THE FEEDING BEHAVIOUR OF THE GHOST ANTS, *TAPINOMA MELANOCEPHALUM* (FABRICIUS) AND *TAPINOMA INDICUM* (FOREL) (HYMENOPTERA: FORMICIDAE)

WONG JING WEN

UNIVERSITI SAINS MALAYSIA
2007

THE FEEDING BEHAVIOUR OF THE GHOST ANTS,

TAPINOMA MELANOCEPHALUM (FABRICIUS) AND

TAPINOMA INDICUM (FOREL) (HYMENOPTERA: FORMICIDAE)

by

WONG JING WEN

Thesis submitted in fulfillment of the requirements

for the degree of

Master of Science

October 2007

To

Daddy & Mommy,
for the endless love, sacrifices and understanding

Sis Yei, Sis Yin & Bro Yeen,
for the love and support

My family and friends

ACKNOWLEDGEMENTS

As we express gratitude, we must never forget that the highest appreciation is not to utter words, but to live by them.
John F. Kennedy

I am deeply indebted to my supervisor, Professor Dr. Lee Chow Yang, who frequently goes above and beyond in helping me, and also for his continued support, concern and understanding throughout these three striving years of completing my masters degree. Of course, for most of all, thanks for every single chance that he has given me in this whole process of learning. He has spent endless time and energy to teach me every skill and knowledge that I needed the most. However, all I can do now is only expressing my deepest gratitude to him in words. Thank you so much, sir.

To Professor Abu Hassan, Dean of School of Biological Sciences, Professor Mashhor Mansor, former Dean of School of Biological Sciences, and all the staff of School of Biological Sciences, Vector Control Research Unit and Universiti Sains Malaysia, thank you for all the facilities that you have provided me and assistance or contribution that have helped me in completing this thesis.

Thanks, to all my seniors; Annie, Edwin, Kean Teik and particularly Say Piau and Pooi Yen for their constructive ideas and comments as well as advises. I've learned so much from them and feel quite blessed that God saw fit for this time of our lives to intersect. Pooi Yen, you are not only my great senior and friend, but the best listener too. Sharing every moment with you especially during our 'working time in the laboratory' has brought me such joy in these past years.

My grateful thanks to all my peers; Lay Tyng, Beng Keok and Boon Hoi for being such wonderful friends and lab mates. We've been through a lot of things together, every up and down when we were working together in the laboratory. I can't imagine doing this job without the friendships.

Not forgetting my two lovely juniors, Steff and Lay Pheng, thank you for being such great friends to me too. Your support and encouraging e-mails cured my sore and keeping me alive whenever I am drown to my deepest depths.

From the bottom of my heart, I thank my dearest friends and house mates; MF, FH, PY, ML and EB for always be there for me and doing 'silly' things with me. You bring me a lot of laughter and fun into my life. Hey buddies, you are great!

I'm surrounded by some of the most amazing people in my life, and I know you know who you are. To the rest of my friends and members of the Urban Entomology Laboratory; Ah Yaw, Soma, Yee Fatt, Sam, Evan, Su Yee, Kim Fung, Kok Boon, Nellie, Ru Yuan and those whose names I failed to mention here, thank you for whatever big or little things that you have done and your kindness will be always remembered and valued.

Lastly, I thank God for all of the many blessings. I know my family and friends are all gifts from you and I truly humbled and grateful. May God bless us all and may be strive daily to reflect His love.

TABLE OF CONTENTS

LIST OF TABLES

Page

LIST OF FIGURES

Page

KAJIAN PERILAKU PEMAKANAN SEMUT MAYAT,

TAPINOMA MELANOCEPHALUM (FABRICIUS) DAN

TAPINOMA INDICUM (FOREL) (HYMENOPTERA: FORMICIDAE)

ABSTRAK

Thesis ini bertumpu kepada perilaku pemakanan dua spesies semut mayat, *Tapinoma melanocephalum* (Fabricius) dan *Tapinoma indicum* (Forel). Perilaku pemilihan, pengagihan dan pencarian makanan bagi kedua-dua spesies dibanding serta pelbagai faktor yang boleh mempengaruhi tindak balas semut-semut ini terhadap makanan dikaji. Dalam kajian pemilihan makanan, saiz partikel didapati mempengaruhi pemilihan semut mayat terhadap makanan tetapi kepekatan dan kelikatan makanan tidak memberi apa-apa kesan. Walau bagaimanapun, semut mayat didapati lebih tertarik (P < 0.05) kepada larutan sukrosa berkepekatan 60% (w/w) pada konsistensi agar 0.5% (w/w). Sakarosa dan sukrosa terutamanya dalam bentuk cecair merupakan makanan berkarbohidrat yang paling diminati. Makanan berprotein seperti makanan anjing yang segar, serbuk lipas Lobster (*Nauphoeta cinerea*), sardin segar dan makanan kucing yang segar telah dipilih sebagai bekalan protein yang utama, sementara itu, telur kuning adalah lipid yang paling digemari. Tiada perbezaan yang signifikan (P > 0.05) didapati dalam perbandingan yang dilakukan ke atas kedua-dua spesies dan ini menunjukkan bahawa kedua-dua spesies semut mempunyai perlakuan pemilihan makanan yang amat serupa. Semut mayat mempunyai kecenderungan untuk memilih makanan berkarbohidrat secara konstan (tetap) sepanjang tempoh kajian yang dijalankan selama 12 minggu

(p > 0.05) dan didapati bahawa perubahan dalam struktur koloni tidak memberi apa-apa kesan terhadap kelakuan ini. Kesan kejemuan terhadap karbohidrat mengakibatkan *T. melanocephalum* memilih makanan berprotein atau berlipid. Di samping itu, *T. indicum* sentiasa menunjukkan kegemaran terhadap makanan berkarbohidrat dan tidak menunjukkan sebarang perbezaan dalam pemilihan makanan akibat daripada kejemuan nutrisi. Sukrosa pada kepekatan dan kelikatan yang berbeza didapati memberi kesan yang berbeza terhadap perkongsian dan pengagihan makanan di dalam koloni. Bilangan semut pekerja yang berkongsi larutan sukrosa 60% (w/w) adalah lebih tinggi daripada bilangan pekerja yang berkongsi larutan sukrosa pada kepekatan 30% (w/w) dan 10% (w/w). Selain itu, pengagihan larutan sukrosa 60% (w/w) di kalangan semut-semut pekerja juga adalah paling pantas (> 75% daripada koloni dalam tempoh masa 24 jam). Pengagihan makanan berprotein dan berlipid secara relatifnya adalah lebih rendah dan mengambil masa yang lebih lama. Didapati tiada semut permaisuri yang mengambil makanan berprotein. Ini adalah kerana kehadiran sumber-sumber protein yang lain di dalam koloni seperti telur trofik, semut pekerja yang sakit dan mati serta telur, larva dan pupa yang cedera boleh mengganggu pengambilan protein melalui makanan. Aktiviti pencarian makanan bagi *T. melanocephalum* dalam keadaan normal mencapai maksimum pada waktu 0730, sementara itu, keadaan tanpa kasta tidak matang dan keadaan tanpa permaisuri tidak menunjukkan sebarang corak waktu pencarian makanan yang jelas. Tambahan itu, juga terbukti bahawa struktur koloni dan jenis makanan bukanlah faktor-faktor yang boleh mempengaruhi aktiviti pencarian makanan bagi kedua-dua spesies semut mayat.

THE FEEDING BEHAVIOUR OF THE GHOST ANTS,

TAPINOMA MELANOCEPHALUM (FABRICIUS) AND

TAPINOMA INDICUM (FOREL) (HYMENOPTERA: FORMICIDAE)

ABSTRACT

This thesis focuses on the feeding behaviour of two species of the ghost ant, namely *Tapinoma melanocephalum* (Fabricius) and *Tapinoma indicum* (Forel). The feeding preference, food distribution behaviour and foraging activity of both species were compared, and several factors that could affect their responses were explored. In feeding preference studies, food particle size was found to affect the feeding of the ants, but no effects of concentrations and viscosities of the food were found. However, ghost ants were found to be significantly ($P < 0.05$) attracted to 60% (w/w) sucrose solution with agar consistency of 0.5%. Saccharose and sucrose in liquid forms were the most preferred carbohydrate, while proteinaceous foods such as fresh dog food, lobster cockroaches (*Nauphoeta cinerea*) powder, fresh sardine and fresh cat food were most preferred. On the other hand, egg yolk was the most preferred lipid source. No significant difference ($P > 0.05$) in feeding preference was found between *T. melanocephalum* and *T. indicum* in all the evaluations, indicating that both species showed a similar feeding preference. Ghost ants showed a constant preference for carbohydrate during the entire 12-week study period, and colony changes did not affect their preferences. Carbohydrate satiation, however, caused *T. melanocephalum* to forage for either lipid, or proteinaceous food. *T. indicum*, on the other hand, showed consistent

preference towards carbohydrate food, irrespective of the food type that they were satiated with. Different concentrations and viscosities of sucrose solution showed an effect in food-sharing behaviour in the colonies studied. The number of workers feeding and sharing 60% (w/w) sucrose solution was found to be higher than 30% (w/w) and 10% (w/w). Besides that, 60% sucrose solution was distributed and shared most rapidly among the worker ants (with >75% workers in the colony receiving it within 24 hours). Distribution of proteinaceous and lipid foods were relatively low and slow in the ant colonies. No queen was found feeding on protein as the presence of alternate sources of protein in the colonies such as trophic eggs, sick or dying workers and injured eggs, larvae and pupae could be possibly affecting the intake of protein through food. Peak foraging activity for *T. melanocephalum* under normal colony condition was at 0730, while broodless and queenless colonies did not demonstrate any clear trend in foraging activity. Colony condition and food type were not affecting the foraging activity in these two species.

CHAPTER ONE: GENERAL INTRODUCTION

In 1800, the people living in cities and large towns represented only about 1.7% of the world population. At that time, human society was mainly rural and still agrarian. Only at the end of the 1800s, the industrial society emerged and began building trend leading toward the global urbanization. As a result, the problems associated with urbanization also arose. These include, the obvious overcrowding, reduced sanitation and increased air and water pollution as well as both communicable and arthropod-borne diseases. Arthropods in the living environment affect the quality of life with their mere presence, or their ability to damage, food, fiber and the structure, or by threatening human health. Some of these animals have become established around the perimeter of structures, while others have adapted to living indoors, in direct contact with people and/or pets. Based on their large numbers present indoors and their occurrence outdoors in sufficient numbers to be a nuisance as well as disrupting the human living comfort, these animals have gained their status as pests (Robinson, 1999).

Prior to the 1990s, pest ants were considered a less important group of household pest than cockroaches and mosquitoes in Asia. Ants began to be viewed upon as pest insects in Malaysia in the mid-90 (Lee et al., 1999). However, its status has recently risen in many developed Asian countries, such as South Korea and Singapore. A household insect pest survey conducted in Malaysia revealed pest ants as one of the most important household pests (Lee & Robinson, 2001, Lee et al., 2002a; 2002b). In addition, ant control as accounted for about 10% of the total business turnover of the pest control

industry in Malaysia (Yap and Lee, 1994; Lee, 2002a) while in several other developed countries in Asia, it has a higher market share (between 10-30%).

Tapinoma melanocephalum (Fabricius) and *Tapinoma indicum* (Forel) are outdoor ant species found nesting in rotten wood, decayed tree parts, in the soil, under flower pots and may be found nesting indoors especially under moist environment (Lee & Tan, 2004). They are generally considered as pest and their characteristics as a tramp ant species makes them even more difficult to control. As a tramp species, they are polygyny, reproduce colony through budding, having the ability to colonize disturbed habitats and relocate nesting sites rapidly, and possess other features such as super colony behaviours and large colony size (Passera, 1994).

Traditional control of ants with insecticides, in spite of its efficiency, is still a problem because of their non-selective toxicity (Leite et al., 2005). Approaches focused on one or two tactics will provide only short-term control, not long-term and sustainable management, as demonstrated by the use of only chemical insecticides (Apperson & Powell, 1984). There is a growing necessity for ant control without ecological injury, one that does not lead to selection of resistant populations, and that can be effective, specific and enduring (Leite et al., 2005). Baiting, however could be a more effective method in managing these problems to control ant infestations.

Baiting is currently a popular method for control of ant infestations and has been studied comprehensively with several species of ants (Baker et al., 1985; Cornelius et al., 1996, Klotz et al., 1996; 1997a; 1997b; Silverman & Roulston, 2001; Ipser & Gardner, 2004; Soproeno & Rust, 2004). Baits require the use of less toxicant with significantly less environmental contamination,

which is an important consideration in controlling ant infestations in urban settings or in native ecosystems. Baiting is also another approach to ant control that attempts to utilize the natural foraging and social behaviour to reduce infestations and provide suppression of the entire colony, instead of just the foraging workers (Knight & Rust, 1991; Williams & Vail, 1993; Klotz et al., 1997a).

In order for a bait to successfully control a target ant, it is especially crucial for the toxicant formulated bait to be palatable, attractive, preferred over competing food sources and has an extended speed of kill for the foragers to have enough time to distribute it to the entire colony (Knight & Rust, 1991; Williams & Vail, 1993; Klotz et al., 1997a). However, formulated baits may have vastly different efficacies against various ant species. The differences may be due in part to feeding preferences and regimes of each particular species. Furthermore, the knowledge and information about the attractiveness and palatability of food materials in producing the bait matrix provided to the target ant species in particular is still very limited. Currently, little is known about specific food preferences of the ghost ants, except that they consist primarily of sweet foods, such as honeydew and dead insects.

The objectives of this study were:

- To learn and gain more information on the feeding behaviour of *T. melanocephalum* and *T. indicum* particularly in their food preference, food distribution and foraging activity, thus believing that this behaviour can be exploited in the baiting strategies for a more successful control program.

- To explore into the feeding behaviour of *T. melanocephalum* and *T. indicum* towards various extrinsic factors that could affect their food preferences such as in terms of nutritional content and physical forms of foods.

- To look into the various intrinsic factors; effects of nutritional satiation and changes within the ant colony that could affect the food selection of both *T. melanocephalum* and *T. indicum.*

- To study how the physical forms of foods such as concentration and viscosity and nutritional contents influence the food distribution in *T. melanocephalum* and *T. indicum* colonies.

- To investigate the foraging activity in *T. melanocephalum* and *T. indicum* colonies and how it is influenced by the different food types and the various colony conditions.

CHAPTER TWO: LITERATURE REVIEW

2.1 ANTS

2.1.1 General

Ants are everywhere on earth. Ants belong to the family Formicidae, a member of the order Hymenoptera. They are among the most wide spread, diverse and dominant life forms, particularly in the tropical regions of the world where their utmost diversity is unearthed (Tobin, 1993). Although ants account for only 2% of all insect species described to date, it is estimated that they constitute more than half of the world's insect biomass. When combined, all ants in the world weigh about as much as all humans (Holldobler & Wilson, 1994).

At present, the number of species world wide are approximately 9, 500 but the true number may eventually reaching 20, 000 or more. Numerous myrmecologists have explored various aspects of ants in the past, yet there is still much left to be discovered and learned (Holldobler & Wilson, 1990; 1994). Less than 0.5% out of the 10,000 identified ant species are known as pests because usually only those that disrupt human living comfort gain such status (Lee & Robinson, 2001). Ants are also believed to be more successful than other social insects because of their high degree of polymorphism and the complex relationships they share with a variety of organisms including man (Wheeler, 1910).

Biology of ants

Ants are one of the most successful types of social insects which live in societies that cooperate in many aspects in order to ensure and maintain the successful survivorship of its colony. Basically, life cycle of an ant can be

divided into three natural stages, each of which is shaped by a distinctive blend of individual-level and colony-level selection. The three periods can be conveniently designated the founding stage, the ergonomic stage and the reproductive stage.

Typically an ant colony consists of a mother queen and her progeny. A colony reproduction starts when a virgin queen departs from the nest in which she was reared, leaving behind her mother, who is the queen of the colony, and her sisters, who are either sterile or virgin reproductive like herself. During her nuptial flight, the queen finds a mate and is inseminated. After it has mated, the queen lost its wings and in the case of hymenopterans (ants, wasps and bees), the male dies (Oster & Wilson, 1978).

During this founding stage, the independent queen finds a suitable nest site in the soil or plant material and starts to construct a first nest cell and rears a first brood of workers on her own. The colony of brood is consisting of eggs, larvae and pupae. When the queens feed the larvae with her own tissue reserves, the caloric content of the little group actually declines as the number of colony members is increased. Since the queen is the only adult present, there can be no division of labour unless the larvae metabolize foodstuffs in specialized ways and pass back nutrients to the queen (Wilson, 1971; Oster & Wilson, 1978).

Soon after reaching the adult stage, these individuals devote themselves and take over the tasks of feeding, foraging, nest enlargement and brood care allowing the queen to confine herself to egg-laying. Unlike the queen, workers would never have wings. Over the coming weeks and months, the population of workers grows and the average size of workers increases and the new physical

castes are sometimes added. After a period ranging from a single warm season to five or more years depending on the species, the colony begins to produce new queens and males (Oster & Wilson, 1978). Monogyny refers simply to the possession by a colony of a single queen, as opposed to polygyny, which is the possession of multiple queens in a colony. Finally, the mode of colony founding is subject to complicated variation among species. It can be accomplished by swarming (a process also called as budding, hesmosis or sociotomy) (Sudd, 1967), in which one or more reproductive forms depart with a force of supporting workers. These reproductives set out to start new colonies, and the colony life cycle begins anew.

Colonies founding is frequently claustral, meaning that the queen seals herself off in a chamber and rears in the first brood in isolation. In this sort of colony, the brood relationship between the queen and the rest of the colony is not so simple and there may be several queens, not necessarily related to one another. Contacts between parent and progeny are not in themselves a criterion of social life. The socialness of ant life lies in the way that the workers carry out portions of this sort of parental behaviour for larvae which are not their own. Rearing the young is the task not of a single natural mother but of a group of foster-mosters (Richards, 1970).

When the first workers enclose as adults, the colony enters the ergonomic stage. During the ergonomic phase, the colony becomes a highly coordinated "growth machine" seemingly designed to maximize the size of the worker population prior to the production of the virgin queens and males. Thus, the ergonomic stage, which occupies most of the life of the colony, is the period in which colony-level selection is paramount and division of labour can be

expected to be the most complex and closely programmed. Now there is a division of labor; the queen reverts mostly or exclusively to egg-laying and the workers assumes the remainder of the tasks. The activities of the colony are exclusively ergonomic in the sense that they are concerned with work devoted to colony growth, rather than with colony-level reproduction or dispersal (Oster & Wilson, 1978).

After the colony reaches a certain "mature" size, it begins to produce virgin queens and males, initiating the reproductive stage. When the reproductive forms depart nuptial flights, the mother colony either dies or is returned temporarily to the ergonomic stage (Oster & Wilson, 1978).

2.2 FEEDING BEHAVIOUR OF ANTS

"The primary force of all animals is the necessity of finding the right type of food and enough of it….The whole structure and activities of the community are dependent upon questions of food supply" (O' Brien, 2005).

Ants like many other animals require food to maintain the living tissues, to grow, to build and repair structural parts, to reproduce and to energize the whole system. Ants owe so much of their diversity and abundance to the evolution of a variety of feeding habits that facilitate utilization of nearly every natural substance (Hagen et al., 1984). They modulate feeding patterns to the diversity of resources available in their environment. Their role as consumers is related to their great numbers in almost all ecosystems and their high consumption which is proportion to their numbers is higher than in the populations of other invertebrates (Petal, 1978). These highly selective consumers tend to achieve a high assimilation or consumption ratio because their food contains more nourishment and they are better adapted to digest it.

Ants show extremes of dietary specialization and generalization. They have certain nutritional requirements and selective of foods with high carbohydrate and protein even when the diet is catholic (Stradling, 1978). In nature, the essential macronutrients such as carbohydrate, protein and lipid, are obtained from a varied diet of insect prey (proteins and fats) and nectar, aphid honeydew and other plant products (carbohydrates). Macronutrients are essential chemical elements which include the big six elements; carbon, hydrogen, nitrogen, oxygen, phosphorus and sulphur, needed by all lives in large quantities for them to function normally. These nutrients provide the vast majority of metabolic energy to an organism. Carbohydrates and lipids serve as

energy sources for the industrious worker population which represent the engine that drives the society. Besides that, lipids are also very important reserve sources. Proteins are the only nutrient that can build, maintain and repair body tissues. Therefore, it is a very important for the reproductive or queens that produce eggs, to the larvae that hatch and grow from these eggs and also after metamophosis in the case of gynes (Peakin, 1972).

Different caste may play a different role in the feeding system of an ant colony. Workers are responsible for food collection, selection and processing. In some cases, they are involved in the assimilation of protein and lipid storage (Peakin, 1972). In addition to the workers, the most important consumer of food in the colony is the developing brood.

Brood stages may be the main concern on how a colony feeds because only the brood is capable of digesting solid food in an ant colony. Besides the availability of food sources, acceptance of food may vary seasonally depending on the presence of brood. They are usually the first to feed from foragers returning with food particles before workers distributed the nutrients to the rest of the colony through trophallaxis. They helped in digestion and even enrichment of nutrients, which are essential to colonial queens (Lim et al., 2005). Petralia & Vinson (1978) and Lim et al., (2005) reported that fourth instars are larvae which are morphologically adapted to feed on solid food. Workers place solid food, of a specific size range, on the antero-ventral region of 4th instars. This region of beards with specialized hairs and spines will hold the solid food while the larvae feeding on it (Petralia & Vinson, 1978).

Besides being potential adult workers, larvae have other roles in a colony. One of these multiple functions may be that larvae are vital protein and nutrient

storage vessels. Workers, who are unable to consume solids and lack the necessary endopeptidase in their foregut to digest them (Stradling, 1978), generally feed solid food protein directly to larvae and queens. In return, the workers would receive the protein from larvae through brood and by feeding larval secretions (Nonacs, 1991). Workers in many species cannibalize apparently healthy larvae even under conditions when food is available *ad libitum* (Sorensen et al., 1983b; Hunt, 1988 as cited by Nonacs, 1991). Workers of *Camponotus floridanus* (Buckley) cannibalize larvae when larvae/worker ratios are too high, or in reaction to perceptions of increasing danger in foraging. The amount and size of a colony's brood may be a reflection not only of the present availability of nutrients, but also a colony's perception of future availability (Nonacs, 1991). Colonies with more protein favoured higher "quality" offspring in that, among ants, larger workers tend to have intrinsically longer life spans (Calabi & Porter, 1989 as cited by Nonacs, 1991). Overall, we can deduce that the changes in nutritional preferences are depending upon the composition of the colony and food intake in a colony is principally dependent on brood development and reproduction.

Liquids comprise a major portion and form an important part of the diet in many social insects (Howard & Tschinkel, 1981a). Stradling (1978) found that 19% of returning *Formica rufa* (Linnaeus) foragers were carrying solid food and the balance of 81% were assumed to be carrying honeydew. According to Paul & Roces (2003), there are two parameters which seem to determine the liquid feeding in ants; the existence of trophallaxis or a comparable liquid food exchange and the associated temporal store of liquids collected during foraging and the existence of a well-developed crop.

Besides the morphological characteristics of the insect's mouthparts, the physical properties of the solution, along with the pressure difference created by the insect while feeding, also may influence the dynamics of liquid intake (Kingsolver and Daniel, 1979 as cited by O' Brien & Hooper-Bui, 2005). According to Paul & Roces (2003), ants were observed to employ two different techniques for liquid food intake, in which the glossa works either as passive-duct like structure (sucking), or as and up- and downloads moving shovel (licking). Workers of ponerine ants licked fluid food during foraging and transported it as a droplet between mandibles, whereas species belonging to phylogenetically more advance subfamilies, with a crop capable of storing liquids, sucked the liquid. Licking has been shown to be a more advantageous technique at higher sugar concentrations than sucking, whereas sucking provided a higher energy intake rate at lower sugar concentrations. Ants which share food with nest mates will choose suction as the preferred methods of liquid feeding. In the higher ants, particularly in the Formicidae and Dolichoderinae, the proventriculus has evolved into a passive dam to increase the capacity of the crop as a storage organ and to reduce the burden on the associated musculature (Eisner & Brown, 1958 as cited by O' Brien, 2005). The advanced proventriculus is characterized by a narrow, rigid, cruciform slit trough which fluids are transported only by active compression of the organ by circular muscles.

Food exchange activity in social insects is one of the main mechanisms for integration between members of a large and complex colony (McMahan, 1963). It has been known that the food exchange is an activity of great importance in social insect colonies especially for members of the society which

cannot or do not forage but depending on their nest mates for nutrition. These are the domestic workers, queens, reproductive and above all, the larvae. Apparently, such exchanges also provide nourishment for the colony members.

Various names have been given to this mechanism such as food exchange, food sharing and food traffic. However, the term "trophallaxis" has been stretched to cover almost all social contacts between ants (Sudd, 1967). Trophallaxis for the majority of many social insects is an open system, where each worker will share food with an unlimited number of nest mates (Wilson, 1971). The flow is not all one way, foragers feed each other and foragers may be fed by domestic workers. How soon this happens depends on the species of ant. These repeated exchanges keep the workers informed of the nutritional status of the colony as a whole. It is possible that, in this manner, foragers are able to access the degree of colony hunger and respond accordingly. Moreover, the different types of nutrient for different metabolic needs such as development and reproduction for the whole colony can be utilized effectively (Sorensen et al., 1985).

The advantage of the social way of life is that it allows the division of labour, not only reproductive and non-reproductive castes, but also into classes of workers fulfilling different functions. The food flow of food within an ant colony is strongly influenced by its division of labour (Abbott, 1978). Workers hold the key to control the caste of the incoming generation among larvae through nutritional regulation (Holldobler & Wilson, 1990). They respond to nutritional regulation need of larvae and consequently resulted in indifferent feeding frequencies. Food supplementation altered the caste ratios in the *Pheidole flavens* (Roger) and suggested that ant colonies determined caste ratios in

response to different variables (McGlynn & Owen, 2002). In fire ants, the foragers are responsible for regulating flow of food from the environment into the nest while other adults and larvae regulating food distribution inside the nest (Cassill & Tschinkel, 1999).

The way in which liquid food is passed from one worker to other workers has often been described for example, as reported by Wallis (1962) as cited by Sudd (1967) on *Formica fusca* (Linnaeus) and other ants from Myrmicinae, Dolichoderinae and Formicinae. A worker which is receiving food from a nest mate lifts its head and the forepart of its body so that its forelegs are off the ground. Its mandibles are closed and its palps directed backwards, but its antennae are folded towards so that their tips converge on the head of the ant which is giving food. It often strokes the other ant's head as it feeds. The ant which is giving food on the other hand raises its head a little and its antennae are folded back at right angles to its head. Its mandibles are opened wide and a drop of liquid appears on its extended tongue.

Another important part of food exchange in trophallaxis in ants is the feeding brood by the adult workers. Larval nutrition in Hymenoptera will influence the body size of various adult forms, development or reproductive systems and also existence of various caste forms (Wheeler, 1994). Although the immature stages of social insects are generally immobile and do not participate directly in feeding activities, they play an important role in feeding as a nutrient storage and enrichment locality of a colony. The ability of larva to regulate colonial nutrient distribution using various factors such as larval size, hunger level, and even food quality as regulator (Cassill & Tschinkel, 1995; Cassill et al., 1998). Therefore, it is also a 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.

The donation of substances between workers and larvae does not occur in one direction only. Larval secretions are collected and consumed by workers in many species, and sometimes actively solicited. Apart from the cuticular secretions which may be attractive to the workers and elicit grooming behaviour, ant larvae frequently produce droplets of clear fluid at the mouth parts, and clear or sometimes milky fluid from the anus. These fluids are sometimes referred to as stomadeal and proctodeal secretions. Stomadeal secretions, produced in the sub-families Myrmicinae, Ponerinae and Formicinae, but not by the Dolichoderinae (Wilson, 1971) are probably formed in the salivary glands.

The radioactive tracers (Markin, 1970; Howard & Tschinkel, 1981b; Sanders et al., 1992), food dye (Ripa et al., 1999; Loke & Lee, 2006a) and paint (Tripp et al., 2000) have enabled the food exchange in an ant colony to be studied. All of these markers have been used to follow the flow of the food within single colonies, food transmission between individual ants and to determine the extent of ant foraging territories. Dyes such as Nile blue A, Neutral Red and fluorescent red, orange and green Day-Glo dust were effective on termites and did not cause significant mortality at low concentration (Su et al., 1991; Haagsma & Rust, 1993; Miller, 1993). These markers may offer an inexpensive and simple way to mark the ants as well. More recently, a red dye (combination of Carmosin S.I.N. 122 and Yellow Crespular S.I.N. 110 dyes) in a sucrose bait successfully marked *Linepithema humile* (Mayr) in a field study with marked ants being found as far away as 52 m from the feeding station

(Ripa et al., 1999). Marker choices have also been limited by health, safety and concerns (especially radiolabelled markers), technique and cost.

2.3 FORAGING BEHAVIOUR OF ANTS

Almost all of the individuals in an insect society share their food within the nest area. Only some of them go out and search for the food. They are the foragers which usually are the oldest and most experienced workers in the colony (Mirenda & Vinson, 1981). Oster & Wilson (1978) have stressed the role of 'tempo' in societies. There is enormous variation in tempo in activity among different species of social insects. The workers of some ant species walk slowly and deliberately. Examples of such species include ants in the subfamilies Ponerinae and Myrmicinae. In contrast, ants of the subfamilies Dorylinae and Dolichoderinae seethe with rapid motion; run excitedly and lively. A species adapted to predictable, rich food sources is likely to operate at a low tempo as it needs to invest very little in searching but a great deal in the protection and exploitation of its resource.

According to Petal (1978), about 80-90% of the members of a colony growth normally stay within the nest, and the rest of the 10-20% of the colony takes part in foraging. Work in the nest is light and complicated whereas outdoor works is heavy and dangerous through requiring sensitivity to environmental cues and intelligent flexibility in navigation, searching, making choices, communication, efficiency, transportation and defense. Resource acquisition by ants is a complex process that involves different activities, realized alone and cooperatively. The great success of ants as a group must be due in some degree to their ability to coordinate individual behaviours into mass action through effective communication. Therefore, communication between individuals and the methods which each forager uses are of paramount importance.

In ecological systems obtaining resources is an important variable and it can be assumed that natural selection favours those individuals that optimize their energetic efficiency, not only through the choice of the best food items, but also by using the best foraging strategies (Bernstein, 1975, Holldobler & Wilson, 1990). The ecological success of ants depends on their ability to adjust their foraging strategies to both resources and environmental constraints. Holldobler & Wilson (1990) recommended four ways of how natural selection modifies behaviour to optimize foraging. These include selection of food items, choice of food patch, allocation of time invested on different patches and regulation of the pattern and speed of movement. According to Schoener (1971) as cited by Baroni-Urbani & Nielsen (1990), ants would either prefer minimize the time spent in searching or maximize the reward of a longer search. When given choices between safe patches with poor food and dangerous patches with better food, the foragers' willingness to take risks is significantly correlated with the costs, in terms of lowered colony growth, of foraging in the safe patch (Nonacs, 1990). Besides that, foraging in ants is energetically an extremely cheap activity (Baroni-Urbani & Nielsen, 1990). Ants are predicted to prefer routes that are relatively cheap in terms of time and energy costs.

Ants do not get a panoramic view of their foraging range and do not possess very well-developed eyes. They depend on chemosensors to recognize their food. Interestingly, ants are able to access its nutritional needs and exploit the foods and to choose the more nutritious food based on the information obtained through these chemosensors. As proven by Barrer & Cherett (1972) as cited by Stradling (1978), the foragers of *Atta cephalotes* (Linnaeus) are more attracted to cut or damaged leaves than to undamaged

one because the ruptured cells are more prone to emit more chemical information. This is probably the similar reason for the attractiveness of injured and dying prey.

The behaviour of ants collecting food can be divided into searching for food and handling it once it has been found. Recruitment generally refers to an increase in the number of feeding ants. Among ants, recruitment by various chemical and mechanical means has been reported by members of four major subfamilies; Ponerinae, Myrmicinae, Dolichoderinae and Formicinae. Even within a species, ants can hence use a wide variety of rectruitment strategies ranging from solitary food collection to mass recruitment. In the relatively primitive system, called 'tandem recruitment' is a system which individual giving signals to another one by direct physical interaction when worker found the food source. Tandem recruitment grades into 'group recruitment', in which chemical signaling by one recruiting a few individuals. More advanced recruitment system, 'mass recruitment' is the system with the greatest efficiency which is performed through independent trail-laying and trail following behaviours (Chadab & Rettenmeyer, 1975).

After a food source is found, ants will gather or transfer back the food to their nest. Gathering and transferring food in an ant colony can be achieved in three ways, based on the physical form of the food. Liquid foods are swallowed, transported and bring back in the crop. Small fragments of food may be directly consumed at the site of capture and the nutrients carried in the crop, or carried whole in the mandibles and maxillae. Larger items of food are either carried back by the groups of workers or broken down into pieces at the site of capture and carried by foragers (Burkhardt, 1998).

Insects, like many other organisms, have evolved in an environment dominated by daily, monthly, annual and, in some cases, tidal periodicities. In natural conditions, or in the artificial light and temperature cycles provided in the laboratory, they may be - with respect to particular activity - either night-active (nocturnal), day-active (diurnal) or twilight-active (crepuscular). Circadian rhythm is defined as an endogenous oscillation with a natural period close to, but not necessarily equal to, that of the solar day (24 hours). The mechanisms controlling these activities may be exogenous (i.e. a direct responses to environmental changes) or endogenous (i.e controlled by an underlying circadian oscillation, which are part of the physiological make-up of the organism) (Saunders, 1976).

Their foraging activity may be restricted to certain times of the diel cycle. According to Bernstein (1975), foraging rhythms confine the outside activity of ants to times when temperature and humidity outside the nest are least harmful to them, the least overlapping schedules of foraging time between coexisting species and also when their food is most easily obtained. Nuss et al. (2005) also reported that *Camponotus pennsylvanicus* (De Geer) foraging ants would prefer daylight foraging because they may encounter additional food resources during the daylight foraging trips and competition with other ant colonies can be reduced.

Besides that, the daily seasonal schedules of foraging activity are also simply consequence of the particular morphological, physiological and behavioural characteristics of the foragers (Berstein, 1979). For examples, daily rhythms of general locomotion, the date of the mating flight each year, time of hibernation in sub-artic ants, feeding and oviposition, in which these activities

are restricted to a particular part of the day or night (Saunders, 1976). This behaviour is more obvious in ants and other poikilotermic eusocial organisms since their metabolic rates are directly dependent on the ambient temperature, water stress, humidity, light intensity and other physical factors that might affect energetic costs of foraging or use of time (Traneillo, 1989; Bonabeau et al., 1998). Feeding may not occur when the temperature is above or below levels of the ambient temperature.

Photoperiodism also involves a clock which measures day- or night-length, the most frequent responses being the seasonal appearance of a dormant stage in the life cycle. Cycles of feeding may be correlated with the supply of food: the classical example of this is probably the "time-memory" (*Zeitgedächtnis*) of bees. According to Beling (1929) as cited by Saunders (1976), bees can be "trained" to visit a food source at a particular time of the day because this mechanisms ensuring that they visit nectar sources every day at the same time.

Nevertheless, animals have developed strategies to counteract or to exploit this periodicity of daily and seasonal changes which may include the violent fluctuations in temperature and humidity. In some insects a circadian rhythm is not merely the direct result of changes and other conditions through the day, for the insect will continue to show peaks of activity at the same time of day if it is imprisoned in the dark at a constant temperature. This shows that the rhythm is partly under the control of an internal 'biological clock'. Virtually, all organisms possess endogenous daily clocks that enable them to prepare in advance to the cyclic 24 hours changes in the environment instead of reacting passively of them (Saunders, 1976).

Biological clocks control a wide variety of behavioural and physiological activities in insects. These include daily rhythms of locomotion, feeding, mating, oviposition, pupation and eclosion, in which these activities are restricted to a particular part of the day or night. These rhythms may be operational either in individual insects or in populations which behave, in this respect, like "superorganisms" (Saunders, 1976).

On the whole, we can deduce that foraging activity is a result of a complex interaction among the phase of colony development, nutritional and climatic factors. Besides external influences; food abundance, competition, temperature and humidity, activities of foragers are directly dependent on the trophic needs of colony (Sorensen et al., 1984). Foraging activity in an ant colony is also promoted by intrinsic characteristics of ant colonies such as level of colony starvation, nest size (Herbers & Choinere, 1996), nutritional demand of workers and condition of the brood. Moreover, Wallis (1962) as cited by Sudd (1967) also discovered that hunger increases ant activity and returning foragers boost the activity of the colony, stimulating more foraging.

2.4 *TAPINOMA* SPP.

Ants in *Tapinoma* sp. are classified in the family Formicidae, subfamily Dolichoderinae under Tapinomini tribe (Holldobler & Wilson, 1990). Dolichoderinae ants can be identified and easily distinguished from ants classified under other subfamilies through their unique characteristics. All Dolichoderinae ants have abdominal pedicel composed of one segment which is usually hidden from view dorsally by the gaster and the tip of the abdomen without a fringe of hairs. Theirs antennae has 12 segments and does not end in a club like in many other species of ants (Wheeler, 1910).

Dolichoderinae ants have no sting but have small sting glands. These anal glands were discovered by Forel and are only present in the female and worker of Dolichoderinae. For some cases, it may be coexist with well-developed poison glands of the bourrelated type (Wheeler, 1910). The defensive function of the sting has been taken over by the anal glands which produce a complex of scented compounds (Sudd, 1967). The secretion by this gland is quite unlike that produced by the poison glands in any other species of ants because it is stickier and having in all Dolichoderinae a very distinctive odour, which calls the "Tapinoma odour". It is very noticeable in the common species such as *Tapinoma erraticum* (Latreille) and *Tapinoma sessile* (Say) (Wheeler, 1910). The common name of *T. sessile*, the odorous house ant, is derived from "rotten coconut-like odour" (Ehmann, 1982 as cited by Thompson, 1990) caused by butyric acid, released when the ant is crushed (Creighton, 1950 as cited by Thompson, 1990). In this case, butyric acid which produced by the anal gland is functioning as the ant's defense (Holldobler & Wilson, 1990). These liquid do not only have repellent and insecticidal properties but in

Tapinoma nigerrimum (Nylander), two components polymerize to viscous oil can immobilize small enemies (Stumper, 1953 as cited by Sudd, 1967). Furthermore, the secretion is fatal, or, in any rate, very irritating, and it constitutes the most efficient protection even for the most diminutive and soft-bodied species like *Tapinoma* (Wheeler, 1910). In *Tapinoma* and other Dolichoderinae ants, the enlarged anal glands produce a specific alarm substance methylheptenone, as well as repellent secretions specifically aimed at attackers, but not to their own nest mates (Wilson & Bossert, 1963 as cited by Sudd, 1967).

2.4.1 Georaphical distribution

Tapinoma is a cosmopolitan genus. All native Australian species belong to the *minitum* group which is distributed throughout the mainland and in Tasmania, occurring in a wide range of habitats (Andersen, 1990). One of the most popular *Tapinoma* ant species, namely *T. melanocephalum*, which is commonly known as the ghost ant, is widely distributed in tropical and subtropical latitudes worldwide (Wilson, 1971) and areas across the Old World and New World in both the northern and southern hemispheres. This is because *T. melanocephalum* can live everywhere that humans live, there is no limit to the latitude where indoor populations of this species may be found (Wetterer, unpublished).

This tropical species has been so widely distributed by commerce that it is difficult to determine its origin. According to Wilson & Taylor (1967) as cited by Espadaler & Espejo (2002) its origin is unknown. As stated in Andersen (1990), it is an introduced species of unknown origin that occurs throughout the