Sexual conflict

Tracey Chapman[1], Göran Arnqvist[2], Jenny Bangham[1] and Locke Rowe[3]

[1]Department of Biology, University College London, Darwin Building, Gower Street, London WC1E 6BT, UK
[2]Department of Animal Ecology, Evolutionary Biology Centre, University of Uppsala, Norbyvägen 18d, SE-752 36 Uppsala, Sweden
[3]Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, Ont., Canada M5S 3G5

Sexual conflict occurs when the genetic interests of males and females diverge. Recent evidence supporting the view that male and female genomes are in conflict has now revolutionized the way in which we interpret interactions between the sexes, and suggests that sexual conflict is a potent force in male–female coevolution. Here, we consider the nature of sexual conflict and what distinguishes it from models of coevolution by sexual selection. There are advantages and pitfalls to the various experimental and comparative approaches now used. More precise predictions derived from theory are essential to evaluate much of the empirical data in support of sexually antagonistic coevolution. Equally, there needs to be a mechanistic understanding of the traits underlying sexual conflict to formulate and test these predictions.

Males and females have divergent interests in reproduction that are rooted in anisogamy and lead to distinct roles, where traits favoured by one sex might be costly to the other. Broadly defined as 'differences in the evolutionary interests between males and females' [1], sexual conflict is, in principle, pervasive among sexual species [1–3], and can occur between the same or different genes, that is when there are different optima for a trait expressed in both sexes (intralocus conflict) or when there is conflict over the outcome of a male–female interaction (interlocus conflict) (Box 1). Here, we focus on how interlocus conflicts drive evolutionary change and how this process differs from that predicted by other models of coevolution.

The traditional view of reproduction was one of cooperation and harmony between the sexes. This view resulted, in part, from an overestimation of the frequency of life-long monogamy in nature. Yet, the uneasy alliance between the sexes was recognized by some. Trivers concluded that 'even when ostensibly cooperating in a joint task male and female interests are rarely identical' [2] and Dawkins commented that 'if there is conflict of interests between parents and children, who share 50 percent of each others' genes, how much more severe must be the conflict between mates, who are not related to each other?' [4]. Parker [1] provided the first formal treatment of the arms race between the sexes that can be generated by sexual conflict, citing the example of yellow dung flies *Scathophaga stercoraria* (Box 1).

How is sexual conflict different from other forms of sexual selection?

Models of coevolution by sexual selection can broadly be classified into those where the female preference is favoured indirectly and those where it is favoured directly. In indirect models, the preference evolves because it becomes genetically associated with genes that confer sexy sons (the Fisher process) and/or high-viability offspring (the good genes process) [5,6]. Such indirect effects probably play at least some role in most coevolution by sexual selection (Box 2), even if the preference is under strong direct selection [5,7]. In direct models, the preference itself is under natural selection. Females expressing the preference might gain resources (e.g. nuptial gifts), greater male parental care, fewer parasites transferred at mating, and so on [8]. The few verbal and formal models of sexually antagonistic coevolution that we have fall into the direct selection class. However, the force driving the evolution of the preference is better described as a general female avoidance of male-imposed costs, rather than, as in traditional direct models, acquisition of benefits from preferred males (e.g. [1,9–11]). Here, the preference is resistance (Box 2). The boundary, if there is one, between traditional models of sexual selection and those of sexual conflict has not yet been carefully explored theoretically.

Sexual conflict theory

Sexual conflict arising from differences in costs and benefits of mating

In addition to Parker's [1] original treatment (Box 1), many other game theoretical models show that asymmetries in interests can generate male–female coevolution (reviewed in [12]). A promising new modelling strategy, using artificial neural networks, addresses male–female coevolution under nonequilibrium conditions. These simulations suggest that females exhibit hidden preferences that can be exploited by males [13], and that neither sex can be said to 'win' a conflict because evolutionary equilibria between male signals and female receptors are never reached [11,13,14].

Using a genetic model, Rice [15] predicted that sexually antagonistic genes should be located on the sex chromosomes, and recent empirical work supports this prediction [16]. Rice showed that alleles of sex-linked genes can spread even when the cost to one sex outweighs the benefit to the other. Gavrilets *et al.* [10] used a quantitative genetic model to address the situation in which female

Box 1. Intra- and interlocus sexual conflict

Two main forms of sexual conflict can be distinguished. When the fitness optima for a trait expressed in both sexes are different in males and females, this is referred to as intralocus conflict. Here, antagonistic selection in males and females, coupled with a genetic correlation between the two sexes, will lead to each sex impeding adaptive evolution in the other [a]. However, selection for sex-limited gene expression could result in independent evolution in the two sexes, thus enabling each sex to reach its adaptive peak [b,c]. Intralocus conflicts are potentially very common, although their evolutionary importance is debated [d,e]. Recently, Chippindale and co-workers provided strong evidence for such conflicts in laboratory stocks of *Drosophila melanogaster* [f]. They found a strong positive genetic correlation between male and female fitness at the larval stage (when the interests of the two sexes are concordant), but a strong negative genetic correlation between adult male and female reproductive success (when the sexes are expected to have different genetic interests). This remarkable result suggests that there is substantial antagonistic adult fitness variation, with genes that benefit males being simultaneously detrimental to females and *vice versa*. However, it is possible that much of the adult fitness variation attributable to unconditionally deleterious mutations have been removed from these laboratory populations with their rather constant environments. This would have the effect of inflating estimates of the contribution to fitness variation by sexually antagonistic alleles. However, studies of genotype × sex interactions for adult fitness components do provide evidence for intralocus conflict [g]. More studies of this nature will enable us to determine how common such loci are.

By contrast, interlocus conflicts occur when there is conflict over the outcome of male–female interactions, so that the optimal outcome is different for the two sexes [h]. Such conflicts can occur over mating frequency, fertilization, relative parental effort, female remating behaviour, female reproductive rate and clutch size. Both sexes are expected to evolve suites of sexually antagonistic adaptations that bias the outcome towards their own interests [i]. The result is sexually antagonistic coevolution between interacting traits in males and females. It was Parker [j] who first pointed to the general importance of such coevolutionary processes. He cited as an example, the drowning of yellow dung fly *Scathophaga stercoraria* females caught up in struggles between male suitors. In this example, males are presumably subject to intrasexual selection for competitive ability. However, this has the side-effect of selecting for sexually antagonistic adaptations in females to lessen the deleterious effects of becoming casualties in battles between males. Parker considered what would happen when a novel male trait, favoured in males by sexual selection, conveyed a cost to females. In spite of the fact that females could benefit from mating with males carrying the novel trait, because of a 'sexy sons' effect, the novel trait was often favourable to males but harmed females. When a male trait and female response were allowed to coevolve under sexual conflict, 'unresolvable evolutionary chases' often occurred. Parker's early work illustrated that sexually antagonistic coevolution can lead to rapid, directionless and unpredictable evolutionary change.

References
a Parker, G.A. and Partridge, L. (1998) Sexual conflict and speciation. *Phil. Trans. R. Soc. Lond. Ser. B* 353, 261–274
b Rice, W.R. (1984) Sex-chromosomes and the evolution of sexual dimorphism. *Evolution* 38, 735–742
c Rhen, T. (2000) Sex-limited mutations and the evolution of sexual dimorphism. *Evolution* 54, 37–43
d Rice, W.R. and Chippindale, A.K. (2001) Intersexual ontogenetic conflict. *J. Evol. Biol.* 14, 685–693
e Badyaev, A.V. (2002) Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. *Trends Ecol. Evol.* 17, 369–378
f Chippindale, A.K. *et al.* (2001) Negative genetic correlation for adult fitness between sexes reveals ontogenetic conflict in *Drosophila*. *Proc. Natl Acad. Sci. USA* 98, 1671–1675
g Vieira, C. *et al.* (2000) Genotype-environment interaction for quantitative trait loci affecting life span in *Drosophila melanogaster*. *Genetics* 154, 213–227
h Rice, W.R. and Holland, B. (1997) The enemies within: intergenomic conflict, interlocus contest evolution (ICE), and the intraspecific Red Queen. *Behav. Ecol. Sociobiol.* 41, 1–10
i Rice, W.R. (1998) Intergenomic conflict, interlocus antagonistic coevolution and the evolution of reproductive isolation. *Endless Forms Species and Speciation* (Howard, D.J., Berlocher, S.H. eds), pp. 261–270, Oxford University Press
j Parker, G.A. (1979) Sexual selection and sexual conflict. *Sexual Selection and Reproductive Competition in Insects* (Blum, M.S., Blum, N.A. eds), pp. 123–166, Academic Press

choice arises from avoidance of direct mating costs. The model assumed an optimal female mating rate and that male fitness increased with increasing mating frequency. The model predicted that the resulting conflict over mating patterns can result in rapid antagonistic coevolution, where male display traits are exaggerated as a consequence of female resistance (Box 2). In this formulation, the costs of resistance to females at equilibrium can be substantial (Box 2; [17,18]).

Parental care and sexual conflict
Trivers stressed that sexual conflict is central to the evolution of parental care [2]. Although outside the main scope of this review, it should be noted that various forms of sexual conflict over parental care occur: each sex should generally prefer the other to 'work harder', because the evolution of increased care by one sex will enable reduced care in the other [14,19,20]. We thus often expect sexually antagonistic coevolution between traits that function to increase provisioning by the other sex, and those that function to resist such manipulations (Box 3). A rich body of game theory models centres on this general prediction,

but also point to the social complexity of such conflicts (reviewed in [21,22]). Genomic imprinting is another possible evolutionary consequence of conflicts over off-spring provisioning in mammals (reviewed in [23,24]).

Sexual conflict and speciation
Sexual conflict clearly has the potential to promote allopatric divergence [25,26]. During allopatry, males and females are expected to coevolve at different rates along separate coevolutionary trajectories, assuming that there are multiple perceptual, mechanical or biochemical biases in females that males can exploit [11,13]. Two recent models have examined situations in which compatibility between males and females determines the outcome of sexual interactions (i.e. reproductive state 'matching'), and have found that sexual conflict promotes both allopatric [27] and sympatric [28] divergence in reproductive traits. In a series of game theory models, Parker and Partridge [29] considered the likelihood of reinforcement when partly diverged populations meet. They showed that sexually antagonistic coevolution could drive increased rates of speciation under some scenarios, but, under

Box 2. Female resistance to reduce mating rate or to 'screen' males?

Substantial evidence demonstrates that females can suffer significant direct costs of mating (e.g. [a]) that are sufficient to explain the frequently observed resistance of females to mating as well as the evolution of male traits functioning to overcome this resistance. Experimental reductions in the level of female resistance can lead to longer and more frequent copulations [b,c]. Moreover, variation in female resistance and resulting sexual selection can be predicted, based on direct fitness tradeoffs [d–f]. In contrast to the view that female resistance is favoured because it decreases the magnitude of direct costs is the suggestion that such costly behaviour is maintained by indirect selection for genetic benefits (e.g. [g]). Under this scenario, female resistance evolved and is maintained as a result of selection to screen among males of different genetic quality. Males that are most persistent in mating attempts are assumed to be the fittest. Females should therefore elevate their levels of resistance to mate with the persistent males, and thus gain greater genetic benefits for their offspring.

However, the increasing evidence that females suffer substantial costs of physical resistance, including death [d,h,i], is inconsistent with the idea that they resist matings with males to screen them. The magnitude of indirect genetic benefits required to offset such costs in females would seem prohibitively high. Even if resistance becomes genetically correlated with male persistence owing to linkage disequilibrium, such indirect benefits are expected to be a weak force in the face of direct selection on resistance (cf. [j]). Although no studies have yet demonstrated indirect selection on resistance, we might expect such effects to occur. Yet, any beneficial screening effect that might be detected (i.e. more resistant females producing fitter offspring) is more likely to represent a reinforcing side effect rather than being the main selective benefit of resistance.

References

a Arnqvist, G. and Nilsson, T. (2000) The evolution of polyandry: multiple mating and female fitness in insects. *Anim. Behav.* 60, 145–164

b Arnqvist, G. and Rowe, L. (1995) Sexual conflict and arms races between the sexes: a morphological adaptation for control of mating in a female insect. *Proc. R. Soc. Lond. Ser. B* 261, 123–127

c Crudgington, H.S. and Siva-Jothy, M.T. (2000) Genital damage, kicking and early death – the battle of the sexes takes a sinister turn in the bean weevil. *Nature* 407, 855–856

d Rowe, L. *et al.* (1994) Sexual conflict and the evolutionary ecology of mating patterns: water striders as a model system. *Trends Ecol. Evol.* 9, 289–293

e Crean, C.S. and Gilburn, A.S. (1998) Sexual selection as a side-effect of sexual conflict in the seaweed fly *Coelopa ursina* (Diptera: Coelopidae). *Anim. Behav.* 56, 1405–1410

f Jormalainen, V. (1998) Precopulatory mate guarding in crustaceans: male competitive strategy and intersexual conflict. *Q. Rev. Biol.* 73, 275–304

g Eberhard, W.G. (1996) *Female Control: Sexual Selection by Cryptic Female Choice*, Princeton University Press

h Clutton-Brock, T.H. and Parker, G.A. (1995) Sexual coercion in animal societies. *Anim. Behav.* 49, 1345–1365

i Jormalainen, V. *et al.* (2001) Costs of intersexual conflict in the isopod *Idotea baltica*. *J. Evol. Biol.* 14, 763–772

j Kirkpatrick, M. (1996) Good genes and direct selection in evolution of mating preferences. *Evolution* 50, 2125–2140

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others, it led to increased gene flow between populations. The contribution of sexual conflict to speciation depended upon the intensity of selection on males *versus* females and the scope for evolutionary change in each sex, both variables that are difficult to determine.

Detecting sexual conflict and its consequences

It was originally thought that sexual conflict would be difficult to study because of problems in accurately measuring relative costs and benefits in males and females [1] and in identifying the underlying genes involved. Adaptation followed by balancing counteradaptation also makes coevolutionary trajectories difficult to observe unless populations are perturbed [3,30]. However, an increasing number of studies have measured the costs and benefits of mating interactions in males and females, and molecular genetic tools have revolutionized the study of sexual conflict in model systems such as *Drosophila melanogaster*. Here, we briefly review such studies, with a focus on more recent advances. Nevertheless, we wish to emphasize that, in the absence of a clear functional understanding of the traits involved, it is currently not possible to isolate sexual conflict as the force leading to a pattern of rapid evolution of reproductive characters or to speciation.

The economics of mating and the evolution of antagonistic traits

A basic requisite for sexual conflict over mating interactions is that optimal outcomes differ for males and females, a finding documented in several recent studies

(e.g. [31–35]). The existence of morphological adaptations in both sexes, which give an advantage to the bearer at the expense of the other sex, suggests the potential for an evolutionary arms race. There is clear evidence of such sexual antagonism in the evolution of morphological adaptations of water striders ([30], reviewed in [31,36]). A recent comparative analysis of 15 congeneric species of these insects showed that evolutionary changes in the balance of armaments between males and females (i.e. clasping and anticlasping adaptations), but not in the absolute level of armament escalation, resulted in evolutionary change in the outcome of sexually antagonistic mating interactions [30].

Bumble bee *Bombus terrestris* females benefit from multiple mating [37,38]. Yet, both genetic and behavioural data show that females mate only once in their lifetime [39]. This is due to male transfer of mating plugs and seminal substances that prevent female remating [40]. Males can apparently successfully prevent female remating in spite of the detrimental effects of monandry to females. In *D. melanogaster*, a negative tradeoff between a component of sperm competitive ability in males and early female mortality was identified [41], suggesting that genes which conferred a sperm competition advantage on males had a deleterious pleiotropic effect on females [3].

Another powerful means of demonstrating the existence of sexual conflict and the function of the underlying traits involved is to manipulate them genetically (Box 4). For any study of the costs and benefits of mating to provide evidence of sexual conflict, net costs and benefits for each sex must be precisely defined and measured. For example,

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Box 3. Sexual conflict over parental care

The genetic interests of males and females often differ with regards to parental care. Fundamental conflicts over mate desertion, over the relative amount of care invested in offspring and over the number of simultaneous mates are common [a]. This sets the stage for sexually antagonistic coevolution between various behavioural adaptations in both sexes. For example, among biparental species with a variable mating system, it is commonly in the interest of a female to monopolize the reproductive effort expended by her mate. Whereas paired males often spend considerable effort on attracting more or additional females, we expect females to exhibit sexually antagonistic adaptations aimed at keeping their mates monogamous. Such female strategies occur in birds, fish and insects, and include: (1) interference with male mate attraction by soliciting superfluous copulations [b] or by directly attacking or otherwise obstructing displaying males [c]; and (2) general aggression towards other females, particularly during the pair formation period [d,e]. Males could, however, reduce female interference by, for example, signalling at some distance away [f,g] or by physically intervening in aggression from females directed towards new potential mates [h]. Such coevolutionary 'tug of wars' between the sexes can sometimes result in highly dynamic mating systems [i], and can generate evolution of mating system components even in the absence of any change in the ecological setting [j].

Sexually antagonistic coevolution between male and female reproductive behaviours that affect parental care is in theory very similar to coevolution between other types of sexually antagonistic traits. Research of sexual conflict should benefit from better integration of theory from different fields and from the incorporation of results from different taxa.

References
a Clutton-Brock, T.H. (1991) *The Evolution of Parental Care*, Princeton University Press
b Eens, M. and Pinxten, R. (1996) Female European starlings increase their copulation solicitation rate when faced with the risk of polygyny. *Anim. Behav.* 51, 1141–1147
c Eggert, A-K. and Sakaluk, S.K. (1995) Female-coerced monogamy in burying beetles. *Behav. Ecol. Sociobiol.* 37, 147–153
d Veiga, J.P. (1990) Sexual conflict in the house sparrow: interference between polygynously mated females versus asymmetric male investment. *Behav. Ecol. Sociobiol.* 27, 345–350
e Sandell, M.I. (1998) Female aggression and the maintenance of monogamy: female behaviour predicts male mating status in European starlings. *Proc. R. Soc. Lond. Ser. B* 265, 1307–1311
f Ratti, O. and Alatalo, R.V. (1993) Determinants of the mating success of polyterritorial pied flycatcher males. *Ethology* 94, 137–146
g Trumbo, S.T. and Eggert, A.-K. (1994) Beyond monogamy: territory quality influences sexual advertisement in male burying beetles. *Anim. Behav.* 48, 1043–1047
h Walter, B. and Trillmich, F. (1994) Female aggression and male peace-keeping in a cichlid fish harem: conflict between and within the sexes in *Lamprologus ocellatus*. *Behav. Ecol. Sociobiol.* 34, 105–112
i Davies, N.B. (1992) *Dunnock Behaviour and Social Evolution*, Oxford University Press
j Rowe, L. and Arnqvist, G. (2002) Sexually antagonistic coevolution in a mating system: combining experimental and comparative approaches to address evolutionary processes. *Evolution* 56, 754–767

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a detected reduction in female longevity could be a consequence of rescheduling the timing and scale of reproduction without necessarily representing a net fitness cost.

Artificial selection
An important line of evidence for detecting sexual conflict comes from studies of experimental evolution in *D. melanogaster*. The first evidence for sexually antagonistic genes was described by Rice [17]. Chromosomal regions were confined to either females (experimental lines), or to both sexes (control lines). Sexual conflict predicts that the gene regions confined to females would be released from any counterselection during expression in males and should therefore accumulate 'female benefit–male detriment' alleles. Fewer males containing these gene regions emerged from cultures than from control lines, suggesting that males from the experimental lines contained alleles that were detrimental for them. The nature of the genes involved remains unclear and it is not known how they benefit females or harm males. Rice [42] also studied the evolutionary consequences of release from sexual antagonism. He used a stock of *D. melanogaster* with chromosomal translocations to provide a standard female phenotype against which males could evolve. Females were discarded every generation and could not counter-evolve to the adapting males. Consistent with a beneficial effect of release from sexual antagonism, adapting males scored more highly in fitness assays compared with controls. Test females also suffered higher mortality when mating with males from one replicate of the adapting

male lines relative to females mated to the other adapting or control line males.

The evolutionary consequences of reduced opportunity for sexual conflict (and sexual selection) have also been studied in *D. melanogaster* by imposing monogamy [18]. Using experimental evolution, monogamous (one male and one female) or polyandrous (one female and three males) lines were created. After 47 generations, females mating with monogamous males had higher subsequent survival than did those mating with polyandrous males. Monogamous females had lower survival than did polyandrous females when paired with polyandrous males. The short-term fecundity of monogamous females was also lower than that of polyandrous females when both were exposed to ancestral, base-stock males. These results suggest that monogamous females were more susceptible to the potentially deleterious effects of mating with males, and that monogamous males were less able to inflict harm to females. Monogamous populations also exhibited a greater net reproductive rate, suggesting a cost to sexual conflict. Pitnick *et al.* [43,44] tested the same lines after 80-plus generations of selection and several differences between regimes were consistent with sexual conflict. However, there were also some unexplained differences between lines within treatments.

The experimental design employed in the *Drosophila* experiments [18], and in similar studies of *Scathophaga* [45], results in higher inbreeding in the monogamous *versus* polygamous lines. This is a potential problem because both sexual conflict and higher inbreeding predict that monogamous males should reduce investment in

Box 4. Sexual conflict and the evolution of male accessory gland proteins in *Drosophila*

In *Drosophila melanogaster*, the major male reproductive tract proteins are the 80 or so accessory gland proteins (Acps) [a] which are transferred to the female with the ejaculate during mating. Such proteins directly affect female behaviour and physiology after copulation in many insect species and their evolution appears to be influenced by sexual conflict, at least in *D. melanogaster*. Acps show high levels of amino acid polymorphism and interspecific divergence, and are estimated to evolve at twice the rate of nonreproductive tract proteins [a]. There is evidence for directional selection on 12 different *Acp* gene sequences. High rates of evolutionary change in loci encoding seminal fluid proteins appear to be common both within and between *Drosophila* species (reviewed in [b]). This is predicted by sexually antagonistic coevolution, but is also consistent with other models of sexual selection.

The Acps involved in conflict in *D. melanogaster* [c] were identified using males genetically engineered to lack them [d]. These males were used to demonstrate that main-cell Acps are necessary for sperm transfer [e] and cause the female cost of mating [f] which appears to result from sexual conflict in this species. Males that lack specific Acps have been used to determine Acp function and involvement in sexual conflict (e.g. [f–i]) by comparing the performance of a knockout mutant with that of a wild-type gene control. Another manipulation for studying function is the overexpression of specific Acps. Using this technique, it was recently shown that overexpression of Acp62F (but not seven other Acps) caused a reduction in adult *D. melanogaster* life span [j]. Acp62F is therefore a candidate for causing the Acp-mediated cost of mating in females. This Acp is one of several protease inhibitors that may protect sperm and/or seminal fluid substances from enzymatic attack in the female reproductive tract [j]. Its deleterious side-effect might be due to interference with essential enzymatic processes inside the female body cavity, as this Acp enters the female haemolymph through the vaginal wall [j].

References
a Swanson, W. *et al.* (2001) Evolutionary EST analysis identifies rapidly evolving male reproductive proteins in *Drosophila*. *Proc. Natl Acad. Sci. USA* 98, 7375–7379
b Chapman, T. (2001) Seminal fluid-mediated fitness traits in *Drosophila*. *Heredity* 87, 511–521
c Chapman, T. *et al.* (1995) Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland products. *Nature* 373, 241–244
d Kalb, J.M. *et al.* (1993) Probing the function of *Drosophila melanogaster* accessory-glands by directed cell ablation. *Proc. Natl Acad. Sci. USA* 90, 8093–8097
e Tram, U. and Wolfner, M.F. (1999) Male seminal fluid proteins are essential for sperm storage in *Drosophila melanogaster*. *Genetics* 153, 837–844
f Neubaum, D.M. and Wolfner, M.F. (1999) Mated female *Drosophila melanogaster* require a seminal fluid protein Acp36DE, to store sperm efficiently. *Genetics* 153, 845–857
g Chapman, T. *et al.* (2000) The role of male accessory gland protein Acp36DE in sperm competition in *Drosophila melanogaster*. *Proc. R. Soc. Lond. Ser. B* 267, 1097–1105
h Heifetz, Y. *et al.* (2000) The *Drosophila* seminal fluid protein Acp26Aa stimulates release of oocytes by the ovary. *Curr. Biol.* 10, 99–102
i Chapman, T. *et al.* (2001) The Acp26Aa seminal fluid protein is a modulator of early egg-hatchability in *Drosophila melanogaster*. *Proc. R. Soc. Lond. Ser. B* 268, 1647–1654
j Lung, O. *et al.* (2002) The *Drosophila melanogaster* seminal fluid protein Acp62F is a protease inhibitor that is toxic upon ectopic expression. *Genetics* 160, 211–224

reproduction and evolve to become more benign to females, relative to polyandrous males [46]. This leads to potentially confounding effects of monogamy and inbreeding.

Comparative studies
Comparative studies provide some evidence that sexual conflict has played a direct role in the evolutionary diversification of natural populations. Sexual conflict is predicted to promote rapid evolutionary change in the underlying genes involved [25,47]. Data consistent with this prediction are now coming from sequence analyses of male reproductive tract proteins, some of which appear to be involved in sexual conflict [48] (Box 4). Unfortunately, we know much less about rates of evolutionary change in the receptors of these proteins. However, unidentified ovary proteins do show elevated levels of divergence in *D. melanogaster*–*Drosophila virilis* species group comparisons, relative to nongonadal proteins [49]. Sequence analysis of the receptors to three mammalian fertilization proteins in a range of different mammalian species has also recently uncovered higher rates of evolutionary change relative to control genes [50]. It will be necessary to identify more of the genes involved in sexual conflict, in both sexes, if we are to understand the role of conflict in genetic divergence.

Two recent studies of morphological traits also support a role for sexual conflict in the rapid coevolution of antagonistic reproductive characters between species. The first study, noted above, provides good evidence for an arms race in water striders [30]. The second study, in diving beetles, suggests antagonistic coevolution of male grasping and female antigrasping traits [51]. Both are notable because they feature traits in both sexes, the function of which in sexual conflict is understood. The degree of evolutionary divergence in genitalic traits of male insects is also significantly elevated in polyandrous relative to monogamous species, as is predicted by the increased potential level of conflict under polyandry [52]. It should be noted however, that it is difficult to make precise inferences about coevolutionary processes from molecular and morphological data that describe trait divergence in one sex only.

Population crosses
A promising line of investigation into the role of sexual conflict in early divergence is to cross closely related allopatric populations. Sexually antagonistic coevolution is predicted to result in differential rates of evolution between different populations and, under some scenarios, evolution along separate coevolutionary trajectories. Although the latter prediction is also a feature of other models of sexual selection, it should be possible to identify conflict as a force in population divergence using predictive theory and careful crosses between populations [29]. For example, females might lack resistance to allopatric males with which they have not coevolved. Several recent studies have crossed populations to investigate interactions between responses in reproductive traits and population

origin [53–58]. Andrés and Arnqvist [55] crossed three strains of the housefly *Musca domestica* in all combinations. Males crossed within two of the three strains induced a lower proportion of their mates to oviposit than did males crossed between strains. There was thus a tendency for weaker responses of females to males with which they had coevolved, but this was not entirely consistent across strains. Brown and Eady [56] compared the results of crosses within and between two populations of *Callosobruchus maculatus* beetles. Males in within-population crosses had higher sperm competitive ability, and induced a longer period of nonreceptivity and higher fecundity in their mates than did males in between-population crosses. The lowered fitness of males in crosses between populations contrasted with the results of Andrés and Arnqvist [55]. Two similar studies, in *Drosophila* [57] and in *Tribolium* [58], also generated partly inconsistent results. In spite of the conflicting results of all these studies, many of the data were interpreted as support for sexual conflict. This suggests that current theory is not sufficient to specify a clear null hypothesis and separate patterns predicted by sexual conflict from those predicted by other processes. One feature currently missing from these studies is a measure of population genetic differentiation. The accumulation of reproductive incompatibilities is eventually expected to lead to reproductive isolation [25,28] and could complicate interpretation of results. Sexually antagonistic traits that vary either quantitatively or qualitatively are also predicted to lead to different outcomes in male–female interactions within and between populations [55]. A mechanistic understanding of conflict is therefore essential to indicate the identity and nature of the relevant traits to study.

Prospects

There is widespread evidence that interactions between the sexes are often characterized by conflict. There is also good evidence that sexual conflict influences the evolution of reproductive traits. We see research along the following lines as being particularly important in the near future.

We need to develop better, generally applicable frameworks and predictive theory for male–female coevolution under interlocus sexual conflict. It is, for example, unclear exactly what is meant by the intensity or strength of sexual conflict, whether and how it can be quantified and manipulated, and how it relates to the rate of sexually antagonistic coevolution. It is a particularly difficult concept, because past conflict can be hidden by adaptation [3,30]. We also need theoretical models that explicitly incorporate female resistance generated by antagonistic coevolution into existing models of female choice, to understand the relative importance of these processes [6, 59].

Self-reinforcing coevolution of armaments, even in the absence of other types of selection, is a central prediction of sexual conflict theory [1,25,60]. But, as yet, we lack a comprehensive understanding of the role of sexually antagonistic coevolution in trait diversification. Although sexually antagonistic coevolution can promote divergence, it is not always predicted to do so, and we need models that will enable us to use patterns of divergence to better distinguish among alternative coevolutionary processes. We need to understand genetic mechanisms to enable us to probe conflict with standard genetic tools. We also need thorough comparative studies, based on traits in both sexes with known function to investigate the role of conflict in trait diversification, and in speciation and extinction.

Finally, much of the research has been confined to a handful of taxa and traits. The taxonomic breadth and range of phenotypic traits that are involved in sexual conflict therefore remain unclear. There is a need for further in-depth empirical studies of sexual conflict, preferably combining economic, functional and comparative studies at the organismal level with studies of the molecular and genetic mechanisms underlying conflict.

References
 1 Parker, G.A. (1979) Sexual selection and sexual conflict. *Sexual Selection and Reproductive Competition in Insects* (Blum, M.S., Blum, N.A. eds), pp. 123–166, Academic Press
 2 Trivers, R.L. (1972) Parental investment and sexual selection. In *Sexual Selection and the Descent of Man* (Campbell, B., ed.), pp. 136–179, Heinemann
 3 Rice, W.R. (2000) Dangerous liaisons. *Proc. Natl Acad. Sci. USA* 97, 12953–12955
 4 Dawkins, R. (1976) *The Selfish Gene*, Oxford University Press
 5 Kirkpatrick, M. and Ryan, M.J. (1991) The evolution of mating preferences and the paradox of the lek. *Nature* 350, 33–38
 6 Kokko, H. *et al.* (2002) The sexual selection continuum. *Proc. R. Soc. Lond. Ser. B* 269, 1331–1340
 7 Rowe, L. and Houle, D. (1996) The lek paradox and the capture of genetic variance by condition dependent traits. *Proc. R. Soc. Lond. Ser. B* 263, 1415–1421
 8 Price, T. *et al.* (1993) Sexual selection when the female directly benefits. *Biol. J. Linn. Soc.* 48, 187–211
 9 Holland, B. and Rice, W.R. (1998) Chase-away sexual selection: antagonistic seduction *versus* resistance. *Evolution* 52, 1–7
10 Gavrilets, S. *et al.* (2001) The evolution of female mate choice by sexual conflict. *Proc. R. Soc. Lond. Ser. B* 268, 531–539
11 Arak, A. and Enquist, M. (1995) Conflict, receiver bias and the evolution of signal form. *Phil. Trans. R. Soc. Lond. Ser. B* 349, 337–344
12 Clutton-Brock, T.H. and Parker, G.A. (1995) Sexual coercion in animal societies. *Anim. Behav.* 49, 1345–1365
13 Arak, A. and Enquist, M. (1993) Hidden preferences and the evolution of signals. *Phil. Trans. R. Soc. Lond. Ser. B*, 340207–340213
14 Wachtmeister, C.A. and Enquist, M. (2000) The evolution of courtship rituals in monogamous species. *Behav. Ecol.* 11, 405–410
15 Rice, W.R. (1984) Sex-chromosomes and the evolution of sexual dimorphism. *Evolution* 38, 735–742
16 Gibson, J.R. *et al.* (2002) The X chromosome is a hot spot for sexually antagonistic fitness variation. *Proc. R. Soc. Lond. Ser. B* 269, 499–505
17 Rice, W.R. (1992) Sexually antagonistic genes – experimental evidence. *Science* 256, 1436–1439
18 Holland, B. and Rice, W.R. (1999) Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. *Proc. Natl Acad. Sci. USA* 96, 5083–5088
19 Westneat, D.F. and Sargent, R.C. (1996) Sex and parenting: the effects of sexual conflict and parentage on parental strategies. *Trends Ecol. Evol.* 11, 87–91
20 Royle, N.J. *et al.* (2002) Sexual conflict reduces offspring fitness in zebra finches. *Nature* 416, 733–736
21 Székely, T. *et al.* (1997) *An evolutionary approach to offspring desertion*

in birds Current Ornithology (Vol. 13) (Nolan, V., Ketterson, E. eds), pp. 271–330, Plenum Press

22 Barta, Z.N. et al. (2002) Sexual conflict about parental care: the role of reserves. Am. Nat. 159, 687–705

23 Tilghman, S.M. (1999) The sins of the fathers and mothers: genomic imprinting in mammalian development. Cell 96, 185–193

24 Haig, D. (2000) The kinship theory of genomic imprinting. Annu. Rev. Ecol. Sys. 31, 9–32

25 Rice, W.R. (1998) Intergenomic conflict, interlocus antagonistic coevolution and the evolution of reproductive isolation. Endless Forms Species and Speciation (Howard, D.J., Berlocher, S.H. eds), pp. 261–270, Oxford University Press

26 Arnqvist, G. et al. (2000) Sexual conflict promotes speciation in insects. Proc. Natl Acad. Sci. USA 97, 10460–10464

27 Gavrilets, S. (2000) Rapid evolution of reproductive barriers driven by sexual conflict. Nature 403, 886–889

28 Gavrilets, S. and Waxman, D. (2002) Sympatric speciation by sexual conflict. Proc. Natl Acad. Sci. USA 99, 10533–10538

29 Parker, G.A. and Partridge, L. (1998) Sexual conflict and speciation. Phil. Trans. R. Soc. Lond. Ser. B 353, 261–274

30 Arnqvist, G. and Rowe, L. (2002) Antagonistic coevolution between the sexes in a group of insects. Nature 415, 787–789

31 Rowe, L. et al. (1994) Sexual conflict and the evolutionary ecology of mating patterns: water striders as a model system. Trends Ecol. Evol. 9, 289–293

32 Warner, R. et al. (1995) Sexual conflict – males with highest mating success convey the lowest fertilisation benefits to females. Proc. R. Soc. Lond. Ser. B 262, 135–139

33 Crudgington, H.S. and Siva-Jothy, M.T. (2000) Genital damage, kicking and early death – the battle of the sexes takes a sinister turn in the bean weevil. Nature 407, 855–856

34 Stutt, A.D. and Siva-Jothy, M.T. (2001) Traumatic insemination and sexual conflict in the bed bug Cimex lectularius. Proc. Natl Acad. Sci. USA 98, 5683–5687

35 Blanckenhorn, W.U. (2002) The costs of copulating in the dung fly Sepsis cynipsea. Behav. Ecol. 13, 353–358

36 Arnqvist, G. (1997) The evolution of water strider mating systems: causes and consequences of sexual conflicts. The Evolution of Mating Systems in Insects and Arachnids (Choe, J.C., Crespi, B.J. eds), pp. 146–163, Cambridge University Press

37 Baer, B. and Schmid-Hempel, P. (1999) Experimental variation in polyandry affects parasite loads and fitness in a bumble-bee. Nature 397, 151–154

38 Baer, B. and Schmid-Hempel, P. (2001) Unexpected consequences of polyandry for parasitism and fitness in the bumblebee Bombus terrestris. Evolution 55, 1639–1643

39 Schmid-Hempel, R. and Schmid-Hempel, P. (2000) Female mating frequencies in Bombus spp. from Central Europe. Insect Soc. 47, 36–41

40 Sauter, A. et al. (2000) Males of social insects can prevent queens from multiple mating. Proc. R. Soc. Lond. Ser. B 268, 1449–1454

41 Civetta, A. and Clark, A.G. (2000) Correlated effects of sperm competition and postmating female mortality. Proc. Natl Acad. Sci. USA 97, 13162–13165

42 Rice, W.R. (1996) Sexually antagonistic male adaptation triggered by experimental arrest of female evolution. Nature 381, 232–234

43 Pitnick, S. et al. (2001) Evolution of female remating behaviour following experimental removal of sexual selection. Proc. R. Soc. Lond. Ser. B 268, 557–563

44 Pitnick, S. et al. (2001) Males' evolutionary responses to experimental removal of sexual selection. Proc. R. Soc. Lond. Ser. B 268, 1071–1080

45 Hosken, D. et al. (2001) Sexual conflict selects for male and female reproductive characters. Curr. Biol. 11, 489–493

46 Sharp, P.M. (1984) The effect of inbreeding on competitive male-mating ability in Drosophila melanogaster. Genetics 106, 601–612

47 Rice, W.R. and Holland, B. (1997) The enemies within: intergenomic conflict, interlocus contest evolution (ICE), and the intraspecific Red Queen. Behav. Ecol. Sociobiol. 41, 1–10

48 Swanson, W.J. and Vacquier, V.D. (2002) The rapid evolution of reproductive proteins. Nat. Rev. Genet. 3, 137–144

49 Civetta, A. and Singh, R.S. (1995) High divergence of reproductive tract proteins and their association with postzygotic reproductive isolation in Drosophila melanogaster and Drosophila virilis group species. J. Mol. Evol. 41, 1085–1095

50 Swanson, W. et al. (2001) Positive Darwinian selection drives the evolution of several reproductive proteins in mammals. Proc. Natl Acad. Sci. USA 98, 2509–2514

51 Bergsten, J. et al. (2001) Intraspecific variation and intersexual correlation in secondary sexual characters of three diving beetles (Coleoptera: Dytiscidae). Biol. J. Linn. Soc. 73, 221–232

52 Arnqvist, G. (1998) Comparative evidence for the evolution of genitalia by sexual selection. Nature 393, 784–786

53 Clark, A.G. and Begun, D.J. (1998) Female genotypes affect sperm displacement in Drosophila. Genetics 149, 1487–1493

54 Clark, A.G. et al. (1999) Female × male interactions in Drosophila sperm competition. Science 283, 217–220

55 Andrés, J.A. and Arnqvist, G. (2001) Genetic divergence of the seminal signal-receptor system in houseflies: the footprints of sexually antagonistic coevolution? Proc. R. Soc. Lond. Ser. B 268, 399–405

56 Brown, D.V. and Eady, P.E. (2001) Functional incompatibility between the fertilization systems of two allopatric populations of Callosobruchus maculatus (Coleoptera: Bruchidae). Evolution 55, 2257–2262

57 Knowles, L.L. and Markow, T.A. (2001) Sexually antagonistic coevolution of a postmating-prezygotic reproductive character in desert Drosophila. Proc. Natl Acad. Sci. USA 98, 8692–8696

58 Nilsson, T. et al. (2002) Patterns of divergence in the effects of mating on female reproductive performance in flour beetles. Evolution 56, 111–120

59 Rosenthal, G.G. and Servedio, M.R. (1999) Chase-away sexual selection: resistance to 'resistance'. Evolution 53, 296–299

60 Dawkins, R. and Krebs, J.R. (1979) Arms races between and within species. Proc. R. Soc. Lond. Ser. B 205, 489–511

future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biol. Conserv.* 112, 63–85

6 Rouget, M. *et al.* (2003) The current configuration of protected areas in the Cape Floristic Region, South Africa – reservation bias and representation of biodiversity patterns and processes. *Biol. Conserv.* 112, 129–145

7 Younge, A. and Fowkes, S. (2003) The Cape action plan for the environment: overview of an ecoregional planning process. *Biol. Conserv.* 112, 15–28

8 Cowling, R.M. and Pressey, R.M. (2003) Introduction to systematic conservation planning in the Cape Floristic Region. *Biol. Conserv.* 112, 1–13

9 Margules, C.R. and Pressey, R.L. (2000) Systematic conservation planning. *Nature* 405, 243–253

10 Lochner, P.A. *et al.* (2003) Aligning the diverse: the development of a biodiversity conservation strategy for the Cape Floristic Region. *Biol. Conserv.* 112, 29–43

11 Gelderblom, C.M. *et al.* (2002) Incorporating conservation priorities into planning guidelines for the Western Cape. In *Mainstreaming Biodiversity in Development. Case Studies from South Africa* (Pierce, S.M. *et al.*, eds), pp. 117–128, World Bank

12 Gelderblom, C.M. *et al.* (2003) Turning strategy into action: implementing a conservation action plan in the Cape Floristic Region. *Biol. Conserv.* 112, 291–297

13 Lombard, A.T. *et al.* (2003) Effectiveness of land classes as surrogates for species in conservation planning for the Cape Floristic Region. *Biol. Conserv.* 112, 45–62

14 Midgley, G.F. *et al.* (2003) Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biol. Conserv.* 112, 87–97

15 Pressey, R.L. *et al.* (2003) Formulating conservation targets for biodiversity pattern and process in the Cape Floristic Region, South Africa. *Biol. Conserv.* 112, 99–127

16 Kerley, G.I.H. *et al.* (2003) Options for the conservation of large and medium-sized mammals in the Cape Floristic Region hotspot, South Africa. *Biol. Conserv.* 112, 169–190

17 Cowling, R.M. and Pressey, R.L. (2001) Rapid plant diversification: planning for an evolutionary future. *Proc. Natl. Acad. Sci. U. S. A.* 98, 5452–5457

18 Rouget, M. *et al.* (2003) Identifying spatial components of ecological and evolutionary processes for regional conservation planning in the Cape Floristic Region, South Africa. *Div. Dist.* 9, 191–210

19 Rodrigues, A.S.L. and Gaston, K.J. (2001) How large do reserve networks need to be? *Ecol. Lett.* 4, 602–609

20 Cowling, R.M. *et al.* (2003) A conservation plan for a global biodiversity hotspot – the Cape Floristic Region, South Africa. *Biol. Conserv.* 112, 191–216

21 Cowling, R.M. *et al.* (2003) The expert of the algorithm? A comparison of priority conservation areas in the Cape Floristic Region identified by park managers and reserve selection software. *Biol. Conserv.* 112, 147–167

22 Heydenrych, B.J. *et al.* (1999) Strategic conservation interventions in a region of high biodiversity and high vulnerability: a case study from the Agulhas Plain at the southern tip of Africa. *Oryx* 33, 256–259

23 Rouget, M. (2003) Measuring conservation value at fine and broad scales: implications for a diverse and fragmented region, the Agulhas Plain. *Biol. Conserv.* 112, 217–232

24 Frazee, S.R. *et al.* (2003) Estimating the costs of conserving a biodiversity hotspot: a case study of the Cape Floristic Region, South Africa. *Biol. Conserv.* 11 2, 275–290

25 Balmford, A. *et al.* (2003) Global variation in terrestrial conservation costs, conservation benefits, and unmet conservation needs. *Proc. Natl. Acad. Sci. U. S. A.* 100, 1046–1050

26 Turpie, J.K. *et al.* (2003) Economic value of terrestrial and marine biodiversity in the Cape Floristic Region: implications for defining effective and socially optimal strategies. *Biol. Conserv.* 112, 233–251

27 Pence, G.V.K. *et al.* (2003) Finding the optimal combination of on- and off-reserve conservation strategies for the Agulhas Plain, South Africa: a financial perspective. *Biol. Conserv.* 112, 253–273

28 Privett, S.D.J. *et al.* (2002) Putting biodiversity to business on the Agulhas Plain. In *Mainstreaming Biodiversity in Development. Case Studies from South Africa* (Pierce, S.M. *et al.*, eds), pp. 101–115, World Bank

Letters

Sexual conflict and female choice

William G. Eberhard[1] and Carlos Cordero[2]

[1]Smithsonian Tropical Research Institute, and Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica
[2]Instituto de Ecología, Universidad Nacional Autónoma de México, Apdo. Post. 70-275, Circuito Exterior, Ciudad Universitaria, Coyoacán 04510, Distrito Federal, Mexico

Chapman *et al.* [1] nicely summarize some recent thinking about male–female conflict, but repeat a widespread inconsistency between old and new versions of sexual conflict, and give an overly optimistic impression of support for new models of antagonistic coevolution.

They define conflict broadly as 'differences in the evolutionary interests between males and females'. Such conflict is hardly a new idea. Traditional darwinian sexual selection by female choice [2] inevitably involves male–female conflicts of interest. Chapman *et al.*'s characterization of the traditional view as 'one of cooperation and harmony between the sexes' misreads history. This broad definition contrasts with how the authors propose to

distinguish sexual conflict from other models of sexual selection. Here, they emphasize the truly new, but much narrower conflict hypothesis: 'the force driving the evolution of the [female] preference is better described as a general female avoidance of male-imposed costs, rather than, as in traditional direct models, acquisition of benefits from preferred males'. Inconsistent use of old, broad definitions, and new, narrow definitions has plagued recent literature on sexual conflict.

How strong is the support for the new, narrower idea of sexual conflict? Some impressions of conflict, based on observing female 'resistance' behavior, or from documenting reproductive costs to females, are misleading [3,4]. A female can gain by being 'manipulated' by a male if her indirect gains via increased manipulative abilities of her

Corresponding author: William G. Eberhard (archisepsis@biologia.ucr.ac.cr).

male offspring are greater than the male-imposed reduction in her own reproduction; under some conditions, female susceptibility to males can be advantageous [4,5]. Chapman *et al.* argue that such 'indirect benefits [to the female] are expected to be a weak force in the face of direct selection on preference', but cite only a theoretical model as evidence. The track record of quantitative conclusions based on mathematical models of sexual selection is rather dismal [2]. Recall, for instance, the now discarded dogma that Fisherian female choice was unlikely because quantitative models had 'proven' that there is little or no heritable variability for sexually selected traits in males. The conflicting demonstrations regarding the feasibility of handicap models constitute another example. In addition, empirical evidence indicates that indirect benefits to the female are not necessarily small [6]. Thus, the studies that Chapman *et al.* cite as documenting the overall cost of manipulation for females, none of which took this possible indirect benefit into account, fail to demonstrate a net cost rather than a net benefit.

A second weakness is that costs and benefits cited by Chapman *et al.* were measured under captive rather than field conditions. It is trite, but nevertheless true [4], that fitness measures made in captivity do not reliably document selection in nature. For instance, reductions in female lifespan in the lab [7] might be irrelevant in nature if females die at earlier ages under natural conditions. Ecological realism is especially important for traits possibly involved in male–female conflict [1], because the demonstration of conflict depends on precise quantitative balancing of costs and benefits. Finally, Chapman *et al.* do not discuss morphological evidence from many other species that speaks strongly against the importance of new male–female conflict models [8–11].

References

1 Chapman, T. *et al.* (2003) Sexual conflict. *Trends Ecol. Evol.* 18, 41–47
2 Andersson, M. (1994) *Sexual Selection*, Princeton University Press
3 Eberhard, W.G. (2002) Female resistance or screening? Male force versus selective female cooperation in intromission in sepsid flies and other insects. *Rev. Biol. Trop.* 50, 485–505
4 Cordero, C. and Eberhard, W.G. (2003) Female choice of antagonistic male adaptations: a critical review of some current research. *J. Evol. Biol.* 16, 1–6
5 Kokko, H. (2001) Fisherian and 'good genes' benefits of mate choice: how (not) to distinguish between them. *Ecol. Lett.* 4, 322–326
6 Møller, A.P. and Jennions, M. (2001) How important are direct fitness benefits of sexual selection? *Naturwissenschaften* 88, 401–415
7 Chapman, T. *et al.* (1995) Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland products. *Nature* 373, 241–244
8 Eberhard, W.G. (1985) *Sexual Selection and Animal Genitalia*, Harvard University Press
9 Eberhard, W.G. (2001) The functional morphology of species-specific clasping structures on the front legs of male *Archisepsis* and *Palaeosepsis* flies (Diptera, Sepsidae). *Zool. J. Linn. Soc.* 133, 335–368
10 Huber, B.A. (1998) Spider reproductive behaviour: a review of Gerhardt's work from 1911–1933, with implications for sexual selection. *Bull. Br. Arachnol. Soc.* 11, 81–91
11 Eberhard, W.G. (1997) Sexual selection by cryptic female choice in insects and arachnids. In *Evolution of Mating Systems in Insects and Arachnids* (Choe, J.C. and Crespi, B.J., eds), pp. 32–57, Cambridge University Press

Sexual conflict

Alex Córdoba-Aguilar and Jorge Contreras-Garduño

Instituto de Ecología, Universidad Nacional Autónoma de México, Apdo. Postal 70-275, Circuito exterior Ciudad Universitaria 04510, Mexico, D.F.

Current positions have redefined the evolution of courtship traits as the takeover of reproductive decisions of one sex by the other sex, giving rise to an unending coevolution, in which one sex (predominantly males) sets the scene (given that selection for siring offspring is frequently stronger in males than in females [1–3]). Chapman *et al.* [3] argue that such sexual conflict is the underlying force during sexual interactions and that males, at the fitness expense of females, usually emerge at the forefront of the coevolutionary race. We perceive two problems with their review and its implications: (1) the evidence that could reject the alternative hypothesis of traditional female choice is still inconclusive. This results from a lack of predictions that can disentangle the hypothesis of traditional female choice from that of sexual conflict; and (2) extreme generalizations of a widespread nature of sexual conflict.

The sexual conflict hypothesis predicts that females become a target of male manipulation that results in mating. Given this, one can be mislead and easily interpret 'aggressive' male traits as a consequence of sexual conflict, even when these traits are also predicted by traditional female choice, with females gaining highly successful sons in spite of being 'harmed' by their mates [2,4]. Lamentably, no studies have separated both hypotheses because no measurements have been collected of direct and indirect benefits for females mated to males differing in their degree of 'aggressive' traits to establish female net fitness payoffs [4]. There are three additional approaches for unraveling both positions. The first is to investigate female reproductive traits involved in fertilization. In spite of being repeatedly claimed as an

Corresponding author: Alex Córdoba-Aguilar (acordoba@uaeh.reduaeh.mx).

important issue both theoretically and experimentally [5], researchers ignore how female reproductive traits intervene during fertilization. Once this is clarified, we can then ascribe female traits as 'resistant' or 'selective'. The second is to study the genetics of the female preference and associated male traits [5]. A genetic correlation is expected between both traits only if traditional female choice is occurring. The third and final approach is to track the rates of origin of female and male traits on phylogenies once resistance or selectivity has been determined. This will explain the prevalence of either process.

Studies of fruit flies and water striders have suggested that negative fitness outcomes for females are a widespread phenomenon, but it is premature to claim that sexual conflict is widespread based on data from relatively few taxa. Related to this, no discussion was made by Chapman *et al.* of recent studies showing how females control both their reproductive decisions and the fitness payoffs accrued by them (e.g. [6–10]). By omitting them, readers might not only believe that the dichotomy of sexual conflict and female choice does not exist, but, if it did, that it has been settled in favour of sexual conflict.

References
1 Holland, B. and Rice, W.R. (1997) Chase-away sexual selection: antagonistic seduction versus resistance. *Evolution* 52, 1–7
2 Parker, G.A. (1979) Sexual selection and sexual conflict. In *Sexual Selection and Reproductive Competition in Insects* (Blum, M.S. and Blum, N.A., eds), pp. 123–166, Academic Press
3 Chapman, T. *et al.* (2003) Sexual conflict. *Trends Ecol. Evol.* 18, 41–47
4 Cordero, C. and Eberhard, W.G. (2003) Female choice of sexually antagonistic male adaptations: a critical review of some current research. *J. Evol. Biol.* 16, 1–6
5 Simmons, L.W. (2001) *Sperm Competition and its Evolutionary Consequences in the Insects*, Princeton University Press
6 Edvardsson, M. and Arnqvist, G. (2000) Copulatory courtship and cryptic female choice in the red flour beetles *Tribolium castaneaum*. *Proc. R. Soc. Lond. Ser. B* 267, 559–563
7 Elgar, M.A. *et al.* (2000) Female control of paternity in the sexually cannibalistic spider *Argiope keyserlingi*. *Proc. R. Soc. Lond. Ser. B* 267, 2439–2443
8 Sakaluk, S.K. and Eggert, A-K. (1996) Female control of sperm transfer and intraspecific variation in sperm precedence: antecedents to the evolution of a courtship food gift. *Evolution* 50, 694–703
9 Tallamy, D.W. *et al.* (2002) Male traits under cryptic female choice in the spotted cucumber beetle (Coleoptera: Chrysomelidae). *Behav. Ecol.* 13, 511–518
10 Tallamy, D.W. *et al.* (2003) Copulatory courtship signals male genetic quality in cucumber beetles. *Proc. R. Soc. Lond. Ser. B* 270, 77–82

Letters Response

Response to Eberhard and Cordero, and Córdoba-Aguilar and Contreras-Garduño: sexual conflict and female choice

Tracey Chapman[1], Goran Arnqvist[2], Jenny Bangham[1] and Locke Rowe[3]

[1]Department of Biology, University College London, Darwin Building, Gower Street, London, UK WC1E 6BT
[2]Department of Animal Ecology, Evolutionary Biology Centre, University of Uppsala. Norbyvägen 18d, SE - 752 36 Uppsala, Sweden
[3]Department of Zoology, University of Toronto, 25 Harbord St. Toronto, ON, Canada M5S 3G5

Eberhard and Cordero [1] begin with a claim that, in our recent *TREE* article [2], we are inconsistent in our use of an older, and new narrower definition of sexual conflict. For the former, we quoted the original views of Parker, Trivers, and Dawkins, and we stand by this usage. The 'narrow' definition noted by Eberhard and Cordero was not a definition at all, but rather an attempt to set recent models of sexual conflict into the broader context of sexual selection theory (direct versus indirect selection, and their signs). Córdoba-Aguilar and Contreras-Garduño [3] imply that we ignore difficulties in disentangling sexual conflict from 'traditional models'. In fact, we were clear that the 'boundary, if there is one, between traditional models of sexual selection and sexual conflict has not yet been carefully explored theoretically' [2]. Yet, we believe that there is much to learn along this road, and initial forays

have supported this view. Eberhard and Cordero consider this an overly optimistic viewpoint.

Eberhard and Cordero also appear to distrust the quantitative predictions of theory, citing, for example, conflicting conclusions about the feasibility of early handicap models. Although these conflicts were real, they did not result from an inherent lack of precision, but from differing underlying assumptions. We see little problem here. However, we do see persistent problems arising from errors in the interpretation and application of theory. For example, in spite of 20 years of contrary research, Córdoba-Aguilar and Contreras-Garduño assert that genetic correlations between female preference and preferred traits are only expected under 'traditional female choice'. This statement is false, a fact that is well known [2]. Such correlations result from assortative mating between males and females bearing alleles for the trait and preference. A hunt for such correlations, although destined for success, would be uninformative in

distinguishing between these processes of coevolution. Similarly, both sets of authors suggest that direct fitness costs of manipulative males might be more than offset by benefits accrued through production of manipulative sons. This view echoes the earlier 'sexy son' hypothesis [4], which has neither theoretical nor empirical support (e.g. [5,6]). In the context of sexual conflict, the idea had been already been modeled in the 1970s [5]. More recently, sexy son effects were investigated in a genetic model of sexually antagonistic coevolution [8]. Although costly female resistance easily led to the exaggeration of manipulative male traits, the inclusion of sexy sons had no effect on the equilibrium values of either trait. This result has a long and consistent history [9].

Another form of indirect selection on female preference, the so-called 'good genes' effects, can shift equilibrium values of male and female traits, and has received little attention in analyses of sexually antagonistic coevolution [7,10]. We noted that these indirect effects are likely to occur, but that theory suggests they will be relatively weak [2]. We do agree with Eberhard and Cordero and with Córdoba-Aguilar and Contreras-Garduño that, in the end, their relative strength in nature will only be resolved by experiments, and that more experiments are required. We do not agree that attempts have not been made to assess indirect benefits in those species where direct costs have been assayed. One of us made an initial attempt at such an experiment (in the field) over ten years ago [11], and more recent experiments, by Holland, Rice, and Promislow [12–14], collectively do not make a strong case for substantial good gene effects. Future experiments might do so.

Córdoba-Aguilar and Contreras-Garduño make several claims that puzzle us. For example, in no place did we argue that males usually emerge at the 'forefront' in conflicts, or that males 'take over' the reproductive 'decisions' of females, or that such takeovers give rise to unending coevolution. The closest we came to this was a healthy distance, when we stated that 'neither sex can be said to win a conflict' [2]. Two of Córdoba-Aguilar and Contreras-Garduño's prescriptions – studying female traits influencing fertilization, and mapping traits on phylogenies –are interesting but ill defined at best, and in spite of their claims, both types have been conducted and were cited [2].

Eberhard and Cordero would like to see fitness assays of direct and indirect selection in wild populations. So would we; although we think that this is a tall order given the obstacles that Eberhard and Cordero note in assaying these same effects in the lab. Both sets of authors would also like to see more taxa included in sexual conflict research. We agree and therefore ended our review with 'The taxonomic breadth and range of phenotypic traits that are involved in sexual conflict…remains unclear' [2]. We hope that our optimism will encourage further theoretical analysis and careful empirical work in a diverse array of taxa.

References
1　Eberhard, W.G. and Cordero, C. (2003) Sexual conflict and female choice. *Trends Ecol. Evol.*, 18, doi:10.1016/S0169-5347(03)00180-0
2　Chapman, T. *et al.* (2003) Sexual conflict. *Trends Ecol. Evol.* 18, 41–47
3　Córdoba-Aguilar, A. and Contreras-Garduño, J. (2003) Sexual conflict. *Trends Ecol. Evol.*, 18, doi:10.1016/S0169-5347(03)00182-4
4　Weatherhead, P.J. and Robertson, R.J. (1979) Offspring quality and the polygyny threshold: 'the sexy son hypothesis'. *Am. Nat.* 113, 201–208
5　Kirkpatrick, M. (1985) Evolution of female choice and male parental investment in polygynous species: the demise of the 'sexy son'. *Am. Nat.* 125, 788–810
6　Ligon, J.D. (1999) *The Evolution of Avian Breeding Systems*, Oxford University Press
7　Parker, G.A. (1979) Sexual selection and sexual conflict. In *Sexual Selection and Reproductive Competition in Insects* (Blum, M.S. and Blum, N.B., eds), pp. 123–166, Academic Press
8　Gavrilets, S. *et al.* (2001) The evolution of female mate choice by sexual conflict. *Proc. R. Soc. Lond. Ser. B* 268, 531–539
9　Cameron, E. *et al.* Sexual conflict and indirect benefits. *J. Evol. Biol.* (in press)
10　Kokko, H. *et al.* (2002) The sexual selection continuum. *Proc. R. Soc. Lond. Ser. B* 269, 1333–1340
11　Arnqvist, G. (1989) Multiple mating in a water strider: mutual benefits or intersexual conflict? *Anim. Behav.* 38, 749–756
12　Holland, B. and Rice, W.R. (1999) Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. *Proc. Natl. Acad. Sci. U. S. A.* 96, 5083–5088
13　Promislow, D.E.L. *et al.* (1998) Adult fitness consequences of sexual selection in *Drosophila melanogaster*. *Proc. Natl. Acad. Sci. U. S. A.* 95, 10687–10692
14　Holland, B. (2002) Sexual selection fails to promote adaptation to a new environment. *Evolution* 56, 721–730

Letters

'Big bang' for Tertiary birds?

Gareth J. Dyke

Department of Zoology, University College Dublin, Belfield Dublin 4, Ireland

I enjoyed Feduccia's [1] recent article in *TREE* where he reiterates his hypothesis that the radiation of modern birds (Neornithes) occurred in an 'explosive manner' in the aftermath of the 'Cretaceous–Tertiary (K–T) cataclysm'

[2]. I note, however, that this argument [1,2] is based primarily on counts of the number of fossil neornithine genera, before and after the K–T boundary. Feduccia's 'big bang' hypothesis does not consider the fact that molecular clock studies are becoming increasingly less discordant with the fossil record as both calibration and rate

Corresponding author: Gareth J. Dyke (gareth.dyke@ucd.ie).