Is Sexual Conflict an "Engine of Speciation"?

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At the end of the last century, sexual conflict was identified as a powerful engine of speciation, potentially even more important than ecological selection. Earlier work that followed—experimental, comparative, and mathematical—provided strong initial support for this assertion. However, as the field matures, both the power of sexual conflict and constraints on the evolution of reproductive isolation as driven by sexual conflict are becoming better understood. From theoretical studies, we now know that speciation is only one of several possible evolutionary outcomes of sexual conflict. In line with these predictions, both experimental evolution studies and comparative analyses of fertilization proteins and of species richness show that sexual conflict leads to, or is associated with, reproductive isolation and speciation in some cases but not in others. Increased genetic variation (especially in females) without reproductive isolation is an underappreciated consequence of sexually antagonistic selection.

By the end of 1990s, studies of sexual conflict and sexually antagonistic coevolution moved to the forefront of experimental and theoretical research in evolutionary biology (Rice and Holland 1997; Holland and Rice 1998; Rice 1998). Although the potential evolutionary importance of sexual conflict was anticipated and articulated from a theoretical point of view by Geoff Parker 20 years earlier (Parker 1979), the explosive interest in this topic was a result of groundbreaking experimental work with *Drosophila melanogaster* by Bill Rice (1993, 1996), which directly showed high potential for sexually antagonistic coevolution.

Sexual conflict is a special case of intragenomic conflict (Rice and Holland 1997; Rice 1998; Crespi and Nosil 2013). Sexual conflict occurs if the interests of the sexes with regard to certain aspects of reproduction differ (Parker 1979; Arnqvist and Rowe 2005). Ultimately, 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). Sexual conflict can occur over mating rate (Rice and Holland 1997; Holland and Rice 1998; Rice 1998), offspring size (Haig 2000), parental care (Smith and Härdling 2000; Barta et al. 2002), the use of sperm (Ball and Parker 2003), epigenetic control of development (Rice et al. 2012), etc.

Sexual conflict can occur through two genetic routes (Chapman and Partridge 1996; Par-

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ker and Partridge 1998). Within-locus conflict occurs when the locus controls a trait expressed in both sexes and the optimum trait values differ between the sexes. As a result, optimizing the trait value in one sex will lead to a fitness reduction in the other sex. Within-locus conflict can be resolved via a number of mechanisms, including the evolution of sex linkage, sex-specific expression of genes, gene duplication, and condition dependence (Bonduriansky and Chenoweth 2009; van Doorn 2009). Between-locus conflict occurs when there are two different (sets of) traits each expressed in one sex only but affecting the fitness of both sexes in opposite directions. In this case, adaptive changes in a trait of one sex cause deleterious fitness consequences for the other sex, which can be negated by the evolution in a trait of the other sex, which in turn will cause deleterious fitness consequences for the first sex. For example, males can evolve adaptations increasing their mating rate, which would be detrimental for females who would then evolve some counteradaptations to decrease the mating rate (Rice 1996).

One particularly exciting idea that has emerged from studies of sexual conflict and sexually antagonistic coevolution is that sexual conflict can be an important "engine of speciation" (Rice 1996, 1998; Howard et al. 1998; Parker and Partridge 1998). In standard modern perspective, speciation is a result of genetic divergence between populations accompanied by the evolution of reproductive isolation (Howard and Berlocher 1998; Schluter 2000; Coyne and Orr 2004; Dieckmann et al. 2004; Gavrilets 2004). Genetic divergence can be driven by a variety of evolutionary factors, including mutation, random genetic drift, and natural, sexual, and social selection. Reproductive isolation can follow from a variety of mechanisms, resulting in incompatibilities (including genetic, developmental, morphological, ecological, and behavioral) of males and females from diverging populations or in a reduced fitness of their offspring. As was argued by Rice (1998), Parker and Partridge (1998), and others (e.g., Howard et al. 1998), sexual conflict can contribute to these processes in a number of ways.

Below, I briefly summarize several, mostly verbal, theories of biological diversification caused by sexual conflict and then move to discussing some of the more concrete mathematical models and empirical data and patterns.

WITHIN-LOCUS CONFLICT AND SPECIATION

In general, if within-locus conflict is not resolved (e.g., via sex-specific expression of genes), one would expect that observed trait values in both sexes will deviate from their respective optima. Also, there will be genetic correlations between the traits expressed in males and females so that selection on one sex can cause a correlated response in the other. Unresolved within-locus conflict can impede any form of genetic divergence, reduce the mean fitness of populations, and increase their extinction rate (Bonduriansky and Chenoweth 2009). These effects will also hinder speciation. At the same time, genetic correlations between the traits expressed in males and females can simplify evolution across a valley of maladaptation toward a new optimum for one sex if the other sex is under strong directional selection. This effect can promote speciation (Bonduriansky and Chenoweth 2009).

If within-locus conflict is resolved and male and female traits have evolved to their own new optima, additional effects can occur (Parker and Partridge 1998). First, independent evolution of sexual dimorphism or sex-limited traits by sexual conflict in two isolated populations can result in hybrid breakdown and postzygotic reproductive isolation (Michalak and Noor 2003). Second, such evolution can, as a by-product, affect mate choice traits, which would lead to premating isolation when secondary contact is made. Note that these two effects are not specific to sexual conflict and can happen as a result of genetic divergence driven by any evolutionary factor (Coyne and Orr 2004). At the same time, one can argue that sexually antagonistic genes are more likely than other genes to contribute to incompatibilities between species, because they are responsible for a large part of the standing additive genetic variation and are therefore likely

to diverge between populations in response to divergent selection.

Recently, Lisle and Rowe (2014) argued that sexual dimorphism evolving to resolve the sexual conflict may represent a key innovation driving, rather than constraining, diversification. This can happen if the newly acquired ability of the sexes to evolve independently allows them to explore novel parts of the morphospace, which would be maladaptive for a sexually monomorphic species.

BETWEEN-LOCUS CONFLICT AND SPECIATION

The main emphasis of Rice and Holland (1997) and Rice (1998) was between-locus conflict over mating rate and its consequences for the evolution of reproductive isolation between allopatric populations. They argued that direct deleterious effects of high mating rates on female fitness (e.g., Rice 1996; Rice et al. 2005) 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 perpetual and rapid coevolution of male and female traits controlling reproduction. As a by-product of this coevolution, different allopatric populations will diverge in these traits quickly, **loosing** mutual reproductive compatibility and, thus, becoming different species.

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REINFORCEMENT AND SEXUAL CONFLICT

Parker and Partridge (1998) have also offered a new perspective on a classical scenario of speciation with gene flow: reinforcement. The standard line of reasoning (Dobzhansky 1940; Butlin 1987; Howard 1993) is that if two partially diverged populations start hybridizing and hybrids happen to have reduced fitness, then selection will favor evolution of reinforced premating isolating mechanisms, which would result in decreasing the frequency of unfit hybrids. An implicit assumption here is that both males and females will benefit from reinforce-

ment. In contrast, Parker and Partridge (1998) argued that although, in general, females are indeed selected to resist such hybridization, males can benefit from it even if offspring has somewhat reduced fitness. As a result, differences in selection acting on females and on males for acceptance of matings in interpopulation encounters can produce a role for sexual conflict in determining whether reinforcement of mating barriers does or does not occur. Parker and Partridge (1998) made three interesting predictions. First, speciation will be more extensive in groups in which females generally win mating conflicts than in those groups in which males usually win. Second, where there is evidence for reinforcement, it will be the females that are responsible for the resulting premating isolation. Third, in those groups in which females tend to win mating conflicts, the genetic variability within species will be less than that in comparable groups in which males tend to win. Some empirical evidence supports these predictions (Parker and Partridge 1998). At the same time, more recent modeling work has shown that in many cases sexual conflict does not have a winner but rather results in an evolutionary compromise between the sexes (see below). This might limit the generality of the above predictions.

ECOLOGICAL CO-OPTATION

Bonduriansky (2011) has recently suggested that sexual conflict (and more generally sexual selection) can play an important role in the evolution and diversification of ecological traits and strategies through the co-optation of sexual traits for viability-related functions. He identifies three mechanisms through which this can happen. First, sexual conflict can displace populations from their local ecological optima. Second, sexual traits can serve as a preadaptation for novel ecological functions. For example, sexual selection in an insect species can favor elongated legs in males for grasping females. Longer legs in males can then open a possibility to invade a new ecological niche, such as foraging on wet surfaces. Third, traits that were sex-limited ancestrally (e.g., horns in beetles) can transfer

between the sexes. A fourth mechanism modeled by van Doorn et al. (2009) is when sexual traits serve as a signal of ecological performance, allowing females to resist mating with a nonlocal male, reducing gene flow between locally adapted populations. Each of these four mechanisms allows populations to explore broader areas of phenotypic space leading to an increase in overall phenotypic diversification and potentially to the emergence of new species.

MODELING CONSEQUENCES OF SEXUAL CONFLICT FOR DIVERSIFICATION

There are three general approaches that have been used for modeling evolutionary consequences of sexual conflict: classical population genetic models of within-locus conflict, game-theoretic models, and dynamic models of between-locus conflict.

Population Genetic Models of Within-Locus Conflict

The very first models of within-locus conflict were built by Owen (1953), Bodmer (1965), Karlin (1972), and Kidwell et al. (1977), who studied one-locus two-allele models of a diploid population subject to sex-differential selection. In their models, fitnesses assigned to three different genotypes—say, AA, Aa, and aa—were different for males and females. These models can be viewed as describing the conflict over traits controlling viability or fertility. The results of mathematical analyses show that depending on the strength of selection, the population can evolve to an equilibrium that is optimal for one sex only or an equilibrium describing an evolutionary compromise between the sexes. The models also show that multiple equilibria can be stable simultaneously so that the evolutionary outcome will strongly depend on initial conditions (Owen 1953; Bodmer 1965). A general conclusion from the population genetic models of within-locus conflict is that the conditions for the maintenance of polymorphism at autosomal sexually antagonistic loci are quite strict, much more so than the conditions for the maintenance of sex-linked polymorphism. In some

situations, the population will not settle to an equilibrium but rather will instead cycle (Gavrilets 1998). More recently, these models were adopted for describing some enigmatic human traits, such as homosexuality (Gavrilets and Rice 2006; Ciani et al. 2008; Rice et al. 2012), and extended to include more loci (Connallon and Clark 2010) and additional evolutionary factors, such as random genetic drift (Connallon and Clark 2012).

Game-Theoretic Models

Parker (1979) coined the term sexual conflict in his theoretical study of the possibility of a conflict over mating decision and its possible resolutions. Parker was building on an earlier idea of the "battle-of-the-sexes" game about the costs of raising offspring, which was introduced and studied by Dawkins (1976). Following Parker's groundbreaking work, most earlier modeling studies of sexual conflict used game-theoretical methods to show its existence, provide measures of its intensity, and identify conditions under which alleles or behaviors causing sexual conflict could invade the population (e.g., Jormalainen et al. 1994; 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). Parker and Partridge (1998) applied this approach to the problem of reinforcement as discussed above.

Evolutionary Dynamics of Between-Locus Conflict

A major component of modeling the evolutionary consequences of between-locus conflict has been done for a conflict over mating rate, an issue playing a prominent role in Rice's arguments. To illustrate the logic of the theoretical approaches used, assume that mating and/or fertilization are controlled by the interaction of trait x in females and trait y in males. Let us specify a mating compatibility function $\psi(x, y)$ giving a probability of mating (or fertilization) between a female with trait x and a male with

trait y. Function ψ is analogous to the preference function in models of sexual selection (Lande 1981; Gavrilets 2004). Let x and y be the average female and male traits in the population. Then function $P = \psi(x, y)$ can be viewed as a measure of how well a female with trait x is compatible with the typical males in her population. Analogously, function $Q = \psi(x, y)$ can be viewed as a measure of how well a male with trait y is compatible with the typical females in his population. With everything else held the same, P and Q can also be viewed as measures of mating rates for the two sexes. For males, reproductive success is expected to increase monotonically with Q (e.g., linearly as in Fig. 1A). In contrast, for females, mating rates that are too high can be detrimental, meaning female fitness is maximized at an intermediate value of P_{opt} as in Figure 1B.

Turning to the function of mating compatibility $\psi(x, y)$, there are two major types capturing different biological mechanisms. First, if mating requires complementarity or matching of the male and female traits, then ψ can be modeled as a unimodal function of the difference $y - x$ (Fig. 1c). In this case, females can achieve an optimum mating rate by evolving their trait x to be larger or smaller than the male trait y. Second, if mating is more of a contest between male "offense" and female "defense" traits in which extreme "offense" trait values would always be beneficial for males, then ψ can be modeled as an increasing function of the difference $y - x$ (Fig. 1d). In this case, females can achieve an optimum mating rate by evolving stronger and stronger "defense" trait x.

Rice's original discussion of the evolutionary consequences of sexual conflict over mating has mostly concentrated on the regime of perpetual coevolutionary chase between the sexes (Rice 1996, 1998; Holland and Rice 1998). Mathematical models have confirmed that such a chase between the average traits x and y in the population is indeed possible. 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 between-locus
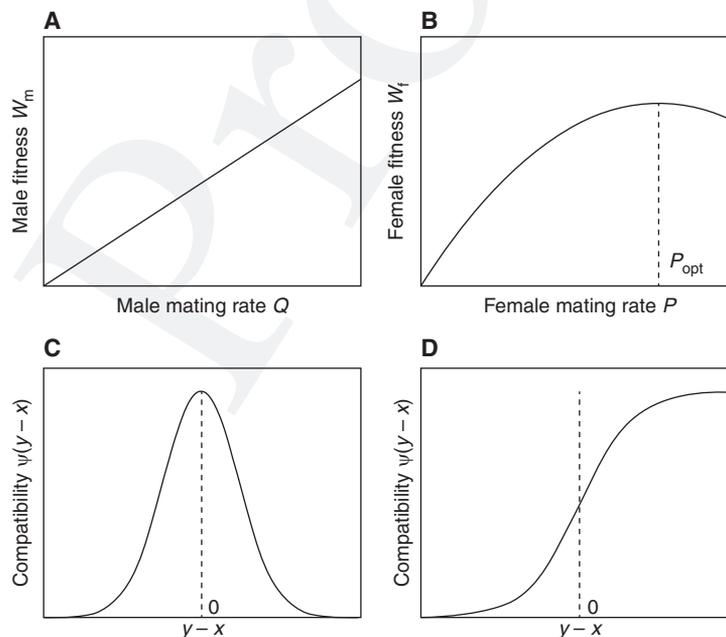

Figure 1. Modeling between-locus sexual conflict. (*A*) Male fitness increases with mating rate. (*B*) For females, there is an optimum mating rate P_{opt}. (*C*) Successful mating requires complementarity of male and female traits ($y = x$). (*D*) Successful mating requires male "offense" trait y to overcome female "defense" trait x.

sexual conflict: continuous coevolutionary chase between the sexes (Gavrilets 2000; Gavrilets et al. 2001; Gavrilets and Waxman 2002; Rowe et al. 2003; Gavrilets and Hayashi 2006), evolution toward an equilibrium (Kondoh and Higashi 2000; Gavrilets et al. 2001; Kimura and Ihara 2009), evolution toward a line of equilibria with subsequent random drift along this line (Gavrilets 2000; Gavrilets and Hayashi 2005; Hayashi et al. 2007), cyclic evolution (Gavrilets et al. 2001; Haygood 2004), Buridan's ass regime involving extensive diversification in female alleles without comparable diversification in male alleles (Frank 2000; Gavrilets and Waxman 2002; Gavrilets and Hayashi 2005; Hayashi et al. 2007), and extensive diversification in both male and female alleles (Frank 2000; Gavrilets and Hayashi 2005; Härdling and Bergsten 2006; Hayashi et al. 2007; Härdling and Karlsson 2009), including a possibility of sympatric speciation (Gavrilets and Waxman 2002; Hayashi et al. 2007). Mathematical models (Gavrilets and Hayashi 2005; Hayashi et al. 2007) also show that different dynamic regimes can be observed with the same set of parameter values but under different initial conditions; populations can switch from one regime to another as a result of stochastic perturbations owing to, say, random genetic drift; different sets of loci controlling mating and fertilization in the same population can follow different dynamic regimes. In short, the behavior of models of sexual conflict is extremely varied and complex (Rowe et al. 2003; Gavrilets and Hayashi 2005). Frequency-dependent selection is well recognized for its ability to result in complex evolutionary dynamics (Altenberg 1991; Gavrilets and Hastings 1995). In the case of between-locus sexual conflict, selection is not only frequency-dependent but also sex-differential, whereas between-sexes interactions include both conflict and cooperation. Therefore, the complexity of resulting evolutionary dynamics is probably not that unexpected.

What does all this tell us about the possibility of speciation by sexual conflict? Out of the six regimes listed above, two regimes are the most intriguing in this regard. The first regime (i.e., continuous coevolutionary chase between

the sexes) will eventually lead to allopatric speciation as a by-product if diverging populations keep evolving in different directions and/or at different rates. 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 will typically lead to increased genetic variation in the population but not to speciation per se.

The question of which outcome—speciation or increased genetic variation without speciation—is more general can hardly be answered. The answer will depend on a number of specific biological factors and details, which will most likely vary between different organisms or populations. Mathematical models, however, do allow us to get a better understanding of the effects of these factors. However, models often make predictions in terms of more abstract model parameters; the challenge, then, is to link them with empirical data.

Lessells (2006) offered an insightful analysis of evolutionary outcomes of sexual conflict in terms of three sets of variables: (1) benefits of male "offense" and female "defense"; (2) costs of "offense" and "defense"; and (3) feasibility of "offense." Obviously, continuous coevolutionary chase is only possible if it is not constrained by natural selection on the alleles and traits underlying reproduction (so that the costs of "offense" and "defense" are low, whereas feasibility of "offense" is high). Parker and Partridge (1998) argued that the cost of resistance for females can be lower than those for males of imposing a mating. At the same time, the opportunity costs for males are expected to be low (Lessells 2006). If mating requires matching or complementarity of male and female traits (as assumed in Fig. 1C), then male "offense" and female "defense" are more likely to be realized without a systematic change in the underlying traits. In this case, costs may be lower and the opportunity for substantial divergence and speciation higher. If mating is more of a contest (as assumed in Fig. 1C), in which success requires a systematic increase in the efficiency of underlying mating traits, then increasing costs are more likely. These costs will prevent perpetual evolu-

tionary change and constrain speciation (Lessells 2006).

However, the absence of constraints does not guarantee that coevolutionary chase will be observed. Modeling shows (Hayashi et al. 2007) that it is also necessary that the population has relatively low levels of genetic variation and that 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. In other words, genetic details are also important.

The absence of clear-cut conclusions can make a disappointed reader question the utility of mathematical modeling sexual conflict, but such modeling did clarify the logic of verbal arguments, make them more precise, identify the most important parameters and relevant timescales, and stimulate novel empirical work. Moreover, mathematical modeling has resulted in several novel conclusions that were not included in earlier discussions of sexual conflict. One example of this is that females can reduce the burden of sexual conflict by diversifying genetically rather than by "running" away from males (Burridan's ass regime) (Gavrilets and Waxman 2002). Genetic variation in females is maintained because sexual conflict generates negative-frequency-dependent selection (i.e., rare female types do better) because the males will tend to optimize their mating rate with whichever female type is most abundant. This situation stands in contrast to models of sexual selection in which the interests of males and females typically align. The diversification in females can be answered by diversification in males, potentially leading to sympatric speciation. The extent of diversification and whether or not 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 the genetics of the traits involved. Another conclusion is that genetic variation in female alleles/traits can be larger than that in males. The level of genetic

variation in both sexes is also predicted to increase with the strength of sexual conflict. Yet another prediction is that 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 one sex but rather there is a (dynamic or static) evolutionary compromise between the sexes.

At the same time, the existing models of sexual conflict are far from being comprehensive (Gavrilets and Hayashi 2005; Lessells 2006). For example, competition between males is not explicitly modeled, spatial models are still lacking, between-sexes interactions are modeled in a rather abstract way despite there being much more currently known about the underlying mechanisms of, say, sperm–egg interactions, the ecological divergence required for coexistence of different species is not considered, and only a single study (Gavrilets and Hayashi 2006) has attempted to model three-way interactions (between male offense, male defense, and female defense) important in Rice's arguments.

EMPIRICAL PATTERNS

Experimental evidence both that high mating rates can be quite detrimental to female fitness and that sexual conflict can drive rapid genetic changes in experimental populations are quite solid (e.g., Rice 1996; Holland and Rice 1999; Pitnick et al. 2001a,b; Rice et al. 2005). How easily these genetic changes result in reproductive isolation and speciation is much less clear-cut. There are three sets of relevant empirical approaches: experimental evolution, analyses of fertilization traits and proteins, and comparative studies of species richness.

Experimental Evolution of Reproductive Isolation

The first study of the evolution of reproductive isolation by sexual conflict under laboratory conditions was that by Martin and Hosken (2003) using populations of the dung fly *Sepsis cynipsea*. In this species, males' armored geni-

talia often injure females internally during copula. Injuries are visible as sclerotized scars in the female ovipositor, and their occurrence increases with mating frequency. Presumably owing to these injuries, mated females show higher mortality (Blanckenhorn et al. 2002). Females typically attempt to dislodge mounted males by harassing them with vigorous shaking. Martin and Hosken (2003) manipulated population densities and then measured copulation success between a male and a female chosen from populations subject to different or the same treatments for 35 generations. They showed that copulation frequency was greater in pairings within conflict populations than those between populations in which conflict was removed, and this effect was stronger in high-density than in low-density populations. Evidence of female (but not male) resistance to flies from other conflict populations implies that sexual conflict drives divergence (Martin and Hosken 2003; Hosken et al. 2009).

However, similar subsequent experiments have largely failed to provide evidence for the evolution of reproductive isolation. These include experiments with *D. melanogaster* (Wigby and Chapman 2006, but see Ghosh and Joshi 2012), *Drosophila pseudoobscura* (Bacigalupe et al. 2007), bruchid beetle populations *Callosobruchus maculatus* (Gay et al. 2009), water strider *Gerris gillettei* (Gagnon and Turgeon 2011), and the bulb mite *Rhizoglyphus robini* (Plesnar-Bielak et al. 2013).

Several factors can explain the negative results: The experiments may be too short to cause a noticeable effect, the populations could have evolved in a similar direction at a similar rate, or the dynamics imposed by the experimental conditions were different from the "coevolutionary chase."

Fertilization Traits and Proteins

A very large 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), indicates that in many diverging taxa, traits and proteins related to fertilization evolve extremely rapidly. At least in the case of marine organisms, there now appears to be a consensus that these data can be explained in large part by selection for avoidance of polyspermy (Levitan et al. 2007; Palumbi 2009; Lessios 2011; Vacquier and Swanson 2011). Sperm is under strong selection for increased efficiency in fertilizing eggs, but if more than one sperm penetrates the egg, the resulting zygote in usually inviable. Polyspermy thus represents an important example of sexual conflict over mating rate (Howard et al. 1998). A variety of mathematical models of the effects of polyspermy all converge on the prediction of a rapid coevolutionary chase between the traits of sperm and eggs with sperm evolving to increase their efficiency and eggs evolving molecular "defense" against sperm (Frank 2000; Gavrilets 2000; Gavrilets and Waxman 2002; Haygood 2004; Tomaiuolo and Levitan 2006; Hayashi et al. 2007). Sperm–egg interactions are more likely to require complementarity at the gene-product level than contest (Fig.1C,D) (Rice 1998, Lessells 2006), which, as discussed above, makes continuous "evolutionary chase" more plausible.

Mathematical models of sexual conflict also provide explanations for certain empirical patterns that were previously rather puzzling. These include apparent deceleration in the evolution of sperm lysin genes in abalone (Yang et al. 2000) and 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).

The data also indicate a potential role for reinforcement, because, in some cases, the rate of evolution and the extent of polymorphism correlate with the number of sympatric species (Vacquier and Swanson 2011). However, rapid evolution of fertilization proteins is not universal. For example, for some allopatric species of

sea urchins that diverged more than 4–9 million years, there is no evidence of positive selection in bindin alleles that evolve very rapidly in other species (Vacquier and Swanson 2011).

Selection for increased female resistance to mating can also potentially explain rapid evolution of genitalia, which has been observed in many organisms (Eberhard 1985). One can then predict 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. This prediction, however, has failed for a large sample of insects and spiders (Eberhard 2004). At the same time, recent comparative studies of water strider populations provide strong evidence for a persistent coevolutionary chase between male and female sexual traits affecting reproductive isolation (Ronn et al. 2007; Perry and Rowe 2012).

Species Richness

The results of comparative studies of the effects of sexual conflict and sexual selection on species richness are equivocal (Parker 2006). 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. Arnqvist et al. (2000) were the first to use comparative data to analyze the effects of sexual conflict on large-scale diversification. These investigators contrasted pairs of related groups of insect species differing in the opportunity for sexual conflict. The latter was characterized by the number of matings per female. Arnqvist et al. (2000) showed that groups in which females mate with many males exhibited speciation rates four times as high as in related groups in which females mate only once. In the hoverflies, higher levels of sexual selection are associated with higher species richness (Katzourakis et al. 2001). Barraclough et al. (1995) showed that species richness correlates with the proportion of sexually dichromatic species within taxa of passerine birds. In birds, taxa with promiscuous mating systems tend to be more species-rich

than their nonpromiscuous sister taxa (Mitra et al. 1996). Data on *Amphibia* show that sexual size dimorphism is associated with increased species richness, diversification rate, and reduced extinction risk (Lisle and Rowe 2014). However, 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), birds (Morrow et al. 2003), and fish (Ritchie et al. 2005). There are some issues with the interpretation of the results of comparative studies attributed to the difficulties for controlling for phylogenetic effects, sexual selection, and extinction (Panhuis et al. 2001; Coyne and Orr 2004).

Female Polymorphism

As was emphasized above, mathematical theory predicts that sexual conflict can lead to speciation only under specific conditions. If these conditions are not satisfied, populations are expected to diversify. In particular, an interesting prediction emerging from theoretical studies is that females can sometimes get the upper hand in sexual conflict and decrease male harassment by diversifying genetically (Franke et al. 2002; Gavrilets and Waxman 2002; Gavrilets and Hayashi 2005; Härdling and Bergsten 2006; Hayashi et al. 2007). Overall, female sexual polymorphisms appear to be overlooked in the past as most studies of sexual selection focused on male–male competition (Svensson et al. 2009). However, by now there are a number of well-studied cases in which female sexual polymorphism has been shown and linked to sexual conflict. These include higher genetic variation in female reproductive traits in carabid beetles (Sota et al. 2000) and apparent polymorphisms in female genitalia in a spider species (Huber and González, 2001), an African bat bug (Reinhardt et al. 2007), the guppy (Evans et al. 2013), black scavenger flies (Puniamoorthy et al. 2010), butterflies (Cook et al. 1994), diving beetles (Härdling and Bergsten 2006), and damselflies (Van Gossum et al. 2008; Svensson et al. 2009). A study in damselflies explicitly looked at frequency- and density-dependent fecundity pat-

terns (Iserbyt et al. 2013). The results are consistent with the hypothesis that the polymorphism is driven by a conflict between sexes over mating rate, with costly male sexual harassment driving negative-frequency-dependent selection on morph fecundity.

CONCLUDING REMARKS

Earlier experimental, comparative, and mathematical work has provided strong support for the idea that sexually antagonistic selection is a powerful engine of speciation. However, we now much better understand the constraints and limitations on the evolution of reproductive isolation as driven by sexual conflict. Modeling work shows that speciation is only one of several possible evolutionary outcomes of sexual conflict and can occur only under specific conditions. In a similar vein, both experimental evolution studies and comparative analyses of fertilization proteins and of species richness show that sexual conflict leads to, or is associated with, reproductive isolation and speciation in some cases but not in others. Sexual conflict is an engine of speciation. But as with other engines of speciation and diversification—ecological selection, sexual selection, and accumulation of incompatibilities between diverging lineages by mutation and drift—it is most efficient when operating under optimal conditions and can stall otherwise.

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Query

Sergey Gavrilets

Q1   "loosing" or "losing"?

Is Sexual Conflict an "Engine of Speciation"?

Sergey Gavrilets

TOC Blurb: Sexual conflict can contribute to the genetic divergence and reproductive isolation of populations, leading to speciation. But speciation is only one of several possible evolutionary outcomes of sexual conflict.