Heredity **86** (2001) 515–521 *Received 10 January 2001, accepted 19 February 2001*

SHORT REVIEW

Conflicts and alliances in insect families

L. SUNDSTRÖM*† & J. J. BOOMSMA‡

†University of Helsinki, Department of Ecology and Systematics, PO Box 17, FIN 00014 Helsinki, Finland and ‡University of Copenhagen, Institute of Zoology, Universitets Parkon 15, DK-2100, Copenhagen, Denmark

Hamilton's principle of inclusive fitness implies that reproductive altruism can evolve, because individuals can pass on genes not only through their own offspring, but also through the offspring of their relatives. Social insects are spectacular examples of how some individuals may be selected to forgo reproduction and instead help others reproduce. Social Hymenoptera are also special because relatedness patterns within families can be asymmetrical, so that optimal sex-ratios, preferred male parentage or preferred mating frequencies become objects of reproductive conflict. The now extensive inclusive fitness theory provides precise qualitative predictions with respect to the emergence of such conflicts. Recent advances in the power of genetic markers applied to resolve family structure in insect societies have brought about a series of studies that have tested these predictions. In support of kin selection as a major evolutionary force, the results suggest that workers frequently control sex allocation. However, the very establishment of such worker control has made new conflicts come to light, between mothers and fathers and between adult individuals and brood. Evidence for these conflicts is only just beginning to be gathered. Recent studies tend to include issues such as 'information' and 'power' (i.e. the ability to perceive signals and the opportunity to act upon this information), and to address selection for selfishness at the individual level with costs of social disruption at the colony level.

Keywords: conflicts, kin selection, male parentage, relatedness, sex ratio, social insects.

Introduction

Much of the ecological success of social insects has been attributed to their mode of life in which some individuals specialize in reproduction, whereas others engage in rearing offspring of nestmates. The emergence of insect sociality represents one of the latest of the major transitions in evolution (*sensu* Maynard Smith & Szathmáry, 1995) and has provided some of the most impressive examples of altruism and cooperation.

The forgoing of direct reproduction in favour of helping others reproduce poses a major evolutionary enigma: how can natural selection, a process based on propagating genes to future generations, produce individuals that never reproduce? Hamilton's (1964) principle of inclusive fitness provides a way out of this dilemma, as it proves that individuals can gain indirect fitness through the sons and daughters of their relatives. Indeed, the members of most social insect colonies are related so that social life can be favoured and maintained through kin selection (Bourke & Franks, 1995; Crozier & Pamilo, 1996).

However, life in societies also entails conflicts because individuals within a colony are not genetically identical. The merit of inclusive fitness theory is that it allows accurate quantitative predictions of reproductive conflicts that can be subjected to empirical testing in the field and the laboratory. A major challenge in modern inclusive fitness thinking is to understand how reproductive disputes are settled without loss of social cohesion (Keller, 1999; Keller & Chapuisat, 1999). Here we review a set of conflicts that arise in colonies of social insects and discuss some of the mechanisms underlying their resolution. For simplicity, we will focus on fairly simple family structures where colonies have a single queen, which may have mated with one or several males.

The sources of conflicts

Potential conflicts arise in all organisms where interacting units are genetically different. A key example is the conflict between parents and offspring over parental investment in present vs. future offspring (Trivers, 1974; Clutton-Brock, 1991), a conflict that ultimately stems from the different fitness interests of the investing mother and her present and future mates. Insects of the order Hymenoptera represent a special case, because offspring usually remain as permanent helpers in the mother's nest and are asymmetrically related to their female and male siblings. In Hymenoptera, females develop from fertilized diploid eggs and males from unfertilized haploid eggs, so full sisters are more closely related to each other (75%) than to their brothers (25%), but equally related to their offspring (50%). This difference in relatedness to sisters vs. brothers, expressed either as a ratio or a proportion, is often referred to as the relatedness asymmetry of workers. Furthermore, males only transfer genes to daughters and therefore have no sons. Finally, females are more closely related to their nephews than to their brothers (Fig. 1a). These relatedness asymmetries induce different fitness returns per unit investment and as a result conflicts over brood composition may arise among

---

*Correspondence. E-mail: liselotte.sundstrom@helsinki.fi

family members. Such a rich variation in relatedness incentives provides one of the most fruitful model systems to test predictions emanating from Hamilton's rule. Recent ramifications of kinship theory have further extended predictions and tests into previously unexplored areas such as sexual selection and mate choice in ants, bees and wasps (Queller, 1993; Ratnieks & Boomsma, 1995; Boomsma, 1996).

Classes of conflicts

Conflicts over sex ratio

By combining Fisherian sex ratio theory and Hamiltonian kin selection theory, Trivers & Hare (1976) predicted a sex allocation conflict between Hymenopteran queens and their daughter workers. This now classical prediction holds that under monogyny (single queen per colony) and monandry (single mating by queens) workers, who are all females, should prefer a threefold investment in females compared to males, whereas the optimum of the mother queen would be an equal investment in the sexes. A further prediction is that the worker and queen optima converge when queens mate with many males, because the degree of relatedness asymmetry then approaches one (Fig. 1). This implies that queens may be under selection to mate multiply if conflicts with their workers are costly and provided that benefits of facultative sex ratio biasing by workers are real (see below) (Queller, 1993; Ratnieks & Boomsma, 1995).

Further theoretical developments have extended this population-wide prediction to account for the commonly observed within-population sex-ratio specialization among colonies (Nonacs, 1986). When colony kin structure varies within populations, split sex ratio theory holds that colonies with a relatedness asymmetry above the average relatedness asymmetry in the population should specialize in female production, whereas those with a relatedness asymmetry below the population average should specialize in male production (Boomsma & Grafen, 1990, 1991). Such within-population variation in relatedness asymmetry arises if the mating frequency of queens varies across colonies (Fig. 1b). When

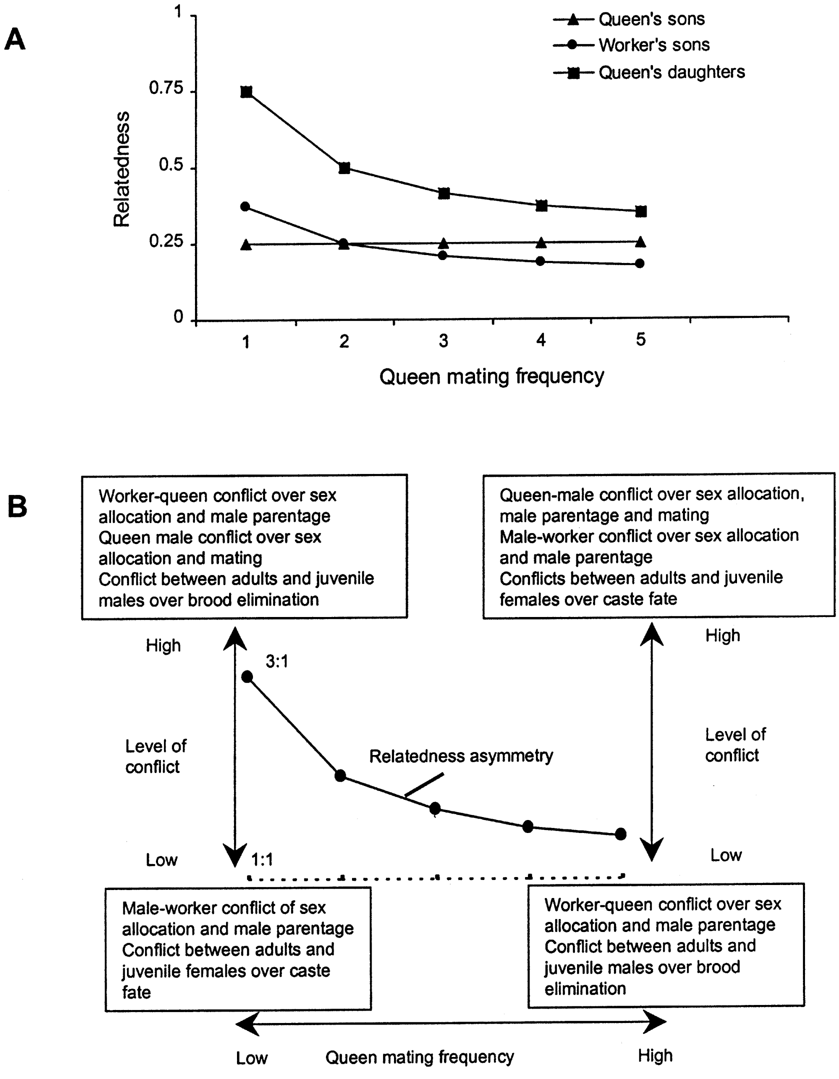

Fig. 1 Relatedness asymmetry and its consequences. A. The relatedness between workers and different categories of brood as a function of queen mating frequency. B. Types of conflict as a function of queen mating frequency and relatedness asymmetry within colonies. The vertical location of the boxes indicates the level of conflict between classes of individuals, whereas the horizontal location of boxes indicates the effect of queen mating frequency. The graph also shows how relatedness asymmetry approaches 1:1 (indicated by the dotted line) when queen mating frequency increases to high values.

workers are able to assess the kin structure of their colony and realize split sex ratios, this conflict between workers and queens is maximal in colonies headed by singly mated queens, and weak or nonexistent in colonies headed by multiply mated queens (Boomsma & Grafen, 1990, 1991).

Conflicts over male parentage

In many species of social insects workers are able to lay unfertilized haploid eggs that develop into males (Bourke & Franks, 1995). When this happens, queens lose fitness because grandsons are raised instead of sons. As a collective, workers may either agree or disagree on male parentage. Assuming no costs to worker reproduction, the trait is favoured at queen-mating frequencies below two, whereas workers are expected to remove (i.e. police) each other's eggs at mating frequencies above two (Ratnieks, 1988). Hence, as relatedness asymmetries decline, the collective interests of the workers come to coincide with that of the queen, and the worker–queen conflict over male parentage disappears (Fig. 1b). However, as an individual, each worker still favours her own sons over anybody else's sons, so that the worker–queen conflict is in fact replaced by a conflict among workers.

Also the conflict over male parentage can be differentially expressed when queen mating frequency varies within populations. A formal model for facultative worker policing has not been developed, but recent evidence indicates that the phenomenon probably follows similar rules as facultative sex allocation (see below).

Alliances across generations and genomes

Sex ratio biasing by workers also affects the fitness of colony fathers because males can only pass on genes through reproductive daughters. Hence, when workers facultatively female-bias colony sex ratios in response to queen mating frequency, they enhance the fitness of their father at the expense of the fitness of their mother (Boomsma, 1996). Conversely, when workers male-bias sex ratios in colonies headed by a multiply mated queen, the males that co-sire a colony may face a very low or zero fitness. In other words, the workers are the sex ratio allies of their joint father when their mother is singly mated, but they become the sex ratio allies of their joint mother when paternity is divided (Fig. 1b) (Boomsma, 1996). Thus the worker–queen conflict over sex allocation ultimately turns into a queen–male conflict over mating and insemination. Male parentage also matters for colony fathers, because they pass on their genes through males produced by their daughter workers but not through males produced by their mate. Thus, males favour single mating by queens, because they attain monopoly on paternity of daughters and maximize the chance that the colony raises worker-derived males.

Social Hymenoptera have several vertically transmitted symbionts. Leafcutter ants rear fungi, *Wolbachia* bacteria occur in most taxa (Wenseleers *et al*., 1998) and carpenter ants (*Camponotus*) are known to have yet another type of intracellular symbiont (Schröder *et al*., 1996). Since they are maternally transmitted, any male offspring produced is a waste for these symbionts. However, it is at present unclear to what extent symbionts can manipulate reproduction in social insect colonies, so that more females and fewer males are raised.

Conflicts over individual destiny

Several authors (e.g. Pamilo, 1991; Nonacs & Tobin, 1992; Ratnieks & Reeve, 1992) have pointed out that a conflict over caste fate might arise between diploid brood and the adult colony members (workers, queens and colony fathers) (Fig. 1b). A female larva may pursue direct fitness as a reproductive instead of inclusive fitness as a worker by overexploiting the common resources of their colony (Frank, 1998; Bourke & Ratnieks, 1999). Kinship and social policing may, however, limit or prevent this tragedy of the commons (Frank, 1998). Self-restraint by larvae is expected under high relatedness, but no prudence is expected under low relatedness. Instead social policing may evolve to prevent unlimited selfishness (Wenseleers *et al*., submitted). Increased caste dimorphism, early caste determination and regulation of larval feeding rate may have evolved to counteract larval selfishness and to secure the interests of the collective (Bourke & Ratnieks, 1999; Reuter & Keller, 2001; Wenseleers *et al*., submitted).

The resolution of conflicts

Several recent studies have tested predictions concerning worker vs. queen control of sex allocation in ants, bees and wasps, and often found that sex allocation patterns follow the predictions under worker control (see Queller & Strassmann, 1998 for a recent review). Further studies have also shown that queens lay mixed sex ratios and that males are apparently eliminated in colonies where workers maximize their inclusive fitness by raising all-female broods (Keller *et al*., 1996; Sundström *et al*., 1996). However, sex ratios and relatedness asymmetries are not always correlated (e.g. Pamilo & Seppä, 1994; Aron *et al*., 1995; Helms, 1999), indicating that either queens sometimes control sex ratios, or that factors other than relatedness play a decisive role.

Worker control of sex ratios affects the fitness of both mother-queens and colony fathers. Sundström & Ratnieks (1998) showed that multiply mated queens in the ant *Formica truncorum* gain a 37% fitness advantage over single mated queens owing to worker sex ratio biasing alone. Conversely, males that sire a colony alone have a fourfold fitness advantage compared to those that co-sire a colony; 80% of this advantage is due to facultative sex ratio biasing by workers (Sundström & Boomsma, 2000). Hence, fitness consequences are indeed dire for one or the other parent when workers bias sex ratios.

This begs the question whether queens and colony fathers can evade the negative consequences of facultative sex ratio biasing by workers. Theory predicts (Ratnieks & Boomsma, 1995) and the above results show that queens can gain from mating with several males. However, genetic studies of a large number of species indicate that, with a few notable exceptions, mating frequencies are usually close to one, indicating that there are almost certainly costs associated with mating multiply (Boomsma & Ratnieks, 1996). Males on their part always stand to win from monopolizing paternity rather than co-siring a colony, and would best pursue their fitness interests by inserting mating plugs (Baer *et al*., 2000) and by avoiding non-virgin females as mating partners, provided later mating opportunities are likely to arise. To date no studies have addressed male mating preferences in species where split sex ratios are known to occur. However, theory has been developed for several such scenarios, predicting that males may either transfer relatively few sperm when mating with a non-virgin queen or may induce sperm clumping in the spermatheca of their partner (Boomsma, 1996). Both mechanisms enhance the relatedness asymmetry between workers and the brood they rear because they create uneven paternity shares and thus enhance the likelihood that workers will increase the investment in females. Observed patterns of paternity skew in *Formica* (Boomsma & Sundström, 1997) and *Lasius* (Boomsma & Van der Have, 1998) ants are consistent with theory, although alternative explanations remain possible. However, we recently found support for sperm clumping as a posthumous male strategy for enhancing the joint fitness of multiple ejaculates stored in the same spermathecae of *Formica truncorum* queens (Sundström & Boomsma, 2000).

Also male parentage has been assessed, especially in bees and wasps (Ratnieks & Visscher, 1989; Arevalo *et al*., 1998; Peters *et al*., 1999; Foster & Ratnieks, 2001). In many of these species workers do lay male eggs in the presence of the queen. In honeybees whose queens typically mate with 10–20 males, workers remove eggs laid by nestmate workers (Ratnieks & Visscher, 1989), whereas no policing was found in the typically singly mated wasps and stingless bees (Arevalo *et al*., 1998; Peters *et al*., 1999). Evidence for facultative worker policing was recently found in *Dolichovespula saxonica* (Foster & Ratnieks, 2000), a species whose queens mate with 1–4 males. In colonies headed by a singly mated queen over 50% of the male brood was worker derived, whereas less than 25% worker-derived males were found in colonies headed by multiply mated queens, because workers selectively removed worker-laid eggs (Foster & Ratnieks, 2000).

Surprisingly few genetic studies have directly addressed the occurrence of worker reproduction in ants. In *Formica* ants worker-derived males seem to be rare in queenright colonies, although effective queen mating frequencies are well below two (e.g. Walin *et al*., 1998). Workers of *Formica fusca* lay male eggs in the presence of the queen, but these are not raised into adults (H. Helanterä, unpublished data). However, in queenless ant species reproductively active workers are attacked, thus preventing worker reproduction (Heinze *et al*., 1994). This suggests that a different mechanism for worker policing may be at work in different contexts.

Any brood manipulation selectively affects the fitness of juveniles. Male larvae could evade culling by disguising their gender up to an age when the costs of their elimination are prohibitive (Nonacs, 1992). Such a disguise could be achieved by mimicking the odour profile of females to prevent workers from discriminating between male and female larvae. However, at least in the ants *Solenopsis invicta*, *Pheidole pallidula* and *Formica exsecta*, males are culled (Aron *et al*., 1995; Keller *et al*., 1996; Sundström *et al*., 1996), although not until close to pupation in *F. exsecta* (Chapuisat *et al*., 1997). It is still unclear whether workers can discriminate between male and female eggs (but see Aron *et al*., 1995). In honeybees workers remove all worker-laid male eggs early on, but are apparently unable to discriminate between queen-produced and worker-produced larvae (Ratnieks & Visscher, 1989). With their high effective queen mating frequency the worker–queen conflict over sex allocation is only slight, so there are no clear incentives for honeybee workers to manipulate sex ratios against the interests of the queen, and both parties benefit from an unambiguous signal.

No empirical work has been done to explicitly address questions of selfish manipulations of destiny by larvae. Among the monogyne insect societies the mass-provisioning *Melipona* bees are interesting, as they tend to produce an excess of females, most of which are culled after eclosion (Imperatriz-Fonseca & Zucchi, 1995). Indeed, the fraction of diploid brood taking the sexual developmental pathway closely fits the value predicted (22%) under self-restraint and maximization of larval inclusive fitness, suggesting that the immature stages have full control over development (Wenseleers *et al*., submitted). The situation may, however, be different for more derived taxa in which workers can control the provisioning rate or where caste determination already occurs at the egg stage.

Proximate mechanisms and constraints on the expression of conflicts

Many recent data indicate that conflicts over sex allocation and male parentage are expressed (i.e. are actual rather than just potential *sensu* Ratnieks & Reeve, 1992) and that one of the conflicting parties prevails. Nonetheless, the ultimate resolution of these conflicts almost certainly also depends on factors associated with productivity and dispersal, information constraints, power asymmetries and interactions between different types of conflicts (Trivers & Hare, 1976; Ratnieks & Reeve, 1992; Bourke & Franks, 1995; Sundström, 1995).

Productivity, dispersal and the cost of conflict

Population-wide sex-allocation ratios may deviate from the expected worker optimum, when variation in colony productivity or sex-biased dispersal (causing local mate or local resource competition) induce additional biases in the sex ratio (Bourke & Franks, 1995; Crozier & Pamilo, 1996). Especially when worker and queen optima converge at lower relatedness asymmetries, factors driven by productivity and dispersal differences are more likely to prevail over genetic factors as determinants of sex allocation (Sundström, 1995; Chapuisat & Keller, 1999).

Costs in terms of reduced colony performance may disfavour worker reproduction at the collective level, although not at the individual level. Hence, worker policing may occur, although relatedness levels would predict otherwise (Foster & Ratnieks, in press; H. Helanterä, unpublished). In this respect ants with perennial colonies differ from wasps and bees with annual colonies. When the time of colony death is predictable, as is the case in annual societies, workers may be selected to sacrifice social cohesion, commit matricide and raise their own sons instead of brothers towards the end of the colony life cycle (Bourke, 1994). In perennial colonies where future reproduction is important there is a significant inclusive fitness premium on preventing social disruption. Differences in life history strategies may thus explain why worker reproduction apparently is more common in bees and wasps than in ants, despite similar genetic benefits. Interestingly, worker reproduction in yellow-jacket wasps appears to be more common in species where nest usurpation is frequent (Foster & Ratnieks, in press), suggesting that social stability and life expectancy of societies may affect the propensity of workers to reproduce.

Information

Successful facultative brood manipulation in response to mating frequencies requires information by which workers can: (1) assess the kin structure of their own colony; (2) discriminate between male and female brood; and (3) discriminate between queen-laid and worker-laid eggs. Unless a direct way of assessment is available (e.g. identifying the sex of the brood based on sexual size dimorphism or location in the nest) such information must be based on heritable or imprinted variation in individual odours. The fact that facultative and selective brood manipulation in response to queen mating frequencies has been found implies that such cues do exist and can be capitalized on.

This begs the question whether males and queens can manipulate odours to pursue their own interests. Queens are in a position to label any eggs they lay, which serves their interests when workers and queens agree upon male parentage. Such odour cue labels have indeed been found in honeybees (Ratnieks, 1995). A recent study of the Cape honeybee has shown that workers of some patrilines also lay such imprinted eggs, which are not removed by other workers (Oldroyd & Ratnieks, 2000). As a result single fathers successfully pass on their genes through males laid by their daughter workers at the expense of the fitness interests of the queen and the other patrilines.

Power

Given that the necessary information is available for workers to act upon, the resolution of conflicts ultimately depends on which party has the power and opportunities to impose its interests. The incentive to pursue personal interests may also differ between parties, as the fitness returns from manipulations may differ among castes. For example, queens suffer a two-fold fitness loss when exchanging sons against grandsons, while workers only get a 1.5-fold fitness gain from producing nephews rather than brothers. Hence, selection may act more strongly on queens to prevent worker reproduction than on the workers to replace brothers with nephews.

Individual vs. collective interests can be pursued both through physical and chemical actions. In queen–worker interactions the queen only stands to lose one member of the collective if she kills a worker, whereas the collective may stand to lose everything if the queen is killed (Trivers & Hare, 1976; Ratnieks & Reeve, 1992). In small societies, caste dimorphism between queens and workers is often less pronounced than in large societies, and direct interactions are often manifest as dominance hierarchies maintained by physical suppression (Wilson, 1971; Alexander *et al*., 1991; Bourke, 1999). In larger societies, caste dimorphism is frequently more pronounced and communication is commonly mediated through chemicals (Bourke & Franks, 1995). Workers will, however, be selected to ignore queen-produced signals unless it is in the inclusive fitness interests of the collective to concede (Keller & Nonacs, 1993). Hence, queens may have little power over workers in large societies, whereas the opposite may be true in small societies.

The juveniles are the potential targets of all manipulations by adults and are under selection to evade elimination and/or manipulation against their interests. Nevertheless, they apparently have very little control over their fate. In bees and wasps larvae develop in special cells confined to specific sections in the nest, so that worker discrimination between classes of brood is easy. In ants eggs and larvae of all castes are kept together, but this does not always prevent discrimination and selective culling (Keller *et al*., 1996; Sundström *et al*., 1996).

Whether a diploid larva develops into a worker or a female depends in many species on provisioning (Bourke & Franks, 1995). Workers who rear the brood can control their feeding rate and thus their fate (Bourke & Ratnieks, 1999). Ultimately queens can gain control by determining the caste already at the egg stage, as seems to be the case in some ants (Hölldobler & Wilson, 1990; for a review see Bourke & Ratnieks, 1999). Such control over larval development by helpers has probably been instrumental for the evolution of sociality, and therefore little larval control may be expected.

In the light of opportunities to exert power it is surprising that the long-dead colony fathers apparently can influence colony sex ratios, albeit through their daughter workers. More remarkably, this occurs against the interests of the colony queen, who stores the sperm she received during a single nuptial flight for her entire life, which in some ant species can be as long as 30 years (Pamilo, 1991a). When workers realize relatedness-induced split sex ratios, queens are selected to mate multiply and to mix sperm to obtain a sex ratio closer to their optimum, but males are apparently able to mitigate at least part of these hypothesized efforts by queens by clumping their sperm (Sundström & Boomsma, 2000). The mechanism by which males can achieve this is, however, unknown.

Conclusion

Social life entails a delicate balance between direct fitness returns through selfish behaviour and indirect fitness returns through collective benefits (Keller & Chapuisat, 1999). The extent to which insect societies can tolerate some selfishness while at the same time realizing optimal compromises between these disruptive forces and the collective interest pose major novel challenges to the study of social evolution. A successful pursuit of individual interests always rests on information and power, but unlimited refinement of such traits may eventually dissolve the society. Selfishness can, however, also promote social cohesion as has been shown for some wasps in their sex ratio biasing activities (Queller *et al.*, 1993; Henshaw *et al.*, 2000). Ultimately, it seems likely that social evolution is mediated by selection both at the individual and the collective level, but studies proving this are still rare.

Acknowledgements

We wish to thank Kevin Foster, Max Reuter and Tom Wenseleers for access to unpublished manuscripts, and Esa Ranta, Andrew Bourke and an anonymous reviewer for comments. This work was funded by grants from the Academy of Finland (grant no. 42725), the University of Helsinki, and The Finnish Society of Sciences and Letters to L. S., and the Danish Natural Science Research Council to J. J. B.

References

ALEXANDER, R. D., NOONAN, K. M. AND CRESPI, B. J. 1991. The evolution of eusociality. In: Sherman, P. W., Jarvis, J. U. M. and Alexander, R. D. (eds) *The Biology of the Naked Mole Rat*, pp. 3–34. Princeton University Press, Princeton, NJ.

AREVALO, E., STRASSMANN, J. E. AND QUELLER, D. C. 1998. Conflicts of interest in social insects: Male production in two species of *Polistes*. *Evolution*, **52**, 797–805.

ARON, S., VARGO, E. L. AND PASSERA, L. 1995. Primary and secondary sex ratios in monogyne colonies of the fire ant. *Anim. Behav.*, **49**, 749–757.

BAER, B., MAILE, R., SCHMID-HEMPEL, P., MORGAN, E. D. *ET AL.* 2000. Chemistry of a mating plug in bumblebees. *J. Chem. Ecol.*, **26**, 1869–1875.

BOOMSMA, J. J. 1996. Split sex ratios and queen–male conflict over sperm allocation. *Proc. R. Soc. B.*, **263**, 697–704.

BOOMSMA, J. J. AND GRAFEN, A. 1990. Intraspecific variation in ant sex ratios and the Trivers–Hare hypothesis. *Evolution*, **44**, 1026–1034.

BOOMSMA, J. J. AND GRAFEN, A. 1991. Colony-level sex ratio selection in the eusocial Hymenoptera. *J. Evol. Biol.*, **4**, 383–407.

BOOMSMA, J. J. AND RATNIEKS, F. L. W. 1996. Paternity in eusocial Hymenoptera. *Phil. Trans. R. Soc. B*, **351**, 947–975.

BOOMSMA, J. J. AND SUNDSTRÖM, L. 1997. Patterns of paternity skew in *Formica* ants. *Behav. Ecol. Sociobiol.*, **42**, 85–92.

BOOMSMA, J. J. AND VAN DER HAVE, T. M. 1998. Queen mating and paternity variation in the ant *Lasius niger*. *Mol. Ecol.*, **7**, 1709–1718.

BOURKE, A. F. G. 1994. Worker matricide in social bees and wasps. *J. Theor. Biol.*, **167**, 283–292.

BOURKE, A. F. G. 1999. Colony size, social complexity and reproductive conflict in social insects. *J. Evol. Biol.*, **12**, 245–257.

BOURKE, A. F. G. AND FRANKS, N. R. 1995. *Social Evolution in Ants*. Princeton University Press, Princeton, NJ.

BOURKE, A. F. G. AND RATNIEKS, F. L. W. 1999. Kin conflict over caste determination in social Hymenoptera. *Behav. Ecol. Sociobiol.*, **46**, 287–297.

CHAPUISAT, M. AND KELLER, L. 1999. Testing kin selection with sex allocation data in eusocial Hymenoptera. *Heredity*, **82**, 473–478.

CHAPUISAT, M., SUNDSTRÖM, L. AND KELLER, L. 1997. Sex ratio regulation: the economics of fratricide in ants. *Proc. R. Soc. B*, **264**, 1255–1260.

CLUTTON-BROCK, T. 1991. *The Evolution of Parental Care*. Princeton University Press, Princeton, NJ.

CROZIER, R. H. AND PAMILO, P. 1996. *Evolution of Social Insect Colonies: Sex Allocation and Kin Selection*. Oxford University Press, Oxford.

FOSTER, K. AND RATNIEKS, F. L. W. 2000. Facultative worker policing in a wasp. *Nature*, **407**, 692–693.

FOSTER, K., RATNIEKS, F. L. W. 2001. Paternity, reproduction and conflict in vespine wasps: a model system for testing kin selection predictions. *Behav. Ecol. Sociobiol.*, **50**, 1–8.

FRANK, S. A. 1998. *Foundations of Social Evolution*. Princeton University Press, Princeton, NJ.

HAMILTON, W. D. 1964. The genetical evolution of social behaviour. *J. Theor. Biol.*, **7**, 1–52.

HEINZE, J., HÖLLDOBLER, B. AND PEETERS, C. 1994. Conflict and cooperation in ant societies. *Naturwissenschaften*, **81**, 489–497.

HELMS, K. R. 1999. Colony sex ratios, conflict between queens and workers, and apparent queen control in the ant *Pheidole desertorum*. *Evolution*, **53**, 1470–1478.

HENSHAW, M. T., STRASSMANN, J. AND QUELLER, D. C. 2000. The independent origin of a queen number bottleneck that promotes cooperation in the African swarm-founding wasp, *Polybioides tabidus*. *Behav. Ecol. Sociobiol.*, **48**, 478–483.

HÖLLDOBLER, B. AND WILSON, E. O. 1990. *The Ants*. Springer Verlag, Berlin.

IMPERATRIZ-FONSECA, V. L. AND ZUCCHI, R. 1995. Virgin queens in stingless bee (Apidae, Meliponinae) colonies: a review. *Apidologie*, **26**, 231–244.

KELLER, L. 1999. *Levels of Selection in Evolution*. Princeton University Press, Princeton, NJ.

KELLER, L., ARON, S. AND PASSERA, L. 1996. Internest sex-ratio variation and male brood survival in the ant *Pheidole pallidula*. *Behav. Ecol.*, **7**, 292–298.

KELLER, L. AND CHAPUISAT, M. 1999. Cooperation among selfish individuals in insect societies. *BioScience*, **49**, 899–909.

KELLER, L. AND NONACS, P. 1993. The role of queen pheromones in social insects: queen control or queen signal? *Anim. Behav.*, **45**, 787–794.

MAYNARD SMITH, J. AND SZATHMÁRY, E. 1995. *The Major Transitions in Evolution*. W. H. Freeman, Oxford.

NONACS, P. 1986. Ant reproductive strategies and sex allocation theory. *Quart. Rev. Biol.*, **61**, 1–21.

NONACS, P. 1992. Male parentage and sexual deception in the social Hymenoptera. In: Wrensch, D. L. and Ebbert, M. A. (eds) *Evolution and Diversity of Sex Ratio in Insects and Mites*, pp. 384–401. Chapman & Hall, New York.

NONACS, P. AND TOBIN, J. E. 1992. Selfish larvae: development and the evolution of parasitic behaviour in the Hymenoptera. *Evolution*, **46**, 1605–1620.

OLDROYD, B. P. AND RATNIEKS, F. L. W. 2000. Evolution of worker sterility in honey-bees (*Apis mellifera*): how anarchistic workers evade policing by laying eggs that have low removal rates. *Behav. Ecol. Sociobiol.*, **47**, 268–273.

PAMILO, P. 1991a. Life-span of queens in the ant *Formica exsecta*. *Insect. Soc.*, **38**, 111–119.

PAMILO, P. 1991b. Evolution of colony characteristics in social insects. I. Sex allocation. *Am. Nat.*, **137**, 83–107.

PAMILO, P. AND SEPPÄ, P. 1994. Reproductive competition and conflicts in colonies of the ant *Formica sanguinea*. *Anim. Behav.*, **48**, 1201–1206.

PETERS, J. M., QUELLER, D. C., IMPERATRIZ-FONSECA, V. L. *ET AL.* 1999. Mate number, kin selection and social conflicts in stingless bees and honeybees. *Proc. R. Soc. B.*, **266**, 379–384.

QUELLER, D. C. 1993. Worker control of sex ratios and selection for extreme multiple mating by queens. *Am. Nat.*, **142**, 346–351.

QUELLER, D. C. AND STRASSMANN, J. E. 1998. Kin selection and social insects. *BioScience*, **48**, 165–175.

QUELLER, D. C., STRASSMANN, J. E., SOLIS, C. R. AND DELOACH, D. M. 1993. A selfish strategy of social insect workers that promotes social cohesion. *Nature*, **365**, 639–641.

RATNIEKS, F. L. W. 1988. Reproductive harmony via mutual policing by workers in eusocial Hymenoptera. *Am. Nat.*, **132**, 217–236.

RATNIEKS, F. L. W. 1995. Evidence for a queen-produced egg-marking pheromone and its use in worker policing in the honey-bee. *J. Apicult. Res.*, **34**, 31–37.

RATNIEKS, F. L. W. AND BOOMSMA, J. J. 1995. Facultative sex allocation by workers and the evolution of polyandry by queens in social Hymenoptera. *Am. Nat.*, **145**, 969–993.

RATNIEKS, F. L. W. AND REEVE, H. K. 1992. Conflict in single-queen Hymenopteran societies – the structure of conflict and processes that reduce conflict in advanced eusocial species. *J. Theor. Biol.*, **158**, 33–65.

RATNIEKS, F. L. W. AND VISSCHER, P. K. 1989. Worker policing in the honeybee. *Nature*, **342**, 796–797.

REUTER, M. AND KELLER, L. 2001. Sex ratio conflict and worker production in social Hymenoptera. *Am. Nat.*, **158**, 166–177.

SCHRÖDER, D., DEPPISCH, H., OBERMAYER, M., KROHNE, G. *ET AL.* 1996. Intracellular endosymbiotic bacteria of *Camponotus* species (carpenter ants): systematics, evolution and ultrastructural characterization. *Mol. Microbiol.*, **21**, 479–489.

SUNDSTRÖM, L. 1995. Sex allocation and colony maintenance in monogyne and polygyne colonies of *Formica truncorum* (Hymenoptera, Formicidae) – the impact of kinship and mating structure. *Am. Nat.*, **146**, 182–201.

SUNDSTRÖM, L. AND BOOMSMA, J. J. 2000. Reproductive alliances and posthumous fitness enhancement in male ants. *Proc. R. Soc. B.*, **267**, 1439–1444.

SUNDSTRÖM, L. AND RATNIEKS, F. L. W. 1998. Sex ratio conflicts, mating frequency, and queen fitness in the ant *Formica truncorum*. *Behav. Ecol.*, **9**, 116–121.

SUNDSTRÖM, L., CHAPUISAT, M. AND KELLER, L. 1996. Conditional manipulation of sex ratios by ant workers: a test of kin selection theory. *Science*, **274**, 993–995.

TRIVERS, R. L. 1974. Parent–offspring conflict. *Am. Zool.*, **14**, 249–264.

TRIVERS, R. L. AND HARE, H. 1976. Haplodiploidy and the evolution of social insects. *Science*, **191**, 249–263.

WALIN, L., SUNDSTRÖM, L., SEPPÄ, P. AND ROSENGREN, R. 1998. Worker reproduction in ants – a genetic analysis. *Heredity*, **81**, 604–612.

WENSELEERS, T., ITO, F., VAN BORM, S., HUYBRECHTS, R. *ET AL.* 1998. Widespread occurrence of the micro-organism *Wolbachia* in ants. *Proc. R. Soc. B.*, **265**, 1447–1452.

WENSELEERS, T., RATNIEKS, F. L. W. AND BILLEN, J. Conflict over caste fate in social insects: a tragedy of the commons examined. *Am. Nat.*, in review.

WILSON, E. O. 1971. *The Insect Societies*. Belknap, Cambridge, MA.