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Original Article

Power and punishment influence negotiations over parental care

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Asymmetries in power (the ability to influence the outcome of conflict) are ubiquitous in social interactions because interacting individuals are rarely identical. It is well documented that asymmetries in power influence the outcome of reproductive conflict in social groups. Yet power asymmetries have received little attention in the context of negotiations between caring parents, which is surprising given that parents are often markedly different in size. Here we built on an existing negotiation model to examine how power and punishment influence negotiations over care. We incorporated power asymmetry by allowing the more-powerful parent, rank 1, to inflict punishment on the less-powerful parent, rank 2. We then determined when punishment will be favored by selection and how it would affect the negotiated behavioral response of each parent. We found that with power and punishment, a reduction in one parent's effort results in partial compensation by the other parent. However, the degree of compensation is asymmetric: the rank 2 compensates more than the rank 1. As a result, the fitness of rank 1 increases and the fitness of rank 2 decreases, relative to the original negotiation model. Furthermore, because power and punishment enable one parent to extract greater effort from the other, offspring can do better, that is, receive more total effort, when there is power and punishment involved in negotiations over care. These results reveal how power and punishment alter the outcome of conflict between parents and affect offspring, providing insights into the evolutionary consequences of exerting power in negotiations.

Key words: **asymmetries, behavioral negotiations, parental care, power, punishment, response rules**

INTRODUCTION

Power, the ability to influence the outcome of conflict, is an elusive feature of social interactions because power is not easily measured. For example, although the outcome of territorial disputes intuitively should be determined by the relative size or physical strength of the interacting individuals, the outcomes of such disputes can also be influenced by differences in motivation or personality (Hurd 2006). Furthermore, how power is determined may depend on the specifics of the system being studied, making it difficult to determine when and why one individual will have power over another (Beekman et al. 2003). One mechanism by which an individual can exert their power over another is through the threat of punishment. Punishment refers to a reduction in the punisher's current payoff to ensure cooperation by its partner in the future (Raihani et al. 2012). As actual conflict can be costly, or even deadly, individuals are predicted to use the threat of punishment and avoid actual conflict (Cant 2011). Such hidden threats only escalate when individuals do not cooperate and thus punishment is rarely observed under natural conditions (Cant 2006). Due to the difficulties in directly observing who has power, theory serves as a valuable tool for understanding how power and punishment influence the outcome of conflicts.

Theory has provided great insight into how power and punishment influence the outcome of conflict in two different contexts: conflict between social group members over reproduction and conflict between parents and offspring over care (e.g., Reeve and Shen 2006; Buston et al. 2007; Hinde and Kilner 2007). Models of reproductive skew make contrasting assumptions about who has power over the partitioning of reproduction in social groups. Some models assume that one dominant individual has complete control over how reproduction is partitioned (Reeve and Ratnieks 1993; Johnstone and Cant 1999; Buston et al. 2007), whereas others make the assumption that there is incomplete control and reproduction is partitioned by costly competition between group members (Reeve et al. 1998; Reeve and Shen 2006). These models explain why some individuals forgo reproduction to help dominants, and empirical tests of these models reveal the role power and punishment can play in maintaining group stability and enforcing cooperation (Beekman et al. 2003). Similarly, models of parent–offspring

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conflict have generated predictions for how resources will be allocated depending on whether the power lies with the parents or the offspring. These models have helped to explain the empirical patterns of coadaptation between parental provisioning and offspring solicitation traits (Cant 2006; Hinde and Kilner 2007). Parents in many animals are frequently observed disciplining overly persistent offspring, for example, by biting or kicking offspring that are attempting to suckle (Clutton-Brock and Parker 1995).

Surprisingly, despite the importance of power and punishment in the resolution of conflicts in these two other social contexts, power dynamics have received virtually no attention in the context of conflict between caring parents. Conflict between parents arises because care is costly, and so each parent can benefit from shifting the burden of care to the other (Trivers 1972). The threat of punishment is expected to play a role in the resolution of conflict between parents for several reasons. First, there are likely power asymmetries between parents, increasing the credibility of the threat and the chance of cooperation by the less powerful to avoid being punished. Second, parental care is a dyadic interaction; therefore, threats and punishment can be easily targeted at the noncooperative individual. And third, parents must interact repeatedly to raise their young, allowing for the benefits of future cooperation to be realized by the punisher (Houston et al. 2005; Cant 2011; Raihani et al. 2012).

The resolution of conflict among caring parents has, however, been the focus of extensive theoretical work, without explicit consideration of power dynamics (Houston and Davies 1985; McNamara et al. 1999, 2003; Johnstone and Hinde 2006; Johnstone et al. 2014). A series of game theoretic models were developed over the past three decades that helped to guide the study of parental conflict. Houston and Davies (1985) developed a framework for explaining how much effort parents should invest in their current offspring by assuming that parents benefit from the total amount of care the offspring receive, but pay a cost to future reproduction that depends only on their own level of effort. The outcome is determined by finding the evolutionarily stable (ES) level of effort that confers the greatest fitness advantage given the ES level of effort of its partner. The model assumes that each parent's investment is a "sealed bid," that is, there is no opportunity to respond to partner effort in behavioral time. A sealed bid is not evolutionarily stable, however, because an individual that can respond in behavioral time will be able to exploit their partner's fixed response (McNamara et al. 1999). In many species, parental effort is plastic (Royle et al. 2014); thus, it is widely recognized that in nature, the assumption that parental effort is fixed in behavioral time is often unrealistic.

McNamara et al. (1999) developed a model that allows individuals to respond to each other by assuming a cost-free period of negotiation where parents alternate bids until they reach a settlement such that each parent's response represents the best response to the other parent. The outcome is a pair of ES response rules that determine how an individual should respond to a change in their partner's effort. The key predictions of this model are that individuals will partially compensate for a change in partner effort and that the resulting ES level of effort will be less than that predicted by the "sealed bid" approach. A meta-analysis in birds revealed that partial compensation is the mean response, but there are many cases in which no compensation or even the opposite response (in which an individual matches a change in partner effort) is observed (Harrison et al. 2009). Further modifications to the original model incorporate how much information each parent has about offspring need (Johnstone and Hinde 2006) and how conditional cooperation between partners (Johnstone et al. 2014) influence the outcome of negotiations. This series of models has provided an explanation for some of the diversity in responses within and across species. However, the role of power has not been explored in the context of parental negotiations despite its potential to improve our understanding of empirical patterns, given that power and punishment likely occur in many interactions among parents.

Here we incorporate power and punishment into the existing negotiation model framework by allowing parents to punish each other in response to parental effort. As a starting point, we assume that there is a large asymmetry in power such that one parent has complete control over punishment. The more-powerful parent is called rank 1 and it can punish (inflict a cost) on the rank 2 as a function of the amount of care the rank 2 provides. We initially assume at first that inflicting punishment comes at no cost to the rank 1, then we relax that assumption to determine how a proportional cost to the rank 1 of punishing influences negotiations. We use this model to answer three questions about how punishment shapes negotiations over parental care: 1) Under what conditions does a parent benefit by inflicting a punishment cost? 2) How do power and punishment affect the response rules and negotiated levels of effort of each parent? 3) How do power and punishment during parental negotiations affect the fitness of the offspring?

MODEL DESCRIPTION AND RESULTS

Original model set-up

In this section, we first review the analysis of the original model by McNamara et al. (1999), which lets two parents undergo a cost-free negotiation in which they determine the optimal amount of effort to invest in their offspring given the response of the other parent. In the next section, we build directly on this analysis to introduce power and punishment, and compare the outcomes with those of the original model. The original model assumes that parents face a trade-off between investing in current versus future reproduction and that there is conflict between parents such that the benefits of parental effort depend on the efforts of both parents, but the cost depends only on the focal individual's effort. This original model (e.g., McNamara et al. 1999) provides a baseline that we use to measure how the inclusion of power and punishment affects predicted patterns of parental effort and their effect on offspring fitness.

The original model can be used to determine when negotiations will be favored by selection and how the negotiated outcome compares with the outcome under alternative models of parental care, for example when parental effort is fixed and parental care is not plastic (Houston and Davies 1985) or when only one parent provides care (McNamara et al. 2003). First, we can show when negotiations will be favored by selection relative to fixed effort, by analyzing general functions for costs and benefits of parental care and making assumptions about the shapes of those functions. Next, specific functions for costs and benefits with the assumed properties can be used to demonstrate the effect of negotiation on the behavioral responses of the parents and the final ES levels of effort that each parent provides after negotiation. Finally, the analysis of these specific functions can be used to reveal the effect of negotiation on the fitness of the offspring, to determine whether the offspring benefit from negotiations between their parents.

The fitness of a parent is given by a benefit, as a function of both its own and its partner's effort, and a cost, as a function of its own effort. The benefit to parent 1 for a given level of effort, u_1, and the effort of its partner, u_2, is given by $B(u_1 + u_2)$. The cost to parent 1 of providing effort at the level u_1 is given by $K(u_1)$. The fitness of parent 2 is found analogously. We assume, as did McNamara et al. (1999), that the benefit is increasing with diminishing returns as function of effort such that $B' > 0$ and $B'' < 0$ and that the cost is increasing and accelerating as a function of effort, such that $K' > 0$ and $K'' > 0$. The total fitness, W, of each parent is the benefit minus the cost of providing care:

$$W_1\left(u_1, u_2\right) = B\left(u_1 + u_2\right) - K\left(u_1\right) \tag{1}$$

$$W_2\left(u_1, u_2\right) = B\left(u_1 + u_2\right) - K\left(u_2\right) \tag{2}$$

The ES fixed level of effort for each parent is found by maximizing the fitness function for each parent, given its partner's best effort (Houston and Davies 1985). If parents undergo a negotiation, however, the optimal level of effort will depend on the response rule of the partner rather than a fixed level of effort by the partner. If parents are responding to each other, the effort of each parent, u_1 and u_2, will be represented in the fitness equation as a function of the other parent's effort. Following McNamara et al. (1999) we call these functions "response rules." The response rule of parent 1 to the effort of parent 2 is $\hat{r}_1(u_2)$ and the response rule of parent 2 to the effort of parent 1 is $\hat{r}_2(u_1)$. The slope of the response rules, $\hat{r}_1'(u_2)$ and $\hat{r}_2'(u_1)$, can be found by differentiating each parent's response rule with respect to partner effort, and represents the responsiveness to a change in partner effort. To simplify the notation, we let $\hat{r}_1'(u_2) = -\lambda_1$and $\hat{r}_2'(u_1) = -\lambda_2$. If λ is positive, the slope of the response rule is negative and a change in partner effort will result in a compensatory (opposing) change in own effort, thus positive λ represents the degree of compensation. Alternatively, if λ is negative, then a change in partner effort results in a matching change in own effort, thus positive λ would represent the degree of matching. Biparental care will only be an ESS when $0<|\lambda|<1$, which results in the response rules intersecting and allowing effort to converge during negotiation (McNamara et al. 1999).

To find the response rules and levels of effort that maximize fitness, we first replace u_2 with the response rule of parent 2, $\hat{r}_2(u_1)$, in the fitness function for parent 1 and u_1 with the response rule of parent 1, $\hat{r}_1(u_2)$, in the fitness function for parent 2:

$$W_1\left(u_1, u_2\right) = B\left(u_1 + \hat{r}_2\left(u_1\right)\right) - K_c\left(u_1\right) \tag{3}$$

$$W_2(u_1, u_2) = B(\hat{r}_1(u_2) + u_2) - K_c(u_2) \tag{4}$$

Next, we differentiate the fitness of parent 1 with respect to u_1 and the fitness of parent 2 with respect to u_2, to determine how an individual's fitness changes with a change in its own effort given that its partner uses the response rule. Differentiating W_1 with respect to u_1 and W_2 with respect to u_2 gives:

$$\frac{\mathrm{d}}{\mathrm{d}u_1}W_1(u_1, \hat{r}_2(u_1)) = (1-\lambda_2)B'(u_1 + \hat{r}_2(u_1)) - K_c'(u_1) \tag{5a}$$

$$\frac{\mathrm{d}}{\mathrm{d}u_2}W_2(\hat{r}_1(u_2),\ u_2,) = (1-\lambda_1)B'(\hat{r}_1(u_2) + u_2) - K_c'(u_2) \tag{5b}$$

Conceptually, we then set the derivatives of both fitness functions equal to 0 and solve for u_1 and u_2, respectively, to find the response rules for each parent that maximize or minimize fitness as a function of partner effort. However, without having either 1) a local approximation or 2) specific functions for the costs and benefits, it is impossible to find an explicit solution.

Original model solution 1: general functions with a local approximation

The first way of finding a solution to the original model uses a local approximation to compare the outcome of negotiation to that of a fixed response (McNamara et al. 1999). If we assume that the ES negotiated levels of effort are close to the ES fixed levels, we can approximate the fitness functions near the ES fixed level from Houston and Davies (1985), u^*, using a Taylor approximation. The Taylor series represents a function as an infinite sum that converges to the true function and thus the first terms can be used to approximate a function near a point. Here we use a quadratic approximation by using the first three terms of the Taylor series and take it to be exact, as in McNamara et al. (1999), which yields the following approximated cost and benefit functions for parent 1 (and analogously for parent 2):

$$\begin{aligned} B(u_1 + u_2) \approx & B(2u^*) + (u_1 + u_2 - 2u^*)B'(2u^*) \\ & + \frac{1}{2}(u_1 + u_2 - 2u^*)^2 B''(2u^*) \end{aligned} \tag{6}$$

$$\begin{aligned} K(u_1) \approx & K(u^*) + (u_1 - u^*)K'(u^*) \\ & + \frac{1}{2}(u_1 - u^*)^2 K'(u^*) \end{aligned} \tag{7}$$

Substituting these approximated functions for the benefits and costs into the fitness function for parent 1 (equation 1), [and analogously for parent 2 (equation 2)], and replacing u_2 with $\hat{r}_2(u_1)$, as in equation (3) and u_1 with $\hat{r}_1(u_2)$, as in equation (4), gives:

$$\begin{aligned} & W_1(u_1, \hat{r}_2(u_1)) \\ & = \begin{bmatrix} B(2u^*) + (u_1 + \hat{r}_2(u_1) - 2u^*)B'(2u^*) \\ + \frac{1}{2}(u_1 + \hat{r}_2(u_1) - 2u^*)^2 B''(2u^*) \end{bmatrix} \\ & \quad - \begin{bmatrix} K(u^*) + (u_1 - u^*)K'(u^*) \\ + \frac{1}{2}(u_1 - u^*)^2 K''(u^*) \end{bmatrix} \end{aligned} \tag{8}$$

Taking the derivative of equation (8) with respect to u_1, setting the result equal to zero, and solving for u_1 gives the response rule of parent 1 in terms of λ_2, the responsiveness of parent 2, and u^*, the ES fixed level of effort. From this analysis and given the assumptions about the shapes of the cost and benefit functions, McNamara et al. show using a focal point for local approximation, u^*, that the negotiated levels of effort under negotiation are less than the case where effort is fixed, and that a responsive individual is doing the best it possibly can with any partner (negotiation is an ESS relative to fixed levels of effort) (Houston and Davies 1985; McNamara et al. 1999).

Original model solution 2: specific functions with an explicit solution

It is also possible to find an explicit solution to the original model using specific functions. McNamara et al. (2003) analyzed a case with quadratic functions for the costs and benefits that have the assumed properties of marginal benefits and accelerating costs. Quadratic functions are useful because they result in an explicit solution with stable, linear response rules, simplifying the analysis and allowing for graphical representations of results. The benefit and cost functions for parent 1 (and analogously for parent 2) are assumed to be:

$$B(u_1 + u_2) = 2(u_1 + u_2) - (u_1 + u_2)^2 \tag{9}$$

$$K(u_1) = ku_1^2 \tag{10}$$

The benefit is an increasing and concave down function (for $u_1 + u_2 < 1$), showing diminishing returns as total effort increases. The costs are an upward-facing parabola, where k is a cost scaling parameter, showing accelerating costs as a parent's own effort increases. Thus they fulfill the assumptions of the case with general functions because $B' > 0$, $B'' < 0$, $K' > 0$, and $K'' > 0$. As described above, we first replace u_2 with $\hat{r}_2(u_1)$, in the fitness function for parent 1 and u_1 with $\hat{r}_1(u_2)$,in the fitness function for parent 2. Next, we differentiate the fitness of parent 1 with respect to the effort of parent 1, and the fitness of parent 2 with respect to the effort of parent 2. Then by setting the results to zero, we can solve for the level of effort of each parent that maximizes or minimizes its own fitness. Because the functions are quadratic, the response rules will be linear functions of partner effort. Where the two lines intersect represents the final negotiated levels of effort for each parent, which we can find by solving the two response rules simultaneously for each parent's effort (McNamara et al. 2003).

Incorporating power and punishment

Our analysis incorporates power and punishment into the original model and parallels the analysis described above to compare negotiated outcomes with and without punishment. First, we use general functions for costs and benefits to determine under what conditions a parent can benefit by exerting their power. Second, we analyze specific quadratic functions for costs and benefits to determine how power and punishment influence the response rules and negotiated levels of effort of each parent. Finally, we use the results from the analysis of quadratic functions to determine how power and punishment influence the fitness of the offspring.

We begin by adding an additional assumption to the original model: that one parent is socially dominant over the other, such that it can punish, that is, inflict a cost on, the other parent in response to the other parent's effort. This assumption will be reasonable in systems where the dominant individual can monitor subordinate effort and inflict a cost at little risk to itself, for example, by causing physical harm or limiting access to resources, according to the amount of subordinate effort provided. At first we assume that the more-powerful parent does not incur any cost from punishing, but then relax that assumption to determine how incurring a cost from punishing, proportional to the cost inflicted, influences our analysis (see Supplementary Appendix).

To represent an asymmetry in power, and be agnostic as to which sex is more powerful, we call the more-powerful parent "rank 1" and the less-powerful parent "rank 2." As before, the benefit to both ranks for their own effort and the effort of their partner is $B(u_1 + u_2)$. The cost to each parent of rank i, of providing effort at the level u_i is now split into two components: the cost to a parent of providing care, K_c, and the cost of being punished, K_p. The cost to rank 1 of providing effort at level u_1 is $K_c(u_1)$ and the cost of being punished is 0 (for this version of our model). The cost to rank 2 of providing effort at the level u_2 is $K_c(u_1)$, and the cost to rank 2 of receiving punishment is $K_p(u_2)$. The total fitness, W, of a parent of rank i is thus the benefit minus the cost of providing care together with the cost of punishing or being punished:

$$W_1(u_1, u_2) = B(u_1 + u_2) - K_c(u_1) - 0 \tag{11a}$$

$$W_2(u_1, u_2) = B(u_1 + u_2) - K_c(u_2) - K_p(u_2) \tag{11b}$$

To find the optimal response rules, we first replace u_2 with the response rule of rank 2, $\hat{r}_2(u_1)$, in equation (11a) and u_1 with the response rule of rank 1, $\hat{r}_1(u_2)$, in equation (11b):

$$W_1(u_1, u_2) = B(u_1 + \hat{r}_2(u_1)) - K_c(u_1) \tag{12a}$$

$$W_2(u_1, u_2) = B(\hat{r}_1(u_2) + u_2) - K_c(u_2) - K_p(u_2) \tag{12b}$$

Next we take the derivative of equation (12a) with respect to u_1 and equation (12b) with respect to u_2:

$$\frac{\mathrm{d}}{\mathrm{d}u_1} W_1(u_1, \hat{r}_2(u_1)) = (1 - \lambda_2)B'(u_1 + \hat{r}_2(u_1)) - K_c'(u_1) \tag{13a}$$

$$\frac{\mathrm{d}}{\mathrm{d}u_2} W_2(\hat{r}(u_2),\ u_2) = (1 - \lambda_1)B'(\hat{r}_1(u_2) + u_2) - K_c'(u_2) - K_p'(u_2) \tag{13b}$$

To find the optimal response rules, we set the derivatives in equations (13a) and (13b) equal to 0 and solve for u_1 and u_2 as functions of partner effort. Because an explicit solution cannot be found using these general functions, we use the two approaches outlined above: 1) using a local approximation and 2) using specific functions for the costs and benefits. These two methods allow us to determine first, under what conditions does a parent benefit by inflicting a punishment cost; second, how punishment influences the response rules and negotiated levels of effort of each parent; and third, how power and punishment influence the fitness of the offspring.

Solution 1: under what conditions does a parent benefit by inflicting a punishment cost?

First, we analyze the case in which parents can respond to each other's effort to reach a negotiated settlement when there is an asymmetry in power and ask under what conditions will selection favor punishment relative to no punishment. When rank 1 can punish rank 2, selection will favor punishment by rank 1 if the fitness payoff to rank 1 with punishment is greater than its payoff without punishment. Given the fitness $W_1(u_1,u_2)$, then the benefit $B(u_1 + u_2)$ must increase, the cost $K_c(u_1)$ must decrease, or the benefit must increase more than the cost, when rank 1 inflicts a cost on rank 2. Because punishment influences u_2, rank 1 is favored to inflict a cost $K_p(u_2)$ on rank 2 if this results in an increase in rank 2 effort relative to when there is no punishment. For this reason, we begin by seeking the level of effort that maximizes the fitness of rank 2 under punishment.

To begin, we assume that the negotiated level of effort with punishment is near the negotiated level of effort without punishment (from the original model), which is realistic if punishment is not so extreme that it dramatically changes parental effort. Next, we can approximate the cost and benefit functions for u_2 near the negotiated level of effort, u_N^*, from McNamara et al. (1999), using a Taylor expansion. To get the negotiated level of effort of rank 2 under punishment and determine when it is greater relative to the classic negotiated level of effort, u_N^*, we use the quadratic Taylor approximation of the cost and benefit functions and take them to be exact:

$$B(u_1 + u_2) \approx B(2u_N^*) + (u_1 + u_2 - 2u_N^*)B'(2u_N^*) + \frac{1}{2}(u_1 + u_2 - 2u_N^*)^2 B''(2u_N^*) \tag{14}$$

$$K_c(u_2) \approx K_c(u_N^*) + (u_2 - u_N^*)K_c'(u_N^*) + \frac{1}{2}(u_2 - u_N^*)^2 K_c''(u_N^*) \tag{15}$$

$$K_p(u_2) \approx K_p(u_N^*) + (u_2 - u_N^*)K_p'(u_N^*) + \frac{1}{2}(u_2 - u_N^*)^2 K_p''(u_N^*) \tag{16}$$

Substituting the cost and benefit equations (14–16) into equation (12a), the fitness function of the rank 1, and replacing u_1 with the response rule of rank 2, $\hat{r}_2(u_1)$ gives the fitness of rank 1 as a function of the rank 2 response (17a).

$$W_1(u_1,\hat{r}_2(u_1)) = \begin{bmatrix} B(2u_N^*) + (u_1+\hat{r}_2(u_1)-2u_N^*)\,B'(2u_N^*) \\ +\frac{1}{2}(u_1+\hat{r}_2(u_1)-2u_N^*)^2 B''(2u_N^*) \end{bmatrix} - \begin{bmatrix} K_c(u_N^*) + (u_1-u_N^*)K_c'(u_N^*) \\ +\frac{1}{2}(u_1-u_N^*)^2 K_c''(u_N^*) \end{bmatrix} \tag{17a}$$

Analogously, substituting equations (14–16) into equation (12b), the fitness function of the rank 2, and replacing u_1 with the response rule of rank 1, $\hat{r}_1(u_2)$, gives the fitness of rank 2 as a function of the rank 1 response (17b).

$$W_2(\hat{r}_1(u_2),u_2) = \begin{bmatrix} B(2u_N^*) + (\hat{r}_1(u_2)+u_2-2u_N^*)B'(2u_N^*) \\ +\frac{1}{2}(\hat{r}_1(u_2)+u_2-2u_N^*)^2 B''(2u_N^*) \end{bmatrix} - \begin{bmatrix} K_c(u_N^*)(u_2-u_N^*)K_c'(u_N^*) \\ +\frac{1}{2}(u_2-u_N^*)^2 K_c''(u_N^*) \end{bmatrix} - \begin{bmatrix} K_p(u_N^*) + (u_2-u_N^*)K_p'(u_N^*) \\ +\frac{1}{2}(u_2-u_N^*)^2 K_p''(u_N^*) \end{bmatrix} \tag{17b}$$

Using this Taylor approximation near u_N^* will allow us to compare how fitness changes with power and punishment relative to the original model. To find the level of effort that maximizes the fitness of rank 2, we take the derivative of its own fitness function with respect to its own effort from equation (17b), set it to 0, and solve for the effort of rank 2, as a function of the rank 1 response rule.

Taking the derivative of the Taylor expanded fitness function with respect to u_2 and setting it equal to zero yields:

$$\begin{aligned} &(1+\hat{r}_1'(u_2))B'(u_N^*) + (u_1+u_2-2u_N^*)(1+\hat{r}_1'(u_2))B''(2u_N^*) \\ &-K_c'(u_N^*) - (u_2-u_N^*)K_c''(u_N^*) \\ &-(u_2-u_N^*)K_p''(u_N^*) - K_p'(u_N^*) = 0 \end{aligned}$$

We set the slope of the response rule $\hat{r}_1'(u_2) = -\lambda_1$ to represent the "responsiveness" of rank 1 to a change in rank 2 effort. We also have the condition that $0<|\lambda|<1$. To simplify the notation, $B''(2u_N^*)$ is written B'', $K_c''(u_N^*)$ is written K_c'', $K_p''(u_N^*)$ is written K_p'', and $K_p''(u_N^*)$ is written K_p'. Finally, solving for the effort of rank 2 as a function of u_1, which we define as the response rule of rank 2, and simplifying gives:

$$u_2 = \hat{r}_2(u_1) = u_N^* + \frac{(1-\lambda_1)B'(u_N^*) - K_c'(u_N^*) + (1-\lambda_1)(u_1-u_N^*)B'' - K_p'}{K_c'' + K_p'' - (1-\lambda_1)B''} \tag{18a}$$

The response rule of rank 1, assuming no cost to the rank 1 of punishing, is found analogously by solving for the effort of rank 1, which is the rank 1 response rule, as a function of u_2 gives:

$$u_1 = \hat{r}_1(u_2) = u_N^* + \frac{(1-\lambda_2)B'(u_N^*) - K_c'(u_N^*) + (1-\lambda_2)(u_2-u_N^*)B''}{K_c'' - (1-\lambda_2)B''} \tag{18b}$$

At equilibrium, McNamara et al. (1999) show that $(1-\lambda_{ESS})B'(2u_N^*) = K_c'(u_N^*)$, where λ_{ESS} is the negative slope of the ES response rule. Assuming λ_1 and λ_2 are close to λ_{ESS}, then $(1-\lambda_1)B'(u_N^*) - K_c'(u_N^*)$ is small. This assumption is reasonable given our assumption associated with the Taylor expansion step, that punishment is not so extreme that it dramatically changes the effort and responsiveness of each parent relative to when there is no punishment. So, to simplify the following analysis, we let $(1-\lambda_{1,2})B'(u_N^*) - K_c'(u_N^*) \approx 0$ and focus on the other terms involving the punishment cost. An additional implicit assumption is that $\lambda_1 - \lambda_2 \approx 0$, which is true if punishment has not changed responsiveness too dramatically, or if an increase in responsiveness by one parent is matched by a decrease in responsiveness by the other parent, relative to the ES responsiveness in the original model.

Using this simplifying step and solving the response rules simultaneously gives the negotiated level of effort for rank 2 when there is punishment:

$$u_2 = u_N^* + \frac{\left(-K_c''\,K_p'\right) + B''(K_p' - \lambda_2 K_p')}{K_c''\left(K_c''+K_p''\right) + B''(K_p''(\lambda_2-1) + K_c''(\lambda_1+\lambda_2-2))} \tag{19a}$$

The effort of rank 1 is solved analogously:

$$u_1 = u_N^* + \frac{-B''(K_p' - \lambda_2 K_p')}{K_c''\left(K_c''+K_p''\right) + B''\left(K_p''(\lambda_2-1) + K_c''(\lambda_1+\lambda_2-2)\right)} \tag{19b}$$

Equation (19a) shows that rank 2 effort will increase relative to the negotiated effort with no punishment, u_N^*, when the second term is positive, and decrease relative to u_N^* when the second term is negative. Rank 1 will therefore benefit from punishing rank 2 when the second term in equation (19a) is positive.

Next, we consider what conditions allow the rank 1 to extract the most care from the rank 2, thereby gaining the greatest possible benefit from punishing. To do this, we compare the change in rank 2 effort, which is the second term in equation (19a), among different forms of punishment cost (Figure 1). If we assume, as in McNamara et al. (1999), that the benefit of care shows diminishing returns and that the costs of care are accelerating with increasing effort, then B'' would be negative and K_c'' would be positive. If K_p' is positive, punishment increases with increasing rank 2 effort (Figure 1a,c), which we do not expect to be a biologically relevant punishment strategy. In support of this, rank 1 never benefits when K_p'' is positive (Figure 1a), and only benefits under a narrow range of conditions when K_p'' is negative (Figure 1c), so we consider the case where $K_p'K_p'$ is negative, that is, the cost of punishment decreases with increasing rank 2 effort (Figure 1b,d). When K_p' is negative the numerator of equation (19a) will be positive, and if K_p'' is positive, that is, concave up (Figure 1b), then the denominator will be positive, and rank 2 effort will increase. This results in an increase in rank 1 fitness. Alternatively, if K_p' is negative then the numerator will be positive, and if K_p'' is negative (as long as it is not large relative to K_c'') (Figure 1d), then the denominator will be positive, and rank 2 effort will increase once more. Not only that, it will increase more than when K_p'' is positive, because the denominator of the increase in effort will be smaller. A greater increase in rank 2 effort would result in greater fitness gains by the rank 1. Therefore, assuming that selection can act on all these different shapes for the punishment cost function, when the relationship between punishment cost and rank 2 effort is decreasing and concave down (Figure 1d), the rank 1 can maximize its fitness gains.

Biologically, a negative K_p' provides an incentive to rank 2 to increase its level of effort and escape punishment. A negative K_p'', then, means that punishment by the rank 1 decreases even more

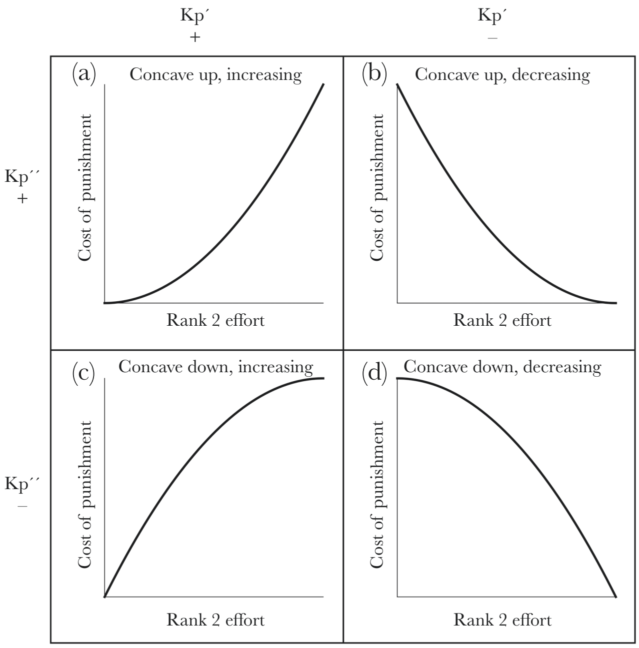

Figure 1
The possible shapes of the function representing how rank 1 inflicts a punishment cost on the rank 2 as a function of rank 2 effort. K_p' is the first derivative of the punishment cost function with respect to rank 2 effort; therefore, a negative K_p' indicates a decreasing function, whereas a positive K_p' indicates an increasing function. K_p'' is the second derivative with respect to rank 2 effort; therefore, a negative value indicates a concave down function, whereas a positive value indicates a concave up function. Shown are the different combinations of punishment types: (a) concave up, increasing—punishment not effective; (b) concave up, decreasing—punishment sometimes effective; (c) concave down, increasing—punishment effective; (d) concave down, decreasing-punishment effective. The punishment strategy of the rank 1 that maximizes fitness gains relative to when there is no punishment is when K_p' and K_p'' are both negative, indicating a decreasing, concave down function.

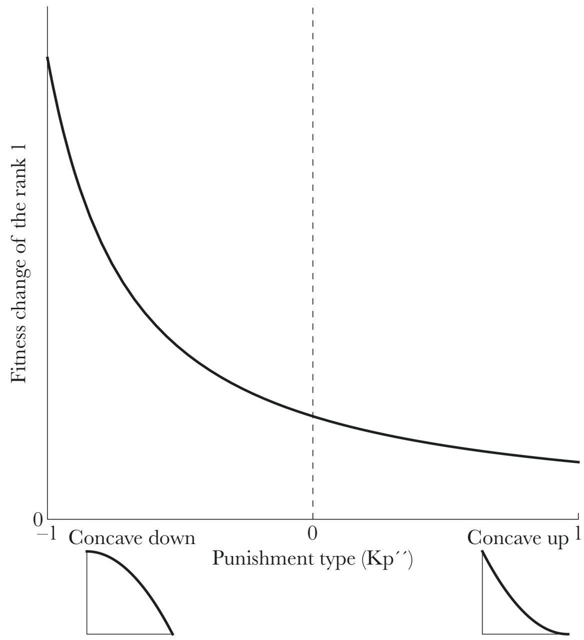

Figure 2
The change in fitness of rank 1, relative to when there is no punishment, when rank 1 inflicts punishment on the rank 2 at different values of K_p'' when all other parameters are held constant and K_p' is negative (the function is decreasing). Negative K_p'' values represent an accelerating reduction in punishment with increased rank 2 effort (concave down), and positive K_p'' represents a decelerating reduction in punishment with increased rank 2 effort (concave up). The fitness change of rank 1 is always positive under these conditions when K_p' is negative and K_p'' is small relative to K_c''. This indicates that under these conditions, selection will favor punishment over no punishment, and concave down forms of punishment over concave up forms of punishment.

when the rank 2 increases its parental effort even more, which is expected as it is a way for the rank 1 to motivate the rank 2 to further increase its effort. Punishment will be favored by selection when the change in rank 1 fitness relative to the original model with no punishment is positive. The change in rank 1 effort is found by plugging in the final negotiated levels of effort from equations (19a,b) into the fitness function for rank 1 and comparing it to the fitness of rank 1 using negotiated effort when the punishment cost is 0. Assuming a negative K_p', we can show graphically that the change in fitness of the rank 1 is greatest when K_p'' is negative (Figure 2). This analysis reveals the range of conditions under which the rank 1 will benefit from punishing the rank 2.

Solution 2: How does punishment affect the response rules and negotiated levels of effort of the rank 1 and rank 2?

The above analysis reveals that when there are no costs to punishing, the higher-ranking parent is predicted to inflict punishment according to the amount of effort the lower ranking parent provides, and the lower-ranking parent is predicted to maintain a high level of effort to avoid more severe punishment. To illustrate the effect punishment has on the response rules and ES negotiated levels of effort, we add a punishment cost to the quadratic cost and benefit functions used in McNamara et al. (2003) and described above. These quadratic functions have the properties assumed in the general case, namely that the benefits of care show diminishing returns (for $u_1 + u_2 < 1$) and the costs of care are accelerating:

$$B(u_1 + u_2) = 2(u_1 + u_2) - (u_1 + u_2)^2 \tag{20}$$

$$K_c(u_{1,2}) = k_c u_{1,2}^2 \tag{21}$$

The above analysis also revealed that the greatest increase in rank 1 fitness compared to the classic negotiation with no punishment occurs when the punishment cost is a decreasing, concave down function. Thus, we set the cost of punishment as a decreasing, concave down function that is positive between 0 and 1 to be biologically realistic:

$$K_p(u_2) = k_p u_2^2 + 1 \tag{22}$$

The punishment cost scaling parameter, k_p, is negative, making this cost a downward-facing parabola. We must also restrict the cost of punishment to be positive, as a negative punishment cost is not biologically realistic. We assume that the benefits of care show diminishing returns, which occurs in the range of $u_1 + u_2 < 1$, meaning u_2 is always less than 1. Under this condition, the cost of punishment is always positive so long as the cost scaling parameter, k_p, is not less than −1. Note that a value of 1 for $u_1 + u_2$ can be thought of as the maximum total amount of effort that the offspring can receive from both parents. An upper limit on combined effort is realistic if, for example, the offspring become satiated and cease to benefit from increased care.

If rank 1 does not pay a cost to punishment, using the specific cost and benefit functions, the fitness of rank 1 and rank 2 become:

$$W_1(u_1, u_2) = 2(u_1 + u_2) - (u_1 + u_2)^2 - k_c u_1^2 \tag{23a}$$

$$W_2(u_1, u_2) = 2(u_1 + u_2) - (u_1 + u_2)^2 - k_c u_2^2 - (k_p u_2^2 + 1) \tag{23b}$$

As with the analysis of the general functions above, to find the optimal response rules for rank 1 and rank 2 given the responsiveness λ_1 of rank 1 and λ_2 of rank 2, we first replace u_2 with $\hat{r}_2(u_1)$ in equation (23a) and u_1 with $\hat{r}_1(u_2)$ in equation (23b). Next, we differentiate the fitness equations with respect to each individual's own effort, set the result equal to 0, and solve for the effort of each parent as a function of the other parent's effort. The solution to this is the effort of each parent as a function of partner effort, which we have defined as the response rule of each parent. The response rules from this analysis are as follows:

$$\hat{r}_1(u_2) = \frac{1 - \lambda_2 - u_2 + \lambda_2 u_2}{1 + k_c - \lambda_2} \tag{24a}$$

$$\hat{r}_2(u_1) = \frac{1 - \lambda_1 - u_1 + \lambda_1 u_1}{1 + k_c + k_p - \lambda_1} \tag{24b}$$

Because we defined λ_1 as the negative slope of the response rule of rank 1 and λ_2 as the negative slope of the response rule of rank 2, λ_1 and λ_2 are found by differentiating equation (24a) with respect to u_2 and equation (24b) with respect to u_1 and reversing the sign:

$$\lambda_1 = \frac{1 - \lambda_2}{1 + k_c - \lambda_2} \tag{25a}$$

$$\lambda_2 = \frac{1 - \lambda_1}{1 + k_c + k_p - \lambda_1} \tag{25b}$$

Solving for λ_1 and λ_2 in terms of k_c and k_p by simultaneously solving equations (25a) and (25b) and plugging those into λ_1 and λ_2 in equations (24a) and (24b) above gives the ES response rules for rank 1 and rank 2 in terms of partner effort and our cost scaling parameters k_c and k_p. These equations are long and difficult to interpret visually; therefore, they are not presented here. However, we can use them to determine which partner compensates more and which provides more effort, as described below and shown graphically (Figures 3 and 4).

In equations (25a) and (25b), $1 - \lambda_1$ occurs in the numerator and denominator, effectively canceling each other out and allowing us to focus on other terms. If k_c is positive and $-1 < k_p < 0$ (remembering that k_p is a scaling parameter of a parabola such that the function $K_p(u_2)$ is always positive under our assumptions), then $\lambda_1 < \lambda_2$ and rank 2 compensates more than rank 1 for a change in their partner's effort. At all values of partner effort, rank 1 is less responsive and provides less effort when using the negotiated rule in which it can punish rank 2 than when using the negotiated rule without punishment. In contrast, at all values of partner effort, rank 2 is more responsive and provides more effort when interacting with the negotiated rule in which it can be punished by rank 1 than when interacting with the negotiated rule without punishment (Figure 3). Finally, at all values of partner effort, rank 2 provides more effort than rank 1, when rank 1 can punish rank 2.

The final, ES negotiated levels of effort for the rank 1 and the rank 2 are found by solving equations (24a) and (24b) simultaneously to get u_1 and u_2 in terms of k_c and k_p. These final levels of effort can then be compared to the classic negotiation case where

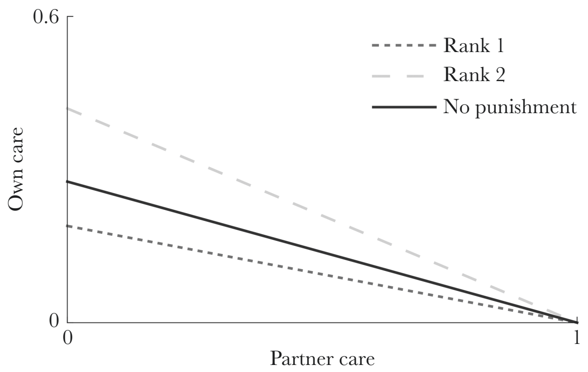

Figure 3
Negotiated response rules indicating the optimal level of effort as a function of partner effort for the rank 1, the rank 2, and both parents when there is no punishment. The slope of the rank 1 response rule when it can punish rank 2 is less than when there is no punishment, whereas the slope of the rank 2 response rule when it can be punished by rank 1 is greater than when there is no punishment. When there is punishment involved, the optimal level of effort for a given level of partner effort is always lower for the rank 1 than for the rank 2, except in the special case where partner care is at 1, where both rank 1 and rank 2 are predicted to provide no effort. Therefore, the rank 1 provides less effort and responds less to a change in partner effort when it can punish rank 2 than when there is no punishment, and the rank 2 provides more effort and responds more to a change in partner effort when it can be punished by rank 1 compared with when there is no punishment.

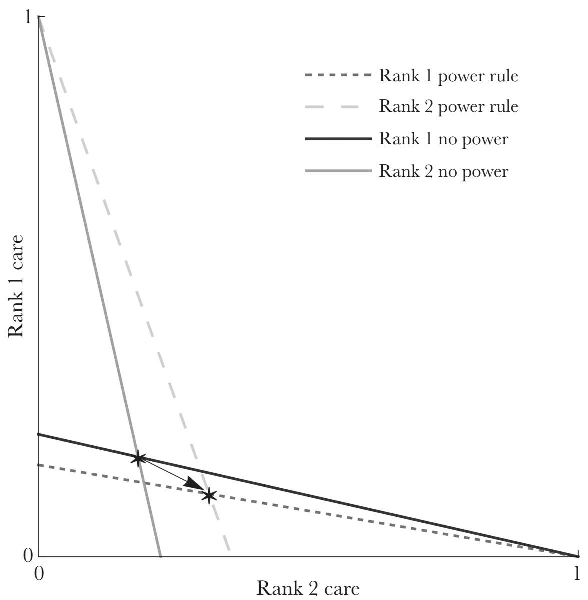

Figure 4
Negotiated response rules as a function of rank 2 effort (rank 2 effort on the x-axis; rank 1 effort on the y-axis). The dotted lines represent the negotiated response rules of the rank 1 and rank 2 when there is no punishment. Where the two dotted lines intersect represents the ES negotiated levels of effort for the rank 2 and rank 1 (*), showing that parents provide the same level of effort after negotiation. The solid lines represent the negotiated response rules when there is power and punishment. Where the two solid lines intersect represents the ES negotiated levels of effort with punishment for the rank 2 and rank 1 (*). The arrow reveals that rank 1 provides less effort than when there is no punishment and the rank 2 provides more effort compared to when there is no punishment.

$k_p = 0$. We found that compared to the classic negotiation case, the final negotiated level of effort is lower for the rank 1 and higher for the rank 2 (Figure 4).

How does punishment during parental negotiations affect the survival of the offspring?

We can show using general functions for costs and benefits that the rank 2 effort increases for certain punishment cost functions, and the rank 1 effort decreases in concert. The second terms in equations (19a) and (19b) show how much each parent's effort changes relative to the case with no punishment. The changes in rank 1 and rank 2 effort relative to the negotiation level with no punishment, u_N^*, are given by:

$$\Delta u_1 = \frac{-B''(K_p' - \lambda_2 K_p')}{K_c''\left(K_c'' + K_p''\right) + B''(K_p''(\lambda_2 - 1) + K_c''(\lambda_1 + \lambda_2 - 2))} \quad (26a)$$

$$\Delta u_2 = \frac{\left(-K_c''\ K_p'\right) + B''(K_p' - \lambda_2 K_p')}{K_c''\left(K_c'' + K_p''\right) + B''(K_p''(\lambda_2 - 1) + K_c''(\lambda_1 + \lambda_2 - 2))} \quad (26b)$$

The change in total effort under punishment, then, is found by adding the changes in each parent's effort:

$$\Delta u_1 + \Delta u_2 = \frac{\left(-K_c''\ K_p'\right)}{K_c''\left(K_c'' + K_p''\right) + B''(K_p''(\lambda_2 - 1) + K_c''(\lambda_1 + \lambda_2 - 2))} \quad (27)$$

Given our assumptions about the shapes of the cost and benefit functions and with the condition that $0 < |\lambda| < 1$, equation (27) is always positive. The total effort received by the offspring is greater in the case with punishment involved than the case with no punishment because the magnitude of the positive change by rank 2 is greater than the magnitude of the negative change by rank 1 (this can be seen in Figure 4 also). Furthermore, when the punishment cost function is a concave down, decreasing function of rank 2 effort, then the total effort will increase as K_p'' gets more negative, assuming K_p'' is small relative to K_c'' (Figure 5). Therefore, assuming that selection can act on all these different shapes for the punishment cost function, when the relationship between punishment cost and rank 2 effort is decreasing and concave down (Figure 1), the offspring will benefit in terms of fitness.

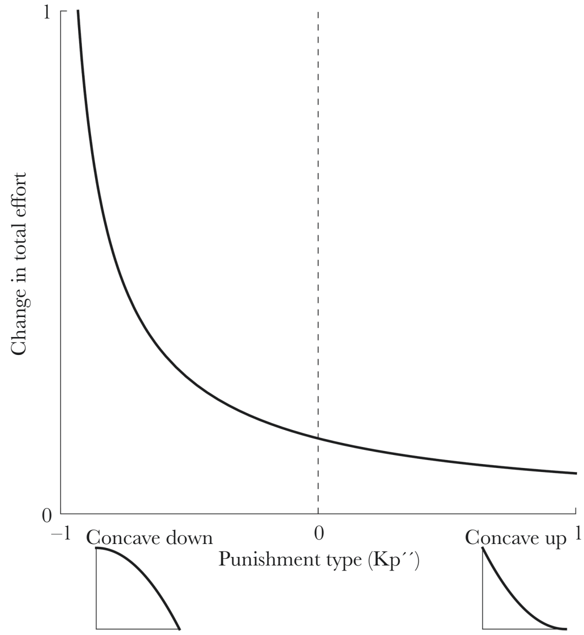

Figure 5
The change in total effort received by offspring relative to when there is no punishment when rank 1 inflicts punishment on the rank 2 at different values of K_p'' when all other parameters are held constant and K_p' is negative (the function is decreasing). Negative K_p'' values represent decelerating punishment with decreased rank 2 effort (concave down) and positive K_p'' represents accelerating punishment with decreased rank 2 effort (concave up). The total care the offspring receive is always positive and therefore greater under punishment compared to the case with no punishment, indicating that under these conditions offspring will benefit.

DISCUSSION

In the original negotiation model, McNamara et al. (1999) show that when parents undergo a negotiation, they will partially compensate for a change in partner effort, but each parent provides less effort than when there is no negotiation and effort is fixed. Because the combined negotiated level of effort is less than the combined fixed level of effort, the offspring receive less total effort when their parents negotiate and in some cases are better off with one parent than with two (McNamara et al. 2003). Here we extend this model to show that when there is an asymmetry in power such that rank 1 can inflict a cost on the rank 2 in response to rank 2's level of effort, it results in greater rank 2 effort and less rank 1 effort than the original negotiation model (this study; McNamara et al. 1999). As in the original negotiation model, when there is power and punishment, a change in partner effort results in partial compensation, but the degree of compensation is asymmetric: the rank 2 compensates more than the rank 1 for a change in partner effort. Because the increase in rank 2 effort outweighs the decrease in rank 1 effort relative to a negotiation with no punishment, our model shows that the offspring do better, that is, receive more total effort, when there is power and punishment in negotiations. When we relax the assumption that there is no cost to punishing, such that the rank 1 incurs a cost from punishing, proportional to the cost inflicted, the results are not qualitatively different (see Supplementary Appendix).

The increase in offspring fitness relative to the original negotiation model results from the rank 2 compensating more and providing more effort after negotiation when under the threat of punishment, which more than offsets the reduction in compensation and final negotiated effort by the rank 1. Because offspring benefit from power and punishment, and thus in having the more-powerful parent underestimate partner effort, offspring strategies that influence power dynamics between their parents might evolve. For example, selection might favor offspring that misrepresent to parent 1 the level of care that they have received from the parent 2, to elicit punishment of parent 2 by parent 1 and elicit greater levels of care from parent 2. Offspring begging behavior provides a mechanism by which offspring can influence parental behavior, which could be selected upon as a means to incite punishment between parents if offspring need serves as a signal of partner effort (Hinde and Kilner 2007).

In this model, although rank 2 has lower fitness than a parent not under the threat of punishment, the rank 2 is in fact doing the best it possibly can because if it reduces its effort, as it will face the cost of being punished by the rank 1 and thus is favored to cooperate and maintain a high level of effort. The rank 2 then is the only loser in negotiations with power and punishment. Whether exploitation of the rank 2 will persist over evolutionary time in a particular system is unclear, however, as the rank 2 may evolve strategies to avoid punishment or regain power. For example, mate choice may allow individuals to choose partners that are less willing or able to inflict punishment. Indeed, although females are predicted to prefer dominant males as mates when those males can provide higher quality resources, many examples exist of females choosing subordinate males (Qvarnström and Forsgren 1998) or assortatively mating (Jiang et al. 2013).

The results of this model fit into a series of alternative models that might help explain the diversity of outcomes of negotiations over parental care (Harrison et al. 2009) and here we provide a set of predictions that might be used to discriminate among models for how parents should respond to a change in partner effort (Table 1). The first in this series of models assumes that effort is a "sealed bid" and predicts that parents do not change their effort in behavioral time but respond only over evolutionary time to changes in partner effort (Table 1, H0; Houston and Davies 1985). Such a "sealed bid" model is relevant to systems where it is difficult to assess partner effort, where there are constraints on the ability to respond, or where negotiation takes place at a different stage of partner interaction, for example as part of courtship or during a previous breeding bout (Houston and Davies 1985; Sanz et al. 2000; Schwagmeyer et al. 2002). If, on the other hand, individuals vary in quality and can observe each other's efforts, then a negotiated outcome should be favored over a "sealed bid," giving us the prediction that parents will partially compensate for changes in partner effort (Table 1, H1; (McNamara et al. 1999).

An important social context that can influence negotiations is the amount of information each parent has about the offspring (Johnstone and Hinde 2006). When one parent is more informed about offspring need, the less-informed parent may be assessing the more-informed parent's effort to determine the needs of the offspring. If this is the case, the more-informed parent is predicted to partially compensate for its partner, whereas the less-informed parent, in contrast with the predictions of the original negotiation model, matches the response of its partner (Table 1, H2; Johnstone and Hinde 2006). Our model incorporating asymmetric power into the negotiation model reveals that if one parent is able to punish their partner for a change in effort, this results in an asymmetric response by the two parents, with greater effort and compensation by the less-powerful parent and lower effort and compensation by the more-powerful parent, distinguishing it from the asymmetric information model (Table 1, H3).

Empirical tests of model predictions generally involve experimentally handicapping one pair member to reduce its parental effort and measuring the response of its partner. A meta-analysis of 54 such studies in birds revealed that partial compensation is the mean response, providing evidence for the original negotiation model (Harrison et al. 2009), but not discriminating among the alternative hypotheses (Table 1). Our model incorporating power and punishment also predicts partial compensation. However, when there is power and punishment, the predictions can be discriminated from those of the original negotiation model in two key ways: first, that the rank 1 will compensate less than the rank 2, and second, when the rank 2 reduces its effort, the rank 1 will inflict punishment. Therefore, existing methods to test for negotiations can also be used to look for evidence of the role of power and punishment simply by recording punishment or threat displays in addition to parental effort. Exploring systems where there is the potential for strong, easily observable power asymmetries, such as the dominance hierarchies based on size found in social fishes (Buston 2004; Bender et al. 2005), meerkats (Clutton-Brock et al. 2004), and naked mole-rats (Reeve 1992), may be a good place to start testing our model.

We further suggest that our model provides an alternative hypothesis that can be explored when empirical results are not fully explained by the original negotiation model alone, and two examples serve to demonstrate the point. First, when males and females differ in the magnitude of their compensatory response (e.g., Sanz et al. 2000; Schwagmeyer et al. 2002; Smiseth et al. 2005), this is not consistent with the predictions of original negotiation model, but it is consistent with the idea of there might be a power differential between the sexes and the predictions of this model. Second, when there differences among partners in their responses to handicapping (e.g., Sanz et al. 2000; Creighton et al. 2015), this is not consistent with the predictions of the original negotiation model, but a lesser response to handicapping by one parent might reflect the fact that it faces a punishment cost if it were to reduce its care further.

Interestingly, a study by Awata and Khoda (2004) demonstrated that in the cichlid *Julidochromis ornatus*, pairs mate assortatively for size and the size difference between parents predicted the amount of care provided by each pair member, such that the smaller parent provided the majority of care regardless of if it was the male or the female. The authors hypothesized that this result was due to power asymmetries between different sized individuals, as larger individuals were socially dominant and aggressive toward their smaller

Table 1

Alternative hypotheses/models for factors that will influence negotiations over parental care, and predicted changes in parental effort that will occur in response to an experimental increase in effort of one parent

Manipulation of one individual's parental effort	Fixed response (H0)	Alternative hypotheses: Original negotiation (H1)	Asymmetric information (H2)	Asymmetric power (H3)
Partner effort ↓	Parental effort – No response	Parental effort ↑ Partial compensation	More-informed parent effort ↑ Partial compensation	More-powerful parent effort ↑ Less compensation + Punishment
			Less-informed parent effort ↓ Matching	Less-powerful parent effort ↑↑ Greater compensation

The symbol ↑ indicates an increase, – indicates no change, and ↓ indicates a decrease in parental effort is predicted.

partners. The model presented here provides a theoretical basis for this hypothesis and could be tested in the context of negotiations via experimental handicapping.

Considering the role of power and punishment is critical to our understanding of how negotiations operate, as these power dynamics have the potential to influence the way parents respond to each other and thus how much care is provided to the offspring and by whom. This in turn could influence the evolution of parent and offspring traits to avoid or incite punishment. Furthermore, asymmetries in power between parents under conflict are likely to be universal. Males and females are often markedly different in size (Lande 1980; McElligott et al. 2001; Dale et al. 2007) or the presence of ornaments and armaments (Berglund et al. 1996; Emlen et al. 2012), which have the potential to give one parent physical power over the other. Even in the absence of sex differences, among-individual differences in traits such as aggression have been widely documented (Dall et al. 2004; Hurd 2006), and thus could result in power asymmetries between parents. Our model shows that if a power asymmetry exists, the rank 1 can gain fitness benefits by inflicting punishment, suggesting that if a parent can exert its power, it should. Explicit tests across different social systems based on predictions about who has power are still necessary to determine whether power and punishment influence the outcome of negotiations.

Tests of negotiations that consider power asymmetries alongside alternative models of negotiations can provide insight into the diversity of observed outcomes of negotiations. However, these models are not necessarily mutually exclusive. For example, if there is an asymmetry in power and information, the relative strengths of the two factors may determine the outcome of negotiation, revealing the need for models that incorporate both power and information into the negotiation framework. Furthermore, we assumed that one parent had complete control over the other, however it is possible that both parents have the ability to punish, but that the amount they can punish depends on some state variable such as size. In addition to physical power, any ability one sex has to influence the behavior of the other can alter power dynamics over parental care, including concealed ovulation by females to confuse paternity (Daniels 1983; Schoröder 1993), genomic imprinting (Haig 2004), or control of partner mating rate (Engel et al. 2016), yet how these types of power differences influence parental negotiations is still an open question. Combining our results with empirical tests of alternative models will further improve our understanding of how parents resolve conflict over care, ultimately helping to explain empirical patterns of care within and among species.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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DATA ACCESSIBILITY

Analyses reported in this article can be reproduced using the data provided by Barbasch et al. (2020).

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