

How does breeding system variation modulate sexual antagonism?

The study of sexually antagonistic (SA) traits remains largely limited to dioecious (separate sex), mobile animals. However, the occurrence of sexual conflict is restricted neither by breeding system (the mode of sexual reproduction, e.g. dioecy or hermaphroditism) nor by sessility. Here, we synthesize how variation in breeding system can affect the evolution and expression of intra- and inter-locus sexual conflicts in plants and animals. We predict that, in hermaphrodites, SA traits will (i) display lower levels of polymorphism; (ii) respond more quickly to selection; and (iii) involve unique forms of inter-locus conflict over sex allocation, mating roles and selfing rates. Explicit modelling and empirical tests in a broader range of breeding systems are necessary to obtain a general understanding of the evolution of SA traits.

Keywords: sexual conflict; sex allocation; selfing; sex chromosomes; simultaneous hermaphroditism; dioecy

1. INTRODUCTION

The evolutionary interests of the sexes (or ‘sex functions’ in hermaphrodites) frequently diverge, potentially generating sexual conflict. Independent trait optimization for each sex (or sex function) is often impossible, owing to interactions between the sexes during reproduction or intersexual genetic correlations (Chapman *et al.* 2003). The resulting conflicts occur through two mechanisms. *Intralocus conflict* occurs when a trait has different male and female optima, thus generating opposing selection pressures (Rice & Chippindale 2001). *Interlocus conflict* occurs when optimal male (female) expression at one locus perturbs females (males) from their optimum at another locus (Parker 1979). It is well established that sexual conflict has important evolutionary consequences in dioecious animals (Arnqvist & Rowe 2005; Parker 2006), but it may also occur in simultaneous hermaphrodites (Charnov 1979; Morgan 1994; Michiels & Koene 2006) and in systems such as plants, where mates do not interact physically during reproduction (Murphy 1998; Bernasconi *et al.* 2004; Levitan 2008). Here, by comparing the expression and the resolution of sexual conflict in the case of simultaneous hermaphroditism and dioecy, we explore how breeding system variation may modify the evolution of sexually antagonistic (SA) traits.

2. INTRALOCUS CONFLICT, SEX-BIASED EXPRESSION AND SEX CHROMOSOMES

At first sight, an SA mutation is predicted to increase in frequency in all breeding systems whenever its net fitness averaged across sexes or sex functions (after appropriate normalization of male and female contributions, see Charlesworth & Charlesworth 1978) is

positive (Rice 1984; Morgan 1994), provided that random genetic drift effects are negligible. However, this prediction assumes that the fitness effect of an allele in each sex stays constant over the course of evolution, i.e. that there is a strict correspondence between genotype and phenotype (Lloyd 1977). This assumption becomes flawed when compensatory evolution and sex-specific gene regulation evolve. In the following, we illustrate how the evolutionary consequences of these mechanisms vary between hermaphroditism and dioecy by considering the fate of a novel SA mutation (figure 1).

First, in dioecious species, the expression (and thus fitness consequences) of such a mutation can be regulated sex-specifically. Sex-biased (or sex-limited) gene expression (Ellegren & Parsch 2007) can reduce the intersexual genetic correlation below 1, lowering the costs of carrying suboptimal alleles and partially resolving intralocus conflict (Cox & Calsbeek 2009). Regarding traits expressed in both sexes (e.g. body size), a similar reduction in the intersexual genetic correlation is impossible in simultaneous hermaphrodites (figure 1*a*). Therefore, it is possible that neither sex function reaches its fitness optimum (Morgan 1994; figure 1*b*).

Second, sex-specific regulation switches off or reduces SA in gonochorists, as no or little, antagonistic selection will act on the sex where the expression is downregulated. Instead, the latter serves as a ‘latent pool’ of alleles, resulting in some kind of ‘sexual masking’. This process slows down allele fixation and can maintain polymorphisms (Reinhold 2000). In hermaphrodites, in contrast, SA alleles are exposed to selection in every individual (figure 1*a*). Fixation (or loss) may therefore occur faster and result in reduced polymorphism.

Hermaphroditic plants present an interesting case, with sex-limited haploid expression of a much higher proportion of the genes than animals during the gametophytic phase (Bernasconi *et al.* 2004; Joseph & Kirkpatrick 2004). An extension of Wright’s (1969) theoretical model to include SA effects in the haploid phase would help understand the evolutionary consequences of such an alternation of selection regimes.

Finally, dioecious species often possess sex chromosomes. Sex chromosome evolution may have been triggered, among other processes (Charlesworth *et al.* 2005; Mank 2009), by the benefits of confining SA genes to one sex (Rice 1984). Moreover, specific selection regimes predispose sex chromosomes to accumulate SA variation (Rice 1984). A theoretical analysis (Van Doorn & Kirkpatrick 2007) further suggested that intralocus conflict could promote a high turnover of sex chromosomes. If this prediction is verified, different parts of the genome would successively become sex chromosomes and accumulate SA variation. Owing to the absence of sexual chromosomes, hermaphrodites have a lower probability of preserving SA polymorphism in their genome.

One contribution of 16 to a Special Feature on ‘Sexual conflict and sex allocation: evolutionary principles and mechanisms’.

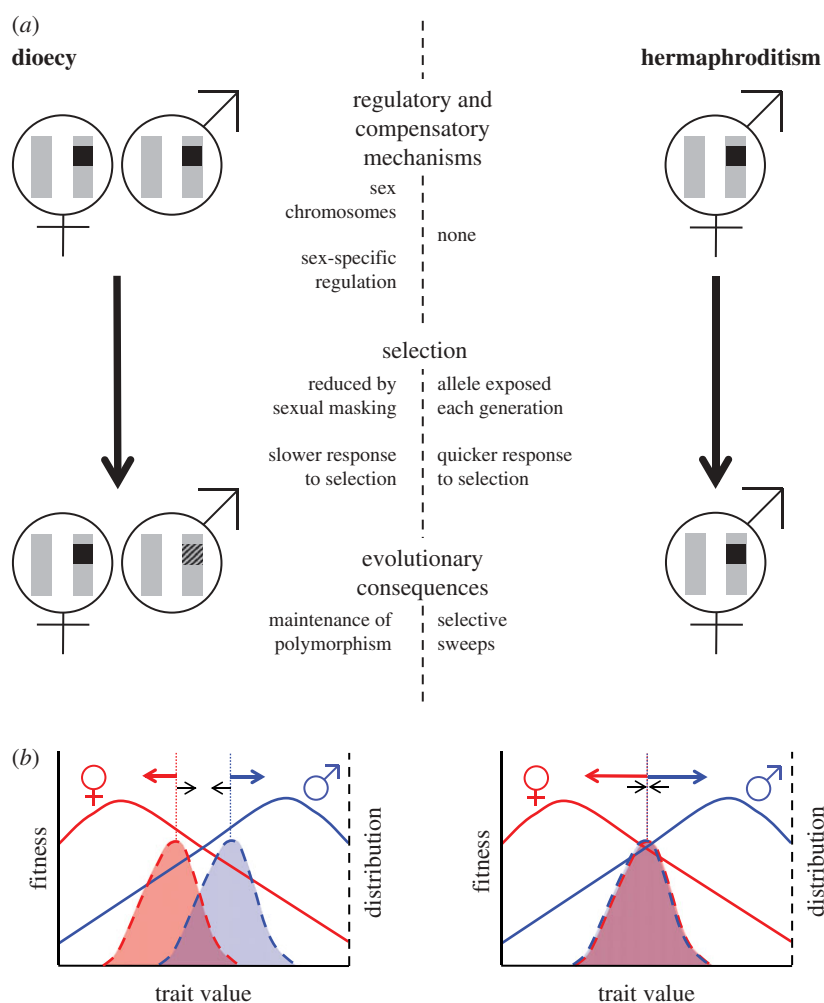


Figure 1. Resolution and outcome of intralocus sexual conflict in dioecious and hermaphroditic species. The figure illustrates a sexually antagonistic mutation (SA, black square) increasing female fitness, but decreasing male fitness. (a) Comparison of the regulatory mechanisms that can occur in response to the presence of an SA allele and the implications for evolution and the intensity of selection. The hatched SA allele represents sexual masking of this allele owing to sex-specific regulation. Sexual masking occurs here in males because the mutation is beneficial to females but would occur in females in the reciprocal case. (b) Representation of the fitness curves (solid lines) and phenotype distributions (dashed lines) for a sexually antagonistic trait. Thick red and blue arrows show female and male selection pressures, respectively. Thin black arrows display the constraint owing to intersexual correlation.

3. INTRA- AND INTER-LOCUS CONFLICTS OVER SEX ALLOCATION

Dioecious carriers of SA alleles are predicted to optimize offspring fitness through mate choice and sex-ratio manipulation (West & Sheldon 2002), as recently verified in side blotched lizards (Calsbeek & Sinervo 2004). Similarly, hermaphrodites may mitigate deleterious effects of SA mutations by adjusting sex allocation (proportion of reproductive resources invested in male versus female reproduction). For example, individuals carrying an allele enhancing female fitness benefit from biasing sex allocation towards their female function (Schärer *et al.* 2001). The existence or subsequent evolution of linkage between the SA and the sex allocation loci provides one potential mechanism, among others (Lloyd 1975; Charlesworth & Charlesworth 1978; Pannell *et al.* 2008) for transitions from hermaphroditism to dioecy.

Hermaphrodite sex allocation may also be a target of interlocus conflict. Sperm donors may benefit from inducing their partners to produce more eggs,

generating diverging post-copulatory sex allocation optima between mates (figure 2a). This conflict could favour the evolution of physiological ‘feminization’ of a partner’s resource allocation (Michiels 1998), for example via manipulative all hormones transferred during copula (Charnov 1979; Koene & Ter Maat 2001). As genes for male and female reproductive pathways are expressed in each hermaphrodite, bioactive compounds for partner manipulation are immediately available (Koene 2005) and only require appropriate means for delivery. Their influence on the partner’s sex allocation, however, remains largely unexplored (Schärer & Janicke *in press*). In plants, patterns of increased female allocation under elevated pollen loads (López & Domínguez 2003) match a scenario of partner feminization.

4. INTERLOCUS CONFLICTS OVER MATING ROLES AND SELFING RATES

Whenever the fitness benefits of remating diverge between sex functions, hermaphrodites should display

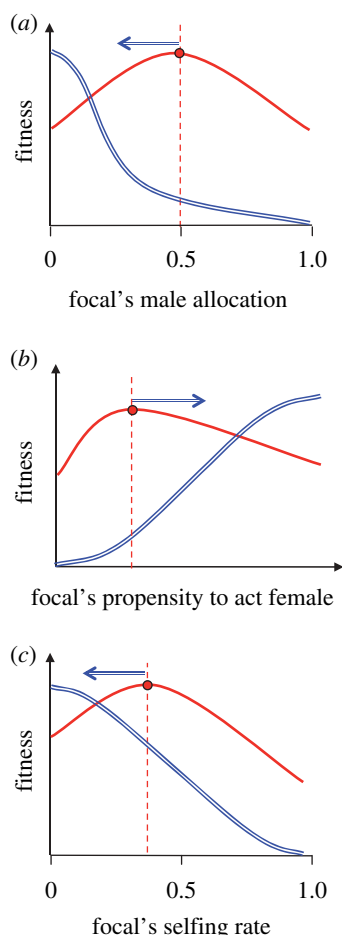


Figure 2. Scenarios for interlocus conflict in hermaphrodites. In all graphs, focal individuals (red curves) express their current trait optimum (dashed line). Their partners maximize fitness at different values than focal trait expression (blue double lines), and therefore aim at removing focals from their trait optimum (double arrow). (a) Hermaphrodites typically maximize fitness at roughly balanced sex allocation, whereas their partners gain most from inseminating focals with highly female-biased sex allocation (conflict over sex allocation). (b) Among prospective mates, the propensity to assume the (sometimes costly) female mating role may be low unless depleted sperm stores make sperm receipt necessary. This may conflict with the partners' interest to achieve insemination (conflict over mating roles). (c) When inbreeding depression is low, focal sperm recipients may prefer to produce some selfed offspring, inevitably conflicting with the interests of a sperm donating partner (conflict over selfing rate).

asymmetric copulation propensities in their male and female functions. Especially if performing one role is costly, prospective mates may face conflict over mating roles (figure 2b). Precopulatory struggles apparently forcing the partner into the female role (e.g. Anthes & Michiels 2007) and mutual sperm trading (Leonard & Lukowiak 1984; Anthes *et al.* 2005) have been interpreted in this context. Yet, whether such behaviours are indeed driven by cost–benefit asymmetries of mating roles remains to be established.

Selfing constitutes a final trait over which the interests of hermaphroditic mates could be at odds. Despite potential costs of selfing (Lande & Schemske 1985), mixed mating systems with intermediate selfing rates are

widespread (Goodwillie *et al.* 2005; Jarne & Auld 2006) and may be evolutionarily stable when selfing is an unavoidable by-product of optimal pollination strategies (Johnston *et al.* 2009). When selfing costs are low, a mother with sufficient sperm or pollen stocks may still benefit from self-fertilizing some of her eggs (doubling her genetic contribution to offspring). This, however, conflicts with the interests of any sperm or pollen donor, generating diverging selection on male and female traits that affect selfing (figure 2c). This idea clearly requires empirical attention, but previous work indicates that sexual conflict over post-pollination changes in stigma receptivity (Lankinen *et al.* 2006; Lankinen & Kiboi 2007) and the degree of outcrossing (Luscher & Milinski 2003) may indeed occur.

Clearly, sexual antagonism takes intriguing forms in hermaphrodites, and the proposed research avenues will help generalizing our picture of its evolutionary consequences.

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