Evolutionary Ecology Research, 2001, **3**: 829–844

Resolution of evolutionary conflicts: costly behaviours enforce the evolution of cost-free competition

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ABSTRACT

A resolution model for evolutionary conflicts of interest is proposed. We assume that two conflicting parties originally have different evolutionarily stable strategies (ESS) with respect to a continuous variable, but that only one value of the variable is simultaneously possible. Individuals from the two parties meet in antagonistic encounters. The side that invests more in the antagonistic behaviours mediating the conflict is able to adjust the variable in its preferred direction. It is shown that the extent of the conflict – that is, the difference between the ESS values of the parties – decreases with increases in investment to antagonistic behaviours. The precondition for this is that the total conflict cost increases with the intensity and frequency of the antagonistic encounters, and that these factors in turn are related to how much the variable is adjusted. The conflict costs then result in a change of ESS level that forces the stronger party to alter its preferred level of the conflict variable. Behaviours that give control in the conflict escalate in an 'arms race', which eventually leads to a compromise solution with one ESS shared by the parties and with a small or no realized cost of conflict behaviour. This result contrasts with the traditional view of evolutionary conflicts, that expressed costs of antagonistic behaviours are necessary for evolutionarily stable resolutions. The model is applied to sexual conflicts, where a stable resolution may result in which apparent conflict behaviours are suppressed, although both parties are ready to engage in costly conflicts. In an explicit model of the compromise resolution of a parent–offspring conflict over parental investment, we demonstrate that the conflict may be resolved so that offspring do not beg. At the solution, parents provide an amount of care intermediate between the original ESS level of the parents and offspring, and the new parental and offspring ESS levels are identical.

Keywords: conflict behaviour, evolutionary conflict, parent–offspring conflict, resolution compromise, sexual conflict.

INTRODUCTION

Evolutionary conflicts of interest exist when there is an asymmetry between two players in an evolutionary game and the players prefer different outcomes to the game (Trivers,

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1972, 1974; Parker, 1979). Such conflicts may drive the evolution of costly antagonistic behaviours. For example, sexual conflicts of interest are probably the reason why fights frequently occur when males try to mate with a reluctant female (Parker, 1979). Other signs of evolutionary conflicts include costly begging by offspring that want more food from their parents (Trivers, 1974; Parker and MacNair, 1979). The aim of evolutionary resolution models (Yamamura and Higashi, 1992; Godfray, 1995) is to find a conflict resolution through the process of natural selection. The type of phenotypic interaction assumed in the conflict resolution model will strongly influence the solution. For example, many conflicts of interest are mediated by fights where the outcome is determined by differences in traits influencing resource-holding potential (Parker, 1974); it may then be reasonable to assume an arms race in these traits. Direct costs of the traits may then bring the arms race to a halt as envisaged by several authors (Parker, 1979; Parker and MacNair, 1979; Yamamura and Higashi, 1992).

If the outcome of the fight is determined by investment in behavioural traits such as aggressiveness or begging intensity, the above model is not easy to apply. The reason is that behavioural conflict costs are often realized only if the opponent counteracts behaviourally. In such a case, increasing direct production cost of the trait influencing conflict resolution may not put a brake on the arms race. The conflict resolution may thus differ from the case with traits influencing resource-holding potential. Here we show that when the realized behavioural conflict cost is integrated into the fitness calculation, a process of escalating contest behaviours may resolve an evolutionary conflict so that, at the evolutionarily stable solution, there are no realized costs of conflict behaviour. This solution arises as a consequence of mutual adjustments of the preferences, made necessary by the increasing conflict costs. Under this model of conflict resolution, the costly behaviours are necessary for the compromise to evolve. On the other hand, when the compromise is reached, there may no longer be any signs of overt conflict. Arms races may thus not always lead to large costs, but to mutual accommodations of the preferences.

A THEORY FOR RESOLVING BEHAVIOURAL EVOLUTIONARY CONFLICTS

Assume two interacting individuals A and B in different roles, with different fitness interests in the value of some continuous variable x. Both individuals are assumed to be able to influence the value that x may take. Let x_a and x_b be the 'bids' or the values in trait space opted for by A and B respectively. If each could choose a value individually and without costs, their individual evolutionarily stable strategies (ESSs) would be different – that is, there is a 'battleground' *sensu* Godfray (1995). To define the 'battleground', let the fitness function of an A individual, which opts for value x'_a in a population where others choose x_a, be $\omega_a(x'_a, x_a) = g(x'_a, x_a)$. The ESS x-value of A can be found from the standard conditions (Maynard Smith, 1982; Eshel, 1983; Taylor, 1989) and is denoted x^{o}_a. In addition, we define $\omega_b(x'_b, x_b) = h(x'_b, x_b)$ as the fitness function of a B individual that opts for value x'_b when the average B population value is x_b. The ESS (x^{o}_b) of B is defined in an equivalent way as for A. The battleground includes all values of x between x^{o}_b and x^{o}_a. We will hereafter assume that $x^{\mathrm{o}}_a < x^{\mathrm{o}}_b$.

If we imagine that the interaction is such that only one value of x is simultaneously possible, so that A and B must agree on some value within the battleground, assumptions about the phenotypic interaction between A and B must be made to find the probable resolution. The type of interactions we will consider is when there are costly behavioural conflicts between A and B. Furthermore, one of the parties is said to be 'in control'. By this we mean that contestants from one side are probable winners in any given antagonistic encounter, because such individuals invest more or have a more efficient way of influencing the outcome. We assume that the side in 'control' through the antagonistic encounters has a stronger influence over x and is able to choose a value of x for its own benefit. Thus if A is stronger than B, and B argues for the value x_b, A can either agree to this value or, by engaging in behavioural conflicts, adjust x to some other value x_a that is better for A. The conflict cost of such an adjustment by A is assumed to depend partly on the intensity of the conflict behaviour and partly on the size of the adjustment – that is, the difference between x_a and the opponent's bid x_b.

The following three cases exemplify that large adjustments should be more costly than small ones when the conflict is mediated by behaviours. First, high mating frequency is often positive for males but negative for females (Parker, 1979). If females are able to reject male mating attempts, they may decrease mating frequency to a level more beneficial for them. Animal fighting behaviour can be expected to be costly (e.g. Neat *et al.*, 1997). The total female cost of rejecting males depends on the cost of repelling any one male and also on the frequency of the mating attempts she refuses. With a high rate of male mating attempts, the increasing cost of repelling males may force her to accept a higher mating frequency than optimal, so-called 'convenience polyandry' (Thornhill and Alcock, 1983; Arnquist, 1992; Rowe, 1992; Watson *et al.*, 1998). Second, male birds may search for additional matings after the start of breeding, while the mated female may be successful in delaying her male's additional matings by aggressively preventing prospecting females from intruding (Slagsvold and Lifjeld, 1994; Sandell and Smith, 1996). The cost of this behaviour should increase with the enforced delay, so that the female may 'accept' male remating when the marginal benefit from a further delay is low enough. Third, in parent–offspring conflicts over parental investment (Trivers, 1974), the offspring may control provisioning rate by begging. If begging behaviour is very costly, this should force the offspring to lower their aspirations and opt for a provisioning rate closer to the rate the parents deliberately provide. Below, we assume that the realized cost of conflict behaviour is proportional to the adjustment made relative to the opponent's preference. This is a consequence of the distinction between the *evolutionary conflict* (i.e. there is a battleground over a trait) and the involved behaviours or *conflict investments* that are instrumental in adjusting the trait value in a battleground.

The amount of control is assumed to depend on some conflict investment, the level of which is denoted by k ($k \geq 0$). This should be thought of as some costly behaviour that is used to enforce one's own preferred outcome of the encounter. Often, this may simply be force; for example, in sexual conflicts it may be female ability to resist mating or male ability to achieve them. Let k_a be the investment of A and k_b be the investment of B. We assume that the individual with the higher investment, k, in conflict behaviour always wins the contest. If k_a is higher than k_b, then A is in control; B is in control if k_b is higher than k_a.

With this behavioural conflict cost, the evolutionarily stable choice of x-value for A can be found by defining the fitness function

$$\omega_a(x'_a, x_a) = g(x'_a, x_a) - C_a(\gamma(x'_a, x_b)k_a) \tag{1}$$

The conflict cost $C_a(\gamma, k_a)$ is assumed to depend on conflict investment and on the adjustment γ relative to the value chosen by the opponent B ($\gamma = x_b - x'_a$). If there is no conflict investment, or without any adjustment of x, there is no realized cost. Conflict cost arises thus only if investments in conflict behaviours are made and if A adjusts the conflict variable – that is, $\gamma > 0$ and simultaneously $k_a > 0$. Assume that A individuals win all antagonistic encounters, so that they have the capacity to produce an agreement on their own terms over the value x should take. Hence, x will move to the ESS x_a^* of A, which must be 'accepted' by B although it means lowered fitness.

The ESS value x_a^* is now the value that solves the following conditions (Maynard Smith, 1982; Eshel, 1983; Taylor, 1989):

$$\left.\frac{\partial g}{\partial x_a'} - \frac{\partial C_a}{\partial \gamma}\frac{\partial \gamma}{\partial x_a'}\right|_{x_a' = x_a = x_a^*} = 0 \tag{2}$$

$$\left.\frac{\partial^2 g}{\partial x_a'^2} - \left[\frac{\partial^2 C_a}{\partial \gamma^2}\left(\frac{\partial \gamma}{\partial x_a'}\right)^2 + \frac{\partial C_a}{\partial \gamma}\frac{\partial^2 \gamma}{\partial x_a'^2}\right]\right|_{x_a' = x_a = x_a^*} < 0 \tag{3}$$

$$\left.\frac{\partial^2 g}{\partial x_a' \partial x_a} + \frac{\partial^2 g}{\partial x_a'^2} - \left[\frac{\partial^2 C_a}{\partial \gamma^2}\left(\frac{\partial \gamma}{\partial x_a'}\right)^2 + \frac{\partial C_a}{\partial \gamma}\frac{\partial^2 \gamma}{\partial x_a'^2}\right]\right|_{x_a' = x_a = x_a^*} < 0 \tag{4}$$

From equation (2), we see that the ESS will depend on the conflict cost. Without conflict cost, A's ESS is the value x_a° as before. With conflict cost, the ESS is located at a higher value where $\partial g/\partial x_a'$ is negative (Fig. 1a). This is necessarily so because the new cost term in (2) is negative (i.e. C increases with γ and γ decreases with x_a'). The expression within the parentheses in equations (3) and (4) is, with the definitions used here, always positive, so that the new ESS is also locally and convergence stable, if the earlier ESS (x_a°) was.

Treating x_b as constant, and remembering that $\gamma = x_b - x_a'$, we can derive from (2) and the implicit functions theorem an expression for how the ESS changes with the cost of the conflict behaviour k_a:

$$\frac{\mathrm{d}x_a^*}{\mathrm{d}k_a} = \frac{\partial^2 C_a}{\partial \gamma \partial k_a} \Bigg/ \left[\frac{\partial^2 C_a}{\partial \gamma^2} - \frac{\partial^2 g}{\partial x_a' \partial x_a} - \frac{\partial^2 g}{\partial x_a'^2}\right] \tag{5}$$

We assume that the cost of a certain adjustment γ is higher the higher the conflict investment k_a; that is, $\partial^2 C_a/\partial\gamma\partial k_a > 0$ in the numerator of (5). As regards the denominator of (5), biologically it is reasonable to assume that $\partial^2 C_a/\partial\gamma^2 \geq 0$; that is, the cost increases linearly or faster with increasing adjustment. The ESS-criterion for convergence stability ensures $\partial^2 g/\partial x_a'\partial x_a + \partial^2 g/\partial x_a'^2 < 0$ around an ESS (Eshel, 1983). We assume this to hold true for all values within the battleground. Then $\mathrm{d}x_a^*/\mathrm{d}k_a$ must be positive – that is, the higher the conflict investment, the higher the value of x_a^* argued by A.

The corresponding fitness function for B becomes

$$\omega_a(x_b', x_b) = h(x_b', x_b) - C_b(\delta(x_b', x_a)k_b) \tag{6}$$

where the adjustment δ relative to the value chosen by the opponent A is $\delta = x_b' - x_a$. By equivalent reasoning as before, it can be shown that x_b^* decreases with k_b (Fig. 1). The net effect is a reduction in the extent of conflict with increasing conflict investments (Fig. 1b). The new evolutionarily stable strategies do not differ as much as when conflict investments were absent.

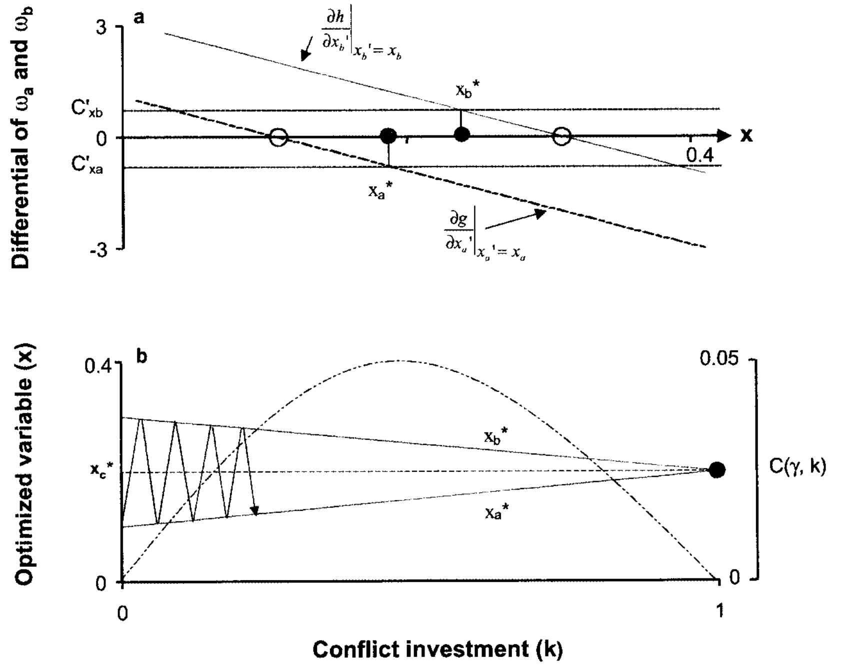

Fig. 1. The convergence of optima. *A*'s fitness function is $\omega_a(x_a', x_a) = g(x_a', x_a) - C(\gamma, k_a)$ and *B*'s is $\omega_b(x_b', x_b) = h(x_b', x_b) - C(\gamma, k_b)$; both are influenced by the trait value x and the conflict cost C. In (a), the two sloping lines show the differentiated fitness functions; the left line $= \partial g/\partial x_a'$ and the right line $= \partial h/\partial x_b'$. Without conflict cost, the optima x for the two parties are at the intersections $\{x_a^\circ, x_b^\circ\}$ with the x axis $\{g'(x_a^\circ) = 0,\ h'(x_b^\circ) = 0$; open circles$\}$. The individuals may affect the value of x by investing in conflict strategies (levels k_a and k_b). With conflict cost, *B* optimizes its fitness at the point x_b^* located at a distance γ from x_a° ($\gamma = x_b^* - x_a^\circ$, given that $x_b^* > x_a^\circ$). This forces *A* to increase its investment in the conflict to take power over *B* and choose the level x_a^*. As k increases, $x_a^*$and x_b^* are adjusted (b). Each individual is expected to increase k by the smallest possible amount that still enables it to get control. The arms race will lead to a point where k is high while *A* and *B* optimize their fitness at the same value (x_c^*) (dot in b). The dash-dot line shows the behavioural conflict cost, which is zero at the compromise. To draw the figure, the following functions were used: $g(x_a', x_a) = x_a'(1 - [x_a' + (n-1)x_a])$, $h(x_b', x_b) = (x_b' - 1)(2 - [x_b' + (n-1)x_b])$, $C = k_i(x_b - x_a)$ $(i = a, b)$. In (b), $x_a^*(k_a) = (1 + k_a)/(n+1)$ and $x_b^*(k_b) = (3 - k_b)/(n+1)$ and $n = 9$.

In other words, the party currently in control must make an accommodation of his or her preferences in the direction of the opponent, because otherwise conflict costs will be too high. As conflict investments increase, the 'bids' of the parties will concomitantly converge (Fig. 1b) and for some conflict investment $k_a = k_b$ there is a compromise $x_a^* = x_b^*$ with identical ESSs that may be reached as a solution to the evolutionary conflict. This x-value is an ESS for both *A* and *B* and simultaneously solves the two equations:

$$\left.\frac{\partial g}{\partial x_a'} - \frac{\partial C_a}{\partial \gamma}\frac{\partial \gamma}{\partial x_a'}\right|_{x_a' = x_a = x_a^*} = 0 \qquad (7)$$

$$\left.\frac{\partial h}{\partial x_b'} - \frac{\partial C_b}{\partial \delta}\frac{\partial \delta}{\partial x_b'}\right|_{x_b' = x_b = x_b^*} = 0 \tag{8}$$

with $\gamma = x_b - x_a'$ in the first equation and $\delta = x_b' - x_a$ in the second. If behavioural conflict is equally costly for both parties, so that an equally large adjustment increases the cost equally for A and B, then

$$\left.\frac{\partial C_a}{\partial \gamma} = \frac{\partial C_b}{\partial \delta}\right|_{|\gamma| = |\delta| = \varepsilon,\ k_a = k_b} \tag{9}$$

Calling the compromise value x_c^*, (7) and (8) can then be expressed as

$$\left.\frac{\partial g}{\partial x_a'}\right|_{x_a' = x_a = x_c^*} = -\left.\frac{\partial h}{\partial x_b'}\right|_{x_a' = x_a = x_c^*} \tag{10}$$

This expression defines a compromise for the evolutionary conflict. Provided that the gradient of C is the same for both parties, the solution is found at a point within the battleground where the fitness gradients of the fitness equations $g(x_a', x_a)$ and $h(x_b', x_b)$ are identical but with opposite signs.

With differing cost functions, the solution will be different. For example, assume that $C_a(\gamma, k_a) = k_a\gamma^2 + k_a\gamma$ and $C_b(\delta, k_b) = mk_b\delta$ and $m > 1$. Then, B is more strongly affected by a small adjustment of x. Larger adjustments are more costly for A than for B (Fig. 2a). The solution is then found where

$$\left.\frac{\partial g}{\partial x_a'}\right|_{x_a' = x_a = x_c^*} = -\frac{1}{m}\left.\frac{\partial h}{\partial x_b'}\right|_{x_a' = x_a = x_c^*} \tag{11}$$

That is, at a point where the fitness gradient of B is steeper than that of A. This is more in the direction of A's interest (Fig. 2b). This shows that the marginal costs of small adjustments are more important in determining the compromise.

As a consequence of their identical evolutionarily stable strategies, neither side may increase fitness by adjusting x in any direction. There is then, by assumption, no behavioural conflict cost (Fig. 1). Nor is it possible to increase fitness by altering the conflict investment; with identical evolutionarily stable strategies, control over x is irrelevant as there is no disagreement. Thus, both parties agree upon the same solution and apparent conflict behaviour will be suppressed. At the compromise, instead of costly behavioural conflicts, both parties will suffer a permanent reduction in fitness because the compromise is not the best choice for either of them in the absence of conflict.

APPLICATION OF THE THEORY TO PARENT–OFFSPRING CONFLICT

Here we provide a more detailed example of the resolution model within the context of parent–offspring conflict (Trivers, 1974). Ever since the potential for evolutionary conflicts between parents and offspring was first pointed out, this field has been one of the most fertile in evolutionary ecology, and the logic is applicable to plants as well as animals (Mock and Parker, 1997). The conflicts arise because genes that influence parental care experience opposite selection pressures if expressed in parents or in young. Offspring genes are selected

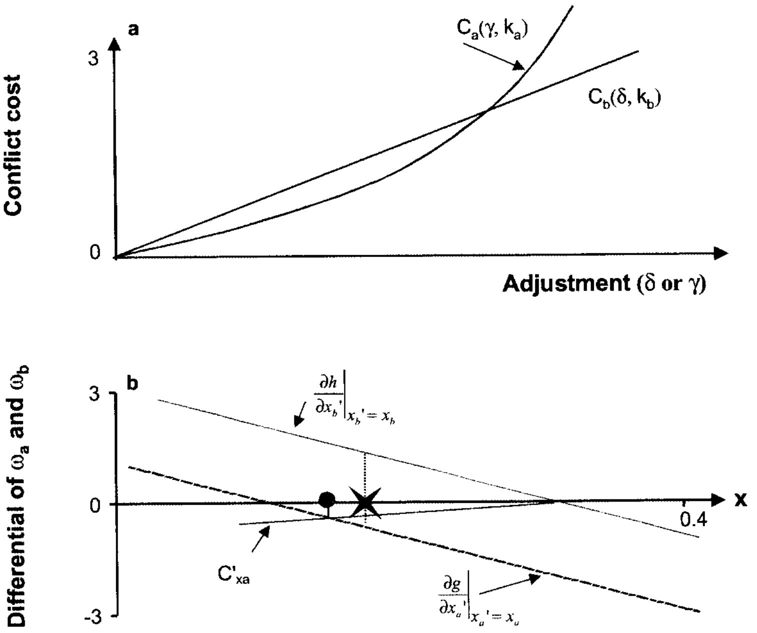

Fig. 2. Conflict resolution with unequal cost functions. We assume $C_a(\gamma, k_a) = k_a\gamma^2 + k_a\gamma$ and $C_b(\delta, k_b) = mk_b\delta$ and $m = 2$. These are shown in (a). In (b), the black dot represents an example of the ESS x_a^* when k_a is low, although higher than k_b. The ESS is located where the rate of cost increase equals the rate of fitness increase. The star shows the location of the compromise defined by equation (11). The compromise is located where the fitness gradient of B is twice as steep as that of A, because of the differing costs. This point is closer to A's interest.

if they obtain a disproportionate share of the parental investment, which increases parental care above that optimal for parents. This is opposed by genes expressed in parents, as a parent is equally related to all of its offspring and should distribute parental care evenly among them (Trivers, 1974).

The notation follows the classical model of parent–offspring conflict (Parker and MacNair, 1978). Consider a single parent, providing for one offspring by collecting food in the surroundings and delivering it at the nest. The parent delivers one food unit at a time, at an even rate. Over the breeding season, the accumulated parental investment is m_p, the deliberately made parental investment. There is an offspring survival function $f(m)$ dependent on the parental investment m received by a young (Fig. 3). We assume that $f(m)$ is zero for low parental investment and increases with parental investment to some maximum < 1. We assume that $f'(m) > 0$, survival increases with parental investment and that $f''(m) < 0$ – that is, there are diminishing returns of parental investment. With M being the total reproductive budget of an individual, let M/m express the lifetime fecundity of the parent.

We make the following assumptions about the phenotypic interaction between parent and young. We assume that the young may beg when the parent is present and, if the amount of begging is higher than an assumed critical parental response threshold, this makes the parent quickly collect and deliver an extra food unit so that the parental

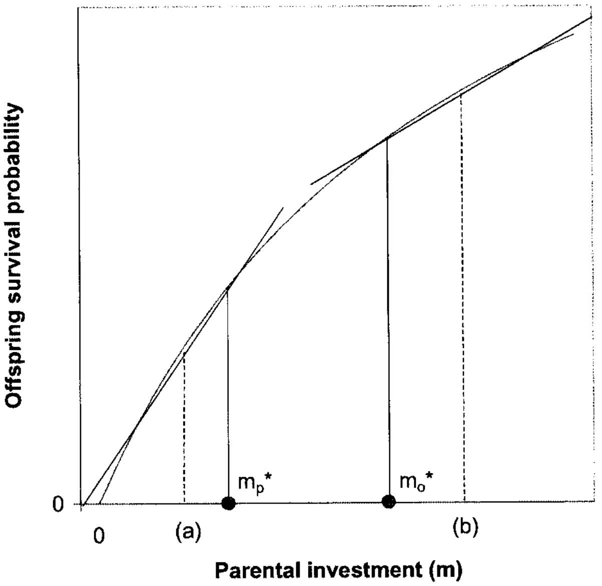

Fig. 3. Compromise resolution model of the parent–offspring conflict. The curved line $f(m)$ shows offspring survival as a function of parental investment. The optimum parental investments for parents (a) and for offspring (b) are shown for the case when there is no conflict cost. Begging is introduced as a costly manipulative strategy, which decreases offspring survival probability. When begging is necessary to obtain more food, the offspring ESS is m_o^*, found where a line from $-m_o^*$ intersects $f(m)$ from above. The parental ESS m_p^* is where a line from the origin intersects $f(m)$ from below. The higher the begging level, the less difference between the two evolutionarily stable strategies.

provisioning rate is increased. To get yet another extra unit of food, the young must on another occasion beg again with the same intensity. Begging decreases survival probability by being energetically costly (Leech and Leonard, 1996; McCarthy, 1996) or by attracting predators (Redondo and Castro, 1992; Haskel, 1994). Thus young pay a survival cost for every extra food unit, and the total conflict cost incurred increases with the total amount of food received by begging. If the parental threshold for responding is high, offspring should lower their aspiration for parental investment because of the necessary high begging costs. For begging costs, let $C(\gamma, k_o)$ be the discount factor of offspring survival probability, being a function of total begging. The term k_o is offspring begging or the cost of begging for one unit of m. The term γ is the difference $\gamma = m_o - m_p$ between the investments opted for by parents and offspring. If $k_o > 0$ and $\gamma > 0$, then $0 < C < 1$, which means decreased survival probability. The explicit function for survival decrease dependent on total begging is assumed to be the function $C = \exp(-k_o\gamma)$, which is a convex function that ranges between 0 and 1.

First, assume the case where the offspring determine parental provisioning rate. The offspring evolutionarily stable (ESS) level of investment is found by first defining the fitness $W_o(m_o', m_o)$ of a mutant offspring that begs so often that it gets the parental investment m_o' when all other offspring get m_o (Maynard Smith, 1982). An evolutionarily stable investment is where, if all offspring adopt it, no other level of investment can increase offspring fitness (Maynard Smith, 1982).

If the normal demand in the population is m_o, a mutant offspring demanding more, m_o', will have higher survival probability $f(m_o')$. With mendelian inheritance, only half of her offspring will inherit the higher level of demand, so that average offspring demand among her offspring is $(m_o + m_o')/2$ (Parker and MacNair, 1978). When offspring control parental provisioning rate by begging, the fitness of young with begging intensity k_o demanding m_o' in a population otherwise demanding m_o, and where parents deliberately provide m_p, can, with the assumptions made, be calculated as:

$$W_o(m_o', m_o, m_p, k_o) = f(m_o')\frac{M}{\left(\frac{1}{2}m_o' + \frac{1}{2}m_o\right)}C(\gamma(m_o', m_p)k_o) \tag{12}$$

With the explicit function for C, the ESS is where the equality

$$f'(m_o^*) - k_o f(m_o^*) = f(m_o^*)/2m_o^* \tag{13}$$

holds. If $k_o = 0$, the offspring may costlessly determine provisioning rate; the ESS in this case is level (b) in Fig. 3. When $k_o > 0$, the ESS m_o^* is found where a line from the point $(-m_o^*)$ on the m-axis intersects $f(m)$ from above. Always with $k_o > 0$, m_o^* is lower than (b) (Fig. 3) and, the higher the k_o, the lower the m_o^*. A sufficient criterion for local stability of m_o^* is that $f(m_o^*)k_o < 2f'(m_o^*)$. By assumption, $f'(m_o^*) > 0$ and $0 < f(m_o^*) < 1$, which means that the solution is always locally stable when begging is low. For convergence stability (Eshel, 1983; Taylor, 1989), the following relation must be true:

$$2f''(m_o^*)(m_o^*)^2 - 4f'(m_o^*)(m_o^*)^2k - 3f'(m_o^*)m_o^* + 2f(m_o^*)(m_o^*)^2k^2 + 3f(m_o^*)m_o^*k + 2f(m_o^*) < 0 \tag{14}$$

As a counter-adaptation to the manipulation, parents may resume control over provisioning by raising their critical level and ignoring the begging (Parker and MacNair, 1979; Harper, 1986), which costs through its effect on offspring survival, because if the offspring gets less than what it opts for, it is assumed to beg when the parent is present. Thus, if offspring begging is high, the parent should keep a high provisioning rate to lower offspring begging costs. The parental counter-adaptation is denoted k_p, the minimum begging when the parents respond and provide an extra unit of deliberate parental investment. If $k_p = k_o + \delta$, so that parents are in control of m, the fitness equation of a parent with investment m_p' where population investment is m_p becomes

$$W_o\,(m_p', m_p, m_o, k_o) = f(m_p')\frac{M}{m_p'}C(\gamma(m_o, m_p')k_o) \tag{15}$$

which may yield the parent ESS. Here, k_p is taken to be approximately equal to k_o (δ is small). With the explicit function $C = \exp(-k_o(m_o - m_p))$, the ESS m_p^* for parents is the solution of

$$f'(m_p^*) + k_o f(m_p^*) = f(m_p^*)/m_p^* \tag{16}$$

If $k_o = 0$, offspring do not beg and the parental ESS in this case maximizes clutch productivity; this level is denoted (a) in Fig. 3. With begging offspring, the ESS is found where a straight line from the origin intersects the survival function from below. This value is always above (a) in Fig. 3, the more so the higher k_o. The condition for local stability of m_p^* is that

$$f''(m_p^*) + 2f'(m_p^*)\,k_o + f(m_p^*)k_o^2 < 0 \tag{17}$$

This is also the criterion for convergence stability, so that a locally stable ESS is always convergence stable. With $k_o = 0$, the ESS is always stable. With increasing k_o, stability depends on the shape of the survival curve. The first term in the condition ($f''(m_p^*)$) is always negative. Therefore, for stability of m_p^*, the second two terms should in general increase slowly with amount of begging. In other words, $f'(m_p^*) + f(m_p^*)k_o$ is low. This is the case if survival increases slowly with parental investment at the ESS and if maximum survival is low.

As long as $m_p^* < m_o^*$, there will be an arms race of k_o and k_p, because if the parent currently is in control, the offspring may increase its fitness by increasing its begging so as to be able to manipulate parental behaviour. Conversely, if the offspring is in control, the parent may increase its fitness by ignoring the begging and choose an optimum provisioning rate. An evolutionary arms race between level of begging and parental threshold leads to a decreased discrepancy between the individual evolutionarily stable strategies.

In the end, a level of begging may be reached with identical ESS for parents and offspring. The two equations

$$\begin{cases} f'(m_c^*) - k_c f(m_c^*) = f(m_c^*)/2m_c^* \\ f'(m_c^*) + k_c f(m_c^*) = f(m_c^*)/m_c^* \end{cases} \tag{18}$$

can then be solved as a linear system in the three variables $f'(m_c^*)$,$f(m_c^*)$ and $f(m_c^*)/m_c^*$. By elimination, we obtain the solution:

$$f'(m_c^*) = 3f(m_c^*)/4m_c^* \tag{19}$$

The compromise parental investment is the solution m_c^*. The conflict investment k_c at this point is $k_c = 1/4m_c^*$. This meets the stability criteria for offspring as can be seen by insertion. Inserting into the sufficient local stability criterion for offspring gives

$$f(m_c^*)k_c < 2f'(m_c^*) = 6f(m_c^*)/4m_c{}^* \tag{20}$$

Thus it must hold true that

$$k_c < 6/4m_c^* \tag{21}$$

This is always true. Inserting into the offspring convergence stability criterion yields

$$2f''(m_c^*)(m_c^*)^2 - f(m_c^*)/8 < 0 \tag{22}$$

which is always true. The parental condition for stability of the ESS is

$$f''(m_c^*) + 7f(m_c^*)/16(m_c^*)^2 < 0 \tag{23}$$

which may or may not be true, dependent on the shape of the survival curve. For example, assume that the survival function can be described by the general expression $f(m) = 1 - \exp(-c(m - a))$. Here a is the minimum investment necessary for offspring survival and c is a shape parameter. Expression (23) then reduces to $7/12 < m_c^* c$. If we arbitrarily choose $a = 1$, numerical analysis shows that this is true for values of $c \geq 0.008$.

The potential compromise solution m_c^* is the deliberately provided parental investment when begging equals k_c. At the same time, m_c^* is the offspring ESS parental investment and, as these two are identical, offspring do not beg. Begging is a way to increase parental provisioning rate, which is unnecessary if parents already provide the offspring ESS amount. For this reason, no begging cost is realized at the resolution: $C = \exp(-k_c(m_c^* - m_c^*)) = 1$.

DISCUSSION

Parent–offspring conflict resolution

Parent–offspring conflict over parental investment in birds often involves a process whereby the parent provides food with a certain frequency and young beg by calling when the parent is present. The amount of begging and the threshold when the parent responds are behavioural traits used for controlling provisioning rate and thus parental investment. As long as control over provisioning rate enables optimization of fitness, begging and parental threshold will increase in an arms race. We have shown that in this process parent and offspring optima will be adjusted, and there is a possible compromise resolution with identical optima of the two parties. This is because the optima are calculated taking into account the behavioural means available to influence parental investment. As these behaviours evolve, the extent of conflict will change because the parental and offspring optima are redefined.

Paradoxically, at resolution the young need not beg for more food. This compromise solution is stable to changes in provisioning. Changing the amount of begging does not increase fitness, as there is no realized begging cost at the compromise because of the identical optima. Lower levels of begging than the compromise level k_c are here selectively neutral and could, in principle, exist simultaneously, which may question the stability of the solution. However, any stochastic changes in food availability will create a disadvantage to these lower begging levels and tend to stabilize the solution. For example, if the condition of the offspring is temporarily lowered, so that their fitness increases faster with an increment in parental investment, the former compromise would not hold any more. There would then be different optima for parents and offspring, and an outbreak of conflict behaviour is expected at elevated levels of begging. Such disturbances would also stop lower levels of begging from invading. Consistent with this, begging is often found to be induced by food deprivation (e.g. Saino *et al.*, 2000). It is possible that such environmental disturbances of the equilibrium could hinder the equilibrium ever being reached in practice.

We used an explicit function for offspring begging cost. Although this made it mathematically easier to find the solution, it restricts the types of survival functions that may satisfy the ESS stability criterion (equation 23). If the survival function levels off very slowly as parental investment increases, the solution may not satisfy the stability criterion for parents. The explicit begging cost function also locates the compromise solution intermediate between the original parent and offspring optima. The reason for this is the symmetrical effect of parental and offspring behaviour on begging cost. Technically, m_o and m_p have equally strong effects on the begging cost C.

Resolution models of parent–offspring conflict (for a review, see Mock and Parker, 1997) suggest that offspring may influence how much food they get by begging, which is costly in terms of fitness, either energetically or because it increases predation risk. The parent may decrease the amount of begging by offspring by providing more food. In the resolution model of Parker and MacNair (1979), the increase in begging is halted by increasing begging costs that decrease fitness at equilibrium. This has been called a 'blackmail' solution (Godfray, 1995), as parents are forced to provide more resources to stop the young from begging. The solution of Yamamura and Higashi (1992) might also be seen as a form of blackmail: parents (the 'donor') provide the investment because of a threat that the offspring ('recipient') will otherwise beg. However, their idea has yet to be applied to parent–offspring conflict. A different resolution model assumes that the offspring begging behaviour provides information about their true need for resources. This can be used by the parent to distribute resources in an optimal way (Godfray, 1991). Stability of this solution is ensured by the costs of begging, and the parent controls the resolution.

The model presented here has similarities with that of Parker and MacNair (1979), in that offspring may influence parental investment by begging and begging is assumed to be costly. However, under our model, it is not these costs that stop the arms race. Following a suggestion by Trivers (1974), we assume that offspring can manipulate their parents psychologically by pretending to be more hungry than they actually are. If an offspring begs loud enough, it gets control over parental investment. Parents are favoured if they are able to 'see through' this, and there will then be an arms race between parents and offspring where parents try to detect increasingly convincing false signals of need. When the parent counteradapts, the offspring is predicted to track this by begging more loudly. Whether this mechanism can be empirically demonstrated clearly requires further research, but some evidence does point in this direction. Kedar *et al.* (2000) showed that house sparrow (*Passer domesticus*) nestlings learn to adjust their begging efforts to the level that rewards them most. If food was only provided after intensive begging, the nestlings performed more begging than nestlings that were fed as soon as they started to beg. In this way, offspring with the same need could be trained to beg at very different levels. Kölliker *et al.* (2000) have shown that variation in the begging call intensity of great tits (*Parus major*) has an additive genetic component. This is important for any resolution model where begging intensity is moulded by natural selection. Although Kölliker *et al.* (2000) could not demonstrate genetic variation in the parental response, there was a genetic correlation between the two traits, which indirectly suggests that additive genetic variation in parental response exists.

Resolution of sexual conflicts

An important class of cases where the model applies is when the variable under conflict may be adjusted in one's own favour by a series of behavioural conflicts that causes the conflict cost to increase cumulatively. Conflict behaviour investment is then costly only when the trait optima of the parties do not coincide. This is frequently the case, as in sexual conflicts over mating frequency.

Consider the following sexual conflict (see Smith and Sandell, 1998, and references therein): In breeding pairs of the starling (*Sturnus vulgaris*), males try to increase their fitness by attracting new females. The reproductive value of additional clutches decreases as the season passes, thus the male optimum time for attraction of new mates is directly after mating with the first female. His mate, on the other hand, should delay his remating attempt, as he will allocate less effort to her brood if he has another clutch. The female optimum timing of male remating is so late that she will not lose any paternal care to the other female. To hinder male infidelity, mated female starlings are aggressive towards intruding females. The male counters by behaving aggressively towards his mate. If the paired female invests enough time and energy in aggressive behaviour, she can force the male to delay his remating attempt at her will. The longer she delays it, the higher her expected cost of evicting intruding females, as the male continuously tries to attract new females. Because of this cumulatively increasing cost, the female optimum time of male remating is somewhat earlier. If the male is in control, he will be able to attract new females. His costs are higher the earlier he starts, since he must stop the already mated female from evicting intruding females. Therefore, he should delay attraction of new females. If there is an arms race of investments in antagonistic behaviours, this will result in increased costs per unit time for the party in power. The male and female optima will in the process tend to be more equal and may eventually become identical. Put differently, the male delays attraction of new females because he expects his mate to be aggressive towards intruder females. Females, on the other hand, at some point stop being aggressive because they expect the male to be aggressive and persistent in his attempt. Female interference should, at equilibrium, be observed rarely or only for a short time unless experimentally provoked.

Another case occurs in amphipods, isopods and many other crustaceans. Here males guard females for a certain time before mating, as the period when fertilization can occur is temporally restricted (for a review, see Jormalainen, 1998). This is costly for females, as it interferes with female sequestering of resources for egg-laying (V. Jormalainen, S. Merilaita and J. Riihimäki, unpublished data). For this reason, costly intersexual fights occur if a male encounters a female mature enough to be within his criterion for guarding and the intensity of the fights is related to female maturity (Jormalainen *et al.*, 2000). Assume that females fight back any male mating attempt until less time than x_f^* is left to her sexual moult. A male that targets females long before this time (male criterion $x_m >> x_f^*$) must pay a higher conflict cost because most females he targets will be reluctant to mate. Thus his behavioural conflict cost increases not only with the cost of each fight, but also with the difference between x_m and x_f^*, forcing him to decrease his guarding criterion. On the other hand, if male criterion is x_m^*, females pay higher conflict costs if they choose a criterion $x_f << x_m^*$, because of more fights. Based on the logic outlined above, the existence of costly behavioural conflict should lead to a shorter period of sexual conflict. Theoretically, this might lead to a resolution where conflict only occurs – for example, because of difficulties in assessing female maturity or uncertain information on the operational sex ratio. For a specific model of this problem, see Yamamura and Jormalainen (1996).

At the resolution of the sexual conflict, there is no difference between the male and female ESS – that is, neither side may increase fitness by changing the conflict investment, as both parties agree upon the same optimal solution. Apparent conflict behaviour will be suppressed, although both parties are ready to engage in costly conflicts. The location of the compromise within the battleground is determined by the differences between the parties in (a) sensitivity of fitness to the variable under conflict and (b) the rate of behavioural cost increase. If behavioural costs are similar, the resolution should be at a point where the increase in marginal fitness, caused by an adjustment of the variable under conflict, is of equal magnitude (although with opposite signs) for both parties (equation 10). In other words, a small adjustment away from the compromise in either direction would mean a fitness gain by one of the parties that equals the fitness loss by the other. For example, in the starling example, the resolution would be located at a time when the increase in female fitness, caused by a further delay in male remating, equals the male benefit from mating again. If the sexes have different conflict behaviour efficiencies, the compromise will be closer to the party with the less cost-consuming conflict behaviour. The costs of small adjustments are, however, critical, which may give rise to counterintuitive compromises as in Fig. 2. There the compromise is closer to the interests of the individual for whom the cost of large adjustments is larger. Our results highlight the importance of considering the behaviour of both sexes in the analysis of sexual conflicts. Male alternative reproductive strategies are often influenced by female behaviour, as has recently been pointed out (Alonzo and Warner, 2000).

Evolutionary conflicts: battlegrounds, arms races and resolutions

We have analysed cases of evolutionary conflict, focusing on stable strategies where evolutionary conflicts are mediated by antagonistic behaviours such as aggression. We have shown that, with an increase in such behaviours, the extent of the evolutionary conflict may decline, so that the costs of conflict eventually decrease. There is a potential evolutionarily stable resolution without apparent conflict or conflict costs. This resolution is in between the original evolutionarily stable strategies of the conflicting parties and can be regarded as a stable compromise. This is the new general result from our resolution model. Reasoning about probable conflict resolution has most often focused on specific systems, with the exception of Yamamura and Higashi's (1992) model of conflict resolution between a donor providing a fixed amount of help to a genetically related recipient. They argued that an arms race between the parties would continue until the inclusive fitness cost for one of the parties became so high that it was no longer advantageous to increase the conflict investment so as to win. That party would then 'give up' and the other would, thereafter, win all conflicts without any extra costs of, for example, fighting. Their solution thus always has one 'winner' and one 'loser' (Yamamura and Higashi, 1992).

The prerequisites for the process in our model are, first, that the variable under conflict is continuous, such as time, mating frequency or provisioning rate, and the two parties have different optima with respect to this variable if allowed to choose the desired value independently from each other. Second, and more importantly, there should be a conflict cost that increases with the conflict investment and also with the range of values between the individual optima.

A common factor in our examples is that either party may adjust the variable under conflict in their own favour by a series of behavioural conflicts. The conflict cost increases cumulatively with the number of conflicts. Conflict behaviour investment is then costly only when the trait optima of the parties do not coincide. In conflicts between the sexes, the number or frequency of fights between males and females causes this cumulative increase. In the parent–offspring example, the survival cost increases with the frequency of offspring begging events.

We have shown that the process of natural selection may lead to an evolutionarily stable compromise resolution in conflicts between individuals. The compromise implies identical evolutionarily stable strategies without conflict costs, but a fitness cost because the compromise is not the best choice when compared with individual optimization without any conflict. Biologically, this would mean that there is never any apparent conflict. Everything else being equal, lower conflict investments would theoretically then be selectively neutral and not be able to invade under natural selection. One could argue that, in the complete absence of sanctions against low investments, these strategies may invade small populations by drift, so that new escalations of conflicts occur and evolution in practice is cyclic. This is unlikely, as even a very small disadvantage to lower investments ensures uninvasibility of the solution. Such a disadvantage may be realistic to assume, for example because of imperfect transfer of information between opponents causing occasional conflicts to occur. Therefore, dependent on specific assumptions about the interaction, it is possible that the resolution point may not always be reached in practice.

ACKNOWLEDGEMENTS

We wish to thank Torbjörn Fagerström, Johannes Järemo, Åsa Lankinen, Olof Leimar, Kate Lessells and John McNamara for their comments on a previous draft of the manuscript.

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