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Should young ever be better off with one parent than with two?

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We analyze models of parental care, providing the first systematic comparison of the care given to young by one parent versus by two parents. In the Houston-Davies model of care, young always do better with two parents rather than with one parent. When one parent decides about its level of care before the other, then the young may do better with one parent when the costs of care for the parents are asymmetric. When the level of parental effort is reached by negotiation, there are cases in which young do better with one parent, even when costs are symmetric. The analysis suggests empirical ways to differentiate between different response rules. *Key words:* game theory, mate removal, negotiation, parental effort. *[Behav Ecol 14:301–310 (2003)]*

How hard a parent should work when rearing its young is a central question in behavioral ecology. The effort that a parent devotes to its current offspring has the benefit that the offspring's prospects of survival and reproduction are improved, but at the cost to the parent in terms of its own future reproductive success. The standard method for predicting the level of parental effort in the face of this trade-off between current and future reproductive success involves maximizing the parent's lifetime reproductive success (Roff, 1992; Stearns, 1992).

In many dioecous species, both parents care for the young (for an overview see Clutton-Brock, 1991). These cases of biparental care cannot be analyzed by optimization alone. Trivers (1972) stressed that there was a conflict of interest between the two members of a pair. Rather than being engaged in a purely cooperative enterprise, each would prefer the other to do most of the work involved in raising the young. This conflict of interest is the basis for the approach to parental care developed by Houston and Davies (1985).

Houston and Davies assumed that in the game between the parents, over evolutionary time each parent should adopt its best effort, given the effort adopted by its mate. The evolutionarily stable strategy (ESS) specifies a level of effort for the male and a level of effort for the female. At the ESS, each parent adopts its best effort given the effort of its mate, so there is no temptation for either parent to change its effort.

The approach adopted by Houston and Davies assumes that each parent makes a single decision about its effort. This decision is independent of the effort adopted by the parent's mate. This means that there is no negotiation between the parents. Other forms of game between the parents are possible. McNamara et al. (1999) model the negotiation between the parents over the level of effort. In this paper we look at the implications of negotiation and nonindependent decisions for the levels of effort adopted by members of a pair.

We are concerned with species in which both parents usually care for the young, for at least part of the time, until the young are independent. The main issue that we address is whether the young might do better when one of the parents is removed or killed as opposed to when both parents care.

We will consider two questions: (1) how does the optimal effort of a single parent of a given sex compare with the evolutionarily stable effort of an individual of this sex when in a pair; and (2) how does the effort of a single parent compare with the total effort of a pair?

It has been shown in insects (Fetherston et al., 1994), fish (see Itzkowitz et al., 2001; Lavery and Reebs, 1994; Mrowka, 1982; Raadik et al., 1990), and birds (see Bart and Tornes, 1989; Duckworth, 1992; Markman et al., 1996; Sasvári, 1986; Whillans and Falls, 1990; Whittingham et al., 1994) that a member of a pair will compensate for the absence of its mate by working harder. The general picture that emerges from these studies is that the measured level of care provided by a single parent is either less than the total care of a pair or is not significantly different from this total care, and that the young never do significantly better when cared for by a single parent.

In contrast to this pattern, Parker (1985; see also Mock and Parker, 1997) presented a model in which the total effort of a pair was less than the effort of a single parent. Thus, in this model, offspring are better off when cared for by one parent than when cared for by two parents.

In this article we demonstrate that the biparental care solution identified by Parker (1985) is not stable. We present a general graphical argument that shows that the total effort of two parents in the Houston-Davies case is greater than the effort of a single parent. We also show that this conclusion may not hold in other forms of the game between the parents.

Although our main concern is the effort of single parents as opposed to members of a pair, we will also discuss the response of a parent to changes in the effort of its mate during a breeding attempt. A central question is to what extent can the effort of a single parent be regarded as the response to no effort by its mate. The Houston-Davies approach deals with how the effort of males and females settles down over evolutionary time. The approach has been seen as a model of the response of one parent to the effort of the other during a breeding attempt, but this view is erroneous; responding in this way is not evolutionarily stable (McNamara et al., 1999). Our analysis offers a new way to differentiate empirically between different response rules.

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The modelling framework

Our approach is to assume that each parent can choose a level of effort that it devotes to its young. (In some cases, a parent's effort may be chosen after a period of negotiation between the parents.) When two parents care for the young, we refer to the parents as parent 1 and parent 2 and denote their efforts by u_1 and u_2, respectively. Each parent obtains a contribution, B, to its reproductive success from the current reproductive attempt. This contribution depends on the total effort, $u_1 + u_2$, of the pair. In general, we assume that B increases with total effort, but that each increment in effort is worth less, i.e., $B' > 0$ and $B'' < 0$. (We weaken the assumption that $B'' < 0$ in a particular case.) The effort that a parent devotes to its young is assumed to reduce the parent's future reproductive success. We represent this reduction by a cost, K. Because male and female parents may differ in various ways, their cost functions may differ. We denote the cost to parent i by $K_i(u_i)$. We assume that cost increases with effort, and that each extra unit of effort is more costly, i.e., $K' > 0$ and $K'' > 0$. Thus, the total reproductive success of parent 1 is maximized by maximizing

$$B(u_1 + u_2) - K_1(u_1), \tag{1}$$

and the total reproductive success of parent 2 is maximized by maximizing

$$B(u_1 + u_2) - K_2(u_2). \tag{2}$$

Here we have implicitly used the decomposition of current reproductive value into the sum of current reproductive success and residual reproductive value given by Williams (1966). For a derivation of this decomposition in a state-structured life-history context see Houston and McNamara (1999). Note that in our formulation, we assume that an individual's future is independent of the mate that it has in the current attempt.

The best response function

The best response function specifies the effort of one parent that maximizes the parent's lifetime reproductive success, given a fixed level of effort by its mate. This function is useful in analyzing the game between parents. Let $\hat{r}_1(u_2)$ be the best effort of parent 1 when the effort of parent 2 is u_2, and $\hat{r}_2(u_1)$ be the best effort of parent 2 when the effort of parent 1 is u_1.

To find the best effort of parent 1, we differentiate Expression 1 with respect to u_1 and set the result equal to zero. This gives us the following equation:

$$B'[\hat{r}_1(u_2) + u_2] = K_1'[\hat{r}_1(u_2)]. \tag{3}$$

To establish the extent to which one parent should compensate over evolutionary time for a change in the effort of its mate, we need to know the slope of the best response curve. We can find this by differentiating Equation 3 with respect to u_2. This gives

$$[1 + \hat{r}_1'(u_2)]B''[\hat{r}_1(u_2) + u_2] = K_1''[\hat{r}_1(u_2)]\hat{r}_1'(u_2)$$

from which it follows that

$$\hat{r}_1'(u_2) = \frac{B''[\hat{r}_1(u_2) + u_2]}{K_1''[\hat{r}_1(u_2)] - B''[\hat{r}_1(u_2) + u_2]}. \tag{4}$$

We have assumed that $K'' > 0$. If we also have $B'' < 0$ (i.e., effort devoted to the young yields diminishing returns), then

$$-1 < \hat{r}_1'(u_2) < 0 \quad \text{for all } u_2. \tag{5}$$

By an analogous argument, when $B'' < 0$,

$$-1 < \hat{r}_2'(u_1) < 0 \quad \text{for all } u_1. \tag{6}$$

We see from Expressions 5 and 6 that when the total effort to the young results in diminishing returns (i.e., $B'' < 0$), the slope of the best response function is negative. This means that when one parent decreases its effort, the other parent increases its effort. It can also be seen that the slope is greater than -1. A slope of -1 corresponds to complete compensation; i.e., the decrease in the effort of one parent is exactly matched by the increase in the effort of the other parent. A slope greater than -1 means a smaller absolute slope and, hence, corresponds to incomplete compensation.

To illustrate some of the effects that arise when $B'' < 0$, we consider the simple case in which B and K are quadratic functions in the range of interest. In this case, both the second derivatives are constant, and so from Equation 4 (and the corresponding Equation for $\hat{r}_2'[u_1]$), $\hat{r}_1'(u_2)$ and $\hat{r}_2'(u_1)$ are both constant. We make the following definitions: $\lambda_1^* = -\hat{r}_1'(u_2)$, and $\lambda_2^* = -\hat{r}_2'(u_1)$.

Then the best response function for parent i is a straight line, and if the mate decreases its effort by unit amount, then parent i increases its effort by λ_i^*. This slope λ_i^* is a measure of the degree to which parent i compensates for the reduction in its mate's effort.

As an example, assume that

$$B(u_1 + u_2) = 2(u_1 + u_2) - (u_1 + u_2)^2, \tag{7}$$

provided that the total effort $u_1 + u_2 < 1$ (with $B = 1$ when total effort exceeds one), and that

$$K_i(u_i) = k_i u_i^2 \qquad i = 1, 2. \tag{8}$$

Then

$$\hat{r}_1(u_2) = \frac{1}{1 + k_1}(1 - u_2) \quad \text{and} \tag{9}$$

$$\hat{r}_2(u_1) = \frac{1}{1 + k_2}(1 - u_1). \tag{10}$$

(See Figure 1.) So in this case

$$\lambda_1^* = \frac{1}{1 + k_1} \quad \text{and} \tag{11}$$

$$\lambda_2^* = \frac{1}{1 + k_2}. \tag{12}$$

The parameter k_i scales the cost of effort to parent i. As k_i and, hence, cost increases, the degree of compensation, λ_i^*, decreases.

The functions used by Houston and Davies (1985) also produce best response curves with a constant slope.

Although we have made the general assumption that $B'' < 0$, it is possible that when total effort is low, B may be an accelerating function, i.e., $B'' > 0$. It can be seen from Equation 4 (and $B'' < K''$ since the best response is a maximum) that the slope of the best response function is still greater than -1 in this case (i.e., compensation is incomplete). It is now possible, however, that the slope is greater than zero. This means that a parent responds to a decrease in the effort of its mate by decreasing its own effort. Let

$$B(u_1 + u_2) = 3(u_1 + u_2)^2 - 2(u_1 + u_2)^3 \tag{13}$$

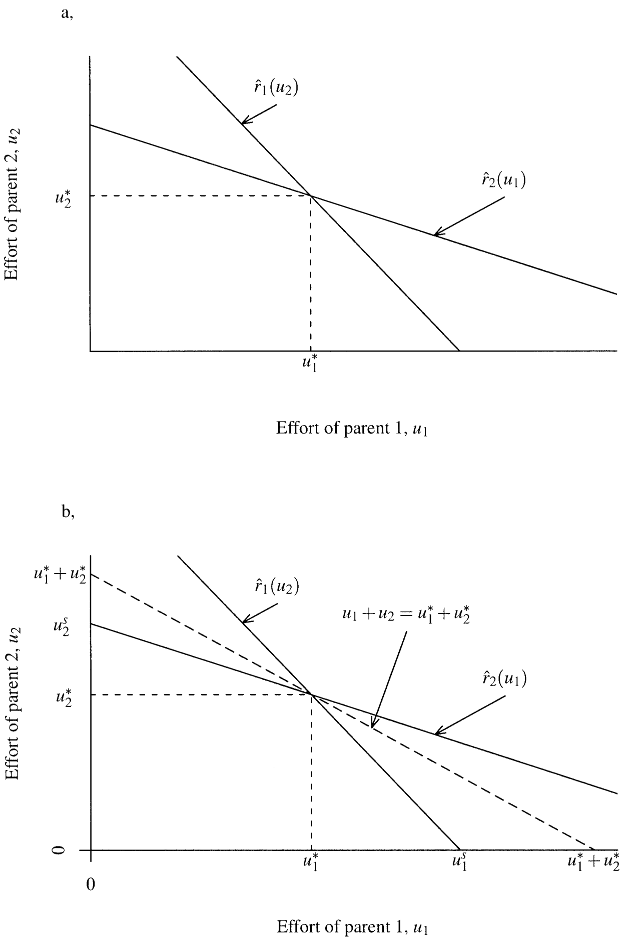

Figure 1
The Houston-Davies solution. (a) The best response functions, $\hat{r}_1(u_2)$ and $\hat{r}_2(u_1)$, and the resulting stable efforts, u_1^* and u_2^*. In the case illustrated, B is given by Equation 7, and K_1 and K_2 are given by Equation 8, with $k_1 = 0.9$ and $k_2 = 0.7$. (b) Graphical demonstration that the effort of a parent when single lies between the effort of that parent under the Houston-Davies solution and the total effort of both parents under the Houston-Davies solution (Equations 15 and 16).

when total effort is less than 1, and

$$K_i(u_i) = 3ku_i^2 \qquad i = 1, 2. \tag{14}$$

In this case, B is first accelerating and then decelerating. Depending on k, best response function may be decreasing or first increasing and then decreasing (Figure 2).

The effort of single versus paired parents

We now compare the optimal effort of a single parent with the evolutionarily stable effort of a parent of the same sex in a pair and the total effort of a pair at this stable equilibrium.

The evolutionarily stable effort of the members of a pair depend on assumptions about the underlying game. We consider four cases: (1) the Houston-Davies solution, (2) the cooperative solution, (3) the Stackelberg solution (one parent decides before the other), and (4) a negotiated solution.

Throughout, we denote the evolutionarily stable effort of parent i when alone by u_i^s $(i = 1, 2)$.

The Houston-Davies solution

The Houston-Davies solution implicitly assumes that each parent makes a single decision about effort without observing the effort of the other parent. The stable outcome over evolutionary time is for each parent to adopt the effort that is the best, given the effort of its mate. In other words, each effort is a best response. Letting u_i^* denote the Houston-Davies effort of i, then $u_1^* = \hat{r}_1(u_2^*)$, and $u_2^* = \hat{r}_2(u_1^*)$. The effort of parent i when alone is $u_i^s = \hat{r}_i(0)$.

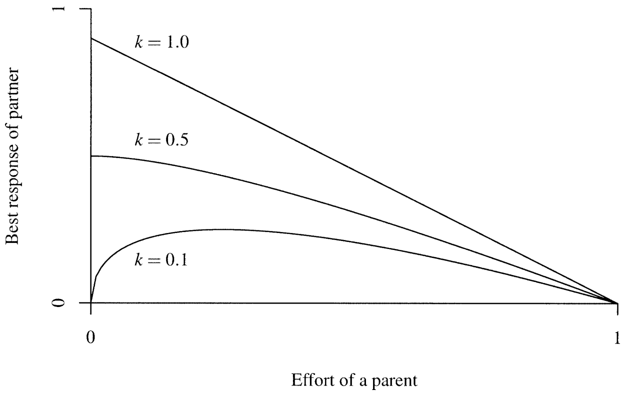

Figure 2
Illustration of the best response function when B is given by Equation 13 and K is given by $K(u) = 3ku^2$.

The simple graphical argument presented in Figure 1b shows that

$$u_1^* < u_1^s < u_1^* + u_2^* \quad \text{and} \tag{15}$$

$$u_2^* < u_2^s < u_1^* + u_2^*, \tag{16}$$

i.e., a parent works harder when alone than when in a pair, but the total effort of a pair is greater than the effort of a single parent. This means that under the assumptions of the Houston-Davies solution, the young are always better off when tended by a pair than when tended by a single parent.

When the degree of compensation is constant, then it can be seen from Figure 1b that

$$u_1^s = u_1^* + \lambda_1^* u_2^* \quad \text{and} \tag{17}$$

$$u_2^s = u_2^* + \lambda_2^* u_1^*. \tag{18}$$

Thus, when the degree of compensation is zero $(\lambda_i^* = 0)$, the effort of a parent is the same when single and when in a pair. As the degree of compensation increases, so does the effort of a single parent relative to that when paired, and in the limit of complete compensation $(\lambda^* = 1)$, the effort of a single parent equals the total effort of a pair.

When the cost functions of both parents are the same (i.e., costs are symmetric), $u_1^* = u_2^* = u^*$, $\lambda_1^* = \lambda_2^* = \lambda^*$ and Equations 17 and 18 reduce to

$$u^s = (1 + \lambda^*)u^*. \tag{19}$$

Parker (1985) considers a model in which each parent breeds repeatedly over its lifetime. The total reproductive effort expended by an individual over its lifetime is fixed, and the individual chooses the effort per bout that maximizes its total lifetime reproductive success. If an individual is a single parent in all its breeding attempts, then (in our notation) lifetime reproductive success is maximized by choosing u to maximize $B_P(u)/u$, where $B_P(u)$ is the reproductive success per bout. Now assume that there is biparental care in each reproductive bout over the lifetime, then the reproductive success of an individual is maximized by choosing its effort, u_1, to maximize

$$B_P(u_1 + u_2)/u_1, \tag{20}$$

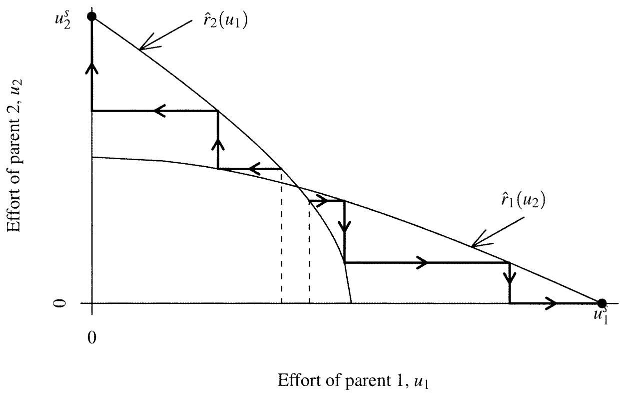

Figure 3
The solution of the biparental care game in the case considered by Parker (1985). The equilibrium at which both parents care is not continuously stable. Consequently, if efforts are not exactly at the equilibrium, they will evolve away from the equilibrium to one of the two stable equilibria in which there is care by one parent alone. B_P given by $B_P(u_{tot}) = 0$ if $u_{tot} \leq 0.493$, $B_P(u_{tot}) = 0.5 - (1.2 - u_{tot})^2$ for $0.493 < u_{tot} < 1.2$, and $B_P(u_{tot}) = 0.5$ for $u_{tot} \geq 1.2$.

where u_2 is the effort of any mate. Parker solves this game by assuming that the effort of each individual is the best, given the behaviour of its mate(s). At Parker's solution, the young do better with one parent than with two. We note that Parker's analysis deals with a situation that is different from the one that we consider in this paper. Parker compares a parent that is single in each breeding attempt with a parent that is involved in biparental care in each breeding attempt. We are concerned with a species in which there is normally biparental care, but in which a parent cares alone in a single breeding attempt because its partner has been removed or killed. In other words, Parker takes future breeding attempts to involve the same number of parents as the current attempt, whereas we take future breeding attempts to be independent of the current attempt. Despite this difference, Parker's model can be converted to a form that is equivalent to the Houston-Davies model. Taking logarithms, maximization of Expression 20 is equivalent to maximization of

$$\log B_P(u_1 + u_2) - \log(u_1). \tag{21}$$

This is equivalent to Expression 1 where the success of the brood is now $B = \log B_P$, and the cost is $K(u_1) = \log(u_1)$. For this form of K, $K'' < 0$. This means that the degree of compensation is greater than 1 (see Equation 4). As a result, if the biparental care solution found by Parker is an ESS, then it is not continuously stable (Appendix A). This means that if the population is perturbed from the Parker solution, it will evolve away from that solution. The only ESSs that are continuously stable involve care by one parent alone (Figure 3). Thus, under the assumptions of Parker's model, biparental care will not occur, and hence, the possibility of an experimental manipulation in which one parent is removed does not arise.

Cooperative solution

The Houston-Davies solution is based on each parent acting so as to maximize its own reproductive success. In other words, the cooperation between the parents is a consequence of each parent pursuing its own selfish interests. To provide a convenient benchmark, we now consider a purely cooperative solution in which each parent acts to maximize the sum of its own and its partner's reproductive success. We confine attention to the special case in which $K_1 = K_2 = K$. B is determined by total effort, $u_1 + u_2$. For any total effort, it follows from Jensen's inequality that the total cost to the pair is minimized when the efforts are equal, and so, it is optimal for efforts to be equal. We therefore assume that $u_1 = u_2 = u$. Under this condition, the sum of the reproductive success of the parents is $f(u) = 2B(2u) - 2K(u)$.

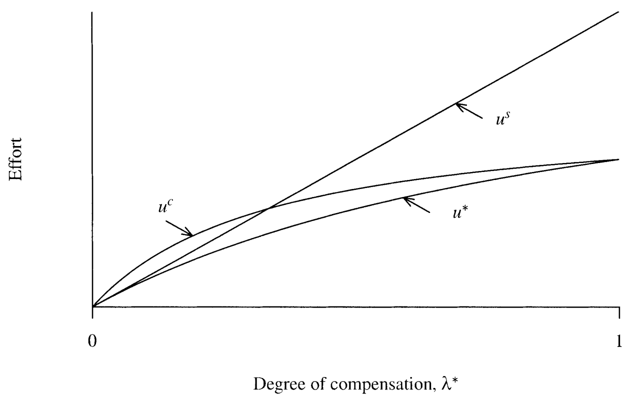

Figure 4
u^s, u^c, and u^* as a function of the degree of compensation $\lambda_1^* = \lambda_2^* = \lambda^*$. Quadratic case, i.e., Equations 7 and 8. Costs are equal, so that $k_1 = k_2 = k$ in Equation 8. λ^* is varied by varying k (see Equations 11 and 12).

Then we can define the cooperative effort, u^c, as the value of effort for each parent that maximizes $f(u)$. It follows that u^c satisfies

$$2B'(2u^c) = K'(u^c). \tag{22}$$

It is easy to show that $u^* < u^c$; i.e., the effort at the co-operative solution is greater than at the Houston-Davies solution (see Appendix B for details).

In the special case of quadratic cost functions with equal costs to each parent (Equations 7 and 8, with $k_1 = k_2 = k$ in Equation 8), we now compare the effort of a single parent with that predicted by the Houston-Davies model and the cooperative solution. In this quadratic case, $\lambda^* = 1/(1+k)$, and we have shown (Equation 19) that

$$\frac{u^*}{u^s} = \frac{1}{1+\lambda^*} < 1,$$

so that

$$\frac{2u^*}{u^s} = \frac{2}{1+\lambda^*} > 1.$$

From Equation 22 we also have

$$\frac{u^c}{u^s} = \frac{2}{1+3\lambda^*}.$$

From this equation, it can be seen that $u^c > u^s$ when $\lambda^* < \frac{1}{3}$. This means that the effort of each member of a cooperative pair is greater than the effort of a single parent for λ^* in this range. From the above equation, it can also be seen that

$$\frac{2u^c}{u^s} = \frac{4}{1+3\lambda^*} > 1.$$

Figure 4 shows u^s, u^*, and u^c as a function of λ^*. As λ^* tends to one, both u^*/u^s and u^c/u^s tend to 1/2. This means that in both cases, the total effort of a pair tends to the effort of a single parent as λ^* tends to one.

Stackelberg game

In a Stackelberg game, the players do not make their decisions independently. Instead, one player makes its decision before the other. We do not claim that decisions

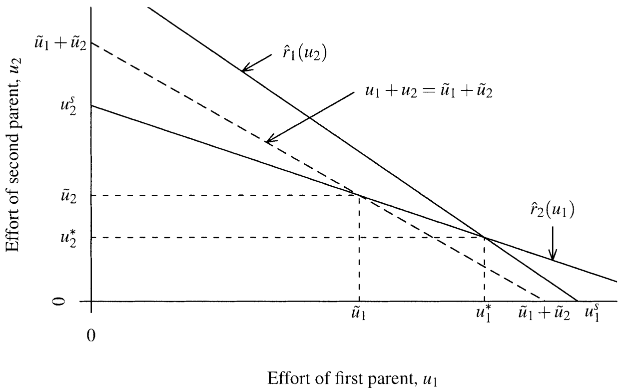

Figure 5
Graphical illustration of the Stackelberg solution. The figure compares the Stackelberg efforts, $\tilde{u}_1$ and $\tilde{u}_2$, with the Houston-Davies efforts, u_1^* and u_2^* (see Equations 23 and 24). The figure also compares the efforts, u_1^s and u_2^s, of each parent when single with the total effort, $\tilde{u}_1 + \tilde{u}_2$, under the Stackelberg solution (see Equations 25 and 27).

about parental effort conform exactly to the Stackelberg framework. Instead, we use this framework as a convenient extreme case of temporal asymmetry in decision making between the two parents (for an example of a Stackelberg game involving parental effort, see Kokko, 1999). Without loss of generality, we assume that parent 1 makes the first decision. If it chooses an effort, u_1, then parent 2 should adopt its best response, $\hat{r}_2(u_1)$. Thus, parent 1 should choose its effort so as to maximize $B[u_1 + \hat{r}_2(u_1)] - K_1(u_1)$.
Let the resulting effort for parent 1 be $\tilde{u}_1$. Then parent 2 adopts effort $\tilde{u}_2 = \hat{r}_2(\tilde{u}_1)$.

The graphical argument presented in Figure 5 shows that

$$\tilde{u}_1 < u_1^* \quad \text{and} \tag{23}$$

$$\tilde{u}_2 > u_2^*. \tag{24}$$

This result says that the first parent works less hard than it would in the Houston-Davies solution, whereas the second parent works harder.

Figure 5 establishes that

$$u_2^s < \tilde{u}_1 + \tilde{u}_2, \tag{25}$$

i.e., the total effort of the pair is greater than the effort of parent 2 when alone. When $K_1 = K_2$, then $u_1^s = u_2^s$, so that we also have

$$u_1^s < \tilde{u}_1 + \tilde{u}_2. \tag{26}$$

If, however, $K_1 \neq K_2$, then it is possible that

$$u_1^s > \tilde{u}_1 + \tilde{u}_2 \tag{27}$$

(Figure 5). In this case, the young do better when cared for by parent 1 alone than at the Stackelberg solution for the pair.

Once again, we use the quadratic functions (Equations 7 and 8) as an illustration. Recall that $\lambda_i^* = (1 + k_i)^{-1}$. In this case it can be shown (Appendix C) that

$$u_1^s > \tilde{u}_1 + \tilde{u}_2 \Longleftrightarrow \frac{1}{\lambda_1^*} + \lambda_2^* < 2 \tag{28}$$

(Figure 6a). The inequality on the right-hand side can only hold in a subset of the region $\lambda_1^* > \lambda_2^*$. In this subset, $k_1 < k_2$. In other words, it is necessary that player 1 pays less cost than player 2. Figure 6b illustrates the dependence of the efforts u_1^s, $\tilde{u}_1$, and $\tilde{u}_2$ on λ_2^* for various values of λ_1^*.

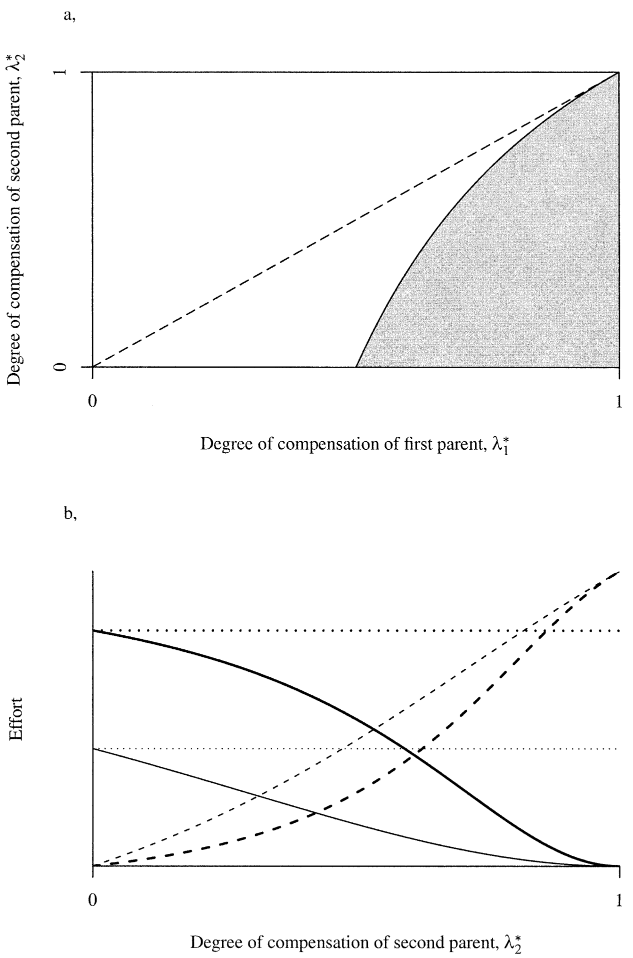

Figure 6
The Stackelberg solution with quadratic functions (Equations 7 and 8). (a) Combinations of values of λ_1^* and λ_2^* for which the effort of the first parent, when single, exceeds the total effort of both parents under the Stackelberg solution (shaded region). (b) The dependence of the effort of the first parent when single, u_1^s, and the Stackelberg efforts $\tilde{u}_1$ and $\tilde{u}_2$ on λ_2^* for various values of λ_1^*. Thin lines indicate $\lambda_1^* = 0.4$; thick lines, $\lambda_1^* = 0.8$. Solid lines indicate $\tilde{u}_1$; dashed lines, $\tilde{u}_2$; and dotted lines, u_1^s.

A negotiated settlement

As we have said above, the best response function that forms the basis of the Houston-Davies solution specifies the best response of a parent to a fixed effort by its mate. It does not give the best response when the mate may adjust its effort. McNamara et al. (1999) present a simple model of the evolutionarily stable outcome when the parents respond to each other's efforts during a breeding attempt. McNamara et al. assume that individuals differ in quality, q, and that the cost to a parent depends on both its effort and quality. There is a costless period of negotiation in which each parent responds to the effort of its mate until an equilibrium is reached at which neither parent changes its effort. At evolutionary stability, the negotiation rule used by each member of the population is the best, given the negotiation rule used by other population members.

The analysis of McNamara et al. deals with the case in which both parents have the same cost function, K. We do likewise, although the analysis is easily extended to the case of unequal costs. McNamara et al. assume that B and K are quadratic functions so that B'' and K'' are constant. The idea behind

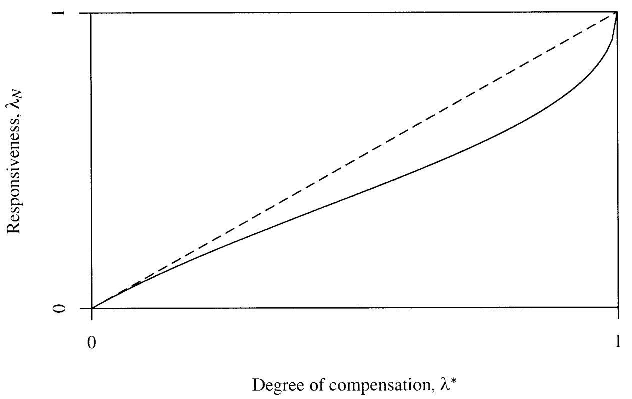

Figure 7
The responsiveness, λ_N, in the model of McNamara et al. (1999) as a function of the degree of compensation, λ^* (see Equations 30 and 31).

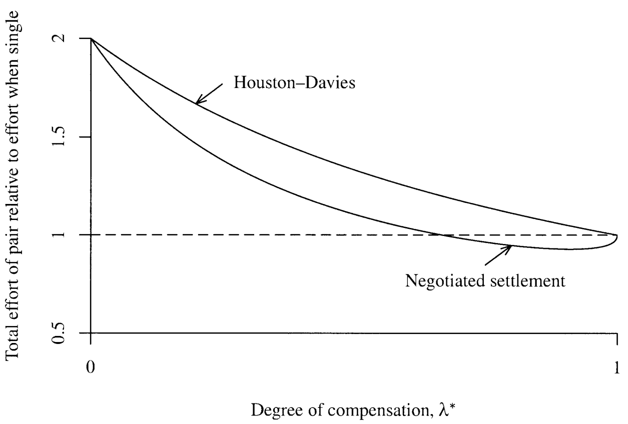

Figure 8
The total effort of a pair under the negotiated settlement and under the Houston-Davies solution relative to the effort of a parent when single (i.e., $2u^N/u^s$ and $2u^*/u^s$) as a function of λ^*.

their analysis is that instead of finding the best effort of a parent given that of its partner, one finds the best responsiveness of a parent given the responsiveness of its partner. To illustrate this approach, suppose that in response to effort, u_1, of parent 1, parent 2 alters its effort to $r_2(u_1) = \gamma(q_2) - \lambda_2 u_2$, where $\gamma(q_2)$ specifies the dependence of the effort of parent 2 on its quality, q_2, and λ_2 is a constant. The responsiveness, λ_2, is the real-time degree of compensation of parent 2 for the effort of parent 1. If parent 1 were to use a fixed effort, u_1, the payoff to this parent would be $B[u_1 + r_2(u_1)] - K(u_1)$.
To find the best fixed effort, we differentiate this expression with respect to u_1 and equate the derivative to zero. On setting $r_2'(u_1) = -\lambda_2$, this gives $(1 - \lambda_2)B'[u_1 + r_2(u_1)] = K'(u_1)$.
As a result of using this effort, after negotiation the efforts u_1 and u_2 of the two parents are related by the formula $(1 - \lambda_2)B'(u_1 + u_2) = K'(u_1)$.
The best effort of parent 1, given the response rule $r_2(u_1)$ of parent 2, can thus be achieved if parent 1 uses response rule $r_1(u_2)$ given by $(1 - \lambda_2)B'[r_1(u_2) + u_2] = K'[r_1(u_2)]$.
This relationship has to hold whatever the quality, q_2, of parent 2 and, hence, must hold for all u_2. Differentiating with respect to u_2, we find that $[1 - \lambda_2][1 + r_1'(u_2)]B'' = K''$.
Because B'' and K'' are constant, so is $r_1'(u_2)$. Setting $r_1'(u_2) = -\lambda_1$ and rearranging gives

$$\lambda_1 = \frac{(1 - \lambda_2)B''}{(1 - \lambda_2)B'' - K''}. \qquad (29)$$

This equation shows how the best responsiveness, λ_1, of parent 1 depends on the responsiveness, λ_2, of parent 2.

The degree of compensation over evolutionary time, λ^*, is the best responsiveness to use in real time if the other parent does not respond at all ($\lambda_2 = 0$). A population in which all individuals used this responsiveness would not be evolutionary stable because it would be invaded by lazy individuals that exploited the willingness of residents to compensate for their lack of effort (McNamara et al., 1999). Instead, the evolutionarily stable responsiveness, λ_N, is the best responsiveness if all other individuals have this responsiveness, and can be found by setting $\lambda_1 = \lambda_2 = \lambda_N$ in Equation 29. In Appendix 4, it is shown that $0 < \lambda_N < \lambda^* < 1$. In fact, λ^* and λ_N are related by

$$\lambda_N = \alpha - \sqrt{\alpha^2 - 1}, \qquad (30)$$

where

$$\alpha = \frac{\lambda^* + 1}{2\lambda^*} \qquad (31)$$

(Appendix D; Figure 7). From Equation 31, $\alpha \to 1$ as $\lambda^* \to 1$. Thus by Equation 30, $\lambda_N \to 1$ as $\lambda^* \to 1$ (Figure. 7).

Turning our attention to the negotiated effort, we assume that both parents have the quality implicit in the Houston-Davies analysis. The general quadratic case is analyzed in Appendix D. For the special case in which $K(u) = ku^2$, the appendix shows that the negotiated effort, u^N, is given by the equation

$$u^N = u^* \frac{1 + \lambda_N^2}{1 + \lambda_N},$$

which means that $u^N < u^*$. It is also shown that we have

$$\frac{u^N}{u^s} = \frac{1 + \lambda_N^2 - \lambda_N}{1 + \lambda_N}.$$

Thus, the total effort of the pair under the negotiated settlement, $2u^N$, is less than the effort, u^s, of a single parent if, and only if, $\lambda_N > 1/2$, which is equivalent to $\lambda^* > 2/3$. Figure 8 shows the dependence of $2u^N/u^s$ and $2u^*/u^s$ on λ^*.

Our results concerning the effort of single versus paired parents are summarized in Table 1. The young are never better off with a single parent as opposed to with a pair, when the pair's effort is given by the Houston-Davies solution or the cooperative solution. In contrast, when the pair's effort is determined by the Stackelberg solution or the negotiated solution, then it is possible for the young to be better off when cared for by a single parent.

Manipulating the effort of one parent

In the previous section, we considered the effect of the complete removal of one parent on the effort of the other parent. Several experiments (see Markman et al., 1995; Saino and Møller, 1995; Whittingham et al., 1994; Wright and Cuthill, 1989, 1990a,b) have manipulated the behaviour of one parent and observed the effect of this change on the effort of the other parent. A fundamental issue is whether the effect of removing the partner can be predicted from the response of the parent to the reduced effort of its partner.

One way to analyze this question is to consider the extreme and to ask whether the effort of a parent caring alone is predicted to be the same as the effort of a parent whose

Table 1
Summary of results

Solution to game between the pair	Effort of given parent greater when single?	Total effort of pair greater?
Houston-Davies	Yes	Yes
Cooperative	Sometimes	Yes
Stackelberg	Yes	Yes (equal costs) No (first parent pays less cost*)
Negotiation	Yes	Yes (if responsiveness low*) No (if responsiveness high*)

* In the special case $K_i(u) = k_i u^2$.

partner is present but is putting in no effort. When a parent adjusts its effort to be the best, given the effort of its partner (i.e., adopts the Houston-Davies best response rule), then these two efforts are the same. This means that the response to removal can be predicted from the response to manipulating the partner's effort. Of course, if the response to manipulation only covers a small range of efforts, then linear interpolation to zero effort by the partner will only be accurate if the best response function is linear. If instead the focal parent responds to the effort of a partner using the negotiation rule of McNamara et al. (1999), then the effort in response to a partner that is present but provides no effort is significantly less than the effort if the partner is absent. An example is given in Figure 9.

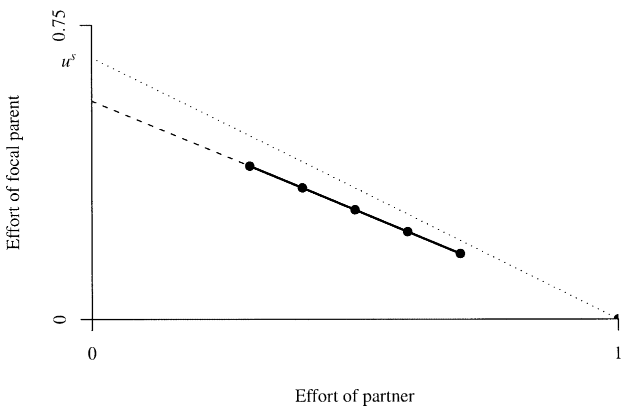

Figure 9
The relationship between the effort of a focal parent when the effort of its partner is manipulated, and its effort when the partner is removed. The solid line gives a response to manipulation that might be obtained from data. The dashed line gives the linear interpolation of this response function. The dotted line is the Houston-Davies best response function. $k = 0.5$ and, hence, $\lambda^* = 2/3$.

DISCUSSION

In this paper, we are concerned with a species in which there is a period during which both parents care for the young. We have compared the level of care received by the young when both parents are present with the level when one parent is removed or dies during this period. We have presented the first systematic investigation of the circumstances in which young will do better when cared for by one parent as opposed to two parents. This analysis might also apply to species in which there is initially a period of biparental care of the young, which is terminated by the desertion one of the parents (e.g., magnificent frigate bird: Osorno, 1999; Kentish plover: Székely and Lessells, 1993). In this case, however, the analysis is complicated by the effect of time per se, and the fact that the decision to desert may be dependent on the state of both the young and the environment (for a review, see Székely et al., 1996).

At the Houston-Davies solution, each parent's effort is the best response to the effort of its partner. We have established that in this case, young always do better with two parents as opposed to with one parent. In contrast to this conclusion, Parker (1985) argues that young do better with one parent in this case. We have shown that the biparental care solution that forms the basis of Parker's claim is not continuously stable and, hence, is not appropriate as a model of biparental care.

We have attempted to capture temporal asymmetrics in the decisions by analyzing a Stackelberg game in which one of the parents chooses its effort first, and then the other parent chooses its effort on the basis of the effort of the first parent.

When the cost functions of the two parents are equal, young always do better with two parents. When the cost functions are unequal and the parent that decides first is less affected by an increase in effort, then the young may do better with just this parent as opposed to with both parents (Figure 6a).

The Houston-Davies solution is based on each parent choosing a fixed effort, independent of the effort of its partner; individuals do not respond directly to one another (McNamara et al. 1999). In contrast, in the model of McNamara et al. (1999), individuals respond repeatedly to each other until they reach a negotiated effort. We analyze this model in the case in which the two parents have the same cost function. Because of the need to avoid being exploited by the partner, negotiated levels of effort are lower than those predicted by the Houston-Davies solution. When parameters are such that the parents are highly responsive to each other's level of effort, young are better off with one parent than with two (Figure 8).

A number of empirical studies have compared care of the young by one versus two parents. In some cases there is evidence that young do better with two parents, and in the remaining cases, there is no significant difference between one parent and two parents (for reviews of data from birds, see Bart and Tornes, 1989; Ketterson and Nolan, 1994; Whittingham et al., 1994).

Experiments in which the effort of one parent is manipulated (e.g., Markman et al., 1995; Sanz et al., 2000; Wright and Cuthill, 1989, 1990a,b) show that parents respond to each other's effort. A fundamental question concerns the rules that parents use when responding. One possibility is that the effort of each parent after the negotiated phase is the best, given the effort of the partner. This means that the pair of efforts would agree with the prediction of the Houston-Davies solution, even though the Houston-Davies model is not based on real-time responding. Another possibility is that the negotiation process is as described in McNamara et al. (1999) and, hence, results in efforts that are not best responses to one another. In this case, the efforts are less than are predicted by the Houston-Davies solution. In a particular system, a knowledge of the cost functions would make it possible to distinguish empirically between these two cases. It is, however, typically very hard to determine the cost functions of parents. Comparing how well young do with one as opposed to with two parents gives us a qualitative method that can distinguish between the two cases under certain circumstances: The Houston-Davies solution never predicts that young do better when cared for by a single parent, whereas the model of McNamara et al.

predicts that this can occur when responsiveness is high. The fact that in a particular case, the data do not provide evidence that the young do better with one parent could be because parents are not following the regulation rule of McNamara et al. But it could also be because the negotiation rule is being used, but responsiveness is not high enough, or that there is too much noise in the data to detect the relatively small effect that is predicted at high responsiveness.

If parents are following the negotiation rule, then one parent will increase its effort in response to a decrease by its partner. If the effort of one parent is reduced by an experimental manipulation, the effort of the other parent will adjust, but not so that it is a best response to the effort of the manipulated parent. In contrast, if one parent is removed, the effort of the other parent should adjust to be the best given that its partner is putting in zero effort. This provides another way of distinguishing between response rules. If the effort of a parent is the best given the effort of its partner, then interpolating from a manipulation of effort to the response to zero effort will predict the effort of the parent when single. In contrast, if animals use the negotiation rule of McNamara et al. (1999), an interpolation to zero effort will underestimate the effort of the parent when single (Figure 9). As far as we know, the only study that combines both manipulation and removal is Whittingham et al. (1994). (The study of Markman et al. [1995] manipulated female orange-tufted sunbirds, but another study by Markman et al. [1996] involved removal of males, so no comparison of treatments within a sex is possible.) Their Figure 2 suggests that there might be a difference between the interpolated effort in response to zero effort and the effort when single, but interpretation of the graph is difficult because of individual variation.

APPENDIX A

Stability in Houston-Davies type models

Consider a population in which there are two types of individual (e.g., males and females). Each type expresses a trait specific to that type (e.g., for a male the trait is male effort). Here we are concerned with conditions for the evolutionary stability of trait values.

Suppose that almost all type i individuals in the population have trait value $\bar{u}_i$ $(i = 1, 2)$. Denote the fitness of a mutant type i individual with trait value u_i by $W_i(u_i, \bar{u}_1, \bar{u}_2)$. Then a necessary conditions that the pair of trait values (u_1^*, u_2^*) be an ESS (Maynard Smith, 1982) are

$$\left.\frac{\partial W_i(u_i, u_1^*, u_2^*)}{\partial u_i}\right|_{u_i=u_i^*} = 0 \qquad i = 1, 2. \tag{A1}$$

$$\left.\frac{\partial^2 W_i(u_i, u_1^*, u_2^*)}{\partial u_i^2}\right|_{u_i=u_i^*} \leq 0 \qquad i = 1, 2. \tag{A2}$$

This criterion for evolutionary stability is based on the idea that if all type i individuals have trait value u_i^* $(i = 1, 2)$, then no mutant individual can do better by adopting a different trait. Eshel (1983) introduced another stability concept, defining a strategy to be continuously stable if evolution takes the whole population to this strategy from strategies near to it. For our two-dimensional case, we adopt the conditions for continuous stability used by Abrams et al. (1993). We assume that the evolution of population trait values are governed by the dynamic system

$$\frac{\mathrm{d}\bar{u}_i}{\mathrm{d}t} = f_i(\bar{u}_1, \bar{u}_2)$$

where

$$f_i(\bar{u}_1, \bar{u}_2) = \left.\frac{\partial W_i(u_i, \bar{u}_1, \bar{u}_2)}{\partial u_i}\right|_{u_i=\bar{u}_i}$$

This formulation assumes that there is no additive genetic covariance between the two traits. An ESS is an equilibrium point (u_1^*, u_2^*) of the dynamics. Following the method of Abrams et al., we take an equilibrium to be continuously stable if it is also a stable point of the dynamics. Let A denote the matrix

$$A = \begin{vmatrix} \dfrac{\partial f_1}{\partial \bar{u}_1} & \dfrac{\partial f_2}{\partial \bar{u}_1} \\ \dfrac{\partial f_1}{\partial \bar{u}_2} & \dfrac{\partial f_2}{\partial \bar{u}_2} \end{vmatrix},$$

where all derivatives are evaluated at (u_1^*, u_2^*). Then a necessary condition for (u_1^*, u_2^*) to be a stable point of the dynamics is that A has both nonpositive trace and nonnegative determinant.

We now apply the above to the case in which $W_1(u_1, \bar{u}_1, \bar{u}_2) = B(u_1 + \bar{u}_2) - K_1(u_1)$, and $W_2(u_2, \bar{u}_1, \bar{u}_2) = B(\bar{u}_1 + u_2) - K_2(u_2)$.

Let (u_1^*, u_2^*) be an ESS for this case. All functions given below are evaluated at this equilibrium. By Equation A2

$$B'' \leq K_i'' \qquad i = 1, 2. \tag{A3}$$

The matrix A is now

$$A = \begin{vmatrix} B'' - K_1'' & B'' \\ B'' & B'' - K_2'' \end{vmatrix}.$$

The trace of A is $(B'' - K_1'') + (B'' - K_2'')$, which is nonnegative by Equation A3. The determinant of A is $[(B'' - K_1'')(B'' - K_2'')] - (B'')^2$, which is nonnegative if and only if

$$K_1'' K_2'' \geq B''(K_1'' + K_2''). \tag{A4}$$

In summary, an ESS must satisfy Equation A3. If the ESS is also continuously stable it must satisfy Equation A4. Conversely, it can be shown that a Nash equilibrium (u_1^*, u_2^*) for which Equations A3 and A4 hold strictly is a continuously stable ESS.

All the Nash equilibria that we present satisfy $B'' < 0$, $K_1'' > 0$ and $K_2'' > 0$. Thus, Equations A3 and A4 hold strictly. These equilibria are therefore continuously stable ESSs.

The game considered by Parker (1985) has $K_1(u) = K_2(u) = \log u$. The ESS found by Parker satisfies $u_1^* = u_2^*$. Thus,

$$K_1'' = K_2'' < 0 \tag{A5}$$

and Equation A4 reduces to

$$2B'' > K_i''. \tag{A6}$$

As can be seen, Equations A3, A5, and A6 cannot all hold. In other words, if the Nash equilibrium found by Parker is an ESS, it cannot be continuously stable.

APPENDIX B

Comparison of cooperative and Houston-Davies efforts

Let $K_1 = K_2 = K$. Define the function g by $g(u) = 2B'(2u) - K'(u)$. Then $g'(u) = 4B''(2u) - K''(u) < 0$ because $B'' < 0$ and $K'' > 0$. Thus, g is a decreasing function.

Because the Houston-Davies effort u* satisfies $B'(2u^*) = K'(u^*)$, we have

$$g(u^*) = B'(2u^*) + [B'(2u^*) - K(u^*)] = B'(2u^*) > 0.$$

Also, by Equation 22 the cooperative effort, u^c, satisfies $g(u^c) = 0$. Thus $u^* < u^c$ because g is decreasing.

APPENDIX C

Stackelberg solution for quadratic functions

Let B be given by Equation 7 and K_i be given by Equation 8. We consider the Stackelberg solution with player 1 choosing first.

By Equations 10 and 12, $\hat{r}_2(u_1) = \lambda_2^*(1 - u_1)$, where $\lambda_2^* = (1 + k_2)^{-1}$. The payoff to player 1 if this player chooses u_1 is thus $2[u_1 + \lambda_2^*(1 - u_1)] - [u_1 + \lambda_2^*(1 - u_1)]^2 - k_1 u_1^2$. This is maximized when $u_1 = \tilde{u}_1$, where

$$\tilde{u}_1 = \frac{(1 - \lambda_2^*)^2}{(1 - \lambda_2^*)^2 + k_1}. \qquad \text{(A7)}$$

The resultant effort of player 2 is then

$$\tilde{u}_2 = \lambda_2^*(1 - \tilde{u}_1). \qquad \text{(A8)}$$

By Equation 9

$$u_1^s = \hat{r}_1(0) = \frac{1}{1 + k_1}. \qquad \text{(A9)}$$

By Equations A7 through A9, $u_1^s > \tilde{u}_1 + \tilde{u}_2 \Longleftrightarrow \lambda_2^* < 1 - k_1$. Because $\lambda_1 = (1 + k_1)^{-1}$, we have

$$u_1^s > \tilde{u}_1 + \tilde{u}_2 \Longleftrightarrow \frac{1}{\lambda_1^*} + \lambda_2^* < 2. \qquad \text{(A10)}$$

APPENDIX D

The negotiated settlement

We assume the model of McNamara et al. (1999). In particular, costs and benefits are quadratic, and the male and female cost functions are the same. For this model, B'' and K'' are constant, and the ESS responsiveness, λ_N, is given by

$$\lambda_N^2 B'' + \lambda_N(K'' - 2B'') + B'' = 0 \qquad \text{(A11)}$$

(McNamara et al. 1999). This equation can also be obtained by setting $\lambda_1 = \lambda_2 = \lambda_N$ in Equation 29. By Equation 4, the degree of compensation is

$$\lambda^* = \frac{-B''}{K'' - B''}. \qquad \text{(A12)}$$

Eliminating B'' and K'' from Equations A11 and A12 yields

$$\lambda_N^2 - \left(\frac{1 + \lambda^*}{\lambda^*}\right)\lambda_N + 1 = 0. \qquad \text{(A13)}$$

This quadratic equation in λ_N has a unique root in the range $0 < \lambda_N < 1$ given by Equations 30 and 31.

Rearranging Equation A13 gives

$$\lambda^* - \lambda_N = \lambda^* \lambda_N(1 - \lambda_N). \qquad \text{(A14)}$$

It thus follows that $\lambda_N < \lambda^*$.

We now consider negotiated effort when $q_1 = q_2 = 0$. In the terminology of this paper, Equation 11 of McNamara et al. (1999) gives

$$u_N = u^* + \left(\frac{1 - \lambda_N}{1 - \lambda_N^2}\right)\rho_N \qquad \text{(A15)}$$

where

$$\rho_N = \frac{-\lambda_N B'(2u^*)}{K'' - (1 - \lambda_N)B''}. \qquad \text{(A16)}$$

Now suppose that when $q = 0$ costs are given by $K(u) = ku^2$. Then $K'' = 2k$. Also, because u^* satisfies $B'(2u^*) = K'(u^*)$, we have $B'(2u^*) = 2ku^* = K''u^*$. Thus, Equations A15 and A16 give

$$\frac{u_N}{u^*} = 1 + \left(\frac{1}{1 + \lambda_N}\right)\frac{\lambda_N K''}{(1 - \lambda_N)B'' - K''}. \qquad \text{(A17)}$$

By Equation A11

$$\frac{B''}{K''} = \frac{-\lambda_N}{(1 - \lambda_N)^2}.$$

Using this to eliminate B'' and K'' from equation A17 gives

$$\frac{u_N}{u^*} = \frac{1 + \lambda_N^2}{1 + \lambda_N}. \qquad \text{(A18)}$$

Because

$$\frac{u^s}{u^*} = 1 + \lambda^*$$

we have

$$\frac{u^s}{u^*} = \frac{1 + \lambda_N^2}{1 + \lambda_N^2 - \lambda_N} \qquad \text{(A19)}$$

by Equation A13. Thus, by Equations A18 and A19,

$$\frac{u_N}{u^s} = \frac{1 + \lambda_N^2 - \lambda_N}{1 + \lambda_N}. \qquad \text{(A20)}$$

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