.
- Parker GA, 1985. Models of parent-offspring conflict, V: effects of the behaviour of the two parents. *Anim Behav* 33:519–533.
- Parker GA, Macnair MR, 1978. Models of parent-offspring conflict, I: monogamy. *Anim Behav* 26:97–110.
- Parker GA, Macnair MR, 1979. Models of parent-offspring conflict, IV: suppression: evolutionary retaliation by the parent. *Anim Behav* 27:1210–1235.
- Price K, Ydenberg R, 1996. Begging tactics of nestling yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, in relation to need. *Anim Behav* 51:421–435.
- Rodriguez-Girones MA, 1999. Sibling competition stabilizes signalling resolution models of parent-offspring conflict. *Proc R Soc Lond B* 266:2399–2402.
- Rodriguez-Girones MA, Enquist M, Lachmann M, 2001. Role of begging and sibling competition in foraging strategies of nestlings. *Anim Behav* 61:733–745.
- Roulin A, 2001a. Food supply differentially affects sibling negotiation and competition in the barn owl (*Tyto alba*). *Behav Ecol Sociobiol* 49:514–519.
- Roulin A, 2001b. On the cost of begging vocalization: implications of vigilance. *Behav Ecol* 12:506–511.
- Roulin A, 2002. The sibling negotiation hypothesis. In: *The evolution of nestling begging: competition, cooperation and communication* (Wright J, Leonard M, eds). Dordrecht: Kluwer; 107–126.
- Roulin A, Kölliker M, Richner H, 2000. Barn owl siblings vocally negotiate resources. *Proc R Soc Lond B* 267:459–463.