

# Influence of the level of polyandry and genetic architecture on division of labour

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## Abstract

Genetic diversity is thought to be a main factor in determining task performance and behavioural plasticity of social insect colonies. This diversity has two main causes. a) Multiple matings by the colony queen (polyandry) and b) the number of regions on the genome that influence a behavioural trait. However experiments exploring the relation between these two factors in influencing division of labour are relatively rare due to the difficulties associated with performing them. We simulate the evolution of a colony of foragers which are offspring of a single queen mating with a variable number of males. The foragers are evaluated based on their ability to bring resources of different types to the nest. We show that the colony foraging efficiency improves significantly with an increment in polyandry as compared to an increment in the number of loci influencing a foraging trait.

## Introduction

Social insects exhibit sophisticated division of labour and behavioural flexibility in order to regulate conditions in the nest under changing environmental conditions. For example honeybees are able to adjust the number of workers foraging for pollen to varying requirements of the colony for pollen and without any centralized decision making system. These workers also forage for nectar, adjusting themselves amongst various nectar sources (flower patches) to improve the quality of nectar collected (Seeley, 1995).

A social insect colony typically consists of one or several queens, a variable number of males called drones and workers. The division of labour exhibited by the workers is influenced by the genetic diversity of the colony. For example, genetically more diverse bee colonies show an increment in the amount of pollen collected (Fewell and Bertram, 1999) and an improvement in their thermoregulation behaviour (Jones et al., 2004). One factor influencing the genetic diversity is the number of drones that mate with the queen to produce the workers (Keller and Reeve, 1994; Crozier and Fjerdingstad, 2001). This mating of the queen with more than one drone is known as polyandry.

A second factor influencing diversity is the genetic architecture of the colony members. The genome of an individual

consists of regions that encode different values of the same behavioural trait. The positions of these regions are known as loci and the values that they encode are known as alleles. The genetic diversity in a colony is influenced by the number of loci that encode for the same behaviour. An increment in the number of loci should result in an increment in the possible combination of the alleles that they encode. This increase in the combination of the alleles encoding for a behavioural trait would result in an increase in phenotypic diversity of this behavioural trait. Three such loci have been found in the *Apis mellifera* genome that are known to influence foraging choice, concentration of nectar and load of pollen collected (Page et al., 2000; Ruppell et al., 2004).

We hypothesize that the number of loci encoding a behavioural trait and the level of polyandry influence division of labour and task performance of a colony. Artificial life methodologies are useful to evaluate this hypothesis in silico mainly due to the difficulties faced in performing such experiments on social insect colonies. The main difficulty is in identifying and varying the alleles that influence the foraging behaviour as well as controlling the level of polyandry.

For performing the simulations of collective foraging, we implement the response threshold model for division of labour (Bonabeau et al., 1996; Bonabeau, 1998). To understand the model, consider an individual that has to perform a task, for example collecting food. The individual has a threshold associated to this task. The model defines a stimulus as a signal containing information on the amount of resources associated with the task. In this case the information would be the amount of food with the individual. The task stimulus is inversely proportional to this number. For example if our individual has no food the task stimulus will be high and if the individual has plenty of food the task stimulus will be low. An individual begins to perform the task when the task stimulus exceeds its response threshold. If the workers of a colony have different response thresholds to a given stimulus, they will display division of labour. Consider the case when individuals of the colony are faced with two tasks. In this case the individual performs the task with the maximum positive difference between the task stimuli

and the corresponding response threshold. If both the task stimuli are below the corresponding response thresholds, the individual remains idle.

In this work, we simulate the evolution of colonies of social insects. Workers of a colony forage their surrounding environment for two types of resources, and bring them back to the nest. This takes inspiration from nature, an example being the diet of a carpenter ant colony, which includes honeydew from aphids, sweets, meat, and fats. Response thresholds for the two foraging behaviours are encoded in the worker’s genome. Simulations have been carried out with variations in the number of drones mating with the queen to produce these workers (level of polyandry) and variations in the number of loci encoding for the two response thresholds.

In the two following sections, we give an overview of our experiment setup, and describe the method used to model the genetic architecture and perform evolution. In Section 4 we present the results which are further discussed in Section 5. Eventually, we conclude in Section 6 and point to some future research directions.

## Experiment Setup

We use a probabilistic agent based simulator (Perez-Uribe et al., 2003), to model the foraging behaviour of the colony of workers, placed in an environment consisting of an equal number of two types of resources, visualized as circular and rectangular objects in Figure 1.

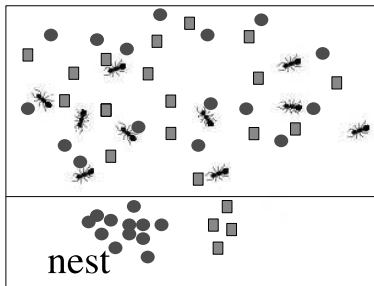


Figure 1: Visualization of the experiment setup consisting of workers foraging for circular and rectangular objects, bringing them back to the nest.

Before evaluating the workers, the colony nest does not contain any object. The colony of workers is evaluated over a set of time steps. At the beginning of each time step, a worker receives two task stimuli signals. These two signals are associated with the number of circular and rectangular objects in the nest. Each worker will forage for the object type corresponding to the largest difference between stimulus and response threshold, or remain idle if both thresholds are higher than the stimuli. A worker has a probability of finding and collecting an object determined by the number of objects left.

## Method

Initially, the environment contains 8000 circular and 8000 rectangular objects. The nest does not contain any objects. A worker has a probability of  $1.25 * 10^{-5}$  to find a rectangular object and an equal probability of finding a circular object. The number of objects in the environment and the probabilities of finding an object have been assigned in order to avoid situations where the workers are not able to find any objects in the environment, even when all of the workers are looking for it. We also want to avoid a situation when the objects in the environment are plenty and just a few workers are sufficient to gather the objects.

During fitness evaluation the rectangular objects in the nest have to be maintained within a lower bound of 140 and an upper bound of 160. These bounds have been set to apply significant selective pressure on the workers to forage for as many circular objects as possible but to balance this by collecting rectangular objects within a given range. If these bounds were not enforced, there would be no need for the workers to switch between the two foraging behaviours in order to maintain a balance between the rectangular and circular objects collected. This need for maintaining a balance between two types of resources is also seen in nature, for example honey bee workers collect as much nectar as possible and yet maintain approximately a one kilogram supply of pollen in the hive (Seeley, 1995).

During evaluation, the objects in the nest are depleted with the probability of 0.25 and 0.5 for the circular and rectangular types respectively. The probabilities are applied at every time step. The higher depletion rate of the rectangular objects increases the frequency of the situation when foraged rectangular objects are not within the preset bounds. This allows for interesting dynamics where workers are motivated to shift between the two foraging tasks to gain a higher fitness. For each time step, we record if the rectangular objects in the nest have been maintained within the preset bounds and we also log the number of circular objects collected at that time step. At the end of 100 time steps, the colony fitness is calculated using Equation 1.

$$Fitness = \sum_{t=1}^{100} w_t * R_c^t \quad (1)$$

$$w_t = 1 \text{ if } 140 \leq R_r^t \leq 160$$

$$w_t = 0 \text{ otherwise}$$

where *Fitness* represents the colony fitness, *t* represents the evaluation time step ranging from 1 to 100.  $R_c^t$  and  $R_r^t$  represent the number of circular and rectangular objects respectively, collected at time step *t*.

The fitness function is meant to award the colony for collecting circular objects and to penalize the colony if the number of rectangular objects collected is not within the bounds.

A population consists of 500 colonies. Each colony consists of a queen, a variable number of drones (which we

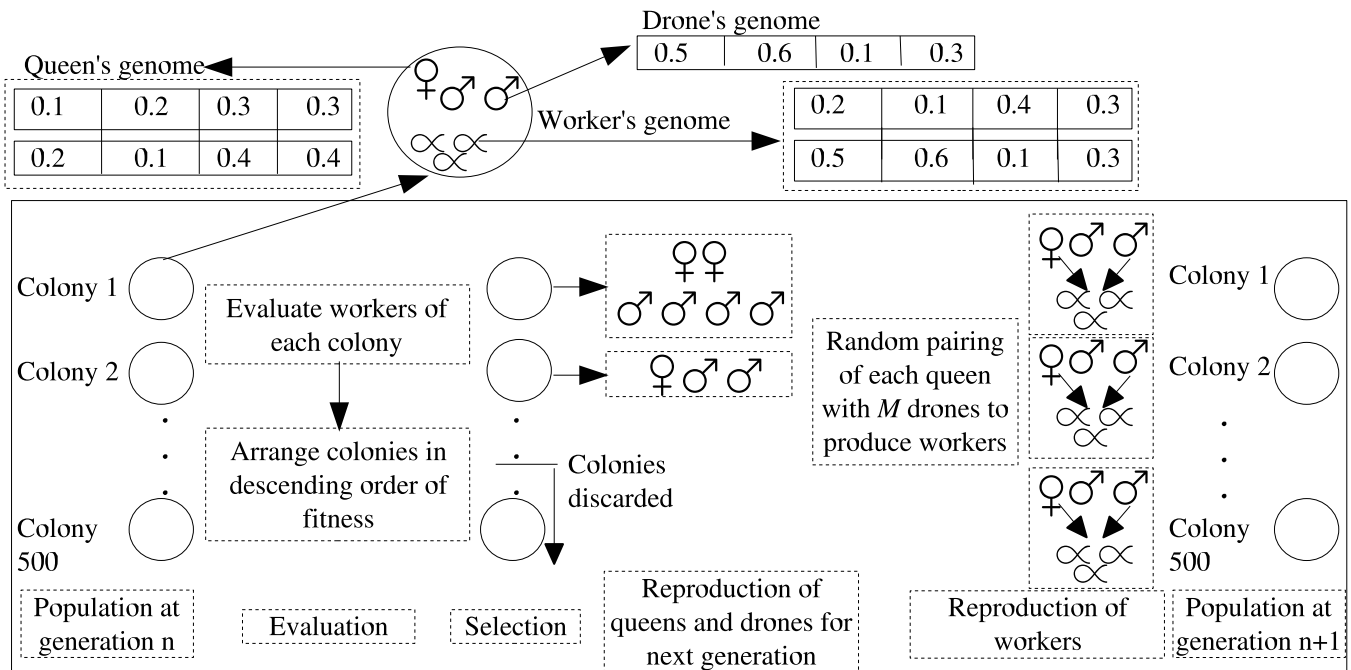


Figure 2: The process of evolution over one generation. Queens and drones for the next generation are produced in proportion to the colony fitness. The numbers in the queen, drone and worker genome represent the allelic effects on behaviour.

shall further denote as  $M$ ) and 1000 workers. The queen and drones mate to produce workers, which are sterile and used to compute the fitness of the colony. Queens and drones also produce other queens and drones for the next generation. The queen has a diploid genetic architecture. This means that her genome consists of pairs of alleles encoding for behaviour. The drones of the colony have a haploid genetic architecture. This means that their genome consists of a single sequence of alleles encoding for behaviour. In both genetic architectures, the effect of the alleles on the behaviour are encoded in the range from 0 to 1 (see top of Figure 2). These genetic architectures are observed in nature, for example in honey bee colonies of the type *Apis mellifera* (Seeley, 1995).

At each generation, the queen and drones of the colony mate to produce workers. These workers are evaluated in our experiment setup, based on which the colony is assigned a fitness value. After all the colonies in the population are evaluated, 150 colonies with the highest fitness in the population are selected to reproduce the queens and drones for the next generation. The rest of the colonies are discarded. In total 500 queens (equal to the number of colonies in the population) and  $500 * M$  drones are produced. Each of the 500 queens form a colony with  $M$  of the  $500 * M$  drones selected at random to produce workers. This marks the beginning of a new generation. The entire process is illustrated in Figure 2.

Figure 3 illustrates the procedure to extract the two re-

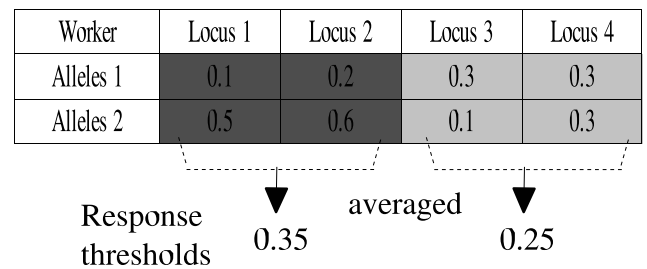


Figure 3: Example of a diploid genetic architecture of a worker. The alleles in the darker and lighter region encode for the first and second response threshold respectively.

sponse threshold from the worker genome. A worker has a set of alleles encoding for a threshold and a subsequent set of alleles encoding for the other threshold. The number of loci that encode for a behaviour will be further denoted as  $N$ .  $N = 2$  in Figure 3. A response threshold is expressed by taking the average of all the allelic effects at the  $N$  loci. An example of this is in Figure 3. The averaging is based on the additive model of gene expression (Hunt et al., 1995). This model is used because we assume a lack of epistasis between alleles, based on empirical evidence (Fewell and Bertram, 1999).

The production of a worker from a queen and multiple drones is illustrated in Figure 4. The worker receives from

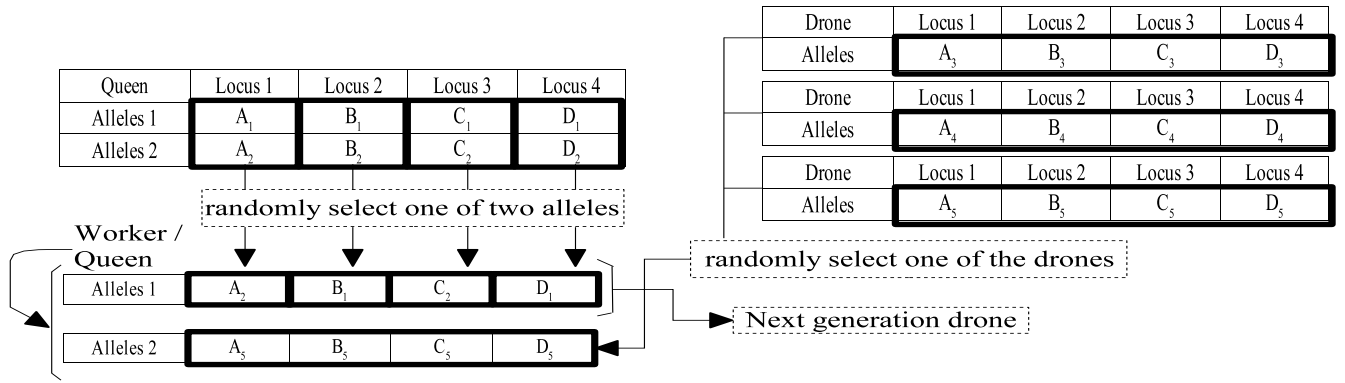


Figure 4: Queen mating with drones to produce a worker or a queen for the next generation. The first allele sequence ‘Alleles 1’ of the reproduced worker or queen genome also illustrates reproduction of the drone for the next generation.

the parent queen for each locus, one of her two alleles, which are randomly selected. The second allele sequence is received from one of the parent drones, selected at random. The same procedure is used to reproduce the queens for the next generation. The drones for the next generation receive all their genetic sequence from the parent queen as illustrated in Figure 4. They do not receive any genetic sequence from the previous generation drones. A worker is not able to reproduce and therefore no mutations are applied to its genome. The alleles of the queens and drones produced are mutated in the range  $\pm 0.1$  following a Gaussian distribution, with the strength of a mutation inversely proportional to its probability of occurrence.

## Results

Evolutionary experiments have been performed for all 25 possible combinations of  $N \in 1, 3, 5, 7, 10$  loci per foraging task and  $M \in 1, 3, 5, 7, 10$  drones. The population fitness at a given generation is calculated as the average of the fitness of all 500 colonies at that generation. A colony is evaluated 20 times (trials). We run ten evolutionary experiments with random initial populations. We plot the average and standard deviation of the population fitness across twenty trials and ten evolutionary runs. The levels of polyandry in the three subsequent fitness plots are captioned as  $x$ D, where  $x = M$  drones.

The fitness of the population while varying  $M$  and keeping  $N = 1$  locus per task is shown in Figure 5. We observe an increment in population fitness with the increment of drones. The fitness of the population while varying  $M$  and keeping  $N = 5$  loci per task and  $N = 10$  loci per task are shown in Figure 6 and Figure 7 respectively. A global perspective of the population fitness while varying the number of loci and matings is shown in Figure 8.

In both the plots, we observe a lower increase in population fitness with an increase in  $M$ . Across the three plots for equal values of  $M$  above 1, we observe a decrease in popu-

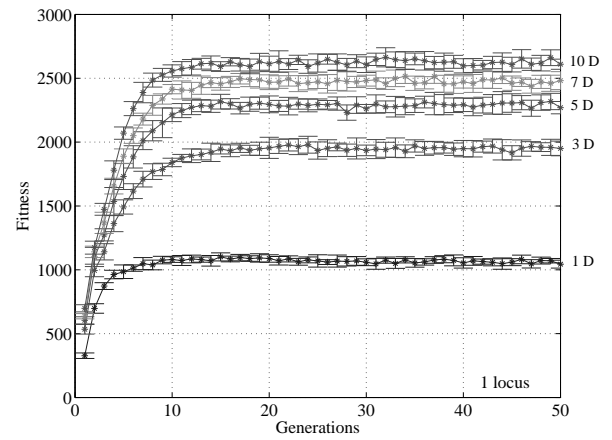


Figure 5: Fitness of the population across 50 generations, with  $N = 1$  locus and  $M \in 1, 3, 5, 7$  and 10 drones.

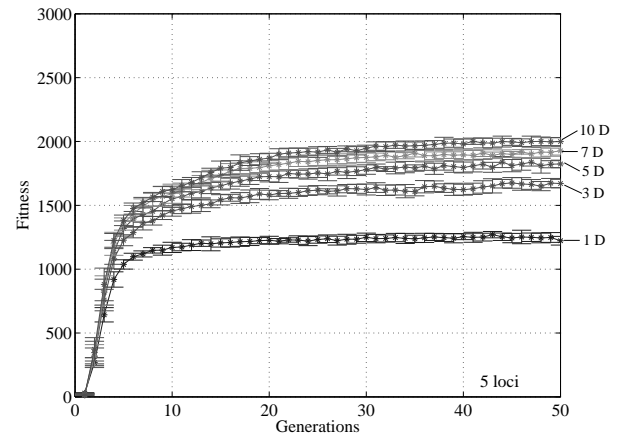


Figure 6: Fitness of the population across 50 generations, with  $N = 5$  loci and  $M \in 1, 3, 5, 7$  and 10 drones.

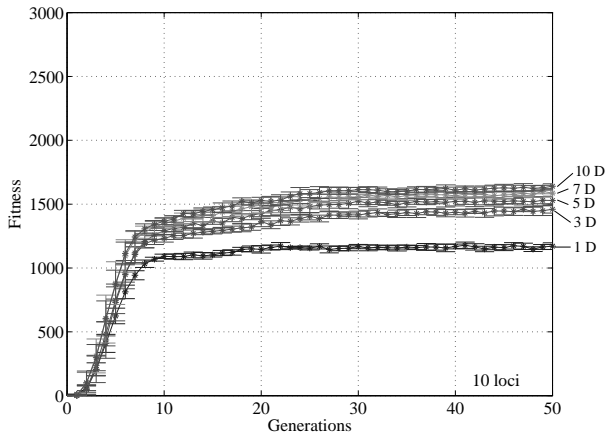


Figure 7: Fitness of the population across 50 generations, with  $N = 10$  loci and  $M \in 1, 3, 5, 7$  and 10 drones.

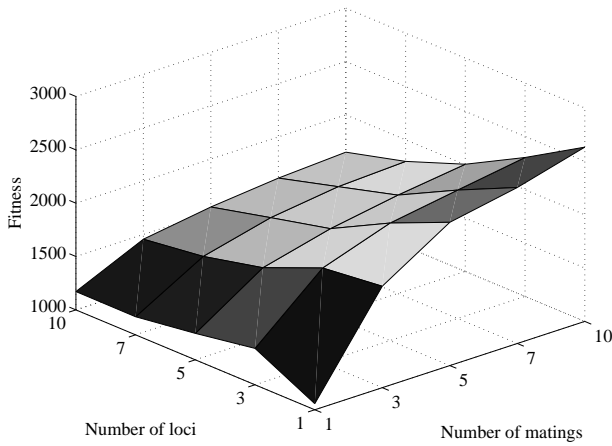


Figure 8: Fitness of the population at generation 50, with  $N \in 1, 3, 5, 7$  and 10 loci and  $M \in 1, 3, 5, 7$  and 10 drones.

lation fitness with an increase in  $N$ . This trend of decreasing fitness is unexpected because an increase in the number of loci should supposedly increase the diversity of the colony and hence the fitness. We would discuss this further in the next section.

## Discussion

We analyse the phenotypic diversity of the population for different values of  $M$  and  $N$ . The phenotypes considered are the response thresholds for the two foraging behaviours. An analysis in this direction will give us information on the amount of diversity in the thresholds, upon which selection can act. To analyse the phenotypic diversity, we plot the contour of worker distributions across the response thresholds at generation 50. The distribution has been averaged over ten evolutionary runs. The number of workers is represented by the intensity of the contour lines as indicated in the bar to

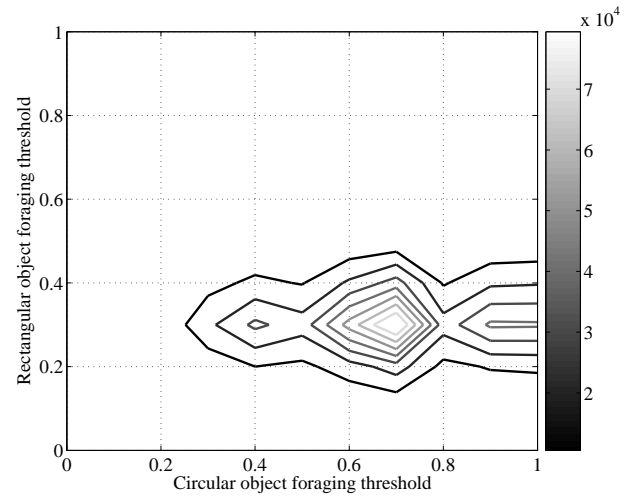


Figure 9: Worker distribution for the population at generation 50, with  $N = 1$  locus and  $M = 1$  drone.

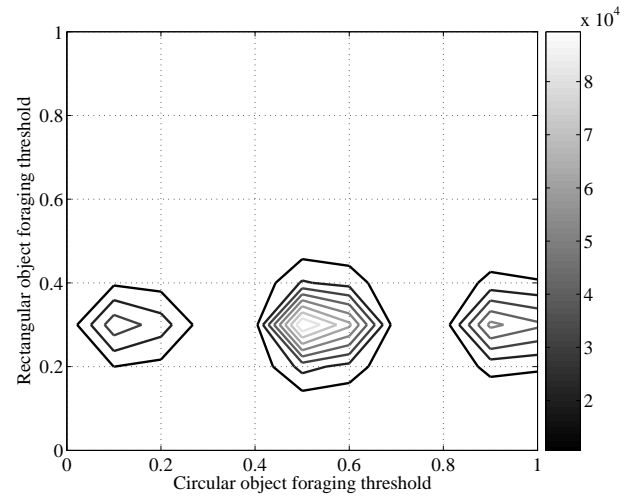


Figure 10: Worker distribution for the population at generation 50, with  $N = 1$  locus and  $M = 10$  drones.

the right of the subsequent plots.

In Figure 9 we observe that when  $M = 1$  drone and  $N = 1$  locus per task, a large number of workers have a high response threshold associated with foraging for circular objects. These workers are specialist foragers for rectangular objects. They only forage for circular objects when the colony has enough rectangular objects in the nest.

On increasing  $M$  to 10 drones and keeping  $N = 1$  locus, we observe an increase in the phenotypic diversity amongst the workers as seen in Figure 10. The workers are distributed in islands of varying specialization across the response threshold landscape. This allows the population to be categorized into workers that are specialist foragers for

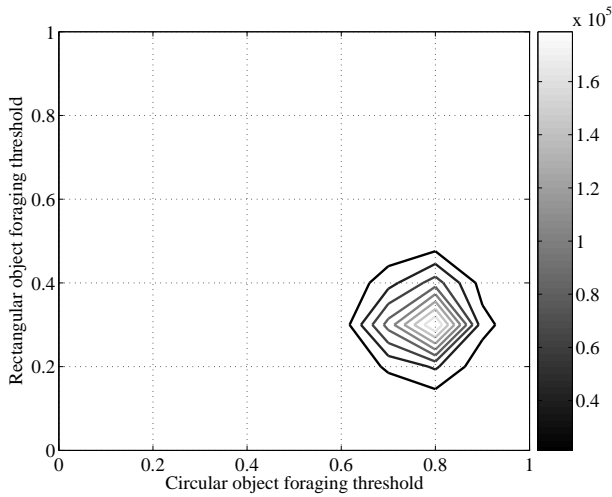


Figure 11: Worker distribution for the population at generation 50, with  $N = 10$  loci and  $M = 1$  drone.

circular objects and workers that are specialist foragers for rectangular objects. We also have workers that are specialist for rectangular objects but have a medium to large threshold (in the range 0.4 to 0.7) of foraging for circular objects.

However increasing  $N$  to 10 loci and keeping  $M = 1$  drone results in a decrease in the response thresholds (circular object foraging) diversity as seen in Figure 11. The reason being that on increasing values of  $N$ , we observe that the number of alleles at different loci influencing the response threshold is  $2 * N$  (two alleles at each locus). The effects of these alleles are averaged to express the response threshold. This averaging with an increasing number of allelic effects makes it difficult for selection to act on individual alleles. The modified allelic effects are lost in the average.

We also observe the worker distribution across the response threshold landscapes for rectangular object foraging. The small difference in this distribution across the three cases displayed above implies that the diversity in this phenotype does not vary much with changes in the value of  $N$  and  $M$ . This has also been observed for other values of  $N$  and  $M$  on which the experiments have been performed.

We also analyse the genotypic diversity of the population for different values of  $M$  and  $N$ . The genotypes considered are represented as fixed length binary strings and the hamming distance is used to calculate the diversity (Mattiusi et al., 2004). The genetic diversity of the population while varying the number of loci and matings is shown in Figure 8. We observe an increase in the genetic diversity with an increase in  $M$ . We also observe lower genetic diversity values when increasing  $N$ .

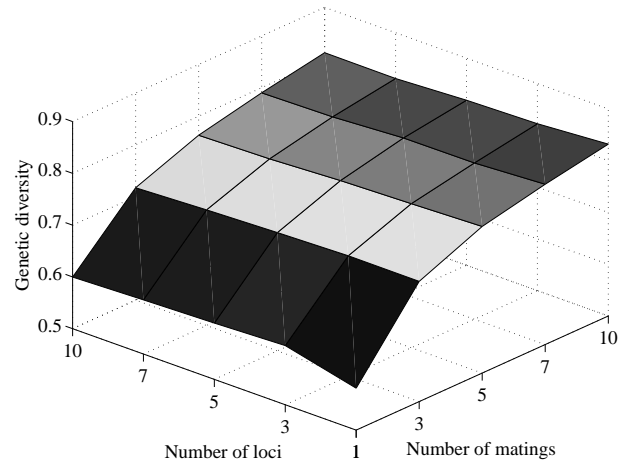


Figure 12: Genetic diversity of the population at generation 50, with  $N \in \{1, 3, 5, 7, 10\}$  loci and  $M \in \{1, 3, 5, 7, 10\}$  drones.

## Conclusion

The results support part of our hypothesis that task performance and division of labour amongst foragers are influenced by the level of polyandry. Multiple matings with different drones increases the number of alleles in the colony. The increment in the number of alleles for each locus results in an increment in the genetic and phenotypic diversity of the colony. Therefore selection on the colony can easily improve its fitness.

On the other hand an increase in the number of loci encoding for a behaviour negatively influences the task performance of the colony. The averaging of the alleles across a large number of diploid loci makes it difficult for selection to act on individual alleles. Advantageous mutations on individual alleles have a small effect on the response threshold and do not result in any subsequent increase in fitness. Therefore increasing the number of loci encoding for a behaviour decreases the fitness. However we do realize that this result is strongly influenced by the additive model of gene expression (Hunt et al., 1995), based on our assumption of lack of epistasis amongst alleles. We would further like to see the effect the number of loci has on fitness when using a simple genetic regulatory network model of gene expression.

This experiment provides interesting insights into division of labour in social insects. It may also prove useful in the field of robotics, when multi-agent systems are needed to solve a problem. In this perspective, it may be argued that using a colony structure similar to that observed in social insects is an unnecessary complexity. However without our colony structure evolving division of labour in a colony consisting of a very large number of agents would require a large number of colonies in the population, the reason being the

large number of combinations of individual genomes in a colony that would need to be evaluated. In our experiments all the genetic information of the workers is represented in the queen and drones of the colony, thus reducing the number of colonies needed. The colony structure and genetic architecture also makes it easier for selection to control the inter-agent diversity, limiting or increasing it depending on the type of behaviour required.

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