ORIGINAL ARTICLE

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Heirs and spares: caste conflict and excess queen production in *Melipona* bees

Abstract The caste conflict hypothesis states that there is potential conflict over the caste fate of totipotent immature females in social insects. In most species, an immature female has little control over her fate because workers control her nutrition. However, in *Melipona* bees, immature females should have considerable control over their own caste fate because they develop on a provision mass in a sealed cell, and because queens are not larger than workers. This may explain why, in *Melipona*, large numbers of queens are reared only to be executed. (Because *Melipona* colonies are founded by swarms very few reproductive opportunities for adult queens occur.) This study uses a one-locus genetic model to determine the optimum proportion of females that should develop into queens from the perspective of immature totipotent females who control their own caste fate. For a population in which all colonies are headed by a single, single-mated queen, which is the typical situation in *Melipona*, the optimum rises from 14–20% as male production by workers declines from 100% to zero. This agrees well with previous studies which, collectively, give an average of 22% of females developing into queens.

Keywords Caste determination · Conflict · Kin selection · *Melipona* · Eusocial Hymenoptera

Introduction

Morphologically distinct queen and worker castes occur in most eusocial Hymenoptera (Wilson 1971). To cause this, developmental pathways divide in an immature stage (Wheeler 1986; Bourke and Ratnieks 1999). Typi-

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cally, the relative numbers of queens and workers reared appears to be appropriate to the needs of the colony. Thus, queens are not normally reared by growing colonies or in seasons inappropriate for reproduction. Similarly, only a few young queens are normally reared in species, such as honey-bees, *Apis* (Seeley 1985; Winston 1987), and army ants, *Eciton* (Hölldobler and Wilson 1990), in which colonies are founded by a queen accompanied by workers. In these species, there is no benefit to the workers in rearing many queens because a queen cannot found a nest on her own (Bourke and Ratnieks 1999). In contrast, species where queens found nests without workers (e.g. *Bombus* bees, most Vespinae wasps and ants) rear large numbers of queens. However, *Melipona* bees do not fit this pattern. Like honey-bees, *Melipona* found new colonies by swarming, yet many young queens, on average approximately 22% of all females (Kerr 1950; Kerr and Nielsen 1966; reviews: Wilson 1971; Michener 1974; Velthuis and Sommeijer 1991) are reared during the reproductive season. Excess queens are executed by workers (Engels and Imperatriz-Fonseca 1990; Koedam et al. 1995) and must be a drain on colony resources. Occasionally, a queen would be needed to supersede a failing mother queen or to head a new colony during swarming. But why rear so many spares when only an occasional heir is needed?

One possible reason is that excess queen production is a selfish strategy of developing female larvae (Bourke and Ratnieks 1999). A female larva can, potentially, enhance her fitness by developing into a queen because she is more related to her own offspring that to a sister's offspring. *Melipona* bees have two unusual features hypothesized to give female larvae greater power, the power of self-determination, over their own caste than is usual in eusocial Hymenoptera (Bourke and Ratnieks 1999). First, cells are mass provisioned – larval food is placed in a cell, an egg is laid on top and the cell sealed (reviews: Wilson 1971; Michener 1974; Engels and Imperatriz-Fonseca 1990; Velthuis and Sommeijer 1991). Second, queens are not larger than workers, so that a provision mass is sufficient to rear either caste

(reviews: Michener 1974; Velthuis and Sommeijer 1991). In contrast, in most eusocial Hymenoptera, queens are larger than workers and workers are also directly involved in larval feeding and so can control the amount and quality of food that larvae receive. Adult workers can also aggress or even kill larvae (Bourke and Ratnieks 1999). In the honey-bee, adult workers have control over female caste because larvae develop in open cells and are progressively fed by the workers. Larvae in queen cells are given special food, royal jelly, and this triggers them to go down the queen devlopmental pathway (Winston 1987).

The hypothesis that the caste fate of a totipotent female is subject to actual conflict between self and other colony members has support from other species. In some trigonine bees, which also have progressive provisioning but unlike *Melipona* have queens that are larger than workers, a larva may break into a neighbouring cell to obtain enough food to become a queen (Engels and Imperatriz-Fonseca 1990; Velthuis and Sommeijer 1991). Dwarf queens also occur in trigonines (Imperatriz-Fonseca et al. 1997; Ribeiro 1998) and may be a strategy by which an immature female can develop into a queen despite limited provisions (Bourke and Ratnieks 1999). Dwarf queens, of similar size and appearance to workers, also occur in ants (Rüppel and Heinze 1999).

This study uses a mathematical model to determine the optimum proportion of females that should develop as queens, assuming self-determination and self-interest. The optimum depends upon the extent of worker production of males and paternity but is close to the 21–22% observed (Velthuis and Sommeijer 1991; Kerr et al. 1966). For example, under single paternity, the optimum is 20% when males are all queens' sons, and 14% when all males are workers' sons.

Excess queen production in *Melipona* has been a long-standing puzzle (Engels and Imperatriz-Fonseca 1990). Part of the puzzle is that development may be under the control of a two-locus two-allele system that makes 25% of the female offspring in every colony potential queens (Kerr 1950; reviews: Wilson 1971; Michener 1974; Velthuis and Sommeijer 1991). Although this study does not model a two-locus system, such a system, if it exists, is less puzzling when considered as a mechanism for generating a proportion of self-determining females close to the optimum.

Model

The model applies to a Hardy-Weinberg population, with all colonies headed by a single queen, all queens mated to either one or two unrelated males, and all males being either queens' sons or workers' sons. The actual situation in most *Melipona* appears to be a single queen mated to a single male (Peters et al. 1999) with considerable variation in the degree of male production by workers (Inoue et al. 1999; Koedam et al. 1999; Sommeijer et al. 1999). The model considers the invasion of a rare allele,

F, causing heterozygote workers, Ff, to develop into queens with probability $Q+d$ versus Q for wild-type females, ff.

The model seeks the value of Q at which there is no value of d at which F can invade. This is the uninvadable or evolutionarily stable strategy (ESS) value. Because ff females can have any probability of developing into queens, the ESSs determined are not subject to any genetic constraints on the proportion of females that develop as queens, as may actually occur in *Melipona* if female caste is determined by a two-locus two-allele system with only heterozygotes developing into queens (Kerr 1950; reviews: Wilson 1971; Michener 1974; Velthuis and Sommeijer 1991). The ESSs are also the optima for developing totipotent females in other swarming species with colonies of the same kin stucture (e.g. *Apis*, *Eciton*). However, because developing females in these species are unlikely to have the power of self-determination of adult caste (Bourke and Ratnieks 1999), the ESSs have little relevance other than to confirm that potential conflict (Ratnieks and Reeve 1992) over caste fate occurs.

Proportion of Ff queens reared in a colony with both ff and Ff female offspring

In colonies in which all the female offspring are Ff, then all young queens reared are necessarily Ff whatever the proportion of Ff females that develop into queens. However, in colonies with both Ff and ff female offspring, genetic differences in the probability of developing into a queen affect the relative proportions of Ff and ff queens reared. (When two genotypes of queens are reared, I assume that the probability that a queen of a specified genotype supersedes the mother queen or heads a new colony during swarming is the proportion of adult queens of that genotype reared in that colony.)

The model only considers situations in which Ff and ff female offspring occur in equal proportions when they co-occur in a colony, either because the queen is mated to one or two males and the F allele is inherited maternally (M-type colonies: Ff queen×f or f,f males) or the F allele is inherited paternally and double mating with equal paternity occurs (P-type colonies: ff queen×F,f males). In such colonies, the proportion of Ff queens reared is:

$$(Q+d)/(2Q+d) \tag{1}$$

The increased proportion of Ff offspring females is the difference between Eq. 1 and 0.5:

$$(Q+d)/(2Q+d)–0.5 = d/(4Q+2d) \tag{2}$$

This increase is caused by a deviation d from Q. Therefore, the increase per unit d is:

$$[d/(4Q+2d)]/d = 1/(4Q+2d) \tag{3}$$

As d tends to zero, Eq. 3 tends to $1/4Q$, which is the marginal value of a small change in queen development prob-

ability as a function of that probability (Fig. 1). When the probability that ff females develop into queens is low, a rare allele increasing queen development probability causes a large increase in the relative proportions of Ff to ff queens. This reduces as the proportion of ff females developing into queens increases. This gives a more quanti-
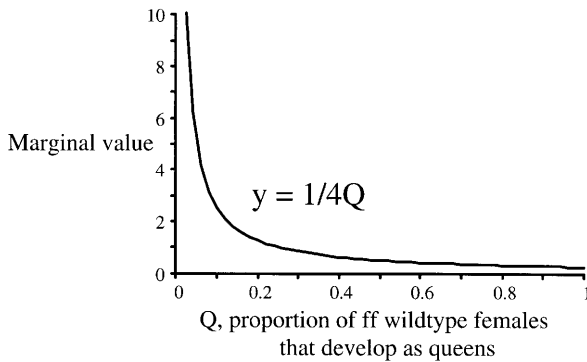

Fig. 1 Marginal increase in the proportion of queens that have Ff genotype as a function of Q, the proportion of ff wild-type females that develop as queens in a colony in which half offspring females are ff and half Ff

Table 1 List of parameters

Q	Proportion of ff females that develop into queens
$Q+d$	Proportion of Ff females that develop into queens
p	Initial frequency of the F allele (equal in both males and females)

tative insight into why we expect the ESS to be an intermediate proportion of females developing as queens.

Effect of queen production on colony productivity

Because young queens perform no work, a colony's total reproduction is a positive function of the proportion of females that develop into workers. Empirical data (Page and Kerr 1990) show that the relationship between colony size (number of workers) and growth is linear in *Melipona*. Therefore, a linear relationship is a suitable approximation of this function and the relative reproductive productivities of colonies with 100% and 50% Ff female offspring are $(1-Q-d)$ and $(1-Q-d/2)$.

Genetic model

The model considers the invasion of the rare allele F, of frequency p in both sexes (see Table 1). Because it is rare, events occurring with probability p^2 or higher power can be neglected (e.g. Ff queen×F male, FF queen×f male, FF queen×F male). Table 2 shows the production of Ff queens and F males in the population, which occur only in the specified M- and P-type colonies. Columns 7 and 8 give the changes in the numbers of Ff queens and F males produced due to the changed proportion of Ff females that develop into queens. Figure 2 gives a geometric view of Table 2 (a).

Table 2 Change in the production of Ff queens and F males in colonies with the rare F allele. Ff females develop into queens with probability $Q+d$, ff females with probability Q. Figure 2 gives a graphic explanation of the entries in columns 7 and 8 of part (a)

| (1) Colony type and parents	(2) Approximate frequency	(3) Female offspring	(4) Proportion of queens reared that are Ff	(5) Proportion of males reared that are F	(6) Colony productivity	(7) Change in Ff queens reared	(8) Change in F males reared
(a) Single paternity, males are all sons of queens							
P-type ff×F	p	All Ff	1	0	$1-Q-d$	$+0$ $-pd$	$+0$ -0
M-type Ff×f	$2p$	0.5 Ff, 0.5 ff	$0.5+d/4Q$	0.5	$1-Q-d/2$	$+2p(d/4Q)(1-Q)$ $-2p(d/2)(0.5+d/4Q)$	$+0$ $-2p(d/2\times0.5)$
(b) Single paternity, males are all sons of workers							
P-type ff×F	p	All Ff	1	0.5	$1-Q-d$	$+0$ $-pd$	$+0$ $-p(d\times0.5)$
M-type Ff×f	$2p$	0.5 Ff, 0.5 ff	$0.5+d/4Q$	0.25	$1-Q-d/2$	$+2p(d/4Q)(1-Q)$ $-2p(d/2)(0.5+d/4Q)$	$+0$ $-2p(d/2\times0.25)$
(c) Double paternity, males are all sons of queens							
P-type ff×F,f	$2p$	0.5 Ff, 0.5 ff	$0.5+d/4Q$	0	$1-Q-d/2$	$+2p(d/4Q)(1-Q)$ $-2p(d/2)(0.5+d/4Q)$	$+0$ -0
M-type Ff×f,f	$2p$	0.5 Ff, 0.5 ff	$0.5+d/4Q$	0.5	$1-Q-d/2$	$+2p(d/4Q)(1-Q)$ $-2p(d/2)(0.5+d/4Q)$	$+0$ $-2p(d/2\times0.5)$
(d) Double paternity, males are all sons of workers							
P-type ff×F,f	$2p$	0.5 Ff, 0.5 ff	$0.5+d/4Q$	0.25	$1-Q-d/2$	$+2p(d/4Q)(1-Q)$ $-2p(d/2)(0.5+d/4Q)$	$+0$ $-2p(d/2\times0.25)$
M-type Ff×f,f	$2p$	0.5 Ff, 0.5 ff	$0.5+d/4Q$	0.25	$1-Q-d/2$	$+2p(d/4Q)(1-Q)$ $-2p(d/2)(0.5+d/4Q)$	$+0$ $-2p(d/2\times0.25)$
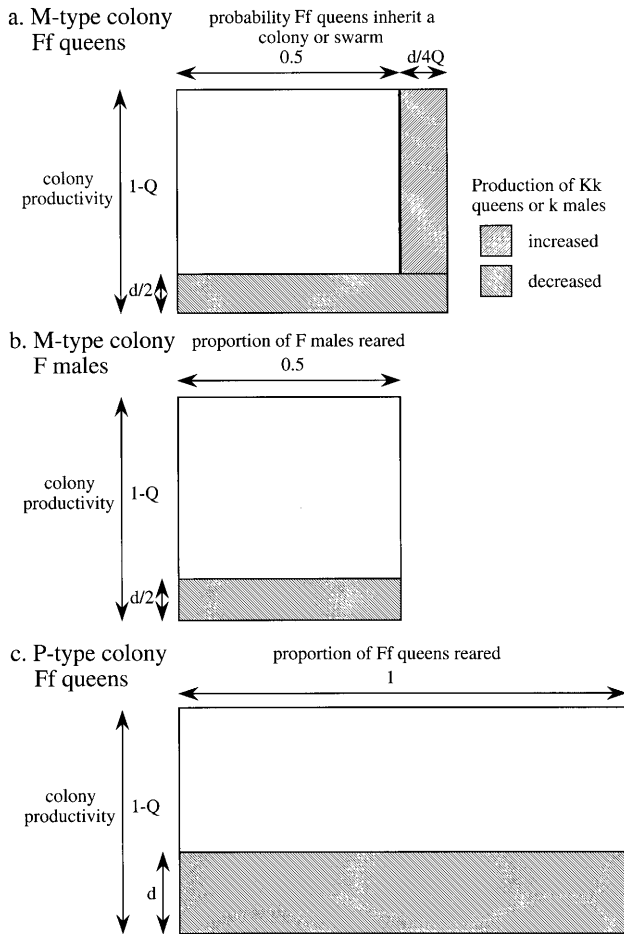
Fig. 2 Graphical representation of the increased production of Ff females (**a**) and decreased production of F males (**b**) and Ff females (**c**) caused by an increase, *d*, in the probability that Ff females develop into queens. The vertical sides of the rectangles represent the reproductive productivity of a colony, which is reduced by *d*/2 or *d* because Ff females have a higher probability of developing into queens than ff females. The horizontal sides represent manipulation of colony reproduction by Ff females. This only occurs in M-type colonies, and only over queen production. This figure corresponds to single mating by queens with all males being queens' sons [Table 2 (a)]. The *double-hatched area* (**a**) is counted as both + and – in Table 2 (a) column 7, and so cancels out

Because the F allele is transmitted to both sexes, it is necessary to combine its effect on the production of both F males and Ff females to determine if it increases or decreases in frequency. In Table 2 (a) and (c), F males and Ff females have equal weight. The F allele is only half the genes at its locus in an Ff female versus all the genes at its locus in an F male, which would give Ff females half the weight of an F male. However, under haplodiploidy with all males being sons of queens, genes in females have twice the reproductive value of genes in males (Crozier and Pamilo 1996), which gives a male half the weight of a female. Overall, therefore, the weights of Ff females and F males are equal. However, when all males are workers' sons [Table 2 (b) and (d)], the reproductive values of males and females are equal (Crozier and Pamilo 1996), so that the weight of an Ff

Table 3 Uninvadable probabilities of developing as a queen

Kin structure of colonies	Probability	
Single mating, males are queens' sons (Table 2 (a)]	1/5	20%
Single mating, males are workers' sons [Table 2 (b)]	1/7	14%
Double mating, males are queen's sons [Table 2 (c)]	2/5	40%
Double mating, males are workers' sons [Table 2 (d)]	1/3	33%

female is half that of an F male. From Table 2 (a), the changes in production of Ff queens and F males, under single paternity and with all males sons of queens, are:

Kk queens: $+2p(d/4Q)(1-Q)-2p(d/2)(1/2+d/4Q)-pd$

K males: $-pd/2$

Setting the value of increased production of F males and Ff females equal to the value of the decreased production makes it possible to solve for the value of *Q* at which no rare allele causing a change in the proportion of females that develop into queens can invade.

$$2p(d/4Q)(1-Q) = 2p(d/2)(1/2+d/4Q)+pd+pd/2$$
$$(1-Q)/2Q = 2+d/4Q = 2 \text{ (as } d \text{ goes to zero)}$$
$$1-Q = 4Q$$
$$Q = 1/5 \tag{4}$$

Equation 4 shows that as *d* tends to zero, *Q* tends to 1/5. This means that when *Q* equals 1/5, the value of *d* at which the costs and benefits of a deviation in queen caste probability to allele F are equal is zero. But when *d* equals zero, the F allele is identical in phenotypic effect to allele f. This means that a self-determination strategy of developing into queens with probability 1/5 cannot be invaded by a rare allele causing a different probability. Table 2 (a) can be modified to consider worker reproduction and double mating [Table 2 (b–d)]. The uninvadable probabilities of developing into queens are given in Table 3 (see also the Appendix).

Discussion

Table 3 shows that the uninvadable probability of queen development under self-determination declines when worker reproduction occurs. This is because worker reproduction reduces the gain in personal reproduction from developing as a queen instead of a worker. Double paternity increases the uninvadable probability because it reduces the relatedness of a female to the reproductives reared in her natal colony (i.e. it reduces the value of indirect offspring via working) but does not affect her relatedness to her own offspring. Looking at things from the gene perspective, double paternity means that the rare allele can also manipulate colony reproduction to its benefit when inherited paternally.

The single-mating cases are of particular relevance to *Melipona*, which has single mating and a variable but often high proportion of male production by workers. The uninvadable queen development probability under single mating increases from 14 to 20% as worker production

of males declines from 100 to 0%. This is in good agreement with empirical data on queen production. In one study (Kerr et al. 1966) of *Melipona quadrifasciata*, 22% of pupae (*n*=276) over 72 mg were queens. During the warm season, when conditions are good, all pupae weigh at least this much. Velthuis and Sommeijer (1991) combined data from several studies of four *Melipona* species and showed that 21% of larvae (*n*=283) given 125% or more of the average natural amount of food developed into queens.

Caste determination mechanisms

In *Melipona*, caste development is suggested to be under the control of a genetic system with two unlinked loci each with two alleles, in which queens are double heterozygotes (Kerr 1950; Michener 1974). In this way, whatever the genotype of a mother queen and her mate or mates, Mendelian segregation in the production of a queen's gametes will give each of her female offspring a 0.25 probability of being a double heterozygote and so having the potential to develop into a queen. However, a double-heterozygote female may become a worker if she has insufficient food.

The model in this paper is not dependent on the actual mechanism which causes alternative caste development pathways. Rather, the model considers whether the actual system will permit the invasion of an allele at another locus that modifies the proportion of queens produced. However, if a genetic mechanism does exist then it may constrain the available strategies (Maynard Smith 1996). In this respect, a two-locus two-allele system, which results in 25% of females being potential queens, is probably closer to the optimum than a single-locus two-allele system, which would give 50% queens, and is approximately as good as a three-locus two-allele system, which would give 12.5%. The empirical data suggest that the actual proportion of queens produced is slightly lower than 25%. This suggests that even if a two-locus genetic system does occur, there may well be other factors which further reduce queen production. The hypothesized two-locus system has never been fully accepted (Velthuis and Sommeijer 1991) and this may be one of the reasons.

The involvement of other loci could modify the caste ratio away from 25%. However, where caste fate depends upon genotype, only the heterozygote system ensures that every colony produces the same ratio. This is important because the uninvadable caste ratio is caused by colony-level factors. A population-level factor – panmictic mating competition – causes an even sex ratio to be the ESS, from the mother's perspective, in a random-mating population because at this sex ratio, both male and female offspring are equally valuable to the mother (Fisher 1958). But in a large population, mothers having all male offspring, all female offspring, or a mixture have equal fitness. In contrast, queens reared in *Melipona* colonies producing different proportions of queens would not have equal fitness. This is similar to local

mating competition (LMC) (Hamilton 1967) which is also driven by local competion for resources. However, in LMC, it is males that are competing for females rather than queens competing for workers. In addition, sex ratio optima under LMC are normally considered from the mother's rather than the offspring's perspective.

Why might a genetic rather than a plastic system have evolved in *Melipona*? When caste is determined by genetic variation among females in a colony, then the only proportions of queens that can be produced in all colonies are 50%, 25%, 12.5% etc. But if caste were determined by a genetic system that did not use genetic variation as its proximate mechanism for determining caste fate, then any proportion of queens could be produced in all colonies. For example, an allele causing 20% queens, such that all females in the population had the same genotype, and this genotype caused all females to have a random probability of 0.2 for developing into a queen. What factors might prevent the evolution of such a genetic system? One possibility is that it is too difficult to obtain the correct developmental probability. However, this seems unlikely. If such a genetic mechanism occurred but produced the wrong probability, then mutant alleles causing a more optimal probability could invade. Given that a single-locus probablistic system could reach the optimum probability, a likely explanation for the existence of a heterozygosity-based two-locus system is that it is an adaptive peak, with the difficulty of reorganizing the caste-determining mechanism acting as a constraint on the evolution of a potentially superior mechanism.

Possible effects on the evolution of the mating system

Could caste conflict have an effect on queen mating frequency? The results show that more females should develop into queens as the paternity of the queen's offspring rises. If, in a population containing both single- and double-paternity families, totipotent immature females developed facultatively in response to paternity, this would select against double mating because double-mated queens would head less productive colonies because these colonies would have fewer workers. Although facultative reproductive strategies with respect to paternity frequency do occur, for example in *Formica* wood ants which have greater male production in colonies headed by a multiple-mated versus single-mated queens (Sundström 1994; Sundström et al. 1996; Sundström and Ratnieks 1998), facultative caste development may be considerably more difficult to achieve than facultative sex allocation. First, any genetic system predisposing females to queen versus worker development must be overcome. In sex allocation, the workers merely have to decide whether or not to kill male larvae. This is a remarkable feat but one which is not constrained by an inherent genetic mechanism. Second, a developing female would have to infer paternity while sealed in her cell away from most potential information

sources (Ratnieks 1990a). However, some information on colony genetic diversity, and hence paternity, would be available because the cell is filled with food, including glandular products, regurgitated by 4–11 worker bees (Kerr et al. 1966 cited in Wilson 1971) and is itself largely made of worker-secreted wax.

Comparative analysis gives a similar conclusion. Single mating appears to be the norm throughout the Meliponinae (Peters et al. 1999); although multiple mating is reported for *Scaptotrigona postica* (Paxton 1999), excess queen production only occurs in *Melipona*. Thus, caste conflict cannot explain why the mating system appears to be highly comparable in all meliponine bees, given that excess queens only occur in *Melipona*. Two hypotheses for single mating in *Melipona* exist, both based upon the costs of diploid male production (Page and Kerr 1950; Ratnieks 1990b).

Testing predictions

The results support the caste conflict hypothesis in that the observed proportions of queens are close to theoretical predictions. If the adult workers or the mother queen were in control, few queens would be reared, as occurs in trigonine bees (Engels and Impertriz-Fonseca 1990; Bourke and Ratnieks 1999). However, the theoretical predictions have a degree of uncertainty because they depend upon the relationship between the proportion of females that develop into workers and colony productivity. Although a linear relationship is probably a good approximation of this (Page and Kerr 1990), it is unlikely to be perfect.

A more powerful test is provided by predicted differences in the uninvadable caste ratio. In *Melipona* species or populations with consistently different average levels of worker reproduction or paternity, the prediction is that the populations with less worker reproduction and higher paternity should have a greater proportion of females developing into queens. Although the model did not explicitly explore it, lower relatedness among offspring can also be caused by multiple queens and this should increase the optimum proportion of females that develop into queens. Multiple-queen colonies are normal in *M. bicolor* (Bego 1989). The queens are related (Bego 1989) so that the relatedness of female offspring is still high, 0.62 (Peters et al. 1999). Multiple queens also occur in *M. nigra* (da Silva 1977; Sakagami 1982). There is one caveat. Testing the hypothesis requires flexibility in the caste determination system. If it is inflexible, perhaps because it is tightly constrained by a two-locus system, then populations will not vary even if the typical kin structure of colonies varies across populations.

Appendix

Calculation of uninvadable probability of developing as a queen from the increased and decreased production of Ff queens and F males given in Table 2.

(a) Single paternity, males are all sons of queens

Kk queens $+2p(d/4Q)(1-Q)-2p(d/2)(1/2+d/4Q)-pd$
K males $\quad -pd/2$

Setting the increased F male or Ff female production equal to the decrease gives:

$2p(d/4Q)(1-Q) = 2p(d/2)(1/2+d/4Q)+pd+pd/2$
$(1-Q)/2Q = 2+d/4Q = 2$ {as d goes to zero}
$1-Q = 4Q$
$Q = 1/5$

(b) Single paternity, males are all sons of workers

When males are workers' sons, the effects on production and value are:

Kk queens $+2p(d/4Q)(1-Q)-2p(d/2)(1/2+d/4Q)-pd$
K males $\quad -3pd/4\times2$ (increased male value) $= -3pd/2$

Setting the increased F male or Ff female production equal to the decrease gives:

$2p(d/4Q)(1-Q) = 2p(d/2)(1/2+d/4Q)+pd+3pd/2$
$(1-Q)/2Q = 3+d/4Q = 3$ {as d goes to zero}
$1-Q = 6Q$
$Q = 1/7$

(c) Double paternity, males are all sons of queens

Kk queens $+4p(d/4Q)(1-Q)-4p(d/2)(0.5+d/4Q)$
K males $\quad -pd/2$

Setting the increased F male or Ff female production equal to the decrease gives:

$+4p(d/4Q)(1-Q) = 3/2+2d/4Q = 3/2$ {as d goes to zero}
$1-Q = 3Q/2$
$Q = 2/5$

(d) Double paternity, males are all sons of workers

Kk queens $+4p(d/4Q)(1-Q)-4p(d/2)(0.5+d/4Q)$
K males $\quad -pd/2\times2$ (double value of males) $= -pd$

Setting the increased F male or Ff female production equal to the decrease gives:

$+4p(d/4Q)(1-Q) = 4p(d/2)(0.5+d/4Q)+pd$
$(1-Q)/Q = 2+2d/4Q = 2$ {as d goes to zero}
$1-Q = 2Q$
$Q = 1/3$

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