

Are mistakes inevitable? Sex allocation specialization by workers can reduce the genetic information needed to assess queen mating frequency

Francis L.W. Ratnieks^{a,b}, Heikki Helanterä^{a,c,*}, Kevin R. Foster^{b,d}

^aLaboratory of Apiculture & Social Insects, Department of Animal & Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

^bWissenschaftskolleg zu Berlin, 19 Wallotstrasse, 14193 Berlin, Germany

^cDepartment of Bio- and Environmental Sciences, P.O. Box 65, FI-00014 University of Helsinki, Helsinki, Finland

^dCenter for Systems Biology, Harvard University, Bauer Laboratories, 7 Divinity Avenue, Cambridge MA 02138, USA

Received 20 December 2005; received in revised form 30 August 2006; accepted 6 September 2006

Available online 12 September 2006

Abstract

Insect workers can increase their inclusive fitness by biasing colony sex allocation towards males when their mother queen is mated to multiple males and females when she is singly mated. Workers need heritable variation in odour diversity to assess queen mating frequency. Here we present a simple one-locus two-allele model, which shows that the sex ratio specialization itself will often select against rare alleles that would provide additional information for the assessment of queen mating frequency. However, under certain rather restricted conditions, such as when sex ratios are highly female biased, and when worker reproduction is rare, sex ratio specialization can select for rare alleles. This suggests that sex allocation biasing by workers will usually reduce the very information that workers need to assess queen mating frequency. Our model is an example where an explicit treatment of underlying genetics and mechanisms of behaviour, such as information use, is necessary to fully understand the evolution of an adaptive behavioural strategy. © 2006 Elsevier Ltd. All rights reserved.

Keywords: Sex ratio; Sex ratio specialization; Conflict; Recognition allele; Mating frequency

1. Introduction

One remarkable thing that ant workers can do is to determine their mother queen's sex life, specifically how many males she has mated with, years after the event. The empirical evidence is convincing. In the wood ants *Formica exsecta* and *F. truncorum*, colonies are typically headed by a single queen who is mated to either one or multiple males. Most colonies headed by a queen mated to a single male specialize their reproductive investment in rearing young queens, whereas most colonies headed by a queen mated to multiple males specialize in rearing males (Sundström, 1994; Sundström et al., 1996). Queens lay the same sex

ratio of eggs in both types of colony (Sundström et al., 1996). By biasing sex allocation in this way the workers enhance their inclusive fitness (Boomsma and Grafen, 1991; Ratnieks 1991a; Bourke and Franks, 1995, Queller and Strassmann, 1998; Mehdiabadi et al., 2003). When the mother queen is single mated, the young queens are the workers' full sisters, and have greater kin value to the investing workers than do brothers. Conversely, when the mother queen is multiple mated, the young queens are a mixture of full and half sisters, and have lower kin value to the workers than brothers.

In eusocial Hymenoptera (bees, wasps, ants) workers have to rely on indirect means to assess their mother queen's mating frequency as the father or fathers are only present as sperm stored in the queen's spermatheca (Wilson, 1971). Workers are thought to assess the number of fathers using heritable traits, such as odours, in the female offspring (Ratnieks, 1990; Boomsma et al., 2003). On average, heritable odour diversity will be greater in colonies headed by a multiple-mated queen than by a single-mated queen

*Corresponding author. Laboratory of Apiculture & Social Insects, Department of Animal & Plant Sciences, Western Bank, University of Sheffield, Sheffield S10 2TN, UK. Tel.: +44 1142220144; fax: +44 1142220002.

E-mail addresses: f.ratnieks@sheffield.ac.uk (F.L.W. Ratnieks), h.helantera@sheffield.ac.uk (H. Helanterä), kfoster@fas.harvard.edu (K.R. Foster).

(Ratnieks, 1990). Although the genetics underlying odour cue diversity is unknown, the fact that some ant workers adjust their colony's sex allocation according to queen mating frequency shows that such diversity exists. Furthermore, studies of several species, including the honey bee *Apis mellifera* (Arnold et al., 1996) and *F. truncorum* (Boomsma et al., 2003), show that workers from the same colony and with the same mother but different fathers often have significantly different cuticular hydrocarbon profiles. In addition, in double-mated colonies of *F. truncorum*, greater male specialization occurs in colonies with greater variation in cuticular hydrocarbons among patriline of nestmate workers (Boomsma et al., 2003).

Recognition based upon heritable cues relies upon genetic diversity which must be caused by diversity at loci coding for these cues (Ratnieks, 1991b; Ratnieks et al., 2006). If all odour-producing loci had one allele, the average odour diversity within all colonies, whether headed by a single-mated or multiple-mated queen, would be identical and assessment of queen mating frequency impossible. More generally, low genetic variation in the information source, that is lower allele diversity at loci coding for odours, will increase assessment errors (Ratnieks, 1990). Data show that some colonies make incorrect assessments of queen mating frequency (Sundström, 1994; Sundström et al., 1996), which indicates that available information may be limited. In support of this, Boomsma et al. (2003) found that heritable odour diversity is indeed low in doubly mated colonies where workers make the wrong assessment about their colony kin structure.

Why is odour diversity so low in some colonies that assessment errors occur? One possible reason is that the acts of discrimination or assessment based upon underlying genetic information act as natural selection against genetic variation (Ratnieks, 1990). For example, queen-rearing nepotism in eusocial Hymenoptera should select against rare alleles under most conditions (Ratnieks, 1991b). Allele diversity will also decrease if colonies with high diversity suffer from costly nepotistic discrimination and so are less productive than colonies with low diversity (Boomsma et al., 2003). In contrast, recognition can also increase genetic variation as in the pollen-stigma incompatibility system of flowering plants, which prevents selfing in many species (de Nettancourt, 1977). A rare allele is at a selective advantage as pollen expressing the rare allele will be rejected with lower probability by the stigmas of other plants in the population (Yokoyama and Nei, 1979).

Here we investigate the effect of sex allocation specialization on genetic diversity at discrimination loci. We use an explicit genetic model to determine whether rare alleles used in the assessment of queen mating frequency will increase or decrease in frequency under haplodiploid sex determination and sex ratio specialization by workers. Our results show that, under many biologically realistic conditions, sex ratio specialization by workers decreases genetic diversity at loci causing heritable effects on odour cues used by workers in assessing queen mating frequency.

2. The model

We use a single-locus two allele model to investigate whether a rare allele, B, causing a novel odour, will increase or decrease in frequency. The model uses recurrence equations to determine the frequency of the rare allele in males and females in the next generation, P'_m, P'_f , as a function of their frequency in the current generation, P_m, P_f (e.g., Godfray, 1986; Bulmer 1994). The dominant eigenvalue, λ , of the 2×2 matrix representing the two recurrence equations tells us whether the frequency of the B allele increases (is selected for) or decreases (is selected against) over time. Neutrality occurs when $\lambda = 1$.

The model investigates the effect of several relevant biological parameters on the frequency changes of the rare allele (Table 1): M , the population-wide proportion of reproductive investment to males; m , the investment to males in colonies in which the rare allele occurs; s , the proportion of the colonies in the population headed by a single-mated queen versus a double-mated queen; p the proportion of males in the population that are workers' sons. We assume that all colonies have the same total productivity of queens and males but that production is more male-biased in colonies with the rare allele, with, on average, a proportion m going into male production instead of the population-wide average of M ($m > M$). This is because colonies with the rare allele have, on average, a higher diversity of alleles leading to a greater diversity of odour cues in the colony and so an increased likelihood of being assessed as "multiple mated" (Fig. 1; Ratnieks, 1990).

Although our model is presented as a two allele model with one rare and one common allele, it is also applicable to situations with more than two alleles, or where alleles have more similar frequencies. The common allele A can be thought of as representing the array of all alleles in the population except the rarest allele. In this situation, a rare allele is less often represented several times in the colony (i.e., is present in two copies in the queen and thus inherited by all

Table 1
Parameters used in the models

P_f	= frequency of B allele in females in the current generation
P_m	= frequency of B allele in males in the current generation
P'_f	= frequency of B allele in females in the next generation
P'_m	= frequency of B allele in males in the next generation
s	= proportion of colonies with a singly mated queen
S_p	= proportion of single mated colonies where B allele is carried by the male
S_m	= proportion of single mated colonies where B allele is carried by the female
D_p	= proportion of double mated colonies where B allele is carried by the male
D_m	= proportion of double mated colonies where B allele is carried by the female
M	= population wide proportion of males in sexual offspring
m	= proportion of males in sexual offspring in colonies where the rare B allele is present
p	= population wide proportion of males produced by workers

her offspring, or is inherited both from the queen and her mate or mates, or from both mates) than is a more common allele (Fig. 1). As a result, a rare allele will on average be associated with increased genetic diversity and hence male biasing ($m > M$) irrespective of how many other alleles there are in the population or their frequencies. Thus, our model should apply to the possible gain or loss of a rare allele in a population whether there is one or more additional alleles. The only exceptions to this are the case of infinite alleles at the recognition locus, when all alleles in all colonies are different so that a rare allele cannot increase genetic diversity in a colony, and the case where all alleles are present in the population at equal frequencies. The latter is highly unlikely due to random drift in finite populations. For simplicity, we also assume that workers base their decision on odours from one polymorphic locus only. Our results, however, should hold even if workers use multiple loci. This is because, the presence of a rare allele at a particular locus used in recognition will always be positively correlated with overall

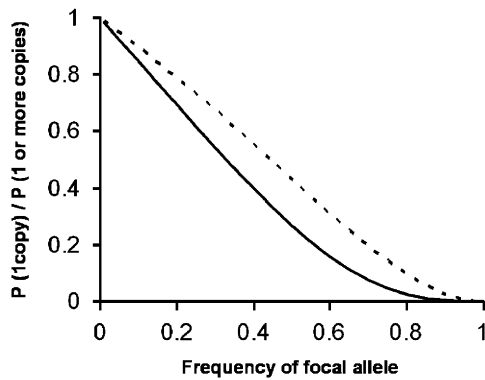


Fig. 1. The proportion of colonies with the focal allele in which it is present in only one copy (i.e. proportion of colonies with 1 copy of focal allele/proportion of colonies with 1 or more copies of focal alleles). The rarer the focal allele, the more often it increases allele number in the colonies where it is present. Dotted line = single mated colonies, solid line = double mated colonies.

Table 2

Numbers of the focal allele, B, in male and female offspring when proportion p of males are workers' sons and workers use number of alleles in assessing queen mating frequency

1. Colony	2. Queen genotype	3. Male genotype	4. Frequency	5. Female offspring	6. Male offspring	7. Proportion of males in sexual offspring
Single mated						
S_p	AA	B	sP_m	AB	$(1-p) \times A, p \times 0.5A, p \times \mathbf{0.5B}$	m
S_m	AB	A	$2sP_f$	0.5AA, 0.5AB	$(1-p) \times 0.5A, (1-p) \times \mathbf{0.5B}$ $p \times 0.75A, p \times \mathbf{0.25B}$	m
Double mated						
D_p	AA	A, B	$2(1-s)P_m$	0.5AA, 0.5AB	$(1-p) \times A, p \times 0.75A, p \times \mathbf{0.25B}$	m
D_m	AB	A, A	$2(1-s)P_f$	0.5AA, 0.5AB	$(1-p) \times 0.5A, (1-p) \times \mathbf{0.5B}$ $p \times 0.75A, p \times 0.25A$	m

Terms in bold give the frequency of the rare allele B.

diversity and male biasing, whether information comes from one or more loci (Fig. 1).

We investigate two assessment scenarios (Ratnieks, 1990: (1) by allele number, where workers assess the number of alleles present in the female offspring in the colony; (2) by genotype number, where workers assess the number of female offspring genotypes present in the colony. Table 2 shows the colony types in which the rare allele, B, occurs, their frequencies and the genotypes and proportions of sexual offspring that are reared, depending on the proportion of queens which are single mated (s) and the proportion of males in the population which are workers' sons (p) when workers use allele number assessment. From these values we can calculate the frequencies of the focal allele in the next generation for both sexes by adding together the numbers of the B allele from each colony type. From Table 2

$$\begin{aligned} \text{Number of B alleles in males} &= sP_mmp/2 + sP_fm p/2 \\ &+ sP_fm(1-p) + (1-s)P_mmp/2 + (1-s)P_fm p/2 \\ &+ (1-s)P_fm(1-p). \end{aligned} \tag{1A}$$

$$\begin{aligned} \text{Number of B alleles in queens} &= sP_m(1-m)/2 + sP_f \\ &\times (1-m)/2 + (1-s)P_m(1-m)/2 \\ &+ (1-s)P_f(1-m)/2. \end{aligned} \tag{1B}$$

These values are normalized into proportions by dividing through by the total number of males, M , and queens, $1-M$, reared in the population, and written in matrix form:

$$\begin{bmatrix} P'_m \\ P'_f \end{bmatrix} = \begin{bmatrix} 0.5(mp/M) & 0.5((2-p)m/M) \\ 0.5((1-m)/(1-M)) & 0.5((1-m)/(1-M)) \end{bmatrix} \times \begin{bmatrix} P_m \\ P_f \end{bmatrix}. \tag{1C}$$

By solving for the dominant eigenvalue, the boundary conditions for the invasion of a rare allele, $\lambda = 1$, are

$$m = M \tag{1D}$$

and

$$m = (1 - 2M)/(1 - p), \tag{1E}$$

which simplify to $m = M$ and $1 - 2M$ under zero worker reproduction ($p = 0$).

A similar procedure for the genotypic assessment scenario is presented in the Appendix, and yields boundary conditions of

$$m = M$$

and

$$m = (1 - 2M)(2 - ps)/(2(1 - p)(1 - s)),$$

which simplifies to $m = (1 - 2M)/(1 - s)$ when worker reproduction, p , is zero.

3. Results

3.1. Assessment based on allele number

Fig. 2 shows the results of Model 1. The figure is divided into 4 main areas by the two boundary conditions, $\lambda = 1$, $m = M$ and $1 - 2M/(1 - p)$. Two of these areas have $\lambda > 1$ and two $\lambda < 1$. The areas where $\lambda > 1$ are the mathematically defined areas in which the rare allele increases in frequency. However, much of this area is not biologically realistic parameter space. Sex-ratio specialization will only increase allele number when the $\lambda > 1$ area overlaps with the area of biologically realistic parameter space, which is shown hatched. First, we know that sex ratio specialization should cause greater male rearing when there is greater genetic diversity, because this correlates with queen mating frequency. Therefore, sex allocation in colonies with a rare allele (m) will be more male biased than average (M). Thus, $m > M$ is realistic parameter space but $m < M$ is not. Second, the population-wide sex allocation ratio will be somewhere between the worker optimum ($M = 0.25$ when all queens are single mated or $M = 0.33$ when all queens are double mated) and the queen optimum ($M = 0.5$) (Trivers and Hare, 1976; Boomsma and Grafen, 1991).

Given these restrictions, it can be seen that the rare allele will only invade in a small part of the biologically realistic parameter space. This is the area where the population-wide

sex-allocation ratio is highly female biased and where the effect of the rare allele on colony sex allocation is small (i.e. sex ratio specialization does not cause male bias to be more extreme than $1 - 2M$). It will only be possible for a rare allele to invade when there is a large proportion of single-mated queens in a population, and where the workers have considerable or complete control over sex allocation. As male production by workers increases from $p = 0$ (Fig. 2b) to 0.5 (Fig. 2c), the mathematically allowed parameter space increases. However, as the proportion of workers' sons increases, the worker optimum sex ratio moves toward more males (Bourke and Franks, 1995), and the biologically allowed parameter space contracts. Furthermore, as P increases, the difference between worker optima at $s = 0$ and at 1 decreases, and the biologically relevant parameter space diminishes further. When workers produce all the males ($p = 1$), the optimum sex ratios of both queen and workers coincide at 0.5, and no biologically allowed parameter space exists. Overall, therefore, male production by workers makes it less likely that a rare allele will increase in frequency.

3.2. Model 2. Assessment based on genotype number

The boundary conditions are $m = M$ and $m = (1 - 2M)(2 - ps)/(2(1 - p)(1 - s))$ which, unlike the allelic discrimination scenario, depend upon the frequency of single versus double mated queens in the population. The invasion conditions plotted for three values of s (Fig. 3) show that the mathematically allowed parameter space is again greatest when most queens are single mated (s close to 1) and where there is no worker reproduction. Furthermore, the mathematically allowed parameter space is somewhat larger than under assessment based on allele number.

4. Discussion

Our model suggests that facultative sex allocation by worker Hymenoptera in response to intrapopulation variation in queen mating frequency will tend to deplete the information necessary for accurate assessment of queen

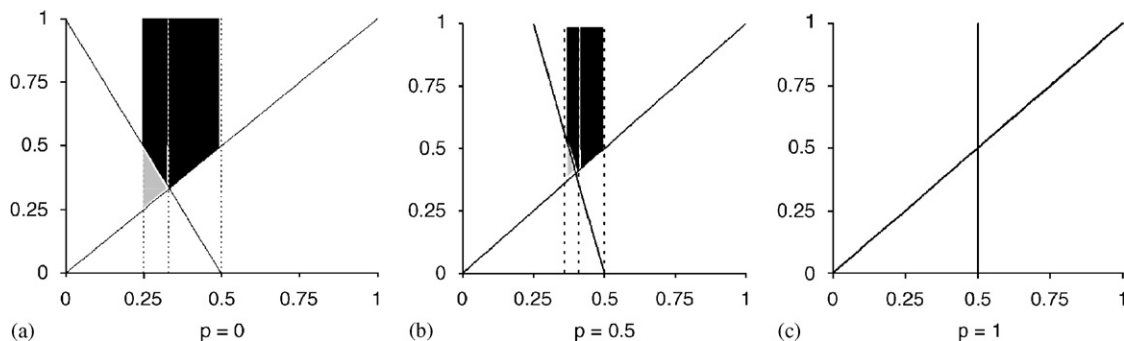


Fig. 2. Invasion under allele assessment, and with different proportions of worker produced males p . X-axis = M , population wide allocation to males, Y-axis = m , allocation to males in colonies with the rare allele. The diagonal (solid) lines represent the mathematical boundary conditions and divide the graph area into four areas. In two of these $\lambda > 1$ meaning that the rare allele will increase in frequency. The shaded areas represent the biologically permitted range of conditions. Black shading indicates biologically relevant conditions outside the invasion area. Grey shading indicates an area of parameter space permitted both biologically and mathematically, and is the zone in which the rare allele can invade. The two vertical (dotted) lines represent sex ratio optima for workers (left line) under $s = 0$ and for the queen (0.5) (right line). In panel C all these lines coincide at $M = 0.5$, so that there is no biologically relevant invasion space for the allele.

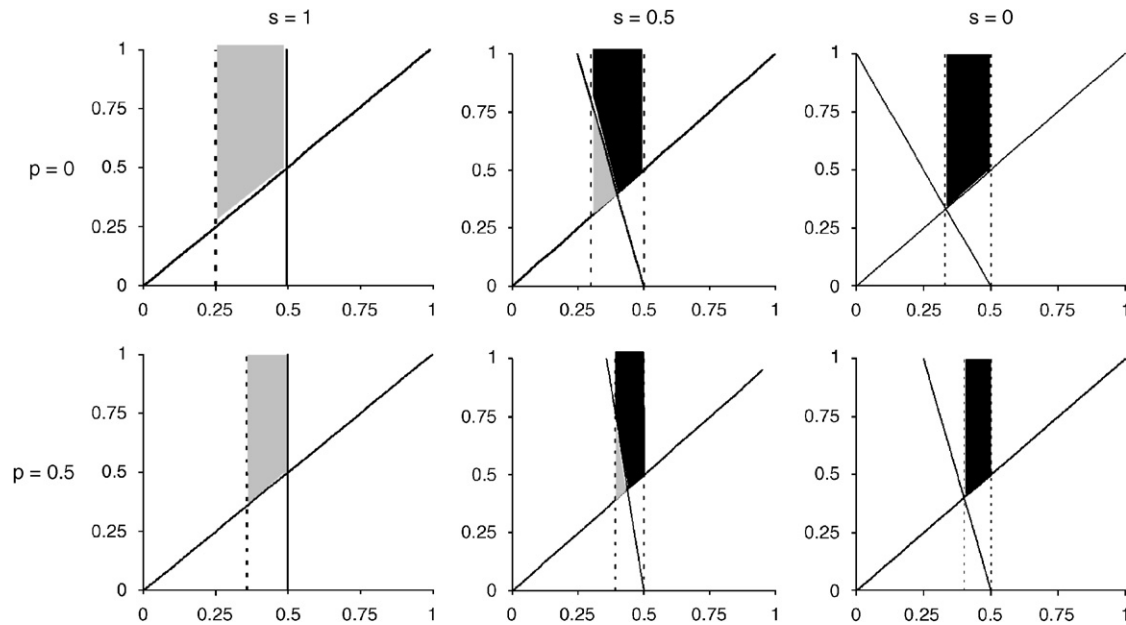


Fig. 3. Invasion under genotype assessment and with different proportions of worker produced males p and single mating s . The diagonal (solid) lines represent the mathematical boundary conditions and divide the graph area into four areas. In two of these $\lambda > 1$ meaning that the rare allele will increase in frequency. Black shading indicates biologically relevant area outside the invasion area, grey shading indicates area permitted both biologically and mathematically, and is the zone in which the rare allele can invade. Vertical (dotted) lines from left to right represent sex ratio optima for workers under the given values of s , and for the queen. When $p = 1$, see Fig. 2c). See legend of Fig. 2 for details.

mating frequency. Low information may, therefore, limit or prevent facultative sex allocation specialization or increase the likelihood that queens are incorrectly assessed in terms of their mating frequency. Rare alleles can only increase in frequency when population sex-allocation ratios are highly female biased, that is close to worker optimum, and when worker reproduction is rare. The model also shows that the average sex ratio biasing effect of an additional allele must be small.

The intuitive logic behind our result is shown in Fig. 4. If a male carries a rare allele, this will tend to cause greater male specialization in his colony. However, because males arise from unfertilized haploid eggs, this father male does not pass on his genes through the additional males reared in the colony (a male has no sons in haplodiploids, only grandsons). As a result, the rare allele will tend to increase the frequency of the sex of reproductive (males) that do not carry the allele, which results in the allele being selected against. The situation is different under worker reproduction because the queen's mate(s) can now pass on their genes (and thus also the rare allele) to future generations via grandsons. This does not, however, increase odour diversity because worker reproduction shifts the worker optimum sex ratio towards more males and thus makes invasion of a rare allele less likely.

Our model only considers one potential mechanism affecting genetic diversity on recognition loci. Thus, even if sex ratio specialization selects against rare alleles, whether rare alleles are favoured or not depends upon the combined effects of all selective forces. In the area of recognition, both nepotistic discrimination (Ratnieks, 1991b) and nestmate

recognition (Ratnieks, 1991b) can affect allelic diversity. Nepotism will normally select against rare alleles, but nestmate recognition can favour rare alleles. However, for this to happen heritable odours must be used, at least in part, in nestmate recognition, and colonies with rarer alleles must be at an advantage perhaps because they can more easily recognize intruders (Ratnieks, 1991b). Furthermore, the primary function of cuticular hydrocarbons is probably not recognition, but to protect the insect from desiccation and microbes (reviewed in Howard and Blumquist, 2005). This will almost certainly select for the best compounds, and may potentially select for allelic diversity if overdominance or some other factor favouring genetic polymorphism exists. Finally, allelic diversity within a population can also be increased or decreased by genetic drift and can be increased by gene flow from neighbouring populations if these are genetically different at loci coding for odours.

Our model assumes a simplified mating system, where queens mate with only one or two males, and where sperm from the two males are used equally in colonies headed by a double-mated queen. These assumptions can be relaxed without undermining our conclusions. Increasing the number of matings above two will shift the worker optimum at $s = 0$ (i.e. when all colonies are multiply mated) towards greater allocation to males, which will not change the conclusion that rare alleles will increase in frequency only between worker optima at $s = 1$ and 0. Unequal sperm use will not affect our conclusions as long as enough offspring of each male are present to be detectable.

How workers actually assess queen mating frequency represents an empirical challenge for the future. We

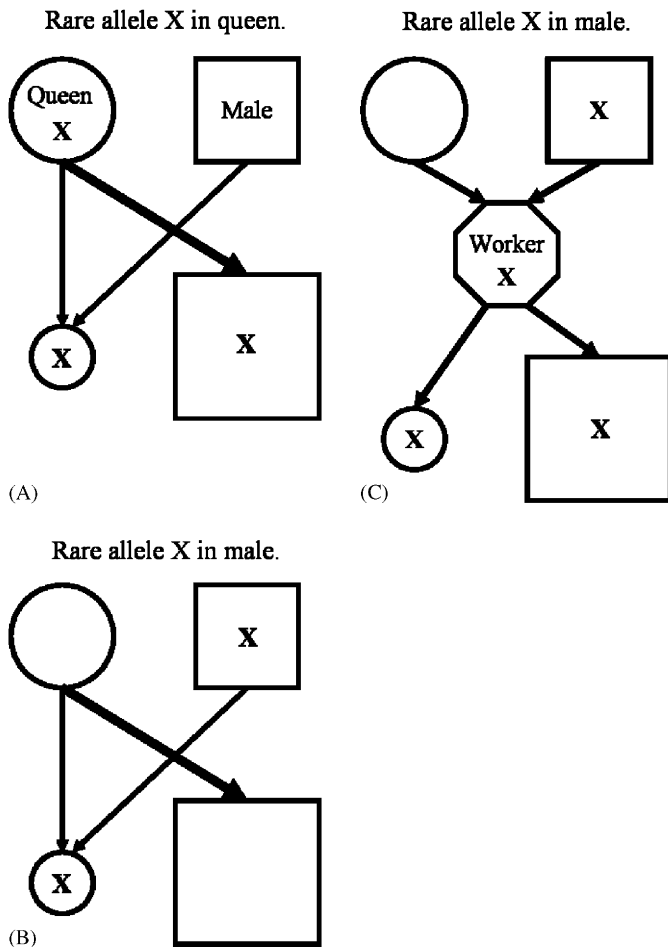


Fig. 4. Intuitive result. Male specialization is adaptive for workers in colonies with a multiple-mated queen. Multiple-mating by the mother queen is detected by the workers by greater than average odour cue diversity. A rare allele has a greater positive effect on colony cue diversity than a common allele. Therefore, a rare allele is more likely to be in a male specialist colony than a female specialist colony. (A) If the rare allele is in a queen then it is preferentially transmitted to males more than females because rare allele colonies have greater allocation to males. (B) Next generation, when it is in a male, male bias still occurs and now the rare allele is weakly transmitted through females and not to males. (C) When males are workers' sons, males transfer genes to grandsons.

considered two different ways that workers may assess queen mating frequency, using either the number of alleles or genotypes in the female offspring in the colony. The basic conclusions are the same for both forms of discrimination but there are also some differences (Figs. 2 and 3). In particular, when there is a high proportion of single-mated queens in the population, a rare allele is much more likely to invade under genotypic than allelic discrimination.

Our model helps to explain in more detail the low levels of information in chemical profiles of workers in colonies of *F. truncorum* headed by a single queen (Boomsma et al 2003). The long-term average sex ratio in the population is 1/3 males, a value around which rare alleles are at best neutral or probably selected against, assuming allele based assessment by workers. Even under genotype assessment, selection against rare alleles is likely, given the large male biases in

doubly mated colonies of *F. truncorum*, and the frequency of single mating in the population $s = 0.61$. Furthermore, our model shows that the more frequent double mating is, the less information there is likely to be for allocation decisions. The resulting errors in the assessment of colony type may slow down the selection for multiple mating by queens (Ratnieks and Boomsma, 1995), shown to exist under facultative sex allocation specialization by workers (Sundström and Ratnieks, 1998). However, the fact that workers in some colonies make the correct assessment and bias sex ratio adaptively suggests that genetic information does exist and must be maintained by some process, whether via selection or not.

More generally, our conclusions suggest interesting feedbacks in the evolution of sex ratio specialization. Greater allele diversity is more likely to occur when sex ratios are close to the population-wide worker optimum. That is, when workers already have control over sex ratio. Moving the population sex ratio towards the queen optimum makes rare alleles less likely to invade (Figs. 2 and 3). Queens may, therefore, need only to exert partial control over sex allocation in order to initiate the collapse of facultative worker sex allocation biasing due to a lack of information. Overall, split sex ratios under monogyny and variable queen mating frequencies are most likely to occur when workers control the sex allocation and worker reproduction is infrequent. These conditions hold at least for *F. exsecta* and *F. truncorum*, but are not necessarily the rule among social Hymenoptera in general. Furthermore, the information available to the workers will be more accurate, and split sex ratios thus more likely, if workers use information produced by many recognition loci (instead of one) and use genotype rather allelic discrimination. The genetic causes underlying the diversity of cuticular profiles are yet to be studied in any species.

More generally, our model is an example where genetic details matter. There has been a long running debate (Schwartz, 2002) over the validity of models that neglect genetics and focus purely on phenotypes (“the phenotypic gambit”, Grafen, 1982). Exceptions to the phenotypic gambit clearly exist and the classic example is sickle cell anaemia, where heterozygote advantage in the presence of malaria maintains an allele that is deleterious in the homozygote (Schwartz, 2002). Our model provides another example where consideration of genetic details, and other mechanistic factors such as how the information is used, provide novel conclusions beyond the scope of a purely phenotypic model. However, we do not take this to mean that phenotypic models should not be used. Rather, it demonstrates the need to consider a range of approaches to any given question and to select the appropriate tools for the job (Kokko, 2005).

Acknowledgments

We thank Tom Wenseleers and the anonymous referees for constructive comments. During this study HH was funded by The Finnish Cultural Foundation and the Academy of Finland (Grant Decision No. 213821).

Table A1

Numbers of the focal allele in male and female offspring when proportion p of males are workers' sons and workers use genotype diversity as a rule for assessing mating frequency of the queen

1. Colony	2. Queen genotype	3. Male genotype	4. Frequency	5. Female offspring	6. Male offspring	7. Proportion of males in sexual offspring
Single mated						
S_p	AA	B	sP_m	AB	$(1-p) \times A, p \times 0.5A,$ $p \times \mathbf{0.5B}$	M
S_m	AB	A	$2sP_f$	0.5AA, 0.5AB	$(1-p) \times 0.5A, (1-p) \times \mathbf{0.5B}$ $p \times 0.75A, p \times \mathbf{0.25B}$	m
Double mated						
D_p	AA	A, B	$2(1-s)P_m$	0.5AA, 0.5AB	$(1-p) \times A, p \times 0.75A,$ $p \times \mathbf{0.25B}$	m
D_m	AB	A, A	$2(1-s)P_f$	0.5AA, 0.5AB	$(1-p) \times 0.5A, (1-p) \times \mathbf{0.5B}$ $p \times 0.75A, p \times 0.25A$	m

Terms in bold give the frequency of the rare allele B.

Appendix A. Invasion conditions under genotype assessment

Table A1 shows the colony types in which the rare allele, B, occurs, their frequencies and the genotypes and proportions of sexual offspring that are reared, depending on the proportion of queens which are single mated (s) and the proportion of males in the population which are workers' sons (p) when workers use genotype assessment. From these values we can calculate the frequencies of the focal allele in the next generation for both sexes.

$$\begin{aligned} \text{Number of B alleles in males} &= sP_mMp/2 + sP_fm p/2 \\ &+ sP_fm(1-p) + (1-s)pP_m m/2 \\ &+ (1-s)P_fm + (1-s)P_fm(1-p)/2. \end{aligned} \quad (2A)$$

$$\begin{aligned} \text{Number of B alleles in females} &= sP_m(1-M)/2 + sP_f \\ &\times (1-m)/2 + (1-s)P_m(1-m)/2 \\ &+ (1-s)P_f(1-m)/2. \end{aligned} \quad (2B)$$

These are normalized into proportions, simplified and written in matrix form.

$$\begin{bmatrix} P'_m \\ P'_f \end{bmatrix} = \begin{bmatrix} 0.5mp(1-s) + psM/M & m(p-2)/2M \\ 0.5((1-m)/(1-M)) & 0.5((1-m)/(1-M)) \end{bmatrix} \times \begin{bmatrix} P_m \\ P_f \end{bmatrix}. \quad (2C)$$

The boundary conditions for $\lambda = 1$ are

$$m = M \quad (2D)$$

and

$$m = (1-2M)(2-ps)/(2(1-p)(1-s)), \quad (2E)$$

which simplifies to $m = (1-2M)/(1-s)$ under zero worker reproduction.

References

Arnold, G., Quenet, B., Cornuet, J.-M., Masson, C., de Scheper, B., et al., 1996. Kin recognition in honeybees. *Nature* 379, 498.

- Boomsma, J.J., Grafen, A., 1991. Colony-level sex ratio selection in the eusocial Hymenoptera. *J. Evol. Biol.* 4, 383–407.
- Boomsma, J.J., Nielsen, J., Sundström, L., Oldham, N.J., Tentschert, J., Petersen, H.C., Morgan, E.D., 2003. Informational constraints on optimal sex allocation in ants. *Proc. Natl. Acad. Sci. USA* 100, 8799–8804.
- Bourke, A.F.G., Franks, N.R., 1995. *Social Evolution in Ants*. Princeton University Press, Princeton, NJ.
- Bulmer, M., 1994. *Theoretical Evolutionary Ecology*. Sinauer, Sunderland, MA.
- de Nettancourt, D., 1977. *Incompatibility in Angiosperms*. Springer, Berlin, Germany.
- Godfray, H.C.J., 1986. Models for clutch size and sex-ratio with sibling interaction. *Theor. Popul. Biol.* 30, 215–231.
- Grafen, A., 1982. How not to measure inclusive fitness. *Nature* 298, 425.
- Howard, R.W., Blumquist, G.J., 2005. Ecological, behavioural and biochemical aspects of insect hydrocarbons. *Annu. Rev. Entomol.* 50, 371–393.
- Kokko, H., 2005. Useful ways of being wrong. *J. Evol. Biol.* 18, 1155–1157.
- Mehdiabadi, N.J., Reeve, H.K., Mueller, U.G., 2003. Queens versus workers: sex-ratio conflict in eusocial Hymenoptera. *Trends Ecol. Evol.* 18, 88–93.
- Queller, D.C., Strassmann, J., 1998. Kin selection and social insects. *BioScience* 48, 165–175.
- Ratnieks, F.L.W., 1990. Assessment of queen mating frequency by workers in social Hymenoptera. *J. Theor. Biol.* 142, 87–94.
- Ratnieks, F.L.W., 1991a. Facultative sex allocation biasing by workers in social Hymenoptera. *Evolution* 45, 281–292.
- Ratnieks, F.L.W., 1991b. The evolution of genetic cue diversity in social Hymenoptera. *Am. Nat.* 137, 202–226.
- Ratnieks, F.L.W., Boomsma, J.J., 1995. Facultative sex allocation by workers and the evolution of polyandry by queens in social Hymenoptera. *Am. Nat.* 145, 969–993.
- Ratnieks, F.L.W., Foster, K.R., Wenseleers, T., 2006. Conflict resolution in insect societies. *Ann. Rev. Entomol.* 51, 581–608.
- Schwartz, J., 2002. Population genetics and sociobiology: conflicting views of evolution. *Perspect. Biol. Med.* 24, 224–240.
- Sundström, L., 1994. Sex ratio bias, relatedness asymmetry and queen mating frequency in ants. *Nature* 367, 266–268.
- Sundström, L., Ratnieks, F.L.W., 1998. Sex ratio conflicts, mating frequency and queen fitness in *Formica* ants. *Behav. Ecol.* 9, 116–122.

- Sundström, L., Chapuisat, M., Keller, L., 1996. Conditional manipulation of sex ratios by ant workers: a test of kin selection theory. *Science* 274, 993–995.
- Trivers, R.L., Hare, H., 1976. Haplodiploidy and the evolution of social insects. *Science* 191, 249–263.
- Wilson, E.O., 1971. *The Insect Societies*. Harvard University Press, Cambridge, MA.
- Yokoyama, S., Nei, M., 1979. Population dynamics of sex-determining alleles in honey bees and self-incompatibility alleles in plants. *Genetics* 91, 609–626.