Sexually antagonistic co-evolution: a model and an empirical test

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Running title: Sexual conflict and sexual size dimorphism

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Abstract

Models reveal that sexually antagonistic co-evolution exaggerates female resistance and male persistence traits. Here we adapt an established model by including directional sexual selection acting against persistence. We find similar equilibria to previous models showing that sexually antagonistic co-evolution can be limited by counteracting sexual, as well as, natural selection. We tested the model using empirical data for the seaweed fly, *Coelopa ursina*, in which body size acts as a persistence and a resistance trait. Our model can generate continuous co-evolutionary cycles and stable equilibria, however all simulations using empirically derived parameter estimates reach stable equilibria. Thus, stable equilibria might be more common in nature than continuous co-evolutionary cycles, suggesting that sexual conflict is unlikely to promote speciation. The model predicts male biased sexual size dimorphism for *C. ursina*, comparable to empirically observed values. Male persistence is shown to be more sensitive than female resistance to changes in model parameters.

Keywords: Sexual conflict, coelopidae, seaweed fly, *Coelopa ursina*, pre-mating struggle, persistence trait, resistance trait, sexual size dimorphism

Introduction

Selection over mating rate is predicted to operate in different directions on the two sexes resulting in conflict over whether or not copulation occurs during a reproductive encounter (Rowe *et al.*, 1994; Clutton-Brock & Parker, 1995; Arnqvist & Nilsson, 2000). Selection to increase mating rate in males and reduce mating rate in females can result in sexually antagonistic co-evolution (Holland & Rice, 1998; Chapman *et al.*, 2003), with females evolving traits that increase their ability to resist male mating attempts, and males evolving persistence traits to overcome any such resistance (Parker, 1979; Gavrilets *et al.*, 2001; Rowe *et al.*, 2005). This results in sexual selection favouring males with the most successful persistence traits (Rowe *et al.*, 1994).

Pre-mating struggles in which males have to withstand female resistance in order to mate have been found to be common in insects occurring in many families including the sepsids (Parker, 1972; Ward *et al.*, 1992; Eberhard, 2002; Mulhauser & Blanckenhorn, 2002; Hosken *et al.*, 2003; Puniamoorphy, 2008), parnopids (Thornhill, 1980), dryomyzids (Otronen, 1984, 1989), asilids (Dennis *et al.*, 1986), gerrids (Rowe *et al.*, 1994), coccinellids (Majerus, 1994), carabids (Takami, 2002), dytiscids (Miller, 2003) and ichneumonids (Teder, 2005). The mating system of all species of seaweed flies (coelopidae) so far studied also involves a pre-mating struggle during which females attempt to dislodge mounted males by kicking and shaking (Day *et al.*, 1990; Crean & Gilburn, 1998; Weall & Gilburn, 2000; Shuker & Day, 2001; Dunn *et al.*, 2002). In high density natural populations of the *Coelopa frigida*, measurement of the willingness to mate of males have estimated that females are mounted as often as once every eight minutes (Blyth & Gilburn, 2006). This is likely to result in strong selection on females to reduce their mating rate. In all species of coelopids so far studied (Crean *et al.*, 2000), large males are known to gain a mating advantage. In *Coelopa ursina* it was shown that this occurs as a result of a positive correlation between ability to withstand female resistance and male size (Crean & Gilburn, 1998). There is a male biased sexual size dimorphism in most species, as might be expected if sexual selection favours large male size (Crean *et al.*, 2000). Furthermore males are much more variable in size than females in most species (Crean *et al.*, 2000).

One of the first mathematical models of sexually antagonistic co-evolution occurring as a result of differential selection on mating rate in the two sexes was presented by Gavrilets and co-workers (2001). In their model directional selection favours males with the highest mating rate, whereas stabilising selection operates on female mating rate. Male persistence and female resistance (via a threshold level) are considered to be individual quantitative traits and mating rate is modelled as a function of the difference between them. The model showed that female resistance and male persistence can indeed co-evolve antagonistically. If natural selection acting against the male persistence trait is included then a stable equilibria or stable limit cycles can occur. Without natural selection on the males, the evolutionary outcome would always be that of an ‘arms race’. The model was later extended by Rowe and co-workers (2005) who allowed the relative sensitivity of female resistance to different male trait values to evolve by varying the slope of the female resistance function. This model suggested that sexually antagonistic co-evolution might occur less often than predicted by the original model, with females sometimes reducing, or even reversing, their sensitivity, thus limiting, or completely preventing, an arms race. Neither of these studies however went on to parameterise their model and determine what type of evolutionary outcome the system achieves using real data.

Both the original models (Gavrilets *et al*., 2001; Rowe *et al*., 2005) assumed that the persistence and resistance traits did not affect other characteristics, although there was natural selection acting to limit the evolution of the trait size in both sexes. However, depending on what the male persistence and female resistance traits are taken to represent, this is not always true. Sexual conflict over whether or not mating occurs is common in insects (Thornhill, 1980; Dennis *et al*., 1986; Otronen, 1989; Arnqvist, 1992, Crean & Gilburn, 1998; Blanckenhorn *et al*., 2000; Eberhard, 2002; Takami, 2002; Miller, 2003; Teder, 2005; Puniamoorphy *et al.*, 2008). One characteristic that often affects both persistence and resistance during pre-copulatory struggles in insects is body size (Arnqvist *et al*., 1996; Crean & Gilburn, 1998; Blanckenhorn *et al*., 2000, 2008; Teder, 2005). A shift in mean body size will also affect many other fitness traits. Thus, sexually antagonistic co-evolution of body size is likely to be more constrained than would be the case for traits whose sole purpose is to aid persistence, such as the arnaments seen in gerrids (Arnqvist & Rowe, 2002). For example, there is sexual selection acting to reduce male size in seaweed flies in the form of reduced male willingness to mate (Dunn *et al*., 1999). Willingness to mate declines even at the smallest male sizes, thus no optimum male size appears to exist with respect to mount rate. Thus, the inclusion of directional sexual selection acting against male persistence would be a more appropriate model for this system.

Here we adopt the same basic framework of the original model of sexually antagonistic co-evolution (Gavrilets *et al*., 2001) but adapt it by incorporating selection more implicitly on male fitness by including directional sexual selection acting to reduce the male trait through lower mount rates. Unlike the model by Rowe *et al*., (2005) we did not vary the sensitivity of the females to the male trait. In contrast to the two previous models, we then use our model to study a specific empirical system, the seaweed fly, *Coelopa ursina*. This parameterisation is much needed in this field as it allows the models to be tested to see if they give reasonable results and, also investigate the evolutionary outcomes generated using empirically derived parameters. Furthermore, we then go on to determine the effects of varying each of the parameters to determine the effect on the final male and female sizes and the evolutionary outcome.

The Model

Here we adapt the co-evolutionary model presented by Gavrilets and co-workers (2001) to investigate sexually antagonistic co-evolution acting on a specific trait, body size, and also within a specific taxon, the coelopids. Although we are modelling a specific system the outcomes will be relevant to other species in which directional selection acts against male persistence.

We denote the average male size by S_M and the average female size by S_F. The term $S_M/S_F = n$ denotes the sexual size dimorphism (average size ratio) between the males and females. A small n ($0 < n < 1$) represents S_F being larger than S_M and a large n ($n > 1$) represents S_M being larger than S_F. Sexual selection functions relating male mating success per attempt to the size dimorphism approximately resemble a sigmoidal curve in coelopids (Crean *et al.*, 2000). To model this mating probability we take the function $\psi(n)$ given by

$$\psi(n) = \frac{1}{1 + e^{-k(n-\alpha_n)}} \tag{1}$$

(Rowe *et al.*, (2005). Here n is the size dimorphism of the male and female, α_n is the size ratio at which the mating success is 0.5 and k is a scaling factor (or female sensitivity *sensu* Rowe *et al.*, 2005). All parameters are positive. This function is a monotonically increasing function of n which approaches 1 for encounters between large males and small females (Fig. 1).

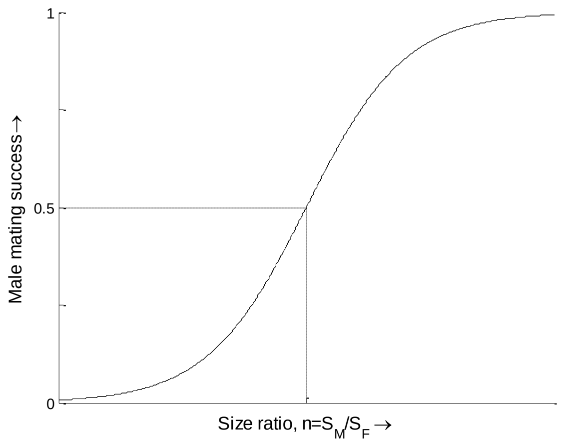

Fig.1 Illustration of the association between ability to overcome female resistance and the size ratio of the sexes, denoted in equation (1), during a particular encounter between a male of size S_M and a female of size S_F, hence with size dimorphism (ratio) $n = S_M/S_F$. The probability of copulation increases with male size and reduces with female size. The size ratio at which the males can overcome resistance 50% of the time is denoted by α_n.

In order to model fitness we assume that during pre-copulatory struggles males aim to maximise their number of mating successes, whereas females aim to mate an optimal number of times to minimise overall costs of mating and resistance. First considering the males, we assume their mating success is proportional to the average number of successful mating occurrences per female per unit time. This, on average, can be written as the product of the number of mating attempts a male will make per unit time multiplied by their persistence success rate. To find the number of mating attempts a male makes, we use the data gathered by Dunn and co-workers (1999). They showed the willingness to mate (proportion of males attempting to mate with a female) is negatively associated with size across several species of coelopids. Thus, even though larger males have a higher probability of mating once mounted, they are subject to constraints that reduce their willingness to mate. Whereas smaller males may have a lower probability of success once mounted but will attempt to mate more often. This association between male size and mount rate is suitably approximated by a (reversed) sigmoidal curve, hence we give the form

$$R(S_M) = 1 - \frac{1}{1 + e^{-m(S_M - \alpha_M)}} \qquad (2)$$

Here α_M is the male size at which 50% of the males attempt to mate with a female per unit time and m is a scaling factor determining the rate at which the willingness to mate (mount rate) decreases. It should be noted that if $m = 0$, the mount rate will stay constant with male size; in this case the model is equivalent to that in Gavrilets *et al*. (2001) and hence gives outcomes equivalent to those. Through our models we assume that m is positive. To gain the fitness of a male (proportional to the average number of females a male successfully mates with) of size S_M in a population where females are of size $\hat{S}_F$ we take the product of the persistence success rate, ψ, and the mount rate, R, and a scaling factor, c_{MM}, (proportional to the average number of females) as follows:

$$W_M(S_M; \hat{S}_F) = c_{MM} R(S_M) \psi(n) + [1 - c_{NM}(S_M - \theta_M)^2] \qquad (3)$$

The term in the square brackets represents natural selection acting upon males. We assume the form of this is similar to that used by Gavrilets *et al*., (2001) and Rowe *et al*., (2005) where θ_M is the optimum male size under natural selection and c_{NM} is the cost of natural selection; however contrasting to the necessity in those studies to include this term to avoid an ‘arms race’, by incorporating the reduction in male willingness to mate (mount rate), we could choose to omit the natural selection on the males and still attain a fitness maximum, avoiding the ‘arms race’. An illustration of the male mating success, in terms of the male size S_M, is shown in Fig. 2.

Fig. 2 Illustration of the male fitness curve (as shown in Equation (3)) for a particular female of size $\hat{S}_F$. The initial increase in mating success is due to the increasing persistence success as male size increases. However this is eventually counteracted by the cost of a lower mount rate suffered by larger males outweighing their persistent success once mounted. The male size which maximises the fitness is denoted by S_M^*. By including this decrease in male mount with increasing size, as an implicit form of sexual selection, the male fitness differs from that modelled by Gavrilets and co-workers (2001) and Rowe and co-workers (2005) in that there exists a fitness maximum preventing an ‘arms race’ without the explicit natural selection term.

Here, as the male size increases, their mating success initially increases due to the increase in their persistence. However as the male size increases further, even though the probability of successfully overcoming resistance increases, their fitness begins to decrease as larger males face the cost of a lower mount rate, a cost which eventually outweighs the benefit of the higher persistence rate. The shape of this curve resembles those derived empirically for coelopids (Fig. 3).

We assume that females aim to mate an optimal number of times. The product of the mount rate and mating success rate, $R(S_M)\psi(n)$, gives the percentage of males each female will mate with per unit time. We denote the optimal percentage of males the females want to mate with per unit time as θ_{Mate}. We therefore take the fitness of a mutant female of size S_F in a population where males are of an average size $\hat{S}_M$ to be of the form

$$W_F(S_F;\hat{S}_M) = 1 - c_{MF}(\psi R - \theta_{Mate})^2 + [1 - c_{NF}(S_F - \theta_F)^2] \qquad (4)$$

Here c_{MF} is the cost per percentage point away from the optimal size. The term in the square brackets represents natural selection acting upon females, where there is an optimum female size for maximising offspring production denoted by θ_F. The cost of each unit of size away from θ_F is denoted by c_{NF}. Therefore females will evolve towards a size that maximises fitness imparted by natural selection and optimal mating rate. An illustration of this fitness curve, in terms of the female size S_F, is shown in Fig. 4. This takes the form of an 'dome-shape' curve with the maximum fitness attained at the optimal female size S_F^*.

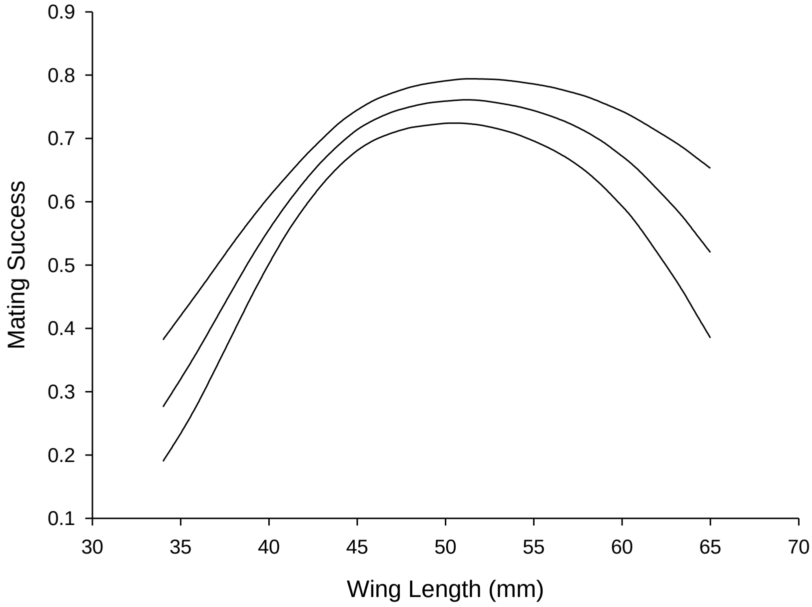

Fig. 3 Sexual selection function for male size in *C. frigida* from Fife (Edward & Gilburn, 2007). The middle curve represents the mean mating success, with the outer lines representing the confidence levels.

Fig. 4 Illustration of the female fitness curve (as shown in Equation (4)) with respect to the average female size S_F, for a particular average male size $\hat{S}_M$. The female size which maximises the fitness is denoted by S_F^*.

The above forms for the male and female fitness, equations (3) and (4), can be used to derive equations that approximate the evolutionary dynamics of the male size, $\bar{S}_M$, and female size, $\bar{S}_F$, using standard techniques where $\bar{S}_M$ and $\bar{S}_F$ represent average values (e.g. Iwasa *et al*., 1991; Abrams, 2001). This gives

$$\frac{d\bar{S}_F}{dt} = \upsilon_F\left[-2c_{MF}R\frac{\partial\psi}{\partial\bar{S}_F}(\psi R-\theta_{Mate})-2c_{NF}(\bar{S}_F-\theta_F)\right]$$

$$\frac{d\bar{S}_M}{dt} = \upsilon_M\left[c_{MM}\psi R\left(\frac{k}{\bar{S}_F}(1-\psi)-m(1-R)\right)-2c_{NM}(\bar{S}_M-\theta_M)\right] \qquad (5)$$

where υ_F and υ_M are constants. Solving these algebraically to give the male and female equilibrium sizes is not possible. In the case when $m=0$, the model becomes equivalent to that in Gavrilets *et al*. (2001), in which it was shown that both stable equilibria and stable limit cycles are possible. We can however quite easily see that if the cost of natural selection is much stronger that the cost of mating, e.g. $c_{NF} \gg c_{MF}$, then the sexes evolve towards their optimum sizes, e.g. θ_F. Although these are not possible to solve algebraically for $\bar{S}_F$ and $\bar{S}_M$, all the numerical simulations run in this study show that there exists a unique and stable evolutionary equilibrium; from which we conclude that, given 'realistic' parameter values for a model of this form, a stable evolutionary equilibrium is the most common outcome**.** At present we have four 'cost' terms: c_{MF}, c_{NF}, c_{MM} and c_{NM}. In running simulations we do not need to explicitly state all four terms, instead we only require the ratio between the two terms for the females, $c_F = c_{NF}/c_{MF}$, and the similarly for the males, $c_M = c_{NM}/c_{MM}$.

These dynamics cause each sex to continually evolve towards their fitness maximum given the current trait size of the other sex. In this example, both sexes reach their respective fitness maximum hence the evolutionary outcome is that of a stable co-evolutionary equilibrium. This can be seen in Fig. 5a where the sizes of the male and female initially evolved (increased in size here) before settling at their respective evolutionary optima. The respective female and male fitness curves, from equations (4), for the final male size S_M^*, and (3), for the final female size S_F^*, respectively, are plotted in Fig. 5b and Fig 5c. Here we see that each sex has attained their fitness maxima, and hence a stable evolutionary equilibrium. Assuming the male and female sizes, S_F and S_M, are of the same scale, and hence directly comparable, then the evolutionary optimum is where the females are larger than the males (with size ratio $n<1$). It should also be noted that here we removed the natural selection term from the male fitness ($c_M = 0$) and this has not affected whether the males attained a fitness maxima or not.

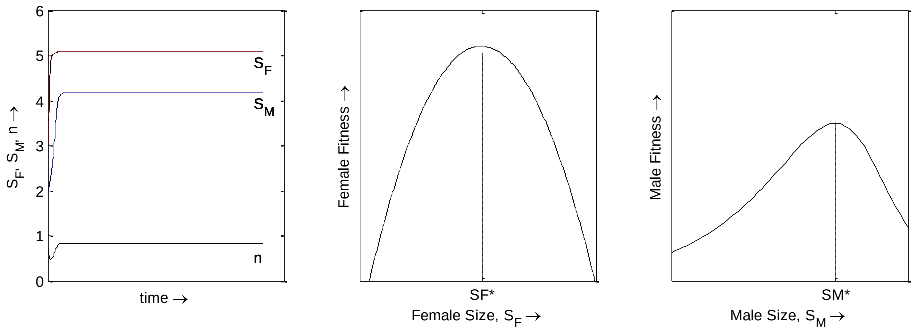

Figure 5a Figure 5b Figure 5c

Fig. 5 Fig. 5a shows how the average male size S_M, average female size S_F and the size dimorphism n, evolve over time, in accordance with the evolutionary dynamics in equation (5), all of which settle to particular (equilibrium) values, S_M^*, S_F^* and n^*. Fig. 5b shows the female fitness function in relation to the female size for the final male size S_M^* and Fig. 5c shows the male fitness in relation to the male size S_M for the final female size S_F^*; the dashed lines represent the final average female and male sizes in Fig. 5b and 5c respectively. The final sizes S_M^*, S_F^* and n^* represent fitness maxima for both the female and male. The parameter values are taken to be $k = 3$, $\alpha_n = 0.9$, $m = 1.6$, $\alpha_M = 5$, $c_M = 0$, $\theta_{Mate} = 0.05$, $c_F = 0.5$ and $\theta_F = 5$. The evolutionary equilibrium size for males and females are $S_M^* = 4.16$ and $S_F^* = 5.07$ respectively, with the size dimorphism being $n^* = 0.82$.

Biological Example: *Coelopa ursina*

To determine the validity of our model, we apply it to a specific example, namely the South African seaweed fly, *Coelopa ursina* (Crean & Gilburn, 1998; Dunn *et al.*, 1999). This species was chosen as it has been shown that male mating success increases with size as a result of size correlating with the duration that the males can withstand resistance (Crean & Gilburn, 1998) and because there is strong negative association found between male size and willingness to mate (Dunn *et al.*, 1999). We have not chosen the better studied species, *Coelopa frigida*, as this species carries a large inversion system which affects persistence, resistance and body size and this would require a much more complex model. Using the male mating success in terms of the size ratio in Crean & Gilburn (1998) we can estimate the parameter values of k and α_n as 2.2 and 1.1 respectively. Likewise, using the male willingness data (Dunn *et al.*, 1999) we can estimate the parameter values of m and α_M as 0.66 and 7.1 respectively.

Estimating the values for remaining parameters, c_M, c_F, θ_{Mate}, θ_M and θ_F, is more difficult due to lack of sufficiently accurate empirical data. For θ_{Mate} we assume the females, in terms of the mating aspect of their fitness, want to mate only a small number of times; hence we estimate θ_{Mate} to be approximately 0.01 (i.e. 1% of the males per unit time). This value might seem very small, however, mount rates of *C. frigida* are known to be very high in nature, and mount rates under laboratory conditions are similar for *C. ursina* and *C. frigida* (Dunn *et al*., 1999). In addition *C. ursina* can occur at high population densities in nature (personal observations). For θ_F and c_F we assume as a result of strong stabilising selection that females are only slightly above their naturally selection optimum, and therefore θ_F will be in the region of 4.8 and c_F will be approximately 0.3. For the males, we assume their evolution is dictated more by sexual selection and that this drives the males to be further from their natural selection optimum and take a value of 4.5 for θ_M and for c_M a value of 0.01. Without strong sexual selection males are usually smaller than females in most animal species.

Running simulations based on the dynamics given in equation (5), the results gained are shown in Fig. 6. Here the males and females evolve towards a stable evolutionary equilibrium, with average male and female sizes are given to be 5.48 and 4.95 respectively. The final sizes from this model are comparable to the actual sizes gained from the data. However we have only estimated the ratio of the cost of natural selection and the cost of mating (females) or mounting (males) for each sex. We therefore investigated what affect varying this ratio has on the final (equilibrium) sizes of the male and female, and whether we can use this model to predict what ratio might be a realistic estimate for *C. ursina*.

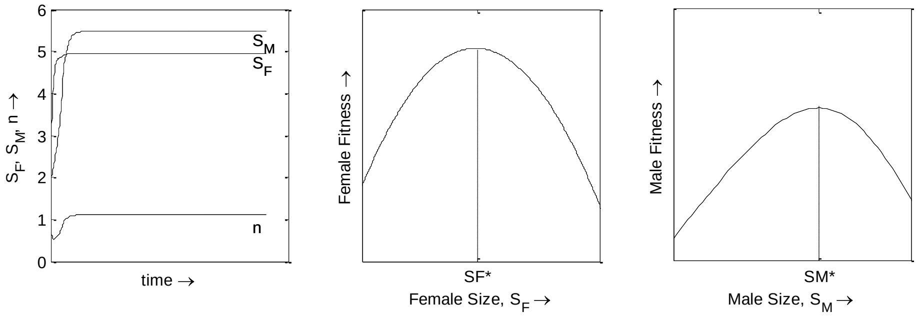

Figure 6a Figure 6b Figure 6c

Fig 6 Figure 6a shows how the average male size S_M, average female size S_F and the size ratio n, of *C. ursina* evolve over time, in accordance with the evolutionary dynamics in equation (5), all of which settle to particular (equilibrium) values, S_M^*, S_F^* and n^*. Figures 6b and 6c each show that the female and male attain their maximum fitness given the final size of the other sex (where the dashed lines represent the final average female and male sizes in Figures 6b and 6c respectively). The parameter values are taken to be $k = 2.2$, $\alpha_n = 1.1$, $m = 0.66$, $\alpha_M = 7.1$, $\theta_{Mate} = 0.01$, $c_F = 0.3$, $\theta_F = 4.8$, $c_M = 0.01$ and $\theta_M = 4.5$.The evolutionary equilibrium size for males and females are $S_M^* = 5.48$ and $S_F^* = 4.95$ respectively, with the size ratio being $n^* = 1.11$. The outcome is comparable to the empirical data from Crean and Gilburn (1998) of mean male size of 5.49 and female size of 4.95 and hence size ratio of 1.11.

In Fig. 7 we plot the final average size of the male and female against, firstly, the ratio of the cost of natural selection and the cost of mating for the females, c_F, and secondly, the ratio of the cost of natural selection and the cost of mating, c_M, for the males.

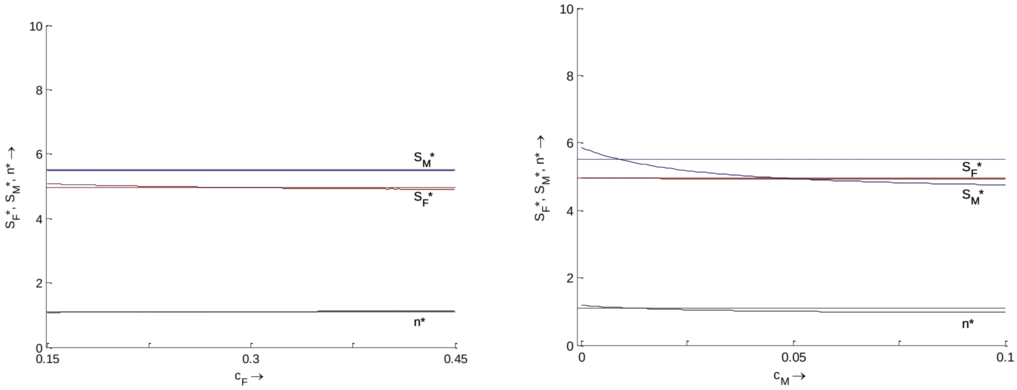

Figure 7a

Figure 7b

Fig. 7 The final size of the female and male, S_F^* and S_M^* respectively, and the size ratio against the ratio of the cost of natural selection and the cost of mating for the females, c_F, in Fig. 7a, and for the males, c_M, in Fig. 7b. The remaining parameter values are taken to be $k = 2.2$, $\alpha_n = 1.1$, $m = 0.66$, $\alpha_M = 7.1$, $\theta_{Mate} = 0.01$, $c_F = 0.3$ (in Fig. 7b), $\theta_F = 4.8$, $c_M = 0.01$ (in Fig. 7a) and $\theta_M = 4.5$. The horizontal dashed lines represent the size of males (top), females (middle) and the size ratio (bottom) as attained by the data.

Providing the cost ratio for the females is larger than approximately 0.2 (in this example) there is little effect on the final sizes of the male and females. However if this cost ratio is less than 0.2, then the resultant effect is to sharply increase the final female size, with a less significant effect on the male size. For these very small ratios (those close to zero for the female cost ratio, representing natural selection being insignificant in comparison to selection on mating rate) the female's sole cost becomes that of mating; hence to minimise this cost, the female evolves to a size that reduces the number of mating occurrences to the θ_{Mate} level. As the females have no way of directly reducing the number of mating attempts the males make, for this to occur requires the female to be considerably larger than the male, thus reducing the probability of the male successfully mating to a level approaching zero. In this case, it might seem obvious for the males to respond by increasing their size in order to increase their probability of mating success. However, this has the repercussion of a lower mount rate. As the females continue to respond, by increasing their size (to decrease the probability of mating), the increasing in size is unsustainable for the males and hence their optimal strategy in this case is to decrease their size and suffer a slightly lower probability of persistence in return for a significantly higher mount rate. It must be noted however, that this is obviously not the case in *Coelopa ursina* as this behaviour is not observed in the data.

In comparison, increasing the cost ratio for the males (Figure 7b) has the effect of decreasing the final male size, with little effect on the female size. This can be explained by the fact that increasing the cost ratio increases the relative cost of natural selection in comparison to the cost of mating, and hence the male's size evolves towards the natural selection optimum in order to reduce this cost.

Testing the sensitivity of our results for changes in the remaining parameters reveals the males are more sensitive to these changes (Table 1). With the exception of the optimal mating rate, optimal female size and female 'cost' ratio, any changes in the parameters will cause a change in the final male size. The females however are insensitive to changes in most of the parameters, with their final size only changing when we changed the female cost ratio and the optimal female size.

	Sensitive to changes	
Parameter	Males	Females
Mating factor^2 k	✓	×
Half mating rate^2 α_N	✓	×
Mount rate^2 m	✓*	×
Half mating size^3 α_M	✓	×
Optimal mating rate^1 θ_{Mate}	×	×
Optimal male size^3 θ_M	✓	×
Optimal female size^3 θ_F	×	✓
Male 'cost' ratio^1 c_M	✓	×
Female 'cost' ratio^2 c_F	×	✓*

Table 1 This shows if the final male and female sizes are sensitive to changes in the given parameter, denoted by ✓, or not, denoted by ×. We define the final sizes being sensitive if they change by more than +/-2.5% away from 5.48 for males and 4.95 for females. The ranges of parameters taken are either 0.0-0.1^1, existing value +/-50%^{2} or +/-20%^{3}. In each case, all the remaining parameter values are as those stated in Figure 6. (* denotes that the final size changes by less than +/-5%.)

Discussion

Previous models (Gavrilets *et al.*, 2001; Rowe *et al.*, 2005) have shown that exaggerated male persistence traits and female resistance to those traits can co-evolve antagonistically. In these models continued exaggeration of male persistence and female resistance occurs in the absence of counteracting natural selection, however with the inclusion of a natural selection term generating an optimal trait size in males then male persistence and female resistance can reach stable equilibria (Gavrilets *et al.*, 2001). Here we developed a similar model but using a different form of selection acting on the male persistence trait. In addition to natural selection favouring an optimum trait size we assumed that there was directional sexual selection acting against exaggeration of the male persistence, with stronger selection acting against more exaggerated forms of the trait. Our aim was to model a specific persistence and resistance trait, body size, in both sexes, and then to test the model using empirical data from coelopids. We included directional sexual selection acting against the male persistence trait as this has been established empirically (Dunn *et al.*, 1999). Based on data from various species of coelopids (Dunn *et al.*, 1999) we estimated that this decrease in mount rate, with respect to the male size, would take the form of a (reflected) sigmoidal curve. Furthermore the use of counteracting directional sexual selection in addition to stabilising natural selection might be a more realistic model for some systems in which variation in male fitness is predominately determined by sexual rather than natural selection. Our model generated comparable results to those found previously by Gavrilets and co-workers (2001) revealing that a stable evolutionary equilibria can be reached. In contrast to those results, including the male natural selection term does not alter the type of evolutionary outcome that occurs. In our model a stable evolutionary equilibrium can be achieved with or without natural selection acting on the male trait.

When the model was run using *Coelopa ursina* as a model species we generated an outcome which reasonably closely reflected the natural situation. This together with our analysis of the sensitivity of changing the parameter values in the model predicted a stable evolutionary equilibrium with final optimal values for the males and females respectively, matching the real-life data for the species. This type of evolutionary outcome contrasts with other studies which report continuous evolutionary chases (reviewed by Gavrilets & Hayashi 2005 and Lessells 2006), whereby adaptation by one sex is met by counter-adaptation by the other, without ever reaching a stable evolutionary equilibrium. These can be an ‘arms race’ or a ‘stable limit cycle’, both of which are seen in the models by Gavrilets *et al.* (2001) and Rowe *et al.* (2005). These same alternative outcomes can also be achieved by our model given appropriate parameter values, however the parameter values needed to achieve these are inconsistent with the empirical values used to model the behaviour of *Coelopa ursina*. Thus, our empirical generate parameters values that generate stable equilibria rather than continuous evolutionary chases. Furthermore, when we tested the sensitivity of the parameters of *Coelopa ursina* we always reached a stable evolutionary outcome. This finding fits with recent empirical tests which have failed to find evidence for sexual conflict playing a role in speciation (Ritchie *et al*. 2005; Wigby & Chapman 2006; Bacigalupe *et al*. 2007) which would be predicted if sexual conflict generated continuous evolutionary chases (Gavrilets & Hayashi 2005). Although most parameters could be predicted from the empirical data, some had to be estimated using our current knowledge of the species; most importantly the cost ratio (which relates the strength of natural selection on body size with the strength of selection on body size as a result of sexual conflict) was unknown. However using this model it is possible to estimate the 'cost ratios', c_F for the females and c_M for the males. More significantly it was found that varying the female cost ratio had little effect on the female resistance and almost no effect on the male persistence traits. Varying the male cost ratio however produced a marked effect on the male persistence trait, with the female trait unchanged. Hence any change in this parameter could result in significant evolutionary change in the males. Extending the sensitivity analysis, the males are sensitive to changes in most of the parameters**,** whereas the females are sensitive to only a few, namely the female's cost ratio and their optimal trait size due to natural selection. The model thus predicts that male persistence traits are likely to be more variable than female resistance traits. In coelopids body size is consistently more variable in males than females for all species (Crean *et al*., 2000). As a result, this suggests that males are generally more sensitive to changes in their characteristics, and potentially those of the environment around them. Therefore we suggest that generating empirical measurements of male parameters might be more important than measuring these for the females.

Although our model was specifically developed to simulate a specific taxon, the results are likely to be more widely applicable as pre-mating struggles in insects are common (Thornhill, 1980; Dennis *et al*., 1986; Otronen, 1989; Arnqvist, 1992, Crean & Gilburn, 1998; Blanckenhorn *et al*., 2000; Eberhard, 2002; Takami, 2002; Miller, 2003; Teder, 2005; Puniamoorphy *et al*., 2008), and body size oftens aids both persistence and resistance (Arnqvist, *et al*. 1996; Crean & Gilburn, 1998; Blanckenhorn *et al*., 2000, 2008; Teder, 2005). Studies of the effects of male size on mount rate do not seem to have been carried out in the other systems so it is unclear whether a negative correlation between mount rate and size is a common feature of insects that display pre-mating struggles. However, the effect is consistent across all coelopid studies (Dunn *et al*., 1999) and quite dramatic in nature with the largest males appearing very sluggish in nature generally in a number of species and sometimes too large to be able or willing to fly (personal observations). Thus, such an association might well be common. We suggest that associations between male persistence traits, such as body size, and male mount rate are studied in other species of insects displaying pre-mating struggles. This will allow an assessment of how widely applicable the results of our model are. It should also be noted our model is applicable to any system in which there is direct sexual selection acting against the exaggeration of the male persistence trait and not just systems in which relative body size determines the outcome of pre-mating struggles.

We show here that any negative effects of exaggerated persistence on mount rate can be enough to create stable equilibria in a model of sexually antagonistic co-evolution without the need for the inclusion of a naturally selected optimum for the male trait. We then used the model to simulate the evolution of a male persistence and female resistance trait in a specific model system, *Coelopa ursina*. Despite exploring the parameter space quite extensively all models of sexually antagonistic co-evolution of body size in *Coelopa ursina* resulted in stable and reasonably realistic outcomes. This is the first time empirically derived parameters have been entered into a model of sexually antagonistic co-evolution. Our consistent outcomes predict that sexual conflict is unlikely to result in unstable co-evolutionary cycles in *Coelopa ursina*, suggesting that sexual conflict is unlikely to contribute to speciation.

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References

Abrams, P.A. 2001. Modelling the adaptive dynamics of traits involved in inter- and intraspecific interactions: an assessment of three methods. *Ecol. Letts.* **4**: 166-175.

Arnqvist, G. 1992. Precopulatory fighting in a water strider: intersexual conflict or mate assessment? *Anim. Behav.* **43**: 559-567.

Arnqvist, G., Rowe, L., Krupa, J. & Sih, A. 1996. Assortative mating by size: a meta-analysis of mating patterns in water striders. *Evol. Ecol*. **10**: 265-284.

Arnqvist, G. & Nilsson, T. 2000. The evolution of polyandry: multiple mating and female fitness in insects. *Anim. Behav.* **60**: 145-164.

Arnqvist, G. & Rowe, L. 2002. Antagonistic coevolution between the sexes in a group of insects. *Nature* **415**: 787-789.

Bacigalupe, L.D., Crudgington, H.S., Hunter, F., Moore, A.J. & Snook, R.R. 2007. Sexual conflict does not drive reproductive isolation in experimental populations of *Drosophila pseudoobscura*. *J. Evol. Biol.* **20**: 1763-1771.

Blanckenhorn, Mülhäuser, C., Morf, C., Reusch, T. & Reuter, M. 2000. Female choice, female reluctance to mate and sexual selection on body size in the dung fly *Sepsis cynipsea. Ethology* **106**: 577-593.

Blanckenhorn, W.U., Birrer, M., Meier, C.M., Reim, C., Teuschl, Y. & Weibel, D. 2008. Size-dependent mating success at various nutritional states in the yellow dung fly. *Ethology* **114**: 752–759

Blyth, J.E & Gilburn, A.S. 2006. Extreme promiscuity in a mating system dominated by sexual conflict. *J. Insect Behav*. **19**: 447-455.

Butlin, R.K., Read, I.L. & Day, T.H. 1982. The effects of a chromosomal inversion on adult size and male mating success in the seaweed fly, *Coelopa frigida*. *Heredity* **49**: 51-62.

Chapman, T., Arnqvist, G., Bangham, J. & Rowe, L. 2003. Sexual conflict. *Trends Ecol. Evol.* **18**: 41-47.

Clutton-Brock, T.H. & Parker, G.A. 1995. Punishment in animal societies. *Nature* **373**: 209-216

Crean, C.S. & Gilburn, A.S. 1998. Sexual selection as a side-effect of sexual conflict in the seaweed fly, *Coelopa ursina* (Diptera: Coelopidae). *Anim. Behav.* **56**: 1405-1410.

Crean, C.S., Dunn, D.W., Day, T.H. & Gilburn, A.S. 2000. Female mate choice for large male size in several species of seaweed flies (Diptera: Coelopidae). *Anim. Behav.* **58**: 121-126.

Day, T.H., Foster, S.P. & Engelhard, G. 1990. Mating behaviour in seaweed flies (*Coelopa frigida*) *J. Insect Behav*. **3**: 105-120

Dennis, D.S., Lavigne, R.J. & Bullington, S.W. 1986. Ethology of *Etheria cressoni* with a review of the comparative ethology of the genus (Diptera: Asilidae). *Proc. Entomol. Soc. Wash.* 88: 42-55.

Ding, A. & Blanckenhorn, W.U. 2002. The effect of sexual size dimorphism on mating behaviour in two dung flies with contrasting dimorphism *Evol. Ecol. Res.* **4**: 259–273

Dunn, D.W., Crean, C.S., Wilson, C.L. & Gilburn, A.S. 1999. Male choice, willingness to mate and body size in seaweed flies (Diptera: Coelopidae). *Anim. Behav.* **57**: 847-853.

Dunn, D.W., Crean, C.S. & Gilburn, A.S. 2002. The effects of exposure to seaweed on willingness to mate, oviposition and longevity in seaweed flies (Diptera: Coelopidae). *Ecol. Entomol*. **27**: 554-564.

Eberhard, W.G. 2002. The function of female resistance behaviour: Intromission by male coercion vs. female cooperation in sepsid flies. *Rev. Biol. Trop.* **50**: 485-505.

Edward, D.A. & Gilburn, A.S. 2007. The effect of habitat composition on sexual conflict in the seaweed flies *Coelopa frigida* and *C. pilipes*. *Anim. Behav.* **74**: 343-348.

Gavrilets, S., Arnqvist, G. & Friberg, U. 2001. The evolution of female mate choice by sexual conflict. *Proc. Roy. Soc. Lond. B* **268**: 531-539.

Gavrilets, S. & Hayashi, T.I. 2005. Speciation and sexual conflict. *Evol. Ecol*. **19**: 167-198.

Holland, B. & Rice, W.R. 1998. Perspective: Chase-away sexual selection: Antagonistic seduction versus resistance *Evolution,* **52**: 1-7.

Hosken, D.J., Martin, O.Y., Born, J. & Huber, F. 2003. Sexual conflict in *Sepsis cynipsea*: female reluctance, fertility and mate choice. *J. Evol. Biol.* **16**: 485-490.

Iwasa, Y., Pomiankowski, A. & Nee, S. 1991. The evolution of costly mate preferences. II. The "handicap" principle. *Evolution* **45**: 1431-1442.

Lessell, C.M. 2006. The evolutionary outcome of sexual conflict. Phil. Trans. R. Soc. B, **361**: 301-317

Majerus, M.E.N. 1994. *Ladybirds*. Harper Collins: London.

Miller, K.B. 2003. The phylogeny of diving beetles (Coleoptera: Dytiscidae) and the evolution of sexual conflict. *Biol. J. Linn. Soc.* **79**: 359-388.

Mülhäuser, C. & Blanckenhorn, W.U. 2002. The costs of avoiding matings in the dung fly *Sepsis cynipsea*. *Behav. Ecol.* **13**: 359-365.

Otronen, M. 1984. The effect of differences in body size on the male territorial system of the fly, *Dryomyza anilis*. *Anim. Behav.* **32**: 882-890.

Otronen, M. 1989. Female mating behaviour and multiple matings in the fly, *Dryomyza anilis*. *Behav.* **111**: 77-97.

Parker, G.A. 1972. Reproductive behaviour of *Sepsis cynipsea* (L.) (Diptera: Sepsidae). I. Preliminary analysis of the reproductive strategy and its associated behaviour patterns. *Behav.* **41**: 172-206.

Parker, G.A. 1979 Sexual selection & sexual conflict. In *Sexual Selection & Reproductive Competition in Insects*. (M.S. Blum & N.A. Blum, eds) pp. 123-166. Academic Press, New York.

Puniamoorthy, N., Su, K.F. & Meier, R. 2008. Bending for love: losses and gains of sexual dimorphisms are strictly correlated with changes in the mounting position of sepsid flies (Sepsidae: Diptera) *BMC Evol. Biol.* **8**:155

Ritchie, M.G., Webb, S.A., Graves, J.A. Magurran, A.E. & Macias Garcia, C. 2005. Patterns of speciation in endemic Mexican Goodeid fish: sexual conflict or early radiation. *J. Evol. Biol.* **18**: 922-929.

Rowe, L., Arnqvist, G., Sih, A., & Kruppa, J.J. 1994. Sexual conflict and the evolutionary ecology of mating patterns: water striders as a model system. *Trends Ecol. Evol.* **9**: 289-293.

Rowe, L., Cameron, E. & Day, T. 2005. Escalation, Retreat and Female Indifference as Alternative Outcomes of Sexually Antagonistic Coevolution. *Am. Nat*. **165**: S5-S18.

Shuker, D.M. & Day, T.H. 2001. The repeatability of a sexual conflict over mating. *Anim. Behav.* **61**: 755-762.

Takami, Y. 2002. Mating behaviour, insemination and sperm transfer in the ground beetle *Carabus insulicola*. *Zool. Sci.* **19**: 1067-1073.

Teder, T. 2005. Male-biased size dimorphism in ichneumonine wasps (Hymenoptera: Ichneumonidae) – the role of sexual selection for large male size. *Ecol. Entomol.* **30**: 342-349.

Thornhill, R. 1980. Rape in *Panorpa* scorpionsflies and a general rape hypothesis. *Anim. Behav.* **28**: 52-59.

Ward, P. I., Hemmi, T. & Roosli, T. 1992. Sexual conflict in the dung fly *Sepsis cynipsea*. *Func. Ecol.* **6**: 649-653.

Weall, C.V. & Gilburn, A.S. 2000. Factors influencing the choice of female mate rejection strategies in the seaweed fly *Coelopa nebularum* (Diptera: Coelopidae). *J. Insect Behav.* **13**: 539-552.

Wigby, S. & Chapman, T. 2006. No evidence that experimental manipulation of sexual conflict drives premating reproductive isolation in *Drosphila melanogaster*. *J. Evol. Biol.* **19**: 1033-1039.