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Evolutionary perspective

Speciation and sexual conflict

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Abstract. We review mathematical models that explicitly consider the dynamics of evolutionary change driven by sexual conflict over mating rate when males are selected for increasing mating success whereas females are selected to restrict mating rate. These models focus on a pair of traits each of which is controlled by a separate set of genes expressed in one sex only. The traits control the probability of mating and/or fertilization. Overall, there are at least six different dynamic regimes observed in models of sexual conflict: (1) continuous coevolutionary chase between the sexes (which can result in allopatric speciation as a byproduct), (2) evolution towards an equilibrium, (3) cyclic evolution, (4) evolution towards a line of equilibria with subsequent random drift along this line, (5) Buridan's Ass regime involving extensive diversification in female alleles without comparable diversification in male alleles, and (6) extensive diversification in both male and female alleles (which can result in sympatric speciation). Mathematical models also show that different dynamic regimes can be observed with the same set of parameter values but under different initial conditions. It is also possible that the same population switches from one regime to another as a result of stochastic perturbations due to, say, random genetic drift. Moreover, different sets of loci controlling mating and fertilization in the same species can follow different dynamic regimes. We attempt to make some generalizations and identify important directions for theoretical and empirical work.

Key words: evolutionary dynamics, mathematical models, sexual conflict, speciation v1646

Introduction

Ultimately, speciation is a consequence of genetic divergence between different populations (or between parts of the same population). Genetic divergence leading to the evolution of reproductive isolation and, eventually, to speciation can be driven by a number of evolutionary factors including random genetic drift, mutation, natural and sexual selection (e.g., Mayr, 1942, 1963; White, 1978; Futuyma, 1998; Gavrilets, 2004). Most of these factors can also oppose genetic divergence in specific biological settings which makes generalizations about speciation difficult. Here, we concentrate on a specific factor known as (inter) sexual conflict which has been recently identified as an important

"engine of speciation" (Rice and Holland, 1997; Holland and Rice, 1998; Rice, 1998; Arnqvist *et al.*, 2000).

Sexual conflict occurs if the interests of the sexes with regard to certain aspects of reproduction differ. For example, sexual conflict can occur over mating rate (Rice and Holland, 1997; Holland and Rice, 1998; Rice, 1998; Arnqvist and Nilsson, 2000), offspring size (Haig, 2000), parental care (Smith and Härdling, 2000; Barta *et al.*, 2002), and the use of sperm (Pitnick *et al.*, 1999; Presgraves *et al.*, 1999; Ball and Parker, 2003). Sexual conflict arises because of the differences in the roles played by the sexes in the process of reproduction which in turn lead to the differences between the sexes in the costs and benefits of mating and reproduction (Bateman, 1948; Trivers, 1972; Parker, 1979). The term *sexual conflict* was apparently first introduced by Parker (1979) who used a game-theoretical approach (e.g., Maynard Smith, 1982) to demonstrate the possibility of a conflict over mating decision and to study its possible resolutions. Parker (1979) was building on an earlier idea of the "battle-of-the-sexes" game about the costs of raising offspring introduced and studied by Dawkins (1976). Following this earlier work, most modeling studies of sexual conflict have used game-theoretical methods to demonstrate its existence, provide measures of its intensity, and to identify conditions under which alleles or behaviors causing sexual conflict can invade the population (e.g., Jormalainen *et al.*, 1994; Hawkes *et al.*, 1995; Parker and Partridge, 1998; Härdling *et al.*, 1999, 2001; Mylius, 1999; Alonzo and Warner, 2000; Smith and Härdling 2000; Reuter and Keller, 2001; Barta *et al.*, 2002; Andres and Morrow, 2003; Ball and Parker, 2003).

Recently, Rice and Holland (1997), Holland and Rice (1998), and Rice (1998) drew attention to one particular consequence of sexual conflict over mating rate for the evolution of reproductive isolation between allopatric populations. They argued that direct deleterious effects of high mating rates on female fitness will continuously select for increased "resistance" of females to mating attempts from males. Increased resistance in females will in turn result in selection for males able to overcome this resistance. As a consequence, sexual conflict over mating rate will drive continuous and rapid coevolution of male and female traits controlling reproduction. As a by-product of this coevolution, different allopatric population will diverge in these traits quickly loosing mutual reproductive compatibility and, thus, becoming different species.

This hypothesis is supported by a number of experimental data and simultaneously provides a plausible explanation for some empirical patterns. In particular, the power of sexual conflict to drive rapid genetic divergence and the evolution of reproductive isolation between isolated population has been demonstrated in experiments with *Drosophila* (Rice, 1996; Holland and Rice, 1999; Pitnick *et al.*, 200la, b) and the dung fly *Sepsis cynipsea* (Martin and Hosken, 2003). In addition, Arnqvist and Rowe (2002) provide strong

empirical evidence for a coevolutionary arms race between male and female armaments (clasping and anti-clasping morphologies) in water striders.

Moreover, a growing amount of experimental data coming from studies of sperm or pollen competition between closely related species (e.g., Arnold *et al*., 1993; Wade *et al*., 1994; Rieseberg, 1995; Howard *et al*., 1998; Howard, 1999) as well as from molecular studies of fertilization proteins (e.g., Aguade *et al*., 1992; Lee and Vacquire, 1992; Vacquier and Lee, 1993; Metz and Palumbi, 1996; Palumbi, 1998; Howard, 1999; Swanson and Vacquier, 2002a, b; Galindo *et al*., 2003; Landry *et al*., 2003; Swanson *et al*., 2003) indicate extremely rapid evolution of traits and proteins related to fertilization in many diverging taxa. At least some of these data can be explained by selection for avoidance of polyspermy (e.g., Howard *et al*., 1998) which represents an important example of sexual conflict over mating rate. Selection for increased female resistance to mating can also potentially explain rapid evolution of genitalia, which has been observed in many organisms (Eberhard, 1985).

Finally, some data show positive correlation between species richness (i.e., the number of species in a clade) and some measures that can be interpreted as proxies for a potential sexual conflict. For example, species richness correlates with the proportion of sexually dichromatic species within taxa of passerine birds (Barraclough *et al*., 1995). In birds, taxa with promiscuous mating systems tend to be more species-rich than their nonpromiscuous sister taxa (Mitra *et al*., 1996). In insects, groups where females mate with many males exhibited speciation rates four times as high as in related groups where females mate only once (Arnqvist *et al*., 2000).

How important is sexual conflict in evolution, in general, and in causing speciation, in particular, and what is its place in relationship to different theories of sexual selection remain very controversial topics (e.g., Getty, 1999; Rosenthal and Servedio, 1999; Chapman *et al*., 2003; Córdoba-Aguilar and Contreras-Garduno, 2003; Eberhard and Cordero, 2003; Pizzari and Snook, 2003). In particular, high mating rates can be beneficial to females rather than detrimental (Andersson, 1994; Jennions and Petrie, 2000) and one can argue that conflict is always present whenever there is female choice (Rosenthal and Servedio, 1999; Eberhard, 2004). Moreover, certain predictions based on the sexual conflict hypothesis do not hold in some groups. For example, the prediction about the positive relationship between the number of species in a clade and a potential for sexual conflict does not hold in some mammals, butterflies, spiders (Gage *et al*., 2002) and birds (Morrow *et al*., 2003). In a similar way, the prediction that the differences in genitalic form among congeneric species in which females are protected from male harassment should be less common than differences among congeneric species in which females are vulnerable to harassment by males has failed for a large sample of insects and spiders (Eberhard, 2004). Finally, many observations mentioned above are equally

consistent with mechanisms other than sexual conflict, in particular, with classical sexual selection.

Our goal here, however, is not to directly contribute to resolving these controversies but rather to summaries what existing mathematical theory tells us about expected dynamic outcomes of sexual conflict as far as the possibility of speciation is concerned. Our focus will be on mathematical models that explicitly consider the dynamics of evolutionary change driven by sexual conflict over mating rate. The conflict discussed here is the one between male traits for increasing mating success and female traits to restrict mating rate. Other important types of conflict, e g., between male traits for discouraging female remating after having mated successfully, and female trail for maintaining the optimal remating rate, are not considered here. Below, we start by reviewing previous modeling work and establishing connections between different models, then we describe our recent numerical work, and finally we attempt to make some generalizations and identify important directions for future work.

Review of previously published models

Parker and Partridge (1998). This was the first paper that invoked mathematical models in a discussion of the effects of sexual conflict on speciation. Although this paper neither studied the dynamics of evolutionary change explicitly, nor was sexual conflict per se the driving force of genetic divergence considered in the paper, we discuss it here both for completeness and because its conclusions have been often quoted in literature. Parker and Partridge (1998) modeled reinforcement, that is, the evolution of premating isolation as a result of selection against hybrids being produced after a secondary contact of two allopatric populations (e.g., Dobzhansky, 1940; Butlin, 1987; Howard, 1993; Servedio and Noor, 2003). In this scenario, evolutionary changes are driven by selection against gamete wastage rather than by sexual conflict. Still, sexual conflict over mating can be present if hybridizing males favor production of low-fitness offspring when for hybridizing females offspring production is deleterious. Parker and Partridge (1998) have used game-theoretical methods to identify the areas in parameter space resulting in sexual conflict in the above sense and to compare the relative gains/losses of the sexes given that hybridization does or does not take place. Parker and Partridge (1998) noticed that if there is a conflict, then males are selected to act as a force for gene flow, whereas females are in general selected to resist it. They also speculated that "speciation will be more in extensive in groups where females generally win mating conflicts than in those groups where males usually win" (Parker and Partridge, 1998, p. 266). We note that, as already acknowledged by Parker and Partridge (1998), their modeling framework does not allow to study evolu-

tionary dynamics as the population structure changes. Moreover, the question who wins sexual conflict does not make sense under many biologically realistic situations because, first, the average fitnesses of sexes are always equal and, second, the realized mating rates are often intermediate between those optimal for males and females (see below). Therefore, Parker and Partridge's conclusion cited above does not seem to be justified yet even under the reinforcement scenario they considered. We agree that the inability of females to evolve choosiness can indeed be interpreted as an evidence that males win sexual conflict. In the same way, the ability of females to evolve choosiness can be interpreted as an evidence that females win sexual conflict with males from the other population (but not with their own males).

The first truly dynamic models describing the evolutionary consequences of sexual conflict appeared in three independent papers published in 2000.

Frank (2000). Polyspermy, that is, near simultaneous fertilization of an egg by more than one sperm usually results in the death of both the egg and the sperm (e.g., Gilbert, 1997). This imposes a strong selection pressure on eggs to increase the average difference in arrival time of the first and second sperm at the inner membrane. At the same time, selection favors sperm to minimize boring time and win the race to the egg's inner membrane. Frank (2000) formulated and studied a population genetic model of evolutionary consequences of this sexual conflict. In his model, there are an egg trait x and a sperm trait y each controlled by a single, multiallele haploid locus. The average boring time from outer to inner membranes is proportional to

$$\alpha|x - y|^{\beta}, \tag{1}$$

where α and β are positive coefficients. The above functional form implies that the boring time is minimized when there is a phenotypic match between sperm and egg. The scale parameter α and the exponent β control how rapidly the boring time grows with the difference in sperm and egg phenotypes. Parameters α and β will repeatedly come back below in other models where they will control the range of compatibility between sperm and egg (or the strength of matching-based nonrandom mating; Gavrilets, 2004). As these parameters increase, the compatibility (or female preference for a male trait) decreases more rapidly with the difference between egg (female) trait and sperm (male) trait.

In Frank's model, both x and y were restricted to the interval [0,1]. Additional model components specify the process of sperm arrival at the outer membrane and allow for genetic relatedness r of different sperm. The relatedness r was defined as the probability that the two sperms are identical genetically.

Frank (2000) used numerical iterations of the corresponding dynamic equations with $\beta = 0.5$, 1.0 and 2.0 to find equilibrium distributions of allele frequencies stable to the invasion of any mutant. There are three general

observations from his simulations. First, all cases show strong diversification of egg character with extreme character values (0 and 1) at frequencies usually close to one-half. Second, the sperm also tend to split into two extreme clusters when the exponent β is 0.5 or 1, but sperm converge to a middle value of 0.5 when $\beta = 2$. When the scale $\alpha \leq 0.5$ and $\beta = 0.5$, convergence towards equilibrium is weak because sperm–egg interactions have little effect on boring time. Third, when the exponent is 0.5, increasing relatedness r causes weak convergence towards equilibrium. On the whole, relatedness values of $r \leq 0.5$ have relatively little effect. Frank's pioneering results demonstrate that sexual conflict can result in the maintenance of genetic variation in eggs only or in both eggs and sperm. Unfortunately his results allowed neither to see clearly the effects of parameters on resulting dynamics, nor evaluate the degree of *prezygotic* reproductive isolation present between different emerging clusters of eggs and sperm.

Kondoh and Higashi (2000). Genomic imprinting is the inactivation of a gene, dependent upon the sex of the parent from which this gene is inherited (e.g., Bartolomei and Tilghman, 1997). In mammals and plants, genes with growth-enhancing effect are often expressed only if inherited from the father, whereas those with growth-suppressing effect are expressed only if inherited from the mother. Kondoh and Higashi (2000) developed an analytical model describing evolutionary consequences of sexual conflict over offspring size. The model assumes that the number of offspring per mother is inversely proportional to the offspring size S, that the offspring size S is the function $S = y/(1 + x)$ of the growth enhancer level y and the growth suppressor level x, and that the survivorship of offspring increases with size S but decreases with both x and y. Both x and y are treated as continuously varying characters. First, Kondoh and Higashi (2000) showed that the optimum values of offspring size S differ between the sexes. Then, they studied the evolutionary consequences of this conflict. The dynamics of x and y was described by a pair of differential equations

$$\begin{pmatrix} \frac{dx}{dt} \\ \frac{dy}{dx} \end{pmatrix} = \begin{pmatrix} G_x & C \\ C & G_y \end{pmatrix} \begin{pmatrix} \frac{\partial \ln W_x}{\partial x'} | x' = x \\ \frac{\partial \ln W_y}{\partial y'} | y' = y \end{pmatrix} \tag{2}$$

Here G_x, G_y and C are (constant) additive genetic variances for x and y and the additive genetic covariance between them, and W_x and W_y are fitnesses of rare mutants x' and y' in a population characterized by values x and y. The system of equation (2) represents a variant of Lande's equations (e.g., Lande, 1979, 1981; Iwasa *et al.*, 1991; Abrams *et al.*, 1993; Gavrilets, 1997). Kondoh and Higashi (2000) proceeded to show that the population always evolves towards an equilibrium state at which the values of x and y are at a certain balance and the offspring size is intermediate between the values optimal from the per-

spective of maternally and paternally inherited genes. The equilibrium values of x and y are expected to be population-specific, e.g., because of local differences in selection on offspring size. Therefore, if two different allopatric populations hybridize, the imbalance in the levels of the paternally inherited growth-enhancer and maternally-inherited growth-suppressor may result in the offspring being too small or too large and, as a consequence, suffering reduced fitness. In this model, sexual conflict over offspring size can drive genetic divergence of allopatric populations which in turn may result in *postzygotic* reproductive isolation as an accidental byproduct. Unfortunately, Kondoh and Higashi's results do not provide an easy way to evaluate how rapidly and how much reproductive isolation evolves by this mechanism.

Gavrilets (2000). This author considered sexual conflict over mating rate using the standard quantitative genetics approach (e.g., Lande, 1979, 1981) analogous to that used by Kondoh and Higashi (2000). Assume that reproductive interactions between the sexes are mediated by two independent sex-limited quantitative traits: a male (or sperm) trait y and a female (or egg) trait x. Let the probability $\psi(x, y)$ that trait x is compatible with trait y, so that mating and fertilization are not prevented by isolating mechanisms, be a quadratic function:

$$\psi(x, y) = 1 - \alpha(x - y)^{\beta}, \tag{3}$$

where α is a positive parameter controlling the strength of female mating preferences and the exponent $\beta = 2$ (Lande, 1981). This *preference function* ψ plays the role similar to that of the boring time in the Frank (2000) model (see Equation (1)). The proportion of the males compatible with female trait x is

$$P(x) = \int \psi(x, y) g(y)\, \mathrm{d}y = 1 - \alpha[G_y + (x - \bar{y})^2], \tag{4}$$

where $g(y)$ is the distribution of y in the population, which has a mean $\bar{y}$ and variance G_y. The proportion $P(x)$ is a proxy of female mating rate. Sexual conflict is incorporated in the model by assuming that the overall female fitness $W_{\mathrm{f}}(x)$ is maximized at an intermediate value P_{opt} of the mating rate:

$$W_{\mathrm{f}}(P(x)) = 1 - s[P(x) - P_{\mathrm{opt}}]^2, \tag{5}$$

where s is a positive parameter measuring the reduction female fitness at non-optimal mating rates ($0 < P_{\mathrm{opt}} < 1$). For example, in sea urchins, egg fitness is maximized at a level of sperm density which is much smaller than levels common under natural conditions (Franke *et al.*, 2002). The success of male y in mating with female x is assumed to be given by a product of $\psi(x, y)$ and a function decreasing with $P(x)$. The latter function describes a reduction in the probability of successful mating with females that are compatible with too

many males as a consequence of the competition among males. The male overall fitness is found by averaging their mating success across all females.

The dynamics of the average trait values $\bar{x}$ and $\bar{y}$ in this model are described by a system of difference equations analogous to Eq. (2) above. To analyze this system, Gavrilets (2000) assumed that both mating preferences and sexual conflict are weak (i.e., α, $s \ll 1$), disregarded the covariance between x and y, and first made the standard simplifying assumption that the additive genetic variances G_x and G_y of female trait x and male trait y are somehow maintained at constant levels (e.g., at a mutation-selection balance). In this case, there are two different dynamic regimes. Let $\Delta P = 1 - P_{\text{opt}}$ be the optimum reduction in the proportion of compatible males, and $\Delta w = s(1 - P_{\text{opt}})^2$ the reduction in female fitness at the maximum possible mating rate. Note that the ratio $\Delta w/\Delta P$ measures an average rate of decline of female fitness with P after the optimum mating rate P_{opt} has been exceeded. That is, this ratio is a measure of the intensity of sexual conflict. Gavrilets (2000) shows that if

$$\frac{1}{2}\frac{G_y/G_x}{\Delta w/\Delta P} > 1, \tag{6}$$

the population asymptotically evolves to an equilibrium state at which the mean trait values match: $\bar{y} - \bar{x} \to 0$. Gavrilets (2000) interpreted this state as corresponding to males winning sexual conflict. [Below we will see that this conclusion is actually an artifact of the assumption that genetic variances do not change.] This regime is promoted if males have higher genetic variance than females (i.e., the ratio G_y/G_x is large) and/or the intensity of sexual conflict is small (i.e., the ratio $\Delta w/\Delta P$ is small). If the inequality (6) is reversed, the difference in the means asymptotically approaches a constant value displaced from zero: $|\bar{y} - \bar{x}| \to \delta$, where the displacement δ

$$\delta = \sqrt{\frac{\Delta P}{\alpha}\left(1 - \frac{1}{2}\frac{G_y/G_x}{\Delta w/\Delta P}\right)}. \tag{7}$$

The value of the displacement δ is intermediate between those that are optimal for males (zero displacement) and females (displacement at a value of $\sqrt{\Delta P/\alpha}$) Thus, neither sex wins the sexual conflict but rather there is a coevolutionary compromise. This compromise is dynamic – neither male nor female trait settles to an equilibrium but both keep simultaneously increasing (or decreasing) along one of the two lines at which the displacement in constant. The lines are defined by equations $y = x + \delta$ and $y = y - \delta$. That is, the population is in a regime of endless coevolutionary chase between the sexes. The rate R of morphological changes (that is, the change in the means per generation) is constant:

$$R = \alpha G_y \delta. \tag{8}$$

Note that both the displacement δ and the rate R increase with increasing the intensity of sexual conflict as measured by the ratio $\Delta w/\Delta P$. The two regimes are illustrated in Figure 1.

Gavrilets (2000) proceeded to allow for genetic variances G_x and G_y to change. Assuming that the distributions of x and y in the population are Gaussian, he showed that G_x and G_y are molded by mutation and selection in such a way that the population *always* enters the regime of endless coevolutionary chase between the sexes. Below we will see that this conclusion is actually an artifact of the Gaussian approximation used.

Gavrilets' results show that sexual conflict over mating rate can indeed result in rapid and continuous evolutionary change in the population. A by-product of this change will be reproductive isolation between isolated populations. Both the rate of change and the degree of reproductive isolation increase with the intensity of sexual conflict. If the latter increases with the population density, the model predicts stronger reproductive isolation between populations maintained at higher densities. This prediction has been supported in experiments with dung flies (Martin and Hosken, 2003).

The Gavrilets (2000) model has a number of important limitations: genetics is incorporated only implicitly, only unimodal phenotypic distributions can be described, no costs of traits were incorporated, and only weak selection was allowed.

Gavrilets et al. (2001). The major focus of this paper was on the evolution of female mate choice as driven by sexual conflict. The model studied was built on that in Gavrilets (2000) with two important modifications. First, the preference function $\psi(x, y)$ was a monotonically increasing (from 0 to 1) S-shaped func-

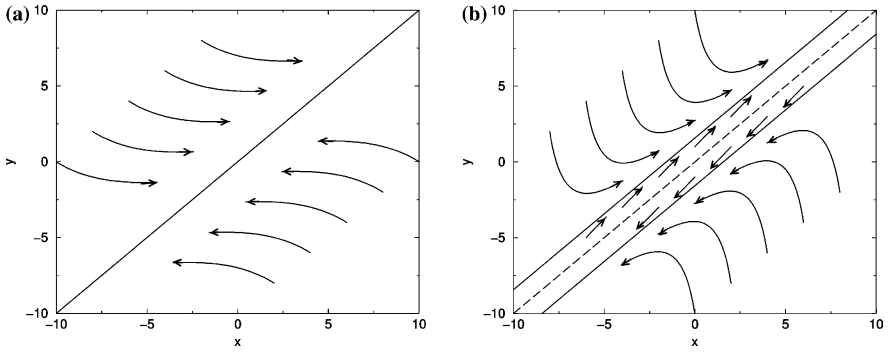

Figure 1. Two dynamic regimes in the Gavrilets (2000) model. (a) Evolution towards a stable line of equilibria $\bar{y} = \bar{x}$. Shown are the line of equilibria and a set of 10 trajectories (corresponding to 100 generations each) starting from different initial states. The direction of change is indicated by arrows. (b) Runaway dynamics along lines $\bar{y} = \bar{x} \pm \delta$. Shown are line of unstable equilibria $\bar{y} = \bar{x}$ (dashed line), the lines of run-away coevolution $\bar{y} = \bar{x} + \delta$ and $\bar{y} = \bar{x} - \delta$ and a set of 20 trajectories (corresponding to 100 generations each) starting from different initial sates. The direction of change is indicated by arrows (from Gavrilets (2000), Figs. 1 and 2).

tion of the difference $y-x$ rather than a unimodal function of $y-x$. This assumption reflects the change in biological interpretation of variables x and y, with y now being interpreted as a "male stimulus" (e.g., a visual or auditory display trait) and x being "female resistance" to mate. Specifically, each female was characterized by a "response curve" $\psi(x, y)$ giving the probability of mating with a male as a function of his stimulus y. Female resistance x was defined as the level of the male stimulus at which the probability of mating is 0.5. Second, the model allowed for natural stabilizing selection on both x and y with intermediate optima. Stabilizing selection was meant to reflect costs of producing elaborate male display traits and costs of female perception system. To analyze the resulting system of dynamic equations Gavrilets *et al.*, (2001) assumed that additive genetic variances did not change.

The model exhibited a number of different dynamic regimes. Continuous coevolutionary chase between male and female traits analogous to that in Gavrilets (2000) was only possible if there was no stabilizing selection (i.e., no costs are present). At this regime, both traits continuously increase maintaining a constant displacement δ. The mating rate is intermediate and the rate of change is

$$R = bG_y\psi'(\delta), \tag{9}$$

where b is a measure of the strength of selection for mating success in males. With stabilizing selection, the population evolves to an equilibrium or to a limit cycle at which the trait values change periodically. An important feature of the model dynamics is the simultaneous stability of different evolutionary attractors so that whether the population evolves to a specific equilibrium or cycle depends not only on parameters but on initial conditions.

Overall and not surprisingly, introducing costs of traits has resulted in reduced potential for allopatric speciation. The model shares most of the limitations of that in Gavrilets (2000). We note that Wachtmeister and Enquist (2000) used a completely different modeling technique – artificial neural networks – to analyze the coevolution of male stimulus and female resistance. Their conclusions parallel those of Gavrilets *et al.*, (2001) in that sexual conflict can indeed drive the evolution of exaggerated male stimuli and female resistance to them.

Rowe et al. (2003). These authors introduced and important modification of the Gavrilets *et al.* (2001) model. They assumed that females are characterized by two traits which they interpreted as the "threshold amount of the male trait required to initiate mating" x_1 and the "sensitivity to male trait" x_2. Female response curve was a linear function of male stimulus y:

$$\psi(x_1, x_2; y) = x_1 + x_2 y. \tag{10}$$

Now females have more flexibility in adjusting their response to male stimulus which they can do by changing both the threshold x_1 and sensitivity x_2. Rowe

et al. (2003) report a limited number of numerical simulations aiming to illustrate the difficulties in making generalizations about the evolutionary consequences of sexual conflict without detailed knowledge of how the relevant preference functions are genetically controlled and evolve. With regard to speciation, they conclude that no simple predictions are likely to emerge either.

Gavrilets and Waxman (2002). Excluding Frank's work, models discussed above used the quantitative genetic framework which does not consider the underlying genetics explicitly. Gavrilets and Waxman (2002) introduced an explicit genetic version of the Gavrilets (2000) model. They considered a very large sexual haploid population with distinct non-overlapping generations. There are two possibly linked multiallelic loci. The alleles $\mathbf{A}_i$ at the first locus are only expressed in females (or eggs), and the alleles $\mathbf{B}_j$ at the second locus are only expressed in males (or sperm). The probability ψ_{ij} that a female (or egg) carrying an $\mathbf{A}_i$ allele is compatible with a male (or sperm) carrying a $\mathbf{B}_j$ allele, so that mating (fertilization) is not prevented by isolating mechanisms, is

$$\psi_{ij} = \exp(-\alpha d_{ij}^{\beta}), \tag{11}$$

where d_{ij} is a measure of genetic distance between female allele $\mathbf{A}_i$ and male allele $\mathbf{B}_j$ and the exponent $\beta = 2$. The major reason for choosing a Gaussian form of ψ given by Equation (11) rather than quadratic form of ψ given by Equation (3) was to allow for stronger female preference α (which has to be relatively small in Equation (3) to avoid negative values of ψ). Let P_i be the proportion of the males in the population that are compatible with females carrying allele $\mathbf{A}_i$. As in Gavrilets (2000), the overall probability that an $\mathbf{A}_i$ female leaves offspring is a unimodal function of P_i that reaches a maximum at a certain value $P_{\mathrm{opt}} < 1$. To clarify the implications of the above assumptions, assume that the population is monomorphic for male allele $\mathbf{B}_j$. Then $P_i = \psi_{ij}$ and the females that have the optimum mating rate and the highest overall fitness are those for which $\psi_{ij} = P_{\mathrm{opt}}$. Using the definition of ψ it is easy to see that the optimum genetic distance of female alleles from the male allele is

$$\delta = \sqrt{\frac{\ln(1/P_{\mathrm{opt}})}{\alpha}}. \tag{12}$$

Note that both increasing the strength of conflict (i.e., decreasing P_{opt}) and decreasing female choosiness (decreasing α) result in increasing the optimum displacement δ.

To study the dynamics of this model, a mutation scheme has to be defined explicitly. Gavrilets and Waxman (2002) used the classical stepwise mutation model, which was previously used for modeling speciation (Nei *et al.*, 1983; Wu, 1985). Specifically, they assume that at each locus there are a large number of alleles labeled by integers $0, \mp 1, \mp 2, \ldots$ and that the x_i allele can only mutate to the alleles x_{i-1} and x_{i+1} and that the y_j allele can only mutate to $y_{\mathrm{j}-1}$ and

y_{j+1}. For simplicity it was also assumed that all possible mutations occur with the small but equal probabilities of $\mu/2$. Genetic distance was defined as the number of mutational steps separating the alleles: $d_{ij} = |i-j|$. In this model, genotype frequencies change deterministically. To avoid artifacts of very small numerical values in deterministic models and also to implicitly introduce effects of the finite population size, each time the frequency of a genotype fell below a small cut-off, Δ, the frequency was set to zero. The inverse of Δ can be thought of as a proxy for the population size.

Gavrilets and Waxman (2002) show that this model exhibits three general dynamic regimes. The first regime is an *endless coevolutionary chase* between the sexes in which females continuously evolve to decrease the mating rate while males continuously evolve to increase it (Holland and Rice, 1998; Gavrilets, 2000; Gavrilets *et al*., 2001; Gavrilets and Waxman, 2002). In this regime, which is only possible if there is no stabilizing selection on or any other cost of the traits, there is a dynamic compromise between the sexes, and the proportion of compatible pairs is intermediate between P_{opt} and 1. The coevolutionary chase is generically observed if the level of genetic variation is not too large which is the case when the mutation rate μ and/or the population size (as characterized by the inverse of Δ) are small. This regime is analogous to that observed in the Gavrilets (2000) model when condition (6) is not satisfied and to that observed in Gavrilets *et al*. (2001) when direct natural selection of the traits is absent.

The two other regimes are observed when the population size or mutation rates are sufficiently large. In the *Buridan's Ass regime*, there is very low variation in male alleles maintained by mutation whereas female alleles split into two clusters both at a genetic distance from the male allele close to the optimum distance δ predicted by Equation (12). In this regime, males get trapped between the two female subclusters and have relatively low mating success. [The name of this regime comes after a metaphor associated with the name of John Buridan (c. 1295/1300 to c. 1360), which has often been invoked in discussions concerning free will and determinism. The hungry animal stood between two haystacks that were indistinguishable in respect of their delectability and accessibility. Unable to decide from which stack to feed, the ass starved to death (Bro, 1995)].

In the *sympatric speciation regime*, males answer the diversification of females by diversifying themselves and splitting into two clusters that start evolving toward the corresponding female clusters. As a result, the initial population splits into different genetic clusters (species) that are reproductively isolated and which have emerged sympatrically. The regime of coevolutionary chase within-species ends after increasing genetic variation in female alleles leads to the splitting of female alleles into two subclusters within each species. By contrast, genetic variation in male alleles remains very low within each

species. At equilibrium, female P_i values are close to P_{opt} whereas males get trapped between two female subclusters and have low mating success. In the limit of very low mutation rates, sympatric speciation occurs if

$$\psi(\delta - 1) + \psi(\delta + 1) > 2\psi(\delta). \quad (13)$$

With large δ this condition is satisfied if function ψ is convex. If condition (13) is not satisfied, the population stays in the Buridan's Ass regime. Sympatric speciation requires small values of P_{opt} implying that sexual conflict over mating rates must be strong. For example, let $\alpha = 0.05$. Then if $P_{opt} = 0.637$, then $\delta = 3$ and condition (13) is not satisfied. If $P_{opt} = 0.450$, then $\delta = 4$ and condition (13) is satisfied, and sympatric speciation occurs. Sufficiently small values of P_{opt} can result in more than two species emerging sympatrically (Gavrilets and Waxman, 2002). The above conclusions are not affected by the recombination rate between the loci. The Buridan's Ass regime and the sympatric speciation regimes are illustrated in Figure 2. Note that Gavrilets and Waxman's (2002) results on these two regimes are analogous to Frank's previous conclusions on the maintenance of genetic polymorphism in female alleles only or in both female and male alleles.

When both male and female alleles split into clusters, reproductive isolation between different clusters can be rather strong. In this model sympatric speciation requires sufficiently strong sexual conflict (i.e., small P_{opt}) and sufficiently strong assortativeness in mating (i.e., large α). Note that costs of being choosy, which typically can easily prevent sympatric speciation (Gavrilets, 2004), are explicitly included in the model (because female fitness is reduced for suboptimal mating rates). That sympatric speciation still occurs is explained by the fact that the loci underlying reproductive isolation also experience direct selection for diversification induced by sexual conflict. In this model, selection does not have to overcome the homogenizing effect of recombination that otherwise can prevent sympatric speciation (Udovic, 1980; Felsenstein, 1981; Rice, 1984; Gavrilets, 2004).

Gavrilets and Waxman (2002) also noticed that other choices of the exponent β in the preference function (11) can lead to a continuous distribution of genotypes across the genotype space rather than to a discrete cluster formation. The important limitations of Gavrilets and Waxman (2002) work are that the population was haploid and that only two loci were considered.

Haygood (2004). This author has built an explicit genetic version of the Gavrilets (2000) model independently of Gavrilets and Waxman (2002). As in the latter paper, there are two multiallelic loci one of which is expressed in females (eggs) only and another expressed in males (sperm) only. Haygood (2004) considered both haploid and diploid populations but allowed for only two alleles at each locus. He concentrated on the conditions for the maintenance of genetic variation and on the possibility of cyclic changes in allele

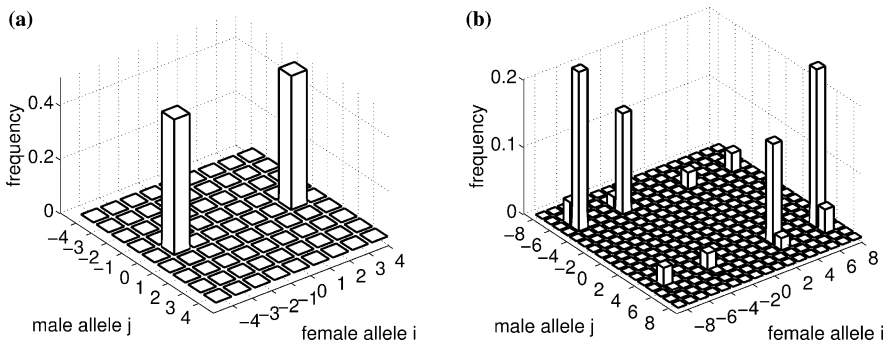

Figure 2. Population genetic states in the Gavrilets and Waxman (2002) model. (a) The Buridan's Ass regime ($P_{\text{opt}} = 0.6$; the average of values P_i is 0.64; there is a single male allele $\mathbf{B}_0$ and two female alleles $\mathbf{A}_3$ and $\mathbf{A}_{-3}$). (b) The sympatric speciation regime ($P_{\text{opt}} = 0.4$; the average of values P_i is 0.42) (from Gavrilets (2003), Fig. 10).

frequencies. In contrast to Gavrilets and Waxman (2002) who assumed that ψ_{ij} was a decreasing function of $i - j$, Haygood (2004) allowed for arbitrary preferences. Haygood (2004) showed that the maintenance of genetic variation requires certain trade-off. Specifically, in the haploid case it is necessary that each female type has preference for a specific (''its own'') male type, that is,

$$\psi_{ii} > \psi_{ij} \tag{14a}$$

for $j \neq i$, but at the same time in a monomorphic population females must do worse with their preferred males than females of the other type, that is,

$$w_f(\psi_{ii}) < w_f(\psi_{ki}) \tag{14b}$$

for $k \neq i$. The latter condition reflects the assumption that females suffer fitness loss from having too many compatible males.

In the diploid case the preference function ψ must be defined as a function of four alleles (two male and two female alleles) which makes the model much more difficult to analyze. Still Haygood (2004) was able to find the conditions for the maintenance of variation which become more restrictive than in the haploid case. First, the trade-offs analogous to those in the haploid case (given by Equations (14)) have to be satisfied for the homozygous genotypes. Second, heterozygotes must resemble homozygotes that have higher fitness in interactions with the other locus (the ''fitter allele dominance'' condition; Haygood, 2004).

In both haploid and diploid models, if genetic variation is not maintained, its loss occurs in a form of a ''chase'' between female and male alleles in which the population spends longer and longer times closer and closer to one of the four monomorphic state before moving to a neighborhood of another monomorphic state. Haygood (2004) did not study explicitly the level

of within-population genetic variation or within-population reproductive isolation.

Numerical results

Simple analytical models discussed above have a number of obvious limitations. In particular, quantitative genetic models treat genetics in an implicit, approximate way, while explicit genetic models consider only a single gene per sex. To train our intuition about effects of explicit genetics and multiple loci on the evolutionary consequences of sexual conflict we have performed individual-based simulations. A large number of model parameters makes thorough numerical investigations very difficult and time consuming. However, the existence of the analytical results reviewed above greatly simplifies numerical analysis by guiding simulations. A detailed description of our numerical results will be given elsewhere. Here, we outline some patterns that appear to be general.

We start with numerical models corresponding to those in Gavrilets (2000) and Gavrilets and Waxman (2002). Briefly, we consider a sexual diploid population of size N individuals. Generations are distinct and nonoverlapping. Each trait is controlled by $\mathcal{L}/2$ possibly linked loci, each with $\mathcal{A}$ alleles. The alleles are labeled by integers from 0 to $\mathcal{A}-1$. Mutation patterns are specified by the stepwise mutation model, so that allele i can only mutate to alleles $i-1$ or $i+1$ each with equal probability $\mu/2$ (e.g., Nei *et al.*, 1983). Alleles 0 and $\mathcal{A}-1$ can mutate only to alleles 1 and $\mathcal{A}-2$, respectively. Each female encounters n randomly chosen males. She mates with a male she encounters with probability $\exp(-\alpha d^2)$, where d is the phenotypic or genetic distance (to be specified below) between her female trait and his male trait (compare with Equation (11)). The overall number of offspring produced by a female is given by equation $B_{\max}\exp[-s(P-P_{\text{opt}})^2]$, where P is the proportion of males (out of the n males encountered) she has mated with, and $B_{\max}$ is the maximum possible number of offspring (compare with Equation (5)). No offspring was produced if $P=0$. Depending on a model version, the offspring can come from a single father or from different fathers.

Additive trait model. In this version, an allele's contribution to the trait is given by the value of its label. The trait value (x in females and y in males) is given by the sum of the contributions of corresponding $\mathcal{L}$ alleles. Phenotypic distance d between a male and a female is simply the difference between their corresponding trait values, i.e., $d=|x-y|$.

First, we discuss the case of only two alleles per locus (0 and 1). When sexual conflict is weak (i.e., P_{opt} is sufficiently large), the population quickly approaches a state at which the average male and female traits match. After

that evolution proceeds by random genetic drift (Fig. 3a). This phase is analogous to the evolution towards the line of equilibria observed in the Gavrilets (2000) model when condition (6) is satisfied (see Fig. la). The female trait x has much larger variance than the male trait y (Fig. 3b). The distribution of x in the population is Gaussian, whereas that of y is non-Gaussian and usually has heavy tails (data not shown). Female mating rate P is intermediate between P_{opt} and 1 (Fig. 3c). That is, genetic variation in both traits decreases the proportion of compatible pairs and, thus, the female mating rate. This happens in spite of the fact that the average trait values are the same in the sexes (Fig. 3a). Therefore, here the evolution towards the line of equilibria should not be interpreted as the ''males win'' situation but rather as a coevolutionary compromise between the sexes.

When sexual conflict is strong (i.e., P_{opt} is small), rapid coevolutionary chase in alternating directions occurs (Fig. 4a). This phase is analogous to that observed in the Gavrilets (2000) model when condition (6) is not satisfied. The direction of evolution changes when the trait values approach a boundary (i.e., 0 or $\mathcal{L}$) or if random genetic drift throws the population across the unstable line of equilibria (see Fig. 1b), so that the population starts evolving in the opposite direction even before the traits reach the boundary. There are substantial fluctuations in genetic variances with females typically having higher variance than males (Fig. 4b). Female mating rate is intermediate between P_{opt} and 1 (Fig. 4c). Both male and female traits generally exhibit Gaussian distributions (data not shown) except at the boundaries of trait range. As P_{opt} decreases, the speed of coevolutionary chase and the variances in both traits increase. The formation of discrete genetic clusters has never been observed.

Strong female preference (i.e., large α) significantly reduces both the genetic variance G_y in male trait and the average displacement δ (in accord with Equation (7)). Female genetic variance G_x generally also decreases with increasing female preference. Simulations show that sufficiently strong female preference slows the rate of evolution. This observation contradicts to Equation (8) which predicts that the rate of evolution is directly proportional to α. The explanation is that increasing α decreases the product of G_y and δ faster than linearly, so that the expression in the right-hand side of Equation (8) actually decreases with α.

Multiallelic model. With multiple alleles, coevolutionary chase between the sexes is the most common outcome. Typically, genetic variances are very small in both sexes. Now, each locus can experience multiple substitutions and continuous change. The direction and speed of evolution at different loci are always very similar (Figs. 5a and 5b).

With multiple alleles (e.g., with $\mathcal{A} = 32$) the formation of discrete clusters becomes possible, although it requires rather strict conditions. Specifically, the Buridan's Ass regime and the sympatric speciation regime can occur only at the

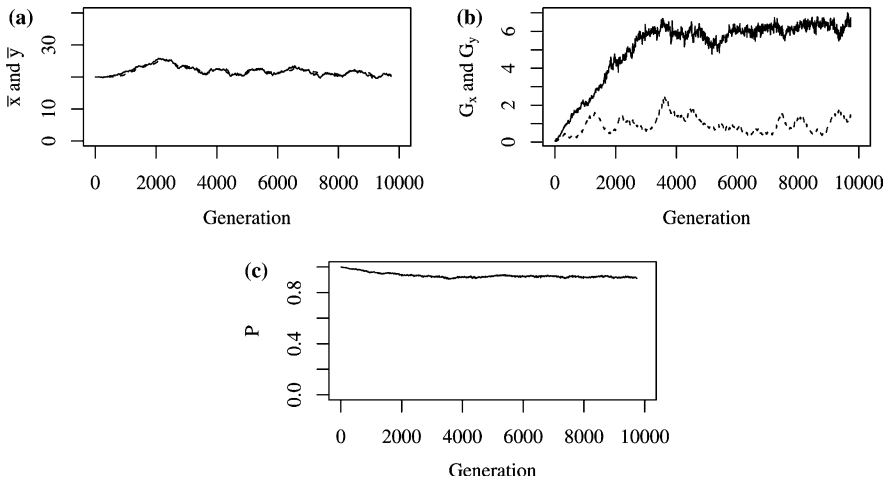

Figure 3. Random genetic drift along the line of equilibria in the additive trait model with 40 unlinked, diallelic loci. (a) Average trait values $\bar{x}$ and $\bar{y}$. (b) Genetic variances G_x and G_y. Solid lines: females, dashed lines: males. (c) Female mating rate. Parameters: $P_{\text{opt}} = 0.8$, $B_{max} = 5$, $n = 100$, $\alpha = 0.01$, $s = 1.02$, $\mu = 10^{-4}$, and population size $N = 3000$.

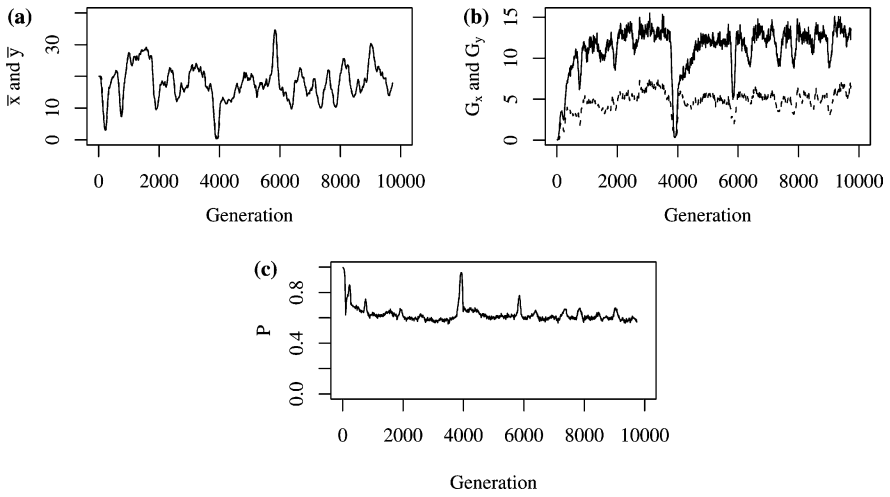

Figure 4. Coevolutionary chase at the additive trait model with 40 unlinked, diallelic loci. (a) Average trait values $\bar{x}$ and $\bar{y}$. (b) Genetic variances G_x and G_y. (c) Female mating rate. Parameters are the same as in Figure 3 except $P_{\text{opt}} = 0.2$ and $\alpha = 0.05$.

boundaries of the trait range and require a sufficiently large number of loci, a sufficiently high mutation rate, and a sufficiently large population size. These regimes occur only in one or two loci while all other loci have very low genetic variation maintained by mutation. For example, Figure 6 illustrates the distributions of allelic effects in a male locus and in a female locus in a simu-

lation that resulted in the emergence of two reproductive isolated clusters of genotypes. Because almost all genetic variation in each trait is attributed to a single locus, one can also interpret this outcome as the evolution of alleles of major genetic effect.

Genetic distance model. In general, compatibility between the sexes (e.g., genetic, behavioral, etc.) is expected to depend on the degree of matching between a number of specific components rather than a difference between a single pair of quantitative traits. We have incorporated such a component-by-component compatibility into the above individual-based model in the following way. There are a number of loci. Each locus can be thought as controlling a separate trait. For mathematical simplicity, we assume that at each locus, alleles with the higher labels are dominant over all alleles with lower labels. For example, this assumption is justified for alleles in a locus controlling wing coloration pattern in butterflies *Heliconius numata* (Joron, 2000). We define the *genic variance* as the sum of the variances of allelic effects at each locus computed using dominant alleles. We define the genetic distance between a female-expressed locus and a complementary male-expressed locus as the absolute difference between the labels of the dominant alleles present at the loci. We define the overall genetic distance d between a male and female genotypes as the sum of genetic distances over all $\mathcal{L}/2$ complementary pairs of male- and female-expressed genes. As before, the probability of "compatibility" between two organisms was given by a Gaussian function $\exp(-\alpha d^2)$.

Diallelic model. The diallelic version of this model shows that the population generally reaches an equilibrium at which female mating rate is close to P_{opt}. When sexual conflict is strong (Figs. 7a and b), most loci are polymorphic with allele frequencies close to 0.5. This large variation in both sexes decreases the proportion of compatible pairs in the population, and, thus, female mating rate. When sexual conflict is weak (Figs. 7c and d), males have significantly smaller variance than females. The number of polymorphic loci and the variance of trait values also decrease in both female loci and male loci. Strong

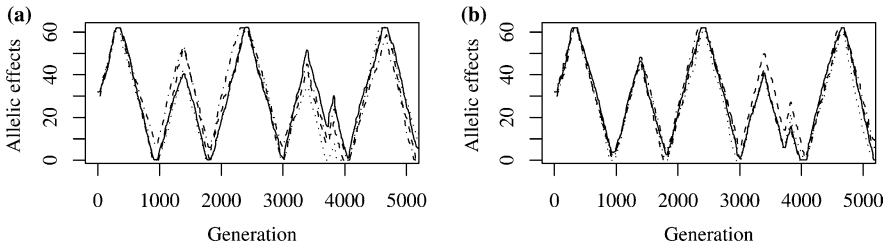

Figure 5. Coevolutionary chase at individual loci in the additive trait model with 8 unlinked loci, each with 32 alleles. (a) The dynamics of the average allelic effects at the four female loci. (b) The dynamics of the average allelic effects at the four male loci. Parameters: $P_{\text{opt}} = 0.4$, $B_{\max} = 5$, $n = 100$,$\alpha = 0.01$, $s = 1.02$, $\mu = 10^{-4}$, and $N = 10{,}000$.

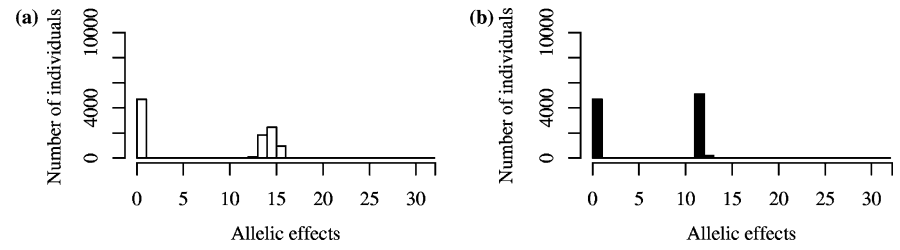

Figure 6. Sympatric speciation in the additive trait model with 20 unlinked loci, each with 32 alleles. (a) The distribution of allelic effects at a single polymorphic female locus. (b) The distribution of allelic effects at a single polymorphic male locus. These polymorphisms have resulted in the population being split into two genetic clusters. The probability of successful mating between the individuals from different clusters is approximately 0.0005. Parameters are the same as in Figure 5.

female preference (i.e., large α) decreases the levels of variation in both sexes. No discrete clusters formation has been observed. Instead the population spreads in the genotype space forming kind of a cloud.

Multiallelic model. The multiallelic version of this model (e.g., with $\mathcal{A} = 32$) exhibits the coevolutionary chase regime if the number of loci, population size, mutation rates, and initial genetic variation are sufficiently small. During the chase, the evolution towards larger trait values is much faster than in the opposite direction (Fig. 8a). This reflects the fact that dominant alleles are easier to fix than recessive ones (e.g., Crow and Kimura, 1970). Genic variance is small in both sexes (Fig. 8b). Female mating rate is intermediate (Fig. 8c).

The Buridan's Ass regime and the sympatric speciation regime are observed if the population size, mutation rates and the initial genetic variation are sufficiently large, and the number of locus is moderate (e.g., $\mathcal{L} = 8$). The sympatric speciation regime is more frequently observed as P_{opt} decreases. The linkage disequilibrium among the loci is generally very small, so that the loci evolve largely independently. Different regimes are often observed at different loci at he same time (Fig. 9). Also, there are rapid stochastic transitions between different regimes by genetic drift (Fig. 10). Note that the Buridan's Ass regime and the sympatric speciation regime are indicated by the large genetic variance only in female loci and in both sets of loci, respectively. Generally, a small number of loci contribute most of genetic variance (Figs. 9 and 10), that is, alleles of major effects evolve. The number of polymorphic loci with very large allelic effects generally increases as P_{opt} decreases. The parameter range required for the discrete cluster formation is much wider than in additive trait models.

However, in the sympatric speciation regime, reproductive isolation among genetic clusters is much weaker than that observed in the Gavrilets and Waxman (2002) model. Genetic clusters are much less distinct because of recombination and segregation (Fig. 11). The haploid network in Figure 11 was computed on the basis of the similarity in the sequences of dominant alleles

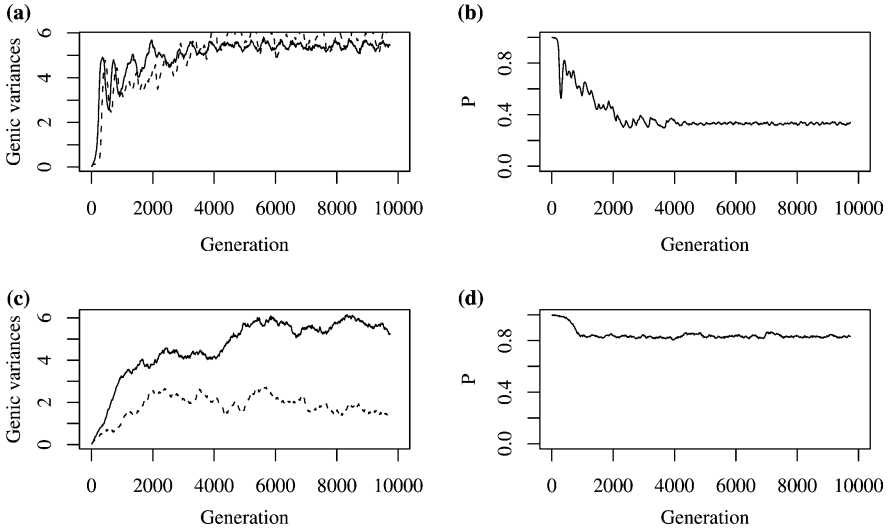

Figure 7. Evolution toward an equilibrium in the genetic distance model with 40 unlinked, diallelic loci. (a) Genic variances, strong sexual conflict ($P_{opt} = 0.2$). (b) Average female mating rate, strong sexual conflict. (c) Genic variances, weak sexual conflict ($P_{opt} = 0.8$). (d) Average female mating rate, weak sexual conflict. Other parameters: $n = 100$, $B_{max} = 5$, $\alpha = 0.01$, $s = 1.02$, $\mu = 10^{-4}$, and $N = 10{,}000$. Solid lines: females, dashed lines: males.

among 100 individuals randomly sampled at generation 50,000. Linkage disequilibrium is generally very small and recombinant genotypes are always commonly observed (unless recombination rate is very low, say $r = 0.005$). There are many small clusters loosely connected with each other, instead of a few large distinct clusters. When the sympatric speciation regime occurs, the number of these small clusters generally increases as P_{opt} decreases.

If the number of loci is large (e.g., $\mathcal{L} = 40$) and also the population size, mutation rates and the initial genetic variation are sufficiently large, the population is at a state at which female mating rate is close to P_{opt} without the discrete clusters formation at any locus. Most female loci generally exhibit unimodal allelic effects distributions with a moderate genetic variance (Fig. 12). Many loci with relatively small effects contribute to the overall genetic variance. The total variance in females is large enough to allow them to achieve their optimal mating rate. Males generally have much smaller genetic variance than females. In this regime, females "spread" in the genotype space without forming any discrete clusters.

Polyspermy model. In the models discussed above, the number of offspring was defined rather heuristically. Here, we explicitly consider a specific biological mechanism of sexual conflict – polyspermy. We assume that each egg can encounter a random number of sperm (drawn from a Poisson distribution

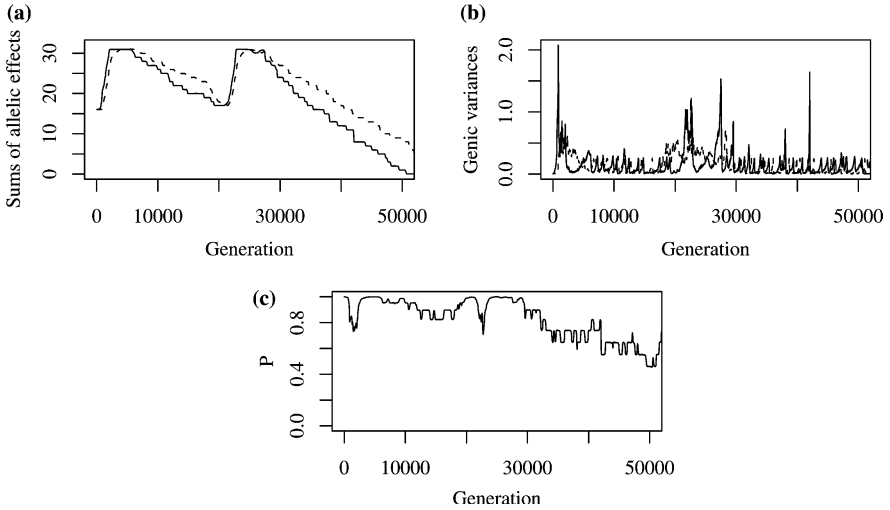

Figure 8. Coevolutionary chase in the genetic distance model with 2 unlinked loci, each with 32 alleles. (a) Sums of dominant allelic effects. (b) Genic variances. (c) Female mating rate. Parameters: $P_{\text{opt}} = 0.2$, $B_{\max} = 5, n = 100, \alpha = 0.01, s = 1.02, \mu. = 10^{-4}$, and $N = 10{,}000$. Solid lines: females; dashed lines: males.

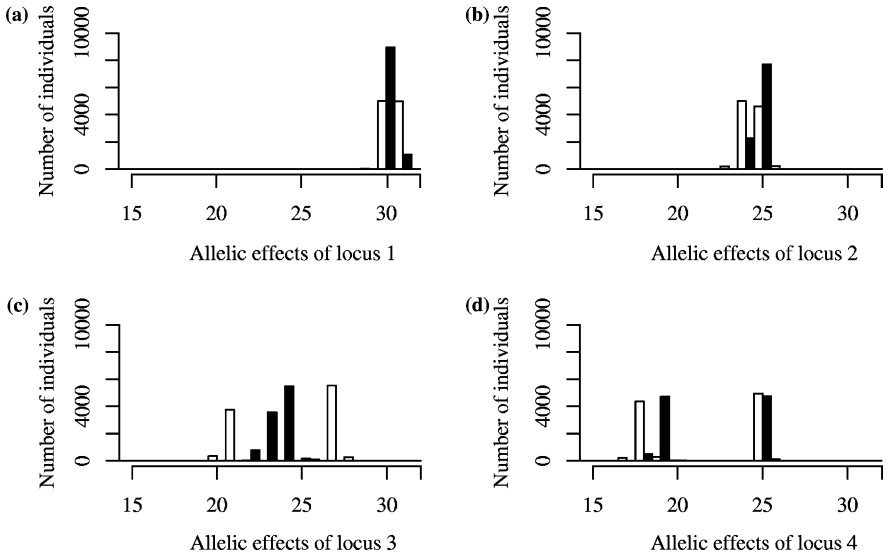

Figure 9. The distribution of allelic effects at generation 50,000 in the genetic distance model with $\mathcal{L} = 8$ unlinked loci and $\mathcal{A} = 32$ alleles. (a), (b) Coevolutionary chase; (c) the Buridan's Ass regime; (d) sympatric speciation regime. White bars: females, black bars: males. Parameters are the same as in Figure 8 except $P_{\text{opt}} = 0.4$.

with average c). Each encountered sperm fertilizes the egg with probability $\exp(-\alpha d^2)$. Polyspermy is incorporated by assuming that the egg dies if it is fertilized by more than one sperm.

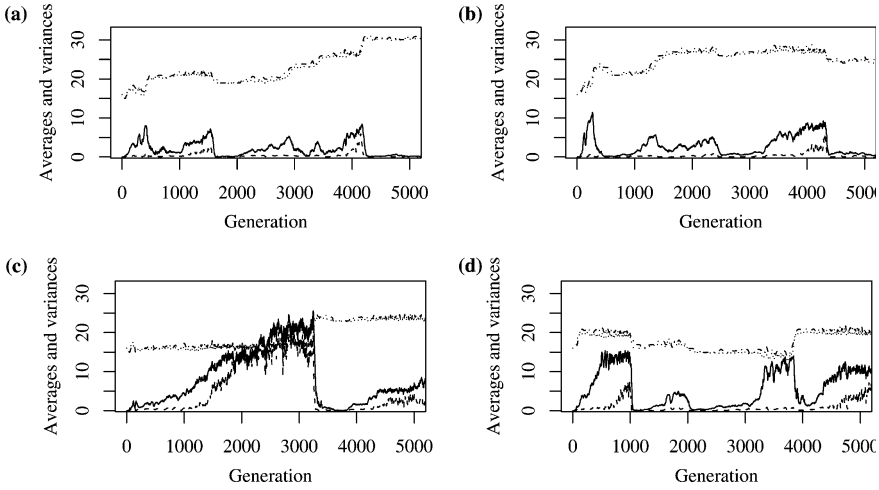

Figure 10. The averages (upper curves) and variances (lower curves) of the allelic effects at each pair of loci during 50,000 generations corresponding to Figure 9. The curves for male and females averages practically coincide.

Figure 13 shows an example of coevolutionary chase in the additive trait model. The average number of fertilizations per egg is between one (which is optimum for female) and c. Eggs' death rate is about 0.6. In an example of the genetic distance model (Fig. 14) the average number of fertilizations per egg is about one and eggs' death rate is about 0.4. At a qualitative level, the polyspermy model corresponds to $P_{\text{opt}} = 1/c$. Overall, the observed dynamics in the polyspermy models are similar to those in the models discussed above. This suggests that using the heuristic approach for describing fitness consequences of sexual conflict provides a good approximation of more realistic scenarios.

Discussion and conclusions

Here, we discuss four general issues relevant to the mathematical models considered above. First, we consider general properties of evolutionary dynamics driven by sexual conflict over mating rate. Then, we discuss the implications of these dynamics for speciation. Finally, we consider the limitations of existing theoretical models and possible avenues for empirical work that would benefit theoretical research.

General dynamic regimes under sexual conflict

Earlier verbal models of the evolutionary consequences of sexual conflict over mating have concentrated exclusively on the regime of continuous coevolutionary chase between the sexes (Rice and Holland, 1997; Holland and Rice,

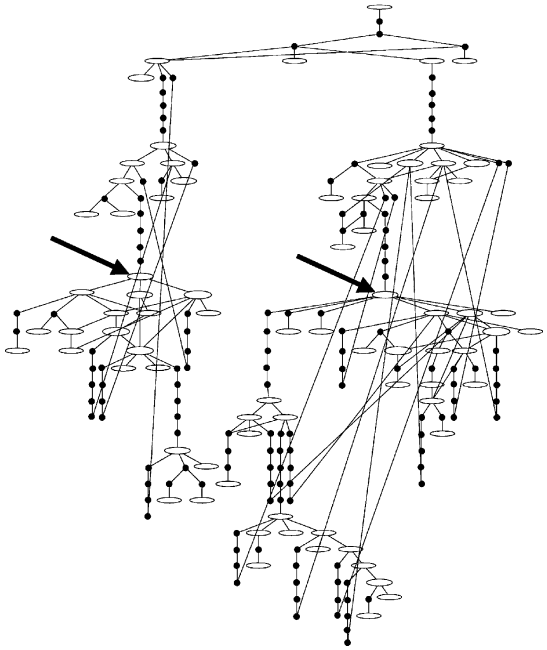

Figure 11. An example of a haplotype network in the genetic distance model with $\mathcal{L} = 8$ and $\mathcal{A} = 32$. The data are from the simulation run shown in Figure 9. Ovals represent groups of individuals with the same genotype. The size of an oval reflects the number of individuals in the group. The number of dots between the ovals represents genetic distance between the corresponding groups. The compatibility between the individuals in the two clusters specified by arrows is approximately 0.25.

1998). Mathematical models have confirmed that such a chase is indeed possible (Gavrilets, 2000; Gavrilets *et al.*, 2001; Gavrilets and Waxman, 2002). However, mathematical models also show that coevolutionary chase is but one of several possibilities. Overall, there are at least six different dynamic regimes observed in models of sexual conflict: (1) continuous coevolutionary chase between the sexes, (2) evolution towards an equilibrium (Kondoh and Higashi, 2000; Gavrilets *et al.*, 2001), (3) cyclic evolution (Gavrilets *et al.*, 2001; Haygood, 2004), (4) evolution towards a line of equilibria with subsequent random drift along this line (Gavrilets, 2000 and numerical studies reported in this paper), (5) Buridan's Ass regime involving extensive diversification in female alleles without comparable diversification in male alleles (Frank, 2000; Gavrilets and Waxman, 2002, and numerical studies reported in this paper), (6) extensive diversification in both male and female alleles (Frank, 2000; Gavrilets and Waxman, 2002 and numerical studies reported in this paper). Mathematical models also show that different dynamic regimes can be observed with the same set of parameter values but under different initial conditions. It is also possible that the same population switches from one regime to another as a

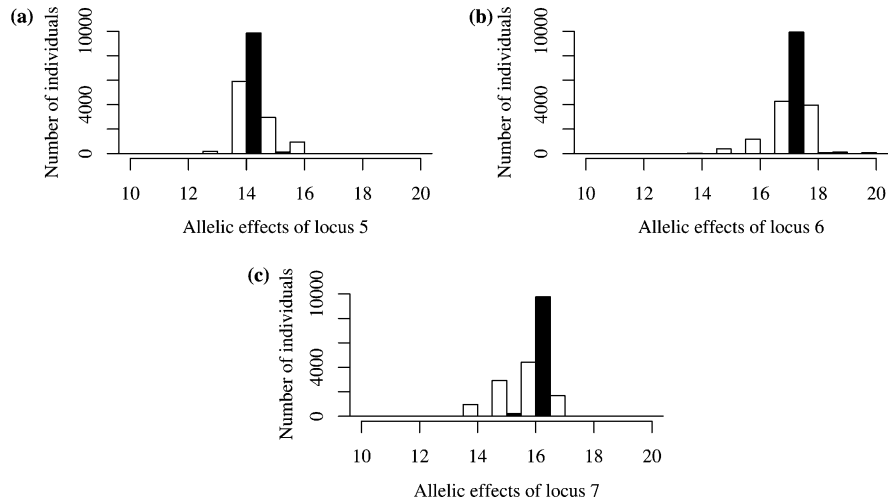

Figure 12. Typical examples of the distributions of allelic effects in the genetic distance models when the female mating rate is close to P_{opt} without the discrete clusters formation. White column: females, black column: males. Parameters are the same as in Figure 8 except $\mathcal{L} = 40$. Population is at generation 50,000.

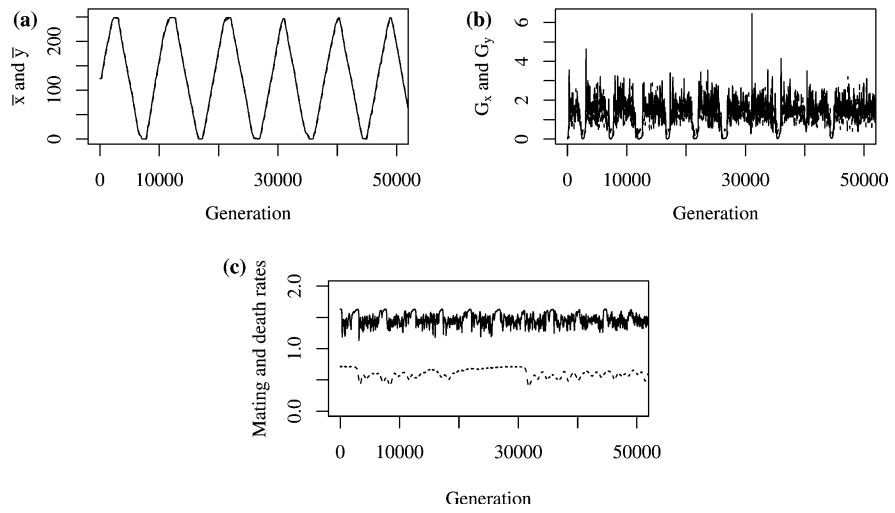

Figure 13. An example of coevolutionary chase in the additive trait model with polyspermy. There are 8 unlinked loci, each with 32 alleles. (a) Average trait values $\bar{x}$ and $\bar{y}$. (b) Genetic variances G_x and G_y. (c) Average number of fertilizations per egg (solid line) and eggs' death rate (dashed line). Parameters: $c = 2$, $\alpha = 0.01$, $\mu = 10^{-4}$, and $N = 10{,}000$.

result of stochastic perturbations due to, say, random genetic drift. Moreover, different sets of loci controlling mating and fertilization in the same species can follow different dynamic regimes. In short, evolutionary dynamics of sexual conflict is extremely rich and complex.

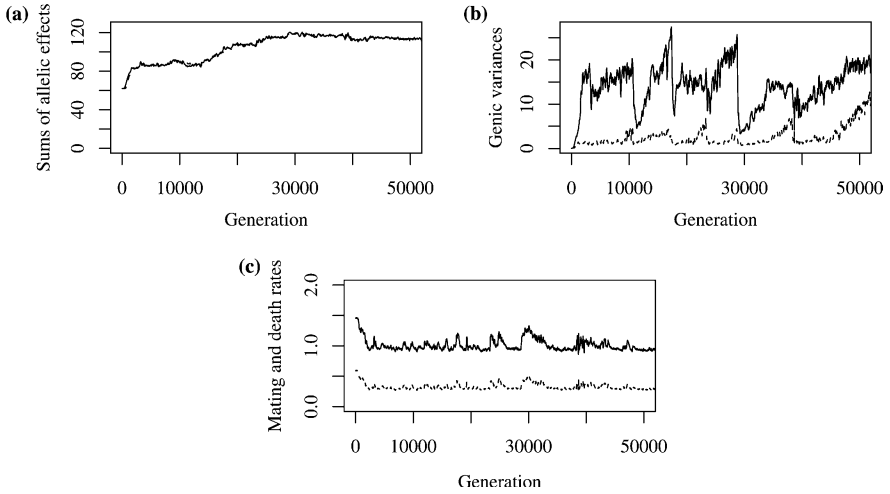

Figure 14. An example of the evolution by random drift along a line of equilibria in the genetic distance model with polyspermy. There are 8 unlinked loci, each with 32 alleles. (a) Sum of dominant allelic effects. (b) Genic variances. Solid lines: females, dashed lines: males. (c) Average number of fertilizations per egg (solid line) and eggs' death rate (dashed line). Other parameters are the same as in Figure 13.

Obviously, continuous coevolutionary chase in the same direction is only possible if it is not constrained by natural selection on the alleles and traits underlying reproduction. However, the absence of such constraints does not guarantee that coevolutionary chase will be observed. Typically, it is also necessary that the population has relatively low levels of genetic variation (which is expected if the population size and mutation rate are small). The plausibility of coevolutionary chase is strongly affected by the genetics of between-sexes interactions. In particular, coevolutionary chase is more plausible if these interactions are mediated by additive quantitative characters than if multiple dominant alleles are involved.

An important novel conclusion emerging from models is that females can reduce the burden of sexual conflict by diversifying genetically rather than "running" away from males. Such a diversification in females can be answered by diversification in males. The extent of diversification and whether it results in the formation of distinct genetic clusters within the population depend on a number of different factors including the strength of sexual conflict, the strength of natural selection, the population size, and genetics of the traits involved.

Given this complexity, making generalizations is difficult. However some additional general observations do emerge. In particular, genetic variation in female alleles and traits is larger than that in males. [Note however that this observation is not specific for sexual conflict. Female preferences, in general,

are expected to induce strong selective pressure reducing variation in male traits.] The level of genetic variation in both sexes increases with the strength of sexual conflict. Recombination rates have little effect unless they are very low. The evolved mating rate is often intermediate between the one optimum for females and the one optimum for males. Therefore, in this case sexual conflict is not won by a sex but rather there is a (dynamic or static) evolutionary compromise between the sexes. In other situations, females can achieve their optimum mating rate by diversifying (Buridan's Ass regime). Sexual conflict can also result in the evolution of alleles of major effects.

Mathematical models show that sexual conflict can explain certain empirical patters which were viewed rather puzzling previously. These include apparent deceleration in the evolution of sperm lysin genes in abalone (Yang *et al.*, 2000), complex genetic clustering in sperm protein bindin in sea urchins (Palumbi, 1999), in sperm lysin genes in abalone (Swanson *et al.*, 2001), and in sea urchin gamete recognition genes (Vacquier and Moy, 1997), as well as higher genetic variation in female reproductive traits in carabid beetles (Sota *et al.*, 2000) and apparent dimorphism in female genitalia in a spider (Huber and González, 2001).

Speciation vs. genetic diversification

Speciation can be viewed as the process of genetic divergence between populations or between parts of the same population accompanied by the evolution of reproductive isolation (Gavrilets, 2003, 2004). In general, genetic divergence and reproductive isolation go along with ecological and morphological divergence.

Mathematical models support the notion that sexual conflict over mating is a powerful engine of genetic divergence. However, out of the six dynamic regimes listed in the previous subsection only two describe speciation. The first regime, i.e., continuous coevolutionary chase between the sexes, will lead to allopatric speciation as a byproduct. The sixth regime, i.e., extensive diversification in both male and female alleles, can lead to sympatric speciation if the diversification is in the form of distinct cluster formation. The four other regimes lead to increased genetic variation in the population but not to speciation per se.

Sympatric speciation in diploid multilocus populations occurs only very rarely and is much more difficult to achieve than in the haploid two-locus model studied by Gavrilets and Waxman (2002). In the cases when sympatric speciation did occur, it was generally due to the divergence in a single pair of loci.

The question which outcome is more general – speciation or increased genetic variation without speciation – cannot be answered yet. The answer will depend

of a number of specific biological factors and details which most likely will vary between different organisms. Mathematical models, however, do already allow a better understanding of the effects of these factors as discussed above.

Limitations of existing models

Theoretical research of the evolutionary consequences of sexual conflict is only a few years old. Existing models are but a scratch on the surface. We need both more models and more realistic models to understand better sexual conflict and to be able to guide empirical research and formulate testable hypotheses.

Most models considered above assume that the effects of mutations are small and that the "preference function" ψ is smooth. However, the interactions between the sexes during reproduction in real organisms can be governed by more complex relationships. For example, sperm–egg recognition in abalone is known to be controlled by the specific interaction between a sperm protein lysin and the egg receptor VERL for it (Galindo *et al*., 2002; Kresge *et al*., 2001). In general, a single mutation can significantly change the protein structure and its binding affinities (e.g., Linder *et al*., 1995; Oshima *et al*., 2000; Nagaoka and Akaike, 2003). Describing such interactions would require introducing preference functions that are "rugged" rather than smooth. The consequences of such preference functions for the evolutionary dynamics and population genetic structure remain unknown.

In models discussed above, mating behavior (e.g., the strength of female preference) does not change in an individual's life. However, the propensity to mate for females can change during the reproductive period, so that the mating behavior can also change (e.g., Snook, 1998; Kodric-Brown and Nicoletto, 2001). The best strategy for female can be to mate with an optimum number of males and never mate with other males after that. Such a strategy may result in qualitatively different mating behaviors before and after the mating with a certain number of males. The propensity to mate can also be strongly affected by competition between males (Rice, 1998). Obviously, the best situation for a particular male is when all females are perfectly compatible with him and not compatible at all with all other males. Competition between males encourages a male to decrease the remating rate of the female that has mated with him previously (Wolfner, 1997; Holland and Rice, 1998; Rice, 1998; Cook and Wedell, 1999; Arnqvist and Nilsson, 2000; Wedell, 2001; Chapman *et al*., 2003; Zeh and Zeh, 2003). How the change in the strength of female preference affects the consequences of sexual conflict remains unknown.

All models considered above are rather unrealistically symmetric in the sense that all loci have equal effects. It is well known that the conditions for the maintenance of genetic variation are much broader in models with equal locus effects than in more realistic models with nonequal effect (e.g., Bürger, 2000).

How introducing asymmetry would affect the conclusions on sexual conflict remains unknown.

Another important area of research that has not been approach yet is models that treat the dynamics of the population size explicitly. Finally, one needs to develop explicit spatial models that would directly address the possibility of parapatric speciation driven by sexual conflict (which has not been considered so far at all).

Limitations of existing data

The development of more sophisticated and realistic mathematical models of sexual conflict is hindered by a lack of precise data. Important directions for empirical work still remain identifying and characterizing in a quantitative way traits and genes underlying the interactions between the sexes during reproduction and characterizing the levels of within- and between-population variation in these traits and genes. Once such traits and genes are identified, quantitative estimates of different parameters and characteristics can potentially be made. Among the most important quantitative characteristics of sexual conflict over mating are the shape of female fitness function $(w_f(P))$, the optimum proportion of compatible males (P_{opt}), the maximum reduction in female fitness from having too many compatible males $(\Delta(w))$, and the effects of population density on the strength of sexual conflict. These characteristics need to be measured in the laboratory or in natural populations if we are to understand whether sexual conflict is as significant in evolution and speciation as some believe it is.

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