

## Research article

# Simulation models of the role of genetic variability in social insect task allocation

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**Summary.** A feature of some species of eusocial Hymenoptera is a high level of intra-colonial genetic diversity, and correlated diversity in the level of the stimulus required for individuals to initiate work. Here we explore the effects of intracolony variability on the responsiveness of colonies to changing needs in task allocation using computer simulation. Our simulations show that colonies comprised of individuals of uniform task threshold are poor at adapting to changing colony needs – that is, they did not allocate the appropriate numbers of workers to tasks. On the other hand, colonies comprised of many groups of differing task threshold adapt quickly and more appropriately to changes in task need. Our simulations suggest that intracolony genetic variability may be an important component of an efficient task allocation system for some species of social Hymenoptera. We speculate that the benefits of an improved task allocation system may have contributed to the high levels of polyandry and polygyny seen in some of these insects.

*Key words:* Self organisation, mathematical modelling, genetic variability, task threshold.

## Introduction

Kin selection theory suggests that the evolution of eusociality in the Hymenoptera was facilitated by high relatedness (and hence low genetic variability) among workers (reviewed in Crozier and Pamilo, 1996). Polyandry and polygyny, however, both generate high levels of intra-colonial genetic variance and low relatedness. Additionally, in the case of polyandry, multiple matings are probably associated with costs to queens (Fuchs and Schade, 1994; Palmer and Oldroyd, 2000). Thus students of social insects have long been puzzled by the widespread occurrence of multiple queens (polygyny) or multiple mates (polyandry) in these species (Keller and Reeve, 1995; Schmid-Hempel and Crozier, 1999).

Both empirical (Cole and Wiernasz, 1999; Fuchs and Schade, 1994; Oldroyd et al., 1992; Tarpay, 2002) and theoretical studies suggest fitness advantages of polyandry and polygyny (reviewed in Crozier and Page, 1985; Oldroyd et al., 1998; Palmer and Oldroyd, 2000). In this paper we explore, using computer simulation, the hypothesis of Crozier and Page (1985) that within-colony diversity permits the enhanced development of ‘task specialisation’ because workers of different genetic background have different thresholds to perform certain tasks, and we speculate that this increases colony fitness.

Social insects need to divide the available workforce among different tasks so that the appropriate number of workers is allocated to each task. It has been demonstrated that effective task allocation systems can emerge from a set of simple rules followed by each individual. These rules can generate information feedback loops from other individuals and the environment. As a simple example, the number of individuals involved in corpse removal could be regulated by the simple rule: ‘if corpses are present then remove corpse’. If the number of corpses is high, the stimulus to act is high, whereas if there are no corpses, individuals are available for other tasks.

Individual workers can be identical or differ in their thresholds for performing a task. Although it can be shown that task allocation systems can emerge from identical individuals following the same rules (e.g. Bonabeau et al., 1996), some societies show considerable variability among individuals in their tendency to perform a task (reviewed in Robinson, 1992) and this variance in task threshold may be an important component of an efficient task allocation system. In some cases, especially honey bees, variance in task threshold seems to be genetically determined; in others, e.g. some termites, whose colonies arise from a single king and queen, variance can arise from environmental factors such as larval feeding (Fraser et al., 1998; Oster and Wilson, 1978).

Here we show that intrinsic variability among families of workers comprising a social insect colony can give a more

finely-tuned task allocation system. Colonies that are genetically diverse can adapt better to changing conditions, because different workers of different families have genetically different propensities to perform certain tasks. For simplicity we will confine our remarks to polyandrous species. However, our arguments are also applicable to polygynous monandrous species, but such polygynous colonies are divided into families, not patrilineal subfamilies.

### Construction of the model

Our simple model is not intended to represent any real species. It is based on that of Page and Mitchell (1998), but has some important differences. We consider a colony of social insects with one hundred workers engaged in foraging or some other critical task. (We have obtained similar results with cohorts of 1000 workers but we chose to work with the smaller number for computational ease). This group of potentially active workers is divided into a number of subfamilies (groups of super-sister daughters of each sire as might be the case for polyandrous honey bee species). In our model, the means of the subfamily thresholds were distributed normally whereas Page and Mitchell (1998) distributed individual thresholds with a uniform random distribution.

The *task stimulus* is defined as an environmental or social variable that will cause some or all workers to commence working or continue working on a task associated with that stimulus. Workers of each subfamily are assumed to have a particular *stimulus threshold*. The stimulus threshold of a particular subfamily is that magnitude of the task stimulus that will cause workers of that subfamily to work on the task. For example, workers of some subfamilies might need to detect a higher temperature before fanning than workers of other subfamilies. For the purposes of our simulations, the stimulus threshold that would cause individuals of a particular subfamily to act was denoted by an integer that was assigned randomly within the range 1–100. The distribution of thresholds from subfamily to subfamily was modelled by a normal distribution with mean 50 and standard deviation 20.

The *task stimulus* in our model is a whole number between 0 and 100 that is a measure of the need for the colony to engage in the task. This number is 0 if the appropriate response is for no workers to engage in the task and 100 if it is appropriate that all 100 workers engage in the task. As a simplification, then, task stimulus was applied externally, and was unaffected by the work of the colony: i.e. work did not alter task demand. It is possible to design a model where the task stimulus decreases as bees work on the task and increases where there are insufficient workers but we have chosen not to do so as this introduces extra assumptions about the rate that the stimulus changes in both the presence and absence of insects working to reduce it. In a general model such as this one, it is desirable to minimise the number of arbitrary assumptions. The fixed task stimulus may be viewed as a measure of the number of bees needed to work on the task to keep the colony at equilibrium. A model where

the bees' work decreased the stimulus would show a different pattern of worker engagement; initially many workers would work to reduce the stimulus but eventually only the bees with lower thresholds would keep working to reduce the stimulus. Our model could be considered as a representation of the last part of this process. Alternatively the stimulus may be viewed as the rate of change of some quantity in the colony, such as the rate that heat is absorbed by the hive or the rate that pollen is consumed by larvae.

Each step in our simulation works like this: a worker is chosen at random. Its stimulus threshold is compared to the current task stimulus. If its task threshold is below the task stimulus it turns 'on' (starts working on the task) if it is 'off' and remains 'on' if it is already 'on'. If the random worker's stimulus threshold is above the current task stimulus it turns 'off' (stops working on the task) if it is working and remains 'off' if it is not working. We describe this series of operations as one time-step or one iteration in the simulation. In the next step, another worker is chosen at random with replacement and an identical process is enacted. The stimulus, which reflects the colony's need for workers on that task, may be changed from time to time to examine how well the colony adapts to changing needs for workers on a particular task. The outputs of the model are the number of the 100 individuals that are available for the task which actually engage in the task. Under the conditions of our model, the optimal response for a simulated colony is for the number of workers that are 'on' to be sufficient to match the task stimulus at all times. Thus a colony genetic architecture (number of subfamilies) is judged as superior if it rapidly responds to a change in task stimulus by closely matching the number of bees that are 'on' to the level of the task stimulus. A genetic architecture is inferior if it is unable to respond to changes in task stimulus, or inappropriately turns all individuals 'on' in response to a relatively low stimulus.

The model was programmed in Matlab implemented on a DEC Unix system.

### Simulations conducted

We first present some examples of outputs from the model showing how individual colonies with various distributions of subfamilies react to different task stimuli. We then explore the effect of the level of task stimulus on colonies' ability to meet task demand and the effects of the number of subfamilies on colonies' speed of adjustment to task stimuli. Finally we explore the cumulative effect of colonies' ability to meet task stimuli by examining what happens in colonies where the task stimulus changes frequently.

#### *The effect of changing the level of the task stimulus over time. Some typical outcomes for various levels of polyandry*

These simulations were started with no workers engaged in the task (all workers were set to 'off') and the task stimulus set at 50. After 400 iterations, the stimulus was reduced to

20 and after a further 400 iterations the stimulus was increased to 80. The purpose of these simulations was to see how colonies with different genetic architectures adapt to a changing environment, and the ways in which some colonies failed to adapt.

The way in which our simulated colonies adapted to these changes depended on the number of subfamilies present and their stimulus thresholds. Colonies comprised of just one subfamily adapted in an all-or-nothing fashion (Fig. 1). The behaviour illustrated in Graph A in Fig. 1 occurs when the stimulus threshold is between 20 and 50 units and that of Graph B when the stimulus threshold is set between 50 and 80 units. If the single subfamily's threshold is set above 80 units, the workers never switch 'on'; if it is below 20 all workers quickly become involved in the task and remain 'on' even when the stimulus is decreased to 20 units and increased to 80. Figure 1, Graph B is an example of a case where a task stimulus of 50 units was insufficient to get any workers engaged in the task, but after the stimulus was increased to 80 units, nearly all workers switched 'on'.

This all-or-nothing behaviour, would be highly maladaptive if every worker in a real colony were to engage in the same task. This model is a highly simplified system and may be regarded as only representing that part of a colony that is able to perform any given task. (For example, foragers are usually only older bees in *Apis mellifera*.) There are, however, in real colonies tasks, such as thermoregulation, where comparatively little variation in individual threshold could be expected (Page et al., 1995). For such tasks the effect of workers' efforts to reduce stimuli need to be considered in order to produce model behaviour which is not all-or-nothing.

Such sub-optimal behaviour is also evident in colonies comprised of two subfamilies, although the extreme cases of either all or none of the workers engaged in the task are unusual. A two-subfamily colony tends to display the additional (and highly desirable) type of behaviour where about half the workers work in response to a stimulus of 50 and almost all workers work in response to a stimulus of 80 (Fig. 1, Graph C). A two-subfamily colony may still be able to ratchet up to a higher work level under a higher task stimulus even if it does not respond to a decrease in stimulus (Graph D).

With five subfamilies there is less variation in the types of behaviour. These colonies show a similar and appropriate response to changes in task stimulus. Figure 1, Graphs E and F are typical examples of the behaviour of five-subfamily colonies, and demonstrate the increased flexibility and responsiveness that genetic variance can bring to a social insect task allocation system. Occasionally, the number of workers switched to 'on' did not decrease when the task stimulus was reduced but did increase when the stimulus increased. With five or more subfamilies the colony almost always tracked changes in task stimulus, although the exact amount of the adjustment made in each case depends on the distribution of subfamily stimulus thresholds. If the mean of the subfamily thresholds is low then workers are more likely to engage on a task and there is generally a high level of activity. If the mean of the subfamily task thresholds is high

then workers are less inclined to be engaged and the general level of activity is low. (Fig. 1, Graph F is an example of this for five subfamilies.)

Generally speaking once there are five or more subfamilies, a spread of thresholds leads to a smoother change in worker numbers in response to stimulus changes. Because the subfamily thresholds are distributed as a normal distribution, increasing the number of subfamilies brings the spread of distributions in the whole colony closer to a normal distribution and so the colony is less likely to be dominated by individuals with thresholds at either extremes. This averaging effect of multiple subfamilies has been demonstrated experimentally by Page et al. (1995), who measured the performance of four single-subfamily colonies and compared this with a four-subfamily colony where the queen was inseminated with semen from the same four drones that were used to create the colonies which had one patriline each. These experiments showed that the performance of the four subfamily colony was close to the average of the single subfamily colonies for most of the 19 quantities that were measured. The averaging effect of multiple subfamilies has also been predicted theoretically in a model for nectar foraging (Cox and Myerscough, 2003).

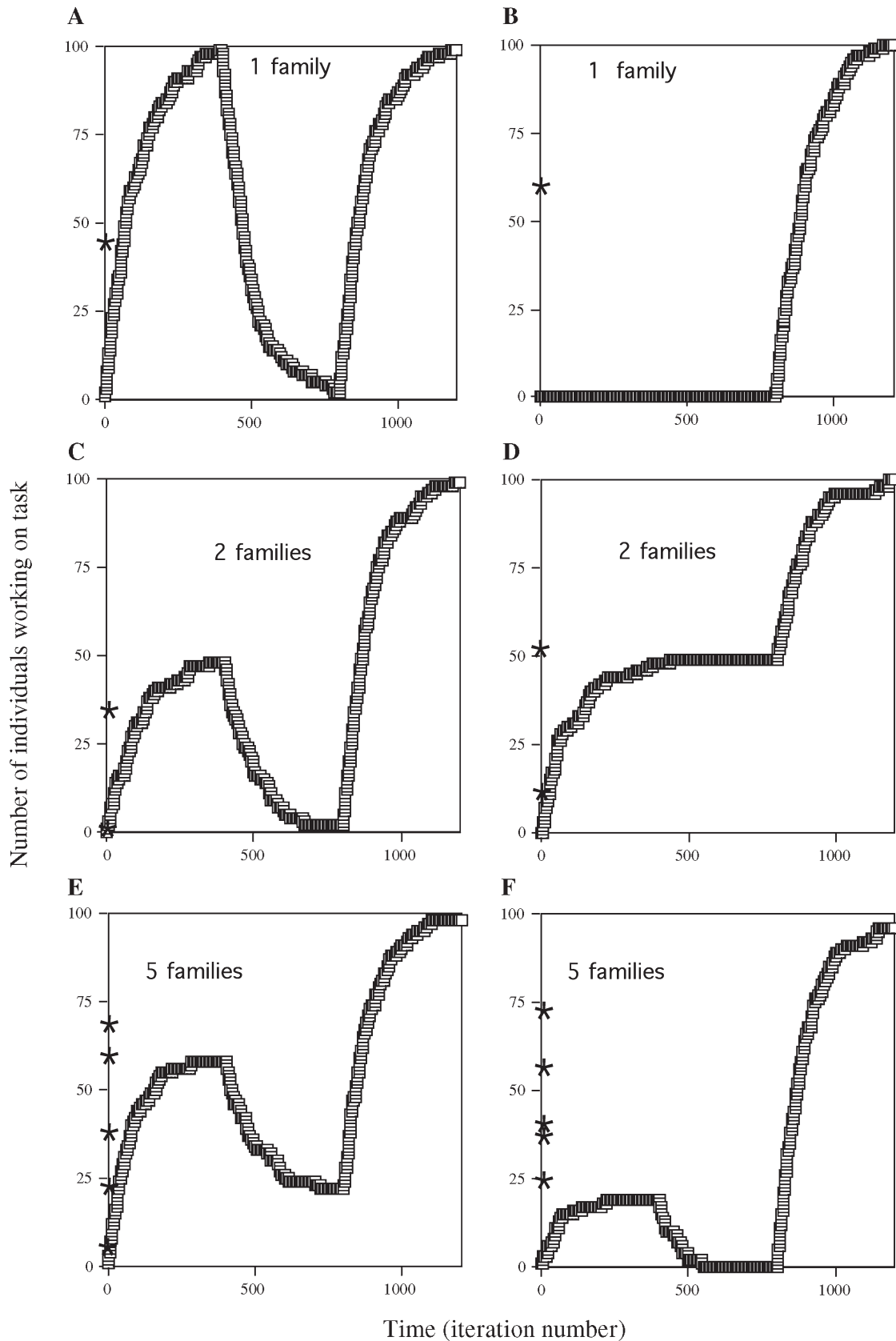
It is interesting to note that most of the advantage of variation in task thresholds is gained in moving from 1 to 5 families. Therefore polyandrous species which mate fewer times than *A. mellifera* will still gain benefit from a spread of genetically determined thresholds.

#### *Effect of stimulus threshold on changes in number of workers engaged in tasks*

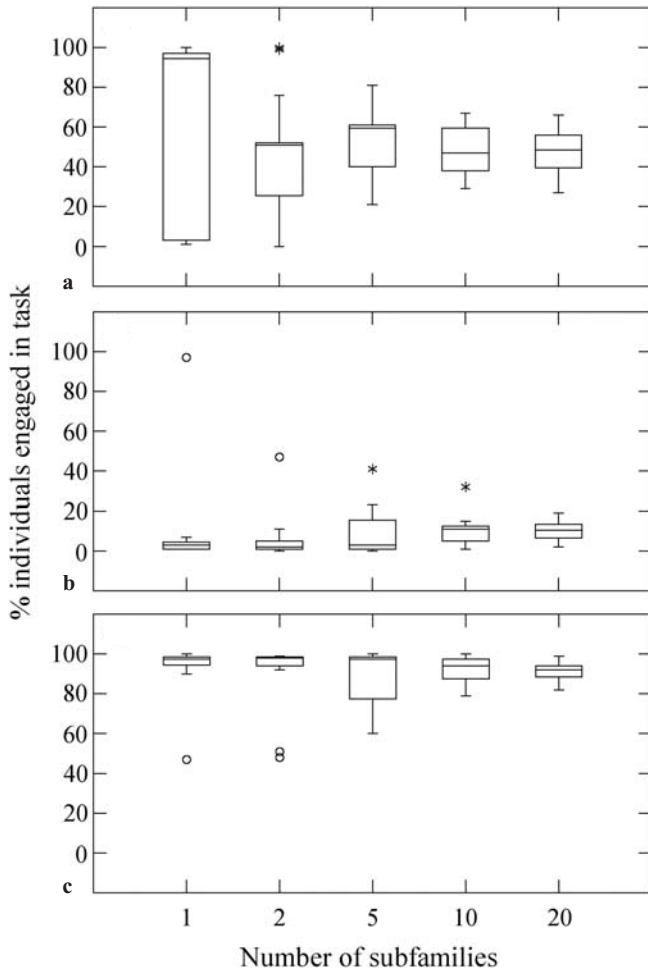
Here we assigned stimulus thresholds to each subfamily in a colony. Initially workers were chosen at random to be 'on'. The simulation was then run until there had been no change in the number of workers 'off' and 'on' for 20 time steps. This was repeated 15 times for each number of subfamilies (1, 2, 5, 10 and 20 subfamilies) for three different set stimulus levels (20, 50 and 80).

Figure 2 presents boxplots of the activity levels for 16 colonies comprised of various numbers of subfamilies. The median of the number of workers active on a task for a mid-range task stimulus of 50 units (Fig. 2a) is closest to 50 for those colonies comprised of large numbers of subfamilies.

The boxplot of the colonies comprised of a single subfamily is somewhat deceptive. An examination of the numerical data shows that these colonies with one subfamily either have almost all or almost none of the available workers at work. For these reasons, the range of activity levels for single subfamily colonies for low level stimulus (Fig. 2b) and high level stimulus (Fig. 2c) is generally much smaller than that of colonies with large numbers of subfamilies (Figs. 2a and c). The median of the number of bees switched to 'on' is much closer to the task stimulus level for colonies with many subfamilies than for colonies with few subfamilies throughout the results presented in Figure 2.



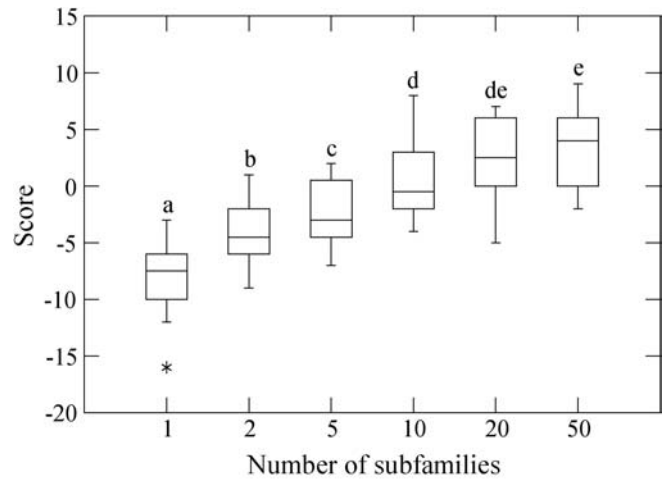
**Figure 1.** Six examples of simulated colonies showing the number of bees engaged in a task over time. The subfamily stimulus thresholds were determined randomly and the stimulus threshold for each subfamily is indicated on the vertical axis by an asterisk. Initially the stimulus was set at 50 units. It was reduced to 20 units after 400 iterations and then increased to 80 units at 800 iterations. A and B: Two exemplar colonies with one subfamily. C and D: Exemplar colonies comprised of two subfamilies. E and F: Exemplar colonies comprised of five subfamilies.



**Figure 2.** The effect of the number of subfamilies on the model colonies' ability to adapt to different task stimuli. The figure shows box plots summarising the results of repeated simulations with fixed levels of task stimuli. Each set of data consists of 16 replicates of the simulation, each with its own randomly chosen allocation of subfamily task thresholds. Colonies with 1, 2, 5, 10 and 20 subfamilies were modelled. (a) Response to a task stimulus of 50 units. (b) 20 units. (c) 80 units

#### Effect of changing stimuli

Stimulus thresholds were allocated to each subfamily and workers were randomly chosen to be 'on' or 'off' at the start of each 'experiment'. Each colony was then given a series of task stimuli in turn and we then monitored how closely the colonies adapted to each new stimulus. For each experiment the stimulus was changed 20 times and the colony was given 400 iterations to adapt to each new stimulus before the stimulus was changed again. Each new stimulus was at least 10 units different from the previous stimulus. If the number of bees that were 'on' in a colony came within 5 units of task stimulus before the task stimulus was changed again, the colony was scored as highly successful in adapting and given one point. If the number of bees that were 'on' did not change by more than 5 units from the number 'on' under the previous task stimulus the colony was classified as failing to



**Figure 3.** Adjustment scores for groups of 100 workers comprised of 1, 2, 5, 10, 20 and 50 subfamilies respectively. Each simulation was replicated 16 times with a randomly selected distribution of subfamily task thresholds and a randomly determined pattern of changes in task stimuli for each replication. Plots with different letters are significantly different at the 5% level (*t*-tests based on an one-way ANOVA).

adapt and given  $-1$  point. Otherwise a colony's response was scored as zero. This gave a score ranging from  $-20$  to  $20$  for each simulated colony. A high negative score meant that a colony changed little in response to new stimuli; a high positive score meant that a colony was generally successful at meeting the demands of changing levels of task stimulus. The 'experiment' was repeated 15 times for each number of subfamilies (1, 2, 5, 10, 20, 50 subfamilies) and the results were tested using *t*-tests to determine if the number of subfamilies had a significant effect on colony performance score (Fig. 3). Generally, the more families, the better a colony's performance was with respect to adapting to changes in task stimulus (Fig. 3). The median score rises from  $-8$  for one subfamily to  $4$  for 50 subfamilies. This suggests that the greater the number of subfamilies, the less likely it is that adaptation fails. It is not until there are 20 or 50 subfamilies that the median score is positive; that is, highly successful adaptations occur more often than failures at the median score. Overall, the simulation experiment results in Figure 3 suggest that when the cumulative effects of adaptation to frequently changing level of task stimulus is considered, there is a definite advantage in having 20 or more subfamilies.

#### Discussion

This study demonstrates that under the assumptions of our model, colonies with a large number of genotypes and consequentially large variability in worker task thresholds can allocate workers to a task with less variation than colonies with low variability.

Colonies comprised of a small number of subfamilies are sometimes able to respond effectively but colonies with a large number of subfamilies are much more reliably efficient in their adjustments to changing stimuli. This is because,

with more subfamilies, the chances of the genetically-based stimulus thresholds being evenly distributed and hence much closer to a continuous normal distribution is much higher than in colonies with just a few subfamilies. Thus it is much more likely that a colony of high genetic diversity will be able to respond to a range of stimuli with roughly the required number of workers for the task.

Mating in polyandrous social insects is likely to be random with respect to task threshold of the future offspring of each male (Fuchs and Moritz, 1998; Moritz and Fuchs, 1998). Thus queens cannot control the spread or clustering of task thresholds in their offspring. Our results suggest that queens, by mating multiply, can increase the probability that their workers' task thresholds will be more evenly spread so that workers will be efficiently allocated to tasks.

How well do the assumptions of our model reflect reality? First, is there genetic variability for task threshold in polyandrous species? We know that individual task thresholds vary greatly in social insects and that this can have a genetic component (reviewed in Beshers et al., 1999; Robinson, 1992). While most of these studies involve the honey bee, *Apis mellifera*, there is evidence that such variability also exists in other polyandrous wasps (O'Donnell, 1996; 1998) and polygynous ants (Snyder 1992; Stuart, 1991). These data support the notion that there is widespread genetic variation for task thresholds within colonies of social insects although they give little or no information about the distribution of such thresholds.

Second, in our simulations the task thresholds of the subfamilies are assumed to follow a normal distribution. The rationale for this assumption rests on the genetic basis of the variation observed. If the variation is essentially quantitative, then the assumption is realistic (Falconer and Mackay, 1996). If a few genes of large effect control most task thresholds, then this assumption is invalid. In honey bees at least, the determination of task threshold has been studied for several behaviours (Giray and Robinson, 1994; Hunt et al., 1995, 1998, 1999; Robinson et al., 1997; Robinson and Huang, 1998; Robinson et al., 1994). These studies suggest that an assumption of quantitative inheritance is reasonable because several genes are involved, each of small effect, and because the environment strongly influences the behaviour of individual bees.

Third, due to constraints in computing resources, we simulated colonies in which 100 workers were available for the task. This is probably a smaller number of workers than would be present in real colonies (though perhaps not substantially so for a small colony for some tasks). Running simulations with a larger number of workers does not appear to substantially change the conclusions obtained here.

We conclude that the effects we observed are plausible. Thus colonies of social insects may gain fitness benefits via polyandry or polygyny because these behaviours can enhance the process of task allocation and self-organization. We acknowledge that variance in task threshold can arise through mechanisms other than genetic variance. For instance, if larval feeding varies, then this could result in life-long variance in task threshold. (This phenomenon would

have its greatest expression when larval feeding results in different morphs such as soldiers and workers (Oster and Wilson, 1978)). Many social insects are not polyandrous or polygynous (Strassmann, 2001), and in these species variance in task threshold may be set environmentally. However for polyandrous species, genetic variance may be a more efficient mechanism for species like honey bees where larval rearing is extremely uniform. Moreover, using an interaction of environment and larval development to set task thresholds might result in correlations between task thresholds. This in turn could reduce maximum possible flexibility among workers. On the other hand, if task thresholds are set by the combination of a large number of interacting loci and the environment, then a genetically mixed colony should be able to efficiently allocate workers to tasks.

The notion that genetic variance and polyandry is a critical factor in the task allocation system requires that there be extensive genetic variance for task thresholds in the population. As selection for task threshold would be weak under the scenario proposed, variance could be maintained at many loci by mutation-drift equilibrium.

Fuchs and Moritz (1998) proposed a model for the evolution of extreme polyandry in the genus *Apis* that is characterised by extremely high numbers of matings (reviewed in Palmer and Oldroyd, 2000). Fuchs and Moritz showed that under the assumption that colonies of this genus require rare specialists (i.e. individuals with a low task threshold for a critical but rarely needed task), high levels of polyandry result in higher fitness than colonies with low levels of polyandry. Our simulations fit well with this model by showing a mechanism by which high variance in task threshold can improve the task allocation system.

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