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# Cooperation and the common good

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In this paper, we draw the attention of biologists to a result from the economic literature, which suggests that when individuals are engaged in a communal activity of benefit to all, selection may favour cooperative sharing of resources even among non-relatives. Provided that group members all invest some resources in the public good, they should refrain from conflict over the division of these resources. The reason is that, given diminishing returns on investment in public and private goods, claiming (or ceding) a greater share of total resources only leads to the actor (or its competitors) investing more in the public good, such that the marginal costs and benefits of investment remain in balance. This cancels out any individual benefits of resource competition. We illustrate how this idea may be applied in the context of biparental care, using a sequential game in which parents first compete with one another over resources, and then choose how to allocate the resources they each obtain to care of their joint young (public good) versus their own survival and future reproductive success (private good). We show that when the two parents both invest in care to some extent, they should refrain from any conflict over the division of resources. The same effect can also support asymmetric outcomes in which one parent competes for resources and invests in care, whereas the other does not invest but refrains from competition. The fact that the caring parent gains higher fitness pay-offs at these equilibria suggests that abandoning a partner is not always to the latter's detriment, when the potential for resource competition is taken into account, but may instead be of benefit to the 'abandoned' mate.

## 1. Introduction

The theoretical literature on the evolution of animal cooperation features many public goods games, in which individuals face a trade-off between investing in some public good of value to all versus investing in their own private good [1–5]. Typically, these models yield inefficient equilibria, at which players invest less in the public good than would maximize mean fitness, as each individual 'free-rides' on the efforts of others. Many biological modelling studies explore mechanisms that might encourage or compel players to invest more in the public good, thus yielding a more efficient outcome [1–5]. Here, instead, we follow economic models [6,7] in focusing on the impact of investment in the public good on conflicts over the distribution of resources.

A well-established result from the economic literature on public goods games, which has received surprisingly little attention within evolutionary biology, is concisely stated in the title of a key paper by Warr [6]: 'The private provision of a public good is independent of the distribution of income'. To expand on this a little, economic models [6,7] suggest that when individuals contribute collectively towards some common goal of benefit to all, they should (under some circumstances at least) refrain from competition over the division of resources or income, because ceding resources to a potential competitor lead to the latter taking on a greater share of the burden of investment in the public good. This finding is relevant to animal cooperation, because it suggests that selection may favour altruistic behaviour towards unrelated individuals because of their involvement in some communal activity that is of collective benefit. Examples might include altruism of one member of a mated pair towards its partner, because this will favour

greater investment by the latter in care of their joint young, or altruism of one group member towards another, because this will favour greater investment by the latter in group defence, predator detection or collective foraging.

Below, we first outline the basic result, and then provide a simple illustration of how it might be applied in a biological context, focusing on the classic Houston–Davies model of biparental care [8], in which two parents work together to raise their joint offspring. We set up a simple instance of the Houston–Davies model, in which each parent has access to a certain amount of resources that can be allocated either to the ‘public good’, i.e. in this case to offspring care, or to their own ‘private good’, i.e. their future survival and reproductive success. We show that, when both parents invest in care to some extent, their levels of investment are uninfluenced by the distribution of resources between them, because claiming (or ceding) a greater share of total resources only leads to a parent (or its mate) investing more in offspring care, such that the marginal costs and benefits of investment remain in balance. To explore the implications of this result for resource conflict, we then extend the game to include a prior step in which the two parents compete with one another over available resources. In this extended, ‘two-step’ sequential game, parents first choose how much effort they will each invest in competition, which determines the division of resources, and then choose how to allocate the resources they each obtain to public versus private good.

## 2. The basic result

We begin by outlining the general result referred to above. Consider interaction among a group of  $n$  individuals, each of whom has access to a limited quantity of some resource, denoted  $x_i$  for individual  $i$ . Each individual must choose how much of this resource,  $y_i$ , to invest in a public good, assuming that it will invest the remainder,  $x_i - y_i$ , in a private good. The model is applicable to many different situations, e.g. we might suppose that the individuals are meerkats choosing how much of their time to invest in scanning for predators (a public good) versus foraging for food (a private good), or in the case  $n = 2$ , on which we will mainly focus in the following sections, the individuals might represent a mated pair choosing how much time or effort to invest in caring for their joint young (a public good) versus foraging for themselves (again, a private good).

Individual  $i$ 's pay-off from the interaction,  $W_i(\mathbf{x}, \mathbf{y})$ , depends upon the vector of initial resource quantities available to each of the  $n$  individuals,  $\mathbf{x}$ , and upon the vector of investment levels  $\mathbf{y}$ , and is given by

$$W_i(\mathbf{x}, \mathbf{y}) = f_i \left( \sum_{j=1..n} y_j \right) + g_i(x_i - y_i). \quad (2.1)$$

It is thus equal to the sum of two terms, the first,  $f_i(\sum_{j=1..n} y_j)$ , a benefit derived from total investment by all group members in the public good, the second,  $g_i(x_i - y_i)$ , a benefit derived from the individual's personal investment in its own private good. We suppose that  $f_i' > 0$  but  $f_i'' < 0$ , so that greater investment in the public good yields increasing benefits, but with diminishing returns; similarly,  $g_i' > 0$  but  $g_i'' < 0$ .

Now, consider a putative evolutionary equilibrium at which each individual invests some non-zero level of resource in the public good, denoted  $y_i^*$  for individual  $i$ . These levels of investment must each satisfy the first-order condition

$$\left. \begin{aligned} \frac{\partial W(\mathbf{x}, \mathbf{y})}{\partial y_i} = 0 \quad \text{for } \mathbf{y} = \mathbf{y}^* \\ \Leftrightarrow f_i' \left( \sum_{j=1..n} y_j^* \right) = g_i'(x_i - y_i^*), \end{aligned} \right\} \quad (2.2)$$

implying that the marginal benefits of greater total investment in the public good must, for each individual, exactly balance the marginal benefits of greater investment in its own private good. Because  $f_i'' < 0$ , and  $g_i'' < 0$  for each individual  $i$ , it follows that for any particular level of total investment in the public good, there is, for each individual, a unique corresponding level of investment in its private good that satisfies this condition. Given a fixed total quantity of resources available to all individuals, there can thus be only one possible stable outcome (at which all individuals invest some non-zero level of resources in the public good), regardless of the distribution of those resources among the individuals in question. Whether one individual has more or less than another to begin with, the total level of investment in the public good that results, and the amount that each retains to invest in its own private good, remain the same. Or, in the economic terminology of Warr [9] ‘the private provision of a public good is independent of the distribution of income’.

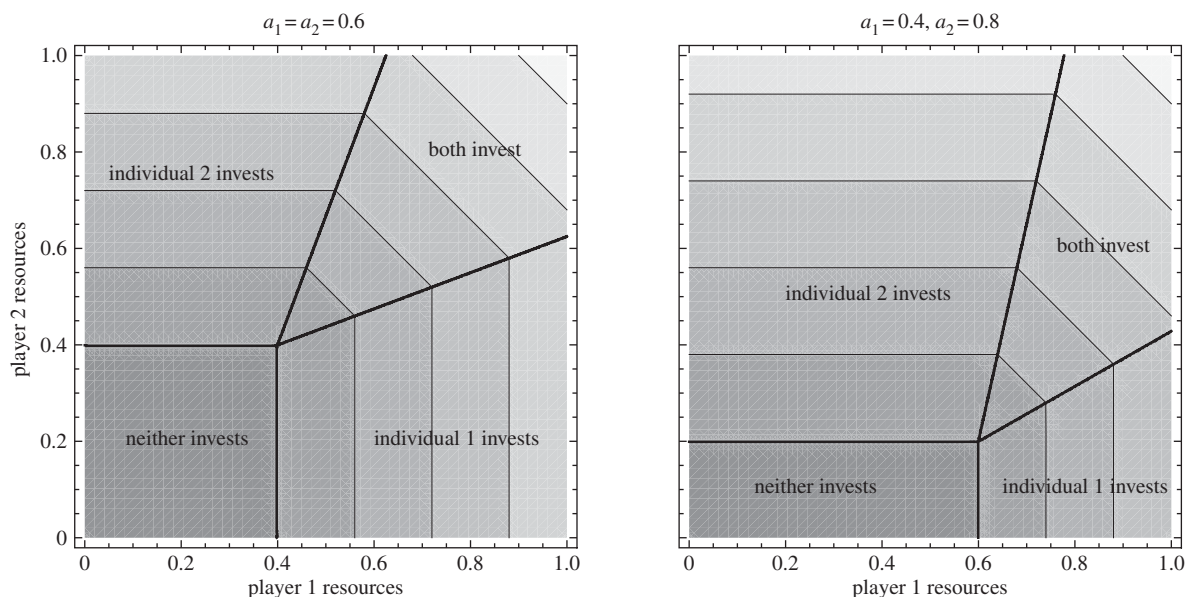
## 3. Application to parental care

We now apply the above approach to a simple example, in which  $n = 2$ , and

$$\left. \begin{aligned} f_i(y_1 + y_2) &= a_i(y_1 + y_2)(1 - \frac{1}{2}(y_1 + y_2)), \\ g_i(x_i - y_i) &= (x_i - y_i)(1 - \frac{1}{2}(x_i - y_i)), \end{aligned} \right\} \quad (3.1)$$

where the parameters  $a_1$  and  $a_2$  (which we assume take values between 0 and 1) specify the value that each of the two individuals place on the public relative to their own private good. We will think of the two individuals, in this illustrative case, as a mated pair choosing how much effort to invest in care of their joint young. The parameters  $a_1$  and  $a_2$  may thus differ because of paternity uncertainty on the part of the male parent, or because one or other has greater prospects for future matings. Note that these particular functions  $f$  and  $g$ , which specify the return on investment in the public good and in each player's private good, attain maxima at one unit of investment; for larger values of their arguments, they have negative slope. We therefore restrict our attention to cases in which the total quantity of resources available is two units or less, ensuring that even when one individual obtains all of the available resources, it pays to invest all of them in either public or private good, and the outcome of the model always falls within the region of positive pay-off slopes.

In this simple case, the stable levels of investment for both individuals,  $y_1^*(\mathbf{x})$  and  $y_2^*(\mathbf{x})$ , each of which depend upon the vector of initial resources,  $\mathbf{x}$  and each of which maximizes the respective individual's pay-off given the other's investment, are given by



**Figure 1.** Regions of parameter space (defined by the resources available to each player,  $x_1$  and  $x_2$ ) in which one or the other individual (or both) invests in the public good. Shading reflects total investment in the public good by both individuals. In the left-hand graph, both place equal value on the public good ( $a_1 = a_2 = 0.6$ ), whereas in the right-hand graph, individual 1 places less value on the public good than does player 2 ( $a_1 = 0.4$ ,  $a_2 = 0.8$ ).

$$y_1^*(\mathbf{x}) = y_2^*(\mathbf{x}) = 0$$

$$y_1^*(\mathbf{x}) = 0, y_2^*(\mathbf{x}) = \frac{x_2(1-a_2)}{1+a_2}$$

$$y_1^*(\mathbf{x}) = \frac{x_1 - (1-a_1)}{1+a_1}, y_2^*(\mathbf{x}) = 0$$

$$y_1^*(\mathbf{x}) = \frac{(1+a_2)(x_1 - (1-a_1)) - a_1(x_2 - (1-a_2))}{1+a_1+a_2}$$

$$y_2^*(\mathbf{x}) = \frac{(1+a_1)(x_2 - (1-a_2)) - a_2(x_1 - (1-a_1))}{1+a_1+a_2}$$

$$\text{for } x_1 \leq 1-a_1, x_2 \leq 1-a_2$$

$$\text{for } x_1 \leq 1 - \frac{a_1(2-x_2)}{1+a_2}, x_2 > 1-a_2$$

$$\text{for } x_1 > 1-a_2, x_2 \leq 1 - \frac{a_2(2-x_1)}{1+a_1}$$

$$\text{for } x_1 > 1-a_1, x_2 > 1-a_2$$

$$\text{for } x_1 > 1-a_1, x_2 > 1-a_2$$

as illustrated in figure 1. From figure 1, one can see that when both individuals have too few resources, neither invests in the public good. Conversely, when both have plenty of resources, both invest. Finally, when the disparity in resources between the two is large, only the player with more resources invests in the public good. As can also be seen from figure 1, when the two individuals differ in the value they place on the public relative to their private good, the player who values the former more is, unsurprisingly, more likely to invest in it.

While the above results are predictable, we can also see from the contour lines in figure 1 that within the zone in which both individuals invest in the public good, total investment ( $y_1^*(\mathbf{x}) + y_2^*(\mathbf{x})$ ), which is given by

$$y_1^*(\mathbf{x}) + y_2^*(\mathbf{x}) = \frac{x_1 + x_2 - (1-a_1) - (1-a_2)}{1+a_1+a_2}, \quad (3.2)$$

depends only on the total quantity of resources ( $x_1 + x_2$ ) available to both individuals, regardless of how these resources are divided between them. This is further illustrated in figure 2, which also shows that each individual's investment in its own private good is likewise uninfluenced by the division of resources. A shift in the initial allocation of resources leads to an equivalent shift in investment in the public good, such that the amount each individual retains for investment in its own private good is left unchanged. This result holds even if both individuals place different values on the public good. Under these circumstances, the player that places less value

on the public good retains a larger quantity of resources to invest in its own private good, but this quantity does not change with the initial division of resources, as long as the total quantity available to both individuals remains fixed.

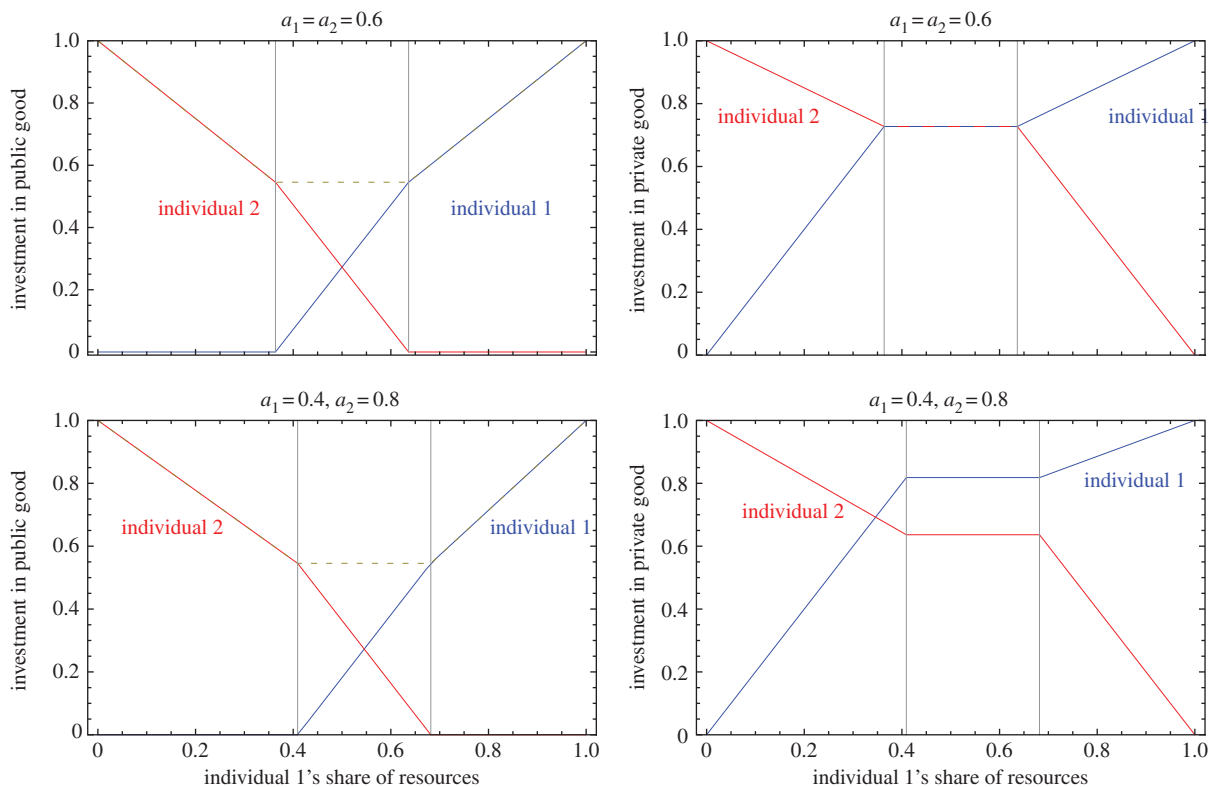
#### 4. Pay-offs and pseudo-relatedness

We have seen that within the region of parameter space in which both individuals invest in the public good, the division of resources does not affect the outcome (in terms of levels of investment by each player in public good and private good). Consequently, within this zone, neither individual should contest resource ownership, because yielding additional resources to the other will merely lead to the latter investing more in the public good, whereas the focal individual invests less, cancelling out any personal costs or benefits. This holds true, regardless of differences between the two individuals in the value they place on the public good, provided that both invest in it to some degree.

We can capture the above effect through calculation of a 'pseudo-relatedness' measure, given by

$$\tilde{r}_{ij} = \frac{\partial W_i(\mathbf{x}, \mathbf{y}^*(\mathbf{x})) / \partial x_j}{\partial W_i(\mathbf{x}, \mathbf{y}^*(\mathbf{x})) / \partial x_i}, \quad (4.1)$$

where  $\mathbf{y}^*(\mathbf{x})$  denotes the vector of stable levels of investment in the public good, given the vector of resources  $\mathbf{x}$ . Here,  $\tilde{r}_{ij}$ , the pseudo-relatedness of individual  $j$  to individual  $i$ ,



**Figure 2.** Investment by individual 1 (blue) and 2 (red) in public (left column) and private (right column) goods, given a fixed total quantity of resources ( $x_1 + x_2 = 2$ ), as one varies the fraction of those resources available to individual 1 rather than to individual 2. Dotted line in left column denotes total investment by both individuals in the public good. In the top panels, both place equal value on the public good ( $a_1 = a_2 = 0.6$ ), whereas in the bottom panels, individual 1 places less value on the public good than does player 2 ( $a_1 = 0.4, a_2 = 0.8$ ). Vertical grey lines demarcate zones that yield qualitatively different outcomes.

expresses the relative marginal benefit (or cost) that individual  $i$  derives from an increase (or decrease) in individual  $j$ 's resources compared with an increase (or decrease) in its own resources, taking into account the impact that any such changes will have on levels of investment in public versus private good. We use the term 'pseudo-relatedness' by analogy with models of kin selection [10–13]. Hamilton's rule tells us that an act that confers a (small) benefit  $b$  on a recipient at a (small) cost  $c$  to the actor will be favoured by selection provided that  $r b - c > 0$ , where  $r$  denotes the relatedness of the recipient to the actor [10]. Similarly, in our model, an act that confers a (small) gain in resources  $b$  on the recipient  $j$  at a (small) cost in resources  $c$  to the actor  $i$  will be favoured provided that  $\tilde{r}_{ij} b - c > 0$ , when we take into account the impact that this act will have on levels of investment in the public good (see §5).

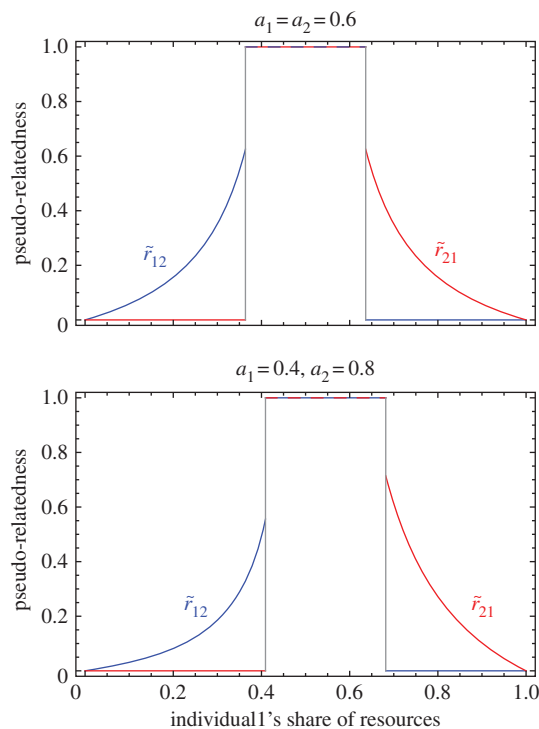
The precise value of  $\tilde{r}_{ij}$  changes across the parameter space of the model as illustrated in figure 3. From figure 3, we see that within the region in which both individuals invest in the public good, the pseudo-relatedness of each to the other is equal to unity, reflecting their indifference over the division of resources. When neither player invests in the public good, the pseudo-relatedness of each to the other is equal to zero, because within this region of parameter space, neither gains anything from an increase in the other's resources, which are all invested in its own private good. When one player invests in the public good, but the other does not, the result is asymmetric pseudo-relatedness. The investor does not gain from an increase in the non-investor's resources, so that the pseudo-relatedness of the latter to the

former is equal to zero. The non-investor, by contrast, does gain from an increase in the investor's resources, because some of that increase will be invested in the public good, leading to a positive pseudo-relatedness of the investor to the non-investor. The precise value of this non-zero pseudo-relatedness, however, depends upon the fraction of any extra resources that the investor will devote to public rather than to private good, which changes with the model parameters.

## 5. Conflict over resources

To see how pseudo-relatedness between players can influence competition over resources, we extend our example to include an explicit model of conflict resolution. We suppose that some total quantity  $T$  of resources is available, over which the two individuals may compete, before engaging in the public good game described in §4, in which each chooses how much of the resources it obtained in the competition phase to invest in public versus private good. During the competition step, each individual must choose some level of competitive effort, denoted  $u_i$  for player  $i$ . Competition is costly and reduces the total quantity of resources available for investment, but at the same time, the share of those remaining resources that an individual obtains increases with the difference between its own competitive effort and that of its competitor. Specifically, we shall assume that the pay-off in terms of resources to individual  $i$  is given by

$$V_i(\mathbf{u}) = T(1 - u_i - u_j)\left(\frac{1}{2} + u_i - u_j\right), \quad (5.1)$$



**Figure 3.** ‘Pseudo-relatedness’ of individual 2 to individual 1,  $\tilde{r}_{12}$  (blue), and of individual 1 to individual 2,  $\tilde{r}_{21}$  (red), given a fixed total quantity of resources ( $x_1 + x_2 = 2$ ), as one varies the fraction of those resources available to individual 1 rather than to individual 2. In the top panel, both place equal value on the public good ( $a_1 = a_2 = 0.6$ ), whereas in the bottom panel, individual 1 places less value on the public good than does player 2 ( $a_1 = 0.4, a_2 = 0.8$ ). Vertical grey lines demarcate zones that yield qualitatively different outcomes.

where  $\mathbf{u}$  is the vector of competitive effort levels, of which element  $u_i$  denotes the focal individual’s competitive effort and  $u_j$  that of its partner.

In the absence of any opportunity to invest in the public good, each individual would do best simply to maximize the amount of resources it obtains from competition, yielding a unique equilibrium at which  $u_1^* = u_2^* = 1/4$  (at which each individual’s competitive effort maximizes its resource pay-off given the other’s behaviour). But because we do allow for the possibility of investment in the public good, an individual’s fitness pay-off depends not only on the quantity of resources it obtains from competition, but possibly also on the quantity its partner obtains, because these quantities determine their subsequent levels of investment in public versus private goods. Taking these subsequent investment decisions into account, the fitness pay-off to player  $i$ , given the vector of competitive effort levels  $\mathbf{u}$ , is given by

$$U_i(\mathbf{u}) = W_i(\mathbf{V}(\mathbf{u}), \mathbf{y}^*(\mathbf{V}(\mathbf{u}))), \quad (5.2)$$

where  $\mathbf{V}$  denotes the vector of resources obtained from competition, and  $\mathbf{y}^*$  the vector of resulting levels of investment in the public good. At an (subgame perfect) equilibrium, the levels of competitive effort  $\mathbf{u}^*$  must (assuming that both are non-zero) satisfy

$$\begin{aligned} U_1(u_1^*, u_2^*) &\geq U_1(u_1', u_2^*) \quad \text{for all } u_1', \quad \text{and} \\ U_2(u_1^*, u_2^*) &\geq U_2(u_1^*, u_2') \quad \text{for all } u_2', \end{aligned} \quad (5.3)$$

which implies that, for each individual  $i$ ,

$$\frac{\partial U_i(\mathbf{u})}{\partial u_i} = 0 \quad \text{for } \mathbf{u} = \mathbf{u}^*. \quad (5.4)$$

Moreover, equation (5.4) may, as suggested in §4, be written in terms of the ‘pseudo-relatedness’ between the two individuals, as follows

$$\left. \begin{aligned} \frac{\partial U_i(\mathbf{u})}{\partial u_i} &= \frac{\partial W_i(\mathbf{V}(\mathbf{u}), \mathbf{y}^*(\mathbf{V}(\mathbf{u})))}{\partial u_i} = 0 \\ &\Leftrightarrow \frac{\partial W_i(\mathbf{V}(\mathbf{u}), \mathbf{y}^*(\mathbf{V}(\mathbf{u})))}{\partial V_i} \frac{\partial V_i}{\partial u_i} + \frac{\partial W_i(\mathbf{V}(\mathbf{u}), \mathbf{y}^*(\mathbf{V}(\mathbf{u})))}{\partial V_j} \frac{\partial V_j}{\partial u_i} = 0 \\ &\Leftrightarrow \frac{\partial V_i}{\partial u_i} + \left( \frac{\partial W_i(\mathbf{V}(\mathbf{u}), \mathbf{y}^*(\mathbf{V}(\mathbf{u})))}{\partial W_i(\mathbf{V}(\mathbf{u}), \mathbf{y}^*(\mathbf{V}(\mathbf{u})))} \right) \frac{\partial V_i}{\partial u_i} = \frac{\partial V_i}{\partial u_i} + \tilde{r}_{ij} \frac{\partial V_j}{\partial u_i} = 0, \end{aligned} \right\} \quad (5.5)$$

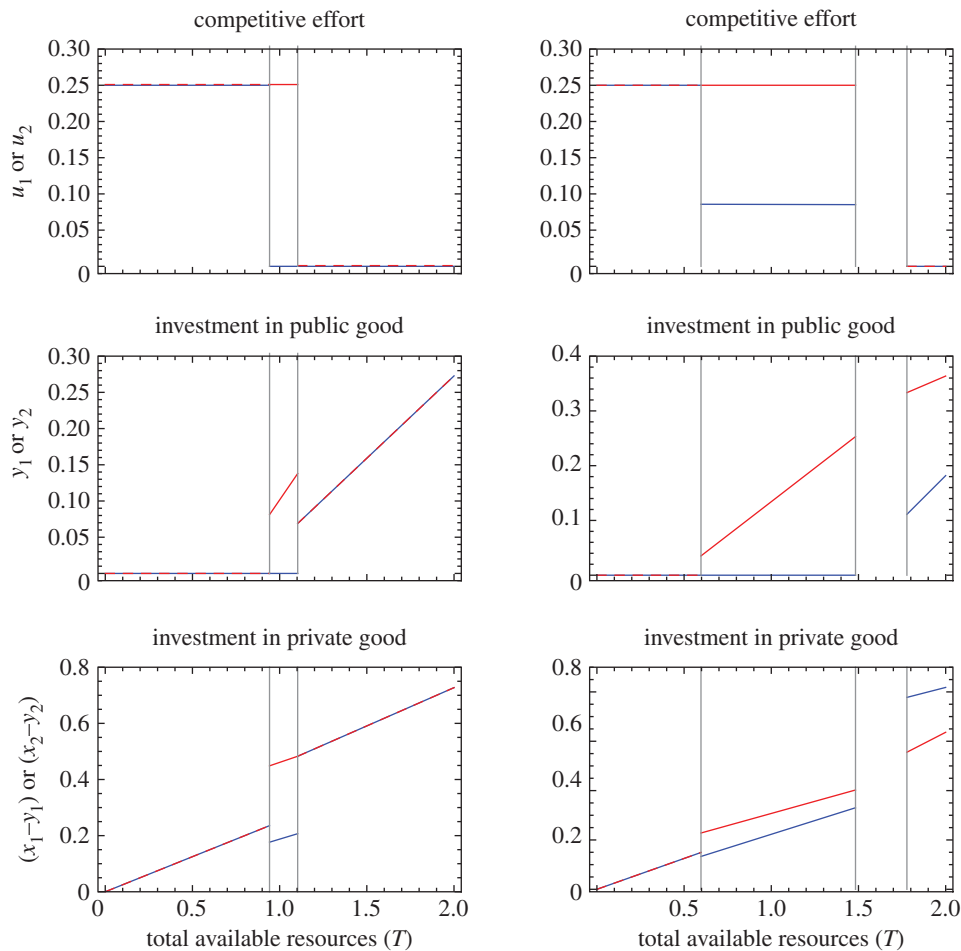
where  $u_i$  and  $V_i$  denote the focal individual’s competitive effort and resulting quantity of resources obtained from competition, and  $u_j$  and  $V_j$  the equivalent values for its partner.

Note, however, that equations (5.4) and (5.5), while necessary for local stability of the equilibrium, are not sufficient to guarantee global stability as does condition (5.3). The reason is that (5.4) and (5.5), and our measure of pseudo-relatedness, focus only on the impact of marginal changes in the quantities of resource obtained by both players. At equilibrium, the marginal costs and benefits of changes in competitive effort must cancel out, but this is not sufficient to guarantee that one or the other individual cannot gain from a larger change in competitive effort, particularly, because such large changes may shift the outcome from one region of parameter space to another, qualitatively altering the outcome. For instance, we have seen that when both individuals invest in the public good, there is no conflict over resource division, and each should therefore refrain from any investment in competition. Yet such an equilibrium might be globally unstable if a sufficiently large increase in one individual’s competitive effort led to an outcome at which one or both players ceased to invest in the public good. In the results discussed in the following, and shown in figure 4, we therefore restrict our attention to equilibria that satisfy (5.3) and are globally stable.

The extended model yields several different types of equilibria, as illustrated in figure 4.

When the total quantity of resources  $T$  is sufficiently small, the outcome described above at which  $u_1^* = u_2^* = 1/4$  remains stable, because the quantity of resources that each player obtains is small enough that neither chooses to invest in the public good at the second stage ( $y_1^* = y_2^* = 0$ ). Under these circumstances, the ‘pseudo-relatedness’ between the two is equal to zero, because neither gains from yielding resources to the other, and each competes as hard as they would do even without the opportunity for investment in the public good.

When the quantity of resources is sufficiently large, by contrast, the extended model yields an equilibrium at which neither player competes at all, and  $u_1 = u_2 = 0$ . This outcome is stable, because each player obtains sufficient resources that both choose to invest in the public good at the second stage, leading to a ‘pseudo-relatedness’ between the two that is equal to unity. There is no competition over resources under these circumstances, because any increase (or decrease) in one individual’s share of resources will be cancelled out by an increase (or decrease) in its level of investment in the public good.



**Figure 4.** Equilibrium levels of competitive effort (top row), investment in the public good (middle row) and in their own private good (bottom row) by players 1 (blue lines) and 2 (red lines), as a function of total available resources  $T$ , when both place equal value on the public good ( $a_1 = a_2 = 0.6$ ; left column), and when individual 1 places less value on the public good than does player 2 ( $a_1 = 0.4$ ,  $a_2 = 0.8$ ; right column). Vertical grey lines demarcate zones that yield qualitatively different outcomes. Note that when both players place equal value on the public good ( $a_1 = a_2 = 0.6$ ; left column), the intermediate zone that yields asymmetric outcomes features two alternative, ‘mirror-image’ equilibria; only one is shown here. When individual 1 places less value on the public good than does player 2 ( $a_1 = 0.4$ ,  $a_2 = 0.8$ ; right column), only one asymmetric equilibrium exists for any given value of  $T$ , as shown; there is also a zone in which the model yields no globally stable equilibrium.

Finally, for intermediate levels of resource availability,  $T$ , the model may yield one or two alternative, asymmetrical equilibria, at which one individual competes strongly for resources, and goes on to invest in the public good, whereas the other competes less strongly or refrains from competition altogether, and does not invest in the public good. In the case in which both players place equal value on the public good ( $a_1 = a_2 = 0.6$ ; left-hand graph in figure 4), there are two equilibria that are mirror images of one another and are stable over the same parameter range—either player 1 competes and invests in the public good, whereas player 2 does not ( $u_1^* = 1/4$ ,  $y_2^* > 0$ ,  $u_2^* = 0$ ,  $y_1^* = 0$ ) or vice versa. The stability of these equilibria reflects the asymmetry in ‘pseudo-relatedness’ between the two individuals when one invests in the public good, but the other does not. The non-investor refrains from competition, because a reduction in its partner’s resources would reduce the amount that the latter invests in the public good (to the non-investor’s disadvantage); by contrast, the investor competes, because a reduction in its non-investing partner’s resources has no impact on provision of the public good.

When the two players differ in the value that they place on the public good, the two alternative equilibria described above are no longer stable over the same parameter range.

Instead, the equilibrium in which it is the player who places greater value on the public good that competes more strongly and invests in it, and the player who places less value that refrains from doing so, is stable over a wider range of parameter values than the alternative (in which it is the player who places less value on the public good that competes more strongly and invests in it, and the player who places more value that refrains from doing so). If the difference in the fitness functions of the two individuals is great enough, then one equilibrium may be lost altogether, as in the right-hand graph of figure 4 ( $a_1 = 0.4$ ;  $a_2 = 0.8$ ). In the asymmetric case, furthermore, there are regions of parameter space in which there is no stable equilibrium at all (see figure 4 again).

One surprising feature of these asymmetric equilibria is that it is typically the individual that competes and goes on to invest in the public good that obtains the greater fitness pay-off than the individual that neither competes nor invests. If one focuses on investment alone, then it might appear that the non-investing parent is free-riding on its partner’s efforts, as in models of parental care in which one parent leaves the young to be looked after by its partner alone. But, when we take into account competition over resources, the actions of the non-investing parent turn out to be beneficial for

both its partner and their offspring, who gain from the non-investor's reduced competitive effort.

## 6. Discussion

Our simple example shows how, even when free-riding leads to under-investment in the public good, selection can favour efficient, conflict-free division of resources (provided that all individuals invest in the public good at least to some extent). Changes in resource distribution lead to changes in investment that cancel out any individual costs or benefits. Consequently, there is nothing to be gained by competing for a larger share of available resources, leading to efficient outcomes with regard to resource division. This result holds true even when individuals differ in the degree to which they benefit from investment in the common good. Those who gain more from such investment will then invest more, whereas those who gain less will invest less and free-ride to a greater extent on the efforts of others, but all are nevertheless still indifferent to the distribution of resources.

There has been much discussion recently in the biological literature of transitions between levels of selection, with models exploring the circumstances under which selection might come to favour traits and behaviours that maximize group rather than individual fitness [9,14]. A frequent assumption in these discussions is that the same processes that favour cooperation in one behavioural context will favour cooperation in all. If high relatedness, for instance, favours cooperation over investment in the public good, then it will also favour cooperation over the division of resources. The economic models we have discussed, however, suggest that cooperation and conflict may coexist within the same group. Even when individuals seek to free-ride on one another's investments, they may nevertheless achieve a high degree of coordination and cooperation over the division of resources. In other words, group-level adaptation is possible with respect to some aspects of behaviour, even if conflict leads to inefficient outcomes with respect to others.

The situation we have considered here might be described as an instance of pseudo-reciprocity, in which one individual invests in another to acquire or enhance benefits that are a side-effect of behaviour by the latter that is of immediate, selfish benefit even in the short-term [15–17]. In classic models of reciprocity, such as the repeated Prisoner's Dilemma, each individual's decision to cooperate in any given 'round' always entails an immediate, short-term cost and hence relies on the promise of reciprocation (or the promise of punishment) in the future. Consequently, if the interaction only lasts a fixed number of rounds, then cooperation cannot persist. In the final, ultimate round, there can be no future interaction, and hence there is no incentive to cooperate, so that individuals do best defect, regardless of their partner's past behaviour. This removes any incentive to cooperate in the previous, penultimate round and so on back to the start of the interaction. By contrast, in our model, an individual that acquires more resources does best to invest more in the public good simply because of the diminishing returns derived from its alternative private good. Consequently, conflict-free division of resources during the first round is stable, even though behaviour during the second (and final) 'round' is uninfluenced by the threat or promise of future interaction. Individuals do best to refrain from competition over

resources during the first 'round', because claiming (or ceding) a greater share only leads, via its impact on pay-offs in the following round, to the actor (or its competitors) investing more in the public good, cancelling out any individual benefits of resource competition.

We have interpreted our results in terms of 'pseudo-relatedness', a measure of the extent to which a focal individual benefits from an increase in others' resources (compared with an increase in its own), which we show can be used to identify locally stable equilibria in the competition over resources. This bears some similarity to Eshel & Shaked's [18] partnership coefficient, and Roberts' [19] measure of interdependence, which quantify the extent to which one individual's fitness depends on that of another. Those measures, however, focus on the benefits that a focal individual stands to gain from an increase in the survival prospects of a potential partner, ensuring that it is more likely to be present in future interactions. By contrast, we focus the benefit that a focal individual derives from a change in the partner's investment behaviour. Refraining from competition, in our model, does not serve to increase the chances of subsequent interaction with the partner (as we do not consider mortality between competition and investment stages); rather, it induces the partner to invest more in the public good. This also distinguishes our analysis from models of group augmentation, in which a focal individual benefits from helping others to raise additional young because of the advantages it and/or other group members derive from the resulting increase in group size [20].

It is also worth noting that our analysis assumes that individuals are able to flexibly adjust their investment in the public good on a behavioural time-scale in response to changes in the distribution of resources (with the further implication that they are able to determine how resources are distributed between themselves and others), but that competitive effort cannot similarly be adjusted in response to investment. In other words, in our sequential model, competition comes first and investment second. In the context of parental care, this is most appropriate for capital breeders, which use stored energy for reproduction, but seems simplistic as a model of investment in income breeders, which use energy acquired during the reproductive period rather than use stored energy [21]. A more realistic approach would allow individuals to simultaneously adjust both competitive effort and investment in response to one another's decisions, with the outcome of the model reflecting the response rules adopted by each player. This kind of approach has been adopted in models of negotiation in parental care and other cooperative interactions [22–27], which have also explored how flexible adjustment of investment in group-beneficial behaviour can alter the outcome of evolutionary games. However, such models to date have focused on behavioural responsiveness within a single behavioural context, individuals adjusting their own level of investment in response to that of others, whereas we emphasize the impact of flexibility in one context (investment in the public good) on behaviour in another (competition over resources). Simultaneous application of the negotiation approach to both competition and investment is beyond the scope of this paper, and remains an interesting possibility for future studies.

While joint investment in a public good can inhibit competition over resource division, substantial asymmetries in resources (or in the value that individuals place on the

public good) can lead to one or more individuals ‘dropping out’ of such investment. The result can be an asymmetrical equilibrium at which some individuals free-ride entirely on others’ investments, but at the same time compete less strongly for resources because of the benefits they gain by ceding resources to those who do invest. In the context of biparental care, for instance, our simple model suggests the possibility of an equilibrium at which only one parent cares, but at which the other refrains from competition (or competes less strongly) in order that the caring parent has sufficient resources to invest substantially in the young. What is striking about this kind of outcome is that the caring parent may enjoy greater personal fitness gains than the non-caring parent. Classical models of parental care have explored under what circumstances biparental care can break down and one parent be left to care for the young alone [28–30], but they have generally done so under the assumption that each parent stands to gain by leaving, and that the individual that remains does so because he or she has been caught in a ‘cruel bind’. Departure, in other words, is interpreted as the ‘selfish’ or ‘exploitative’ option. By contrast, when resource competition is taken into account, the model suggests that departure may actually be of benefit to the caring parent, because it frees up resources for the latter and for the young.

Support for the above notion comes from a recent study of parental care in burying beetles [31], which showed that females indeed benefit from male desertion prior to offspring independence. Forcing males to stay until larvae dispersed

resulted in shorter subsequent female lifespans than did earlier male removal, even when controlling for mass of the brood and of the carcass on which they are fed, and for maternal investment. The authors of the study suggest that male departure allows females to recoup the costs of care by feeding from the carcass themselves, whereas the presence of a male throughout the breeding attempt prevents this, perhaps through competition for food. Furthermore, they cite a previous study showing that male desertion occurred sooner on smaller carcasses [32], matching our model’s prediction that joint investment in care is stable when resources are abundant, but breaks down when less is available. The fact that burying beetles rely on a limited food supply, the carcass on which both parents and offspring feed, may mean that resource competition is particularly pronounced in this case. It is not clear, therefore, whether such clear-cut benefits of desertion are likely to be common in other species with different forms of care. However, we suggest that expanding the focus of studies to consider the benefits as well as the costs of ‘abandoning’ offspring may offer new insights into the evolution of parental care more generally.

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**Data accessibility.** No data were used in this paper.

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**Competing interests.** We have no competing interests.

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## References

- Motro U. 1991 Co-operation and defection: playing the field and the ESS. *J. Theor. Biol.* **151**, 1145–1154. (doi:10.1016/S0022-5193(05)80358-3)
- Parker GA, Royle NJ, Hartley IR. 2002 Intrafamilial conflict and parental investment: a synthesis. *Phil. Trans. R. Soc. Lond. B* **357**, 295–307. (doi:10.1098/rstb.2001.0950)
- Foster KR. 2004 Diminishing returns in social evolution: the not-so-tragic commons. *J. Evol. Biol.* **17**, 1058–1072. (doi:10.1111/j.1420-9101.2004.00747.x)
- Reeve HK, Hölldobler B. 2007 The emergence of a superorganism through intergroup competition. *Proc. Natl Acad. Sci. USA* **104**, 9736–9740. (doi:10.1073/pnas.0703466104)
- Frank SA. 2010 A general model of the public goods dilemma. *J. Evol. Biol.* **23**, 1245–1250. (doi:10.1111/j.1420-9101.2010.01986.x)
- Warr PG. 1983 The private provision of a public good is independent of the distribution of income. *Econ. Lett.* **13**, 207–211. (doi:10.1016/0165-1765(83)90087-3)
- Bergstrom T, Blume L, Varian H. 1986 On the private provision of public goods. *J. Publ. Econ.* **29**, 25–49. (doi:10.1016/0047-2727(86)90024-1)
- Houston AI, Davies NB. 1985 The evolution of cooperation and life history in the dunnoek, *Prunella modularis*. In *Behavioural ecology: ecological consequences of adaptive behaviour* (eds RM Sibly, RH Smith), pp. 471–487. Oxford, UK: Blackwell Scientific.
- Akçay E, Van Cleve J. 2012 Behavioral responses in structured populations pave the way to group optimality. *Am. Nat.* **179**, 257–269. (doi:10.1086/663691)
- Hamilton WD. 1964 The genetical evolution of social behaviour. I and II. *J. Theor. Biol.* **7**, 1–52. (doi:10.1016/0022-5193(64)90038-4)
- Charnov EL. 1977 An elementary treatment of the genetical theory of kin-selection. *J. Theor. Biol.* **66**, 541–550. (doi:10.1016/0022-5193(77) 90301-0)
- Lehmann L, Keller L. 2006 The evolution of cooperation and altruism: a general framework and a classification of models. *J. Evol. Biol.* **19**, 1365–1376. (doi:10.1111/j.1420-9101.2006.01119.x)
- Rodrigues AMM, Gardner A. 2013 Evolution of helping and harming in heterogeneous groups. *Evolution* **67**, 2284–2298. (doi:10.1111/evo.12110)
- Gardner A, Grafen A. 2009 Capturing the superorganism: a formal theory of group adaptation. *J. Evol. Biol.* **22**, 659–671. (doi:10.1111/j.1420-9101.2008.01681.x)
- Connor RC. 1986 Pseudo-reciprocity: investing in mutualism. *Anim. Behav.* **34**, 1562–1566. (doi:10.1016/S0003-3472(86)80225-1)
- Leimar O, Connor RC. 2003 By-product benefits, reciprocity, and pseudoreciprocity in mutualism. In *Genetic and cultural evolution of cooperation* (ed. P Hammerstein), pp. 203–222. Cambridge, MA: MIT Press.
- Connor RC. 2007 Invested, extracted and byproduct benefits: a modified scheme for the evolution of cooperation. *Behav. Proc.* **76**, 109–113. (doi:10.1016/j.beproc.2007.01.014)
- Eshel I, Shaked A. 2001 Partnership. *J. Theor. Biol.* **208**, 457–474. (doi:10.1006/jtbi.2000.2232)
- Roberts G. 2005 Cooperation through interdependence. *Anim. Behav.* **70**, 901–908. (doi:10.1016/j.anbehav.2005.02.006)
- Kingma SA, Santema P, Taborisky M, Komdeur J. 2014 Group augmentation and the evolution of cooperation. *Trends Ecol. Evol.* **29**, 476–484. (doi:10.1016/j.tree.2014.05.013)
- Jönsson KI. 1997 Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* **78**, 57–66. (doi:10.2307/3545800)
- McNamara JM, Gasson CE, Houston AI. 1999 Incorporating rules for responding into evolutionary games. *Nature* **401**, 368–371. (doi:10.1038/43869)
- McNamara JM, Houston AI, Barta Z, Osorno J-L. 2003 Should young ever be better off with one parent than with two? *Behav. Ecol.* **14**, 301–310. (doi:10.1093/beheco/14.3.301)
- Johnstone RA, Hinde CA. 2006 Negotiation over offspring care—how should parents respond to each other’s efforts? *Behav. Ecol.* **17**, 818–827. (doi:10.1093/beheco/arl009)



25. Johnstone RA. 2011 Load lightening and negotiation over offspring care in cooperative breeders. *Behav. Ecol.* **22**, 436–444. (doi:10.1093/beheco/arq190)
26. Akçay E, Simms EL. 2011 Negotiation, sanctions, and context dependency in the legume–rhizobium mutualism. *Am. Nat.* **178**, 1–14. (doi:10.1086/659997)
27. Van Cleeve J, Akçay E. 2014 Pathways to social evolution: reciprocity, relatedness and synergy. *Evolution* **68**, 2245–2258. (doi:10.1111/evo.12438)
28. Maynard Smith J. 1977 Parental investment: a prospective analysis. *Anim. Behav.* **25**, 1–9. (doi:10.1016/0003-3472(77)90062-8)
29. Lazarus J. 1990 The logic of mate desertion. *Anim. Behav.* **39**, 672–684. (doi:10.1016/S0003-3472(05)80378-1)
30. Yamamura N, Tsuji N. 1993 Parental care as a game. *J. Evol. Biol.* **6**, 103–127. (doi:10.1046/j.1420-9101.1993.6010103.x)
31. Boncoraglio G, Kilner RM. 2012 Female burying beetles benefit from male desertion: sexual conflict and counter-adaptation over parental investment. *PLoS ONE* **7**, e31713. (doi:10.1371/journal.pone.0031713)
32. Bartlett J. 1988 Male mating success and parental care in *Nicrophorus vespilloides* (Coleoptera: Silphidae). *Behav. Ecol. Sociobiol.* **23**, 297–303. (doi:10.1007/BF00300576)