Opinion piece

Sexual conflict as a partitioning of selection

Sexual conflict appears to be a powerful force in evolution. We suggest that selection theory can readily be adapted for cases of sexual conflict and illustrate how it can provide a new perspective on what traits cause conflict and might respond to its presence. Use of selection theory resolves some terminological confusion, provides operational measures of conflict and generates a conceptual tool for parsing the causes and consequences of conflict in complex systems of male–female interactions.

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Mating patterns and the bizarre variety of associated morphological and behavioural traits have long fascinated scholars in many disciplines. That these traits result from discordant evolutionary forces (i.e. sexual conflict) is a relatively recent idea, but one that is rapidly growing in acceptance. In a seminal paper, Parker (1979) explored how interactions between the sexes produced opposing selective pressures on a variety of traits. He originally defined sexual conflict as ‘a conflict in the evolutionary interests of individuals of the two sexes.’ Numerous refinements of this definition exist (e.g. see table 7.1 in Arnqvist & Rowe 2005); most differ in how traits are defined and fitness is incorporated. This diversity reflects confusion about the core meaning of the concept. To clarify, Parker & Partridge (1998) introduced the now widely accepted terms ‘intralocus’ (when allelic variation influences a trait expressed in both sexes and selection favours different optima in each sex) and ‘interlocus’ (when alleles at different loci have sex-limited expression, but in interactions between the sexes produce antagonistic selection pressures) sexual conflict to separate two seemingly disparate categories of ‘differing’ evolutionary interests. Although this terminology has been useful, it creates misleading assumptions about genetics which can occlude a clearer understanding of how sexual conflict influences evolution. Here we offer a parallel approach from selection theory that provides several novel insights.

Selection theory partitions fitness variation into components and explores the covariance between traits and fitness (Crow 1958; Price 1970; Lande & Arnold 1983). It explicitly separates the issue of genetics from selection, as in the breeders’ equation ($R = h^2S$) in which evolutionary change (R) results from the product of selection (S) and heritability (h^2). In selection theory,

fitness can be described by the following equation:

$$w = c + \beta z_i + \varepsilon, \quad (1)$$

where w is fitness, c is a constant (fitness unrelated to z_i), β is the linear selection gradient associated with individual variation in the expression of the i -th trait (z_i) and ε is the error term that accounts for random variation in fitness not attributable to selection (and assumed to be uncorrelated with all traits, Lande & Arnold 1983).

Sexual conflict introduces two types of complications to equation (1). The first is that selection may act differently on traits in males than in females. Second, the fitness of individuals of one sex will depend on the phenotype of individuals of the other sex with whom they interact. The latter is a form of social selection, which has already been incorporated into selection theory (Queller 1992; Wolf *et al.* 1999) generally, and explored briefly for sexual conflict by Moore & Pizzari (2005). Following Wolf *et al.* (1999), we can partition fitness for both sexes as follows:

$$w_m = c_m + \beta z_{mi} + \beta_{Sf} z'_{fi} + \varepsilon, \quad (2a)$$

$$w_f = c_f + \beta z_{fi} + \beta_{Sm} z'_{mi} + \varepsilon, \quad (2b)$$

where β_{Sf} and β_{Sm} are new terms describing the linear social selection gradients associated with the expression of a trait (denoted as z' with subscript fi or mi indicating the j -th or i -th trait in females or males) in the individuals’ sexual partners. These equations reveal two types of sexual conflict. *Sexually discordant selection* (SDS) occurs when a trait that is correlated between the sexes experiences different selection gradients in the two sexes (figure 1a). In SDS, the covariance between fitness and the trait depends on the sex expressing the trait but is independent of the trait values of sexual partners. SDS might be considered a selection theory version of ‘intra-locus conflict’ (Parker & Partridge 1998) without reference to genetics. *Sex-based social selection* (SSS) occurs when the selection gradient acting on a trait in one sex (e.g. βz_{mi}) is of opposite slope from the fitness effect of the trait on opposite sex partners (e.g. $\beta_{Sm} z'_{mi}$), where z_{mi} and z'_{mi} are the same trait (figure 1b; Westneat & Stewart 2003). If Z_{mi} and Z_{fi} are different and antagonistic then SSS corresponds with interlocus conflict, but SSS can exist if they are the same trait (see below) or if there is no antagonism between different traits. The central idea of SSS is how fitness of individuals of one sex is affected by a social interaction with individuals of the other sex having particular phenotypes.

This partitioning of selection illustrates that the two forms of sexual conflict can occur simultaneously. For example, consider northern elephant seals (*Mirounga angustirostris*), where males can be 10 times heavier than females (Ingles 1965). SDS is likely to be the explanation for this sexual dimorphism (Lande 1980). In the range of observed values, strong selection favours a larger body size in males (strongly positive βz_m) and a smaller body size (negative βz_f , figure 1a) in females. But, because males and females interact during mating, the large size of a male could also harm females (Mesnick & Le Boeuf 1991). In other words, the strongly positive βz_m term in equation (2a) could co-occur with a negative $\beta_{Sm} z'_{mi}$ term in equation (2b) (figure 1b).

Now consider male claspers (z_{m1}) and female spines (z_{f2}) in water striders (Gerridae). Claspers improve male mating success by allowing them to hold resistant females more effectively (Arnqvist & Rowe 2002); βz_{m1}

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Figure 1. Graphs illustrating the distinctions between (a) sexually discordant selection (SDS) and (b) sex-based social selection (SSS). Both graphs show fitness plotted against a trait to illustrate selection gradients. Males, solid lines; females, dotted lines. In (a), the trait is expressed in both sexes, and the zone of conflict is indicated in grey. The symbols and arrows are path diagrams showing the effect of male and female traits (labelled z_m and z_f) on their own fitness (w_m and w_f). SDS is interesting evolutionarily if there is a genetic correlation (r_{mf}) between the traits, as is likely if the same alleles influence both traits. In (b), SSS occurs when a trait in males has an effect on the fitness of its bearer as well as on any females the bearer interacts with. Conflict is again indicated by the shaded area. Symbolically, selection on the male trait (z_m) is indicated by the path to male fitness (w_m) labelled (β). The effect of the male trait on female fitness (w_f) is indicated by the path labelled (β_{Sm}). This is the conflict gradient and illustrates the novel opportunity for selection on female traits induced by variation in a male trait.

in equation (2a) is therefore positive. When females experience mating costs, there is a negative effect of claspers on female fitness (negative $\beta_{Sm}z'_{m1}$ in equation (2b)). Spines in females have a similar effect; β_{zf2} is positive in equation (2b) and $\beta_{Sf}z'_{f2}$ is negative in equation (2a). Thus, we have a case of reciprocal (sexually antagonistic) SSS for two traits. Because both traits seem distinct, SDS would seem irrelevant, but because females could express clasper-like structures (z_{f1}) and males could have spines (z_{m2}), SDS could explain why the sexes are reciprocally dimorphic for both these traits. Thus partitioning selection in this way reveals the potential for both SDS and SSS forms of conflict simultaneously in examples traditionally described as intralocus (elephant seals) or interlocus (water striders). This is a consequence of focusing on selection rather than the underlying genetics of traits.

We explore SSS in more detail. In social selection, the terms $\beta_{Sf}z'_{fj}$ and $\beta_{Sm}z'_{mi}$ are not formally selection gradients (Wolf *et al.* 1999; Moore & Pizzari 2005). Rather, these terms represent sources of variance in fitness and hence opportunities for selection. Equations (2a) and (2b) complement game theory models of sexual conflict,

for example if z_{mi} is the same trait as z'_{mi} (male copulatory persistence) and z_{fj} is the same as z'_{fj} (female resistance, e.g. Dawkins 1976; Parker 1979). Game theory solves for an evolutionarily stable strategy, given a particular set of cost–benefit (payoff) functions. In contrast, selection analyses quantify the actual cost–benefit relations underlying sexual conflict. In addition, selection theory offers novel insights. By defining conflict as an opportunity for selection, we can ask (i) which among many traits in partners cause conflict and (ii) once conflict has been identified, which among many traits might experience conflict-induced selection. Any trait that covaries with a β_S and reduces its absolute value experiences selection as a result of conflict. For example, if copulation is costly to females but beneficial to males, then female resistance reduces the negative impact on female fitness of male attempts to copulate. Resistance is just one trait that could incur selection as a result of this conflict (Lessells 2006); others include increased refuge use (e.g. Sih & Krupa 1995) and shifts in resource allocation to minimize fitness costs of mating. Multivariate selection analyses (e.g. Phillips & Arnold 1989) could simultaneously address how multiple traits influence either SDS or SSS. In addition, social selection theory accommodates multiple social partners each with potentially different trait values (Wolf *et al.* 1999).

SSS is unusual because the fitness of males and females are not free to be any value; when the sex ratio is balanced, mean fitness of males is identical to that of females. A trait might increase a male's fitness by increasing the number of partners at the expense of their fitness, but some portion (a_f) of the fitness cost to any female partner (e.g. $a_f\beta_{Sm}z'_{mi}$) may decrease the fitness benefit to the bearer (βz_{mi}). Thus there may be bounds on whether a trait that induces conflict can continue to evolve irrespective of any subsequent evolution of partners, although such constraints will depend on how much of the partner's fitness contributes to the male's. The proportion (a_f) should be bigger than (a_m) since male fitness depends on female fecundity whereas female fitness is more dependent on her own fecundity (Trivers 1972; Jennions & Kokko 2008), although exceptions may occur (e.g. female desertion of a parental male).

A partitioning of selection emphasizes that conflict is induced by traits expressed by individuals of the different sexes, not the sexes as a whole, and this has some broad implications. Consider, for example, sexual selection through mate choice. The fitness consequences of a male ornamental trait (z_{m1}) include those effects outside of interactions with females (e.g. natural selection or male–male competition, βz_{m1}) as well as the effects of female behaviour towards males. Suppose that all females prefer to mate with an extreme male, but vary in choosiness from none to highly choosy. Male fitness can thus be partitioned as follows:

$$w_m = c_m + \beta z_{m1} + \beta_{ISf} z_{m1} z'_{f2} + \varepsilon \quad (3)$$

where the effect of female choosiness (z'_{f1}) on male fitness is a consequence of an interaction between the male trait and female choosiness ($\beta_{ISf} z_{m1} z'_{f2}$). Males with high values of z_{m1} (preferred) have enhanced fitness owing to social selection (choosy females mate disproportionately with them), whereas males with low values of z_{m1} (non-preferred) experience a cost (they get mates

only if females mate randomly). If female choosiness is under positive directional selection in females, then it induces sexual conflict, but only on males who lack the preferred trait value. Choosiness then induces an opportunity for selection on some other trait in the unpreferred males. We postulate that this component of variance in fitness drives the evolution of some alternative mating strategies (Shuster & Wade 2003). Any trait expressed in unpreferred males that circumvents female choosiness (e.g. forceful matings, satellite behaviour, sneaking, etc.) is favoured if it allows unpreferred males to obtain matings despite female preferences.

A selection theory approach to sexual conflict is entirely consistent with Parker's (1979, 2006) definition of 'differing evolutionary interests', yet it adds clarity. The generality of Parker's definition is also its problem—the word 'interests' is interpreted variably and hence leads potentially to confusion. A selection theory definition clarifies this idea explicitly in terms of selection gradients, providing an operational measure of conflict that can be estimated with field or laboratory data. Selection gradients can be further partitioned to develop additional theory. Selection theory is compatible with approaches using game theory, but we suggest it adds new insights. More broadly, selection theory integrates well with quantitative genetics to provide robust models for evolutionary change. This has been done for interacting phenotypes in general (Moore *et al.* 1997). Moore & Pizzari (2005) illustrate this potential specifically for sexual conflict. They explore how SSS combined with indirect genetic effects of heritable traits in one partner on trait expression in the other partner can have complex and fascinating implications for sexually antagonistic coevolution. Finally, because the framework focuses on understanding variance in fitness, it can be adapted to a variety of systems even where partitioning sources of variance in fitness might be done quite differently. In hermaphrodites, for example, partitioning fitness variation would distinguish trade-offs between components tied to sexual function within individuals from variation caused by interactions between individuals. Many other unique systems of male–female coevolution exist, all of which may be better understood by clearly defining sources of variance in fitness.

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