Opinion piece

Sex allocation conflict in insect societies: who wins?

Sex allocation in colonies of eusocial Hymenoptera is one of the best studied social conflicts. We outline a framework for analysing conflict outcome through power and the costs of manipulation and suggest that the conflict will often be unresolved because both major parties of interest, the queen and the workers, should manipulate allocation even at considerable costs to the colony. We suggest future work for analysing power in the conflict between queen and workers over sex allocation and discuss the extent of male power.

Keywords: social insects; kin selection; sex allocation; conflict; sexual conflict; power

1. INTRODUCTION

Non-clonal social groups are subject to reproductive conflict among group members (Ratnieks *et al.* 2006). Sex allocation in eusocial Hymenoptera is a conflict where the selective basis and behavioural mechanisms have been extensively studied. Haplodiploidy leads to sex allocation conflicts between and within sexes and generations and within genomes of individuals (table 1). We present a framework for analysing conflict outcome through comparative and experimental work. The framework is based on power, i.e. the ability of different parties to act towards their inclusive fitness interests, specifically the benefit of exerting power in terms of manipulating sex allocation versus the cost on the reproductive performance of the colony. We also discuss power in sex allocation conflicts between mating partners.

2. POTENTIAL AND ACTUAL CONFLICT

Due to arrhenotoky, where males develop from haploid unfertilized eggs and females from diploid fertilized ones, workers are related to full sisters by three-quarters but to brothers by one-quarter. In an outbred population, where each colony has a single queen that has mated with one male, this leads to a 3F:1M worker optimum investment ratio. The queen, who is equally related (one-half) to both sexes of offspring, favours a 1F:1M ratio (Trivers & Hare 1976). Multiple mating by the queen, worker production of males and polygyny reduce potential conflict between queen and workers as these cause the worker optimum to converge on the queen optimum of 1F:1M (Ratnieks *et al.* 2006).

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Both parties have means to bias sex allocation towards their inclusive fitness optima. Queens coerce workers into increased male rearing by limiting the number of female eggs (Passera *et al.* 2001; Rosset & Chapuisat 2006) or by laying female eggs that can be reared into workers only (de Menten *et al.* 2005). Workers increase female bias by redirecting resources from male brood to females (Sundström *et al.* 1996) or by biasing the development of females into queens instead of workers (Hammond *et al.* 2002).

Sex allocation of colonies may vary around the population mean according to variation in queen mating frequency, queen number, colony size, resource levels and local competition over resources or mating partners (Bourke & Franks 1995; Kümmerli & Keller *in press*). In addition to these colony-level factors, which influence the optima of different parties, an additional major factor affecting sex allocation, at both colony and population levels, is whether the queen(s) or workers have power (Beekman & Ratnieks 2003; Kümmerli & Keller *in press*). While power in the conflict between mating partners is not well understood (Parker 2006), power over sex allocation in hymenopterian societies can be linked to measurable factors. Power as a conflict determinant is not a new idea, but empirical work has concentrated on explaining patterns in single species. We focus on testable predictions for comparative and experimental work. Our framework is based on costs and benefits, factors that have been difficult to quantify and test in kin selection studies.

3. WHAT DETERMINES POWER?

Population-wide sex allocation in social Hymenoptera is generally female biased (Bourke & Franks 1995; Ratnieks *et al.* 2006) which suggests at least partial worker control. However, there are strong reasons to expect mixed control. First, both parties have means to manipulate allocation, as described above. Second, sex allocation conflict may often not be resolved (*sensu* Ratnieks *et al.* 2006) to a level where colony costs are small (Ratnieks *et al.* 2006). This is because the benefit to one party in biasing allocation increases as the population-wide sex allocation ratio moves away from their optimum. The more a party is losing, the greater the incentive to fight back, and the colony-level cost that is worthwhile to cause in biasing sex ratio towards the optima (figure 1; Reuter & Keller 2001; Ratnieks *et al.* 2006).

The key to power is the degree of bias achieved for a given cost to the colony (figure 1). Importantly, for future research, the costs of manipulation can be linked to measurable factors (table 2; box 1 in the electronic supplementary material). A key consideration is how much the future loss of workers (i.e. rearing of queens instead of workers) decreases colony survival and productivity (Reuter *et al.* 2004). Factors such as large number of workers and large queen–worker dimorphism should increase the power of workers to invest into queens at little cost to the colony (table 2). Queen power is increased, for example, if sexuals are reared in a specific cohort so the queen can limit the availability of female eggs to rear into queens without limiting the number of female eggs available to rear into workers at other times.

Figure 1. Sex allocation conflict and the interests of males, females and workers. At the worker optimum sex-allocation ratio (3F:1M), the mother queen (solid line) can enhance her inclusive fitness if she manipulates colony reproduction to rear an extra unit of males, provided that this costs less than three units of females. The situation is reversed at the queen-optimum sex-allocation ratio (1F:1M). Here, workers (dashed line) can enhance their inclusive fitness by manipulating colony reproduction to trade off three or less units of allocation to males to one unit of queens. As male mates (dotted line) of the queen are unrelated to young males, they are selected to bias allocation towards females (1F:0M) at all population sex ratios even if this causes considerable costs to colony reproduction. The more a party loses control of the sex allocation, the greater is its incentive to fight back, and the greater the costs that may be caused.

Table 1. Sex allocation optima for different parties of interest in a haplodiploid insect society, for the situation in which young males and queens are offspring of a single mother queen mated to a single unrelated male.

party of interest within colony	optimum allocation to young queens (%)
queen (mother)	50
male (father)	100
daughter workers (female offspring)	75
male (male offspring of queen)	50
patrigenes ^a in female offspring	100
matrigenes ^b in female offspring	50

^aPatrigene = a gene inherited from the father.

^bMatrigene = a gene inherited from the mother.

There are two kinds of factors underlying power. First, several factors, such as queen–worker dimorphism, vary between species and it is unreasonable to assume a facultatively varying response within a species. Such factors are unsuitable for experimental study but appropriate for comparative analyses. Comparative analyses can provide information on how kin structure and other factors affect sex allocation. We predict the variation around the trend predicted by kin structure should be largely determined by the power factors in table 2. Second, there are factors to which a facultative response may occur, such as colony size, and which can be manipulated experimentally or studied using natural variation within species (table 2).

Comparative and experimental work needs to be complemented by theoretical modelling of conflict

outcome based on power, and the costs parties are prepared to inflict (table 2). Theory should also take into account other reproductive conflicts, such as conflict over caste fate, allocation into sexuals versus workers (Reuter & Keller 2001), worker reproduction and policing (box 1 in the electronic supplementary material; Foster & Ratnieks 2001) and competition between multiple queens (box 1 in the electronic supplementary material; Fournier *et al.* 2003). The models should also consider the information different parties base their decisions on (Pen & Taylor 2005; Ratnieks *et al.* 2007).

4. MALE INTERESTS OVER SEX ALLOCATION

Haplodiploidy also creates male–female conflict over sex allocation (table 1). The queen's mate(s) are selected to favour extreme female allocation since young males carry no paternal genes. But do males have any power to do this? When allocation decisions are made, the males are only present as sperm in the queen's spermatheca and lack direct power to influence colony decisions (but see Sundström & Boomsma 2000). However, the methylation machinery that can potentially imprint genes according to their parental origin suggests a mechanism for father power (Kronforst *et al.* 2008). Paternally derived genes in workers and developing females share the interests of their father. They are predicted to favour worker–brood and brood–brood interactions that increase female bias (Queller 2003). Because fathers favour 1F:0M investment, imprinted genes that harm colony productivity considerably may be

Table 2. Factors affecting the balance of power between queen and workers over sex allocation, evidence and suggestions for empirical tests.

	evidence/predictions
<i>queen power increases if</i> the queen is able to bias the caste fate of eggs	queens of <i>Pheidole pallidula</i> are able to bias the caste fate of female eggs through juvenile hormones. Monogynous colonies where caste fate of eggs is limited produce a male-biased sex ratio, and population allocation is between queen and worker optima (de Menten <i>et al.</i> 2005). Comparative analyses should look for a correlation between less female bias and early caste determination of brood, which presumably reflects queen power to limit caste fate
sexuials are reared in a distinct cohort	species, populations or colonies with distinct workers and sexual cohorts should have more queen control and less female bias (Pamilo 1982) when compared with those where females of both castes are reared at the same time
workers are not rearing the brood	slave-making ants have allocation ratios closer to the queen optimum than free-living species (Bourke 1989; Herbers & Stuart 1998). Comparative work should look for more female bias in free-living species, compared with their socially parasitic, inquiline or slave-making relatives. In facultative slave makers, sex ratios should be more female biased in free living populations or colonies
workers cannot lay male eggs	species where workers have lost functional ovaries may have more queen control because the workers cannot respond by laying male eggs if the queen limits the availability of diploid eggs. The best support for queen control of sex ratios comes from <i>Solenopsis</i> and <i>Pheidole</i> where workers are sterile (Helms 1999; Passera <i>et al.</i> 2001). A comparative test should look for a relationship between worker fertility and female bias across species
<i>worker power increases if</i> the number of female eggs is not limiting	workers in colonies with queens that limit number of female eggs produce less females than the worker optimum in <i>Formica selysi</i> (Rosset & Chapuisat 2006) and <i>Solenopsis invicta</i> (Passera <i>et al.</i> 2001). Adding diploid eggs to colonies of <i>Pheidole desertorum</i> increases female allocation (Helms <i>et al.</i> 2000). Furthermore, if resource levels are low, and not all eggs can be reared, worker power increases, because egg number is not limiting anymore (Reuter <i>et al.</i> 2004). Experimental tests should look for increase in female bias as an effect of decrease in resource levels
workers have good information on sex of the brood	early expression of sex specific cues should correlate with worker power and female bias (Nonacs & Carlin 1990). Mass provisioning may decrease worker power. For example, in stingless bees, the queen may have good abilities to prevent the under rearing of males because all broods are reared in sealed cells and the males are reared in identical cells to workers. Comparative work should look for a positive correlation between female bias and progressive provisioning
workers have good information on kin structure	diversity of genetically determined cues in a colony should correlate with worker power to optimize sex allocation (Boomsma <i>et al.</i> 2003). This means that singly mated queens lose since workers in their colonies will produce a female biased brood
productivity returns of worker number are diminishing	colonies at a maximum size should have female biased allocation (Reuter <i>et al.</i> 2004). An experimental increase in worker numbers in colonies should result in increase in female bias
a lot of resources can be invested in a single queen	large size of queens compared with workers should correlate with female biased investment (Reuter & Keller 2001). Comparative work should look for a correlation between female bias and queen–worker size dimorphism
queen number increases	other things being equal, workers should have more power in colonies with multiple unrelated queens compared with monogynous colonies (box 1 in the electronic supplementary material; Fournier <i>et al.</i> 2003), and in species where there are multiple unrelated queens compared with monogynous species where the queen limits number of diploid eggs
resource recycling is efficient	workers of carnivorous species, such as some ants, should have increased power compared to non-carnivorous species such as bees. This is because if male larvae are culled, the resources invested in them are in a more readily available form for species with a carnivorous diet

selected for (figure 1). However, maternally imprinted genes are selected to counteract this, and if the female bias is higher than 3F:1M, so are any unimprinted genes. Availability of genomic data makes imprinting a promising area for future research. First, differences between male and female gametes in methylation of genes potentially involved in brood interactions would strongly support the conflict theory of genomic imprinting (Queller 2003), especially if combined

with caste-specific gene expression data (Kronauer 2008). Second, intragenomic conflicts may lead to an ‘arms race’ between different parties, and ‘signatures of selection’ in the gene sequences would be strong evidence of conflict (Summers & Crespi 2005). Third, evolutionary arms races resulting from imprinting play a role in speciation (Coleman *et al.* 2009) and suggest a role for reproductive conflict as a driver of social insect diversity.

Sex allocation conflict between sexes also affects the conflict over female mating frequency. As in non-eusocial animals, a male benefits from being the only sire of the female's offspring. This benefit may be even stronger in haplodiploid social insects because colonies headed by multiple-mated queens allocate more to males that carry no paternal genes, to the benefit of the mother queen (Sundström & Ratnieks 1998). Males of eusocial Hymenoptera may thus benefit doubly from traits that decrease re-mating, such as mating plugs and harming the female (Wigby *et al.* 2004; Parker 2006). In social insects, a male that has mated with a multiple-mated female potentially faces very low fitness, and harming to prevent re-mating could be favoured even at extreme costs to the colony. Also the conflict over mating frequency is shown to drive speciation through coevolutionary arms races (Arnqvist *et al.* 2000), and the extreme conflict between male and female interests in social Hymenoptera suggests that this may be worth special attention in future studies.

5. CONCLUSION

Sex allocation is an area where the optima and constraints to adaptation are well understood (West & Sheldon 2002). The study of sex allocation conflict in eusocial Hymenoptera, where by definition at least one of the parties will not achieve its optimum, is an important area within this. Power relations, especially the costs and benefits of manipulating colony sex allocation as influenced by the idiosyncrasies of natural history among different taxa, are crucial for understanding which party of interest is expected to win in a conflict situation.

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