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. Haploidy 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 arrenotoky, 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).

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; Kümmel & 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; Kümmel & Keller in press). While power in the conflict between mating partners is not well understood (Parker 2006), power over sex allocation in hymenopteran 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.


One contribution of 16 to a Special Feature on ‘Sexual conflict and sex allocation: evolutionary principles and mechanisms’.

Received 24 June 2009
Accepted 13 July 2009
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 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.

<table>
<thead>
<tr>
<th>party of interest within colony</th>
<th>optimum allocation to young queens (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>queen (mother)</td>
<td>50</td>
</tr>
<tr>
<td>male (father)</td>
<td>100</td>
</tr>
<tr>
<td>daughter workers (female offspring)</td>
<td>75</td>
</tr>
<tr>
<td>male (male offspring of queen)</td>
<td>50</td>
</tr>
<tr>
<td>patrigenes&lt;sup&gt;a&lt;/sup&gt; in female offspring</td>
<td>100</td>
</tr>
<tr>
<td>matrigenes&lt;sup&gt;b&lt;/sup&gt; in female offspring</td>
<td>50</td>
</tr>
</tbody>
</table>

<sup>a</sup>Patrigene = a gene inherited from the father.

<sup>b</sup>Matrigene = a gene inherited from the mother.
Table 2. Factors affecting the balance of power between queen and workers over sex allocation, evidence and suggestions for empirical tests.

<table>
<thead>
<tr>
<th>Evidence/Predictions</th>
<th>Examples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Queen power increases if the queen is able to bias the caste fate of eggs.</td>
<td>Queens of <em>Pheidole pallidula</em> 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 et al. 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.</td>
</tr>
<tr>
<td>Sexuals are reared in a distinct cohort.</td>
<td>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.</td>
</tr>
<tr>
<td>Workers are not rearing the brood.</td>
<td>Slave-making ants have allocation ratios closer to the queen optimum than free-living species (Bourke 1989; Herbers &amp; 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.</td>
</tr>
<tr>
<td>Workers cannot lay male eggs.</td>
<td>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 <em>Solenopsis</em> and <em>Pheidole</em> where workers are sterile (Helms 1999; Passera et al. 2001). A comparative test should look for a relationship between worker fertility and female bias across species.</td>
</tr>
<tr>
<td>Worker power increases if the number of female eggs is not limiting.</td>
<td>Workers in colonies with queens that limit number of female eggs produce less females than the worker optimum in <em>Fornica selysi</em> (Rosset &amp; Chapuisat 2006) and <em>Solenopsis invicta</em> (Passera et al. 2001). Adding diploid eggs to colonies of <em>Pheidole desertorum</em> increases female allocation (Helms et al. 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 et al. 2004). Experimental tests should look for increase in female bias as an effect of decrease in resource levels.</td>
</tr>
<tr>
<td>Workers have good information on sex of the brood.</td>
<td>Early expression of sex specific cues should correlate with worker power and female bias (Nonacs &amp; 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.</td>
</tr>
<tr>
<td>Workers have good information on kin structure.</td>
<td>Diversity of genetically determined cues in a colony should correlate with worker power to optimize sex allocation (Boomsma et al. 2003). This means that singly mated queens lose since workers in their colonies will produce a female biased brood.</td>
</tr>
<tr>
<td>Productivity returns of worker number are diminishing.</td>
<td>Colonies at a maximum size should have female biased allocation (Reuter et al. 2004). An experimental increase in worker numbers in colonies should result in increase in female bias.</td>
</tr>
<tr>
<td>A lot of resources can be invested in a single queen.</td>
<td>Large size of queens compared with workers should correlate with female biased investment (Reuter &amp; Keller 2001). Comparative work should look for a correlation between female bias and queen–worker size dimorphism.</td>
</tr>
<tr>
<td>Queen number increases</td>
<td>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 et al. 2003), and in species where there are multiple unrelated queens compared with monogynous species where the queen limits number of diploid eggs.</td>
</tr>
<tr>
<td>Resource recycling is efficient</td>
<td>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.</td>
</tr>
</tbody>
</table>

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 (Arnvist 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.

We thank Tracey Chapman for the invitation and comments, and the anonymous referees for comments. H.H. was funded by the Academy of Finland (121078).

Heikki Helanterä1,2,* and Francis L. W. Ratnieks1
1Laboratory of Apiculture and Social Insects, Department of Biological and Environmental Science, University of Sussex, Palmer, Brighton BN1 9QG, UK
2Department of Biological and Environmental Sciences, PO Box 65, University of Helsinki, FI-00014 Helsinki, Finland
*heikki.helantera@helsinki.fi.


Kümmerli, R. & Keller, L. In press. Patterns of split sex ratio in ants have multiple evolutionary causes based on different within-colony conflicts. Biol. Lett.


