Brood Arrangement and Food Distribution Among Larvae Under Different Colony Conditions in the Pharaoh's Ant, *Monomorium pharaonis* (Hymenoptera: Formicidae)

by

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ABSTRACT

The Pharaoh's ant, *Monomorium pharaonis* (L.) is one of the most widely distributed and most successful tramp species in the Formicidae family. It is an important pest ant in many parts of the world. Therefore, it is essential to understand the feeding behavior of this species to further enhance the efficiency of baiting. In the first part of this study, we observed the trend in brood arrangement in an ant colony. This was accomplished by feeding them with dried tuna fish stained with blue food dye. 10 colonies consisting of 0.3 g of mixed-stages brood, 4 queens and 300-400 workers were set up. Digital still photographs were taken 1 day after they were given dyed tuna. The arrangement of brood in each colony was observed and discussed. In the second part of our study, we simulated 8 different colony conditions to observe the trend in food distribution among two larval stages (Instar 2 and 3). The two major groups were colonies with old larvae and colonies with mixed-stages of brood. These were further separated into queenless/queenright colonies and fed/unfed colonies. Each condition was replicated five times. Dried tuna fish (stained with blue food dye) was used to determine the number of larvae that were fed with it. Digital still photographs were taken at different time intervals (2H, 4H, 8H, 24H, & 72H). They were later used in counting the number of larvae fed by the workers. Data were subjected to one-way ANOVA followed by Tukey HSD ($P < 0.05$). Results indicated that both instars' feeding in all the colonies differed from one another only after 24 hours. The differences in all eight conditions are discussed.

Keywords: *Monomorium pharaonis*, brood arrangement, food distribution, baiting.

INTRODUCTION

Growth, maintenance and reproduction are three major life processes that need to be sustained through ingestion of nutrition (Casill *et al.*

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1998). In insect colonies, intake of food is governed by both external and internal factors. These include colony composition, size, hunger, nutritional needs, division of labor and environmental factors (Sudd 1967; Wilson 1971; Abbott 1978; reviewed in Sorensen *et al.* 1985).

Even though ants have a catholic diet and show extremes of dietary preference, they are selective of foods with high protein and carbohydrate concentrations (Stradling 1978). Animal flesh is a source of high quality protein and desirable food although the collection of prey often involves a large amount of indigestible cuticle.

Production of new reproductives is extremely commanding of high intake of protein and lipid in the larval stage and also after metamorphosis in the case of gynes (Peakin 1972). Food intake is therefore related to brood development and reproduction.

A constant exchange of food between adults and larvae has been observed among social insects such as termites, ants, and wasps (Ishay & Ikan 1968). The larvae of many social hymenopterans digest solid food and regurgitate the liquids to the workers (Wilson 1971). Janet (1895) and Roubaud (1916) (Reviewed by Ishay & Ikan 1968) believed that these oral secretions are highly palatable to the adults. Larval saliva was also reported to play a role as food sources for the male in vespine wasps (*Vespula*) (Montagner 1964).

The role of ant larvae in food exchange is also arguable (Sorensen *et al.* 1983). Larval secretions are consumed by workers and actively implored (Abbott 1978). Maschwitz (1966) found that larval secretions of *Tetramorium caespitum*, *Myrmica ruginodis* and *Formica sanguinea* contained high concentrations of amino acids and proteins but not carbohydrates. Furthermore, there was evidence in *T. caespitum* that amino acids were actively secreted by the salivary glands. Wust (1973) later found that Pharaoh's ants' oral secretions to contain similar composition, origin and function.

Although there have been previous studies on food utilization and food flow in foraging adults of the imported fire ant (Vinson 1968) and in a number of other species of ants (LeMasne 1953; Eisner & Wilson 1958; Gosswald & Kloft 1963), very little research of this nature was done on the larvae (Petralia & Vinson 1978). In 1980, Petralia *et al.* found that labial glands in *S. invicta* larvae secrete a proteinaceous substance rich in digestive enzymes. The presence of high levels of proteinase activity in larval midguts, labial glands and oral secretions compared with the low levels found in adult midguts suggested that the larvae might be responsible for protein digestion in the colony (Ricks & Vinson 1972).

It has been hypothesized that workers hold the key to control the caste of the incoming generation among larvae through nutritional regulation (Hölldobler & Wilson 1990). Therefore, it is of paramount importance that we understand the mechanisms of food distribution among larvae, not only as an insight into caste structure but also of colony growth and reproduction.

Reproduction success in a wide variety of insects is largely determined by nutrition during the larval period. Adult fecundity is directly affected by larval nutrition that influences female body size. In social Hymenoptera, larval nutrition takes on a special importance because it can influence the caste of the resulting adult (Wheeler 1994).

Social feeding is a potential mechanism for regulating the adult caste by means of nutritional switches because immobile larvae depend on adults to feed them (Wheeler 1986, 1990, 1994; as cited by Casill & Tschinkel 1995). Through this, various female castes that make up a colony emerge. Hence, larval feeding may be a central regulatory process in colony ontogeny.

Generally, workers sort brood according to their age. Eggs and first instar larvae are separated from older ones within the same brood chamber while the pupae are kept in a different and drier brood chamber (Carlin 1988; Deneubourg *et al.* 1991; Franks & Sendova-Franks 1992; Vander Meer & Morel 1995). Proteinaceous foods are given primarily to larvae and queens while sugars are fed mainly to other workers. Through this observation, scientists suggest that larvae communicate either directly or indirectly, to make their nutritional requirements known to workers (Brian 1956; O'Neal & Markin 1973; Abbott 1978; Petralia & Vinson 1978; Howard & Tschinkel 1980, 1981a, 1981b; Sorensen *et al.* 1980; Sorensen & Vinson 1981; Wheeler 1994).

In 1992, Franks & Sendova-Franks postulated that the different brood members are sorted in such a way to alleviate the particular type of care they beseech. For example, the largest larvae, which require the most nutrition, are placed on the boundary. This positioning makes them very accessible to food-carrying ants. The eggs and the prepupae, which do not require feeding, are placed in the center of the brood pile where they are groomed.

Communication between larvae and workers may be a two-way system because larvae provide the necessary ingestible protein sources to workers via glandular regurgitations (Markin 1970; Sorensen *et al.* 1983). Caste in honeybees is determined by differential feeding of female larvae. Beetsma (1979) reported that larvae destined to be queens receive more food compared to worker-to-be larvae. Consequently, differential feeding leads to very distinct worker and queen castes with

unique characters (Allsopp *et al.* 2003). This shows that dietary pattern plays a role in caste determination.

MATERIALS AND METHODS

Arrangement of brood in ant colonies

Ten colonies (R1 - R10) were set up using stock colonies of the Pharaoh's ant. These colonies consisted of 300-400 workers, 0.3 g of mixed-stages brood and four queens. They were acclimatized for three days in the aluminium trays measuring 40.0 x 24.5 x 8.0 cm with food and water supplied *ad libitum*. The food source used in this study was dried canned tuna fish stained with Bush Boake Allen's True Blue food dye (Star Brand) 10% W/W. After acclimatization, stained tuna was given to all ten colonies. Digital still pictures were taken 24 hours after administration of dyed tuna. These photos were used in evaluating the brood arrangement pattern in Pharaoh's ants.

Effects of colony condition on the distribution of food to larvae

Eight different colony conditions were simulated using laboratory-reared Pharaoh's ants. These colonies were set up in fluon-coated aluminium trays measuring 40.0 x 24.5 x 8.0 cm. The eight conditions were as follows with reference to brood age, queen's presence and level of starvation respectively; each of which was replicated five times.

(A) Mixed-stages + Queenright + Unfed
(B) Mixed-stages + Queenless + Unfed
(C) Mixed-stages + Queenright + Fed
(D) Mixed-stages + Queenless + Fed
(E) Old brood + Queenright + Unfed
(F) Old brood + Queenless + Unfed
(G) Old brood + Queenright + Fed
(H) Old brood + Queenless + Fed

In the mixed-stages colonies, approximately 0.1 g of brood was used where all different stages of brood (from eggs to pupae) were present. Conversely, the old brood colonies only consisted of instars L2, L3 and L4 (Fig. 1). Old broods were separated by isolating visually larger larvae from the brood pile. Larvae with well-formed mouthparts were considered older larvae, similar to the classification done by Edwards (1986). Smaller larvae with less prominent mouthparts and bearing similar size with eggs were grouped as younger broods. Meanwhile, in the queenright colonies, four queens were present as opposed to the queenless colonies where none was present. The fed colonies were

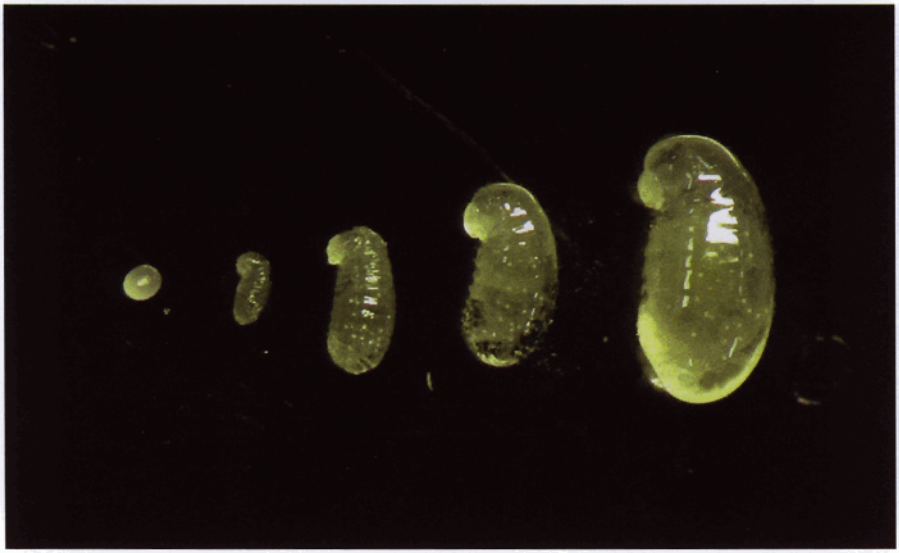

Fig. 1. Different stages of larvae.

never starved from food and in contrast, the unfed colonies were starved from food for three days until the experiment was initiated. All of these colonies contained 500-600 workers.

Dried tuna fish was used as the food source. Prior to the experiment, it was stained with a non-toxic blue food dye (True Blue, Star, Bush Boake Allen, London) 10% W/W. Sugar water was also given daily as a source of carbohydrate. Data was taken at fixed intervals by taking digital still pictures. The intervals were 120 minutes, 180 minutes, 480 minutes, 24 hours and 72 hours. Ants' larvae were then counted using these pictures and the number of dyed larvae at each time interval for each condition was recorded. Data accumulated was subjected to One-Way ANOVA and the means were separated using Tukey HSD ($p < 0.05$).

RESULTS AND DISCUSSION

Arrangements of brood in ant colonies

In this study, we manipulated the information which reported that solid food is normally given to larger larvae. Dried tuna fish stained with blue food dye was fed primarily to larger larvae. After feeding on stained tuna fish, the ten replicates in this study showed that Pharaoh's ants arrange their brood in a conspicuous pattern (Fig. 2 & Fig. 3). Observations of each experimental colony illustrated a ring of dyed brood on the outer layer of the brood pile. Closer inspections

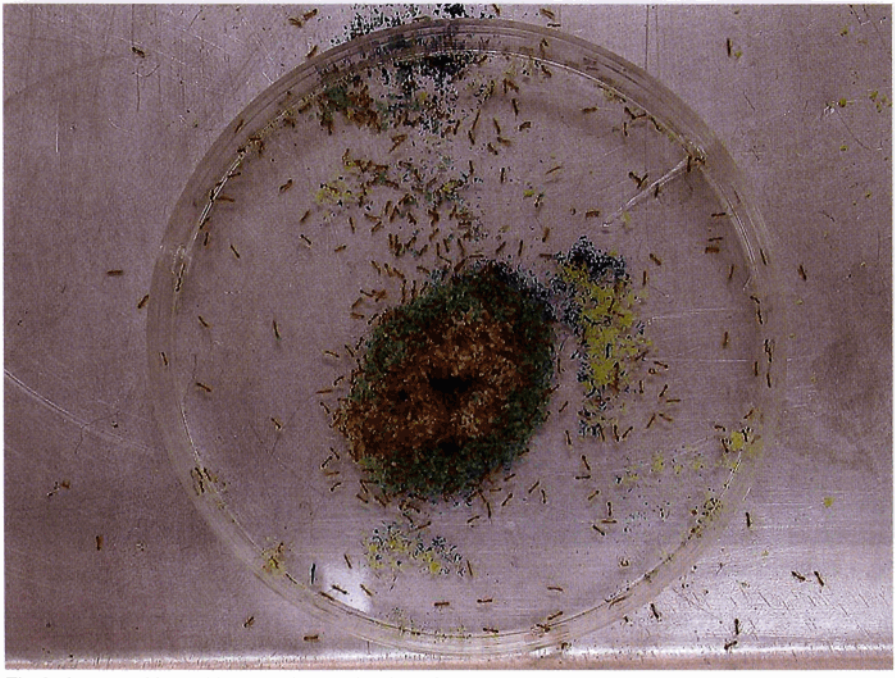

Fig 2. Arranged brood in experimental colony I.

showed three distinct rings in each brood pile. The outermost layer contained older broods, mostly L2 and L3. The center pile consisted of eggs and L1 while the pupae and prepupae were found to be placed in the intermediate ring in between these two.

This finding was concurrent with those of Franks & Sendova-Franks (1992) where *Leptothorax unifasciatus* colonies were also found to have a distinct pattern in brood arrangement. One of the key criteria of eusocial insects is the caring for brood by adults (Hölldobler & Wilson 1990). Earlier works on brood sorting has focused on ants shifting certain brood types into different brood chambers (Headley 1941; LeMasne 1953; Hölldobler & Wilson 1990; reviewed by Franks & Sendova-Franks 1992).

Franks & Sendova-Franks suggested that the creation of a spatial pattern helps to organize the work of brood care. In a way, they are of adaptive significance because the ants rapidly recreate such patterns when they relocate to a new nest.

These patterns also make it easier for specialized caring of certain brood types. For instance, by placing broods that needs extra nutrients or the hungriest ones at the periphery, they become more accessible

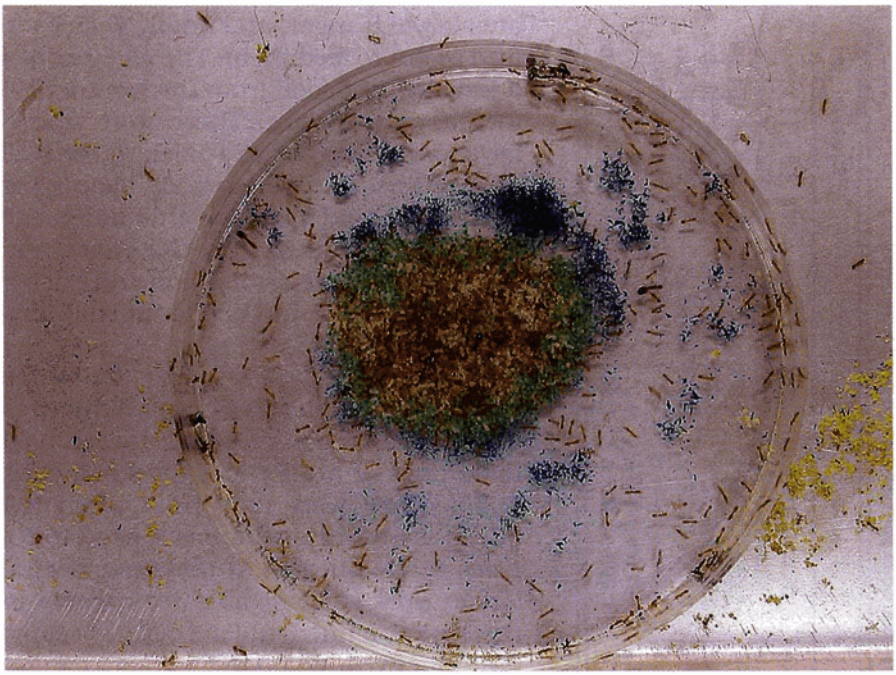

Fig. 3. Arranged brood in an experimental colony II.

to food-carrying workers. In such a system, the most valuable larvae are fed first and subsequently progressed towards the center.

However, they did not provide a possible suggestion as to why the smallest broods are placed in the center or how the broods send hunger signals to the workers in order to be placed at the border of the brood pile to receive maximum nutrients. O'Toole *et al.* (2003) suggested the young are placed in a more protected space. For instance, an intruder would have to break two barriers (the large larvae and the pupae) before reaching the youngest brood pile.

Equal distribution of brood care is a crucial problem faced by brood-tending ants (Hatcher *et al.* 1992). If unattended for too long a time, they may perish. Since Morel & Vander Meer (1988) proved strongly that ant brood pheromones do not exist, there is zero possibility that they emit pheromone signals to indicate their hunger. Therefore, how exactly do they tell the workers that they are hungry and vice versa?

Cassill & Tschinkel (1995) observed four main rules for allocation of food to larvae by workers of the fire ant, *Solenopsis invicta*. They found that each worker nurse patrols the brood pile constantly and contact is made with each larva every few seconds, each nurse worker evalu-

Table 1. Mean[1] percentage of fed L2 under different colony conditions after feeding on dyed tuna over time.

Colony condition	2 Hours	4 Hours	24 Hours	72 Hours
(A) Mixed-stage + Queenright + Unfed	0.000 ± 0.000'a	0.000 ± 0.000 a	70.996 ± 14.733 a	74.002 ± 14.119 a
(B) Mixed-stage + Queenless + Unfed	0.000 ± 0.000 a	0.000 ± 0.000 a	74.692 ± 8.582 a	64.284 ± 4.365 ab
(C) Mixed-stage + Queenright + Fed	0.992 ± 0.992 a	0.000 ± 0.000 a	0.000 ± 0.000 b	39.636 ± 16.104 abc
(D) Mixed-stage + Queenless + Fed	0.000 ± 0.000 a	0.000 ± 0.000 a	0.000 ± 0.000 b	20.990 ± 8.020 abc
(E) Old brood + Queenright + Unfed	0.000 ± 0.000 a	0.000 ± 0.000 a	0.000 ± 0.000 b	9.780 ± 7.636 bc
(F) Old brood + Queenless + Unfed	7.126 ± 7.126 a	8.046 ± 8.046 a	21.222 ± 13.003 b	0.000 ± 0.000 c
(G) Old brood + Queenright + Fed	0.000 ± 0.000 a	0.000 ± 0.000 a	4.152 ± 3.698 b	3.774 ± 2.601 c
(H) Old brood + Queenless + Fed	0.000 ± 0.000 a	0.000 ± 0.000 a	0.000 ± 0.000 b	30.500 ± 20.131 abc

[1] Means with the same letter are not significantly different ($n = 5$, Tukey HSD, $p > 0.05$)

ates larval hunger, and finally decides to feed or not to feed them. The likelihood of a larva getting food from the worker also increases with size. There were also a few larvae that got extra attention as well as food from the workers. By identifying the source and cause of this difference in hunger cue strength, the cause and source of caste determination and worker polymorphism could be identified (Casill & Tschinkel 1995).

Pharaoh's ant may adopt the same system in production of reproductives where potential reproductives are said to be present at all times (Peacock *et al.* 1955). They were only bred when the queen is absent or there is a need to replace senile queens. At this time, sexual larvae may send signals to workers to receive extra nutrients needed to become reproductives. When the workers receive this signal, they will provide extra care and attention to these future royalties.

Effects of colony condition on the distribution of food to larvae

Observations from this study showed that feeding amongst larvae was significantly affected under different colony conditions. Although L2 started feeding on dyed tuna within the first 2 hours, results from L2 did not differ significantly during the first four hours (Table 1). Significant differences were only seen in L2 after 24 hours. They were of Colony A and Colony B. These two colonies were starved colonies with mixed-stages of brood. The difference in these colonies was the presence of queens. When compared with Colony E and Colony F, the difference was the brood stages.

Brood stages may be the main concern on how a colony feeds. A complete mixture of all stages of brood may be needed for a colony to

feed normally, regardless of whether queen is present or not. Hunger is only a factor that contributes to the speed of how fast they feed. This conclusion was drawn when after 72 hours, all colonies with mixed stages of brood recorded higher number of dyed broods. Howard & Tschinkel (1981a) suggested that colony starvation leads to larvae being put to the top of the priority list when amino acids are shared.

In L3, feeding too did not differ significantly amongst all colonies within the first four hours (Table 2). After 24 hours, Colony A has the highest number of dyed individuals. Colony E, which only had old broods, not only showed the lowest amount of consumption but the numbers were also significantly different from Colony A. These two colonies are different in terms of brood content where Colony A contained mixed-stages while Colony E only contained older ones. When queens are absent in colonies with old broods (Colony F), feeding of L3 increased to a point where it was not significantly different from Colony A.

This phenomenon could be derived from the absence of queens. Under such condition, workers may have fed larvae with extra food with the intentions to raise sexual larvae. Differential feeding leads to very distinct unique characters in worker and queen castes (Allsopp *et al.* 2003).

In honeybees, differential feeding determines the caste of female larvae. Under such conditions, larvae destined to be workers are fed with lesser food compared to queen-to-be larvae. These foods are also reported to be of different composition (Beetsma 1979).

McGlynn & Owen (2002) found that food supplementation altered caste ratios in the *Pheidole flavens* and sug-

Table 2. Mean[1] percentage of fed L3 under different colony conditions after feeding on dyed tuna over time.

Colony condition	2 Hours	4 Hours	24 Hours	72 Hours
(A) Mixed-stage + Queenright + Unfed	3.276 ± 3.276 a	8.054 ± 8.054 a	80.568 ± 7.445 a	91.380 ± 3.891 a
(B) Mixed-stage + Queenless + Unfed	0.000 ± 0.000 a	1.944 ± 1.944 a	69.036 ± 12.423 a	86.708 ± 10.754 ab
(C) Mixed-stage + Queenright + Fed	3.916 ± 2.401 a	4.416 ± 2.727 a	46.204 ± 17.791 abc	86.080 ± 6.476 ab
(D) Mixed-stage + Queenless + Fed	0.000 ± 0.000 a	0.000 ± 0.000 a	3.936 ± 2.595 bcd	72.454 ± 11.548 ab
(E) Old brood + Queenright + Unfed	1.804 ± 1.804 a	1.618 ± 1.480 a	2.106 ± 2.106 d	32.838 ± 12.204 bc
(F) Old brood + Queenless + Unfed	8.734 ± 7.902 a	10.102 ± 9.766 a	44.192 ± 11.548 ab	80.000 ± 20.000 ab
(G) Old brood + Queenright + Fed	0.000 ± 0.000 a	0.000 ± 0.000 a	14.582 ± 8.360 bcd	14.326 ± 5.985 c
(H) Old brood + Queenless + Fed	0.000 ± 0.000 a	0.000 ± 0.000 a	3.206 ± 3.206 cd	12.114 ± 6.533 c

[1] Means with the same letter are not significantly different (n = 5, Tukey HSD, p > 0.05)

gested that ant colonies determine caste ratios in response to different environmental variables. In addition, Pereboom *et al.* (2003) proposed that caste fate is predetermined and caste specific differences are manifested physiologically in the larvae of bumblebees, *Bombus terrestris*. This makes all the difference when workers respond to nutritional needs of larvae and consequently resulted in different feeding frequencies. Besides that, larvae are also known to play a role as foodstores in ant societies (Wilson 1976). They are the digesting machinery of solid food in an ant colony.

Edwards (1984) described that there is no evidence that either quantitative or qualitative food differences change castes in Pharaoh's ants. It was proposed that egg-signal mediates worker to rear worker, males or queens and works simply by the presence of eggs in a colony. Any reduction of eggs/workers will initiate the production of more reproductives (Edwards 1987). However, the mechanism that workers adopt in rearing was not fully explained. There may not be a special food similar to that of the royal jelly in the creation of reproductives in honey bees but preferential feeding may be enough to produce reproductives.

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