Behavioral Plasticity in Polyethism of *Monomorium* spp. (Hymenoptera: Formicidae)

by

Annie G.H. Eow[1], Alexander S.C. Chong[2] & Chow-Yang Lee[1,3]

ABSTRACT

A laboratory study was conducted to determine the influence of colony size, caste composition and foraging area on the behavioral plasticity of polyethism in monomorphic workers of the Pharaoh's ant, *Monomorium pharaonis* (Linnaeus) and *Monomorium floricola* (Jerdon). Results indicated that larger absolute worker number (> 2.39 individual cm^2) and foraging area did not affect the percentage of foragers in both *Monomorium* spp colonies; however, the influence of these two factors was significant at a smaller absolute worker number (~0.60 individual cm^{-2}). Under caste ratio of 1 queen: 0.02 g brood: 100 workers, the percentage of foragers ranged from 18 – 30% and 34 – 47% for *M. floricola* and *M. pharaonis* colonies, respectively. When caste composition changed, particularly with an increase in brood numbers, more *M. floricola* workers were retained in the nest to compensate the increase load of brood-care, but this observation was not recorded in the case of *M. pharaonis*. Under abnormal colony repertoires (absence of either foragers, or nurses), both ant species showed behavioral plasticity in task switching within the colony. The implications of these findings on regulation of task allocation were discussed.

Keywords: behavioral plasticity, polyethism, *Monomorium pharaonis*, *Monomorium floricola*, monomorphic worker.

INTRODUCTION

Polyethism (division of labor) is fundamental to the organization of ant colonies and is thought to be one of the principal factors in their ecological success (Robinson 1992). Worker ants are probably the most commonly sighted caste and are often seen in large numbers. In an ant colony, worker ants perform a wide variety of tasks ranging from foraging, nursing, food relaying, nest sanitation, nest construction and defense. The distinctions in task allocation are generally predisposed

[1]Urban Entomology Laboratory, Vector Control Research Unit, School of Biological Sciences, Universiti Sains Malaysia, 11800 Penang, MALAYSIA.
[2]Laboratory of Fish Biology, School of Biological Sciences, Universiti Sains Malaysia, 11800 Penang, MALAYSIA..
[3]To whom reprint requests should be addressed: Email: chowyang@usm.my

by fixed internal factors (e.g. size, age, genetic) and transient external factors (e.g. environmental stimuli) (Gordon 1996). The plasticity in polyethism, in response to changes in internal and external conditions, is accomplished via behavioral flexibility of the individual workers (Robinson 1992). For instance, when a colony food requirement changes, or when food resource becomes easily available, an ant colony may adjust the number of workers engaged in each task (Gordon 1996). Thus, task allocation is always dynamic; the number of workers engaged in any given task may continually change, as circumstances require.

Several studies have demonstrated the dynamics and determinants of task allocation and regulations of polyethism in several ant species and other social insects such as honeybees and social wasps (Gordon 1986, 1987, 1989, 1996; Calabi 1988; Calabi & Traniello 1989; Herbes & Cunningham 1983; Hölldobler & Wilson 1990; Mirenda & Vinson 1981; Oster & Wilson 1978; Robinson *et al* 1989; Robinson 1992). However, no empirical study has been carried out to investigate the colony behavior in eliciting plasticity of polyethism in response to environmental stimuli, particularly on monomorphic ant species.

This study was conducted based on the understanding that age-dependent polyethism exists primarily in monomorphic ant species (Wilson 1971). Nurses and foragers are the two commonly accepted groups in the worker ant caste (Edwards 1986, Mirenda & Vinson 1981). Foragers generally consist of older adult workers which wander outside the nest, searching for food and water, while the nurses are the younger individuals which normally reside within the nest, caring for the queen and brood, and are also involved in nest maintenance (Wilson 1971, Edwards 1986). This study was done to examine behavioral plasticity in polyethism of two *Monomorium* species (*M. pharaonis* and *M. floricola*), particularly on the number of foragers and nurses affected by factors such as colony size, caste composition and foraging area.

MATERIALS AND METHODS

The *M. pharaonis* and *M. floricola* colonies used in this study were from established stock cultures reared in the Urban Entomology Laboratory, School of Biological Sciences, Universiti Sains Malaysia since 1999. A series of colony types (A – G) of different colony size, caste composition and foraging area was set up and is as described in Table 1. The C-type colony was considered as the control colony for this experiment. Foragers and nurses of both species were separated from the stocks. The worker ants that remained outside their nest or harborage in stock cultures were considered foragers, while those that

Table 1: Colony type and experimental setup in this study.

Colony type	Caste composition			Test arena
	workers (ratio)[1]	brood	queen	(cm^2)
A	500 (1: 1)	0.1 g	5	836
B	2000 (1: 1)	0.4 g	20	836
C	5000 (1: 1)	1.0 g	50	836
D	5000 (1: 1)	2.0 g	50	836
E	5000 (1: 0)	1.0 g	50	836
F	5000 (0: 1)	1.0 g	50	836
G	5000 (1: 1)	1.0 g	50	1850

[1]Ratio = Foragers: Nurses.

remained in the nest (harborage), tending the brood were considered nurses. When separating brood to be weighed, the nurses were removed and collected. Generally, the foragers (older workers) were noticeably darker in color, when compared to the nurses (younger workers).

Callow workers and young queens were not chosen for this study. All immature stages (eggs, larvae, pupae) were present in the weighed brood. All colony types were placed in aluminium pans (measuring 38 x 22 x 8 cm), with exception to G-type colony which was placed in a larger foraging arena (measuring 50 x 37 x 9 cm). A plastic petri dish with black-painted lid and holes drilled along its side was used as harborage and placed at the center of the test arena. All colony types were replicated six times and were acclimatized for 3 days with food and water.

After the acclimatization period, the colonies were each transferred to a new test arena without food, to avoid recruitment of workers to food. They were acclimatized for 12 hours. All colonies were examined for foragers. This was done by removing the harborage/nest, and the remaining workers in the test arena (foragers) were counted from a digital photograph taken on the test arena. To avoid possible influence of daily foraging rhythm, two replicates each were conducted in the morning, afternoon and night. Based on the known total number of worker ants, the percentage of foragers could be determined. This value was then subjected to arc-sine transformation before analysis of variance. Means were separated using Tukey's HSD ($P = 0.01$).

RESULTS

The results obtained were shown in Table 2. For *M. floricola*, the percentage of foraging workers in control colony (C-type) was 27.4 % at the caste ratio of 1 queen: 0.02 g brood: 100 workers. Although B- and

Table 2: Mean (%) workers which remained outside the nest of different colony types

Colony type	Mean (%) workers outside the nest ± S.E.M.[1]			
	n	*M. pharaonis*	n	*M. floricola*
A	6	33.8 ± 2.0 a	6	21.7 ± 1.7 a
B	6	44.3 ± 0.8 b	6	29.9 ± 0.7 b
C	6	45.0 ± 0.8 b	6	27.4 ± 1.4 b
D	6	39.5 ± 0.7 ab	6	18.0 ± 0.6 a
E	6	60.1 ± 1.1 c	6	53.2 ± 1.0 c
F	6	12.0 ± 1.0 d	6	2.7 ± 0.1 d
G	6	47.1 ± 2.5 b	6	28.0 ± 0.6 b

[1]Means within the same column followed by different letters are significantly different (Tukey HSD; $P < 0.01$).

C-type colonies varied in colony sizes (but with the same caste ratio), the percentage of foragers did not differ significantly ($P > 0.01$). The smallest colony (A-type) showed a significantly lower percentage ($P < 0.01$) of foragers than those of the former two colony types (B and C), but the difference was only 5.7%. An additional brood of 1.0 g in colony D also showed a significant decrease ($P < 0.01$) in percentage of foragers to 18.0%. Under abnormal (absence of nurses or foragers) colony repertoires, behavioral flexibility in task allocation was observed. E-type colony, which consisted of 100% foragers introduced initially showed a significantly higher ($P < 0.01$) percentage of foraging workers after reorientation. Conversely, the F-type colony, which consisted of all nurses showed a very low percentage of foraging workers (2.7%). When a similar type of colony as C-type was introduced into a larger foraging arena (G-type), the number of foragers did not differ significantly from that of the control.

An almost similar trend was obtained in experiments on *M. pharaonis* (Table 2) although the number of foragers in this species tended to be higher. In control colony (C-type), 45% of its workers were foragers, which is 40 % more than the total foragers of *M. floricola* with the same colony size. This suggested that forager's number in a colony could be species-dependent. Previous studies reported that there was only a small percentage of the worker ants which were foragers (Sudd 1960, Abbott 1978), and only about 5 – 10% *M. pharaonis* were foraging at any given time in the field (Edwards 1986). Another study reported that there was no more than 20% of fire ant (*Solenopsis invicta*) workers engaged in foraging activity (Tschinkel 1986).

DISCUSSION

The outcome of these experiments demonstrated that foraging area and a larger absolute worker number (>2.39 individual cm^2) did not affect the percentage of foragers in both *M. pharaonis* and *M. floricola* colonies, but the effect was significant ($P < 0.01$) at a smaller absolute worker number (~0.60 individual cm^{-2}). Earlier, Gordon (1987, 1994, 1996) proposed *worker – worker interaction rate* hypothesis that colony size and foraging area may affect task decisions of workers at individual-level on harvester ants (*Pogonomyrmex barbatus*). Thus, our results only partially supported Gordon's hypothesis. This discrepancy could be due to the fact that monomorphic worker ants were used in this experiment, compared to Gordon's study which engaged a polymorphic species.

In type A, B, C, D and G colonies of the *Monomorium* species, both nurses and foragers were equally assembled prior to the experiment. If the task allocation is solely determined by caste-specification of these species, the ratio of nurses and foragers should remain the same even after reorientation. However, only 45% of *M. pharonis* and 27.4% of *M. floricola* remained outside the nest at the end of the experiment for C-type colony. These differences may indicate the probable existence of 'intermediates' or 'reserve' workers which are inactive and remain in the nest most of the time under normal colony condition (Herbers & Cunningham 1983). These inactive individuals form a pool of uncommitted reserves that can immediately begin to work when stimulated by external condition (Michener 1964, Gordon 1989, Lenoir 1987, Wilson 1983).

Numerous studies have shown that workers from highly eusocial species retain some forms of behavioral plasticity associated with more primitive species to enable colonies to respond appropriately to changing conditions (Oster & Wilson 1978, Robinson 1992). The plasticity in task allocation was observed in this study under an abnormal caste repertoire. Experimental manipulation of colony age demography could cause accelerated, retarded, or reversed behavioral development (Robinson 1992); however, only accelerated and reversed behavioral development were observed in this study. In the absence of nurses, at least half of the former foragers of *M. floricola* and one-third of *M. pharaonis* were retained in the nest to perform the task of nurses (behavioral reversion). On the contrary, a relatively smaller percentage of nurses remained outside the nest in the absence of foragers (behavioral acceleration). This behavioral plasticity has been reported earlier in *Pheidole dentata* (Calabi & Traniello 1989), *Solenopsis invicta*

(Sorensen *et al.* 1984), *Pogonomyrmex barbatus* (Gordon 1986, 1987, 1989) and honey bees (Naumann & Winston 1990, Robinson *et al.* 1989).

For colony type D, it was observed that a larger quantity of brood present in colonies of *M. floricola* would retain significantly more workers in the nest, but this observation was not seen in the case of *M. pharaonis*. This is because an additional 1.0 g of brood in both species did not amount to the same number of individuals. Due to the difference in size, 1 g of *M. floricola* brood may consist up to 20700 individuals of mixed stages, compared to only 12900 individuals in *M. pharaonis* brood (AGHE, unpublished data). Thus, this may explain why more nurses were needed to remain within the nest of *M. floricola*. In *M. pharaonis*, although the brood amount was increased by 1 g in colony type D (when compared to colony type C), it did not result in a decrease of foragers (Table 2). This may support the hypothesis that reserve workers were present, and could have likely been activated to perform brood care as nurses, before the behavioral reversion of foragers.

The experimental design was biased towards brood care more than food foraging, because no food was provided in the experiment. Thus, this may explain the relatively low percentage of former nurses that were required to perform foraging task.

We hypothesize that task allocation in monomorphic polygynous species is internally influenced by age and genotypic variability. Both are also determinants to the presence of worker subcastes. The behavioral plasticity of worker subcastes in response to environmental stimuli depend on their response thresholds. Normally, nurses have the lowest response threshold to brood care stimulus, while it is otherwise for the foragers. The reserves' response threshold to brood care stimulus is intermediary.

The age-dependent response thresholds have been reported to be mediated by changes in juvenile hormone titer in honey bees (Robinson *et al.* 1987, Robinson 1992, Robinson *et al.* 1989), in which low titers are associated with activity within the nest whereas the higher titers are associated with the onset of foraging. Although Robinson *et al.* (1989) have demonstrated that hormonal and behavioral switching can occur rapidly (within 24 hours prior to perturbation), the role of juvenile hormone in task allocation of the ant colonies remains an intriguing aspect that warrants further investigation.

This study dealt with the foraging worker ants that remain outside the nest without the presence of food or pheromonal trail. In the presence of food resources, task allocation would definitely reorient as mass recruitment is involved. Nevertheless, this laboratory study

provides a good prediction of the subject matter because empirical study is difficult under field situations as the nests of most monomorphic ant species such as *M. pharaonis* and *M. floricola* are hard to locate and usually inaccessible. In addition, it is also difficult to trace the forager ants without disturbing them.

In summary, under a caste ratio of 1 queen: 0.02 g brood: 100 workers, the percentage of foragers ranged from 18 – 30%, and 34 – 47% for *M. floricola* and *M. pharaonis* colonies, respectively, irrespective of absolute worker number (> 2.39 individuals cm^{-2}) and foraging area. However, when the caste composition changed, particularly with an increase in brood numbers, more workers were retained in the nest. Both ant species showed plasticity in polyethism within the colony under the absence of either foragers or nurses.

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