Parent–offspring conflict: the full-sib–half-sib fallacy

C. M. Lessells^{1*} and G. A. Parker²

¹*Netherlands Institute of Ecology, Boterhoeksestraat 22, PO Box 40, 6666 ZG Heteren, The Netherlands*

²*Population Biology Research Group, School of Biological Sciences, Nicholson Building, University of Liverpool, Liverpool L69 3BX, UK*

R. L. Trivers used Hamilton's rule regarding the evolution of altruistic behaviour to demonstrate the occurrence of parent–offspring conflict and concluded that this would be more severe when future offspring were half siblings rather than full siblings of the offspring currently receiving investment. Here we show that Trivers' formulation applies in a limited range of circumstances and offer an alternative formulation that is universally applicable. Under this formulation the optimal investment from the offspring's point of view in species with uniparental care and, hence, the extent of parent–offspring conflict depends on the cost of the caring parent's investment to the future fitness of the non-caring parent.

Keywords: parent–offspring conflict; Hamilton's rule; half siblings; full siblings

1. INTRODUCTION

Trivers (1974) revolutionized evolutionary biology when he pointed out that parent–offspring relationships are not, as hitherto thought, cooperative relationships in which the evolutionary interests of both parties coincide but are instead battlefields on which conflict resulting from genetic asymmetries between the different parties is played out. He considered the case of one parent caring alone for a single offspring in order to demonstrate the occurrence of parent–offspring conflict over the amount of parental investment. He argued that, if the benefit to the caring parent in terms of increased survival of the current young (B) and cost to the caring parent in terms of decreased production of future young (C) are expressed as functions of the amount of parental investment (i), then the optimal investment for the caring parent (P) occurs where $B - C$ is a maximum, that is where

$$B' = C', \quad (1)$$

where a prime indicates the first derivative with respect to i (graphically, the slope of the B or C curve plotted against i ; figure 1a). (In addition, for equation (1) to give the maximum value, rather than a minimum or stationary value, the second derivative must be negative (see Appendix A). Also, we assume throughout that the expected number of young raised is an adequate measure of fitness. When this is not the case, C and B must be calculated in other units.) However, the current offspring is related to the future offspring of the caring parent by a factor r , so that the cost to the current offspring of any investment should be weighted by that factor (Hamilton 1964) and the offspring's optimal investment received occurs where $B - rC$ is a maximum, that is where

$$B' = rC', \quad (2)$$

(figure 1a). If, as seems biologically reasonable, the benefit curve shows diminishing fitness returns and the cost curve is linear or accelerating with respect to the amount of investment, the caring parent's optimum is less than the offspring's optimum and the difference between the optima increases with decreasing relatedness r (Trivers 1974; Lazarus & Inglis 1986). The latter conclusion is interpreted as implying that parent–offspring conflict should be more severe when future siblings are half rather than full siblings (i.e. when $r = 0.25$ rather than 0.5). Other authors have followed Trivers (1974) in focusing on whether future siblings are full or half siblings in predicting the extent of parent–offspring conflict (Lazarus & Inglis 1986; Clutton-Brock 1991; Clutton-Brock & Godfray 1991; Godfray & Parker 1991; Godfray 1999; but see Parker 1985).

Trivers (1974) did not state explicitly how r should be calculated, nor what other assumptions he made in his formulation of parent–offspring conflict. However, it seems that he intended that the value of r used in calculations for a given species should reflect the average relatedness in the population between current offspring and their future siblings and not any change brought about in this proportion as a result of parental investment ('Other things being equal, species in which different, unrelated males commonly father a female's successive offspring are expected to show stronger... conflict than species in which a female's successive offspring are usually fathered by the same male' (Trivers 1974, p. 252)). Remembering that Trivers (1974) was considering uniparental care, where one sex (the female in his writing) is the caring parent and the other (the male in his writing) is the non-caring parent, we take his writing to imply that

$$r = 0.25(1 + \hat{p}_c), \quad (3)$$

where $\hat{p}_c$ is the proportion for the population of future offspring of caring parents that are full siblings

*Author for correspondence (lessells@cto.nioo.knaw.nl).

Figure 1. (a) Trivers' (1974) model of parent-offspring conflict. When the benefit (B) and cost (C) of parental investment by one parent caring alone are expressed as a function of the amount of investment, the parent's optimum investment (P) occurs where $B - C$ is a maximum. The current offspring is related by r to its future siblings and, therefore, devalues the cost of investment by that amount, so that the offspring's optimum investment occurs when $B - rC$ is a maximum. Trivers (1974) concluded that the offspring's optimum is higher when future siblings are half siblings (offspring's optimum = H ; $r = 0.25$) than when they are full siblings (offspring's optimum = F ; $r = 0.5$). (b) The correct calculation of optimum investment by the parent and offspring takes into consideration the costs to the caring (C_c) and non-caring (C_n) parents separately, in terms of their respective number of future offspring. The caring parent's optimum (P) occurs where $B - C_c$ is a maximum, but now the offspring's optimum (O) occurs where $B - (C_c + C_n)/4$ is a maximum and does not additionally depend on whether future siblings are full or half siblings (see the text). C_n shown here is not a constant proportion of C_c (see the text).

(as opposed to half siblings) of the current offspring (so that $r = 0.25$ when all future offspring are half siblings and 0.5 when all future offspring are full siblings, as Trivers (1974) stated). Moreover, Trivers' formulation clearly implies that the extent of parent-offspring conflict can be predicted from knowledge of the fitness cost of investment to the caring parent and the proportion of full and half siblings among future offspring alone and that no indepen-

dent information about costs to the non-caring parent is needed. Here we show that this is true only in a limited range of circumstances; concentrating on the proportion of future offspring that are full and half siblings may be misleading in other circumstances (see also Parker 1985). We offer an alternative formulation that focuses on the separate costs incurred by the caring and non-caring parents. This formulation is universally applicable, offers a framework that identifies the costs that must be measured in empirical systems in order to predict the extent of parent-offspring conflict and gives rise to new general insights about the extent of parent-offspring conflict.

2. TRIVERS' FORMULATION REAPPRAISED

A problem with Trivers' formulation is revealed when it is reconsidered with costs and benefits expressed in units of 'caring parent's fitness' instead of offspring produced. B is thus the increase in the caring parent's fitness that accrues through the increased survival of the current young and C the decrease in the caring parent's fitness that is caused by decreased production of future young (who happen to be full or half siblings of the current young). The caring parent's optimum again occurs where $B - C$ is a maximum (i.e. $B' = C'$). Because the current offspring is twice as related to itself as the caring parent is to the current offspring, the benefit to the current offspring's fitness through itself is twice as great as the benefit to its caring parent's fitness (i.e. the fitness benefit of investment to the current offspring is $2B$). On the other hand, because the current offspring is only half as related to the caring parent as the caring parent is to itself, the cost to the current offspring's fitness through the caring parent's future reproduction is half the cost to the caring parent (i.e. the fitness cost of investment to the offspring is $0.5C$). The offspring's optimal investment thus occurs where $2B - 0.5C$ is a maximum. This is where $B' = 0.25C'$. In other words, by simply changing the units in which the calculation is made, it apparently no longer matters whether future siblings are full or half siblings; the optimum is always that predicted by Trivers (1974) for half siblings.

The solution to this paradox is that Trivers' calculation ignores the fact that future full siblings are not 50% related via the caring parent, but 25% via each parent. When this is taken into account, it is no longer relevant to ask whether future siblings are usually full or half siblings, but rather what happens to the non-caring parent's future reproduction as a consequence of the caring parent's investment. If future siblings are usually (in the population as a whole) full siblings, but the caring parent pays a survival cost and the other parent remates without any loss of reproductive success if its mate dies, then the current offspring has full siblings replaced by half siblings (i.e. it loses the equivalent of half siblings) rather than losing full siblings. This argument concurs with the calculation based on the caring parent's fitness (i.e. the offspring's optimum is given by $B' = 0.25C'$). Essentially, Trivers' formulation assumes that the non-caring parent is not compensated at all for the full-sibling offspring that it loses as a result of its mate's investment (figure 2a), whereas the formulation based on the caring parent's fitness assumes that it is fully compensated through an

Figure 2. Costs to the non-caring parent of the caring parent's investment. As a result of investment in the current offspring, the expected future reproduction of the caring parent (caring, 1) is reduced by two offspring (offspring outlined with broken lines). The non-caring parent's loss of future fitness through offspring that are full siblings of the current offspring may (a) not be compensated, so the cost to the non-caring parent equals the cost to the caring parent ($C_n = C_c$), (b) be partially compensated by offspring produced with a different caring parent (caring, 2) or (c) be fully compensated by offspring produced with a different caring parent, so there is no cost to the non-caring parent ($C_n = 0$). Which of these occurs will depend on the exact mating system (see the text). Shading of the offspring indicates the parental origin of the offspring's genotype.

increase in half-sibling offspring (figure 2c). For example, suppose that only females invest in offspring that they produce one at a time with the same (non-investing) male. Increased investment by the female causes her to die earlier, so that she produces fewer offspring (two offspring fewer as shown in figure 2). Both the female and male have lost potential future offspring that would have been full siblings of the existing offspring. Under Trivers' formulation, the male is not compensated for this loss and gains no future offspring (figure 2a). In contrast, the formulation based on the caring parent's fitness assumes that he is fully compensated by producing further offspring with another female (figure 2c), although these are half siblings of the existing offspring.

3. COSTS TO THE NON-CARING PARENT OF PARENTAL INVESTMENT BY THE OTHER PARENT

In the first example given in the previous section, the non-caring parent's future reproduction was not damaged by the caring parent's investment because it continues reproduction elsewhere (figure 2c), but this will not always be the case. For instance, if the pair usually remain together when both survive and the female cares and pays a cost in reduced fecundity instead of survival, the male's future reproductive success will be reduced by an amount dependent on the female's fecundity cost and the probability of the pair breeding together again. Similarly, if the female pays a survival cost and the male can remate, but the reproductive success of newly formed pairs is reduced (Scott 1988; Emslie *et al.* 1992), the male's

future reproductive success will also be reduced by the female's parental investment. In the extreme when there is obligate lifelong monogamy in both sexes so that remating is impossible ('true monogamy', an extremely rare phenomenon; Parker 1985), the cost to the non-caring parent will be the same as the cost to the caring parent, as in figure 2a. The costs to the two parents will also be the same if there is obligate lifelong monogamy in the caring sex and the reproductive success of the non-caring parent with other mates is independent of the caring parent's investment (e.g. when females invest by provisioning eggs and mate only once during their lifetime; Parker & Macnair 1978).

The cost to one parent of investment by the other may also vary within superficially homogeneous mating systems. In species where males hold harems, the cost to the father's future reproduction will depend on what limits future harem size. If harem size is determined by the size of the group that the male can control and potential harem members are superabundant then, if the mother dies, the size of the male's future harem will be unaffected, so he will pay no cost. On the other hand, if harem size is limited by the availability of females to coopt into the harem, the cost to the father will be the same as the cost to the mother, because if the mother dies the male's future harem will be one female smaller than it would otherwise have been. It is even possible for the cost to the father to be larger than the cost to the mother if female harem members cooperate in such a way that their individual reproductive success is higher in larger harems (Burt & Trivers 1998).

4. THE CORRECT FORMULATION OF PARENT-OFFSPRING CONFLICT

One way of incorporating the above considerations is to separate the relatedness of offspring with future siblings into components via each of the parents before applying Hamilton's rule. (A similar approach has been suggested by Burt & Trivers (1998) in modelling the conflicts of interest involved in genomic imprinting.) The costs to the caring (C_c) and non-caring (C_n) parents are then considered separately in terms of their respective future offspring. It should be noted that both of these costs result from the investment of the single caring parent and that a reduction in the number of future full siblings of the current offspring contributes to both C_c and C_n . The optimum amount of parental investment for the caring parent (P) then occurs, as before, when $B - C_c$ is a maximum (i.e. when $B' = C'_c$). However, bearing in mind that, when current and future offspring share a parent, their relatedness via that parent is 0.25 whether or not they also have the other parent in common as well, the optimal amount of parental investment for the offspring (O) occurs when $B - 0.25C_c - 0.25C_n$ is a maximum, that is when

$$B' = 0.25(C'_c + C'_n), \quad (4)$$

(see equation (A4) and figure 1b).

Essentially, this formulation accounts for the relationship between the current and future offspring via each parent separately. Thus, the overall cost to the offspring is the product of the number of future offspring lost by each parent and the coefficient of relationship between the current and future offspring via that parent (i.e. 0.25), summed over the two parents (i.e. $0.25(C_c + C_n)$). When the cost involves the loss of a future full sibling, this is treated as the loss of one sibling related by 25% via the caring parent, plus the loss of one sibling related by 25% via the non-caring parent, instead of the more familiar accounting of the loss of one sibling related by 50% via the two parents combined. This method of accounting appears unnecessarily cumbersome at first sight, but has the major advantage of focusing on the information that is needed in empirical studies to assess the extent of conflict. C_c is the cost to the caring parent and is the same as in Trivers' formulation. The new variable is C_n , the cost to the non-caring parent. This is the net reduction in the number of future offspring of the non-caring parent (irrespective of who the other parent of these offspring is) as a result of the caring parent's investment. If the caring parent can remate without cost, this net reduction will be zero. At the other extreme, the cost to the non-caring parent may be as large or larger than the cost to the caring parent (see §3). The important empirical question is how C_n varies with investment: in other words, to what extent the future reproductive output of the non-caring parent is affected by investment by the caring parent.

An alternative formulation involves partitioning the costs into the changes in the number of full siblings (C_f), half siblings via the caring parent ($C_{c,h}$) and half siblings via the non-caring parent ($C_{n,h}$). The caring parent's optimal parental investment is then given by

$$B' = C'_f + C'_{c,h}, \quad (5)$$

and that of the offspring by

$$B' = 0.5C'_f + 0.25(C'_{c,h} + C'_{n,h}), \quad (6)$$

(see Appendix A, equation (A5)). The two formulations given in this section are exactly equivalent (see the appendix). In addition to the advantage explained above, the former is easier to present graphically (figure 1b) and also avoids the need to deal with negative values of $C_{n,h}$ when the non-caring parent is partly or fully compensated for the loss of offspring with the caring parent. What follows refers to the first of the two formulations.

The cost function for the non-caring parent is not necessarily simply a constant proportion (between 0 and 1) of the cost function for the caring parent (see also Burt & Trivers 1998). For example, if females care and pay a fecundity cost at low levels of investment and a survival cost at high levels, males that remain with their mates may suffer a higher cost at lower levels of maternal investment (but in this situation mate fidelity would probably be selected against). Under the biologically realistic assumption that the cost function for the non-caring parent increases monotonically (and the benefit function for the current offspring is, as before, decelerating), a cost to the non-caring parent will reduce the offspring's optimum and, hence, the amount of parent-offspring conflict below that expected without a cost to the non-caring parent. Another important point is that the optimum amount of effort depends on the slope of the cost curves and not the absolute value of the costs. This can have the consequence that a cost to the non-caring parent can reduce the offspring's optimum (and, hence, the extent of parent-offspring conflict) below that predicted by Trivers (1974) when future siblings are full siblings, even when the cost to the non-caring parent is less than that to the caring parent (cf. figure 1a,b). In the extreme case when the non-caring parent's cost curve is more than three times as steep as the caring parent's cost curve at the parental optimum, the offspring will have the same or lower optimum than the parent and parent-offspring conflict will be abolished or reversed. However, while theoretically possible, such a difference in the slopes of the cost curves of the two parents seems biologically implausible.

5. WHEN IS TRIVERS' FORMULATION ADEQUATE?

Our interpretation of Trivers' formulation defining the offspring's optimal parental investment is

$$B' = 0.25(1 + \hat{p}_c)C'_c, \quad (7)$$

(equation (A3)), where $\hat{p}_c$ is the proportion of the population of future offspring of caring parents that are full siblings (as opposed to half siblings) of current offspring. Our formulation, taking into account all costs to both parents, can be expressed as

$$B' = 0.25((1 + p_c)C'_c - p'_c N_c + C'_{n,h}), \quad (8)$$

(see Appendix A, equation (A7)), where p_c is the proportion of future young of the caring parent that are full siblings of the current offspring and N_c is the number of future offspring produced by the caring parent, both expressed as functions of the amount of parental investment. A comparison of equations (7) and (8) allows the

conditions under which Trivers' formulation is adequate to be identified. In general, these equations will only give the same value for the offspring's optimal parental investment when the proportion of future offspring that are full siblings (as opposed to half siblings via the caring parent) does not change with the amount of investment (i.e. $p'_c = 0$ and $\hat{p}_c = p_c(i)$) and there is no change in the number of future half siblings produced by the non-caring parent as a result of investment (i.e. $C'_{n,h} = 0$). These conditions are fairly restrictive, but do include the case mentioned above when the caring parent mates only once in its lifetime. They also include the case when future offspring of the caring parent are never full siblings of the current offspring. At these extremes, focusing on whether future offspring are full or half siblings will predict the offspring's optimal parental investment correctly. However, such cases are rare and the universal occurrence or absence of full siblings among future offspring of the caring parent must be absolute. When an intermediate proportion of future offspring are full siblings of the current offspring, a survival cost to investment will tend to alter the number of future half siblings produced by the non-caring parent and a fecundity cost that acts unequally across future reproductive attempts will tend to alter the proportion of full siblings (as opposed to half siblings via the caring parent) among future offspring. For example, a fecundity cost falling predominantly on the immediately succeeding reproductive attempt will reduce the proportion of full siblings among future offspring.

Another case in which these conditions are met is when all conflict occurs over the allocation of investment within the current brood. Trivers (1974) considered the case of a single offspring competing for investment with future siblings ('interbrood conflict'), but competition can also occur between siblings in families of two or more young ('intra-brood conflict'; Macnair & Parker 1979; Briskie *et al.* 1994). When conflict occurs between litter-mates only (e.g. when the resource allocated to a brood is fixed), the proportion of future offspring that are full siblings (as opposed to half siblings via the caring parent) and the number of future half siblings via the non-caring parent are unaffected (i.e. $p'_c = C'_{n,h} = 0$). Then, arguments based on full and half sibship via the caring parent will yield the same conclusion as our formulation. However, although either approach can be used for intra-brood conflict, only the approach separating the costs to each parent can be used when there is an element of interbrood conflict that affects p_c or $C_{n,h}$.

We note in passing that the optimal parental investment for the offspring can indeed be defined without explicit reference to the cost to the non-caring parent (equation (A8)):

$$B' = 0.25[(1 + p_c)C'_c - p'_c N_c] + [(p'_n/p_n^2)p'_c N_c + (1/p_n - 1)(p_c C'_c - p'_c N_c)], \quad (9)$$

where p_c and p_n are the proportions of future offspring of the caring and non-caring parents, respectively, that are full siblings (as opposed to half siblings) of the respective parent's current offspring and N_c is the number of future offspring of the caring parent, all as a function of parental investment. Thus, it can be argued that Trivers (1974) was

in some sense correct in focusing solely on the cost to the caring parent and the frequency of full and half siblings. However, p_c and p_n are functions of the amount of investment, not population averages and it is necessary to include the proportion of full siblings for both the caring and non-caring parents separately. Moreover, the equation also includes the number of future offspring produced by the caring parent (N_c), as well as the change in this variable as a result of investment (i.e. the cost C_c). Trivers made no mention of these extra variables (p_n and N_c) and we do not believe that this is what he had in mind.

6. DISCUSSION

Trivers' formulation of his path-breaking concept of parent-offspring conflict has led more recent authors to focus on the proportion of future offspring that are full or half siblings of the current offspring as an important determinant of the extent of parent-offspring conflict. Trivers did not explicitly state how the relatedness (r) between current and future offspring should be calculated, but we show here that a formulation based on a population average, as his writing implies, is correct only under limited circumstances. Our alternative formulation does not suffer from these limitations.

It can be argued that Trivers was in some senses correct. First, the cost to the non-caring parent will probably be loosely correlated with whether future siblings are full or half siblings. When future siblings are always half siblings (e.g. Cockburn *et al.* 1985), it is unlikely that there will be any cost to the non-caring parent. When future siblings are nearly always full siblings, the cost to the non-caring parent may vary between zero and the biologically plausible upper limit of the cost to the caring parent. However, it is the cost to the non-caring parent rather than the average relatedness between siblings which determines the extent of parent-offspring conflict. When most future siblings (in the population as a whole) are full siblings, but there is no cost to the non-caring parent, parent-offspring conflict will be as severe as when all siblings are half siblings.

Second, Trivers' (1974) 'other things being equal' condition (see quote above) can be taken to include the future reproductive success of the non-caring parent through half siblings of the current offspring (i.e. $C_{n,h} = 0$). However, without explicit elaboration, it can equally be taken to include the total future reproductive success of the non-caring parent (i.e. $C_n = 0$). This second assumption is the one that is usually made in models of biparental care (e.g. Houston & Davies 1985) and results in the offspring's optimal parental investment being given by $B' = 0.25C'_c$ and, hence, being independent of the proportion of future offspring that are full or half siblings.

Third, although we show that the offspring's optimal parental investment can be defined without explicit reference to the cost to the non-caring parent (equation (9)), some of the variables used in this formulation are not mentioned by Trivers (1974).

The correct definition of the offspring's optimal parental investment under uniparental care (and, hence, the extent of parent-offspring conflict) can be formulated in a number of ways, including equations (4) and (6). Equation (4) lends itself more readily to graphical presentation in a

form similar to that used by Trivers (see figure 1b). It also helps to focus on the question of central importance in empirical studies: to what extent is the future reproductive output of the non-caring parent affected by investment by the caring parent? §3 illustrates how the answer to this question may vary with subtle differences in mating system.

One of us (Parker 1985) has also previously warned against equating the coefficients of 0.5 or 0.25 in equations specifying the offspring's optimum with the coefficient of relatedness between the current and future offspring. Explicit population genetics models were examined which incorporated assumptions about the mating system and resource allocation to parental care. These assumptions determine the extent to which the reproductive success of the non-caring parent is constrained by offspring genes for the amount of care demanded (essentially equivalent to the cost of parental investment to the non-caring parent). These earlier models correspond with the extreme cases in which the cost to the non-caring parent is either zero ($C_n = 0$) or the same as for the caring parent ($C_n = C_c$). The phenotypic formulation of parent-offspring conflict presented here not only confirms these earlier conclusions, but also provides a means of modelling continuous variation in the cost to the non-caring parent and particularly to situations in which C_n is not a constant proportion of C_c .

Trivers' (1974) argument assumes that genes in the offspring for the amount of care demanded are equally expressed whichever parent they are inherited from. However, Haig (1992, 1997a) has pointed out that genomic imprinting (in which genes are molecularly labelled according to their parental origin) implies that an offspring's strategy should be conditional on the parent from which it inherits the gene. These cases can be dealt with using explicit population genetics models. Alternatively, they can be modelled phenotypically by being regarded as sexual conflict between parental characters expressed in the offspring (Dawkins 1982; Lessells 1999) rather than as parent-offspring conflict (Godfray 1999).

The concept of a cost to non-carers of another individual's parental investment is also illuminating in other cases of conflict. Costs to the future reproduction of one parent of the other's investment (as well as a 'current cost' of the other's investment; Lazarus & Inglis 1986; Lessells 1999) may be important in tempering the extent of conflict between parents (Lessells 1999). As argued above, calculations based on the frequency of half and full siblings (e.g. Haig 1997b) will be misleading. Costs to the other parent of each parent's investment could also be included in models of biparental care. In this case, the total cost to each parent would be a function of both parents' investment and would be represented graphically as a surface in three dimensions (with two axes, x and z , for the parental investment by each parent; cf. figure 1). Each of the parent's own optima would occur where there was maximum vertical separation between their cost surface and the benefit surface. Determining the evolutionarily stable pattern of investment would require a game-theory approach (e.g. Houston & Davies 1985). Eventually, models of parental investment should take parent-offspring conflict, sibling competition and sexual conflict

into consideration simultaneously. In the meantime, the models presented here provide a reminder that, even under uniparental care, the non-caring parent has a defined optimal level of investment by the other parent (given by $B' = C_n'$) and that parental investment is consequently a game involving the entire family (Mock & Parker 1997).

Trivers' (1974) argument for the occurrence of parent-offspring conflict has stood the test of time remarkably well (Godfray 1999). However, we show here that the key variable influencing the strength of parent-offspring conflict is not whether future siblings are in general full or half siblings, but the cost to the non-caring parent of the caring parent's investment.

The paradox outlined above was first brought to the attention of C.M.L. in a paper by Richard Sibly that she refereed about a decade ago. We are also grateful to Troy Day, Charles Godfray, Peter Taylor and various anonymous referees for comments on previous versions of this paper. This is publication 2548 of the Netherlands Institute of Ecology.

APPENDIX A

Trivers (1974) argued that, when B , the benefit in terms of increased survival of the current young and C_c , the cost to the caring parent in terms of loss of future young are expressed as functions of i , the amount of parental investment, the optimal investment for the caring parent (i_p^*) occurs when $B - C_c$ is a maximum, i.e. when

$$B' = C_c', \quad (\text{A1})$$

where a prime indicates the first differential with respect to i . For equation (A1) to give a maximum value rather than a minimum or stationary value, the second derivative of $B - C$ with respect to i must also be negative. This condition that the second derivative of the appropriate function of costs minus benefits must be negative applies to all parental investment optima specified in this paper. This condition will be met when the cost curve is accelerating and the benefit curve decelerating.

Trivers also argued that the optimal investment for the offspring (i_o^*) occurs when $B - rC_c$ is a maximum, i.e. when

$$B' = rC_c'. \quad (\text{A2})$$

We interpret Trivers to mean that $r = 0.25(1 + \hat{p}_c)$, where $\hat{p}_c$ is the proportion of future offspring of caring parents that are full siblings (as opposed to half siblings) of current offspring, so that i_o^* is also given by

$$B' = 0.25(1 + \hat{p}_c)C_c'. \quad (\text{A3})$$

We argue that, because siblings are related by 0.25 via any parent they have in common, the costs to the caring (C_c) and non-caring (C_n) parents in terms of loss of future offspring must be separated before applying Hamilton's rule. i_o^* then occurs when $B - 0.25C_c - 0.25C_n$ is a maximum, i.e. when

$$B' = 0.25(C_c' + C_n'). \quad (\text{A4})$$

C_c and C_n can be further subdivided according to whether the affected offspring are full or half siblings of

the current offspring (indicated by additional subscripts f and h, respectively). Then i_o^* occurs when $B - 0.25C_{c,f} - 0.25C_{c,h} - 0.25C_{n,f} - 0.25C_{n,h}$ is a maximum. Since the cost through the loss of full sibling offspring must be the same for both parents, the offspring's optimum occurs when $B - 0.5C_f - 0.25C_{c,h} - 0.25C_{n,h}$ is a maximum, i.e. when

$$B' = 0.5C_f' + 0.25C_{c,h}' + 0.25C_{n,h}', \quad (A5)$$

where C_f is the cost to each parent in terms of the loss of future offspring that are full siblings of the current offspring.

The cost to the caring parent can be rewritten in terms of the number of future offspring produced by the caring parent (N_c) and the proportion of future young of the caring parent that are full siblings of the current offspring (p_c), both expressed as functions of the amount of parental investment (i). (Hence, $N_c(0)$ and $p_c(0)$ are the respective values of these variables when no investment is made.)

$$C_c(i) = N_c(0) - N_c(i),$$

$$C_{c,f}(i) = p_c(0)N_c(0) - p_c(i)N_c(i),$$

and

$$C_{c,h}(i) = (1 - p_c(0))N_c(0) - (1 - p_c(i))N_c(i), \quad (A6)$$

so that

$$0.5C_{c,f} + 0.25C_{c,h} = 0.25[(1 + p_c(0))N_c(0) - (1 + p_c(i))N_c(i)].$$

Then i_o^* occurs when $B - 0.25[(1 + p_c(0))N_c(0) - (1 + p_c(i))N_c(i)] - 0.25C_{n,h}$ is a maximum, i.e. when

$$B' = 0.25(-(1 + p_c)N_c' - p_c'N_c + C_{n,h}').$$

It follows from equation (A6) that $C_c' = -N_c'$, so i_o^* is also given by

$$B' = 0.25((1 + p_c)C_c' - p_c'N_c + C_{n,h}'). \quad (A7)$$

Finally, $C_{n,h}$ can also be rewritten in terms of the number of future offspring produced by the caring parent, the proportion of future young of the caring parent that are full siblings of the current offspring and the proportion of future young of the non-caring parent that are full siblings of the current offspring (p_n). The number of future offspring produced that are full siblings of the current offspring must be the same for both parents, so that $p_c(i)N_c(i) = p_n(i)N_n(i)$, where $N_n(i)$ is the number of future offspring produced by the non-caring parent as a function of i . Hence, $N_n(i) = p_c(i)N_c(i)/p_n(i)$. i_o^* therefore occurs where $B - 0.25[(1 + p_c(0))N_c(0) - (1 + p_c(i))N_c(i)] - 0.25[(1 - p_n(0))p_c(0)N_c(0)/p_n(0) - (1 - p_n(i))p_c(i)N_c(i)/p_n(i)]$ is a maximum, i.e. where

$$\begin{aligned} B' &= 0.25([-(1 + p_c)N_c' - p_c'N_c] \\ &\quad + [(p_n'/p_n^2)p_cN_c - (1/p_n - 1)(p_cN_c' + p_c'N_c)]) \\ &= 0.25([(1 + p_c)C_c' - p_c'N_c] \\ &\quad + [(p_n'/p_n^2)p_cN_c + (1/p_n - 1)(p_cC_c' - p_c'N_c)]). \end{aligned} \quad (A8)$$

REFERENCES

- Briskie, J. V., Naugler, C. T. & Leech, S. M. 1994 Begging intensity of nestling birds varies with sibling relatedness. *Proc. R. Soc. Lond. B* **258**, 73–78.
- Burt, A. & Trivers, R. 1998 Genetic conflicts in genomic imprinting. *Proc. R. Soc. Lond. B* **265**, 2393–2397.
- Clutton-Brock, T. H. 1991 *The evolution of parental care*. Princeton University Press.
- Clutton-Brock, T. H. & Godfray, H. C. J. 1991 Parental investment. In *Behavioural ecology* (ed. J. R. Krebs & N. B. Davies), pp. 234–262. Oxford: Blackwell Science.
- Cockburn, A., Scott, M. P. & Scotts, D. J. 1985 Inbreeding avoidance and male-biased natal dispersal in *Antechinus* spp. (Marsupialia: Dasyuridae). *Anim. Behav.* **33**, 908–915.
- Dawkins, R. 1982 *The extended phenotype*. Oxford: W. H. Freeman.
- Emslie, S. D., Sydeman, W. J. & Pyle, P. 1992 The importance of mate retention and experience on breeding success in Cassin's auklet (*Ptychoramphus aleuticus*). *Behav. Ecol.* **3**, 189–195.
- Godfray, H. C. J. 1999 Parent-offspring conflict. In *Levels of selection in evolution* (ed. L. Keller). Princeton University Press. (In the press.)
- Godfray, H. C. J. & Parker, G. A. 1991 Clutch size, fecundity and parent-offspring conflict. *Phil. Trans. R. Soc. Lond. B* **332**, 67–69.
- Haig, D. 1992 Genomic conflict and the theory of parent-offspring conflict. *Semin. Dev. Biol.* **3**, 153–160.
- Haig, D. 1997a Parental antagonism, relatedness asymmetries, and genomic imprinting. *Proc. R. Soc. Lond. B* **264**, 1657–1662.
- Haig, D. 1997b The social gene. In *Behavioural ecology* (ed. J. R. Krebs & N. B. Davies), pp. 284–304. Oxford: Blackwell Science.
- Hamilton, W. D. 1964 The genetical evolution of social behaviour. *J. Theor. Biol.* **7**, 1–52.
- Houston, A. I. & Davies, N. B. 1985 The evolution of cooperation and life history in the dunnock *Prunella modularis*. In *Behavioural ecology* (ed. R. M. Sibly & R. H. Smith), pp. 471–487. Oxford: Blackwell Science.
- Lazarus, J. & Inglis, I. R. 1986 Shared and unshared parental investment, parent-offspring conflict and brood size. *Anim. Behav.* **34**, 1791–1804.
- Lessells, C. M. 1999 Sexual conflict in animals. In *Levels of selection in evolution* (ed. L. Keller). Princeton University Press. (In the press.)
- Macnair, M. & Parker, G. A. 1979 Models of parent-offspring conflict. III. Intra-brood conflict. *Anim. Behav.* **27**, 1202–1209.
- Mock, D. W. & Parker, G. A. 1997 *The evolution of sibling rivalry*. Oxford University Press.
- Parker, G. A. 1985 Models of parent-offspring conflict. V. Effects of the behaviour of the two parents. *Anim. Behav.* **33**, 519–533.
- Parker, G. A. & Macnair, M. R. 1978 Models of parent-offspring conflict. I. Monogamy. *Anim. Behav.* **26**, 97–111.
- Scott, D. K. 1988 Breeding success in Bewick's swans. In *Reproductive success* (ed. T. H. Clutton-Brock), pp. 220–236. University of Chicago Press.
- Trivers, R. L. 1974 Parent-offspring conflict. *Am. Zool.* **14**, 249–264.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.