

Power over reproduction in social Hymenoptera

Madeleine Beekman^{1,2*} and Francis L. W. Ratnieks²

¹*Schools of Biological Sciences & Mathematics and Statistics, University of Sydney, A12, Sydney, NSW 2006, Australia*

²*Laboratory of Apiculture and Social Insects, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK*

Inclusive fitness theory has been very successful in predicting and explaining much of the observed variation in the reproductive characteristics of insect societies. For example, the theory correctly predicts sex-ratio biasing by workers in relation to the queen's mating frequency. However, within an insect society there are typically multiple reproductive optima, each corresponding to the interest of different individual(s) or parties of interest. When multiple optima occur, which party's interests prevail? Presumably, the interests of the party with the greatest 'power'; the ability to do or act. This article focuses on factors that influence power over colony reproduction. In particular, we seek to identify the principles that may cause different parties of interest to have greater or lesser power. In doing this, we discuss power from two different angles. On the one hand, we discuss general factors based upon non-idiosyncratic biological features (e.g. information, access to and ability to process food) that are likely to be important to all social Hymenoptera. On the other hand, we discuss idiosyncratic factors that depend upon the biology of a taxon at any hierarchical level. We propose that a better understanding of the diversity of reproductive characteristics of insect societies will come from combining inclusive fitness theory with a wide range of other factors that affect relative power in a conflict situation.

Keywords: reproduction; potential and actual conflict; kin selection; social Hymenoptera; social insects; power

1. INTRODUCTION

Social insects have long been a favourite metaphor of human society. For Shakespeare in *King Henry V* (act 1, scene 2), a bee colony was a benevolent despotism, with the workers carrying out complementary tasks and living in harmonious obedience to a monarch, much like Elizabethan England. To this day, ants and bees often serve as an example of an ideal human society (Ridley 1996). However, we also know that insect societies are the scene of numerous potential and actual conflicts with different parties having different interests and often manipulating colony reproduction to their advantage. Conflicts occur because insect societies are non-clonal. This leads to potential conflict among individuals or groups of individuals over colony reproduction (Ratnieks & Reeve 1992). In particular, different individuals or groups of individuals have different optima with respect to colony reproduction and their actions sometimes reflect these differences (Ratnieks 1998). Several conflicts have long been known, for example conflicts over sex allocation or male production. Others have only recently been 'discovered' both in theoretical and empirical senses, for example conflict over the caste fate—queen or worker—of female brood (Bourke & Ratnieks 1999; Ratnieks 2001).

The study of reproductive conflicts in insect societies has its theoretical base in the work of Hamilton (1964).

Serious empirical study of conflict began a decade later with the influential paper of Trivers & Hare (1976). Trivers & Hare (1976) used the theory of Hamilton (1964) to show that the worker-optimum sex-allocation ratio in hymenopteran societies is female biased. The worker optimum depends upon several factors but is 3:1 (75%:25%) females (young queens) to males in a Hardy-Weinberg population in which each colony is headed by one single-mated queen who is the mother of all the colony's male and female offspring.

Trivers & Hare (1976) also considered another party of interest, the queen, whose sex-allocation optimum in the absence of local resource competition, local mate competition (Alexander & Sherman 1977) and inbreeding is an even ratio. The prediction of female bias was supported by reviewing published data on sexual production in field surveys of ant populations. With 64% female (see Boomsma (1989) for a reanalysis of the data of Trivers & Hare (1976)), investment was significantly more female biased than 50 but less than 75%. That Trivers & Hare (1976) were able to detect female bias at all indicates that the queen was not in complete control of colony reproduction. (The alternative explanation, local mate competition (Alexander & Sherman 1977), is now considered unlikely to be of general value (Nonacs 1986).) Although the results of Trivers & Hare (1976) have often been taken to mean that the workers are in full control of sex allocation they are, in fact, often more compatible with sex allocation being under joint queen and worker control. Alternatively, the observed 64% allocation to queens could be due to worker control but with the worker-

*Author and address for correspondence: Schools of Biological Sciences & Mathematics and Statistics, University of Sydney, A12, Sydney, NSW 2006, Australia (mbeekman@bio.usyd.edu.au).

optimum less female biased than 75%. Factors reducing optimum female bias include multiple mating by queens, multiple related queens per colony, and male production by workers, all of which occur in ants. Although in theory many combinations of these factors can reduce the workers' optimum sex allocation to 64%, alone they are probably insufficient (see Boomsma & Ratnieks 1996).

Inclusive fitness modelling has been very successful in predicting variation in the reproductive characteristics of insect societies, such as the female bias described above. But clearly it cannot be the sole predictor because the theory frequently produces multiple reproductive optima, each corresponding to the interest of a different individual or group of individuals within the colony. The actual reproductive characteristics of a colony must also reflect the varying power of individuals or groups in manipulating colony reproduction. Trivers & Hare (1976) gave a good example. In slave-making ants sex allocation is not female biased, probably because the workers have no power. Their lack of power is because the brood are reared by slaves of another species. In this case, all power rests with the queen because brood are reared by unrelated workers who have not been selected to bias the sex ratio in this novel context. Presumably, the queen can choose the sex ratio via her egg laying and slaves are not selected to vary this ratio because their fitness is not affected in any way by the sex ratio of the brood they rear. This prediction, equal investment in males and queens, has been confirmed for three outbreeding species of slave makers (Bourke (1989); Bourke & Franks (1995); but see also Herbers & Stuart (1998) for exceptions).

Inclusive fitness is a fundamental principle in understanding reproductive conflicts. But, as we argue in the previous paragraphs, it cannot alone explain colony reproductive characteristics because it typically predicts multiple reproductive optima. Power is a key factor in determining who influences reproduction, but what principles determine who has power? Indeed, are there any general principles? Here, we focus explicitly on power with the aim of making a first attempt at identifying some of these principles. As we will show, there are some general principles that are likely to apply to all social Hymenoptera, for example asymmetry among parties of interest in their access to information or food. Similarly, a group will usually have power over an individual, although there are important exceptions. In many cases, however, there can be some feature of the biology that is non-general but revolutionizes power relations. These idiosyncrasies may characterize a taxon at any hierarchical level and are often extremely revealing. At the order level, hymenopteran males and brood are generally assumed to be powerless because their societies are numerically dominated by adult females (workers and queens). Hence, until recently males (e.g. Sundström & Boomsma 2000) and brood (Bourke & Ratnieks 1999) have not been the focus of study. At the genus level, individual workers of the queenless ponerine ant *Diacamma* have little power because gemmae mutilation of newly eclosed and physically weak workers prevents them from mating, and hence prevents them from ever replacing the mated worker (gamergate) who heads the colony and plays the queen role (Peeters & Higashi 1989; Sommer *et al.* 1993; Tsuji *et al.* 1998). In *Diacamma* the bizarre idiosyncrasy of gemmae and their mutilation

gives the gamergate and the workers collectively power over individual workers. Gemmae are unknown in other ants, yet they are fundamental to understanding reproduction in *Diacamma*.

Before we discuss principles that affect power, we will first provide examples of the wide range of different reproductive optima that can occur in insect societies, with respect to different reproductive contexts (sex allocation, male and female production) and parties of interest. Our aim in doing this is not to review this relatively well-understood area but explicitly to show the great diversity of reproductive optima and parties of interest, many of whom, such as males and brood, are often ignored because they are implicitly assumed to have no power. However, as we will show, the normally powerless can have power under certain idiosyncratic conditions. Although our main focus is on the social Hymenoptera, we conclude by comparing Hymenoptera with Isoptera, social insects with social vertebrates, and birds with mammals. The aim of this final comparison is not to provide a thorough review, but to show that the idea of power, and its many biological idiosyncrasies, apply broadly and to encourage researchers studying these organisms to consider power explicitly.

2. DIFFERENT PARTIES OF INTEREST, REPRODUCTIVE CONTEXTS AND MULTIPLE OPTIMA

The reproductive interests of different parties, and hence their conflicts of interest, depend upon two main factors: colony kin structure and reproductive context. Kin structure is determined by several factors such as diploidy versus haplodiploidy, number and relationship of mother queens, number and relationship of mates per mother queen, and outbreeding versus inbreeding. Even in the simplest case which we will use here, a society with a single queen mated to a single unrelated male, there are many different parties of interest: the queen, workers individually, workers collectively, offspring males, father males, and brood (i.e. female larvae who still have the potential to develop into either queens or workers). Different parties of interest for three reproductive contexts: sex allocation, male production and female production, are given in table 1.

A party of interest can be either a group or an individual. The largest group is that of the workers collectively, who are in conflict with the queen but not in conflict with each other over sex allocation. In sex allocation the non-reproducing workers collectively have the same interest and are opposed to the queen (single-individual party). Where male production is concerned, individual workers are single-individual parties with opposing interest to both the queen and the non-reproducing workers. Hence, the parties of interest depend on the exact reproductive conflict and one individual can be part of the group in one and a single-individual party in another.

The diversity of reproductive optima among different parties of interest within a colony is clearly shown by considering sex allocation. In addition to the asymmetry in relatedness caused by haplodiploidy, the effective mating frequency of the queen (Boomsma & Grafen 1990, 1991; Ratnieks & Boomsma 1995, 1997) and the proportion of males produced by workers (Bourke 1988; Pamilo 1991)

Table 1. Parties of interest under different reproductive contexts when colonies have a single queen (either singly or multiply mated) and queen and worker caste are morphologically distinct. (When conflicts change owing to multiple mating, this is denoted in *italic*. Conflicts are based on relatedness only (i.e. costs of manipulative acts are ignored).)

parties of interest and their interest under single mating	under multiple mating (effective paternity > 2)
<u>area of conflict: sex allocation^a</u>	
queen—1 : 1 (m : f) allocation ratio	queen—1 : 1 (m : f) allocation ratio
workers collectively—1 : 3	<i>workers collectively—1 : < 2^b</i>
workers individually—1 : 3	<i>workers individually—1 : < 2^b</i>
female larva—1 : 3	<i>female larva—1 : < 2^b</i>
queen's mate (father)—0 : 1	queen's mate (father)—0 : 1
offspring males—1 : 1	offspring males—1 : 1
<u>area of conflict: male production</u>	
queen—sons > grandsons	queen—sons > grandsons
workers collectively (female larva)—nephews > brothers	<i>workers collectively (female larva)—brothers > nephews</i>
workers individually—own sons > any other male	workers individually—own sons > any other male
queen's mate (father)—worker's sons > queen's sons	queen's mate (father)—worker's sons > queen's sons
offspring males—brothers > sons of other females	offspring males—brothers > any other males
<u>area of conflict: female production—nepotism</u>	
no conflict	<i>queen—no preference</i>
	<i>workers collectively and individually—own > other patriline</i>
	<i>female larva—self > sister</i>
	<i>queen's mate (father)—daughter > daughter of other male(s)</i>
	<i>offspring males—no preference if they are queen's sons; if they are worker's sons, their preference will be to their own patriline</i>
<u>area of conflict: female production—caste fate^c</u>	
female larva—develop into queen > worker	although the potential for conflict increases with multiple mating (owing to reduced relatedness among potential queens), the nature of the conflict does not change if the queen mates more than once ^e
queen and adult workers—prefer to rear fewer queens than is optimal for individual female larva ^d	
<u>area of conflict: replacement of breeder^f</u>	
workers collectively—prefer to replace the mother before she wants to be replaced	less conflict between the workers collectively and the breeding female because the current breeder is more valuable than the replacement female.
workers individually—each individual wants to become the new breeder	more conflict among different patrilines over who will replace the breeder

^a Assuming all males are produced by the queen and the absence of ergonomic constraints (i.e. optimal sex ratio is solely determined by kin structure).

^b In the case where there are colonies with singly and multiply mated queens in the same population, sex investment ratios may be split. Workers in colonies headed by a singly mated queen will then prefer female-biased investment, and workers in colonies headed by multiple mated queens will prefer a male-biased investment ratio. Male-biased investment is not in the interest of the father because his relatedness towards queen-produced males is zero (Boomsma 1996; Sundström & Boomsma 2000).

^c In some ants (such as *Cardiocondyla*) there are two types of males: winged males that disperse and ergatoid males who stay in the nest and kill rivals (Cremer & Heinze 2002). A male may prefer to be either one or the other.

^d The optimal proportion of queens from an individual perspective is $(1 - r_f)/(1 + r_m)$ in which r_f is the relatedness among female offspring and r_m is the relatedness to males reared in the colony assuming that colony productivity is directly proportional to the proportion of females that are workers (Bourke & Franks 1995; Crozier & Pamilo 1996).

^e Bourke & Ratnieks (1999).

^f Here, we refer to insect societies that lack a morphological queen caste. All (female) individuals are totipotent, in that each can potentially mate and replace the principal breeder. However, only high rankers are likely to replace the breeder. Examples are queenless ponerine ants.

also affect kin structure in ways that affect the optimum sex allocation ratios. For example, because males never father sons, father males benefit from 100% reproductive investment in females (i.e. queens) unless their daughter-workers produce some or all of the males (Boomsma & Grafen 1990, 1991; Pamilo 1991). Offspring males (queen's sons) normally have no interest in workers bias-

ing the sex ratio towards females if that means they will be killed. The different sex-allocation optima of the parents (queen, father male) and offspring (workers, offspring males), are shown in figure 1. The queen's optimum is always the same, irrespective of her mating frequency and the contribution of worker-produced males in the population because neither affects the relative kin values of

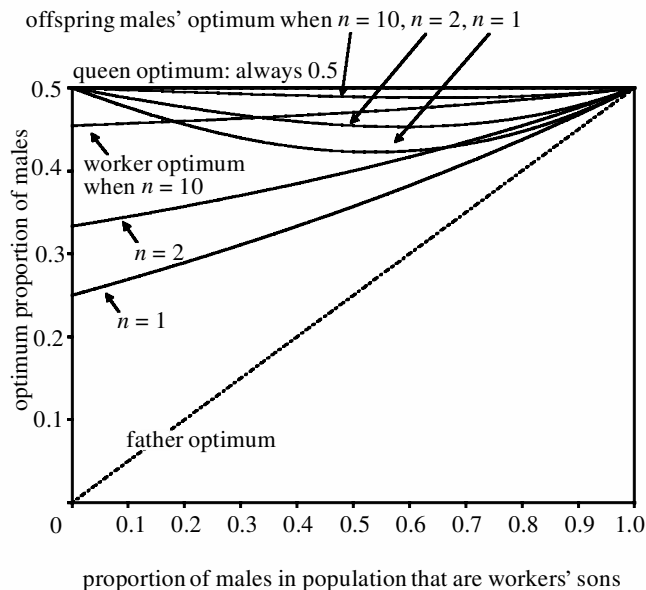


Figure 1. The optimum proportion of males in relationship to the proportion of worker-produced males in the population. The optimum proportion of males is calculated using $1/(1 + (r_f V_f / r_m V_m))$, in which r_f and r_m are the relatedness of the focal individual(s) to females and males, respectively, and V_f and V_m the sex-specific reproductive value of females and males, (Boomsma & Grafen 1991; Pamilo 1991). $r_f V_f / (r_m V_m)$ is the kin value of females (males) (Ratnieks & Reeve 1992) and $r_f V_f / r_m V_m$ is the optimal ratio of males and females. The ratio of the kin values of males and females changes with the proportion of worker-produced males in the population, except for the queen (Ratnieks & Reeve 1992). Workers and offspring males have different optima depending on the mating frequency of the queen (n). The mating frequency does not affect the optimum proportion of males from the queen's point of view nor that of her mate (father).

male and female reproductives (Crozier & Pamilo 1996). The optimum of the queen's mate(s) however, changes with the proportion of males produced by his daughter-workers because this is his only means of passing on genes via the males produced within a colony (Boomsma & Grafen 1991; Pamilo 1991). The optima for workers and offspring males are both affected by the proportion of worker-produced males and the queen's mating frequency. This is because the queen's mating frequency affects their relative relatedness to males and females (r_m and r_f) while the proportion of worker-produced males changes the sex-specific reproductive value of males and females (V_m and V_f ; Boomsma & Grafen 1991; Pamilo 1991).

3. FACTORS AFFECTING POWER

Trivers & Hare (1976) were probably the first to mention power. They predicted that workers collectively would have greater power over sex allocation than the queen, because they tend and feed the brood and because they outnumber the queen. They also stated two mechanisms by which the queen would have power over male production: aggression towards reproducing workers and remembering or learning which eggs were hers and killing

any other egg. It seemed more likely to Trivers & Hare (1976) that the queen could exert power over a single act (preventing a worker from laying an egg) than multiple acts (feeding of brood). The main reason why the queen is likely to have considerable power over preventing egg laying by a worker is because of asymmetry in aggressive encounters. If a worker kills the queen, this will greatly reduce the worker's inclusive fitness because by doing so she not only loses the specialized egg-layer but also the producer of highly valuable sisters. Moreover, the worker runs the chance of killing the whole colony by killing the queen, whereas if the queen kills a daughter-worker this will have a minor effect on both the queen's fitness and colony survival.

This discussion of Trivers & Hare (1976) shows that power has sometimes been considered explicitly. However, who has power is usually an implicit assumption in the study of reproductive conflicts in insect societies. Typically, it is assumed that one party, usually the workers, or prior to Trivers & Hare (1976) the queen, has the power to fully control colony reproduction. But it could well be that a party of interest has only partial power. The extent to which a party with partial power can exercise power may then depend on the costs of manipulating. A party who can only exercise power at a considerable cost to itself or the colony as a whole would have little power in relation to a party who could exercise power at a low cost. Although costs do not directly affect the physical power of different parties, costs are important because they determine the inclusive fitness consequences of any physical act of manipulation.

In § 3a–e we discuss factors that affect power with the aim of identifying general principles based on the mechanisms available to different parties of interest to influence colony reproduction (table 2).

(a) *Physical presence*

It seems generally necessary to be physically present to influence colony reproduction. One class of individuals, who represent several parties of interest, are absent for much of the time: males.

In social Hymenoptera, fathers are present only as sperm stored in the queen's spermatheca. Diploid parents are not in conflict over sex allocation because both transmit genes to sons and daughters. However, under arrhenotoky (haplodiploidy with haploid males) fathers pass on their genes only to daughters because a male has no father. Thus, hymenopteran parents are in conflict over sex allocation. In colonies in which the workers assess the queen's mating frequency and adjust the sex allocation accordingly (female-biased sex allocation when the queen has a low mating frequency; Boomsma & Grafen 1990, 1991), fathers might exert power by clumping their sperm when the queen is inseminated by more than one male. By contrast to diploids, where sperm of a single male are potentially in conflict, the interests of every single sperm cell of a hymenopteran male are identical making it more likely that sperm clumping occurs because it can lead to more females being produced than when no clumping occurs (Simmons 2001). (But note that even though sperm of several fathers in a queen are in agreement in that they want a female-biased sex ratio, and hence may benefit by not mixing—i.e. they remain in clumps—they

Table 2. Basic mechanisms that determine power over reproduction.

party	mechanism
queen	fertilize egg
worker	activate ovary and lay eggs feeding brood killing males
male and female brood	obtaining food/cannibalize siblings
female larva	choose developmental pathway
father male ^a	clump sperm ^b leave mating plug ^c avoid non-virgins ^d conditional sperm transfer ^b

^a Mechanisms that can be used by father males are all indirect mechanisms, i.e. the father is not physically present during the period in which conflicts over reproduction occur. Another possible indirect mechanism is genomic imprinting, where paternal genes can (in theory) influence the behaviour of the female individual they are in, in favour of their own spread (Haig 1992b; Queller & Strassmann 2002). However, paternal genes can only do this if they 'know' that they are derived from the father (Queller & Strassmann 2002), a situation similar to asymmetry in information in, for example, *Dinoponera quadricaps* where the high-ranking workers cannot act owing to limited information.

^b These mechanisms are aimed at workers assessing the colony as singly mated. This would then result in the workers biasing the sex ratio towards females, which is in the interest of the father (Boomsma 1996).

^c By leaving a mating plug a male can prevent other males from mating with the queen (Baer *et al.* 2001).

^d Under very strict conditions the father avoids siring workers that will bias the sex ratio towards males by avoiding mating with non-virgins. This requires: (i) a population in which workers bias the sex ratio depending on the mating frequency of the queen; (ii) the ability of males to determine whether or not a female is a virgin; and (iii) all colonies headed by multiple-mated queen should always produce male-only sex ratios (Boomsma 1996).

are still in conflict over whose sperm fertilizes the eggs that develop into queens.) When sperm are clumped, even if the queen has mated multiply, the effective paternity will be low (Trivers & Hare 1976; Boomsma 1996; Boomsma & Ratnieks 1996; Sundström & Boomsma 2000). This results in the colony being effectively single mated for the period of time in which sperm of the same male is used (Boomsma & Ratnieks 1996) which could result in the workers assessing the colony as singly mated and therefore biasing the sex ratio towards females, which is in the male's interest. Hence, males potentially have some indirect means to exert power even though they are present only as stored sperm. Such indirect effect has recently been shown to occur in *Formica truncorum* (Sundström & Boomsma 2000). Sperm of males of *F. truncorum* were shown not to be used evenly over time and this resulted in workers raising more females than expected based on the overall relatedness asymmetry owing to multiple mating if sperm were used evenly and equally over time.

Offspring males, although of the same generation as their sister workers, are not present for most of the year in most species. As a result, if sexuals are reared in one cohort adult offspring males are not around to manipulate the colony's reproductive output. However, there may be situations where an offspring male has some power. One example is the stingless bee *Trigona postica*. When more than one egg is laid in a cell, for example owing to both the queen and a worker laying, the male, who hatches first, eats the female egg (Beig 1972).

The importance of physical presence (or absence) is not restricted to males. In mass provisioners (e.g. stingless bees (Michener 1974) and some bumble-bee species (Free & Butler 1959)), adult workers have no physical presence in a cell, giving greater power to the larva (or larvae) inside. In many species, there is only one larva per cell and this larva cannot compete directly, except in the case mentioned above when two eggs are laid in the same cell. However, in so-called pocket-making bumble-bee species, a single cell contains many larvae and cannibalism can occur (a possibility discussed by Hamilton (1964)). But physical presence is clearly not sufficient because one could be present but have no access. In some ant species, such as weaver ants and the attine ants *Atta* and *Acromyrmex*, there is only one queen but several brood chambers (Hölldobler & Wilson 1990). The workers transport brood to these brood chambers for rearing. This results in locations that may be inaccessible to the queen and hence will be out of her direct control.

(b) Physical strength

In rare cases power over reproduction is just a matter of sheer physical power. In multiple foundress associations, where several mated females initially initiate a nest but where foundresses fight as soon as the first workers have emerged, the strongest female is often the female that kills the others and inherits the nest (Bernasconi & Strassmann 1999). In most other social insects, queens are often larger than workers, which may give them an advantage in physical dominance. In small societies, queens can have considerable power over worker reproduction through egg eating and physical domination (queen policing; Oster & Wilson 1978). Queen policing is well documented in ponerine ants (Monnin & Ratnieks 2001), polistine wasps (Spradbery 1991), halictine bees (Brothers & Michener 1974; Fletcher & Ross 1985) and bumble-bees (Free *et al.* 1969; Fletcher & Ross 1985). However, it seems unlikely that queen policing will be a feasible mechanism in large societies simply because there are too many workers for the queen to physically control (Seeley 1985; Ratnieks 1988; Keller & Nonacs 1993).

(c) Power of numbers: brood rearing and the individual versus the collective

Workers outnumber the queen and normally rear the brood. Therefore, it is generally assumed that they have the greatest power over sex allocation, except in slave makers. In addition, workers collectively 'agree' on which sex to favour: the sex that is more valuable to them. It therefore seems likely that the queen is relatively powerless against the manipulation by her workforce when conflicts occur. But, as we discuss in the following paragraphs, there are exceptions in which the queen, although only a

single individual and not involved in brood rearing, may be able to control sex allocation.

The power of the collective is evident in worker policing, the selective removal of worker-laid eggs by other workers. In insect societies with a single queen mated to two males or more, the workers collectively and the queen 'agree' on whose sons are reared: i.e. the queen's sons (Ratnieks 1988). However, the interests of an individual worker are at variance with the workers collectively because each worker is more related to sons (0.5) than any other type of male that could be reared in the colony (brother 0.25; full sister worker's son 0.375). In honeybees these eggs seldom result in worker-produced males because other workers kill worker-laid eggs (Ratnieks & Visscher 1989; Ratnieks 1993; Visscher 1996; Barron *et al.* 2001).

When conflict occurs between the workers and the queen over sex allocation, workers have two main manipulative mechanisms. They could selectively kill queen-produced males or they could adjust the food fed to larvae and rear queens instead of workers. There is convincing evidence for sex-ratio biasing by workers in several ant species (for instance in *Solenopsis invicta* (Aron *et al.* 1995), *Pheidole pallidula* (Keller *et al.* 1996), *Linepithema humile* (formerly *Iridomyrmex humilis*) (Passera *et al.* 1995), *Formica truncorum* (Sundström 1994) and *F. exsecta* (Sundström *et al.* 1996)), presumably by selective killing of males. The second mechanism, preferentially rearing queens from totipotent female brood (i.e. brood that can be reared into workers and queens), occurs in the ant *Leptothorax acervorum* (Hammond *et al.* 2002).

Several factors (access to brood, ability to recognize gender and maternal origin of brood when sexual and worker brood are reared) affect whether the workers can bias the brood sex ratio in a more female direction (i.e. in the direction of their optimum when the primary sex ratio reflects the queen's optimum) or selectively remove brood of the un-preferred maternity (as in worker policing).

If workers do not have access to brood or do not provision brood, such as in slave makers or in species where brood are reared in sealed cells on a provision mass, the power of workers to manipulate sex allocation will be minimal. But even when workers do have access to brood, they must be able to discriminate between males and females. If they can discriminate at an early stage, for example eggs or young larvae, this will lower the costs of sex-ratio biasing, especially when the mechanism is selective killing (Nonacs 1993). When workers cannot distinguish between haploid and diploid brood at an early stage or when error rates are high, the costs of eliminating male brood will be much higher and sex-ratio biasing is not likely to be favoured. However, there is one exception, and that is when investment made in males can be re-allocated towards females. This could even result in the usage of males as food storage when the food itself cannot be stored and when female and male brood are present at the same time, as is the case in many ants. This is probably the reason why in the wood ant *F. exsecta* larval males are killed only when nearly full grown (Chapuisat *et al.* 1997). Male brood are killed when the developing female larvae need large amounts of food, and it was suggested by Chapuisat *et al.* (1997) that workers feed males to female brood, thereby re-allocating investment made in males to

females. Ants are primarily carnivorous, as are wasps, and this pre-adapts them to this mechanism by contrast to herbivores, such as bees, and fungivores, such as attine ants.

Even though power is often in numbers, there are various factors that can give power to individuals. For example, anarchistic honeybees are workers that lay eggs that are not policed thereby allowing them to reproduce in queenright colonies in which normal worker-laid eggs are policed (Oldroyd & Ratnieks 2000). Queens can have increased power over sex allocation by laying diploid eggs for which the caste fate has already been determined or by laying only one type of egg (either all haploid or diploid) during the period in which sexuals are reared thereby forcing workers to invest in whichever sex the queen chooses. Queen power over sex allocation has been shown in *Pheidole desertorum* (Helms 1999) and the monogyne form of the fire ant *Solenopsis invicta* (Passera *et al.* 2001). Colonies of *P. desertorum* and *S. invicta* produce either all males, almost exclusively males, or all females yielding a population sex ratio that is close to 1 : 1, which is the queen's optimum (Trivers & Hare 1976). These split sex ratios are not caused by differences in relatedness asymmetry, because all colonies are headed by one singly mated queen. The colony's sex ratio is determined solely by the queen because she lays either only haploid eggs or only diploid eggs during the period in which sexuals are produced. (However, it could be that in male-specialist colonies the queen does lay diploid eggs during the reproductive period but the queen somehow ensures that these eggs are destined to develop into workers, which prevents the workers from biasing the secondary sex ratio. Whether caste determination in the egg stage occurs is currently unknown (K. R. Helms, personal communication).) Because half of the colonies produce only or almost exclusively males, queens of the other colonies are selected to produce only females, resulting in a population sex ratio that is close to equality (Helms 1999). When queenless *P. desertorum* workers from male-specialist colonies were given brood of both sexes, workers reared reproductive females but failed to rear males, showing that the workers of male-specialist colonies do prefer to rear queens but are prevented from doing so by their queen (Helms *et al.* 2000). Swapping *S. invicta* queens from male-specialist colonies to female-specialist colonies, and vice versa, resulted in the host colonies producing the same sex ratio as the donor colony (Passera *et al.* 2001). This clearly shows that in these cases it is the queen that controls the sex ratio in *P. desertorum* and *S. invicta*. Interestingly, queen control does not seem to be universal in *S. invicta*. Aron *et al.* (1995) showed that in their monogynous colonies the secondary sex ratio was more female biased than the primary sex ratio, suggesting some worker control.

(d) *Access to food*

In most social Hymenoptera with morphologically distinct female castes, caste differentiation depends on differential feeding in the larval stage. Queens are typically larger and require more food, or, in some species such as honeybees, special food. This means that when brood are unable to influence their food intake, they are not likely to have much power over their own caste fate. In all social Hymenoptera brood consists of legless larvae which, in most species, completely depend on the workers that feed

them. Hence, there seems little opportunity for brood to influence either their colony's reproduction or even, in the case of females, their own caste fate.

An individual female larva can potentially increase her fitness by developing into a queen instead of a worker, because any female is more related to her own offspring than to a sister's offspring (Bourke & Ratnieks 1999; Ratnieks 2001). Brood power is evident in *Melipona* stingless bees in which workers and queens develop in sealed cells of similar size. Although there is worker–queen dimorphism, the queens are not heavier than workers on emergence (T. Wenseleers, personal communication) so that a normal provision mass is sufficient to rear either a queen or a worker. This, combined with the absence of worker–brood interaction owing to sealed cells and mass provisioning, should give female larvae the power to determine their own caste fate (Bourke & Ratnieks 1999; Ratnieks 2001), which results in large numbers of queens being reared. The resulting conflict between the developing female brood and the workers is finally resolved with the workers killing newly emerged queens (Imperatriz-Fonseca & Zucchi 1995; Koedam *et al.* 1995). The idiosyncratic ability of *Melipona* larva to determine their own caste fate, combined with the absence of differences in size between queens and workers, allows us to see the actual caste-fate conflict which is potential in all social Hymenoptera. In this respect, *Melipona* can be seen as the exception that proves the rule.

When there is queen–worker size dimorphism, such as in Trigonini (sister clade to *Melipona*, the only genus in Meliponini), workers control food intake by building large and small cells. But even then female brood may still influence their own caste fate. In some trigonine bees, a larva reared in a worker cell may break into a neighbouring cell and thereby have enough food to develop into a queen (Engels & Imperatriz-Fonseca 1990; Velthuis & Sommeijer 1991). In other Trigonini dwarf queens occur (Imperatriz-Fonseca *et al.* 1997; Ribeiro 1998) and these are suggested to be a female strategy to develop into a queen on a food mass insufficient for a full-sized queen (Bourke & Ratnieks 1999). Dwarf queens have lower, but still considerable, fecundity, suggesting that a dwarf queen of a swarming species can adequately head a colony (Ribeiro & Alves 2001) and that a larva can benefit from becoming a dwarf queen even if the success of the colony is less than one headed by a full-sized queen.

(e) *Asymmetry in information*

Information is fundamental in the organization of cooperative activities in insect societies. For example, honeybees communicate distant food locations (Beekman & Ratnieks 2000) and the whole colony is able to focus foraging on the most rewarding flower patches (Seeley 1995). Information is also used in the regulation of reproduction, and can greatly affect power relations. Information can increase the power of an individual over a group, but it can also favour a group over an individual. A good example of information benefiting the group is worker policing by egg eating in the honeybee. The honeybee queen marks her eggs thereby ensuring that queen- and worker-laid eggs can easily be distinguished, ensuring the removal of the latter by other workers (Ratnieks 1995; Ratnieks & Visscher 1989). The signal is favoured because there is no

conflict between the workers as a collective and the queen, and hence both the signal receiver and producer benefit. When eggs are marked, so that queen-laid and worker-laid eggs can be distinguished, the workers could use this information to kill either type of egg. Worker policing by killing of worker-laid eggs has been detected in three species of *Apis* honeybees (Barron *et al.* 2001) and also in three species of Vespinae wasps (Foster & Ratnieks 2001a,b). In *Vespa crabro*, queenless colonies show 'reverse' policing (Foster *et al.* 2002). That is, queen-laid eggs are killed. This is probably because queen supersedure with a related queen does not occur in annual Vespinae wasps, whereas queen takeover by an unrelated queen does (Foster *et al.* 2000). Thus, if queen-laid eggs appear in a queenless nest they will have been laid by an unrelated queen rather than by related sister workers (see also Ratnieks *et al.* (2001)). This example suggests that the same information can be used to favour opposing groups under different reproductive circumstances.

In some cases, one party may have better information and thereby have more power. In the queenless ant *Dinoponera quadriceps* each colony is headed by a single worker, known as the gamergate, mated to an unrelated male. Workers of *D. quadriceps* show a linear hierarchy with high-ranking workers occasionally laying (haploid) eggs (Monnin & Peeters 1997). The eggs laid by the gamergate are chemically distinct from those laid by the high-ranking workers (Monnin & Peeters 1997). Presumably, therefore, both gamergate and high rankers can distinguish eggs laid by the other party. Owing to single mating the workers are more related to worker's sons (relatedness to sons and nephews 0.5 and 0.375, respectively) than the gamergate's sons (brothers 0.25). However, egg eating consists almost entirely in the gamergate eating worker-laid eggs. Workers rarely eat gamergate-laid eggs. Given that the information on egg maternity is, presumably, available to both gamergate and high rankers, why is it only the gamergate who eats eggs? The probable reason is that even though the information on egg maternity is symmetrical, the information it provides is insufficient for the workers, but not for the gamergate, to police eggs without great cost to the colony. In particular, the eggs laid by the gamergate are mostly female eggs. If these are killed by workers this will reduce colony growth. Conversely, the workers are all unmated and their eggs are, therefore, male. The gamergate can kill these without affecting colony performance. If the workers cannot determine the gender of the gamergate's eggs, why not wait until they hatch and kill male larvae? Evidence from other ant species suggests that the gender of larvae can be detected (Peacock *et al.* 1954; Brian 1981; Vargo & Fletcher 1986a; Aron *et al.* 1995), although this may not be true for all ant species (e.g. Nonacs & Carlin 1990). But data from the honeybee also suggest that the maternal origin of eggs cannot be determined in the larval stage (Ratnieks & Visscher 1989). In other words, workers never know both the gender and maternal origin of either eggs or larvae. Only the gamergate has sufficient information to gain from killing eggs laid by the other party. It is sometimes said that 'information is power'. A gamergate of *D. quadriceps* appears to be an example of this.

There are other examples where the breeder female may magnify her power via better information. Bumble-bees

have an annual life cycle in which at first only workers are produced (ergonomic phase) followed by a reproductive phase (Macevicz & Oster 1976; Beekman *et al.* 1998). Only in the reproductive phase will the queen lay haploid eggs and will diploid brood be reared into queens. The queen in the bumble-bee *Bombus terrestris* presumably knows when she starts to lay haploid eggs whereas the workers do not. Because the queen mates only once (Estoup *et al.* 1995) she and the workers collectively are in conflict over male parentage. Early males will have a higher mating success (Bulmer 1983; Bourke 1997; Beekman & Van Stratum 1998), hence workers can only increase their fitness by producing males early. *B. terrestris* shows split sex ratios with approximately half of the colonies specializing in male production and half in females (Duchateau & Velthuis 1988; Beekman & Van Stratum 1998). Because sister-queens are highly valuable to the workers (especially given the fact that the population sex ratio is male biased; Bourke 1997; Beekman & Van Stratum 1998), workers should only try to produce males themselves if this does not jeopardize the production of queens (Beekman 1998). This gives the queen power, because by not laying haploid eggs before queens are being raised, the queen assures the co-operation of her workers in colonies that specialize in queens (Bourke & Ratnieks 2001). In colonies that specialize in males, the workers should try to reproduce as soon as they notice the presence of queen-produced male brood (Bourke & Ratnieks 2001). However, the workers probably do not know that the queen is producing males for some time. By the time they do, it is no longer worthwhile to replace brothers for worker-produced males, because these males will emerge too late to have sufficient chances to mate (Beekman 1998; Beekman & Van Stratum 1998; Bourke & Ratnieks 2001). The bumble-bee queen thus has more power because she 'knows' the sex of the eggs she lays whereas the workers do not.

But even though information is power, there are possible counter-strategies to manipulations relying upon information advantages. Ant workers could carry their eggs around to prevent them from being policed by the queen or gamergate. How successful this will be probably depends on the colony size, because in small colonies the queen could easily check workers for eggs and kill them (Monnin & Ratnieks 2001). Alternatively, workers could hide their eggs in the egg pile (see reference in Bourke (1994)) thereby making them harder to check and also mixing the egg odour with odours from other eggs (cue scrambling), which occurs in, for example, the ponerine ant *Pachycondyla obscuricornis*. Marking your own eggs as if they were queen-laid eggs, as the anarchistic honeybees apparently do (Oldroyd & Ratnieks 2000), is also a counter-strategy.

4. THE DEVIL IN THE DETAILS

In § 3 we have given examples of biological details that give one party of interest more power, for instance the ability to determine one's own caste fate in mass provisioners when there is no worker-queen dimorphism. Here, we focus more generally on how power can be affected by many details of the biology which can be idiosyn-

cratic at any taxonomic level, from order to subspecies. At the order level, Hymenoptera and Isoptera (termites) differ in many ways that affect power. Hymenoptera are homometabolous and all brood stages are immobile and relatively helpless. Isoptera, however, are hemimetabolous. Working individuals are nymphs but in many species they retain the ability to transform themselves into reproductives via ecdysis and metamorphosis (De Wilde & Beetsma 1982). Because the worker morphs are not terminal instars (except in Termitidae), developmental strategies in termites are more flexible (De Wilde & Beetsma 1982). This developmental plasticity probably allows termite juveniles to have more power over their own caste fate. For example, in the lower termites (Termopsidae) any juvenile can function as a temporary worker, develop into a specialist fighting morph (soldier) or become a replacement reproductive at any moult after the third developmental stage, and before the penultimate moult (Castle 1934; Light & Weesner 1951; Miller 1969; Shellman-Reeve 1997). In addition, immatures can delay, speed up or even reverse their physiological and morphological development (Light & Weesner 1951; Miller 1969; Noirot 1985; Roisin 1988; Shellman-Reeve 1997). Offspring males work (De Wilde & Beetsma 1982) and the reproductives of both sexes are present in the colony so that male termites may have more power compared with hymenopteran males. Although termites are diploid, conflicts over the sex ratio and/or the replacement of one or both primary reproductives exists in species in which genetic material is transmitted to the next generation of the same sex via rings or chains (Vincke & Tilquin 1978; Luykx 1987; Martins 1999). These rings or chains can consist of up to 50–60% of all the chromosomes and thus result in relatedness asymmetries between the two sexes and consequently in potential conflicts between the sexes (Roisin 2001). Being physically present in the colony as male helpers gives termite helper-males the power to bias the sex ratio, something that is impossible for hymenopteran offspring males. However, physical presence may not necessarily be an advantage for the male reproductive, the king. In the fungus-growing termites (Macrotermitidae) both the king and queen are confined to a royal chamber that is built by the workers (Bruinsma 1979; De Wilde & Beetsma 1982) and this does not seem to be much different from being present only as stored sperm.

As we discussed in the previous paragraph, the way hymenopteran brood are reared can have a large effect on power. Across the social Hymenoptera, the types of cells used in brood rearing vary considerably among social groups, and at a variety of taxonomic levels. Table 3 gives an overview of the different types of brood rearing found among social Hymenoptera and its possible effect on power. Earlier we discussed the power of brood when brood are reared in sealed cells and are mass provisioned. When brood and food mass are together, larvae have more control over food intake. Similarly, when more than one larva is present in a cell, cannibalism can occur, again giving an individual more power. The absence of cells may also give brood more power. Ants do not rear their brood in cells but sort brood according to size. This means that ant brood may have more power over food intake compared with brood of bees and wasps that depend on their sisters to feed them, because ant brood have the possibility

Table 3. Features of brood rearing that affect the basic mechanisms of power over reproduction as mentioned in table 2. (The plus signs refer to an increase in power and the minus signs to a decrease.)

brood-rearing feature	example taxa	effect on power	mechanism	context
no cells	ants	+ adult workers	aggression towards queen-destined brood	caste fate
		- female brood	food control	
		+ adult workers - brood	killing male larvae biasing female rearing towards more queens	sex allocation
		+ individual larva	cannibalism	caste fate (female) survival (male)
many eggs per cell	pocket-making ^a bumble-bees	+ individual larva	food control cannibalism	caste fate (female) survival (male)
open cells, one egg per cell	Vespidae wasps honeybees	- individual larva	food control cannibalism	caste fate (female) survival (male)
mass provisioned cells of same size	<i>Melipona</i> bees	+ queen	selective male killing by workers not possible	sex allocation
		+ female brood	food control	caste fate
sexuials reared in distinct cohort	<i>Formica</i> ants ^d	+ queen	workers less able to rear more queens ^b	sex allocation
only one type of egg present (haploid/diploid)	<i>Solenopsis invicta</i> <i>Pheidole desertorum</i>	+ queen	less able to bias sex ratio ^c	sex allocation

^a In pocket-making bumble-bees eggs are laid on a provision mass in one cell.

^b Workers cannot easily trade-off workers for queens.

^c Workers cannot easily trade-off males for queens.

^d L. Sundström (personal communication).

to cannibalize on siblings. However, access to brood also gives the adult workers more power. In several polygynous ant species, workers starve, attack or cannibalize queen-potential larvae (Brian 1973; Vargo & Fletcher 1986a,b; Edwards 1987, 1991; Keller *et al.* 1989; Vargo & Passera 1991; Keller & Passera 1992). This either leads to the larvae being killed, or it may cause them to develop into workers rather than queens (Bourke & Ratnieks 1999). Hence, although in general we can say that access to food and the ability to process food affects power, idiosyncrasies related to brood rearing ultimately determines which party is the most powerful.

Sometimes idiosyncrasies can be highly unusual or bizarre. The Cape honeybee, *Apis mellifera capensis*, is the only subspecies in which workers lay female eggs by thelytoky rather than male eggs by arrhenotoky. This results not only in worker reproduction being less costly to the colony because workers' offspring turn into new workers (Greeff 1996) but also gives unmated workers the possibility to produce queens. In the ponerine ant *Diacamma* the presence of gemmae is another bizarre idiosyncrasy. It seems difficult to imagine that these gemmae are important in reproductive conflicts, yet they are necessary for mating and provide adult workers and the gamergate a method by which power over individual workers can be exercised. Interestingly, gemmae mutilation does not occur in all species of *Diacamma* (Peeters *et al.* 1992).

5. SOCIAL HYMENOPTERA VERSUS SOCIAL VERTEBRATES

Social Hymenoptera are not the only social animals. To what extent do the generalizations above apply to vertebrate societies? As in social insects (social Hymenoptera and termites), many general factors may affect power relations in vertebrate societies, such as colony or group size (which determines how many subordinates must be controlled), information (birds may find it harder to recognize the maternity of an egg, whereas it is probably easier to determine who is the mother of a mammalian young), as well as a wide variety of taxon-specific details. One important difference is that hymenopteran societies are basically single-sex societies whereas in vertebrates (and termites) males and females are both important parties in the control of reproduction and the conflict over it. The presence or absence of males has significant implications for the importance of mating in the regulation of reproduction. For example, in many primate societies a male may be able to control reproduction by preventing another male from mating with an oestrous female. In hymenopteran societies, mating is rarely part of social life. Where it is, as in the ant *Cardiocondyla*, there are interesting male-male conflicts and special fighting male morphs (Cremer & Heinze 2002). So, in comparison with hymenopteran societies, vertebrate societies introduce a major

new conflict, that over mating, into social life. In Hymenoptera the conflicts are mainly around aspects of egg laying, brood rearing and the replacement of the breeder rather than who mates with whom.

Another major idiosyncrasy between social Hymenoptera and social vertebrates is the haplodiploid sex determination system. This allows precise control over the sex ratio of offspring and gives the breeder female far more power because she can choose different sex ratios as discussed earlier. Although conflicts over sex ratios owing to asymmetrical relatedness do not occur in (social) vertebrates, there are often other reasons why breeding pairs can benefit from a biased sex ratio. For example, if helpers enhance the fitness of the breeding pair and only offspring of a certain sex help, parents could profit from biasing the sex ratio towards the helper sex. Sex-ratio biasing is known to occur in some social birds (e.g. in Seychelles warblers (Komdeur 1996; Komdeur *et al.* 1997); see also West & Sheldon (2002) for a recent meta-analysis on sex-ratio biasing) and may be facilitated in birds where it is the female that is the heterogametic sex contrary to (social) mammals where sex-ratio biasing seems to be absent (see Brown (2001) for a review on sex ratios in non-human primates).

Finally, both social birds and mammals have helpers at the nest and it may well be the case that reproduction by bird subordinates is easier than for mammal subordinates. Pregnancy is probably harder to conceal than the much briefer and less overtly obvious period in which a female bird is maturing an egg. Similarly, egg laying is much briefer than giving birth.

6. GENERAL DISCUSSION

The purpose of this paper is to explicitly discuss the concept of power over reproduction and present factors that give an individual or a group more or less ability to manipulate colony reproduction. Power enables an individual or a group to influence the colony's reproductive output against the interest of other individuals or groups within the same colony. In theory this may result in an arms race between different parties of interest with selection acting on the losing party to regain control. Hence, one could say that power is inherently unstable and that the winning party of today will be the losing party of tomorrow. However, there could be parties of interest that are never likely to gain power because there is nothing to select for to regain power. Honeybee workers can be selected to lay eggs that escape policing, as the anarchistic honeybees show. But it is hard to imagine how a newly enclosed *Diacamma* worker can prevent being mutilated. And when a queen has full control over caste determination of the diploid eggs she lays, it is hard to see how selection on workers can remove that power from her.

The concept of power is not unique to social insects or social animals. Power is important wherever individuals interact and conflicts occur. Alexander (1974) and Trivers (1974) mentioned power in relation to parent-offspring conflict where there is disagreement between the parent (usually the mother) and the offspring in the amount of investment made in offspring by the parent. General consensus is that it is the parent that has the most power, simply owing to physical superiority. But the offspring

could exert power in a more subtle, or 'psychological', way by reverting to gestures and behaviours normally employed in a much earlier developmental stage (Trivers 1974). Because parents are likely to be selected to respond positively towards signals of need emitted by young offspring, by pretending to be younger, offspring can manipulate their parents into providing more resources than the parent would normally want to give (Trivers 1974).

Conflicts occur even in our own bodies, as we consist of genetic material originating from our mother and our father, and the interests of both may not necessarily coincide (Haig & Westoby 1989; Haig 1992a). Or we may contain self-promoting elements that try to manipulate their 'host' so as to promote their own spread at the expense of altruistic genetic material (Hurst *et al.* 1996). In genetic conflicts, the parties of interest are the self-promoting element and its suppressor and all genes that do not benefit by the manipulation. The relative power of the parties of interest determines the ultimate outcome in much the same way as we have described for social Hymenoptera (Hurst *et al.* 1996). As in social insects, certain potential conflicts may never result in actual conflicts owing to idiosyncrasies that give complete power to one party. An example is genomic imprinting. Here, there is a potential conflict between the paternal and maternal genome in that the fetal paternal genes want the foetus to obtain more resources from the mother than the fetal maternal genes would prefer. The expression of such conflicts is possible in mammals and angiosperms where the contact between foetus and mother is intense. The same potential conflict is present in birds, but here this is not likely to result in an actual conflict because the chick develops independently of the mother (Hurst *et al.* 1996).

Our aim has been to identify some general principles of power that can complement factors such as kin structure in understanding the reproductive characteristics of insect societies. Unlike the inclusive fitness theory of Hamilton (1964), power is not a general theory although there are some general principles. Information, access to brood or to food, and numbers are all important general principles affecting power across social insects as well as other social animals. Although not as elegant as the 'c, b and r' of Hamilton's rule (1964), these general principles provide some guidelines for further study. Alongside these general principles, power has a myriad of biological details which can be important, even crucially important. These biological details can be found at any taxonomic level. These idiosyncrasies could be at a high taxonomic level and have to do with some basic element of its biology (haplodiploidy versus diploidy) or some small detail like the gemmae of *Diacamma*. Here, we have only touched upon some principles, both general and idiosyncratic, that determine power over reproduction in insect societies. This is because we do not know all the factors that determine power. But we hope that we have provided enough examples and delineated sufficient principles to act as a catalyst for other researchers to do the same and to look at their own study species from a new angle.

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