



Fighting costs stabilize aggressive behavior in intersexual conflicts

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Abstract. We analyze the evolution of aggressive behavior in intersexual conflicts, with a special reference to mate guarding behavior in crustaceans. An analysis of a discrete-strategy game shows that an ESS with only one of the sexes being aggressive prevail if fighting costs or fitness values of winning are asymmetric. Non-aggressiveness of both sexes is stable if fighting behavior is very costly for females and if the cost is at least partly paid independent of the strategy of the opponent. Most interestingly, the solutions of both sexes being aggressive prevails only if both sexes have some probability of winning, and if fighting costs are small. Second, we solve for the expected levels of aggressiveness in a game with continuous strategies. The form of the fighting cost function largely determines the stability of the solution. When fighting cost increases linearly with aggressiveness, mutual aggressiveness fluctuates cyclically instead of stabilizing at an ESS. However, if there is an asymmetry in fitness payoffs, a solution with only the sex having most to lose being aggressive alone is possible. With quadratically increasing fighting costs an ES combination of mutual aggressiveness may exist. It is predicted that fights between the sexes should be hardest when payoffs are symmetric, and that an overt behavioral conflict will always take place as long as there is a fitness loss to each of the sexes if losing the conflict and both sexes have a chance to win. We discuss the models in the context of fights preceding precopulatory guarding, but the models offer a general frame for analyzing any intersexual conflict.

Key words: aggressiveness, fighting cost, intersexual conflicts, mate guarding

Introduction

Male fitness increases with mating success usually at a faster rate than female fitness (Arnold and Duvall, 1994), a fact which is attributable to the fundamental sexual differences in reproductive allocation (Trivers, 1972; Clutton-Brock and Parker, 1992). Because of this, males are expected to compete with each other over access to matings and to develop traits which are beneficial in the competition, even if these traits carry some negative consequences for the fitness of the females (Parker, 1979; Rice and Holland, 1997). For example,

reduced feeding opportunities or increased predation risk due to male mate-guarding (Rowe *et al.*, 1994; Jormalainen, 1998), risk of injury while being harassed by males (Parker and Thompson, 1980), and reduced paternal care (Lifjeld and Slagsvold, 1991; Westneat and Sargent, 1996) may represent fitness costs for females. When such costs exist, females are expected to evolve behavioral means to resist mating attempts, which in turn may lead to costs for male fitness in terms of lost mating opportunities or increased investment into persistence in contests (Alexander *et al.*, 1997).

Mating behavior of aquatic crustaceans with precopulatory mate guarding provide an example of intersexual conflict. Typically, opportunity for fertilization is temporally limited and males monopolize females by guarding them for a certain period before the copulation (Parker, 1974). Such a male strategy has been suggested to lead into a conflict, if mate guarding incurs some fitness costs for females (Parker, 1979; Jormalainen and Merilaita, 1993; Jormalainen *et al.*, 1994). It is probable that the intersexual fights, which often precede precopulatory guarding, have evolved because of such a conflict (Jormalainen, 1998).

Although behavioral contests between the sexes are common, the evolution of costly fighting behavior in itself is much less examined. In theory, the amount of investment into the behavioral contest should depend on the fitness payoffs of winning, on the powers of the contestants, and the costs of fighting (Yamamura and Higashi, 1992; Clutton-Brock and Parker, 1995; Yamamura and Jormalainen, 1996). However, the exact way that asymmetries between sexes determine optimal aggressiveness, or, what determines evolutionary stability of mutual aggressiveness, is poorly known (but see Enquist and Leimar, 1983; Hammerstein and Parker, 1987). Below, we analyze the conditions under which aggressive behavior is expected to evolve. Following Parker (1979) and Maynard Smith (1982), we treat the problem as an asymmetric game, and solve for conditions that allow males, or females, or both of them simultaneously, to behave aggressively. We begin by assuming two discrete strategies, aggressive or non-aggressive, for males and females. We then allow the aggressiveness of both sexes to vary continuously, and seek for a stable combination of male and female aggressiveness. We show that under certain circumstances mutual aggressiveness of both sexes may be a stable solution, and that the relationship between the fitness cost and the level of aggression is crucial for the evolutionary stability of aggressiveness. We apply our results in a specific context of mate guarding conflict in order to exemplify the usage of these otherwise general models.

Discrete female and male strategies

The breeding period begins with mate search by males. Each female copulates only once during a mating cycle. Upon meeting a mature female, the male is

assumed to approach her in order to start precopulatory guarding. Let W_u represent the expected number of eggs the female is able to lay if not guarded by the male. We assume two discrete pure strategies, non-aggressive (N) and aggressive (A). A non-aggressive male can keep his hold only if the female does not resist. An aggressive male is persistent in his attempt but if the female escapes anyway, he has to continue mate search. We assume that (i) the aggressive behavior of the male costs $C_1 > 0$ in male fitness if the female is resisting, but that (ii) only a fraction h ($0 \leq h \leq 1$) of the cost C_1 is paid if the female is not resisting. A failure in mate guarding (iii) leads to a cost y on male fitness. (iv) A non-aggressive female never resists and can therefore never escape from a male attempting to guard. (v) Precopulatory guarding costs z in female fitness so that she only lays $W_u - z$ eggs. (vi) An aggressive female resists, which costs $C_2 > 0$ on female fitness if the male is persistent. If he is not, (vii) it only costs her a fraction h of C_2 to be aggressive, just as in males. We assume further that female resistance has two consequences: (viii) aggressive females always escape from the hold of non-aggressive males, and (ix) they escape from aggressive males with a probability e ($0 \leq e \leq 1$; see Table 1 for definition of parameters). (x) If able to guard the female, the male will get W_p offspring, which equals the expected number of eggs the female will lay after guarding.

Predictions: precopulatory guarding and temporal patterns of aggressive behavior

The analysis of the game is found in Appendix 1. We found four possible evolutionary stable solutions for the game (Table 2). The solution of the game may not lead to behavioral contest between the sexes, that is, stability of the

Table 1. List of symbols used in the models and their definitions

Symbol	Definition
p	The frequency of aggressive individuals among males
q	The frequency of aggressive individuals among females
y	Male cost of losing an opportunity to mate
z	Female cost of being in precopula until molt
C_1	Male cost of fighting
C_2	Female cost of fighting
h	The proportion of the fighting cost paid if the opponent is passive
e	The probability of escape in encounters of two aggressive individuals
b	Male level of aggressiveness
c	Female level of aggressiveness
W_u	Number of offspring possible without female costs of either fighting or guarding
$W_p = W_u - z$	Value of the female to the male
r	Rate of increase of fitness cost of aggressiveness

Table 2. Evolutionary stable pairs of pure strategies (N = non-aggressive and A = aggressive) for males and females according to the conditions defined in the Appendix 1, and under assumptions of at least some cost of aggressiveness ($0 < h \leq 1$) or no cost of aggressiveness ($h = 0$) in encounters between an aggressive and a non-aggressive individual

ESS-pairs	Strategy	$0 < h \leq 1$	$h = 0$
ESS1	Male N	$C_1 > 0$	Not possible
	Female N	$hC_2 > z$	
ESS2	Male N	$C_1 > y(1 - e)$	$C_1 > y(1 - e)$
	Female A	$hC_2 < z$	$C_2 < \infty$
ESS3	Male A	Not possible	$C_1 < y(1 - e)$
	Female N		$C_2 > ez$
ESS4	Male A	$C_1 < y(1 - e)$	$C_1 < y(1 - e)$
	Female A	$C_2 < ez$	$C_2 < ez$

solution where both sexes are aggressive. In the case of ESS1, there is no escalation because both sexes behave non-aggressively. The same concerns ESS2 because now the male will detach immediately if the female resists, and ESS3, because the female is completely passive and the male will never have to escalate the conflict. In contrast, ESS4 represents a stable solution where both sexes are motivated to fight. A necessary but not sufficient condition for ESS4 is that both the male and the female have a chance to win the conflict (Appendix 1).

In mate-guarding crustaceans the start of precopulatory guarding is often preceded by a period of intersexual contests (reviewed by Jormalainen, 1998). These contests may have three possible outcomes: (a) female resists violently and escapes, (b) male detaches the hold, or (c) permanent precopula is established (Styron and Burbanck, 1967; Strong, 1973; Jormalainen and Merilaita, 1993). The first and second possibilities are incorporated in our parameter e defined as the probability that the female escapes, i.e. no permanent precopula is established. Consequently, females have a chance to escape and therefore we have here a potential case of both males and females having adopted an aggressive strategy.

The present analysis focuses in encounters with males and females at a given moment of the female molt cycle. Therefore, for instance, ESS2 may prevail during some part of the molting cycle, but not during the entire cycle because this strategy pair will never end with a permanent precopula. A possibility to deduce a potential sequence of solutions during the female molting cycle is to consider $y(t)$ and $z(t)$ as variables that vary as a function of time to female ecdysis (t). As suggested by Jormalainen *et al.* (1994) and Yamamura and Jormalainen (1996), the optimal time to start precopula in the female molting cycle may be different for males and females when females face some cost due to guarding.

According to these previous models a common situation leading to a behavioral contest was that the male optimum guarding duration t_m exceeded the female optimum t_f , i.e. males aim to longer guarding than what is optimal for females. Then, males should not be interested in to start guarding females that are further from their molt than the male optimum. At the male optimum $y(t)$ will be zero, and after that positive increasing towards the day of female sexual molt as the value of the female to him increases (Fig. 1). In the case of females, $z(t)$ will be positive above the female optimum, and will gradually decline toward 0 when approaching the female optimum (Fig. 1). Cost curves $y(t)$ and $z(t)$ will intersect each other both being positive only when the male optimum (t_m) exceeds the female optimum (t_f). In Figure 1, we have treated the costs of aggressiveness and e as constants and assumed further that $C_1 = C_2 > 0$.

If we now apply the solutions of the present game (Table 2: $0 < h \leq 1$) to Figure 1, we get the following succession for male and female behavior when t approaches 0:

1. When $t_3 < t$, then males N and females A.
2. A period of conflict: When $t_2 < t < t_3$, then both A. When $t_1 < t < t_2$ then no pure ESS.
3. When $0 < t < t_1$ then both N.

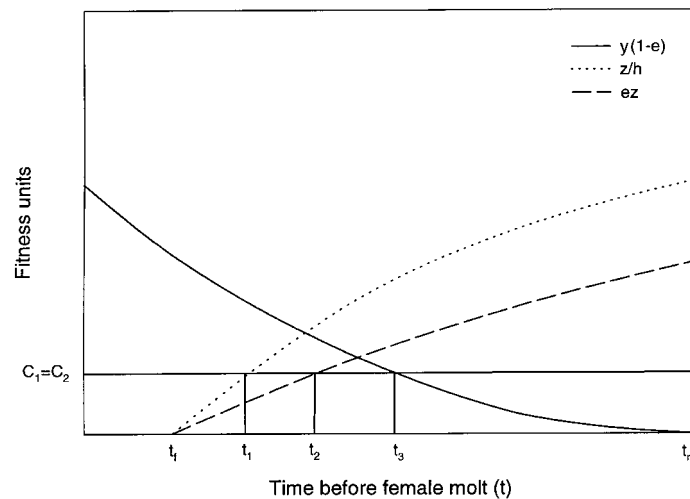


Figure 1. Hypothetical sequence of the different ESSs before the female molt when male and female costs are dependent on time, and some fighting cost is paid also in encounters with a passive opponent, i.e. $0 < h < 1$. Male optimum guarding time is t_m and female optimum guarding time is t_f . The intersections between the cost line $C_1 = C_2$ and the curves define when the ESSs are changed. As t approaches zero, the sequence is Male N, Female A ($t_3 < t$), Both A ($t_2 < t < t_3$), No ESS ($t_1 < t < t_2$), and both N ($t < t_1$). For $h = 0$ the sequence is Male N, Female A ($t_3 < t$), Both A ($t_2 < t < t_3$), and Male A, Female N ($t < t_2$).

So during the first period, females are aggressive because $z(t)$ is high relative to the cost of aggressiveness, whereas $y(t)$ is low and hence males are not motivated to fight. This should be interpreted as females being prepared to escalate, but males withdrawing immediately. A period of conflict follows when $z(t)$ declines and $y(t)$ increases enough ($t_2 < t < t_3$, Fig. 1). Now males are highly motivated to start a permanent precopula, but females are not. After this follows a period when there is no pure ESS solution to the game. Finally, as the day of female molt approaches, females become non-aggressive and a permanent precopula will be the result.

A slightly different schedule is followed if $h = 0$, i.e. if there is no cost for fighting with a non-aggressive partner. As in the previous case, there is first a period when males are non-aggressive and females aggressive (ESS2), followed by a period with both sexes aggressive (ESS4). When females are more mature, the solution will be that females are non-aggressive and males aggressive (ESS3). In this case, however, males will not have to take females by force, as they do not resist males' guarding attempts.

This hypothetical latter sequence fits especially well to the descriptions of the sexual behavior of several mate-guarding crustaceans (e.g. Strong, 1973; Jormalainen and Merilaita, 1993): When being far from the sexual molt females resist heavily, and males often retreat. Later, both sexes fight heavily and contests last for longer. Finally, after the start of guarding female resistance ceases completely. Our model naturally describes at best only some general patterns of sexual behavior that may be found. More detailed analyses are, however, possible only if aggressiveness is assumed to be a continuous parameter (cf. Grafen and Sibly, 1978).

Continuous strategies and fighting costs

We continue by formulating a game between males and females where aggressiveness is allowed to vary continuously, seeking evolutionary stable solutions for male and female aggressiveness when both are ready to escalate. As before, let W_u represent the number of eggs a female is able to lay if she is unguarded before mating. Guarding will decrease this number by the factor z so that she only lays $W_u - z$ eggs and z is assumed to increase with guarding duration. Let y represent the fitness cost for a male if he does not succeed in holding the female. The fitness of the male will then be $W_p - y$. The cost y comes from the low probability of finding a new female of equal value as the lost one. Both sexes can affect the outcome of a contest by showing some level of aggression, which we call persistence (b) for males and resistance (c) for females. There is a fitness cost (C) of fighting, in terms of energy or otherwise. In Appendix 2, we derive fitness equations for males and females as a function

of their mutual aggressiveness. We proceed by finding the levels b^* and c^* which are the best responses for an individual with respect to the aggressiveness of the opponent. These are functions $b^*(c)$ and $c^*(b)$ that are best responses in the sense that they maximize individual fitness given that an opponent showing a certain aggressiveness is met (Maynard Smith, 1982). We analyze two cases; we let the fitness cost of fighting increase either linearly or with an accelerating rate with the level of aggressiveness.

First consider the case when the fitness costs of fighting increase linearly with the level of aggressiveness. If the cost of aggressiveness for both sexes increases faster than the fitness benefits, the ESS is for both not to show any aggressiveness (see Appendix 2). With lower cost increase rate, and if simultaneously the costs of loosing the conflict are symmetric, there will be cyclical dynamics of mutual aggressiveness. From the initial case of no aggressiveness both b and c will start to increase (Fig. 2a). However, as the fighting costs are steadily increasing with aggressiveness, at some level of b or c further escalation will become so costly that it will give higher fitness for one of the parties to decrease its aggressiveness to zero. This will move the combination of c and b from the region of increasing aggressiveness into the region of decreasing aggressiveness. We will end up at one of the intersection points between an axis and a best response line. At this intersection point, it is always possible for the passive part to increase fitness by showing some aggression (Fig. 3). This moves the combination (c, b) again into the region of increasing aggressiveness, and we have completed a full cycle (Hårdling, 1999).

In contrast, when there is an asymmetry between the sexes with respect to potential fitness loss ($y \neq z$) there is one locally stable solution (Fig. 2b). This is found at the intersection point between the axis and the best-response line of the sex with the most to lose. In other words, the asymmetry determines the solution of the game, as it is always possible to get a solution where the one with the most to lose is the only aggressive part. However, this solution is locally, but not globally stable, because by increasing aggressiveness by a relatively large amount it is still possible to increase fitness (Fig. 3).

A completely different evolutionary dynamics of aggressiveness arises when we let the fitness cost increase with an accelerating rate as more effort is put into fighting. The best response functions $c^*(b)$ and $b^*(c)$ now intersect so that there is a combination of c and b which are the best responses to each other (Fig. 2c). This point is a stable ES combination (Appendix 2). In other words, we can now expect certain, stable levels of aggressiveness for both parties to evolve.

We have assumed that a mating between two non-aggressive individuals took place with a probability of 0.5. However, even if mating would always follow from such encounters it would not change the main results. When females are not resisting, then it never pays males to be aggressive. So, we

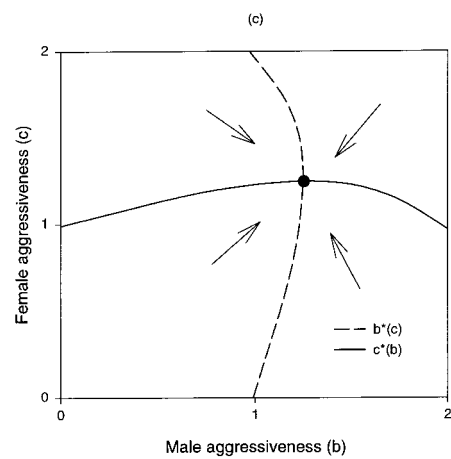
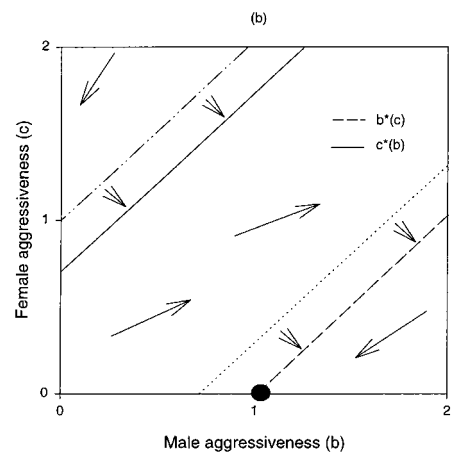
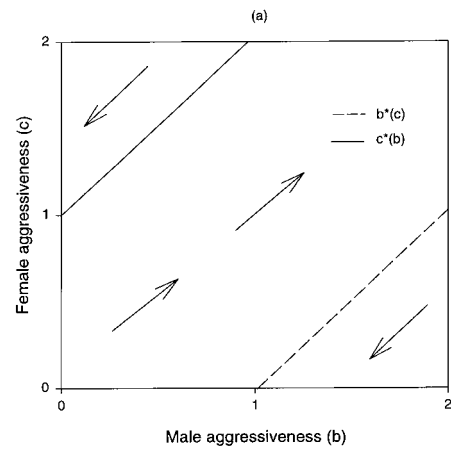
Figure 2. The best response curves and the resulting vector fields for the continuous model under varying assumptions on symmetry of conflict costs and the relationship between aggressiveness and fitness costs of fighting. (a) Fighting costs are linearly increasing, and conflict costs are symmetric. Between the lines there is a region with increasing aggressiveness, and outside the lines aggressiveness is decreasing. The figure is drawn for $z = 2$, $y = 2$, $r = 1/5$. (b) Linearly increasing fighting costs, but asymmetric conflict costs for the sexes, i.e. $z = 1$, $y = 2$, $r = 1/5$. In addition to the best response lines, the dotted line shows the function $c(b)$ that minimizes female fitness. The dash-dot-dot line shows the corresponding function $b(c)$ for male fitness (see Appendix 2). There is a stable point at one of the intersection points between an axis and a best-response line. (c) Fighting costs are exponentially increasing. At the intersection point between the two best-response curves, there is a stable point, towards which all the trajectories direct. The figure is drawn for the values $z = 2$, $y = 2$, $r = 1/5$.

would not expect males to start being aggressive. On the other hand, females will have much to gain by showing even a little bit of resistance, as they would, with a minimal cost, get a greater than 0.5 chance of escaping. Thus, females would start being aggressive, pushing the levels of aggressiveness into the region of fighting, and we would anyway end either to the cyclical dynamics or to the stable combination of mutual aggressiveness.

Predictions: Costs and stable levels of aggressiveness

The result from the continuous game shows the crucial importance of fighting costs in stabilizing aggressiveness in games, in which one individual in the conflict may gain something at a cost to the fitness of the other. In the case of linear fighting cost functions, there is no stable combination of the male and female aggressiveness. However, if the conflict costs increase quadratically with the chosen aggressiveness, it is possible to find a stable level of aggressiveness for both sexes. This is a biologically interesting case, as it can be used to predict the levels of aggressiveness and the probable outcomes of actual fights.

Intersexual conflicts typically have asymmetric gains (e.g. Parker, 1979). The conflict over the start of guarding is especially interesting because asymmetries change with the reproductive stage of the female. By defining the precise way in which they change, it is possible to get predictions on how the mutual aggressiveness should change with the female maturity. Instead of giving exact values for z and y , we have shown the effect of the degree of asymmetry in these cost on the stable levels of aggressiveness (Fig. 4a). Analogously with the example in Figure 1, we may assume that when being far away from the female molt the cost of loosing is high for the female, but low for the male. That would be the case at the far right of the horizontal axis in Figure 4a. With the approaching sexual molt of the female this asymmetry changes as the cost of losing decreases for the female but increases for the male. This change in asymmetry is shown when moving to left along the horizontal axis in



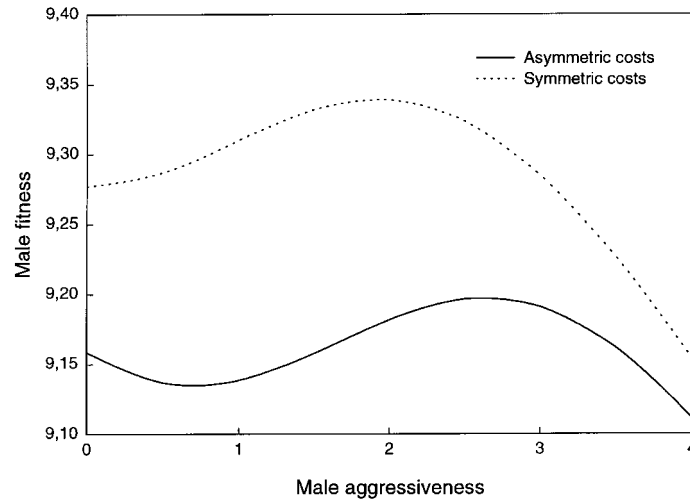


Figure 3. Male fitness as a function of male aggressiveness when the female fights with the best response to a passive individual, as defined by Equation (A2.7) for $b = 0$. Symmetric Costs: The fitness when conflict costs are equal for both sexes (drawn for values: $z = 1$, $y = 1$, $r = 1/5$). Asymmetric Costs: The fitness for the sex with the smallest cost when costs are unequal ($z = 1.5$, $y = 1$, $r = 1/5$).

Figure 4a. As can be seen, the optimal aggressiveness level varies depending on who has the most to lose in the conflicts. The one with the higher potential loss in the conflict is expected to invest more in aggressiveness. As long as it is costly in terms of fitness to lose the fight, it is always beneficial for both parts to show some aggressiveness; the only points where it is optimal to be passive, i.e. adopt b or $c = 0$ is when z or $y = 0$ (Fig. 4a). When both have equal costs if losing, both sexes have equal aggressiveness. Also, the probability of either one of winning the contest is then 0.5, whereas in other cases the sex having the higher aggressiveness has a better chance of winning (Fig. 4b). Therefore, we expect the most intense and prolonged fights at the time when the conflict costs are the same for both of the sexes. Before that time, the encounters are likely to result in separation of the individuals, and after that, the probability of precopula formation increases as the male aggressiveness exceeds the one of the female.

The case of linearly increasing fitness cost of aggressiveness, in which an asymmetry in the costs of losing created a locally stable point where only the sex with the most to lose was expected to be aggressive gives a result similar to that of Yamamura and Jormalainen (1996). They suggested that the conflict could be resolved by a 'compromised guarding criterion', found where the level of the maximum acceptable fighting costs, i.e. amount of the fitness gain if winning the contest, was the same for males and females. In contrast, the case with

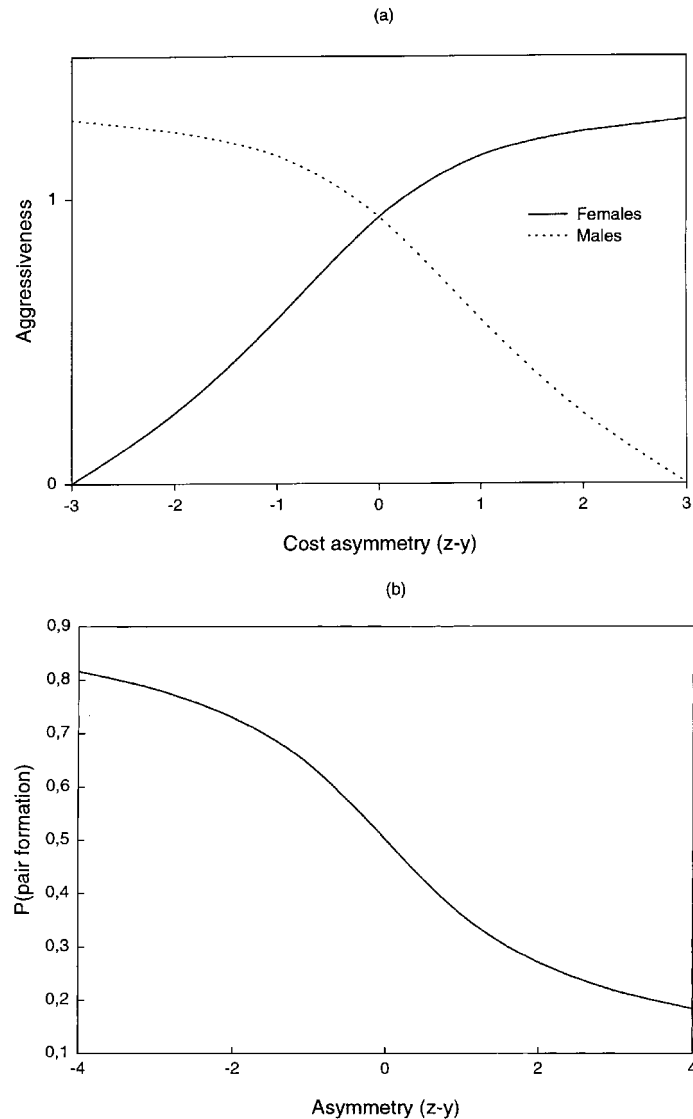


Figure 4. (a) Stable aggressiveness levels for different conflict cost asymmetries when the fitness cost of fighting is exponentially increasing. (b) The probability of pair formation expected from the stable aggressiveness levels from (a). The graphs are drawn for $r = 1/5$ and $z + y = 3$.

quadratically increasing fitness cost of fighting, predicts that both sexes should show aggression, i.e. overt contests should always follow, when both parties have something to lose. Contests are most pronounced when the fitness gains of winning are close to each other, but even if they are not, showing at least some aggression may be beneficial as there may be a slight chance of winning.

Discussion

The models presented here analyze evolutionary conflict between the sexes in the sense that male and female fitness depends on the phenotypic strategy of the opposite sex. Our treatment of the game with discrete male and female strategies is similar to Parker (1979), although there are differences. The most important is that we allow aggressiveness to have some costs also in encounters between an aggressive and a non-aggressive individual, which may often be more realistic. In Parker's game this cost was never paid because the passive party was overcome without aggressiveness. When costs are present in contests between an aggressive and a non-aggressive individual ($h > 0$), the set of solutions was different from Parker's results. The condition for both sexes being aggressive is the same, but one ESS is lost (ESS3) and one is added (ESS1) (Table 2). In addition it is now possible to get a solution without any ESS at all. In this case, the frequencies of aggressive males and females cycle. The population might in this case be polymorphic for aggressiveness, or the sexes may adopt a mixed strategy, or the population may most of the time adopt one of the pure ESSs although these rapidly change whenever there is an appropriate mutant (Maynard Smith, 1982).

We can assume that initial condition would be a population without aggressiveness, and that mating always takes place in encounters with two non-aggressive individuals. In such a case, aggressiveness would first emerge from a non-aggressive state as a female strategy for resisting and escaping males. However, the proportion of the aggressiveness cost paid in an encounter with a non-aggressive individual (h) effectively restraints emergency of aggressiveness. The higher this proportion, the lower the acceptable fighting cost can be. The probability that the strategy pair of both sexes being non-aggressive (ESS1) prevails then increases (Appendix 1). The strategy pair of males being aggressive and females not, is now impossible because it will never pay males to accept the cost of aggressiveness if females are passive (Table 2).

The relationship of fighting costs to what can be achieved by winning (Clutton-Brock and Parker, 1995) as well as whether or not these costs are dependent on the opponent (Parker, 1979; Haig and Rose, 1980; Johnstone and Norris, 1993) are generally important determinants of the resulting strategies in game theoretic models. This, together with the mutual chance of winning the contest, was also emphasized by the results from our discrete model. The results from the model with continuous strategies further extended the role of fighting costs for the stability of the solution. For the case when the fitness cost of fighting increased linearly with the level of aggressiveness, we found two possible solutions. If there was symmetric fitness gains to both of the sexes, there was no single stable solution to the game. Instead, male and female aggressiveness would escalate in an arms race until for one of them the fighting

cost overrides the fitness gain if winning. Then with no prospects of winning this party is selected for passiveness, which selects for decreased aggressiveness of the counterpart. This cycle will be repeated over and over again, i.e. the dynamics of mutual aggressiveness is fluctuating and no stable state will be reached (Härdling, 1999).

If there is an asymmetry in the gains so that it is more costly for males to lose the contest than for females, or vice versa, there is also a possibility for a locally stable solution. This solution is for the sex with the most to lose to be aggressive and for the other one to remain passive. A necessary assumption for this solution is that only small consecutive increments in aggressiveness are possible. This could be the case for example if aggressiveness is genetically determined, and, assuming that one mutation can only slightly change the level of aggressiveness. Then the passive part cannot increase fitness by choosing a small aggressiveness level (cf. Fig. 3). However, if it is possible to make big momentary changes in the level of aggressiveness, it is always possible to increase fitness by increasing aggressiveness. In this interpretation, more apt to describe a behavioral contest, there is no stable solution of the game, and we have again fluctuating dynamics.

The main result of the continuous model was that the stability of the mutual aggressiveness was sensitive to the form of the fighting cost function. Accelerating fighting costs may stabilize aggressiveness to a certain level, determined by the rate of increase of these costs and the fitness benefits if winning the conflict. At this level, the opponent cannot do better by withdrawing and assuming total passivity. Thus, the type of accumulation of fighting costs is extremely important. Unfortunately, not much empirical data exists for evaluating the reality of the accumulation of the fitness cost of fighting. In a detailed study on energetic costs of fighting between house cricket males, Hack (1997) found that several tactics, with different energetic costs, were used during a fight, and that the net oxygen consumption increased linearly with the fight duration. However, the energetic cost of fighting as such does not tell much about the form of fitness cost. In house crickets the fighting cost was large enough to constitute a significant portion of the daily energy budget and to reduce mating success by limiting spermatophore production (Hack, 1997). Resource depletion due to fighting may thus lead to exhaustion and need for foraging, both of which may lead to lost mating opportunities and increased predation, and decreased fecundity. These effects of resource depletion and foraging costs may well imply an accelerating increase in the fitness cost of fighting with the aggressiveness. The same may be true with the fitness costs of female resistance in pre- or post-mating struggles in water striders; the energetic costs of struggling increase with the level of resistance (Watson *et al.*, 1998), and at the same time struggling may increase predation risk (Rowe, 1994).

To conclude, both the discrete and continuous model presented here showed that mutual aggressiveness can be an evolutionary stable solution to an intersexual conflict, thus, providing an analytical tool to understanding behavioral contests, and their dynamics, so commonly found as a part of mating behavior (e.g. Clutton-Brock and Parker, 1995; Arnqvist, 1997; Jormalainen and Merilaita, 1993; Jormalainen, 1998). In water striders, sexes fight over both pre- and post-copulatory guarding (Arnqvist, 1997). In the fly *Dryomyza anilis*, males try to mate repeatedly with the same female. The female resists this as it delays oviposition (Otronen, 1994). Behavioral conflict over the type of breeding association occur in species as widely separate as burying beetles (Eggert and Sakaluk, 1995) and starlings (Sandell and Smith, 1996). Furthermore, the form of the fitness cost of aggressiveness plays a crucial role in defining evolutionary stability of aggressive behavior. The mutual levels of aggressiveness in intersexual conflicts may show either fluctuating evolutionary dynamics or stability determined by the fitness gains of winning. Showing some aggressiveness may always pay if there is something to win and even a slight chance of winning. Therefore, overt contests should almost always follow, being most pronounced when the fitness gains of winning are close to each other's. We conclude that the influence of fighting costs on the evolution of aggressive behavior deserves further theoretical and empirical investigation.

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Appendix 1

Let us assume that there are two strategies available for males: E_1 (Aggressive, (A)) and E_2 (Non-aggressive, N) present in frequencies p and $1 - p$. The mixed strategies $(p, 1 - p)$ for males are denoted \mathbf{p} . Females have the same strategies to choose from, and the frequency of A among females is q and the frequency of N is $1 - q$. Hence the mixed strategies are \mathbf{q} . We will denote the payoff matrix for males by M and the payoff matrix for females by F . The payoffs are then $\mathbf{p} \cdot M\mathbf{q}$ for males and $\mathbf{q} \cdot F\mathbf{p}$ for females. A pair (\hat{p}, \hat{q}) is a Nash equilibrium when \hat{p} is the best reply to \hat{q} and \hat{q} is the best reply to \hat{p} (Hofbauer and Sigmund, 1998), i.e. if

$$\mathbf{p} \cdot M\hat{q} \leq \hat{p} \cdot M\hat{q} \text{ for all } \mathbf{p} \text{ and} \quad (\text{A1.1})$$

$$\mathbf{q} \cdot F\hat{p} \leq \hat{q} \cdot F\hat{p} \text{ for all } \mathbf{q}. \quad (\text{A1.2})$$

Let

$$M = \begin{bmatrix} W_p - C_1 - ey & W_p - hC_1 \\ W_p - y & W_p \end{bmatrix},$$

$$F = \begin{bmatrix} W_u - C_2 - (1-e)z & W_u - hC_2 \\ W_u - z & W_u - z \end{bmatrix}.$$

Symbols are explained in the text and Table 1. ESS implies strict Nash equilibrium, i.e. inequalities in Equations (A1.1 and A1.2). Then no mixed strategies can be part of an ESS (Selten, 1980; Hofbauer and Sigmund, 1998).

When males and females pair randomly with respect to their behavioral strategies, the fitness of male strategy (E_i) in the pair-wise contests is $W_m(E_i) = (M\mathbf{q})_i$ and similarly for females the fitness of strategy (E_i) is $W_f(E_i) = (F\mathbf{p})_i$. This implies that aggressiveness is favored in the male population, $W_m(A) > W_m(N)$, if

$$C_1 < \frac{qy(1-e)}{(h+q-hq)} \quad (\text{A1.3})$$

and that aggressiveness is favored in the female population, $W_f(A) > W_f(N)$, if

$$C_2 < \frac{(1-(1-e)p)z}{(h+p-hp)} \quad (\text{A1.4})$$

As said ESS must consist of pure strategies, thus we will only consider $p = 0$ or 1 and $q = 0$ or 1. The conditions for the respective ESS are given in Table 2.

Assuming $h > 0$, we obtain three evolutionary stable pairs of male and female strategies (Table 2): both N (ESS1), male N female A (ESS2), and both A (ESS4) (Fig. 5a). The third remaining pair (ESS3) is not possible in this case as it requires $hC_1 < 0$, contrary to our assumptions. The condition for ESS1 is straightforward. It does not pay females to be aggressive if the cost of being aggressive towards a non-aggressive partner exceeds that of precopulatory guarding. If, on the other hand, all females are non-aggressive, it does not pay males to be aggressive if the aggressive behavior is costly. These conditions naturally follow from our assumption that an encounter with two non-aggressive individuals results in mating.

The two other evolutionary stable strategies need some further thought. If all males are non-aggressive, it pays females to be aggressive if the cost of being guarded exceeds the costs of rejecting a non-aggressive male with force (ESS2). If all females are aggressive, the precopulatory attempts by non-aggressive

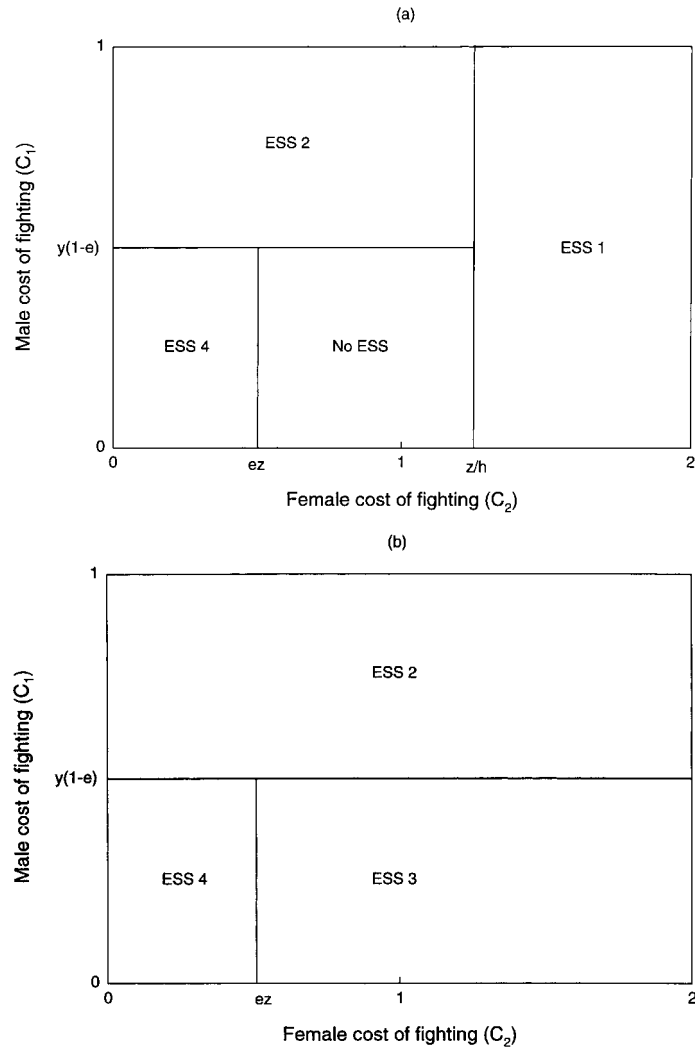


Figure 5. Regions in $C_1 - C_2$ space where the conditions for the different ESSs hold, assuming (a) $h = 0.8$ and (b) $h = 0$. The conditions are given in Table 2. The graphs were drawn assuming $C_1 = 1$, $C_2 = 1$, $z = 1$, $e = 0.5$, $y = 1$.

males always leads to a failure, while aggressive males succeed with a probability $1 - e$. Passive males will have the fitness $W_p - y$, or $W_p - ey - (1 - e)y$. Aggressive males will have the fitness $W_p - C_1 - ey$. If $C_1 > (1 - e)y$ then all males should be passive.

The requirements for ESS4 are especially interesting because they imply a behavioral contest between the female and male, and because the probability of escape (e) influences choices of both sexes. Rewriting the condition of ESS4 gives

$$\frac{C_2}{z} < e < \frac{y - C_1}{y} \quad (\text{A1.5})$$

where C_2/z determines the lower boundary indicating that e , the probability that a resisting female escapes, must be sufficiently high otherwise females N. On the other hand, $(y - C_1)/y$ gives the upper boundary for e above which males N. As C_1 and C_2 are both >0 , ESS4 is not possible unless the probability of escape (e) assumes values somewhere between 0 and 1. In other words, both sexes must have a chance of winning the contest.

For $ez < C_2 < z/h$ and $y(1 - e) > C_1$, instead of a pure ESS, there is an equilibrium (\hat{p}, \hat{q}) where $\hat{q} = hC_1/(y(1 - e) - C_1(1 - h))$ giving $M(\text{N}) = M(\text{A})$ and $\hat{p} = (z - hC_2)/(C_2(1 - h) + z(1 - e))$ giving $F(\text{N}) = F(\text{A})$. In such a situation, ESS1 does not hold because $hC_2 < z$; neither ESS2 because $C_1 < y(1 - e)$; and ESS4 does not hold because $C_2 > ez$ (cf. Table 2). If males are aggressive it pays females to be non-aggressive, but if females are non-aggressive then so should males be. If males are non-aggressive females should be aggressive, and if females are aggressive then males should also be aggressive. We are back to where we started, and cycles are certain in this situation. However, the final outcome of the situation is uncertain. Maynard Smith (1982) has suggested that the population will temporarily be at some solution, but that the vulnerability to invasions means that there will be a change to a new solution whenever appropriate mutations appear. Hofbauer and Sigmund (1998) allow mixed strategies in this situation and describe the evolution of the frequencies of pure strategies by systems of differential equations. The behavior of the system depends on exactly how the evolution is approximated by the differential equations. One possibility is that the equilibrium is neutrally stable, i.e. the frequencies of p and q cycle around the equilibrium point with a constant amplitude. With other forms of system dynamics, the equilibrium is asymptotically stable so that p and q will eventually settle at the equilibrium values (\hat{p}, \hat{q}) (see also Maynard Smith, 1982). This fifth solution is possible unless both h and $e = 1$, in which case the region vanishes where the condition for C_2 holds (Fig. 5a).

In the special case in which aggressiveness does not have any cost at encounters with a non-aggressive individual ($h = 0$), the set of stable strategies will be different (Table 2, Fig. 5b); male N and female A (ESS2), male A and female N (ESS3) and both A (ESS4). ESS1 is now impossible, which has a simple explanation. If males are not persistent, it always pays females to be aggressive, because she does not have to pay the cost of aggressiveness anyway. She will only gain by being able to overcome the males guarding attempts. On the other hand, this set of solutions contains ESS3, males A and females N, which is impossible unless $h = 0$. It may seem strange why males should be aggressive although females are passive, but we must remember that the cost for male aggressiveness will never be actually paid. If males are aggressive, it is

best for the females to be passive. The ESSs with only one of the sexes being aggressive should be interpreted as only one of the sexes is prepared to escalate. In this set of solutions there is no region without a pure ESS (Fig. 5b).

Appendix 2

We formulate the fitness equations for males $W_m(b, c)$ and females $W_f(b, c)$ with a basic fitness and additive benefit and cost components:

$$W_m(b, c) = W_p - y + B_m(b, c) - C_m(b) \quad (\text{A2.1})$$

$$W_f(b, c) = W_u - z + B_f(b, c) - C_f(c) \quad (\text{A2.2})$$

$P(b, c)$ is the probability that a male fighting at the level b wins a behavioral conflict over a female fighting at the level c .

$$P(b, c) = \frac{1}{1 + e^{c-b}} \quad (\text{A2.3})$$

This function increases with b in a sigmoidal fashion and reaches between 0 and 1, assuming the value 0.5 when $b = c$. Therefore, when both sexes are investing the same level in behavioral contest, the probability of precopula formation is 0.5. The value of the fight for males is y , and thus the male benefit function is $B_m(b, c) = yP(b, c)$. The female benefit of resisting is similarly given by $B_f(b, c) = z(1 - P(b, c))$. We first consider a linear form of cost function, with r measuring the rate of cost increase with increasing aggressiveness. When a female tries to resist a male, the fitness equation of the female meeting a male with aggressiveness b is

$$W_f(b, c) = W_u - rc - z + \frac{z}{1 + e^{-(c-b)}} \quad (\text{A2.4})$$

and the fitness equation for the male is

$$W_m(b, c) = W_p - rb - y + \frac{y}{1 + e^{c-b}} \quad (\text{A2.5})$$

A unique local ESSs of Equation (A2.4) i.e. a single strategy $c^*(b)$ that is immune against invasion by any c mutant is called the females best response to a given level of b . This can be found by solving the usual ESS condition

$$\left. \frac{\partial W_f}{\partial c}(b, c) \right|_{c=c^*} = 0 \quad (\text{A2.6})$$

(Maynard Smith, 1982). In our case there are two solutions, one corresponds to a fitness maximum and one to a minimum. The fitness maximum solution gives

the best response, and the condition for maximum is that the second derivative of $W_f(b, c)$ is negative. The females' best response $c^*(b)$ (Motro, 1994) is in the case of linear cost functions the straight line

$$c^*(b) = b - \ln\left(\frac{z - 2r - \sqrt{z(z - 4r)}}{2r}\right) \quad (\text{A2.7})$$

The fitness minimum solution gives another function $c(b)$, for the value of c that minimizes fitness against b , which is also a straight line and identical to (A2.7) except that the minus sign before the square-root is exchanged for a plus sign. The best response $b^*(c)$ for males is because of symmetry otherwise identical to the best response for females (A2.7), but exchanging the b on the right-hand side for c , and z for y .

There is no intersection point between the two lines of best responses, i.e. there is no evolutionarily stable combination (b^*, c^*) and we must proceed in another way to find the probable outcome of the game. Evolutionary change can be regarded as guided by the fitness gradient (Brown and Vincent, 1987; Abrams *et al.*, 1993; Dieckman and Law 1996), which in one dimension is the slope of the fitness function on the trait value. If two traits evolve independently, the evolution of each trait is guided by the derivative of the corresponding fitness function. Thus in each point in $b - c$ space the vector

$$u(b, c) = \left(\frac{\partial W_m}{\partial b}(b, c), \frac{\partial W_f}{\partial c}(b, c)\right) \quad (\text{A2.8})$$

gives the direction of evolutionary change in b and c . The elements in the vector are always negative if $r > y/4$ and $r > z/4$, and in this case the ESS is $(b^*, c^*) = (0, 0)$. If r is lower than this, b and c can be under positive selection pressure. In Figure 2 the arrows show the direction of $u(b, c)$, found by calculating the signs of the elements in the vector. By plotting the vector field $u(b, c)$ for different parameter values, we can find ES combinations of b and c . In the vicinity of a convergence stable equilibrium the field is directed towards the eq. point. We have made such an analysis for the cases of symmetric (Fig. 2a) and asymmetric (Fig. 2b) gains.

In Figure 2a, the $b - c$ trait space is divided into three regions by the best-response lines. Between the best-response lines there is a region where both elements of $u(b, c)$ are positive, and outside this region, both elements are negative. Because of the symmetric gains in this case, the line for best response of one sex coincides with the fitness minimum line of the other sex. Due to the asymmetry these lines do not coincide in Figure 2b, and there are thus five different regions limited by the best-response lines and the fitness minimum lines. In the two narrow regions where b increases and c decreases (Fig. 2b), the first and second element of $u(b, c)$ are positive and negative, respectively.

Accelerating cost

We propose the quadratic form $C_i(x) = rx^2$ to describe this situation, changing the fitness expressions to

$$W_m(b, c) = W_p - rb^2 - y + \frac{y}{1 + e^{c-b}} \quad (\text{A2.9})$$

and

$$W_f(b, c) = W_u - rc^2 - z + \frac{z}{1 + e^{-(c-b)}} \quad (\text{A2.10})$$

The best response lines now intersect (Fig. 2c). The stability of this ES combination is seen from the vector field as all evolutionary trajectories point towards the stable combination of c^* and b^* (Fig. 2c). We used an iterative procedure to find the numeric values for this combination: Initially setting $b = 0$, we found the best response $c^*(0)$. The best response b^* to this level of c was then found from the best-response function $b^*(c)$. This procedure was then continued until only a very small change in either b or c was recorded. The resulting combination of c^* and b^* then approximates the stable ESS combination of fighting levels.

References

- Abrams, P.A., Matsuda, H. and Harada, Y. (1993) Evolutionary unstable fitness maxima and stable fitness minima of continuous traits. *Evol. Ecol.* **7**, 465–487.
- Alexander, R.D., Marshall, D.C. and Cooley, J.R. (1997) Evolutionary perspectives on insect mating. In: J.C. Choe and B.J. Crespi (eds) *The Evolution of Mating Systems in Insects and Arachnids*. Cambridge University Press, Cambridge, pp. 4–31.
- Arnold, S.J. and Duvall, D. (1994) Animal mating systems: a synthesis based on selection theory. *Am. Nat.* **143**, 317–348.
- Arnqvist, G. (1997) The evolution of water strider mating systems: causes and consequences of sexual conflicts. In: J.C. Choe and B.J. Crespi (eds) *The Evolution of Mating Systems in Insects and Arachnids*. Cambridge University Press, Cambridge, pp. 146–163.
- Brown, J.S. and Vincent, T.L. (1987) Coevolution as an evolutionary game. *Evolution* **41**, 66–79.
- Clutton-Brock, T.H. and Parker, G.A. (1992) Potential Reproductive Rates and the Operation of Sexual Selection. *Q. Rev. Biol.* **67**, 437–456.
- Clutton-Brock, T.H. and Parker, G.A. (1995) Sexual coercion in animal societies. *Anim. Behav.* **49**, 1345–1365.
- Dieckman, U. and Law, R. (1996) The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.* **34**, 579–612.
- Enquist, M. and Leimar, O. (1983) Evolution of fighting behavior: decision rules and assessment of relative strength. *J. Theor. Biol.* **102**, 387–410.
- Eggert, A.K. and Sakaluk, S.K. (1995) Female-coerced monogamy in burying beetles. *Behav. Ecol. and Sociobiol.* **37**, 147–153.
- Grafen, A. and Sibly, R. (1978) A model of mate desertion. *Anim. Behav.* **26**, 645–652.
- Hack, M.A. (1997) The energetic costs of fighting in the house cricket, *Acheta domesticus* L. *Behav. Ecol.* **8**, 28–36.
- Haig, J. and Rose, M.R. (1980) Evolutionary game auctions. *J. Theor. Biol.* **85**, 381–397.

- Hammerstein, P. and Parker, G.A. (1987) Sexual selection: Games between the sexes. In: J.W. Bradbury and M.B. Andersson (eds) *Sexual Selection: Testing the Alternatives*. John Wiley and Sons, Chichester, pp. 119–142.
- Hofbauer, J. and Sigmund, K. (1998) *Evolutionary Games and Population Dynamics*. Cambridge University Press, Cambridge.
- Hårdling, R. (1999) Arms races, conflict costs and evolutionary dynamics. *J. Theor. Biol.* **196**, 163–167.
- Johnstone, R.A. and Norris, K. (1993) Badges of status and the cost of aggression. *Behav. Ecol. Sociobiol.* **32**, 127–134.
- Jormalainen, V. (1998) Precopulatory mate guarding in crustaceans – from male competitive strategy to intersexual conflict. *The Quarterly Review of Biology* **73**, 275–304.
- Jormalainen, V. and Merilaita, S. (1993) Female resistance and precopulatory guarding in the isopod *Idothea baltica* (Pallas). *Behaviour* **125**, 219–231.
- Jormalainen, V., Tuomi, J. and Yamamura, N. (1994) Intersexual conflict over precopula duration in mate guarding Crustacea. *Behav. Proc.* **32**, 265–283.
- Lifjeld, J.T. and Slagsvold, T. (1991) Sexual conflict among polygynous pied flycatchers feeding young. *Behav. Ecol.* **2**, 106–115.
- Maynard Smith, J. (1982) *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.
- Motro, U. (1994) Evolutionary and continuous stability in asymmetric games with continuous strategy sets: the parental investment conflict as an example. *Am. Nat.* **144**, 229–241.
- Otronen, M. (1994) Repeated copulation as a strategy to maximize fertilization in the fly, *Dryomyza anilis* (Dryomyzidae). *Behav. Ecol.* **5**, 51–56.
- Parker, G.A. (1974) Courtship persistence and female guarding as male time investment strategies. *Behaviour* **48**, 157–184.
- Parker, G.A. (1979) Sexual selection and sexual conflict. In: M.S. Blum and N.A. Blum (eds) *Sexual Selection and Reproductive Competition in Insects*. Academic press, New York, pp. 123–166.
- Parker, G.A. and Thompson, E.A. (1980) Dung fly struggles: a test of the war of attrition. *Behav. Ecol. Sociobiol.* **7**, 37–44.
- Rice, W.R. and Holland, B. (1997) The enemies within: intergenomic conflict, interlocus contest evolution (ICE), and the intraspecific Red Queen. *Behav. Ecol. and Sociobiol.* **41**, 1–10.
- Rowe, L. (1994) The costs of mating and mate choice in water striders. *Anim. Behav.* **48**, 1049–1056.
- Rowe, L., Arnqvist, G., Sih, A. and Krupa, J.J. (1994) Sexual conflict and the evolutionary ecology of mating patterns: water striders as a model system. *Trends Ecol. Evol.* **9**, 289–293.
- Sandell, M. and Smith, H. (1996) Already mated females constrain male mating success in the European Starling. *Proc. R. Soc. Lond. B. Biol. Sci.* **38**, 743–747.
- Selten, R. (1980) A note on evolutionarily stable strategies in asymmetrical animal conflicts. *J. Theor. Biol.* **84**, 93–101.
- Strong, D.R. (1973) Amphipod amplexus, the significance of ecotypic variation. *Ecology* **54**, 1383–1388.
- Styron, C.E. and Burbanck, W.D. (1967) Ecology of an aquatic isopod, *Lirceus fontinalis* Raf., emphasizing radiation effects. *Am. Midl. Nat.* **78**, 389–415.
- Trivers, R.L. (1972) Parental investment and sexual selection. In: B. Campbell (ed.) *Sexual Selection and the Descent of Man*. Aldine Press, Chicago, pp. 136–179.
- Watson, P.J., Arnqvist, G. and Stallmann, R.R. (1998) Sexual conflict and the energetic costs of mating and mate choice in water striders. *Am. Nat.* **151**, 46–58.
- Westneat, D.F. and Sargent, R.C. (1996) Sex and parenting: The effects of sexual conflict and parentage on parental strategies. *Trends Ecol. Evol.* **11**, A87–A91.
- Yamamura, N. and Higashi, M. (1992) An evolutionary theory of conflict resolution between relatives: altruism, manipulation, compromise. *Evolution* **46**, 1236–1239.
- Yamamura, N. and Jormalainen, V. (1996) Compromised strategy resolves intersexual conflict over precopulatory guarding duration. *Evol. Ecol.* **10**, 661–680.