

Caste fate conflict in swarm-founding social Hymenoptera: an inclusive fitness analysis

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Abstract

A caste system in which females develop into morphologically distinct queens or workers has evolved independently in ants, wasps and bees. Although such reproductive division of labour may benefit the colony it is also a source of conflict because individual immature females can benefit from developing into a queen in order to gain greater direct reproduction. Here we present a formal inclusive fitness analysis of caste fate conflict appropriate for swarm-founding social Hymenoptera. Three major conclusions are reached: (1) when caste is self-determined, many females should selfishly choose to become queens and the resulting depletion of the workforce can substantially reduce colony productivity; (2) greater relatedness among colony members reduces this excess queen production; (3) if workers can prevent excess queen production at low cost by controlled feeding, a transition to nutritional caste determination should occur. These predictions generalize results derived earlier using an allele-frequency model [*Behav. Ecol. Sociobiol.* (2001) 50: 467] and are supported by observed levels of queen production in various taxa, especially stingless bees, where caste can be either individually or nutritionally controlled.

Introduction

Societies of eusocial Hymenoptera (ants, and many bees and wasps), are characterized by a high degree of cooperation (Wilson, 1971; Hölldobler & Wilson, 1990; Seeley, 1995). However, the nonclonal structure of their societies also causes conflict. Traditionally, four major conflicts have been studied (Bourke & Franks, 1995; Crozier & Pamilo, 1996): (1) queen-worker conflict over the sex ratio, (2) conflicts over male parentage, (3) conflicts over female parentage ('nepotism'; Ratnieks & Reeve, 1992) and (4) conflict over reproductive dominance (e.g. in foundress groups). Recently, however, an additional conflict – that over female caste fate – has

attracted considerable attention (Ratnieks, 1989, 2001; Bourke & Ratnieks, 1999; Reuter & Keller, 2001; Strassmann *et al.*, 2002). In social Hymenoptera, immature females are generally genetically totipotent, and in species with morphological castes each can be reared irreversibly into either a queen or a worker (Wilson, 1971). However, according to caste conflict theory, females would often benefit if they could develop as queens rather than workers, in order to gain greater direct reproduction (Bourke & Ratnieks, 1999; Ratnieks, 2001). In social Hymenoptera without morphological castes, where all females are totipotent, conflicts over who takes on the breeding role have long been recognized (e.g. West-Eberhard, 1967, 1978, 1981; Strassmann, 1989) and their study continues to be an important area of research (e.g. Reeve & Nonacs, 1992; Monnin & Ratnieks, 1999, 2001; Monnin *et al.*, 2002). However, that the same conflict can also occur in species with morphological castes is a relatively new idea (Ratnieks, 1989, 2001; Bourke & Ratnieks, 1999). Yet, the consequences of caste conflict on the functioning of the

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colony can be profound. When females can control or influence their own caste fate, caste conflict is predicted to lead to more females selfishly choosing to develop as queens than is optimal for colony function (Ratnieks, 2001; Reuter & Keller, 2001; Strassmann *et al.*, 2002). With more females developing into queens the workforce is diminished leading to a reduction in total lifetime colony reproduction (i.e. a smaller colony reproduces less, survives less or both).

Although caste conflict in social Hymenoptera is expected under a wide range of conditions (Bourke & Ratnieks, 1999; Ratnieks, 2001; Reuter & Keller, 2001; Strassmann *et al.*, 2002), in societies with morphological castes, it is usually present only in latent or 'potential' form (Bourke & Ratnieks, 1999). This is because in such species, the passive female brood rarely have the ability to control their own caste fate, as caste is usually determined by the amount or quality of the food given to larvae by workers ('nutritional caste determination'; Wilson, 1971; Michener, 1974; Wheeler, 1986). By food control, the adult workers can coerce immature females to develop as workers. For example, in honeybees, female larvae develop into queens only when fed large amounts of special food, royal jelly, provisioned in special queen cells (Winston, 1987).

However, in one group of highly eusocial insects, *Melipona* stingless bees, the caste fate of female brood can be controlled by the immature female individual herself (Bourke & Ratnieks, 1999, reviewed by Wenseleers & Ratnieks, 2003). This is because *Melipona* queens and workers are of the same size and are reared from identical, mass-provisioned sealed cells (Wilson, 1971; Michener, 1974). These conditions prevent the adult workers from coercing the immature females and allow caste to be self-determined – prerequisites for actual caste conflict to be observed. In agreement with this prediction, *Melipona* produce a great excess of queens. Stingless bees reproduce by swarming (Engels & Imperatriz-Fonseca, 1990). That is, daughter colonies are founded by queens accompanied by a swarm of workers. Colonies, therefore, require only few queens to be reared, just enough to permit seasonal swarming or supersedure of a failing mother queen. In *Melipona*, however, up to 25% of all females are reared as queens, and most of these are executed by the workers within hours or days of emergence (Kerr, 1950; Engels & Imperatriz-Fonseca, 1990; Imperatriz-Fonseca & Zucchi, 1995). Although such queen overproduction has long been considered paradoxical (Engels & Imperatriz-Fonseca, 1990), it can now be explained on the basis of caste conflict theory (Ratnieks *et al.*, 2001). In other stingless bees (Trigonini), queens are normally larger than workers, and caste is determined by nutrition, as in the honeybee (Engels & Imperatriz-Fonseca, 1990; Wenseleers & Ratnieks, 2003). In trigonine stingless bees few queens are reared, in keeping with colony

needs (e.g. in *Tetragonisca angustula*, only approximately four queens are reared over an entire season; van Veen & Sommeijer, 2000).

Although the above observations provide good general support for caste conflict theory, additional, more detailed, tests would be desirable. However, such tests require a solid theoretical basis in order to make predictions about the expected level of excess queen production. Ratnieks (2001) showed that for swarm-founding social Hymenoptera, the optimum or 'evolutionarily stable' proportion of females that should develop as queens ranges from 14 to 20% depending on whether the colony's males were produced by the workers or the queen (workers in many species of eusocial Hymenoptera, including *Melipona*, retain ovaries and can lay unfertilized, male, eggs). These predictions were derived using an allele-frequency model and although rigorous, this method has several disadvantages. In particular, it requires evolutionary stable strategy (ESS) ratios to be derived separately for each colony kin structure (e.g. single or double mating) which is impractical for all but the simplest colony structures (e.g. one queen mated to one or two males).

The aim of this paper is to develop caste conflict theory using inclusive fitness methods (Hamilton, 1964; Frank, 1998). We develop our model specifically for swarm-founding social Hymenoptera, as *Melipona*, the prime example where overt caste conflict occurs, is swarm-founding and because it is only in swarm-founding species that predictions can easily be tested (Bourke & Ratnieks, 1999). This is because colonies only need a few queens to swarm, so that excess queen production is easily quantified (i.e. all queens are basically excess). By comparison, in species with queens that found nests independently the colony optimum would also be to produce many queens and it would be hard to determine what fraction of them represents an excess (i.e. reared in excess of the optimum of the queen and workers collectively). A major conclusion of the model is that when caste fate is under larval control, an excess of queens should occur that is inversely proportional to intracolony relatedness. For simple relatedness structures, we rederive the earlier results (Ratnieks, 2001). But the new model also makes more complex social structures, such as extreme polyandry (multiple mating by queens) or polygyny (multiple queens occurring in a single colony) open to prediction. These additional predictions will allow critical tests of caste conflict theory once more data are available, and will also suggest key species for data collection. We also analyse how the colony-level cost of excess queen production influences the expected ESS ratios. Finally, we consider when a transition from individual to social control over caste fate is expected (Bourke & Ratnieks, 1999), that is, when workers should attempt to prevent immature females from developing as queens.

The model

Individual caste allocation interests

First we derive the optimal probabilities with which individual females should develop as queens vs. workers in swarm-founding social Hymenoptera. We use the direct-fitness method of Frank (1998), whereby the direct fitness of various classes of relatives is written as a function of the individual and average behaviour of individuals in the group. In our case, this behaviour is the probability with which females develop as queens. We use y , z and Z to denote the focal individual, group-average and population-average probabilities with which females develop as a queen (Table 1 summarizes the notation used in this paper). Note that the model analyses optimal caste allocation (worker vs. queen production), rather than reproductive (worker vs. sexual, male + queen) allocation (Pamilo, 1991a; Bourke & Chan, 1999; Herbers *et al.*, 2001).

It is clear that total colony reproduction, the production of males and swarms, is a decreasing function of z . The more females that develop as queens (higher z), the fewer that develop as workers, leading to less work and a lowered ability of the colony to rear males or produce swarms. For simplicity, and as in the model of Ratnieks (2001), we initially use a linearly decreasing function, $1 - z$, for the absolute productivity of the focal colony, but we consider other cost functions later. Relative colony productivity, i.e. the productivity of the focal colony relative to a random colony in the population is

then given by $G = (1 - z)/(1 - Z)$. We also assume that queen overproduction reduces male production to the same extent as swarm production. This assumption is also relaxed later. Clearly, at the level of the colony, it is undesirable to have many females develop as queens (high z). However, at the individual level, there are distinct benefits associated with becoming a queen rather than a worker: if females develop as queens with higher than average probability, it allows them to increase their chances of inheriting a daughter swarm. Formally, over the course of a single queen replacement or swarming event, the relative probability for a female to inherit a daughter colony is y/z , the ratio of the individual probability with which it becomes a queen and the probability with which other females in the colony become queens.

We can now write the fitness through male (W_m) and swarm (W_f) production as a function of the individual (y) and average (z) probabilities with which female larvae become queens within the colony:

$$\begin{aligned} W_m &= \frac{1 - z}{1 - Z} \\ W_f &= \frac{y}{z} \cdot \frac{1 - z}{1 - Z} \end{aligned} \quad (1)$$

In these equations, $(1 - z)/(1 - Z)$ is the relative productivity of the colony in terms of male and swarm production (relative group success G) and (y/z) is the success of any female larva relative to another (relative individual success I). In these equations we also assume that the population is in sex ratio equilibrium, so that the relative valuation of the sexes is not affected by it. The above model is closely related to that of Frank (1995b), which was developed to determine the optimal level of exploitation within social groups. The only difference is that we specifically address the hymenopteran situation where only females can vary their level of exploitation (i.e. become queens rather than workers) but costs are to both sexes.

Whether an increased probability of developing as a queen is favoured can be calculated from a simple Hamilton's rule condition (Hamilton, 1964) with three affected parties: (1) self, (2) sisters and (3) males. The personal benefit of developing as a queen is given by $\partial W_f / \partial y = (1 - z)/[(1 - Z)z]$ (for a full account of the method used, see Frank, 1998). In other words, the benefit of becoming a queen is proportional to the relative productivity of the colony, $(1 - z)/(1 - Z)$, because this sets the ability for the colony to produce workers and swarms, but is inversely proportional to the number of competing queens (z), because a female that develops as a queen will only inherit the colony or swarm with a probability of $1/z$. Similarly, the personal cost that occurs as a result of other females developing into queens is given by $-\partial W_f / \partial z = y/[z^2(1 - Z)]$. As the role of any female in the colony is symmetrical, this is also the cost of developing as a queen to a sister. Lastly,

Table 1 Parameters and terminology used in this paper.

W_f	Fitness through queen (swarm) production
W_m	Fitness through male production
G	Relative group success (lifetime colony productivity)
I	Individual success of one female relative to another
y	Probability with which a focal female larva develops into a queen
z	Average probability with which female larvae develop into queens in the colony
Z	Population average probability with which female larvae develop into queens
z^*	ESS probability of developing as a queen
k	Parameter describing how excess queen production affects total colony reproduction (swarm and male production) ($k = 1/2$: square law, $k = 1$: linear, $k = 2$: quadratic, etc.)
k_s	Parameter describing how excess queen production affects swarm production ($k_s = 1/2$: square law, $k_s = 1$: linear, $k_s = 2$: quadratic, etc.)
k_m	Parameter describing how excess queen production affects male production ($k_m = 1/2$: square law, $k_m = 1$: linear, $k_m = 2$: quadratic, etc.)
M	Effective maternity (number of laying queens)
P	Effective paternity
c	Cost of preventing excess queen production
R_f	Life-for-life relatedness to sister queens reared in the colony
R_m	Life-for-life relatedness to males reared in the colony

the cost to male production is given by $\partial W_m / \partial z = -1 / (1 - Z)$, that is, relative to the population average productivity of a colony $(1 - Z)$, a unit change in the proportion of females that develop into queens causes a corresponding reduction in the net production of males. Following kin selection theory (Hamilton, 1964), we need to weigh these costs and benefits with the relatedness to the affected parties, that is self ($r = 1$), sisters (life-for-life relatedness R_f), and males (life-for-life relatedness R_m), to calculate the change in frequency of the caste determining gene. Summing the three relatedness-weighted costs and benefits, the net inclusive fitness benefit of developing as a queen with probability y is given by

$$\frac{(1-z)}{(1-Z)z} \cdot 1 - \frac{y}{(1-Z)z^2} \cdot R_f - \frac{1}{1-Z} \cdot R_m \quad (2)$$

Near the ESS, all female larvae will evolve to become queens with the same probability, so we can set $y = z = Z$. Setting the resulting equation to zero and solving for Z yields the ESS probability with which female larvae should develop into queens:

$$z^* = \frac{1 - R_f}{1 + R_m} \quad (3)$$

In equivalent form, females should develop into queens or workers in a ratio of

$$[1 - R_f \text{ queens}] \text{ to } [R_f + R_m \text{ workers}] \quad (4)$$

The intuitive explanation is that a female gains from becoming a queen in proportion to its own value (1) relative to that of the sisters it is competing with (value R_f), whereas becoming a worker has indirect benefits in terms of increased swarm (value R_f) and male production (value R_m). A similar derivation from a levels-of-selection perspective is also possible (see Appendix). Note that the fact that most *Melipona* queens are killed upon eclosion (Kerr, 1950; Engels & Imperatriz-Fonseca, 1990;

Imperatriz-Fonseca & Zucchi, 1995) does not make it less profitable to develop as a queen. This is because if the queens were allowed to survive this would only delay the time at which one was 'chosen'. Or if the queens could share reproduction this would divide each queens share of colony reproduction by the number of queens. Therefore, queen killing does not alter the expected payoff. Rather, it just converts it from a small equal payoff to a large jackpot won by one individual.

Extending the result for nonlinear colony cost functions is straightforward. Instead of using a linear colony-level cost function, we use a power function $(1 - z)^k$ (or any other monotonically decreasing function) for colony productivity, instead of the linear $(1 - z)^1$. This gives a family of convex ($k < 1$) and concave ($k > 1$) curves. Relative colony productivity G is now equal to $(1 - z)^k / (1 - Z)^k$ and analysis by the same methods as before yields the ESS

$$z^* = \frac{1 - R_f}{1 - R_f + k(R_f + R_m)} \quad (5)$$

This optimum is plotted for different values of k in Fig. 1a. It is also possible that the costs of excess queen production to male and swarm production are different, because they are very different modes of reproduction. We can generalize the model by describing costs to male and swarm production with separate power functions with coefficients k_m and k_s . Fitnesses through male and swarm production then become

$$W_m = \frac{(1-z)^{k_m}}{(1-Z)^{k_m}} \quad (6)$$

$$W_f = \frac{y}{z} \cdot \frac{(1-z)^{k_s}}{(1-Z)^{k_s}}$$

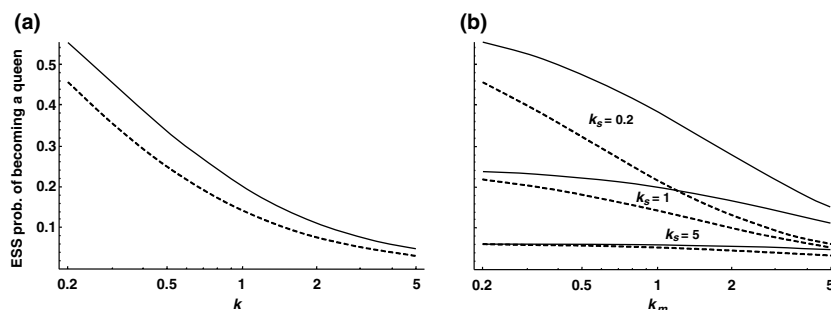


Fig. 1 ESS probability z^* for a female larva to become a queen in a colony headed by a single once-mated queen, assuming different colony-level cost functions. The optimum is plotted for cases when all males are either queen (full line) or worker (dashed line) produced. (a) Queen overproduction reduces male and swarm production equally, and the cost function follows a power law with coefficient k (plotted from eqn 5). (b) Queen overproduction reduces male and swarm production unequally with costs to swarm and male production following power laws with coefficients k_s and k_m .

Analysis as before yields the ESS

$$z^* = \frac{1 - R_f}{1 - R_f + k_f R_f + k_m R_m} \quad (7)$$

This optimum is plotted for arbitrary values of k_s and k_m (Fig. 1b).

From eqns (3)–(5), the prediction is that larvae should selfishly develop as queens with a higher probability when the relatedness to sister larvae or males or both is

lower (Fig. 2), or when the costs to colony function are less severe ($k < 1$, i.e. with a convex colony productivity function, Fig. 1a).

Table 2 shows some numerical examples for typical colony kin structures as they occur in *Melipona* and honeybees. Most *Melipona* are headed by a single once-mated mother queen (Kerr *et al.*, 1962; da Silva *et al.*, 1972; Kerr, 1975; Contel & Kerr, 1976; Peters *et al.*, 1999;

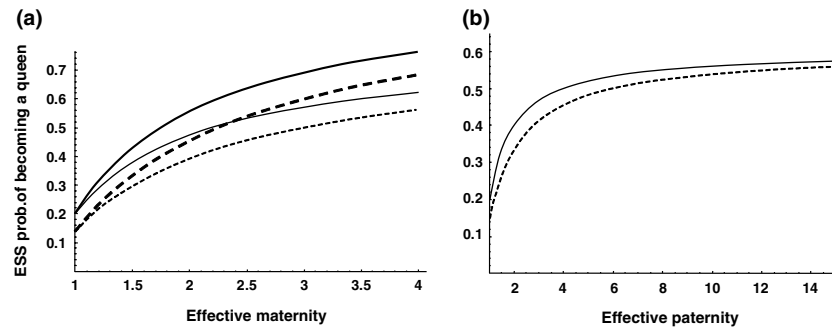


Fig. 2 ESS probability z^* for a female larva as a function of the colony kin structure. It is assumed that queen overproduction linearly reduces total colony reproduction. (a) Optimal levels of queen production when the colony is headed by multiple, once-mated queens. The figure is plotted for effective maternities (M) ranging from 1 to 4, assuming that the males are either the queens' (unbroken line) or the workers' sons (dashed line). The bold and fine curves are for when the mother queens are unrelated or related by 0.5. (b) Optimal levels of queen production when the colony is headed by a single multiple-mated queen. The optimum is plotted for effective paternities (P) ranging from 1 to 15, with all males either queen (full line) or worker produced (dashed line). The optima are calculated from eqn (3) with relatedness values $R_f = (1 + 2/P + 0.5(M - 1))/4M$ and $R_m = (1 + 0.5(M - 1))/4M$ (all males queen produced) or $R_f = R_m = (1 + 2/P + 0.5(M - 1))/4M$ (all males worker produced) (Pamilo, 1991b).

Table 2 Kin structure of various stingless bees and the honeybee *Apis mellifera* and the individual-optimum probabilities for females to develop as queens. Lower sister–sister relatedness causes more females to develop as queens while worker production of males has the opposite effect as the cost of queen overproduction is then borne by closer relatives – workers' sons (nephews) rather than queens' sons (brothers). Life-for-life relatedness to females (R_f) and males (R_m) is the product of regression relatedness (r_f , r_m) and the sex-specific reproductive value (the contribution of a given sex to the future gene pool). The relative reproductive value of males is $1 + p$ where p is the population proportion of males that are queens' sons (Pamilo, 1991b).

Species	Kin structure	$r_f = R_f$	r_m	Relative reproductive value of males, v_m	$R_m = r_m v_m$	Optimal probability for females to develop as queens* = $(1 - R_f)/(1 + R_m)$, %	References
<i>Melipona favosa</i>	Single once-mated queen, nearly all males workers' sons	3/4	3/4	1	3/4	0.14	Sommeijer <i>et al.</i> (1999), Chinh <i>et al.</i> (2002)
<i>Melipona beecheii</i>	Single once-mated queen, nearly all males queens' sons	3/4	1/2	1/2	1/4	0.20	Paxton <i>et al.</i> (2001)†
<i>Melipona bicolor</i>	Multiple-related queens, most males probably workers' sons	0.6	1/2–3/4	1/2–1	1/4–3/4	0.23–0.32	Nogueira-Neto (1970), da Silva <i>et al.</i> (1972), da Silva (1977), Bego (1989), Peters <i>et al.</i> (1999), D. Koedam (personal communication)
<i>Apis mellifera</i>	Single multiple-mated queen	0.3	1/2	1/2	1/4	0.56	Estoup <i>et al.</i> (1994)

*Assuming that queen overproduction linearly reduces total colony reproduction (eqn 3). The optimum is higher or lower with a convex or concave productivity function (eqn 5).

†Double mating by queens was erroneously reported for *M. beecheii* due to the accidental inclusion of workers that drifted between colonies (Paxton *et al.*, 1999).

Paxton *et al.*, 2001), so that $R_f = 0.75$. In one species, *M. bicolor*, however, the colony can be headed by one or several (2–7) related queens, and the average R_f has been estimated at 0.6 (Peters *et al.*, 1999; Table 2). The relatedness to the males (R_m) reared in a single-queen colony can range from 0.25 to 0.75 as a result of variable degrees of worker reproduction (Tóth *et al.*, 2002). For example, in *M. favosa*, nearly all males are workers' sons, so that $R_m = 0.75$, whereas in *M. beecheii*, all males are the queens' sons, so that $R_m = 0.25$ (Table 2). Assuming a linear cost function ($k = 1$), the prediction for *Melipona* is that larvae should develop as queens with a probability of $(1 - 0.75)/(1 + 0.25) = 20\%$ when all males are the queens' sons ($R_m = 0.25$), or with a probability of $(1 - 0.75)/(1 + 0.75) = 14\%$ when all males are workers' sons ($R_m = 0.75$, Table 2). When all males are workers' sons the optimum is lower because the cost of individual selfishness then falls on more closely related males (nephews, $R_m = 0.75$ rather than brothers, $R_m = 0.25$). From a colony-level perspective both of these values represent great queen overproduction as only few queens are needed for swarming. These values agree with those obtained from the exact genetic model (Ratnieks, 2001), but the current method is more general as it makes any colony kin structure open to prediction. For example, in *M. bicolor*, as a result of polygyny, females should develop as a queen with even higher probability, 23–32% (Table 2). Similarly, in the honeybee, polyandry causes very low relatedness among sisters ($R_f = 0.3$; Estoup *et al.*, 1994), and the individual optimum is to develop as a queen with a probability of 56% (Table 2). Figure 2 shows the optimum for different levels of polygyny and polyandry.

The numerical predictions above are for the case where queen overproduction linearly reduces total colony reproduction (production of males and swarms). The predictions for other colony-level cost functions are plotted in Fig. 1. Figure 1a plots the optima when both male and swarm production are affected in a nonlinear way. As can be seen, the optimum probability to develop as a queen is higher when the colony-level cost is less severe (with a convex colony productivity function, $k < 1$, Fig. 1a), or lower when it is more severe (with a concave colony productivity function, $k > 1$ (Fig. 1a). Figure 1b plots the optima when effects of queen overproduction on male and swarm production differ. As can be seen, the relative influence of relatedness is the same in all cases, but the predicted optima are different, both in terms of magnitude and range. In other words, predictions are affected quantitatively but not qualitatively [Maynard Smith (2002) comments that biological systems are generally too complex for precise quantitative predictions, but strong qualitative predictions can be made]. However, if the cost functions were different for the different species, then that might obscure the predicted effect of relatedness. Currently, no information is available on the shapes of the cost functions. It would

be hard to determine them empirically as a colony normally only swarms once every few years (Engels & Imperatriz-Fonseca, 1990) but can produce males over a long period, even the whole year (Moo-Valle *et al.*, 2001).

In deriving the optimal level of queen production (eqn 3) we make no assumptions as to how it may be caused at the proximate level. For *Melipona*, Kerr (1950) hypothesized a two-locus two-allele genetic system that would give 25% queens, on average, in each colony. But such a genetic system, which still lacks strong empirical support (Velthuis & Sommeijer, 1991), is not strictly required. If it did occur, however, it might constrain what ratios can be attained (Ratnieks, 2001). In the model above, we assumed there are no constraints. Instead, we assumed a very large number of alleles, each of which could slightly alter the probability with which females develop as queens, and with the allele that codes for the optimum going to fixation.

Worker interests

Immature females benefit from developing as a queen with a high probability because they value themselves more highly than their sisters. The adult workers, however, should value all developing females equally as they are equally related to all of them (this is neglecting the possibility of strong nepotism which could potentially occur under polyandry or polygyny). Formally, from the perspective of a worker, the relatedness to a potential beneficiary in eqn (3) is R_f rather than 1, which yields the optimum $z^* \equiv 0$. The caste fate optimum of the adult workers is thus the same as the colony optimum of near-zero allocation to queens. By the same argument, the mother queen also favours the production of few queens.

A direct consequence of this is that workers (or the mother queen) should be willing to police larvae that try to selfishly become queens in much the same way as parents should try to prevent young from being overly greedy (Clutton-Brock & Parker, 1995; Mock & Parker, 1998). As larval manipulation of caste fate brings colony productivity down from 1 to $1 - z^*$ (cf. eqn 1) with $z^* = (1 - R_f)/(1 + R_m)$ (eqn 4), workers are expected to prevent larvae from becoming queens if this can be done at a lesser cost (c), i.e. when

$$c < \frac{1 - R_f}{1 + R_m} \quad (8)$$

(The cost of policing is measured as that which would occur in a colony where all females would become workers; for a more formal derivation see Wenseleers, 2001.)

From eqn (6), the prediction is that workers should try to gain social control over larval caste determination whenever it can be achieved at low cost. This is more

probable when queens are larger than workers, as workers can then withhold food from larvae to hinder them from developing into a queen (Bourke & Ratnieks, 1999). However, costs, such as accidental starving of larvae, may be larger in societies of low relatedness, as policing of larval selfishness can then cause greater potential increases in colony productivity. This parallels the conclusion of Frank (1995b) that low relatedness is conducive to the spread of policing although his result, due to the simpler kin structure modelled, was simply that policing is favoured when $c < 1 - r$. Even in societies of high relatedness, however, policing may be expected if it is not too costly. For example, in societies with a once-mated queen, workers could prevent larvae from becoming queens if social control had a cost of <20% (eqn 6).

Empirical support for caste conflict theory

Strong general support for the model predictions comes from the clear association between queen overproduction and conditions allowing individual control of caste fate. In *Melipona*, where queens and workers are reared from the same cells, there is great queen overproduction: on average between 5 and 15% of all females usually develop as queens across different species (e.g. Kerr, 1950; Darchen & Delage-Darchen, 1975; Koedam *et al.*, 1999; Moo-Valle *et al.*, 2001; Gioli & Bego, 2002; Sommeijer *et al.*, 2003). Similarly, excess queens develop in some trigonine stingless bees where females have the ability to develop as dwarf queens from worker cells – a situation that has been specifically likened to *Melipona* (Engels & Imperatriz-Fonseca, 1990; *Schwarziana quadripunctata*: production of 25–30 gynes in 10 days, Ribeiro & Alves, 2001; *Plebeia julianii*: Juliani, 1962, 1967; *Plebeia remota*: production of up to six gynes per month, Ribeiro *et al.*, 2003). In most species, however, excess queen production can be effectively prevented by nutritional control. When queens are larger than workers, developing females can be forced into a worker role by giving them insufficient food to allow them to develop as queens. This is a type of social policing (Ratnieks, 1988), and could be termed ‘caste fate policing’. Nutritional caste control can be extremely effective at preventing excess queen production. Taxa where feeding control is possible, such as army ants, honeybees and most trigonine stingless bees (with the exception of the genera that produce dwarf queens), all produce few queens, in keeping with colony needs. *Apis mellifera*, for example, produces about 15–25 queens vs. 150 000 workers over one season when swarming occurs (Seeley, 1985; Winston, 1987). This implies that the chance for a female to be reared as a queen is only 0.01–0.02%. Similar ratios have been observed in the trigonine stingless bee *Tetragonisca angustula* (van Veen & Sommeijer, 2000), where approximately four queens develop over a single season, amounting to 0.01–0.02% of the female brood.

In army ants, finally, where queens are 50 times the size of workers, few queens are generally reared (*Aenictus gracilis*: <6, Macevicz, 1979; *Dorylus wilverthi*: 1–2, Raignier, 1959; *Eciton hamatum*: 1–14, Schneirla & Brown, 1952; Schneirla, 1971; Franks & Hölldobler, 1987; the concurrent worker brood ranges in size from 30 000 to 300 000; Schneirla, 1971). That caste conflict is resolved so efficiently is surprising given the huge potential for conflict that is present. As mentioned above, in the honeybee relatedness is low ($R_f = 0.3$; Estoup *et al.*, 1994) because of polyandry and the inclusive fitness interest of an individual female is to become a queen with a probability of 56% (assuming a linear cost function).

In future, more detailed predictions of the theory could also be tested. For example, it is predicted that fewer females should selfishly develop as queens when all males are workers' sons (Table 2). Unfortunately, there are currently good data on male parentage and caste ratios for only few species. Therefore, a meaningful test will be possible only once more data have accumulated. One species that would be particularly valuable for a more detailed test is *M. bicolor*. In this species, the predicted queen production is higher than in other *Melipona* as a result of polygyny, which reduces relatedness (Table 2). Although no detailed caste ratio data are available for *M. bicolor*, da Silva *et al.* (1972) noted that *bicolor* is exceptional within *Melipona* in that it ‘produces an unusual [high] quantity of virgin queens’. If *M. bicolor* larvae could detect how many laying queens there are in the colony, they would also benefit by facultatively adjusting their probability of becoming a queen (Ratnieks, 2001). Given that there are other examples of facultative adjustment of reproduction in social Hymenoptera, a facultative response seems quite possible (e.g. Sundström *et al.*, 1996; Foster & Ratnieks, 2000). Future studies could attempt to test this.

Discussion

In this paper, we have investigated a key topic in insect sociobiology – the conflicts associated with the rearing of individuals of different reproductive and working ability. More than 20 years ago, Oster & Wilson (1978) noted that ‘the interaction of individual-level and colony-level selection complicates the evolution of caste in ways that are just beginning to be explored’. Indeed, this is exactly what our current analysis shows. The decision to become a queen or a worker depends upon an interaction of individual benefits and costs to the whole colony. Feeding control of larvae by adults can maximize the success of the colony by preventing excess numbers of individuals from selfishly developing as queens. For example, in the honeybee, only 1 in 10 000 females are reared as queens (Seeley, 1985; Winston, 1987), although the individual optimum is to become a queen with a probability of 56%. Clearly, nutritional caste

determination is a very powerful form of social suppression, which makes individuals work for the benefit of society even when this goes against their inclusive fitness interests. In general terms, our results reinforce the view that parental or sibling manipulation, in addition to kin selection, is of major importance in resolving social conflicts (Alexander, 1974, 1987; Michener & Brothers, 1974; Hamilton, 1975; Leigh, 1977; Frank, 1995b; Monnin & Ratnieks, 2001; Strassmann *et al.*, 2002).

If the honeybee illustrates a situation where caste conflict is efficiently resolved by social control then *Melipona* illustrates the reverse. Weak size differences between queen and worker and rearing in sealed cells away from any interference by adults allow every female larva to control her own fate. In line with predictions, queens in *Melipona* are produced in great excess of colony needs. Excess queen production also occurs in some trigonine stingless bees where females evade social control by developing as dwarf queens in worker cells (Engels & Imperatriz-Fonseca, 1990; Ribeiro *et al.*, 2003). Significantly, excess queen production only occurs in those trigonines where self-determination is possible. This represents good and phylogenetically independent evidence for caste conflict theory.

Our inclusive fitness model also makes more detailed predictions on the expected level of excess queen production as a function of the colony kin structure. For single mating, the model recovers the predictions of Ratnieks (2001) that between 14 and 20% of all females should develop as a queen depending on male parentage. But the model also makes several new predictions, for example, deriving the optima under polygyny (Table 2), or for nonlinear colony-level cost functions. These additional predictions will be useful for future tests of caste conflict theory.

Recently, Strassmann *et al.* (2002) gave evidence for caste conflict in the swarm-founding epiponine wasp *Parachartergus colobopterus*. They suggest that in epiponines, caste conflict may lead to occasional episodes of queen overproduction, leading to the colony becoming polygynous. *Parachartergus colobopterus* is a species without morphological castes, and who becomes a queen depends purely on whether females mate and activate their ovaries (Strassmann *et al.*, 2002). Caste conflict in *P. colobopterus* is, therefore, over an individual female's behavioural rather than morphological caste fate. Consistent with the interpretation of caste conflict, queens in polygynous societies tend to be aggressively suppressed by the workers (Herman *et al.*, 2000; Strassmann *et al.*, 2002). Aggression can force queens to work rather than reproduce, which has the advantage that neither they nor the other workers have to pay the cost of queen killing, as in *Melipona* (Herman *et al.*, 2000; Strassmann *et al.*, 2002). It is possible, however, that aggressive suppression does eventually cause a reduction in queen number, and that it helps to drive the queen number

cycles typical of epiponine wasps (Jeanne, 1991). An additional observation consistent with occasional queen overproduction is that polygyny does not increase colony productivity (Forsyth, 1980). Strassmann *et al.* (2002) also developed a model to show why *P. colobopterus* only produces excess queens when there is just a single mother queen left. The conclusion of their model was that this could be the result of collective worker interests, which favour the adoption of new queens especially at low queen number (because they would then replace full siblings). An alternative that was not discussed, however, is that females may benefit most from becoming a queen at low queen number, as they will then have fewer competitors.

Although our discussion has been primarily concerned with caste conflict in the social Hymenoptera it is worth considering whether similar conflicts occur in the other major group of social insects, the termites. In particular, in the 'lower' termite families Kalotermitidae and Termopsidae, overt caste conflict might be expected, as all individuals (except soldiers) are totipotent and can moult into either a queen or king (Shellman-Reeve, 1997; Thorne, 1997; Myles, 1999). In fact, replacement reproduction, the process whereby some individuals moult into a queen or king in case of accidental loss of the royal pair, seems formally identical to caste conflict. Any individual would benefit from becoming a replacement reproductive, but future colony productivity would be reduced if an excess do so (for a review, see Myles, 1999). Indeed, removing the royal pair in some species results in a vast overproduction of replacement reproductives (up to 50%), and the excess are subsequently killed (Termopsidae: *Porotermes adamsoni*, Mensa-Bonsu, 1976; Kalotermitidae: *Cryptotermes brevis*, Lenz *et al.*, 1985; *Kalotermes flavicollis*, Lüscher, 1952, 1964; Ruppli, 1969; *Neotermes connexus*, Myles & Chang, 1984; *Neotermes jouteli*, Nagin, 1972). This closely resembles the queen cull in *Melipona*. Similar conflicts also occur at other evolutionary levels. For example, in slime moulds, the decision of a cell to become either a reproductive spore or a sterile stalk cell parallels the decision of a social insect larva to develop as a queen or a worker (Bourke & Ratnieks, 1999). As in caste fate conflict, conflict over cell-fate is expected especially at low relatedness, which can arise as a result of the mixing of different clones during fruiting body formation (Hudson *et al.*, 2002). Indeed, chimaerism appears common in nature (Strassmann *et al.*, 2000), and there is some evidence that actual conflict does occur (Atzmony *et al.*, 1997; Csaba & Balázs, 2000). This shows how the concept of caste conflict will probably help towards the understanding of a wide variety of social conflicts.

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Appendix. Caste conflict from a levels-of-selection perspective

Caste conflict is expected because females are more highly related to own offspring than to a sister's offspring. Alternatively, one could say that females benefit from developing as queens because this increases their reproductive success relative to other females within the colony, although this might reduce the total reproduction of the group. This leads to an equivalent interpretation of caste conflict as a levels-of-selection problem, which can be analysed using the multilevel Price equation (Price, 1972; Frank, 1995a). For structured populations (e.g. individuals structured into groups), Price (1972) showed that selection may be partitioned into two components, one due to the differential success of individuals within groups, and the other due to the differential success of groups. Price's (1972) equation for gene frequency change, in simple form, ignoring mutation and drift, is $\beta_{Gz}V_B + \beta_{Wz}V_W$, where β_{Gz} is the effect of the average level of selfishness on group productivity (i.e. the group cost), β_{Wz} is the effect of the individual level of selfishness on individual fitness (i.e. the individual benefit) and the V_B and V_W are between- and within-group genetic variances, respectively, which give appropriate weightings to the group and the individual as units-of-selection. Hamilton (1975) showed that when groups are large, the between-group genetic variance is proportional to relatedness, and the within-group genetic variance is proportional to 1-relatedness. The Price equation, therefore, both resolves the kin vs. group selection controversy and offers a precise answer to the dilemma of what really is the unit of selection (Brandon & Burian, 1984; Gliddon & Gouyon, 1989; Maynard Smith, 1998): groups can be considered units of selection in proportion to intragroup relatedness while individuals are units of selection in proportion to 1-relatedness. When groups are clones, natural selection simply strives for maximal group success and for maximal intragroup altruism. On the other hand, when groups are composed of unrelated individuals, natural selection favours high within-group selfishness, leading to lowered group

success. In our case, the within-group variance is proportional to $1 - r_f$, but the between-group variance has two components, one for the genetic variation present in females, r_f , and one for the genetic variation present in males, r_m (r_m does not feature in the within-group selection component as males do not actually express the caste determination phenotype. Therefore, no within-colony selection can act on them. However, between-colony selection does occur, as males contain copies of the caste determination gene, and fewer of these will be passed on if the colony productivity is reduced.) The individual benefit β_{wy} is $\partial W_f / \partial z = [(1 - z)/(1 - Z)](y/z)$, i.e. $(1 - z)/[(1 - Z)z]$; the group cost β_{Gz} is $-1/(1 - Z)$ as $G = (1 - z)/(1 - Z)$ and $\partial G / \partial z = -1/(1 - Z)$. Equilibrium

occurs when components of selection, weighted by reproductive value, balance each other:

$$\frac{(1 - z)}{(1 - Z)z} \cdot V_W = \frac{1}{1 - Z} \cdot V_B \quad (9)$$

with $V_B = R_f + R_m$ and $V_W = 1 - R_f$. This equilibrium condition is exactly the same as that derived using the kin selection approach (eqn 2). The only difference is that the logic and calculation to arrive at the result were different. This reinforces the view that kin and group selection are merely two different ways of analysing gene frequency change (e.g. Hamilton, 1975; Wade, 1980; Wilson, 1983; Queller, 1992; Dugatkin & Reeve, 1994; Keller, 1999).