

Introduction. Sexual conflict: a new paradigm?

On 9–10 May 2005, over 200 people met at the Royal Society in London to discuss sexual conflict. Papers by 12 of the speakers are presented in this volume. In this introductory note we briefly discuss whether we have, or in fact need, a universal definition of sexual conflict. We briefly summarize what for us were the main messages emerging from the meeting in relation to where the field of sexual conflict currently stands, before finally attempting to distil some of the important unanswered questions for the future. Our motivation for organizing the meeting was that it seemed to us that in the last ten years or so, there has been a dramatic shift in the prevailing view of matings as being essentially ‘a good thing’ for both participants, to one in which they are regarded as ‘bad’ for females. This change has been driven primarily by some very elegant empirical work, which has generated some passionate advocacy (and some equally passionate resistance) for the importance of conflict. However, whether evolutionary biologists were mistakenly viewing male–female interactions as more benign than they actually are, or whether there is now a tendency to over-emphasize the importance of conflicts of interest, is a major question that warrants consideration. This discussion meeting provided an opportunity to explore the state of the art and whether sexual conflict is indeed a new paradigm. This was made possible by the hard work of the participants, whom we would like to take this opportunity to thank.

1. SEXUAL CONFLICT: DEFINITIONS AND HISTORY

In his book ‘Adaptation and natural selection’, G. C. Williams uses the term ‘sexual conflict’ and provides what may be the first discussion of an ‘evolutionary battle of the sexes’ (Williams 1966, p. 184), although he credits Fisher with the original insight. This concept received little immediate attention, and the dominant view continued to be that sexual reproduction was mostly a harmonious cooperation between mates. In the 1970s, the field was brought to life by Trivers’ chapter on ‘parental investment and sexual selection’ (Trivers 1972) and Dawkins’ chapter 9 in ‘The Selfish Gene’ (Dawkins 1976) devoted to conflicts of interest between mates over parental care and to the evolution of male ornaments. A few years later, Parker’s now classic chapter on ‘sexual selection and sexual conflict’ expanded the concept from investment in offspring to consider conflicts over whether a mating takes place. Parker provided the theoretical basis for the entire field and for the first time sought to define what was meant

by sexual conflict, using the term to refer to ‘a conflict between the evolutionary interests of individuals of the two sexes’ (Parker 1979; Parker 2006).

Since Parker’s seminal work and particularly in the last decade, the concept of sexual conflict has caught the imagination of evolutionary biologists and the number of papers using the term has increased exponentially. Inevitably, there has been some divergence in the use of ‘sexual conflict’, which has contributed to a degree of confusion about the concept itself (Pizzari *et al.* 2003; Arnqvist 2004; Pizzari & Snook 2004). Biologists are often reluctant to commit themselves to narrow definitions of concepts, a habit that sometimes mystifies physical scientists leading them to suspect that a degree of woolly thinking may be taking place. When we asked the participants in our discussion meeting to define the term, several replied that they did not believe a definition was useful. The definitions that were offered could be divided into three broad types: (i) those that addressed only conflicts mediated by interactions between sex-specific adaptations (inter-locus conflict: see below); (ii) those that made an explicit distinction between intra-locus and inter-locus conflicts (see below); and (iii) those that combined both inter- and intra-locus conflicts (of which Parker’s original definition is one). In reading the definitions provided by the leading researchers in the field, the reason for the reluctance of some to provide them becomes apparent: it is hard to provide one that is both succinct, accurate and which does not require further qualification or limit thinking.

Early discussions of sexual conflict were concerned with conflict occurring between individual males and females over issues such as how much to invest in offspring and whether or not to mate. These types of conflicts have been termed ‘inter-locus conflicts’ because they are typically mediated by phenotypes encoded by alleles at different loci (for instance in the form of a toxin and an antidote). A second distinct form of conflict occurs when a specific gene has beneficial effects in one sex, but detrimental effects in the other (where selection on the specific locus in question is sexually antagonistic). This form of conflict, termed ‘intra-locus conflict’, is implicit in discussions of the evolution of sex differences (Lande 1987) and was explicitly discussed in relation to the evolution of sex chromosomes by Rice (1984). Somewhat confusingly, it is possible for inter-locus conflicts to be mediated by alleles found at the same locus in males and females (for instance size may affect ability to impose and resist matings). However, the important point is that selection can recruit alleles at different loci in response to inter-locus conflicts, whereas intra-locus conflicts are constrained to a single locus and do not involve interactions between a male and a female.

One contribution of 13 to a Discussion Meeting Issue ‘Sexual conflict: a new paradigm?’.

A number of definitions of sexual conflict cleverly cover both these forms of conflict, and it was these types of definition that we mainly received from our meeting participants. These include Parker's original (Parker 1979) definition (above) as well as: 'when the optimal value of a trait differs between the two sexes'; 'when one sex evolves a trait that does not maximize the fitness of the other sex'; 'the load created by disruptive selection between the sexes on fitness related characters'; and so on. It is possible to quibble over aspects of all these definitions, but our view is that all of them are essentially accurate and are admirable in their economy and scope. However, what these pithy definitions really have in common is that they are, to some extent, incomplete. To fully understand them and their implications, the reader needs to think carefully about the meaning of each word, and it is noteworthy that all such definitions were accompanied by several lines of explanation about the implied meanings of the terms involved. Our view is that the study of sexual conflict in all its forms is probably not well served by a search for a perfect definition, even though this may be an engaging intellectual and semantic pursuit. Definitions can constrain as well as clarify and the search for precise definitions can end up wasting time, as has arguably been the case in relation to species definitions. Also, inadvertent exclusions and logical errors made in attempting to formulate definitions can create yet more confusion.

The original concept of sexual conflict had its genesis in a time when sexual reproduction was viewed as a harmonious venture. In relation to inter-locus conflicts, we are now aware that any interaction between individuals that are not clonally related involves conflicts of interest, and that situations where these conflicts are completely avoided may never occur in nature. The wonder is not only that there are conflicts between individuals of different sexes, but that the benefits of sexual reproduction are apparently sufficiently large (at least at some point in evolutionary time) to allow it to evolve. In relation to intra-locus conflicts, the fact that the same alleles find themselves in such different genetic and phenotypic backgrounds makes it inevitable that the direction of selection will frequently be different in one carrier relative to another. This may be because individuals are of opposite sexes or because they are of different ages or in different environments. We suggest that it is important for researchers to be explicit about the exact nature of the genetic conflict they are describing. In this context, it seems useful to make the distinction between intra-locus and inter-locus conflicts. Also, it is important to distinguish between the potential for conflicts of interest, whether they actually occur and if so, their magnitude, before proceeding to discuss the selection created by adaptive genetic variation resulting from such conflicts. For instance, intra-locus sexual conflicts can be resolved through the evolution of sex limitation, so an allele that in theory is under antagonistic sexual selection, may completely escape such selection through not being expressed in the 'wrong' sex. The potential for conflict is ubiquitous. It is when such conflicts result in selection that is sufficiently strong to drive evolutionary change that this potential is realized.

2. SEXUAL CONFLICT: THE STATE OF THE FIELD

Given that the existence and evolutionary potential of sexual conflict was laid out in the 1970s (see §1), it is puzzling that empirical investigations on this topic have become common only relatively recently. Some approaches such as the genetic manipulations used by Rice and colleagues, and the molecular data and approaches utilized by Swanson *et al.* have been contingent on technological advances. However, for theoreticians and researchers using comparative techniques and life-history investigations of costs and benefits, the reason for the delay in realizing the potential importance of sexual conflict is less clear. One suggestion is that because the operation of sexual conflict may be entirely cryptic, it was simply not apparent to empiricists, and existed only as an interesting but untested theoretical possibility. It was perhaps only with the advent of techniques in which it was possible to perturb the balance of interests between mates (e.g. Rice 1992, 1996) that sexual conflict as a phenomenon was revealed and its evolutionary potential became apparent. It also seems likely that earlier observations were interpreted according to a prevailing mind-set, and that greater acceptance of new ideas has led to a genuine shift in the dominant paradigm, with researchers seeing conflict where before it would have been ignored.

It was clear from the meeting that our thinking about sexual conflict has become more sophisticated and that empirical tests of theory continue to provide new insights (Arnqvist & Rowe 2005). Here we highlight a few areas discussed at the meeting where there has been clear progress since Parker's seminal (Parker 1979) paper. We have attempted to synthesize views presented in talks and discussed with participants, but inevitably have our own biases.

(a) *The costs of conflict*

Following the work of several authors (Johnstone & Keller 2000; Hosken *et al.* 2003; Morrow *et al.* 2003; Lessells 2005), it is clear that the harm inflicted on females by their mates can come about in several ways. It may be divided up into: (i) the fitness disadvantage due to an individual being shifted away from its optimum value for a trait over which conflict occurs (the 'shared trait' (Rowe & Day 2005) or 'conflict trait' (Lessells 2006), an example might be the energetic costs to females of mating more frequently than is optimal; and (ii) harm which reduces fitness through direct effects on traits that are not subject to sexually antagonistic selection, for instance female lifespan may be reduced by seminal fluid chemicals, but lifespan is not actually a trait over which there is any conflict of interest. This second type of harm can be further divided into 'adaptive harm', where it is the costs of the harm inflicted that leads to a female changing the value of the shared trait, and 'collateral harm' which is a negative side effect in one individual of a conflict driven adaptation in another. Collateral harm is under directional selection to be reduced in both sexes, but persists because the beneficial effects of the adaptation to individuals of one sex outweigh the costs. This type of harm has been called 'pleiotropic harm' (Morrow *et al.* 2003); however, as Lessells (2006) points out, this

term is misleading, since manipulation of the trait through the direct effect of harm is also a pleiotropic effect of the harm. In addition to these costs of sexual conflict, populations also suffer the costs of bearing conflict traits. Sexually antagonistic coevolution takes place against a backdrop of directional selection to reduce harm to females and to reduce the costs of adaptations and counter-adaptations to both sexes.

(b) *Coevolutionary and non-coevolutionary responses to conflict*

Part of the excitement over sexual conflict stems from the potential for antagonistic selection to drive coevolutionary arms races between the sexes. However, Lessells (2006) points out that in addition to coevolution, manipulative traits are likely to have pleiotropic effects that are not beneficial to either mating partner and which will lead to selection for palliative adaptations that are not under antagonistic selection and which may be beneficial to both sexes. It is also likely that female counter-adaptations that shift the value of the conflict back to where it had been before an earlier male adaptation may frequently fail to completely remove costs imposed by the male adaptation. For instance, males might evolve a chemical that increases female oviposition rate, but reduces lifespan. Females may then evolve a counter-adaptation that reduces the sensitivity of their oviposition control system to the male chemical. This would ameliorate the harm due to the change in the shared trait, but the poisonous effect of the male chemical would remain. Hence, the 'evolutionary dance' that has been used as a metaphor to describe the process of sexually antagonistic coadaptation (Rice 1998) may be better regarded not simply as a couple moving across a dance floor, but as a couple who leave a trail of destruction that they must negotiate as they move around.

(c) *Using population comparisons to understand sexual conflict*

Inter-sexual coevolutionary arms-races are expected to result in unpredictable evolutionary trajectories, because there are many possible adaptations and counter adaptations and the direction of evolution is likely to depend on the chance occurrence of mutations. Hence, there is a prediction that if you cross populations that have been isolated from one another you should expect to see interactions between male and female genotypes affecting traits that are exposed to sexually antagonistic selection. There have now been a number of studies in which this population cross approach has been utilized (Clark *et al.* 1999; Andres & Arnqvist 2001; Hosken *et al.* 2002; Nilsson *et al.* 2002, 2003; Attia & Tregenza 2004; Fricke & Arnqvist 2004) culminating in the study presented by Long *et al.* (2006). However, there seems to be a general consensus that the existence of interactions between male and female genotypes over shared traits, or even the finding that females have higher fitness when mating with males from their own population, cannot be considered diagnostic of sexual conflict (Rowe *et al.* 2003). Although this approach was initially claimed as a powerful tool for examining coevolution between male and female mating signals, it is now clear

that sexually antagonistic evolution should not be expected to produce any particular pattern, and as Long *et al.* (2006) show, that substantial variation in the outcome of crosses between the same populations can occur between experimental blocks for no obvious reason. Future experiments of this type are unlikely to offer substantial insights unless they are based on better understanding of the proximate causes of genotypic differences in inter-sexual interactions and how these affect fitness.

(d) *Evidence for coevolution and rapid evolution*

Empirical work on sexual conflict continues apace. The rapid evolution of male accessory gland proteins (Acps) and female reproductive proteins in *Drosophila melanogaster* remains the best-studied system to date in sexual conflict. New approaches, including large-scale screens to detect associations between different Acp variants and the performance of males bearing those variants in sperm competition assays (Fiumera *et al.* 2006), are providing new insights into this system. Fiumera and colleagues' work reveals some significant, and sometimes antagonistic, associations between Acp alleles and performance as either the first or second mate of a female. Tests for association between allelic variants of Acps and Acp expression levels and a male's ability in sperm competition reveal that allelic variation seems to be generally more closely related to sperm competition phenotype than does Acp expression level, but how robust this result is and why this should be the case are avenues for future study. Intriguingly, there is some functional similarity and cross-reactivity between *D. melanogaster* Acps (e.g. the sex peptide, Acp 70A) and sex peptide in moths (e.g. *HexPSP*). This implies that seminal fluids are hijacking physiological pathways regulating female reproduction that are conserved across taxa. Future development of genomic and post-genomic techniques will hopefully allow detailed examination of gene function to be expanded to non-model species such as moths. This may shed some light on why seminal factors have been found to be both very rapidly evolving and yet conserved across very distantly related groups (Wedell 2005). Simply finding rapid evolution is not evidence for sexual conflict, future studies need to demonstrate a relationship between costs to females and the rate of evolution of potentially manipulative substances such as Acps.

(e) *Direct costs versus genetic benefits*

There has been considerable debate over the last few years about whether females mating with manipulative males suffer a loss of fitness or whether they actually gain overall, because costs of mating are more than balanced by indirect genetic benefits accrued to their offspring. This issue has now been tackled both theoretically (e.g. Kirkpatrick 1996; Cameron *et al.* 2003) and empirically (Rice *et al.* 2005). The general consensus of this meeting seemed to be that indirect genetic benefits surely exist, but that they are probably not sufficiently large to offset the large direct costs that can be incurred by females. It is also noteworthy that discussion of indirect benefits has been somewhat lopsidedly dominated by possible benefits of having manipulative sons, with little consideration of possible

costs of having daughters that are less resistant to males. Further measurement of the magnitude of both sets of costs is needed to allow a more informed debate, and this issue looks set to rumble on.

3. FUTURE RESEARCH

(a) *Evidence for coevolution*

As discussed above and by Lessells (2006), a distinction can be made between coevolutionary adaptations and those that simply ameliorate the negative effects of adaptations to conflict but which do not directly affect shared traits. For instance, a male seminal chemical that reduces female re-mating will create selection for a coevolutionary adaptation in females to re-mate more readily, but it may also have the side effect of reducing female lifespan, creating selection for immunity to this toxic effect. Increased re-mating by females will increase selection on males to reduce it again, whereas immunity to toxicity will not drive coevolution, because it is in the interests of both mating partners. This distinction is important because coevolutionary adaptations and counter-adaptations have the potential to drive perpetual evolutionary change, whereas palliative adaptations do not. More data are needed on the types of adaptation that occur in response to sexual conflict and on their fitness implications for both sexes. These data could reveal whether coevolution is retarded by the build up of negative side effects of conflict adaptations. Additionally, they could throw light upon the extent to which the trajectory of conflict-driven evolution is determined by its past history as opposed to random variation due to the availability of new mutations. It would also be very interesting to know the relative importance of standing genetic variation and new mutations in providing fuel for conflict arms-races.

(b) *Sexual conflict and population ecology*

There comes a time in the development of any field of evolutionary biology when it becomes possible to consider how insights into evolutionary dynamics will affect population ecologies. It is clear that for sexual conflict, this point has arrived. There is already evidence from various taxa that ecological parameters such as colony size affect male adaptations to sperm competition (e.g. Pitcher *et al.* 2005) with inevitable consequences for conflicts of interest over mating rate. Kokko & Rankin (2006) point out that it is also essential to consider the opposite interaction: the influence of population ecology (specifically density) on the level of sexual conflict. There is a clear need for further work examining the interaction between ecology and conflict evolution, with an awareness of the bidirectional nature of this interplay.

(c) *Sexual conflict and speciation*

The area where the study of sexual conflict impinges most dramatically on the 'big questions' in biology is over its potential role in driving speciation. Theoretical models suggest that coevolutionary changes driven by sexually antagonistic selection have the potential to drive speciation (Gavrilets 2000). Within populations sexual conflict may drive divergence if females can

reduce harassment by evolving two different evolutionary states. Males hence become stranded between the two female phenotypes (a phenomenon known as 'Buridan's Ass'). There is then the potential for a split among males, with some adapting in response to each female phenotype. Whether this type of phenomenon has the potential to lead to population differentiation or speciation is currently unknown. Recent theoretical work (Gavrilets & Hayashi 2006) highlights the potential complexity of these situations and the dependence of the outcome on the costs and benefits of matings to females. There is clearly a great deal of theoretical work left to be done, both in reducing the number of simplifying assumptions and in producing models that lend themselves to testing. There is some empirical support for a role of conflict in speciation particularly from studies of sperm-egg interactions such as Swanson *et al.*'s work on abalone (2005), which reveals that interspecific crosses have reduced efficiency of sperm-egg membrane interactions. But progress will be aided by more theories than make clear predictions and more experiments that test them.

(d) *Range of sexual conflict*

Allied to the above, it will be extremely important to expand sexual conflict theory and empirical investigations to include a broader range of traits and scenarios. For instance, conflict over female mating rate ranges from situations where females that mate more frequently have much lower fitness to situations where they gain very large direct benefits from matings resulting in dramatically different outcomes. There is much scope for integrating the study of sexual conflict within a broader context of evolutionary change driven by coevolutionary processes. For example, in what way is sexually antagonistic coevolution distinct, if it is from coevolution between parasites and their hosts, predators and prey, etc.

(e) *Intra- versus inter-locus sexual conflict*

There was little discussion in this meeting of comparisons between intra- and inter-sexual conflict. It will be of interest in the future to investigate whether these two processes are quantitatively or qualitatively different from one another in terms of theoretical predictions, for example the extent to which they may promote or constrain evolutionary change. Other important questions are to determine how important sexual conflict is in driving evolutionary change and to investigate the relative contributions of intra- versus inter-sexual conflict in determining such change.

(f) *The nature of female harm*

It will be valuable to establish the ways in which females are harmed as a result of reproductive processes. This may help to distinguish whether the harm done is a direct result of the male manipulation, or whether the damage is collateral. The types of selection that are likely to promote the evolution of female resistance to harm are likely to differ significantly depending upon which of these alternatives is the predominant one. For example, if females are continually being subjected to new conflicts as a result of being shifted off their optimum strategy, then selection pressures against

harm are likely to be variable and fitness costs of harm unpredictable.

(g) Making predictions about the evolutionary dynamics of conflict

The population crosses approach illustrates a general issue in the field, which is that there is a lack of predictive theory which empiricists can use to design experiments. Part of the reason for this deficiency is discussed by Rowe & Day (2006), specifically that the dynamics of conflict-driven evolution are expected to be very different during its initial establishment and spread, compared to the situation in which adaptations have gone to fixation. Hence, the detection of sexual conflict when it is being maintained at equilibrium requires a different methodology from that necessary during the origin and establishment phases. It is sometimes suggested that it may be possible to determine signatures of sexual conflict from examination and comparisons of sequence information. However, it is unlikely that such signatures, as distinct from those due to processes such as sperm competition and/or cryptic female choice, will be distinguishable from analysis of sequence data alone. There is a need to put such analyses together with information about the underlying mechanisms of sexual conflict in order to provide a theoretical framework that empiricists can use to make progress. As discussed by Arnqvist (2006), an important distinction can be made between the maintenance of traits that have evolved in response to conflicts of interest and their origin, with the possibility that female sensory biases may be a much more common way of establishing sexual conflict than previously thought.

(h) Sexual conflict is not confined to fruitflies

It was notable that of the seven empirical talks at the meeting, four were predominantly concerned with one small fly. *Drosophila melanogaster* has proved to be a superb model system for the study of sexual conflict and has been brilliantly exploited. However, the time is ripe for researchers to branch out into other fields. Although they tend to lack the molecular genetic tools that are available for flies, other systems have different advantages: insects such as bed-bugs have dramatic interspecific variability in conflict related traits (Siva-Jothy 2006) and marine invertebrates allow direct observation of sperm-egg interactions (Swanson *et al.* 2006). There is a pressing need to investigate systems where the costs and benefits of mating do not confirm to a typical Bateman (1948)-type scenario in which males continue to gain benefits from large numbers of matings but females require only a few. For example, there are many instances where female remating is beneficial and hence direct costs of mating may not exist instead creating new conflicts over female receptivity. However, this does not preclude the operation of sexually antagonistic coevolution driven by sexual conflict. Instead, it will become important to identify traits whose effects conform to an antagonistic scenario. Investigation of species in which the sex roles are reversed, and in which the balance of power is assumed to have been altered between the sexes, should also prove extremely interesting. Even less studied in

relation to sexual conflict is the entire plant kingdom where genetic systems that must surely result in antagonistic selection abound. Haig & Wilczek (2006) discuss the cryptogams, plants with alternating diploid and haploid generations that are interdependent. Here, the haploid 'female' nourishes the diploid offspring setting up a conflict, not only between mother and offspring, but also between the maternal and paternal genomes as the paternal genome of offspring is likely to be unrelated to the mother. Postzygotic sexual conflict is predicted to promote genomic imprinting in bryophytes (i.e. liverworts, mosses and hornworts), where females invest in multiple offspring (that can be produced both sexually and asexually), and hence sexual conflict is expected to be rampant. Future research should provide evidence of the extent to which maternal resource provisioning to diploid offspring result in parent-offspring and maternal-paternal conflict in this understudied group.

4. IS SEXUAL CONFLICT A PARADIGM SHIFT?

The general impression from this meeting was that sexual conflict is a potentially significant force for driving evolutionary change. The antagonistic selection that characterizes sexual conflict distinguishes it from existing theory and ideas of sexual selection as envisaged by Darwin. Hence, in our view, the acceptance of sexual conflict as an evolutionary force can acceptably be called a paradigm shift. It seems to us that the change in view associated with the rise of the concept of sexual conflict has invigorated the field of sexual selection. Mating systems are now being reappraised in a new light, and original and exciting thinking abounds. The challenge within this field is now to provide a theoretical framework that can be used as a basis for empirical testing and to develop new and existing model systems to deliver studies that address the unique features of evolution driven by conflict as opposed to other forms of sexual selection.

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