Opinion piece

Sexual conflict, sex allocation and the genetic system

Decisions over what sex ratio to produce can have far-reaching evolutionary consequences, for both offspring and parents. However, the extent to which males and females come into evolutionary conflict over aspects of sex allocation depends on the genetic system: when genes are passed to the next generation unequally by the two sexes (as in haplodiploidy, for example), this biased transmission can facilitate a range of conflicts not seen in diploids. However, much less attention has been paid to these forms of sexual conflict, not least because it has not always been clear how the conflicts could be realized. Here we consider how biased gene transmission, as expressed in different genetic systems, enhances the opportunity for sex ratio conflict and give empirical examples that confirm that males and females have the opportunity to influence sex ratios.

1. INTRODUCTION

Since Parker (1979), evolutionary biologists have identified numerous sexual conflicts over patterns of mating, parental care and life history (Arnqvist & Rowe 2005). Despite this interest, one reproductive decision has received less attention: sex allocation. Sex allocation describes how resources are partitioned between male and female offspring, including the proportion of each sex produced (the sex ratio, defined here as the proportion of male offspring). For brevity, we will equate sex allocation with sex ratio, although we acknowledge that they may differ, especially if parental investment extends beyond egg provisioning. In this article, we consider the scope for sexual conflict over sex ratio, focusing on the role of different genetic systems and giving empirical examples in which both males and females can influence sex ratios.

2. SEXUAL CONFLICT OVER SEX RATIO

In the classic Düsing–Fisher scenario, frequency-dependent selection acts on sex allocation to equalize the marginal fitness returns of male and female offspring (Charnov 1982; Edwards 2000). In addition, in diploid species, the average reproductive success of males and females has to be the same. Together these two facts have given the impression that sexual

conflict over sex ratio may be rather limited in scope (Arnqvist & Rowe 2005). However, the Düsing–Fisher scenario does not rule out conflict as the fitness consequences of male and female offspring can vary due to either genetics or the environment.

In terms of genetics, in the conventional diploid case at sex ratio equilibrium, mothers and fathers obtain equal fitness through both sons and daughters, and there is no sexual conflict. Under alternative genetic systems, however, the reproductive value of sons and daughters can differ markedly for mothers and fathers (Trivers & Hare 1976). For instance, in haplodiploids, genes in fathers are only transmitted through daughters, with sons being of no reproductive value to males. Females, on the other hand, gain fitness benefits through both sons and daughters, setting the scene for possible conflicts over sex ratio. Although the most familiar non-diploid organisms are the haplodiploid Hymenoptera (ants, bees and wasps), haplodiploid and related systems are found in more than 15 per cent of animal species, including among thrips, beetles, scale insects and mites (Hedrick & Parker 1997). These 'asymmetric' genetic systems are therefore non-trivial.

The classic scenario can also mislead because of environmental effects on offspring fitness, for instance, if selection favours being a member of the rarer sex (Trivers 1974; Pen 2006), or if the fitnesses of sons and daughters are condition dependent (Trivers & Willard 1973). These environmental effects initiate conflicts between parents and offspring over sex allocation, and it is known that selection on sex ratio depends on whether parents or offspring are in 'control' (Trivers & Hare 1976). However, condition-dependent fitness differences between male and female offspring can also create sexual conflict, and offspring that manipulate the sex ratio to their advantage will be selected (making sex ratio a conflict trait for broodmates of the opposite sexes). In these situations, conflict can arise under diploidy as well as under other systems, although the extent of the conflict (the difference in sex ratio optima) may be smaller in diploids (see Wild & West 2009 for a thorough treatment). Genes and the environment can shape the conflict together of course, for instance if a species' ecology influences the mating system and pattern of inbreeding (potentially selecting for biased sex ratios: Hamilton 1967; Charnov 1982). The degree of male–female conflict will then depend on the extent and direction of any sex ratio bias and what this means for maternal and paternal gene transmission.

To summarize, we can consider sexual conflict over sex ratio to occur in two broad categories. First, there may be male–female parental conflict over the sex ratio, with changes in sex ratio leading to changes in the transmission of paternal or maternal genes. This category will be intimately associated with the genetic system and typically occur outside diploids. Second, male–female conflict may be a consequence of the sex an individual has been assigned and the sex ratio of the brood it is in. Changes in sex ratio lead to changes in the reproductive advantages of being male or female, and traits that lead to the manipulation of the sex ratio by offspring can be favoured. This means that there will often be an intimate relationship between sexual conflict and other genetic conflicts

(parent–offspring and sibling rivalry) when it comes to sex allocation. Again, these conflicts are more likely to be apparent outside diploids.

However, for potential conflicts to become actual conflicts, both males and females must be able to influence sex ratio (Beekman & Ratnieks 2003). While this is often assumed to be true for females, the opportunities are less intuitively clear for males (Werren & Beukeboom 1998). Our brief empirical sketch of the possible scope for sexual conflict over sex ratio will therefore focus on what evidence we have of male effects on sex ratio.

3. PARENTAL CONFLICT OVER SEX RATIO

Genetic conflict over sex ratio has been best studied in the social Hymenoptera. The relatedness asymmetries generated by haplodiploidy in social insect colonies are well known to affect the optimal sex ratios for different colony members (Sundström & Boomsma 2001). Since brood production is predominantly shaped by interactions between workers and queens, it has been assumed that males as fathers have little opportunity to influence sex ratio and increase daughter production. However, there is evidence that in multiply mated species, males deliberately try to 'clump' their sperm together. This sperm clumping inside a queen means that cohorts of brood are singly fathered, keeping the relatedness asymmetry high between male and female brood, which in turn favours the production of female-biased sex ratios (Boomsma 1996). Males could also promote a high relatedness asymmetry in the brood by avoiding non-virgin females, reinforcing any other selection for male choice of virgin queens. Mechanisms by which males influence sex ratio may be even more indirect however. For instance, in the mud-daubing wasp *Trypoxylon politum*, males that guard the nest end up with more daughters (Brockmann & Grafen 1989). This is not due to direct manipulation, but rather nest-guarding enables females to invest more time in foraging and so provision more female brood (the costlier sex). Males guard nests in order to copulate, but they also indirectly decrease the sex ratio, increasing their genetic success. The costs to fathers of male production may not just be associated with the missed opportunity to sire a daughter however in autoparasitoid wasps such as *Encarsia*, females develop on 'normal' (whitefly) hosts, whereas males can hyperparasitize the female larvae of their own species (Hunter & Woolley 2001). This means that not only do male offspring fail to pass on paternal genes, but their development destroys paternal genes that manage to make it into daughters.

For Hymenoptera, since sex determination is via egg fertilization (Heimpel & de Boer 2008), the key process for sex ratio control is sperm usage during oviposition. Can males influence this? One possibility is via seminal proteins. Although the effects of seminal proteins on female reproductive physiology are mostly known from *Drosophila* (Wolfner 2002), there is some evidence for the action of seminal fluid on females in *Bombus* bumblebees (Baer *et al.* 2001). Seminal fluid could affect the sex ratio by increasing the 'leakiness' of the female's spermatheca, increasing the

fertilization rate. Suggestive (but by no means conclusive) evidence of a male effect on fertilization rate comes from the work by Shuker *et al.* (2006) on the parasitoid wasp *Nasonia vitripennis*. They showed that variation in sex ratio varied with the genotype of the inseminating male, in a study that attempted to exclude effects of sperm limitation or gametic incompatibility. Moreover, sperm competition adaptations in haplodiploids that improve the likelihood that sperm is preferentially used could also be favoured if they generally increase the sperm usage (and daughter production), regardless of sperm competition. In the parasitoid wasp *Dinarmus basalis*, Chevrier & Bressac (2002) showed that multiply mated females laid a greater proportion of daughters, which could result from male attempts to influence sperm usage (or, more prosaically, from multiply mated females avoiding sperm limitation).

Resolving the extent to which selection has acted on males to influence sex ratio may not be straightforward in Hymenoptera, as variation among males in sperm quality or quantity may give the appearance of male control, since females need sperm to produce daughters (but not sons). However, a different group of insects may offer more opportunities to test the role of sexual conflict over sex ratio. Scale insects exhibit an array of genetic systems, including haplodiploidy and paternal genome elimination (PGE) (Gullan & Kosztarab 1997). The mealybug *Planococcus citri* exemplifies the scope for conflict. It has PGE whereby in males the paternally inherited chromosomes are condensed via DNA heterochromatinization and, while present but untranscribed in somatic tissues, these chromosomes are lost during meiosis in the germ line (Nur 1980). Male offspring are a dead-end for paternal chromosomes, and selection would favour males that either managed to subvert the destruction of their chromosomes in prospective sons or induced females into producing more daughters (as in haplodiploids). In terms of mechanisms, the role of genomic imprinting may be crucial. Scale insects boast widespread genomic imprinting, and imprinting of the paternal chromosomes underpins PGE and sex determination (Buglia & Ferraro 2004; Normark 2006). Paternal chromosomes that could hide their origin when transmitted would be at a selective advantage. Intriguingly, in *P. citri*, the one place genomic silencing of paternal chromosome has failed is in the male germ tissue, suggesting that paternally inherited genes may still have the ability to influence the fate of paternal chromosomes in the germ line.

That paternal chromosomes may sometimes 'escape' destruction and be transmitted to the offspring forms the basis of Herrick & Seger's (1999) hypothesis for the evolution of the various forms of PGE in scale insects, with males and females selected to control the fate of chromosomes trying to enter the germ line. This hypothesis highlights that conflict may not only be facilitated by alternative genetic systems, but may also drive the evolution of those genetic systems. For example, females able to exclude male gametes from some of their offspring gain an immediate transmission advantage, favouring the evolution of haplodiploidy and systems such as PGE (Bull 1979).

4. CONFLICT BETWEEN MALE AND FEMALE BROOD

The relatedness asymmetry generated by haplodiploidy means that in social Hymenoptera colonies, female workers are more related to their sisters than their brothers (the basis of the queen–worker conflict), and brood sex ratio manipulation by the destruction of male brood by their (worker) sisters has been well documented (Ratnieks & Boomsma 1995). While this can be interpreted in terms of parent–offspring conflict over sex ratio, this is also a sexual conflict between the male and female brood themselves, arising as a consequence of the queen's pattern of sex allocation. A similar conflict arises in some species of polyembryonic wasp in which sex ratio is controlled by the offspring, both through embryonic proliferation and the production of (female) soldier larvae that preferentially kill males (Gardner *et al.* 2007). Male larvae have also been known to kill female larvae though, for instance in the bee *Trigona postica* (Beig 1972), and it is perhaps likely that more such conflicts will be uncovered, perhaps among gregarious parasitoids with asymmetric larval competition (Sykes *et al.* 2007).

5. CONCLUSIONS

Some genetic systems may be more predisposed to sexual conflict over sex ratio than others, given the links between sex ratio and gene transmission. Males cannot be assumed to be passive players in sex allocation, although as yet we have little more than an idiosyncratic collection of interesting items of biology, rather than a compelling body of empirical work. One of the main challenges will be that the boundaries between traditional conflicts such as parent–offspring, sibling and sexual conflicts may often be blurred. However, resolving how these forces interact will give us a much clearer picture of the evolutionary importance of genetic conflict, both in terms of sex allocation and more generally.

David M. Shuker[1,*], Anna M. Moynihan[1]
and Laura Ross[2]
[1]*School of Biology, University of St Andrews, Harold Mitchell Building, St Andrews, Fife KY16 9TH, UK*
[2]*Center for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands*
*david.shuker@st-andrews.ac.uk.

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