

Introduction

Sexual conflict and sex allocation**1. INTRODUCTION**

The year 2009 is very remarkable, being 200 years since the birth of Charles Darwin and 150 years since the publication of *On the origin of species by means of natural selection* (Darwin 1859). The phenomena of sexual conflict and sex allocation, which are the subjects of this special issue of *Biology Letters*, are rooted very firmly in the scientific observations made by Darwin. It is interesting, therefore, to consider what information has become available that has allowed us to extend the initial Darwinian tenets of evolutionary biology into the mature study of conflicts over sexes and sex functions that we have today. There are many technological advances of course that allow ever-greater insights into mechanisms. However, the important advances since the time of Darwin, in terms of understanding evolutionary conflicts of interest, are the incorporation of the mechanism of heredity into evolutionary biology, and the universal explanatory power of taking a gene's eye view of evolution (Hamilton 1964; Dawkins 1976).

It is a mark of the genius of Darwin that he realized when there were general problems that needed to be explained. For example, he noted that the peacock's tail was an example of an obvious 'non-utilitarian' trait, which seemed to decrease survival. This was problematic because it was not obvious how such phenotypes could be favoured under natural selection. The problem was resolved, however, when Darwin had the fundamental insight that non-utilitarian phenotypes could be selected if they increased the mating success of their bearers. This idea formed one of the two major themes of *The descent of man and selection in relation to sex* (Darwin 1871). A similar paradox pertains to the study of sexual conflict: how it is that phenotypes that harm females but benefit males can be selected? The answer comes from adopting, either explicitly or implicitly, a gene-centred view of evolution, a perspective that was first developed in the 1930s by the population geneticists Fisher (1930), Wright (1931) and Haldane (1932). The importance of taking a gene's eye view in the study of behaviour was not realized until the seminal works of Hamilton (1964), Maynard Smith (1964), Trivers (1972, 1985), Dawkins (1976) and Parker (1979), and collectively this research revolutionized the study of social evolution, sex allocation and sexual conflicts. For example, in terms of sexual conflict, it was realized that phenotypes that increase male reproductive success, but at a cost to the current female mating partner,

can be selected because they can lead to more efficient transmission of the genes that control those phenotypes. The conflict is ultimately rooted in the different optima for reproductive processes in males and in females (Parker 1979), or in male versus female function (Charnov 1979). The result is that the evolutionary interests of the sexes or sex functions are often not completely aligned (except under complete and lifetime monogamy). The coevolution between males and females that can result from sexual conflict seems to be a particularly potent evolutionary facilitator, leading to the evolution of reproductive novelty, reproductive isolation and, potentially, speciation.

In this special issue, we bring together contributions on sexual conflict and sex allocation. This brief introduction aims to highlight how each of the contributions expand upon major themes that were first laid out in a series of important works that covered sexual conflicts and sex allocation in non-social and social species with and without separate sexes (Fisher 1930; Trivers 1972, 1985; Benford 1978; Charnov 1979; Parker 1979). I draw together where possible, shared themes to look for commonalities and for emergent properties. The effective integration of the study of sexual conflict and sex allocation adds an extra dimension to our understanding of evolutionary conflicts in general. The hope is that the collection of papers in this special issue may help to facilitate this.

2. IMPORTANT THEMES IN SEXUAL CONFLICT AND SEX ALLOCATION**(a) Sexual, parental and sibling-sibling conflicts**

Trivers (1972) showed the crucial importance of Bateman's (1948) work on the potential differences in the variance in reproductive success for males versus females, with the variance most often being higher for males than for females. This led Trivers (1972) to define a set of conflicts over parental investment. Parker (1979) realized the central importance of this idea with respect to sexual (and other) conflict(s), and constructed game theory models to investigate the outcomes when a sexual selection benefit to the male conveys a cost to the female. As noted by Parker (1979), there are many interesting parallels between conflicts that occur between different parties, and two of the contributions in this special issue provide further examples. A startling example of sibling-sibling sexual conflict is provided by Korsten *et al.* (in press) who show that female red deer with a male twin have a lower birth weight than females born with a female twin. This suggests that active sexual conflict is ongoing during gestation. A new model by Patten & Haig (in press) investigates the sex-specific effects that mothers can have on their offspring, ideas that are prompted by data from behavioural studies showing that there are striking differences in how sons and daughters can be treated by their mothers.

(b) Measurements of costs and benefits

Parker (1979) originally suggested that it might be difficult to measure costs arising from sexual conflict. However, this has not proved to be as difficult as initially thought, and measurements of costs and benefits of adaptations shaped by sexual conflicts are

One contribution to a Special Feature on 'Sexual conflict and sex allocation: evolutionary principles and mechanisms'.

extremely valuable, and can be accurately measured under a wide variety of different environments (Fricke *et al.* in press). What is now realized is that the local environment and individual condition are extremely important in determining the existence, magnitude and sign of sexual conflict costs and benefits (Fricke *et al.* in press). Westneat & Sih (in press) make the useful suggestion that there may also be significant advantages in applying techniques from selection theory to the study of sexual conflict, in order to clarify concepts and integrate conflicts across a wider field of study. As well as studies of the economics of mating interactions, selection experiments and breeding designs can also usefully elucidate sexual conflicts, even in non-model species such as butterflies (Wedell *et al.* in press). In species such as butterflies and moths, there are also potential, and as yet relatively unexplored, parallels to investigate between reproductive (fertilizing) versus non-reproductive (sterile) sperm, and divisions between the germ-line and soma.

(c) Importance of genetic mechanisms and the genetic system on the extent of sexual conflict and conflicts over sex allocation

Parker (1979) showed the importance of the effects of dominance and of allele frequencies on the invasion of sexually antagonistic adaptations. Some of the ways in which this work has been extended are provided in two of the contributions here. Shuker *et al.* (in press) investigate the effect of different genetic systems on sexual conflicts and assess the effect on sexual conflict and sex allocation of biased gene transmission (e.g. loss of one set of parental chromosomes). The influence of the sex chromosome system on the degree of sexual conflict is investigated by Rice *et al.* (in press) in a study that reveals the interesting result that individuals with genomes which do not share the same sex chromosomes may exhibit sibling conflicts. This is effectively an integration of kin structure into the study of sexual conflicts as encouraged by Bourke (in press, see also below). As noted above, there may be interesting synergies and emergent properties from the consideration of conflicts over an ever wider context.

(d) Sexual conflict, coevolution, evolutionary chases and reproductive isolation

The tight coevolution between males and females that can be caused by sexual conflict can result in several types of evolutionary dynamics (Parker 1979). One of these is reproductive isolation and, potentially, speciation. Two contributions investigate this experimentally. Gay *et al.* (in press) test the prediction that under models of sexual conflict, larger rather than smaller population sizes may lead to more rapid reproductive isolation. Hosken *et al.* (in press) illustrate, using data from two experimental evolution studies in flies, that the experimental manipulation of sexual conflict can provide evidence for reproductive isolation in some species but not others. There is therefore as yet no clear picture emerging from the relative importance of sexual conflict in driving speciation versus

intraspecific reproductive diversification, and more studies are required to identify the explanatory factors involved.

(e) Sexual conflict—who wins?

The concepts of which sex ‘wins’ in a conflict, and which sex may have most power to enforce its evolutionary interests was discussed by Parker (1979) for non-social species. This concept has been rooted in the study of social animals for a long time and has been developed further here for the eusocial hymenoptera, the paper by Helanterä & Ratnieks (in press). This work helps to further integrate data from social and non-social species on the fundamental factors that initiate and maintain actual sexual conflicts.

(f) Variance in reproductive success between sex functions in hermaphrodites

Following the ideas of Trivers (1972), Charnov (1979) laid out the potential for sperm competition and for male–female conflicts to play important roles in the evolution of hermaphroditism. Differences in variance between sex functions are also therefore important in species without separate sexes. Schärer & Janicke (in press) nicely extend this approach by examining conflicts over sex allocation between sperm donors and sperm recipients in hermaphrodites, and the importance of post-copulatory sexual selection. Sperm-trading and the influence of conflicts of interest between different hermaphrodite partners are themes that were also tackled by Charnov (1979). These ideas are extended here by Michiels *et al.* (in press), who present an intriguing investigation into the pattern of unilateral male matings, reaching the conclusion that these interactions are driven by conflict rather than cooperation.

(g) Unifying sexual conflicts across social and non-social species

The seminal papers in the field of sexual conflicts did not focus on sexual conflicts in social species. The reason for this is not clear, as conflicts have been, from the start, rigorously defined in a social context. It is clear that there is much work to do to fully integrate sexual conflicts across social and non-social systems. Several of the contributions are fruitful in this respect. For example, the remarkable phenomenon of sex allocation via split sex ratios, where colonies specialize on the production of either female or male sexuals, has usually been explained in terms of kin structure. However, Kümmerli & Keller (in press) show how split sex ratios may be caused by a wider variety of factors and are perhaps, therefore, a more general phenomenon. In social insects, kin structure is well studied and it predicts the existence of conflicts within social groups and also optimal sex ratios. Kin structure is also important because it will affect the strength and incidence of sexual conflict (Bourke in press). However, it has been much less well emphasized outside social species (though see Rice *et al.* in press). For example, sexual conflict will be less likely if there is a high probability of current mating partners meeting again in the future and if

current mating partners are related. Hence, there will be much to gain from the consideration of kin structure across *all* studies of sexual conflict. Schärer & Janicke (in press) also do much to highlight the fact that the links between sex allocation and sexual conflict deserve further study across hermaphrodites and organisms with separate sexes. Similarly, Bedhomme *et al.* (in press) initiate a discussion of the differences in how traits selected under the influence of sexual conflict will behave in hermaphrodites in comparison to plants and animals with separate sexes.

In conclusion, it is clear that a full integration of conflicts over sex and sexes, and of conflicts in general across many levels of organization, will yield significant benefits and will allow emergent properties and contrasts to become evident (Chapman 2006). In this year in which we are celebrating the work of Charles Darwin, who was perhaps the greatest ever synthesizer of ideas from disparate disciplines, we can only hope that he would have thought this to be a worthwhile endeavour.

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Correction

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There was an error in the above paper on page 660, in §2*a*. The fifth sentence in this section should have stated:

‘A startling example of sibling–sibling sexual conflict is provided by [Korsten *et al.* \(2009\)](#) who show that female Soay sheep with a male twin have a lower birth weight than females born with a female twin.’

Korsten, P., Clutton-Brock, T., Pilkington, J. G., Pemberton, J. M. & Kruuk, L. E. B. 2009 Sexual conflict in twins: male co-twins reduce fitness of female Soay sheep. *Biol. Lett.* **5**, 663–666. (doi:10.1098/rsbl.2009.0366)