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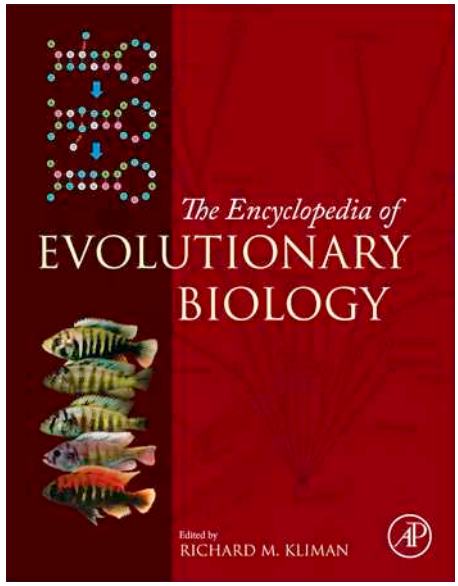

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Speciation, Sexual Conflict and

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Glossary

Chase away model The evolution of exaggerated secondary sexual characteristics through sexually antagonistic coevolution.

Interlocus sexual conflict Occurs when the expression of a locus in one individual compromises the fitness of its mate with expression of different loci acting to counteract the negative effects. One possible outcome is sexually antagonistic coevolution.

Intralocus sexual conflict Occurs when the same combination of alleles exert opposite effects on fitness when expressed in a male versus a female.

Reproductive isolation Any factor that restricts gene flow to produce independently evolving populations that, in the extreme, yields distinct species. Barriers may act prior to mating (premating isolation), after mating but prior to zygote formation (premating, prezygotic isolation (PMPZ), gametic isolation), or after zygote formation (postzygotic isolation).

Sexually antagonistic coevolution A possible outcome of interlocus sexual conflict whereby selection on one sex favors reproductive traits that induce a fitness cost on its mates. Selection on the mate, in response, favors evasive adaptations to reduce the negative effects, leading to a cycle of male and female trait evolution.

Sexual conflict Differing optimal reproductive strategies of sperm donor and recipient individuals that induces opposing selective pressures on the sexes.

What is Sexual Conflict?

The kernel of the idea that those traits shared between the sexes can experience different fitness optima in each sex – sexual conflict – traces to Darwin (1871), and yet reproduction was, nevertheless, widely viewed as an entirely cooperative endeavor prior to the 1970s. As we now recognize, the fitness interests of mating partners are seldom harmonious in all aspects of the 'economics' of reproduction (Parker, 1979), and instead, male and female reproductive interests often conflict. The fundamental root of conflicting interests between the sexes lies in the production of different sized gametes (anisogamy): smaller male gametes (sperm) essentially parasitize the larger, resource-rich female gametes (eggs) (primordial sexual conflict: Parker *et al.*, 1972; Parker, 1978). This asymmetry in gametic investment in reproduction sets the stage for further layers of conflict to arise between males and females in any traits that elevate the reproductive success of one sex at the expense of the other. Students of sexual selection now apply the term 'sexual conflict' to these disparities between the sexes in their fitness interests, the resulting selective pressures, and evolutionary responses (Parker, 1979; Arnqvist and Rowe, 2005).

Sexual conflict is widespread across taxa (Arnqvist and Rowe, 2002), with conflict over parental investment taking many forms, including mating rate (Rice and Holland, 1997; Holland and Rice, 1998; Rice *et al.*, 1998), sperm selection by females (Ball and Parker, 2003), and epigenetic control of development (Rice *et al.*, 2012). These antagonistic interactions between the sexes contrast with exaggeration of secondary sexual traits through other forms of sexual selection that involve female preference and male–male competition. Rapid nonantagonistic trait evolution mediated by Fisher's (1930) runaway selection model or Zahavi's (1975) handicap 'good genes' hypothesis can contribute to interpopulation divergence and the evolution of reproductive isolation. Likewise, evolutionary responses to sexual conflict also can promote trait exaggeration, via the chase away model involving sexually antagonistic coevolution (Holland and Rice, 1998), to produce population divergence and speciation in a manner potentially even more potent than other modes of sexual selection (reviewed in Gavrilets, 2014). Distinguishing sexual conflict from other forms of sexual selection, however, remains a challenge (Rowe and Day, 2006).

Sexual conflict generates sexually antagonistic selection that discriminates among heritable variation in male traits and in female traits (Rice, 1984), whereby selection favors one trait value to maximize the reproductive success of one sex and a different trait value for the other sex. For example, more numerous matings typically will improve male reproductive success disproportionately greater than female reproductive success because female reproductive output often is limited by total offspring production, independent of the number of matings (Bateman, 1948). Consequently, selection will favor alleles that confer on males a propensity to mate numerously and promiscuously, as well as favoring alleles that enable females to engage in few, select 'high-quality' matings. This tension can lead to the evolution of mating rates that are suboptimal from the point of view of one or both sexes, or can instigate coevolutionary arms races in traits that influence the balance of sexual costs and benefits for each sex (Arnqvist and Rowe, 2005). The roles of which sex inflicts and receives disproportionate fitness costs depend on the organism and its stage in the coevolutionary process, sometimes with females inflicting higher fitness costs on males (e.g., sexual cannibalization of male mantids: Lelito and Brown, 2006) or vice versa (e.g., traumatic insemination of female bedbugs: Stutt and Siva-Jothy, 2001). However, sexual conflict need not necessarily result in harmful behavior, nor is harm a required feature for sexually antagonistic coevolution to occur (see Rowe *et al.*, 2005; Lessells, 2006).

The vocabulary employed for concepts in sexual conflict are tailored toward organisms with distinct and separate sexes

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(gonochorism or dioecy: see Schärer *et al.*, 2014). However, sexually antagonistic selection also occurs in hermaphroditic mating systems, which provided some of the first observations and insights into sexual conflict (Charnov, 1979). Recently, Schärer *et al.* (2014) defined and clarified the nuances of sexual conflict theory in hermaphrodites in order to bring attention back to them as powerful examples of sexual conflict, coming from simultaneously hermaphroditic organisms in which an individual expresses both sexes at the same time, such as the 'love dart' in snails (Koene and Schulenburg, 2005), as well as from sequential hermaphrodite species in which a single individual changes from one sex to the other over time (reviewed in Abbott, 2011). Given that hermaphroditism is taxonomically widespread, with ~70% of animal phyla and >90% of plant genera containing hermaphrodite representatives (Renner and Ricklefs, 1995; Jarne and Auld, 2006), neglecting sexual conflict in hermaphrodites could impede progress toward deciphering general principles and implications of sexual conflict for the production of biodiversity (Schärer *et al.*, 2014). The dual connections of evolutionary transitions in reproductive mode with speciation itself (Goldberg and Igić, 2012) and with shifts in the cost-benefit structure of sexual conflict suggest that consideration of both of these factors simultaneously might prove fruitful in discerning the driving forces in species diversification.

Despite the prevalence of circumstances like multiple mating and sex chromosomes that are conducive to sexual conflict across organisms (Charlesworth, 1991; Zeh and Zeh 1996, 1997; Baur *et al.*, 1998; Michiels *et al.*, 1998; Jennions and Petrie, 2000), sexual conflict is unlikely to provide a prominent selective pressure in several key types of systems. In particular, organisms with reproductive modes dominated by asexuality and parthenogenesis, extremely high self-fertilization, and true monogamy should severely limit the extent to which sexual conflict can contribute to evolutionary change. For example, species with true lifelong genetic monogamy, such that mating with other individuals is not possible for either sex, display completely codependent reproductive success for the two sexes and so escape most sexual conflict (Wedell *et al.*, 2006); any strategy that decreases partner fitness will simultaneously reduce self-fitness, and consequently be opposed by selection. The extreme rarity of monogamy in animals has led to doubts about the existence of this ideal in nature (Birkhead, 1997; Wedell *et al.*, 2006; Hosken *et al.*, 2009b), although asexual and selfing reproduction arise commonly in both plants and animals (Jarne and Charlesworth, 1993).

How Can Sexual Conflict Promote Speciation?

Speciation results from the accumulation of genetic divergence between populations, which fosters the evolution of reproductive isolation. As populations evolve independently, incompatibilities amass and manifest as mismatches in mating behaviors or morphologies, ecological preferences, postmating gametic interactions, or as fitness deficiencies in genetically admixed, hybrid individuals. Sexual selection on mating traits can drive them to diverge rapidly from preexisting genetic variability, but the distinctiveness of such daughter populations may be temporary as they are susceptible to subsequent fusion (Servedio and Bürger, 2014). Similarly, while extrinsic genotype-by-environment interactions can represent a powerful selective pressure to restrict gene flow, transience of environmental conditions can collapse multiple nascent species back into a single evolutionary unit (Seehausen *et al.*, 2008; Futuyma, 2010). While such ecological speciation is most typically framed in terms of divergent local adaptation (Rundle and Nosil, 2005), modulation of the strength of sexual selection by ecological conditions could influence population divergence under sexual conflict in a similar way under some circumstances (Seehausen *et al.*, 1997). By contrast, a permanent reproductive barrier to enforce restricted gene flow evolves when population divergence involves new, derived alleles that create genetically intrinsic reproductive isolation by way of reduced viability or reproductive success of hybrid offspring, for example, via Dobzhansky–Muller incompatibilities affecting development or behavior (Dobzhansky, 1937; Coyne and Orr, 2004; Gavrilets, 2004). Rapid coevolution that results from sexually antagonistic selection provides an intuitively appealing way to explain how trait divergence can foster the production of new reproductively isolated populations or maintain restricted gene flow between nascent species that originated from other evolutionary circumstances.

Sexually antagonistic coevolution has the potential to provide a more potent and rapid source of interpopulation divergence compared to other forms of intersexual selection such as female mate-choice or assortative mating (Panhuis *et al.*, 2001; Kirkpatrick and Ravigné, 2002). A perpetual arms race between the sexes that follows from sexually antagonistic coevolution can bring about rapid and potentially limitless evolutionary change (Parker, 1979), for example, through iterated female evolution of resistance adaptations in response to male persistence adaptations. By comparison, other forms of intersexual selection typically involve an evolutionary response in female preference favoring an exaggerated male trait rather than resistance to an exaggerated male trait. The evolutionary tethering of the expression of female preference to those male traits that provide an indirect or direct benefit to females leads to trait responses constrained within the scope of females' ability to perceive them (Fisher, 1930; Berglund *et al.*, 1996). By contrast, female evasion of male traits under antagonistic coevolution, rather than trait tracking, creates more opportunity for the evolution of novelty and, subsequently, population divergence in allopatry (Gavrilets, 2000; Gavrilets *et al.*, 2001; Martin and Hosken, 2003) or even in sympatry (Gavrilets and Waxman, 2002). Sexually antagonistic coevolution also predicts the evolution of multiple male traits under a wide range of conditions (Arak and Enquist, 1995; Gavrilets *et al.*, 2001) and a greater number of genetic trajectories for the sexes and populations to pursue, resulting both in rapid exaggeration and diversification (Gavrilets, 2000). In some cases, such sexual traits could be co-opted for ecological innovation and provide the basis for divergent natural selection and so indirectly contribute to the origin of new species (Bonduriansky, 2011).

It is straightforward to see how gene flow may be disrupted in early stages prior to mating or in later stages after zygote formation: easily observable traits like species-specific

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courtship songs in birds (Grant and Grant, 2010) and sterile hybrids in *Drosophila* (Masly *et al.*, 2006) provide compelling and clear-cut bases of reproductive isolation. By contrast, reproductive barriers that occur midway through the reproductive process at the gametic level – following mating, but prior to zygote formation, termed postmating, prezygotic reproductive (PMPZ) barriers – can involve phenotypically subtle but reproductively crucial divergence, owing to coevolution between the gametes or between the female reproductive tract and the sperm or components of the seminal fluid (Eady, 2001). As we discuss the ways that sexually antagonistic selection can participate in the speciation process, one must consider the potential for evolution of reproductive isolation to manifest through any of these phases: premating barriers, PMPZ incompatibilities, and postzygotic isolation.

The Dual Genetic Bases of Sexual Conflict

Two genetic pathways can produce sexual conflict, whereby sex-specific selection can occur between different loci (interlocus conflict) or within a locus (intralocus conflict). Interlocus conflict can induce an evolutionary arms race between the sexes, while intralocus conflict results in an evolutionary tug-of-war for each sex to reach their own fitness optimum. Both modes may derive from either simple (one- or two-locus systems) or complex (polygenic, quantitative genetic) genetic architectures. Below we differentiate between the two types of sexual conflict and discuss how each can facilitate, or restrain, the process of speciation.

Interlocus Conflict and Speciation

Conflict over the outcome of male–female interactions that are mediated by genetic factors encoded with different loci is known as interlocus sexual conflict. Conflicts between the sexes can occur over a diversity of traits, with commonly considered traits including mating rate, parental investment, remating behavior, and female reproductive rate. Different traits encoded by loci with sex-biased expression in each sex enable males and females to reach their sex-specific fitness optima in a given intersexual context (Rice *et al.*, 1998). As the intersexual context changes, interlocus conflict can drive continuous selective pressure for allelic replacement at the interacting loci in both sexes (Rice and Holland, 1997). Such recurrent conflictual selection will potentially spur a sexually antagonistic coevolutionary arms race between one set of loci that confers benefits to one sex at the expense of the other sex, and a distinct set of loci that control responding traits in the alternative sex. If given the opportunity for a male trait and female response to coevolve under sexual conflict, 'unresolvable evolutionary chases' might result, whereby neither sex reaches their optima (Parker, 1979). Under such conditions, sexually antagonistic coevolution can promote rapid evolutionary change (Parker, 1979).

Such a perpetual arms race that involves multiple loci promotes divergence between separated populations that evolve along independent evolutionary trajectories of trait change and counter-change (Rice, 1996; Rice and Holland, 1997; Holland and Rice, 1998; Rice *et al.*, 1998; Chapman *et al.*, 2003). When new mutations arise with sex-limited expression at sexually antagonistic loci subject to interlocus conflict, selection in one sex will favor their fixation and the same allele will be selectively neutral when it occurs in the other sex. Consequently, iterated over time, sex-limited selection can lead to repeated fixation of new sexually antagonistic alleles. Allopatric divergence accrues between populations as their trait evolution traces independent genetic trajectories, with coevolution driving distinct genotypic solutions to ongoing sexual conflict involving sex-biased adaptations and counter-adaptations. Because any source of evolutionary divergence, especially divergence involving new derived mutations (Orr, 2005), will increase the probability of genetic incompatibilities arising that could impede gene flow between populations, an interlocus genetic basis to sexual conflict can facilitate speciation (Rice *et al.*, 1998).

A perpetual arms race between the sexes represents just one possible evolutionary outcome of interlocus sexual conflict predicted by theory (reviewed in Gavrilets, 2014). Another possibility is the accumulation of many alleles at loci expressed in each of the sexes (Gavrilets and Hayashi, 2005; Härdling and Bergsten, 2006; Hayashi *et al.*, 2007; Härdling and Karlsson, 2009), that can potentially lead to sympatric speciation (Gavrilets and Waxman, 2002; Hayashi *et al.*, 2007). Other evolutionary outcomes of interlocus sexual conflict can generate elevated genetic variation in the population, but not facilitate formation of new species (Gavrilets, 2014), such as evolution toward an equilibrium (Kondoh and Higashi, 2000; Gavrilets *et al.*, 2001; Kimura and Ihara, 2009), and cyclic evolutionary dynamics (Gavrilets *et al.*, 2001; Haygood, 2004). Additionally, stochastic perturbations like genetic drift have the potential to switch the attracting evolutionary regime expected by deterministic theory (Gavrilets and Hayashi, 2005; Hayashi *et al.*, 2007). An alternative outcome to sexually antagonistic coevolution is that females can evolve indifference to male traits rather than resistance, and in extreme cases may select against these traits (Rowe *et al.*, 2005). The indifference that females express to male traits could halt the coevolutionary process, thus preventing further divergence that would otherwise facilitate the speciation process (Rowe *et al.*, 2005).

Intralocus Conflict and Speciation

Intralocus sexual conflict, as a mode of sexually antagonistic selection, favors alternative alleles at the same locus differentially between the sexes and generally acts as a force promoting maintenance of genetic variation (Rice and Holland, 1997; Parker and Partridge, 1998). In intralocus sexual conflict models with a one-locus two-allele genetic system, the strength of selection determines the evolutionary outcome: whether a population reaches an evolutionary compromise between the sexes or, instead, the population reaches an equilibrium that optimizes the fitness of only one sex (reviewed in Gavrilets, 2014). With a polygenic trait subject to intralocus sexual conflict owing to a sex-by-genotype interaction, the same combination of alleles exert opposite effects on the fitness of each sex (Fisher, 1930; Lande, 1980). The resulting conflicting

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selection acting to produce an optimal phenotype in males thus, collaterally, impedes selection for the optimal phenotype in females (Rice, 1996). This scenario results in an evolutionary tug-of-war in which neither the male nor female trait value might obtain their sex-specific optima, owing to the evolution of an intermediate phenotype for both sexes and maintaining genetic variation for the trait in both sexes.

Importantly in the context of speciation, this tendency of intralocus sexually antagonistic selection to maintain polymorphism, rather than to drive individual alleles to fixation, will retard the accumulation of divergence between populations. Consequently, we should expect this genetic architecture of sexual conflict to impede, or at least not facilitate, the speciation process. However, sexual antagonism via intralocus conflict might not be able to maintain genetic variation effectively at more than a very small number of loci (Turelli and Barton, 2004), suggesting that the scope for intralocus conflict to constrain divergence might have been overstated in extrapolations of single-locus models unless epistasis among intralocus conflict loci is pervasive (Arnqvist *et al.*, 2014). Intralocus conflict also can impede divergence between populations by interfering with coevolutionary dynamics mediated by interlocus conflict (Pennell and Morrow, 2013). Nevertheless, intralocus sexual conflict could promote speciation when one sex experiences sufficiently strong directional selection, as it could drag traits expressed in the other sex across sex-specific maladaptive troughs of fitness, potentially fostering formation of new species (Bonduriansky and Chenoweth, 2009). Also, interestingly, epistasis among loci that each experience intralocus conflict can lead to 'equity effect' allelic fixation at different loci that could contribute to population divergence if different allele combinations fix in different populations (Arnqvist *et al.*, 2014), though it is unclear whether secondary contact of divergent populations might simply resurrect the sexual conflict rather than contribute to reproductive isolation between them.

Resolutions to intralocus sexual conflict can evolve that alleviate the selection pressure for maintenance of alternative alleles at a locus that confer sex-limited costs and benefits. Specifically, translocation mutations of loci to a sex chromosome, regulatory mutations that induce sex-limited expression, gene duplication that permits each gene copy to evolve to sex-specific fitness optima, or genetic imprinting can all provide evolutionary routes to eliminate intralocus conflict (reviewed by Bonduriansky and Chenoweth, 2009; Stewart *et al.*, 2010). The consequences of such evolutionary solutions to intralocus sexual conflict, however, might then themselves foster the evolution of reproductive isolation, as the resulting genetically decoupled male and female trait evolution respond independently to selection (Parker and Partridge, 1998; Pennell and Morrow, 2013). For example, when the evolution of sex-specific gene expression resolves intralocus conflict to create sexual dimorphism in a trait like body size, further selection on dimorphism can drive diversification whereby the dimorphic population can access and exploit previously inaccessible resources (De Lisle and Rowe, 2015). Moreover, as the sexes evolve independently, exaggeration of a male trait to an extent that it compromises female fitness could then spark a sexually antagonistic coevolutionary arms race via interlocus conflict. For example, genes with different expression between males and females (sex-biased genes), especially for paralogous copies of duplicates, could represent the resolution of intralocus sexual conflict (Wyman *et al.*, 2012; Ingleby *et al.*, 2015), as there can be rapid turnover in sex-biased gene expression (Harrison *et al.*, 2015). In this circuitous manner, the resolution of intralocus sexual conflict might ultimately predispose populations to evolution by interlocus conflict and lay the genetic groundwork for interpopulation divergence (Pennell and Morrow, 2013).

In turn, the independent evolution of separated populations for such evolutionary resolutions to sexual conflict, involving unique genetic causes, would provide the raw substrate for forming genetically intrinsic reproductive incompatibilities through Dobzhansky–Muller interactions in hybrid individuals (Orr, 1995). As a by-product of hybrid genetic incompatibilities, female choosiness in selecting mates might promote premating isolation under secondary contact that could subsequently evolve to an exaggerated extent by reinforcement or reproductive character displacement (Servedio, 2001). Because sexually antagonistic genes might contribute much of the genetic variation in fitness within a population, these loci offer plausible substrates for divergent selection to generate intrinsic incompatibilities between emerging species (Gavrilets, 2014).

How Can the Genetic Architecture of Sexually Antagonistic Selection Impact Evolutionary Responses?

Interlocus conflict provides a more effective potential source of population divergence and reproductive isolation than does intralocus conflict (Gavrilets, 2014). Such disparity between these two genetic modes of sexual conflict arises because of the tendency for intralocus selection to maintain polymorphism, rather than to drive allelic fixation, and for interlocus conflict to generate coevolutionary arms races between alleles with sex-biased expression at different loci. These conclusions ought to hold true regardless of the simplicity (one or two loci situations) or complexity (polygenic, quantitative genetic situations) of the genetic architecture of sexually antagonistic loci (Gavrilets, 2014), with the caveat that polymorphism maintenance via intralocus conflict for polygenic traits might not be stable in the absence of epistasis (Turelli and Barton, 2004; Arnqvist *et al.*, 2014). Whether sexually antagonistic selection operates primarily on standing genetic variability or on new mutations also represents a critical determinant of the potential for sexual conflict to generate irreversible constrictions on gene flow between populations. Responses to selection will always be more rapid when genetic differences are immediately available, meaning that trait divergence can accumulate especially quickly. But such rapid shifts in trait means from selection on additive genetic variation may easily be undone (Servedio and Bürger, 2014). The persistence of divergent populations as genetically distinguishable entities requires that barriers to hybridization are not leaky, and it is genetically intrinsic reproductive incompatibilities from new mutations that are more likely to enforce restricted gene flow even in the face of mating between nascent species, owing to irreversible hybrid dysfunction. Given that new mutational input might be

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a rate-limiting step, even for conflict loci for which selection greedily favors novel alleles, it remains a challenging problem to assess the importance of distinct contributors to the genetic architecture of sexual conflict in the accretion of enduring divergence.

What Signatures of Sexual Conflict Reveal Its Influence on Speciation?

It remains a pernicious challenge to discriminate evolution by sexual conflict from other modes of sexual selection (Rowe and Day, 2006), making it especially difficult to demonstrate empirically an association with speciation. Compelling examples of rapid genetic changes in experimental populations owing to sexual conflict nevertheless do not generally make direct links to diversification and the accumulation of reproductive isolation (e.g., mating rates in *Drosophila*: Rice, 1996; Holland and Rice, 1999; Pitnick *et al.*, 2001a,b; Rice *et al.*, 2005). Despite a few examples illustrating proof of principle (but see Martin and Hosken, 2003; Hosken *et al.*, 2009a), given the inability of laboratory evolution to mimic natural conditions (Arbuthnott *et al.*, 2014) and other studies failing to demonstrate divergence coupled to reproductive isolation (e.g., Wigby and Chapman, 2006; Gay *et al.*, 2009; Gagnon and Turgeon, 2011), it remains unclear empirically how broadly antagonistic coevolution might apply to the speciation process.

An alternative to experimental evolution for inferring processes of male–female coevolution and their influence on speciation is to conduct interpopulation or interspecies crosses and examine traits indicative of reproductive isolation, such as mating rate, offspring production, and survivorship (Parker and Partridge, 1998; Andrés and Arnqvist, 2001). Genital structures evolve most rapidly and divergently by intersexual selection as genitalia typically differ, even between closely species (Arnqvist, 1998, reviewed in Hosken and Stockley, 2004). In particular, the male genitalia of *Drosophila* varies across the genus (Bachli and Vilela, 2002), within the *Drosophila melanogaster* species subgroup (Yassin and Orgogozo, 2013), and even within a natural population (Andrade *et al.*, 2009). Sexually antagonistic coevolution can explain why male genitalia are divergent between some species of *Drosophila* (Kamimura and Mitsumoto, 2012), but not all (see Eberhard and Ramirez, 2004). For example, females of *Drosophila yakuba* have coevolved structures (cavities with sclerotized platelets) to minimize infection risk caused by wounding with sclerotized spikes on the male genitalia (Kamimura, 2012), in contrast to females from the sister species *Drosophila santomea* that lack these cavities, as they have coevolved with males with rounded genitalia (Kamimura, 2012). Interspecies matings revealed enhanced mating costs from the risk of microbial infection, owing to genital mismatch and indicating sexually antagonistic coevolution within each species. Similarly, interspecies matings of *Caenorhabditis* nematodes revealed dramatic fitness costs, manifesting as sterilization and premature death to maternal nematodes (Ting *et al.*, 2014). Gametic barriers to fertilization define a potent contribution to reproductive isolation between *Caenorhabditis* species, mediated by heterospecific male sperm that induce the harmful effects by displacing conspecific sperm and by mislocalizing within the maternal gonad and to nonreproductive tissues (Ting *et al.*, 2014). The findings implicate a role of sexually antagonistic coevolution whereby female resistance adaptations to aggressive sperm evolved along different trajectories in different species. However, it remains unclear whether conflictual selection might have occurred during speciation per se or after other drivers of reproductive isolation had already created 'good species.' Moreover, caution must be taken in interpreting interpopulation crosses, as some outcomes are not necessarily unique to or required from sexually antagonistic coevolution (Rowe *et al.*, 2003).

Comparative phylogenetic analysis provides yet another avenue to evaluate a role for sexual conflict in species diversification. One such analysis identified higher species richness in clades with polyandrous compared to monandrous species, as a proxy for sexual conflict (Arnqvist *et al.*, 2000). Despite being consistent with a role for sexual conflict in promoting speciation, additional and more fine-grained analyses are warranted that might better distinguish conflict from other modes of sexual selection, incorporate quantitative measures of reproductive isolation (Rabosky and Matute, 2013; Yukilevich, 2013), and that exploit recent advances in partitioning speciation and extinction rates on phylogenies (FitzJohn, 2010).

How Might Sexual Conflict Hinder Speciation?

Speciation represents a compelling possible evolutionary outcome of sexual conflict and sexually antagonistic coevolution (see Lessells, 2006; Gavrilets, 2014). Sexual conflict could instead hinder speciation, however, and increase the risk of extinction (Rowe and Day, 2006; Rankin *et al.*, 2011). Sexual conflict could elevate extinction rates by reducing the mean fitness of populations (Doherty *et al.*, 2003; Rowe and Day, 2006), which can also occur when unresolved intralocus conflict impedes genetic divergence (Lande, 1980; Bonduriansky and Chenoweth, 2009). Populations can also be driven to extinction when sexual conflict over mating is a 'tragedy of the commons,' whereby traits favored by antagonistic selection are simultaneously beneficial to individuals and costly to the group (Hardin, 1968; Rankin *et al.*, 2007). For example, in the pursuit of increasing mating rates, excessive harassment by males might directly compromise female survival, creating a male-biased population that feeds back in turn until the population collapses (Rankin *et al.*, 2011; Grayson *et al.*, 2014). A possibility worthy of further investigation is to what extent sexual conflict might promote both speciation and extinction, perhaps contributing to more rapid species turnover but little to net diversification.

Conclusions

The prevalence of sexual conflict across the tree of life, combined with its capability to propel rapid evolutionary change, motivates the logic that sexually antagonistic selection might play a creative role in the speciation process or in the maintenance of nascent species' integrity. However, the genetic architecture that underlies sexual conflict (intralocus vs.

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interlocus conflict, few vs. many loci, standing variation vs. new mutation) can drastically alter the implications regarding the potential for and permanence of population divergence. Evolutionary responses to antagonistic selection can, in some circumstances, retard population divergence, increase the likelihood of population extinction, or contribute to post-speciation enforcement of restricted gene flow instead of providing the causative feature to species origination. More generally, it remains difficult to confidently ascribe a causal role to sexual conflict in the speciation process, despite the conceptual attractiveness of this idea, making especially important all future mechanistic studies of sexual conflict at premating, gametic, and postzygotic levels in the evolution of reproductive isolation.

See also: Ecological Speciation and Its Consequences. Hermaphrodites. Reinforcement. Reproductive Isolation, Postzygotic. Reproductive Isolation, Prezygotic. Sexual Conflict. Sexual Selection, Theory of. Speciation, Sexual Selection and. Species Concepts and Speciation

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