

Negotiation over offspring care—how should parents respond to each other's efforts?

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Models of biparental care predict that parents should compensate incompletely for any change in their partner's investment. Experimental tests have, however, yielded results that range from full compensation, through a lack of any reaction, to a matching response. Here we suggest a new, adaptive explanation for such variation. Building on an approach developed by McNamara et al., we incorporate uncertainty regarding brood need or value into a game-theoretical model of biparental negotiation over offspring care. We show that when each parent has only partial information, greater effort invested by one serves as a signal to the other of brood need. This favors a matching response by the focal parent's mate, whereas the impact of increased effort on the marginal value of investment favors a compensatory response. The net outcome depends on the relative strength of these two effects. The greater the variation in brood need compared with parental state, the weaker the predicted level of compensation, and the more likely matching is to occur. Our model also suggests why males and females might respond differently to each other. If there is an informational asymmetry between them, then the parent that is better informed about brood need should work harder, respond more strongly to changes in brood need, be less sensitive to changes in the cost of feeding, and compensate more strongly for changes in partner effort. If the asymmetry is very great, the poorly informed parent may even match changes in its partner's work rate. *Key words:* game theory, negotiation, parental care, sexual conflict. [*Behav Ecol* 17:818–827 (2006)]

In species that exhibit biparental care, an evolutionary conflict arises between mates over investment in their joint young (Trivers 1972; Chase 1980; Houston et al. 2005). Each parent benefits from effort invested by its partner but usually escapes at least some of the associated costs (see Lessells and Parker 1999). Thus, each parent benefits if the other does more of the work involved in raising their offspring. How is this conflict over care resolved? This question has been the subject of much attention, both theoretical and empirical.

Focusing first on theoretical predictions, Chase (1980) and Houston and Davies (1985) modeled the conflict over investment as an evolutionary game, in which each parent may be expected (at an evolutionarily stable equilibrium) to invest a fixed level of effort that maximizes its own fitness, given the effort invested by its mate. They showed that biparental care will prove stable if a change in one parent's effort selects for incomplete compensation by the other parent, that is, a change in the opposite direction, but of smaller magnitude, and that such compensation is to be expected if brood productivity is an increasing but decelerating function of total parental effort, and the costs of such effort for an individual parent are nondecelerating (see also Winkler 1987; Ratnieks 1996; Jones et al. 2002). Greater investment by a partner then leads to a decline in the marginal benefit of investment by the focal parent, which favors a compensatory reduction in effort.

Subsequently, McNamara et al. (1999, 2003) have extended this basic framework to incorporate behavioral negotiation between parents (although Chase [1980] emphasized the importance of behavioral negotiation, his analysis did not explicitly distinguish between behavioral and evolutionary timescales). In their analyses, each parent may adjust its own effort in response to that of its partner, on a behavioral timescale. It is the “response rules” that parents follow that constitute the

strategies in this “negotiation game,” rather than the effort levels they adopt per se. The evolutionary outcome of the negotiation game, that is, the negotiated effort levels that result when parents adopt the evolutionarily stable response rules, differs in detail from the outcome of Houston and Davies' original “sealed bid” analysis. Compensation is predicted to be less marked in the negotiation game, and total parental investment lower. Nevertheless, the model still predicts incomplete compensation—in this case on a behavioral timescale.

Theoretical predictions that parents should respond to a change in partner effort with incomplete compensation have prompted numerous empirical tests, most commonly in species of bird that exhibit biparental care (for similar studies of insects see Hunt and Simmons 2002; Smiseth and Moore 2004). Techniques such as feather cutting, tail weighting, testosterone manipulation, and selective playback of begging calls have been used to modify the level of care provided by one parent (for a review see Hinde 2006) or by one carer in a cooperatively breeding species (e.g., Wright and Dingemanse 1999; MacGregor and Cockburn 2002). The responses by partners of manipulated birds, however, vary across these studies from full compensation (Wright and Cuthill 1990a, 1990b; Ketterson et al. 1992; Hunt et al. 1999; Sanz et al. 2000; Stoehr and Hill 2000) to partial compensation (Wright and Cuthill 1989; Markman et al. 1995; Saino and Møller 1995), to a lack of any significant response (Slagsvold and Lifjeld 1988, 1990; Whittingham et al. 1994; Lozano and Lemon 1996; Moreno et al. 1999; Sanz et al. 2000; Schwagmeyer et al. 2002), and even beyond this to a matching response, such that the partner responds to a change in the manipulated individual's effort with a change in the same direction (Hegner and Wingfield 1987; Hinde 2006). Moreover, males and females have been found in some cases to respond differently to a change in partner effort (e.g., Sanz et al. 2000, females compensated and males did not).

How can the simple predictions of existing models be reconciled with this diversity of results and, in particular, with the occurrence of matching rather than compensatory responses? One approach to this question would be to focus on possible

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side effects of the experimental manipulations—for example, feather-cutting experiments, especially if performed early on (some have been before egg laying; Slagsvold and Lifjeld 1990), may decrease the apparent quality of the focal parent, lowering the perceived value of parental investment to their partner. Conversely, increasing male testosterone levels also increases male attractiveness (Saino and Møller 1995; Stoehr and Hill 2000; Van Duysel et al. 2002), which may favor greater female investment.

Here, however, we take the empirical results at face value and attempt to develop a possible adaptive explanation for variation in parental responses to partner effort. Building on the approach developed by McNamara et al. (1999, 2003), we incorporate uncertainty regarding brood “value” or “need” into the negotiation game. Our suggestion is that changes in partner effort may influence parental investment not only through their impact on the marginal value of care but also because of the information they convey about the value or long-term need of the brood. As we show, the interplay between these two effects can lead to a surprisingly wide range of outcomes. In particular, when increased partner effort provides a strong indication of high brood value or need, selection can favor a matching rather than a compensatory response, without destabilizing biparental care.

THE MODEL

Two parents each provide food to their joint brood of young, which boosts the total productivity of the brood (i.e., the number of young that successfully fledge) at a cost to the parents’ own future fitness (i.e., expected future reproductive success). The magnitude of the productivity benefit depends on the total amount of food delivered by both parents and on the level of brood need or value (for clarity, we will use only the term need from now on; this specifies the degree to which the brood will benefit from additional investment, which could depend on the genetic quality or value of the young, their long-term history of growth, current hunger, and possibly other factors as well). Formally, we will write $B(n, x)$ for the total benefit given a brood of need n and total provisioning of level x ($= x_f + x_m$, where x_f and x_m denote provisioning by the female and by the male parent, respectively). Equally, the magnitude of the fitness cost that a parent pays for a given level of provisioning depends on its state, denoted m_f and m_m for the female and male, respectively (this single measure of state subsumes the foraging ability of the parent, its level of energetic reserves, and any other factor that influences the cost of provisioning). Formally, we will write $C(m, x)$ for the fitness cost paid by a parent in state m if it provisions at level x (note that, for simplicity, we assume that this cost function is the same for both males and females; we also assume that costs incurred by one parent do not impact on the fitness of the other). A full list of model parameters and variables is given in Table 1.

Each parent is unaware of the other’s state (but has full knowledge of its own). Moreover, each has only imperfect information regarding brood need. Formally, we assume that female and male state m_f and m_m are independently drawn from a normal distribution with mean \bar{m} and variance σ_m^2 . The level of brood need n is independently drawn from a normal distribution with mean \bar{n} and variance σ_n^2 . Each parent must base its provisioning decisions on its own state and on its perception or estimate of brood need, denoted p_f and p_m for the female and male, respectively. A parent’s perception of need is equal to the true need n plus a random error term, denoted e_f and e_m for the female and male, respectively. These error terms are independent and are drawn from normal dis-

Table 1
Parameters and variables of the model

α_f, α_m	Constant term in female’s/male’s response rule
β_f, β_m	Slope of female’s/male’s response rule with respect to her/his own state
$B(n, x)$	Productivity benefit from provisioning a brood of need n at level x
$C(m, x)$	Cost paid by a parent in state m who provisions at level x
δ_f, δ_m	Slope of female’s/male’s response rule with respect to partner’s work rate
γ_f, γ_m	Slope of female’s/male’s response rule with respect to perception of brood need
\bar{m}	Mean parental state
m_f, m_m	Female/male state
p_f, p_m	Female’s/male’s perception of brood need
σ_m^2	Variance in parental state
σ_n^2	Variance in brood need
$\sigma_{pf}^2, \sigma_{pm}^2$	Error variance in female’s/male’s perception of brood need
\bar{n}	Mean brood need
x	Total provisioning level (by both parents combined)
x_f, x_m	Provisioning by the female/male, respectively

tributions with mean 0 and variance σ_{pf}^2 for the female and σ_{pm}^2 for the male.

Each parent may also adjust its own level of provisioning in response to the behavior of the other. Following McNamara et al. (1999, 2003), we will assume that after some unspecified period of negotiation, in which the parents take turns in each choosing their own level of feeding in response to the other’s most recent choice, the choices of both settle down to stable limiting values, which we refer to as the outcome of negotiation. The behavior of each parent during this negotiation process is described by a response rule: for the female, the rule $\hat{x}_f(m_f, p_f, x_m)$ specifies the level of food provisioning she will choose as a function of her state, m_f , her perception of brood need, p_f , and the male’s most recent choice of investment x_m ; the equivalent male rule is denoted $\hat{x}_m(m_m, p_m, x_f)$.

The payoff to each parent depends solely on the final outcome of negotiation and not on choices made earlier during the negotiation process. One may thus compare the expected payoffs to parents that adopt alternative response rules, by focusing on the negotiated outcomes to which these rules give rise, for different levels of parental state and perceived brood need. In “Solving the Model,” we outline how to derive (for a particular class of fitness functions specified below) stable pairs of linear response rules, each of which is strictly optimal for the relevant parent given that the behavior of the other parent is described by the other rule. We also show that these pairs of rules do indeed lead to a stable outcome of negotiation, as originally assumed.

The above negotiation game may be contrasted with a sealed bid version of the model, in which parents do not have the opportunity to respond to each other’s behavior but instead must simultaneously (and independently) choose a fixed effort level based only on their own state and their own perception of brood need. In this case, the stable levels of effort are directly specified by the strategies the parents adopt, rather than emerging as the result of a negotiation process (alternatively, one could say that the negotiation does occur in the sealed bid game but that the process terminates immediately because neither parent will alter its original level of investment in response to the other’s behavior). We derive the stable strategies in this simpler game in the Appendix, chiefly to allow comparison with the results of the negotiation game.

Fitness functions

For the sake of simplicity, we will assume that $B(n, x)$ and $C(m, x)$ are given by the quadratic formulae below:

$$B(n, x) = \begin{cases} nx - x^2, & \text{for } 0 \leq x < n/2 \\ n^2/4, & \text{for } x \geq n/2 \end{cases}, \quad (1)$$

$$C(m, x) = mx + x^2$$

as illustrated in Figure 1. These formulae are chosen primarily because (unlike more commonly used functions) they yield stable response rules that are linear in form. This renders the model tractable (as we are unable to solve for stable, nonlinear response rules). However, we emphasize that our cost and benefit functions satisfy all the common assumptions about the nature of the costs and benefits of provisioning—namely, that additional food yields diminishing benefits that are lower for a less needy brood and that greater levels of provisioning carry an accelerating cost for the parent. Perhaps, the only unusual feature of the formula for $B(n, x)$ is that it implies that there is a maximum level of provisioning above which offspring gain nothing from additional food (whereas most previous models have assumed no upper limit on the amount of food from which the young can benefit). This seems, however, a plausible assumption as there is bound to be an upper limit on the rate of energy assimilation by offspring (e.g., Karasov 1996).

Each parent is assumed to maximize the expected sum of current brood productivity and its own future reproductive success (so that, as previously stated, costs incurred by one parent do not impact on the other's payoff).

Solving the model

We seek a pair of response rules, $x_f^*(m_f, p_f, x_m)$ and $x_m^*(m_m, p_m, x_f)$, such that each rule maximizes the expected fitness payoff of the parent that adopts it, given that the remaining parent responds according to the other rule.

As stated above, the fitness functions we have assumed yield a stable pair of linear rules of the form

$$x_f^*(m_f, p_f, x_m) = \alpha_f + \beta_f m_f + \gamma_f p_f + \delta_f x_m, \quad (2)$$

$$x_m^*(m_m, p_m, x_f) = \alpha_m + \beta_m m_m + \gamma_m p_m + \delta_m x_f.$$

Below we explain how this pair of rules may be derived. First, we show that if the male parent adopts a linear rule of the above form, then the optimal female rule is also linear, and we derive equations that the coefficients of this optimal female rule (α_f , β_f , γ_f , and δ_f) must satisfy (in terms of the coefficients of the male rule, α_m , β_m , γ_m , and δ_m). Second, we give the corresponding equations for the coefficients of the optimal male rule. We then outline how joint solution of these equations may be used to identify the stable rule pair (and how one can derive predictions regarding mean and variance in female and male effort on the basis of this stable rule pair). Note, however, that we do not consider the possibility of alternative, stable rule pairs that are nonlinear.

The optimal female rule

The fitness payoff to a female parent at the end of the negotiation process, given that the brood is of need n , she is in state m_f , she provisions at level x_f , and the male provisions at level x_m , is given by

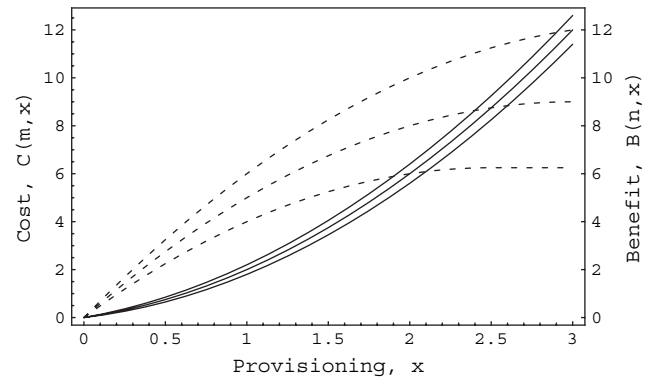


Figure 1

The costs (solid lines) and benefits (dashed lines) of provisioning (as defined in Equation 1 in the main text) for three different values of parental state ($m = 0.8, 1.0, 1.2$, corresponding to successively higher curves) and three different values of brood need ($n = 5, 6, 7$, corresponding to successively higher curves), respectively.

$$W(n, m_f, x_f, x_m) = B(n, x_f + x_m) - C(m_f, x_f) \\ = n(x_f + x_m) - (x_f + x_m)^2 - m_f x_f - x_f^2. \quad (3)$$

Consequently, the marginal change in the female parent's fitness resulting from an increase in her provisioning, taking into account the effect this will have on provisioning by the male parent, is given by

$$M(n, m_f, x_f, x_m) \\ = \frac{\partial W(n, m_f, x_f, x_m)}{\partial x_f} + \delta_m \frac{\partial W(n, m_f, x_f, x_m)}{\partial x_m} \\ = (1 + \delta_m)n - 2(1 + \delta_m)(x_f + x_m) - m_f - 2x_f. \quad (4)$$

The above formula gives the marginal fitness consequences of provisioning for the female, as a function of brood need n . However, the true level of brood need, n , is unknown to the female, instead, her decision must be based on her perception of need p_f and on the male's provisioning level x_m , which reflects his perception of need p_m (as well as his state m_m ; note that the female could do no better by attending to the history of the negotiation process than she can by responding simply to the male's most recent choice of provisioning level—given that the male adopts a linear rule of the form specified in Equation 2, observation of his response to different choices of x_f does not help to reduce the female's uncertainty regarding the values of n and m_m). To determine the female's optimal response rule, we therefore need to determine the expected marginal fitness consequences of an increase in her provisioning, conditional on p_f and x_m .

The prior distribution of brood need n is normal, with mean \bar{n} and variance σ_n^2 . For any particular value of n , the female's perception of need, p_f , is drawn from a normal distribution with mean n and variance $\sigma_{p_f}^2$. Equally, for given values of n and x_f , the male's provisioning effort, assuming he follows a linear response rule of the form specified in Equation 2, is independently drawn from a normal distribution with mean

$$\alpha_m + \beta_m \bar{m} + \gamma_m n + \delta_m x_f,$$

and variance

$$\beta_m^2 \sigma_m^2 + \gamma_m^2 \sigma_{p_m}^2.$$

Using Bayes' rule to determine the expected value of n conditional on p_f and x_m , we thus obtain

$$E[n | p_f, x_m] = \frac{\sigma_{pf}^2 s^2 \bar{n} + \sigma_n^2 s^2 p_f + \sigma_{pf}^2 \sigma_n^2 \left(\frac{x_m - \alpha_m - \beta_m \bar{m} - \delta_m x_f}{\gamma_m} \right)}{\sigma_{pf}^2 s^2 + \sigma_n^2 s^2 + \sigma_{pf}^2 \sigma_n^2}, \quad (5a)$$

where

$$s^2 = \frac{\beta_m^2 \sigma_m^2 + \gamma_m^2 \sigma_{pm}^2}{\gamma_m^2}. \quad (5b)$$

Combining Equations 4 and 5, the expected marginal change in the female parent's fitness payoff with an increase in provisioning, conditional on p_f and x_m , is given by

$$\begin{aligned} \bar{M}(m_f, p_f, x_f, x_m) &= E[(1 + \delta_m)n - 2(1 + \delta_m)(x_f + x_m) - m_f - 2x_f | p_f, x_m] \\ &= (1 + \delta_m)E[n | p_f, x_m] - 2(1 + \delta_m)(x_f + x_m) - m_f - 2x_f \\ &= (1 + \delta_m) \left[\frac{\sigma_{pf}^2 s^2 \bar{n} + \sigma_n^2 s^2 p_f + \sigma_{pf}^2 \sigma_n^2 \left(\frac{x_m - \alpha_m - \beta_m \bar{m} - \delta_m x_f}{\gamma_m} \right)}{\sigma_{pf}^2 s^2 + \sigma_n^2 s^2 + \sigma_{pf}^2 \sigma_n^2} \right] \\ &\quad - 2(1 + \delta_m)(x_f + x_m) - m_f - 2x_f. \end{aligned} \quad (6)$$

It cannot pay the female to deviate from her optimal response rule, which implies that the marginal expected fitness consequence of such a deviation must be 0. Formally,

$$\bar{M}(m_f, p_f, \hat{x}_f(m_f, p_f, x_m), x_m) = 0. \quad (7)$$

(Note that provided $\delta_m > -2$, the second derivative of $W[n, m_f, x_f, x_m]$ with respect to x_f is negative, and hence, any value of x_f satisfying Equation 7 represents a fitness maximizer rather than a minimizer.) Combining Equations 6 and 7, we find that, given our assumption of a linear male response rule, the female's unique optimal response rule must take the form

$$\begin{aligned} x_f^*(m_f, p_f, x_m) &= \alpha_f + \beta_f m_f + \gamma_f p_f + \delta_f x_m, \quad \text{where} \\ \alpha_f &= \frac{(1 + \delta_m) \sigma_{pf}^2 (\bar{n} (\beta_m^2 \sigma_m^2 + \gamma_m^2 \sigma_{pm}^2) - \gamma_m \sigma_n^2 (\alpha_m + \beta_m \bar{m}))}{X}, \\ \beta_f &= - \frac{\beta_m^2 \sigma_m^2 (\sigma_{pf}^2 + \sigma_n^2) + \gamma_m^2 (\sigma_{pf}^2 \sigma_{pm}^2 + \sigma_{pf}^2 \sigma_n^2 + \sigma_{pm}^2 \sigma_n^2)}{X}, \\ \gamma_f &= \frac{(1 + \delta_m) \sigma_n^2 (\beta_m^2 \sigma_m^2 + \gamma_m^2 \sigma_{pm}^2)}{X}, \\ \delta_f &= -((1 + \delta_m) \\ &\quad \times (2\beta_m^2 \sigma_m^2 (\sigma_{pf}^2 + \sigma_n^2) + 2\gamma_m^2 (\sigma_{pf}^2 \sigma_{pm}^2 + \sigma_{pf}^2 \sigma_n^2 + \sigma_{pm}^2 \sigma_n^2) \\ &\quad - \gamma_m \sigma_{pf}^2 \sigma_n^2)) / X \end{aligned} \quad (8a)$$

and

$$\begin{aligned} X &= 2(2 + \delta_m) \\ &\quad \times (\beta_m^2 \sigma_m^2 (\sigma_{pf}^2 + \sigma_n^2) + \gamma_m^2 (\sigma_{pf}^2 \sigma_{pm}^2 + \sigma_{pf}^2 \sigma_n^2 + \sigma_{pm}^2 \sigma_n^2)) \\ &\quad + \delta_m (1 + \delta_m) \gamma_m \sigma_{pf}^2 \sigma_n^2. \end{aligned} \quad (8b)$$

The optimal male rule

A precisely equivalent argument leads to the conclusion that if the female adopts a linear rule, then the male's unique optimal response rule must take the form

$$\begin{aligned} x_m^*(m_m, p_m, x_f) &= \alpha_m + \beta_m m_m + \gamma_m p_m + \delta_m x_f, \quad \text{where} \\ \alpha_m &= \frac{(1 + \delta_f) \sigma_{pm}^2 (\bar{n} (\beta_f^2 \sigma_f^2 + \gamma_f^2 \sigma_{pf}^2) - \gamma_f \sigma_n^2 (\alpha_f + \beta_f \bar{m}))}{Y}, \\ \beta_m &= - \frac{\beta_f^2 \sigma_f^2 (\sigma_{pm}^2 + \sigma_n^2) + \gamma_f^2 (\sigma_{pm}^2 \sigma_{pf}^2 + \sigma_{pm}^2 \sigma_n^2 + \sigma_{pf}^2 \sigma_n^2)}{Y}, \\ \gamma_m &= \frac{(1 + \delta_f) \sigma_n^2 (\beta_f^2 \sigma_f^2 + \gamma_f^2 \sigma_{pf}^2)}{Y}, \\ \delta_m &= -((1 + \delta_f) \\ &\quad \times (2\beta_f^2 \sigma_f^2 (\sigma_{pm}^2 + \sigma_n^2) + 2\gamma_f^2 (\sigma_{pm}^2 \sigma_{pf}^2 + \sigma_{pm}^2 \sigma_n^2 + \sigma_{pf}^2 \sigma_n^2) \\ &\quad - \gamma_f \sigma_{pm}^2 \sigma_n^2)) / Y \end{aligned} \quad (9a)$$

and

$$\begin{aligned} Y &= 2(2 + \delta_f) \\ &\quad \times (\beta_f^2 \sigma_f^2 (\sigma_{pm}^2 + \sigma_n^2) + \gamma_f^2 (\sigma_{pm}^2 \sigma_{pf}^2 + \sigma_{pm}^2 \sigma_n^2 + \sigma_{pf}^2 \sigma_n^2)) \\ &\quad + \delta_f (1 + \delta_f) \gamma_f \sigma_{pm}^2 \sigma_n^2. \end{aligned} \quad (9b)$$

The stable rule pair

Any simultaneous solution of Equations 8 and 9 yields a pair of linear response rules, each of which is optimal given the other. Provided that

$$|\delta_f \delta_m| < 1, \quad (10)$$

these rules lead to a stable outcome of negotiation, as assumed in the above analysis. Under these circumstances because each rule is optimal given the other, the pair represents an evolutionarily stable solution of the parental negotiation game. Unfortunately, we are unable to derive a general analytical solution to Equations 8 and 9 (although we have obtained some partial analytical results, to be described later). It is not difficult, however, to calculate solutions numerically. In the next section, therefore, we present results based on stable pairs of rules obtained in this way.

We can also consider whether an evolutionarily stable rule pair is locally convergently stable. In other words, we can ask whether a population adopting a linear pair of rules that deviate slightly from the evolutionarily stable pair will evolve toward the evolutionarily stable strategy (ESS) (we do not consider convergence stability within the larger space of nonlinear rules). To address this question, we make the assumption that evolutionary change is described by the continuous-time adaptive dynamics of Hofbauer and Sigmund (1998). Thus, the pair of rules adopted in a population are described by the vector of parameters $(\alpha_f, \beta_f, \gamma_f, \delta_f, \alpha_m, \beta_m, \gamma_m, \delta_m)$, and we assume that the rate of evolutionary change in each element of this vector is given by the partial derivative of mutant fitness with respect to the parameter in question. We can then determine whether an evolutionarily stable pair of rules is also convergently stable by calculating the eigenvalues of the Jacobian matrix of the vector of partial derivatives at the equilibrium.

Strategies in the negotiation game specify how males and females respond to their partner's effort level. These responses are determined by the parameters δ_f and δ_m , which describe the increase (or decrease) in female or male effort level per unit change in partner effort. The sealed bid version of the game (analyzed in the Appendix), by contrast, does not allow for negotiation and thus corresponds to a special case of the present model in which δ_f and δ_m are both fixed at 0. We

emphasize, however, that under some circumstances, the negotiation game too may yield a stable solution for which δ_f or δ_m or both are equal to 0. Under these circumstances, the model implies that sealed bid behavior on the part of the female or male (or both) is actually adaptive, even when one allows for the possibility of negotiation. Lack of responsiveness, in other words, may emerge as a prediction of the negotiation model, whereas it is simply assumed in the sealed bid model.

Implications of the stable rule pair

Having obtained a stable pair of linear rules, we can use them to predict the expected level of provisioning by the female and the male parent and the variance in these values. Joint solution of the equations given in Equation 2 yields the levels of provisioning at the end of the negotiation process, for particular values of m_f , m_m , p_f , and p_m :

$$\begin{aligned} x_f(m_f, m_m, p_f, p_m) &= \frac{\alpha_f + \beta_f m_f + \gamma_f p_f + \delta_f(\alpha_m + \beta_m m_m + \gamma_m p_m)}{1 - \delta_f \delta_m}, \\ x_m(m_f, m_m, p_f, p_m) &= \frac{\alpha_m + \beta_m m_m + \gamma_m p_m + \delta_m(\alpha_f + \beta_f m_f + \gamma_f p_f)}{1 - \delta_f \delta_m}. \end{aligned} \tag{11}$$

From Equation 11 it follows, given our assumptions about the distributions of m_f , m_m , p_f , and p_m , that the expected levels of female and male provisioning are given by

$$\begin{aligned} E(x_f) &= \frac{\alpha_f + \beta_f \bar{m} + \gamma_f \bar{n} + \delta_f(\alpha_m + \beta_m \bar{m} + \gamma_m \bar{n})}{1 - \delta_f \delta_m}, \\ E(x_m) &= \frac{\alpha_m + \beta_m \bar{m} + \gamma_m \bar{n} + \delta_m(\alpha_f + \beta_f \bar{m} + \gamma_f \bar{n})}{1 - \delta_f \delta_m} \end{aligned} \tag{12}$$

and that

$$\begin{aligned} \text{Var}(x_f) &= \frac{\beta_f^2 \sigma_m^2 + \delta_f^2 \beta_m^2 \sigma_m^2 + (\gamma_f + \delta_f \gamma_m)^2 \sigma_n^2 + \gamma_f^2 \sigma_{pf}^2 + \delta_f^2 \gamma_m^2 \sigma_{pm}^2}{(1 - \delta_f \delta_m)^2}, \\ \text{Var}(x_m) &= \frac{\beta_m^2 \sigma_m^2 + \delta_m^2 \beta_f^2 \sigma_m^2 + (\gamma_m + \delta_m \gamma_f)^2 \sigma_n^2 + \gamma_m^2 \sigma_{pm}^2 + \delta_m^2 \gamma_f^2 \sigma_{pf}^2}{(1 - \delta_f \delta_m)^2}. \end{aligned} \tag{13}$$

It is also possible to calculate, in a similar way, the correlation between the provisioning levels of the two parents and the slope of the regression of male or female provisioning effort on brood need, although we will not give these formulae here.

RESULTS

In this section, we present results based on numerical solution of Equations 8 and 9. These solutions were obtained using the FindRoot function in Mathematica (Wolfram Research Inc 2001), which employs Newton’s method, with initial values of the coefficients in the search procedure corresponding to the sealed bid solution of the game, derived in the Appendix (though other starting values were found to yield the same solution). Over the ranges of parameter values for which results are presented, we confirmed numerically that all evolutionarily stable solutions are also locally convergently stable and yield a stable outcome of negotiation. We begin by pre-

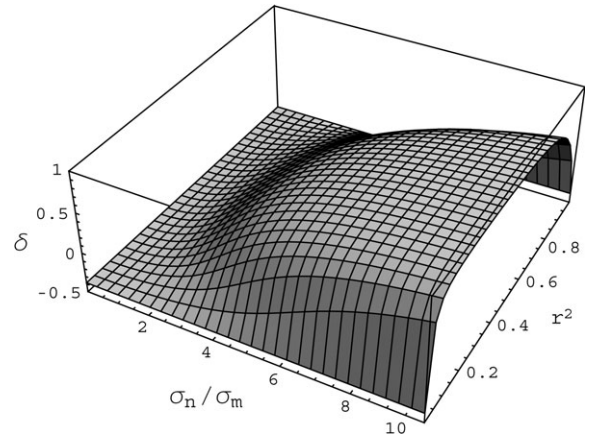


Figure 2

The response of either parent to a change in the other’s level of provisioning (i.e., the stable value of δ), as a function of the standard deviation of brood need relative to that of parental state (σ_n/σ_m) and the accuracy with which each parent can determine brood need (measured as the correlation r^2 between perceived and true need). Negative responses indicate compensation (such that if one parent works harder, the other will work less hard), whereas positive responses indicate matching (such that if one parent works harder, the other will work harder too). As stated in the main text, these results do not depend on the value of σ_m . Other parameter values are $\bar{m} = 1$ and $\bar{n} = 6$.

sending results for the symmetrical case in which $\sigma_{pm}^2 = \sigma_{pf}^2 = \sigma_{pm}^2 = \sigma_{pf}^2$ (i.e., in which both parents are equally well or poorly informed about brood need), so that at equilibrium $\alpha_f = \alpha_m = \alpha$, $\beta_f = \beta_m = \beta$, $\gamma_f = \gamma_m = \gamma$, and $\delta_f = \delta_m = \delta$ (i.e., both parents adopt the same response rule).

Results of the symmetrical case

We focus first on the way in which parents respond to each other’s effort, that is, on the value of δ at equilibrium (illustrated in Figure 2). This depends only on the relative levels of variation in parental state (σ_m), variation in true need (σ_n), and error variation in perceived need (σ_p); it is independent of the absolute values of these parameters and of the values \bar{m} (mean parental state) and \bar{n} (mean brood need). For simplicity, we plot δ as a function of two composite parameters: σ_n/σ_m , the ratio of the standard deviation in offspring need to standard deviation in parental state and, r^2 , the squared correlation between perceived and true need (which depends on σ_n , the variation in true need, and σ_p the error in perception). This latter value, r^2 , is essentially a measure of how well or poorly informed parents are about offspring need; $r^2 = 0$ implies that parents have no information, $r^2 = 1$ implies that they have perfect information, and intermediate values imply partial information.

When there is little or no variation in brood need compared with the variation in parental state (as in previous analyses), or when parental assessment of brood need is either very accurate or very inaccurate, then each parent responds to a change in the other’s level of provisioning with an incomplete compensatory change in the opposite direction (i.e., the stable value of δ is negative; see Figure 2). Thus, if the male works harder, the female reduces her level of provisioning (but not so far as to completely cancel out the male’s greater contribution), and vice versa. By contrast, when variation in brood need is large compared with variation in parental state and when each parent has partial but incomplete information as to the precise level of need, then each will respond to a change in the other’s level of provisioning with a matching, though

less pronounced change in the same direction (i.e., the stable value of δ is positive; see Figure 2). Thus, when the male works harder, the female works harder too, and vice versa. So as variation in brood need increases from 0, we see a shift from significant compensation (negative δ), through 0 (a complete lack of response to partner effort), to significant matching (positive δ).

Although we are unable to derive a general analytical solution to the model, we can (in the symmetrical case) obtain an expression for the boundary separating the region in which parents exhibit compensatory responses from the region in which they exhibit matching responses. The model predicts matching when

$$\frac{\sigma_n}{\sigma_m} > \frac{2 + r^2}{2\sqrt{r^2(1 - r^2)}}.$$

When parents respond to a change in each other's level of provisioning with a compensatory response in the opposite direction, then the expected level of provisioning that the brood receives is lower than at the sealed bid solution. In other words, negotiation leads to lower levels of effort at equilibrium (see McNamara et al. 1999, 2003). By contrast, when parents respond to a change in each other's level of provisioning with a matching change in their own level of effort, equilibrium provisioning is greater than at the sealed bid solution. Parental negotiation, under these circumstances, leads to greater investment in brood care.

Finally, when there is little variation in brood need (compared with parental state) and parents exhibit strong compensatory responses to each other's effort, then (in the absence of any correlation between the qualities of mates) their levels of provisioning tend to be negatively correlated. As variation in brood need increases (favoring weaker compensation or even matching), however, their effort levels become positively correlated. Note, however, that correlations between the qualities of mates (arising, for instance, from assortative mating) may in reality obscure these effects of negotiation (unless experimentally controlled, see e.g., Smiseth and Moore 2004).

Informational asymmetry

We now move on to consider asymmetrical versions of the model, in which the female and male parents differ in the extent of their information regarding brood need (we focus solely on informational asymmetry and continue to assume that the costs of care are on average the same for both sexes). We assume that the female parent is better informed because females often spend more time with the young (e.g., in great tits, *Parus major*; females typically brood the young during the early nestling phase, whereas males defend the territory—see Sanz et al. 2000). In addition, there may be maternal effects on begging, either genetic (e.g., Kolliker et al. 2000) or mediated by egg hormones such as testosterone (e.g., Eising and Groothuis 2003), ignorance of which would presumably reduce the information regarding brood need that fathers can derive from begging (see Kilner 2002). There is, however, no real loss of generality here because the case in which the male is better informed yields precisely the opposite results.

When the female is better informed about brood need than is the male, the model predicts that she will exhibit more marked compensation, that is, will respond to a change in the male's level of provisioning with a more marked change in the opposite direction (see Figure 3). The magnitude of compensation by the male will decrease as his information regarding brood need deteriorates, eventually passing through 0 and becoming negative. Thus, when the informational asymmetry is very great—such that the female has

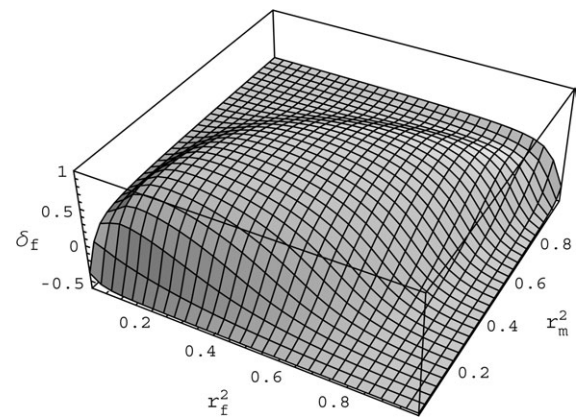


Figure 3 The response of the female parent to a change in the male's level of provisioning (i.e., the stable value of δ_f), as a function of the accuracy with which each parent can determine brood need (measured as the squared correlation between perceived and true need, denoted r_f^2 for the female and r_m^2 for the male). Negative responses indicate compensation (such that if the male parent works harder, the female will work less hard), whereas positive responses indicate matching (such that if the male parent works harder, the female will work harder too). Other parameter values are $\bar{m} = 1$, $\sigma_m = 0.1$, $\bar{n} = 6$, and $\sigma_n = 0.5$. Note that the graph of male response to a change in the female's level of provisioning is an exact mirror image of the one shown here.

highly accurate information about brood need, whereas the male has very little information—the model predicts compensation by the female but matching by the male. Given a less pronounced asymmetry—such that the female has moderately better information about brood need than does the male—the model predicts stronger compensation by the female and weaker compensation by the male.

The better-informed parent is also predicted to invest on average more effort in brood care than is the less well-informed parent (see Figure 4), to exhibit a greater response to changes in the level of brood need (see Figure 5), and a lesser response to changes in its own state or the cost of

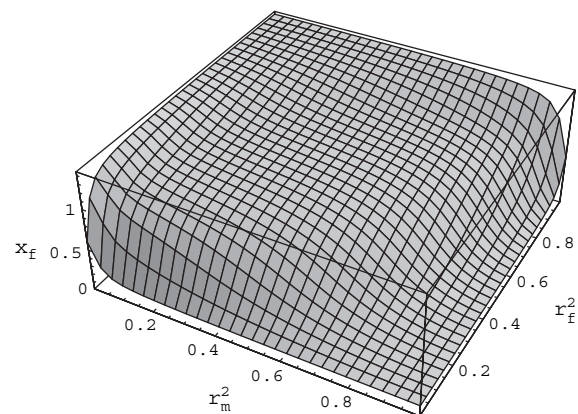


Figure 4 The mean level of provisioning by the female, as a function of the accuracy with which each parent can determine brood need (measured as the squared correlation between perceived and true need, denoted r_f^2 for the female and r_m^2 for the male); note that the axes have been swapped compared with those in Figure 3 (so that the shape of the graph can be more clearly seen). Other parameter values are $\bar{m} = 1$, $\sigma_m = 0.1$, $\bar{n} = 6$, and $\sigma_n = 0.5$. The graph of male provisioning is an exact mirror image of the one shown here.

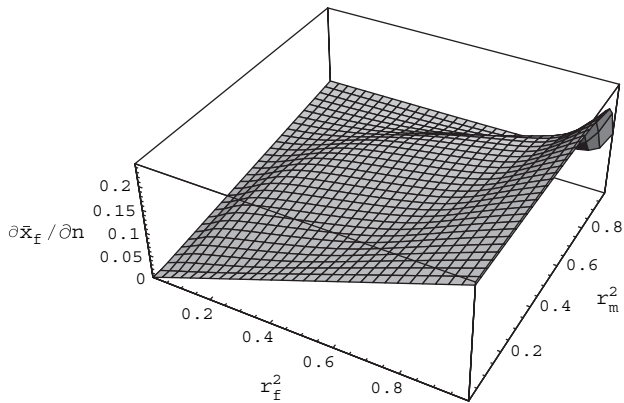


Figure 5

The slope of the regression of mean female provisioning on brood need, as a function of the accuracy with which each parent can determine brood need (measured as the squared correlation between perceived and true need, denoted r_f^2 for the female and r_m^2 for the male). Other parameter values are $\bar{m} = 1$, $\sigma_m = 0.1$, $\bar{n} = 6$, and $\sigma_n = 0.5$. The graph of male provisioning is an exact mirror image of the one shown here.

feeding it experiences (see Figure 6). Thus if, as assumed above, females are better informed than males, then they are predicted to work harder than males to compensate more strongly for changes in male effort, to respond more markedly to variation in brood need, and to adjust their own effort less in response to changes in the cost of feeding.

DISCUSSION

When one parent changes its level of investment in offspring care, this may influence the behavior of the other parent for two reasons. First, a change in the focal parent's effort may directly affect the benefits of additional investment by its mate. If investment yields decelerating returns (as usually assumed), then greater effort by the focal parent leads to a decline in the marginal benefit of care. This favors a compensatory reduction in investment by its mate. Second, a change in the focal parent's effort may indirectly affect the behavior of its mate because of the information it conveys. The behav-

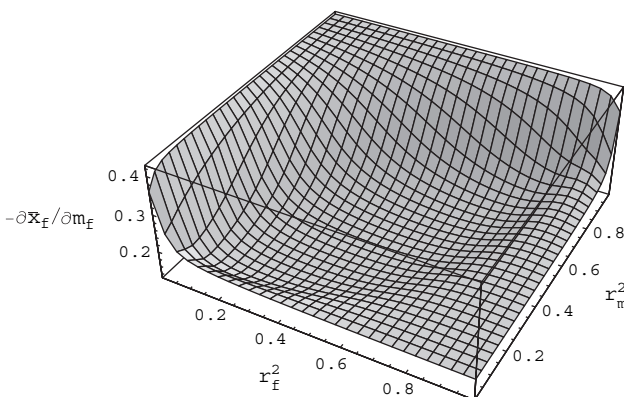


Figure 6

The slope of the regression of mean female provisioning on female state, as a function of the accuracy with which each parent can determine brood need (measured as the squared correlation between perceived and true need, denoted r_f^2 for the female and r_m^2 for the male). Other parameter values are $\bar{m} = 1$, $\sigma_m = 0.1$, $\bar{n} = 6$, and $\sigma_n = 0.5$. The graph of male provisioning is an exact mirror image of the one shown here.

ior of the focal parent is likely to reflect its own state, its perception of brood need, the availability of food, and perhaps other factors too (e.g., its perception of its mate's quality). Consequently, its mate may be expected to respond to a change in effort as indicating a change in one or more of these factors.

Previous analyses have focused on the direct impact of a change in parental effort and have paid little attention to the exchange of information between parents. Consequently, they have predicted compensatory responses to changes in partner effort. Here, we have extended the framework developed by McNamara et al. (1999, 2003) to incorporate uncertainty regarding brood need. When each parent has only partial information regarding need, greater effort invested by one serves as a signal to the other that the focal individual perceives the brood as needy. This favors a matching increase in the other parent's own investment.

Why should we assume that parents possess only partial information about brood need? There is now good evidence that chick begging reflects current hunger (reviewed by Kilner and Johnstone 1997; Godfray and Johnstone 2000), which suggests that parents could assess this aspect of "need," and, by inference, the work rate of their partner by monitoring chick behavior (Wright and Cuthill 1990a; Wright and Dingemanse 1999). Nevertheless, assessment of short-term need via begging may well be less than perfectly accurate (Schwagmeyer et al. 2002, and for a review of theoretical debate on this issue, see Johnstone and Godfray 2002). Additionally, more cryptic components of brood need in our sense include the "long-term" condition and quality of the chicks (see Christe and Richner 1996; Iacovides and Evans 1998; Wright et al. 2002). It seems unlikely that parents can untangle all these factors in their evaluation of offspring display, especially if short-term fluctuations in hunger mask the longer term effects. Hence, we suggest that parents may often be able to glean extra information about the need or value of the brood from the behavior of their partner, which can be integrated with the information obtained by their own assessment of offspring begging.

The information conveyed by an increase in one parent's effort should tend to elicit a matching response by its mate, whereas the direct impact of this increase on the marginal value of investment favors a compensatory response. As we have shown, the net outcome depends on the relative strength of these two effects. If there is little variation in brood need compared with variation in parental state, then the informational effect is weak. Under these circumstances, parental effort reflects the state of the parent more than it does brood need. Consequently, high effort is unlikely to encourage a matching response and we expect to see compensation. By contrast, when there is little variation in parental state compared with variation in brood need, then greater parental effort is likely to indicate more needy young. This will (to a degree) encourage greater effort by the partner, weakening the level of compensation that we expect to see. In the extreme, it can even cancel out the compensatory response altogether (giving rise to a sealed bid outcome, despite the potential for negotiation) or lead to a net matching response.

The extent to which parents respond to each other's efforts as indicative of brood need also depends on the degree of independent information that each has. If neither parent can independently assess brood need, then neither can learn anything from the other. At the other extreme, if each can independently assess brood need with great accuracy, then neither needs to learn anything from the other. Only if parents have partial information do we expect them to rely on each other's behavior as a guide to brood need. Even in this case, as we have said, each will integrate the information

obtained from the other with its own assessment of offspring need. Indeed, combining direct assessment with information from a partner's work level will be likely to enhance or give extra information about the chicks' state. Nevertheless, greater effort by one parent will then tend to favor a matching response by the other.

At this point, the reader may well question whether matching responses are compatible with stable biparental care. Might they not lead to runaway escalation or decay in the level of investment, as a result of positive feedback? In fact, there is nothing intrinsically destabilizing about matching responses. Stability depends on the magnitude of each parent's response to the other, not on the direction of this response. Complete or overcompensation leads to instability (though see Jones et al. 2002) and so does complete or overmatching. By contrast, incomplete matching results in a stable negotiated solution just as does incomplete compensation. In terms of our model, as stated in condition (10), the process of negotiation will lead to a stable outcome provided that the product of the slopes of the two parents' response rules is of magnitude less than 1 (regardless of whether these slopes are positive or negative), and this is true of all the evolutionarily stable pairs of response rules that we have considered.

Explaining the data

Our analysis thus suggests one reason why different empirical studies might report different levels of compensation. Strong compensation should arise when there is little variation in brood need compared with parental state (or when parents can independently determine brood need with great accuracy). By contrast, when there is marked variation in brood need compared with parental state, we should expect compensation to be weak or absent, or even to see matching responses. But how can we assess the magnitude of variation in brood need compared with variation in parental state? One possible measure might be the repeatability of provisioning rate among parents over breeding attempts. If, for instance, brood need varies from one breeding attempt to the next (e.g., due to variation in clutch size) to a greater extent than does a parent's state, high repeatability suggests that variation in individual parental ability is substantial compared with variation in need, whereas low repeatability suggests that variation in individual quality is low compared with variation in brood need (see Schwagmeyer and Mock 2003). We should then predict a positive relationship between the repeatability of individual effort and the strength of compensation.

Informational considerations also suggest that the time at which an experimental manipulation is carried out may affect the results of an experiment. If mates can gain information about each other over the course of a breeding season, there may be less uncertainty about partner state later on. Consequently, handicapping a bird may be less likely to affect its partner's perception of its state if this is done late in the nesting period. This would lead to stronger compensation later in the season (as partner work rate is then less indicative of partner state and more indicative of brood need).

We emphasize, however, that ours is not the only possible explanation for variation in the extent of compensation. Existing analyses suggest that the shape of the function describing investment costs will affect parental responses (Winkler 1987; Ratnieks 1996; Sanz et al. 2000). If costs are steeply accelerating, for instance, it may be more difficult for a parent to compensate for a drop in its partner's effort. However, this idea is very hard to test—to determine whether the costs of investment are more or less strongly accelerating is far from easy (though for an attempt to infer cost curves from the pattern of response to experimental handicapping, see Sanz

et al. 2000). By contrast, repeatability of individual effort is simpler to assess. In addition, it is difficult to account for matching responses simply in terms of the shape of the cost function (though if the benefit curve is accelerating rather than decelerating, matching may be possible; such a situation, however, is unlikely to prove stable and seems to us less plausible than the informational explanation offered here).

Differences between the sexes

Our analysis also suggests why males and females might respond differently to each other's efforts. If there is an informational asymmetry between the sexes (as discussed in Results), then the parent that is better informed about brood need should (all other things being equal) work harder, respond more strongly to changes in brood need (leading to lower repeatability of individual effort across broods), be less sensitive to changes in its own state or the cost of feeding it experiences, and show more marked compensation for changes in partner effort. Its less well-informed mate should display weaker compensation or possibly no response at all. If the asymmetry is very great, the poorly informed parent may even be expected to match any change in its partner's work rate.

Intriguingly, the study by Sanz et al. (2000) of differential responses by males and females to manipulation of partner contribution in the great tit (*Parus major*) reports findings that match our predictions if females are better informed regarding brood need than are males—females adjusted their own effort levels less in response to experimental feather cutting but compensated more strongly for changes in partner effort. The study even yielded some indication of matching by males (males with a handicapped partner did not show any compensation and even tended to decrease their feeding rates). Moreover, an informational asymmetry between the sexes is plausible in great tits because (as stated above) the tasks of male and female parents differ in the early nestling phase, with females brooding the young, whereas males have to defend the territory.

Advantages and limitations of the negotiation model

The modeling approach we have adopted here, based on McNamara et al. (1999, 2003), explicitly allows for "negotiation" between mates over investment in care, on a behavioral timescale. By contrast, earlier models focused on evolutionary dynamics alone, with the strategies of mates specifying a fixed level of investment, that is, a sealed bid. We view the negotiation approach as a step forward because it directly addresses the response of parents to experimentally induced changes in partner effort. Schwagmeyer et al. (2002) have argued, based on both their own findings on house sparrows and a number of previous studies (Slagsvold and Lifjeld 1988, 1990; Lozano and Lemon 1996; Sanz et al. 2000), that "effort levels that are largely independent of the mates' efforts (fitting the implicit sealed bid assumption of the earlier ESS models) may be more common than is generally recognised." However, even if sealed bid models are applicable in some species, they cannot hope to explain why insensitivity to partner contributions has not been replaced by behavioral negotiation in these cases. For such models, the absence of negotiation is an assumption rather than a prediction. By contrast, our model shows that within the negotiation framework, we can explain both why parents of some species should respond to each other's efforts and why parents of other species should not. Indeed, we can attempt to predict when males should respond more than females and vice versa. In other words, negotiation or the lack of it is not assumed but predicted by the model.

Despite the advantages of the negotiation framework, however, our analysis of parental interaction remains incomplete. Two limitations of the present model stand out. First, we have focused only on the stable outcome of negotiation, given fixed parameters specifying the costs and benefits of begging and feeding. We can predict how parents will respond in the short term if this stable situation is perturbed, but the model does not address the longer term changes in parental interaction due to offspring growth, depletion of parental reserves, changes in food availability, etc. To do so, however, it would require a fundamentally different approach, in which the interaction between parents is modeled as a state-dependent dynamic game (see e.g., McNamara et al. 2000; Barta et al. 2002).

Second, we have dealt only with the interaction between parents, treating offspring as passive receptacles for parental investment. In reality, of course, parent-offspring interaction and sibling competition may play a key role in family conflict resolution and may even mediate negotiation between the parents themselves (Wright and Cuthill 1990a; Wright and Dingemans 1999; Parker et al. 2002). Some previous models have explored negotiation between offspring, while omitting negotiation between parents (Godfray 1995; Johnstone and Roulun 2003; Johnstone 2004); others have looked at negotiation between a single parent and a single offspring, ignoring sibling competition and parent-parent interaction (Hussell 1988; Johnstone 1999; Parker et al. 2002; RA Johnstone, in preparation). We suggest that the next step forward will be to integrate these approaches in a unified model of family negotiation that incorporates the responses of each family member to all the others.

APPENDIX

The sealed bid solution

In this section, we derive the sealed bid solution to the model presented in the main text. That is, we solve a modified version of the model in which the parents are unable to respond to each other's behavior, but each must instead choose a fixed level of provisioning based only on its own state and its own perception of brood need.

As before, the model yields an evolutionarily stable pair of linear strategies, in this case of the form

$$\begin{aligned} x_f^*(m_f, p_f) &= \alpha_f + \beta_f m_f + \gamma_f p_f, \\ x_m^*(m_m, p_m) &= \alpha_m + \beta_m m_m + \gamma_m p_m. \end{aligned} \quad (\text{A1})$$

Bearing in mind the lack of any possibility of negotiation in the sealed bid version of the game, the marginal change in the female parent's fitness resulting from an increase in her provisioning, assuming that the brood is of need n , she is in state m_f , she provisions at level x_f , and the male provisions at level x_m , is given by

$$\begin{aligned} M(n, m_f, x_f, x_m) &= \frac{\partial W(n, m_f, x_f, x_m)}{\partial x_f} \\ &= n - m_f - 4x_f - 2x_m. \end{aligned} \quad (\text{A1})$$

As before, the true level of brood need, n , is unknown to the female and must be estimated based on her perception of need p_f . In addition, the male's level of provisioning x_m (which depends on his state and perception of brood need) is also unknown at the time the female makes her decision. To determine the female's optimal strategy (given that the male adopts a linear strategy of the form specified in Equation A1), we therefore need to determine the expected marginal fitness

consequences of an increase in her provisioning, conditional on p_f . Using Bayes' rule, we obtain

$$\begin{aligned} \bar{M}(m_f, p_f) &= \left(\frac{\sigma_{p_f}^2 \bar{n} + \sigma_n^2 p_f}{\sigma_{p_f}^2 + \sigma_n^2} \right) - m_f - 4x_f \\ &\quad - 2 \left(\alpha_m + \beta_m \bar{m} + \gamma_m \left(\frac{\sigma_{p_f}^2 \bar{n} + \sigma_n^2 p_f}{\sigma_{p_f}^2 + \sigma_n^2} \right) \right). \end{aligned} \quad (\text{A2})$$

Setting the above equal to 0 and solving for x_f we find that (given our assumption of a linear male strategy) the female's optimal strategy must take the form

$$\begin{aligned} x_f^*(m_f, p_f) &= \alpha_f + \beta_f m_f + \gamma_f p_f, \quad \text{where} \\ \alpha_f &= \frac{\sigma_{p_f}^2 (1 - 2\gamma_m) \bar{n} - 2(\sigma_{p_f}^2 + \sigma_n^2)(\alpha_m + \beta_m \bar{m})}{4(\sigma_{p_f}^2 + \sigma_n^2)}, \\ \beta_f &= -\frac{1}{4}, \\ \gamma_f &= \frac{\sigma_n^2 (1 - 2\gamma_m)}{4(\sigma_{p_f}^2 + \sigma_n^2)}. \end{aligned} \quad (\text{A3})$$

(Note that the derivative of M with respect to x_f is negative, so that the strategy specified by Equation A3 is fitness maximizing rather than fitness minimizing.) A precisely equivalent argument leads to the conclusion that if the female adopts a linear strategy, then the male's optimal strategy must take the form

$$\begin{aligned} x_m^*(m_m, p_m) &= \alpha_m + \beta_m m_m + \gamma_m p_m, \quad \text{where} \\ \alpha_m &= \frac{\sigma_{p_m}^2 (1 - 2\gamma_f) \bar{n} - 2(\sigma_{p_m}^2 + \sigma_n^2)(\alpha_f + \beta_f \bar{m})}{4(\sigma_{p_m}^2 + \sigma_n^2)}, \\ \beta_m &= -\frac{1}{4}, \\ \gamma_m &= \frac{\sigma_n^2 (1 - 2\gamma_f)}{4(\sigma_{p_m}^2 + \sigma_n^2)}. \end{aligned} \quad (\text{A4})$$

Joint solution of Equations A3 and A4 yields a unique, evolutionarily stable pair of linear rules, defined by

$$\begin{aligned} \alpha_f &= \frac{(2\sigma_{p_f}^2(\sigma_{p_m}^2 + \sigma_n^2) - \sigma_{p_m}^2 \sigma_n^2) \bar{n}}{3Z} + \frac{\bar{m}}{12}, \\ \beta_f &= -\frac{1}{4}, \quad \gamma_f = \frac{\sigma_n^2 (2\sigma_{p_m}^2 + \sigma_n^2)}{2Z}, \\ \alpha_m &= \frac{(2\sigma_{p_m}^2(\sigma_{p_f}^2 + \sigma_n^2) - \sigma_{p_f}^2 \sigma_n^2) \bar{n}}{3Z} + \frac{\bar{m}}{12}, \\ \beta_m &= -\frac{1}{4}, \quad \gamma_m = \frac{\sigma_n^2 (2\sigma_{p_f}^2 + \sigma_n^2)}{2Z}, \end{aligned} \quad (\text{A5})$$

$$\text{where } Z = 4\sigma_{p_f}^2 \sigma_{p_m}^2 + 4\sigma_{p_f}^2 \sigma_n^2 + 4\sigma_{p_m}^2 \sigma_n^2 + 3(\sigma_n^2)^2.$$

The above values (setting $\delta_f = \delta_m = 0$) are used as the starting point for the numerical search procedure (described in the main text) when calculating solutions to the full model.

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