FOOD PREFERENCE, FORAGING ACTIVITY, INTER- AND INTRASPECIFIC AGGRESSION AND BAITING OF THE CRAZY ANT, *Paratrechina longicornis* (LATREILLE) (HYMENOPTERA: FORMICIDAE)

By

SAM SIAO JING

Thesis submitted in fulfillment of the requirements
for the degree of
Master of Science

June 2010

This thesis especially dedicated to my beloved mom

Thank you for your endless love and support

I know you always looking after me no matter where you are...

To my dad, sis Hong, sis Ying and brother Wei

Thank you for your caring and misunderstanding

Thank you once again and I'm lucky to have all of you as my dearest

ACKNOWLEDGEMENT

I would like to express my utmost gratitude to my supervisor, Professor Dr. Lee Chow Yang, who is always willing to spend his time and energy to teach and advise me in order to complete this thesis. I'm deeply indebted to him for giving me the opportunity to learn from him and also providing me numerous chances to attend local and international conferences. Thank you once more for your understanding, support and concern throughout these three wonderful years.

To Professor Abu Hassan, Dean of School of Biological Sciences, Associate Professor Dr. Zairi Jaal, the coordinator of Vector Control Research Unit as well as all the staff of the School of Biological Sciences and Vector Control Research Unit, Universiti Sains Malaysia, thank you for providing all the facilities and assistances that helped me in completing this thesis.

Not forgetting Dr. Michael Lenz and Mrs. Lenz, thank you for your effort in reviewing my thesis.

Many thanks to Yee Fatt, Kok Boon and Evan for their statistical analysis advice, constructive comments and support. Of course, I would never forget all the laughter and joyfulness that you guys brought to me. Those great times are some of the best moments in my life.

Hui Siang, thank you very much for accompanying me through the ups and downs during these years. Your cheerful character and jokes lift me up when I'm down, always willing to lend me your helping hand. Thanks again.

Thanks to the rest of the past and present members of the Urban Entomology Laboratory; Sui Yaw, Su Yee, Chee Kit, Nellie Wong, Ru Yuan, Yu Chong, Li May, Jia Wei, Ling Hui, Veera, Rivo, Foong Kuan, Ching Chen, Tomoki and Beng Keok etc., thank you for all the big and small things that you have done and your kindness will be always be valued. Many thanks to my direct junior, Nadiah for always giving me a helping hand with my research.

Special thanks to Vanessa Yu, for the encouragement and support. Last but not least, I thank God for all the blessings and filling my life with my lovely and caring family members.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

PEMILIHAN MAKANAN, AKTIVITI PENCARIAN, INTER- DAN INTRASPECIFIK AGRESI DAN PENGUMPANAN CRAZY ANT, PARATRECHINA LONGICORNIS (LATREILLE) (HYMENOPTERA: FORMICIDAE)

ABSTRAK

Tesis ini menumpu pada kajian mengenai pemilihan makanan, aktiviti pencarian, interaksi inter- dan intraspecifik agresi dan pengumpanan *Paratrechina longicornis* (Latreille). Antara semua kelas makanan karbohidrat dan lipid, *P.longicornis* lebih menyukai gula sakarose dan kuning telur ($P < 0.05$). Semut in juga lebih menggemari ikan bilis kering antara makanan lain dalam kelas protein tetapi pilihan ini tidak signifikan ($P > 0.05$) berbanding dengan udang kering, ikan tuna dan sosej. Species ini lebih tertarik kepada makanan yang kurang likat tetapi berkepekatan tinggi ($P < 0.05$). Selain itu, *P.longicornis* menggemari diet dalam bentuk cecair dan juga makanan berprotein dan lipid dalam bentuk pepejal ($P < 0.05$). Sebaliknya, makanan separa pepejal kurang menarik perhatian semut ini ($P < 0.05$). *Paratrechina longicornis* menggemari partikel makanan yang agak besar tetapi saiznya tidak melebihi 1900µm. Aktiviti pencarian oleh *P.longicornis* lebih dipengaruhi oleh suhu persekitaran berbanding dengan kelembapan relatif. Tambahan pula, hujan mempengaruhi aktiviti pencarian semut dengan darjah yang berbeza-beza bergantung kepada jangka masa dan kekerapan hujan. Dua puncak aktiviti pencarian dicatat, satu antara 5.00-7.00 petang dan satu antara 1.00-5.00 pagi. Pada waktu puncak ini, suhu adalah antara 24-32^{0}C dengan kadar kelembapan relatif yang tinggi. Pemilihan makanan bermusim menunjukkan bahawa semut "crazy" tertarik kepada karbohidrat (sakarose dalam larutan) hamper

sepanjang tempoh percubaan. Pada bulan Mei dan Julai, *P.longicornis* memberi perhatian kepada semua jenis diet dan ini mungkin berkolerasi dengan pertumbuhan koloni dan pertambahan keperluan. Semasa interaksi dengan species asing, *P.longicornis* lebih agresif dalam ujian berkumpulan berbanding ujian secara individu. *Oecophylla smaragdina* (Fabricius) menyebabkan kadar kematian yang tinggi pada *P.longicornis* dalam kedua-dua ujian secara berkumpulan dan individu. Semut "crazy" yang terkorban berkolerasi dengan kelebaran mandibel dan saiz musuh. Selain itu, reaksi agresif *P longicornis* juga berkolerasi dengan darjah kerapatan taksonomi antara species dan ini dibuktikan sewaktu interaksi intraspecifik. Umpan gel Optigard® berjaya menurunkan jumlah pekerja *P. longicornis* sebanyak lebih daripada 95% pada akhir ujian manakala umpan gel Advion® hanya mencapai 42% penurunan. Tambahan pula, hanya kesan Optigard® yang menunjukkan perbezaan yang bererti dalam rawatan kawalan ($P < 0.05$).

FOOD PREFERENCE, FORAGING ACTIVITY, INTER- AND INTRASPECIFIC AGGRESSION AND BAITING OF THE CRAZY ANT, *PARATRECHINA LONGICORNIS* (LATREILLE) (HYMENOPTERA: FORMICIDAE)

ABSTRACT

This thesis focuses on the study of food preferences, foraging activity, inter- and intraspecific interactions as well as baiting of *Paratrechina longicornis* (Latreille). Amongst all the carbohydrate and lipid foods, *P. longicornis* preferred saccharose sugar and egg yolk ($P < 0.05$) the most. Crazy ant also highly preferred dried anchovy and it was significantly ($P < 0.05$) preferred over the other candidates except dried prawn, tuna fish and sausage. This species are also more attracted to lower viscosities but higher concentrations of food ($P < 0.05$). Besides that, *P. longicornis* favoured their diet in liquid solution as well as protein and lipid food in solid form ($P < 0.05$). In contrast, semi-solid food was less appeal to these ants ($P > 0.05$). *P. longicornis* preferred relatively large food particles but not above 1900 µm in size. Foraging activity of *P. longicornis* was influenced more by ambient temperature compared to relative humidity. In addition, rain would affect the foraging activity of ants in varying degree depending on the duration and intensity of rainfall. Two peaks of activity were recorded, on between 5.00-7.00 pm and the other between 1.00-5.00 am. During these peak periods, temperatures ranges from 24^{o}C to 32^{o}C with relatively high humidity. Seasonal food preferences revealed that crazy ants are attracted to carbohydrates (saccharose solution) throughout most of the trial period. In May and July, all food groups were given more attention by *P. longicornis* and it may be related to colony growth and expansion. During interactions with other ant species, *P. longicornis* were more aggressive in group test than individual test. *Oecophylla smaradigma* (Fabricius) inflicted the highest mortality rate on *P. longicornis* in both individual and group tests. Casualties of the crazy ants were correlated with the mandible width and size of the opponents. Besides that, the aggressive response from *P. longicornis* also correlated with the degree of taxonomic closeness between the species and this was especially evident during the intraspecific interactions. Optigard® gel bait managed to reduce *P. longicornis* workers by more than 95% at the end of the test while Advion® gel bait achieved only about 42% reduction rate. Furthermore, only the impact of Optigard® was significantly different from the control treatment ($P < 0.05$).

CHAPTER ONE

GENERAL INTRODUCTION

Ants are highly adaptable to various environments characteristic threat has driven their success and appearance in almost every corner of the world except for Antarctica and some of the inaccessible islands (Schultz, 2000).Of approximately 10,000 species of ants known to science, only less than 0.5% are considered pests in the human environment (Lee & Robinson, 2001).

In Asia prior to the 1990, less attention was paid to pest ants compared to cockroaches and mosquitoes. However, since the mid-90s, ants have become increasingly important as one of the key household pests in Malaysia and other Asian countries, such as Singapore and South Korea (Lee, 2002). A 2001 survey revealed that pest ants have not gone unnoticed by the Malaysian pest control industry and that their importance was ranked third after termites and cockroaches (Lee, 2002). Even in the United States, ants have been the number one pest since 1998 (Robinson, 1999), and according to Gooch (1999) ants were the most difficult pest to control.

Paratrechina longicornis (Latreille), more commonly known as the crazy ant due to its erratic movement are highly adaptable to the environment and can nest either indoors or outdoors (Smith, 1965; Trager, 1984). *P. longicornis* colonies have multiple queens and may contain more than a thousand workers (Passera, 1994). Foragers of crazy ants are opportunists (Andersen, 1992). They are omnivorous and feed on various items such as dead insects, fruits, and household foods (Smith, 1965). They usually occur in abundance, which makes them a nuisance (Harris et al., 2005). In addition, crazy ants also have been reported to replace native ants in a greenhouse due to their overwhelming numbers (Wetterer et al., 1999).

P. longicornis is a common tramp ant which invades buildings and structures (Harris et al., 2005; Nickerson & Barbara, 2000). In Penang, Malaysia, surveys showed that *P. longicornis* was one of the most dominant pest ants found in residences (Yap & Lee, 1994; Na & Lee, 2001). A survey of food outlets revealed that crazy ants were often found in large numbers (Lee et al., 2001). Crazy ants were often found in some of the hospitals in Brazil, and may transmit pathogens mechanically (Fowler et al., 1993). According to Wetterer (2008), crazy ants are pests in agriculture due to their habit of providing protection to and distributing crop damaging insects such as aphids and mealy bugs.

Common control methods for ants consist of chemical residual treatments and baiting. Residual insecticide sprays will only provide short term control, as these chemicals only kill visible foragers (Knight & Rust, 1990), which make up about 10% of the total nest population (Adams et al., 1999). This control method has other limitations, including degradation of the insecticide due to weather (e.g. rain and heat) (Knight & Rust, 1990) and treated surfaces (Rust et al., 2003). Baiting is gaining in popularity and is effective in controlling pest ants (Knight & Rust, 1991; Lee, 2000; Lee, 2007). Baits exploit the social behaviour trophallaxis of ants, where food is shared among colony members (Silverman & Roulston, 2001). By utilising this process, baits which contain the insecticides are distributed throughout the colony (Knight & Rust, 1991), and eventually the whole colony is eliminated. Other advantages of baiting are the smaller quantity of toxicant needed and the lack of need to locate the nest. The latter is important when it comes to combating crazy ants because they can forage far away from the nest (Smith, 1965).

The effectiveness of baits to control ants lies within the bait formulation. The bait must be more attractive and palatable to the ants compared with other food sources. In addition, the insecticide must exhibit delayed toxicity in order for the foragers to have enough time to distribute it throughout the entire colony. However, different ant species display inconsistent responses to the baits due to different behaviour and biological characteristics. Baiting can only be successful if the correct baits and strategies are applied accordingly. Therefore, it is crucial to learn and understand the behaviour and biology of the target pest ant. Despite its importance, there is little information available about *P. longicornis*. Therefore, the objectives of this study are:

a. To gain more information on the feeding preferences of *P. longicornis* in terms of their choice of food qualities, consistencies, different food forms as well as food particle sizes.

b. To study the foraging activities and seasonal food preferences of *P. longicornis*.

c. To study the level of aggression displayed by *P. longicornis* during interactions with other common local pest ants.

d. To evaluate the effectiveness of two commercial ant baits against *P. longicornis*.

CHAPTER TWO

LITERATURE REVIEW

2.1 Ants

Ants are one of the most successful groups of social insects. They belong to the family Formicidae in the order Hymenoptera, which also includes bees and wasps. Ants existed during the mid-Cretaceous period, about 110 to 130 million years ago, and became ecologically dominant after they diversified following the rise of flora around 100 million years ago (Grimaldi & Agosti, 2001; Moreau *et.al*, 2006; Wilson & Hölldobler, 2005). They remain amongst the most abundant and species-rich taxa on the planet (Hölldobler & Wilson, 1990).

Ants live in colonies ranging in size from a few dozen to millions of individuals. Such large colonies are highly organised and may occupy a large area (Oster & Wilson, 1978). Every species of ant has its own distinct characteristics and behaviour regarding food preferences, distribution, and methods of dispersal. (Haack & Granovsky, 1990).

2.2 Biology of ants

An ant can be divided into three distinct body segments; head, thorax and abdomen or gaster. The petiole is formed by one or two nodes and is located between the thorax and the abdomen. The reproductive members, such as queens and males have two pair of wings. The forewings are larger than the hind wings. Like all insects, ants have an exoskeleton that acts like a protective casing and as a place of attachment for the muscles. Ants also have compound eyes which are good at detecting acute movement but do not give a high resolution (Haack & Granovsky, 1990; Borror et al., 1989). Some also have three small ocelli (simple eyes) that detect light intensity (Fent & Rudiger, 1985). An ant's head also has a pair of antennae which are used to detect chemicals, air currents and vibrations. Moreover, it is also used to play a vital role in communication by transmitting and receiving the signals through touch. The head also has two strong mandibles that are used to construct the nest, carry or manipulate objects and for defence. In the abdomen some of the important systems such as excretory, reproductive and respiratory systems are located. In the workers of some species, their egg laying structures are modified into stings that are used for defence and to paralyse prey (Haack & Granovsky, 1990; Borror et al., 1989).

The life cycle of ants consist of four different stages which are the egg, larva, pupa and adult. This shows that ants undergo complete metamorphosis (holometabolous). Eggs are usually white in colour and microscopic in size but vary among different species (Lee & Chong, 2003). The larva is highly immobile and is fed by a process called trophallaxis (see below for more details). The larva will go through a series of moults before turning into a pupa (Gillott, 1995). The pupa will then develop into an adult. The newly hatched adult is also known as a callow due to its fair body colour but as it grows older, its colours will darken (Lee & Chong, 2003).

Ants practise caste system in their colonies. Basically, a colony consists of two castes; namely the reproductive individuals and the non-reproductive individuals. The queens and alates, both male and female, belong to the reproductive group while the other colony members include the workers, immature stages or brood and are considered non-reproductive individuals (Lee & Chong, 2003). The differentiation of caste into queens and workers and also different castes of workers is believed to be determined by the nutrition the larvae obtain (Hölldobler & Wilson, 1990). The queen is the largest individual in the colony. Ant colonies which contain multiple queens are called polygynous while those with only one queen are known as monogynous colonies. However, there are also some ant nests that can exist without queens and the workers have the ability to reproduce and are called gamergates (Peeters & Hölldobler, 1995). During the breeding period, the alates will swarm from the nest, mate and after that, female alates will shed their wings, seek a suitable place to lay eggs and become the queen of the newly established colony while the male alates will die within two weeks (Haack & Granovsky, 1990). The only role of the queen is to lay eggs. The female alate has the ability to store sperm and only has to mate once in order to reproduce continuously thorough out her life (Hölldobler & Wilson, 1990). The workers are sterile females and are the most abundant individuals in the colony (Haack & Granovsky, 1990).

In a colony, younger workers usually stay within the nest and take care of the broods and queens. Older workers are responsible for foraging for food and building the nest. Ant species which only have workers of a single size are called monomorphic while in species that have workers of two or multiple sizes are known as dimorphic and polymorphic workers respectively. Dimorphic workers consist of major and minor workers, while polymorphic workers consist of minor, median and major workers. Basically the larger ants will have disproportionately larger heads and with a pair of stronger mandibles. Sometimes these individuals are called "soldiers". However, their duties do not vary greatly from the minor or median workers (Wilson, 1953). Median workers are absent in a few species while some other ants, for example, *Pheidologeton diversus* (Jerdon), show continuous variation in the size of workers (Moffett & Tobin, 1991). Larger ants usually function as foragers, nest builders and protect the colony from enemies. Lighter task such as tending the brood and queens will be carried out by the minor workers (Lee & Chong, 2003). Meanwhile, the brood that includes the eggs and immature stages are highly immobile and vulnerable; they have to be fed and groomed by the workers (Haack & Granovsky, 1990).

Swarming and budding are two methods that are mainly used by ants to establish new colonies. During the reproductive period, a mature colony will produce female and male alates. These alates will mate on the ground or perform the nuptial flight (swarming). After mating, the female will shed its wings and find a suitable place to lay eggs while the male will die shortly afterwards (Hölldobler & Wilson, 1990). During the colonies founding period, queens usually will forage for prey in order to feed her first brood. On the other hand, some of the queens are shown to be facultatively claustral which means they will seal off the chamber and tend the first batch of brood in isolation (Wilson, 1963a). The first batch of workers is usually weak and smaller than later workers. After that, the queen will only act solely as an egg-laying machine as the workers begin to serve the colony (Hölldobler & Wilson, 1990). For other species, some of the mated queens will leave the nest along with some workers to establish a new colony at a new site. This process is also known as budding. In some cases, queens show temporary parasitic behaviour where they invade other host colonies in order to found their own colonies (Wilson, 1963a) and for a few species, the workers are able to produce new queens to start a new colony through special feeding of the larvae (Lee & Chong, 2003).

2.3 Feeding behaviour

Generally, ants are omnivorous and feed on a great variety of foods ranging from sugar-rich items to grease and oils as well as plant and animal materials (Nash, 1969). Some ants even cultivate fungus in the nest as their main source of nutrition such as the leafcutter ants (*Atta sp.* and *Acromyrmex sp.*). The specialised workers will choose suitable plants that are non-toxic and will carry back pieces of cut leaves to their colonies and grow fungi on them. Leafcutter ants will feed on structures produced by the fungi called gongylidia (Schultz, 1999). There are ants that form symbiotic association with other insects in order to obtain their daily nutritional needs. Ahpids and some hemipteran insects such as mealybugs and whiteflies will secrete a sweet liquid called honeydew when they feed on plant sap. The sugar in honeydew is a high energy source that provides the ants with their daily carbohydrate needs. In return, ants will provide protection for the hemipterans and ward off other ants, parasites and predators (Tynes & Hutchins, 1964; Wetterer, 2008). On the other hand, Dacetine ants (Myrmicinae) are good predators. Most species specialise in preying on soft-bodied insects such as springtails (Collembola) because those small organisms are rich in protein and calories (Wilson, 1962a). Another rich source of protein can be gained from the nests of other social insects. For example, *Termitopone* ants frequently raid termite colonies while army ants frequently raid the nest of other ants. Seed collecting behaviour has also been recorded many times especially in the Myrmicinae (Creighton, 1950; Cole, 1968; Bernstein, 1971) Seeds have a high nutritional value (high in lipid and nitrogen content) (Baker, 1972; Janzen, 1971). Due to the specific functions of different foods, this will influence their distribution within an ant colony (Abbott, 1978). Carbohydrates are the primary energy source for the workers which carry out various tasks such as brood tending, foraging and defending the colony. Meanwhile, protein and lipids are very important to brood development and reproduction (Peakin, 1972). Therefore, the queens and the growing larvae are the main consumers of these two nutrients. Lipids act like an alternate source of energy for the workers but are more suitable as a reserve material and large amounts are given to the larvae to store (Abbott, 1978).

Workers foraging for liquid foods will ingest it until the abdomen is swollen and bring it back to the nest and share it among other colony members (Lee & Chong, 2003) especially with the younger larvae for which liquid foods are a very important dietary component (Abbott, 1978). In many ant species, the workers will give the solid food to the 3rd larval instar for digestion. The workers lack the endopeptidase enzymes in their foregut which are required for digesting solid food (Stradling, 1978), but this larval stage possesses them. Food particles will be placed on the mouthparts of the larvae and they will be allowed to consume and digest the food (Abbott, 1978). After that, the larvae will regurgitate the digested food back to the workers and subsequently the workers will feed it to other colony members. This process of exchanging food is called trophallaxis (Lee & Chong, 2003).

Food exchange is a very common practice that happens in an ant colony but the rate of exchange depends on the temperature, species and season. Even the different types of food will influence the pattern of exchange (Khamala & Büschinger, 1971). For example, carbohydrates are not always distributed evenly within the colony. Gösswald & Kloft (1956) found out that the larger workers of *Formica rufopratensis* (Forel) usually received a bigger share of the sugar solution than the smaller workers. Similarly, in *Formica polyctena* (Foerster) the foragers are usually the first to receive the honey and in a larger proportion than the larvae (Schneider, 1972; Länge, 1967). According to Wilson & Eisner (1957), little food exchange happens in *Pogonomyrmex badius* (Latreille) colonies compared to the rapid sharing within the colonies of the two *Formica spp.* (Eisner & Wilson, 1958). Proteins as mentioned earlier are taken more by the brood and queens compared to the workers whereas lipids are not just spread among the workers but also given to the larvae as an energy reservoir. Food exchange which involves larvae appears to be more complex due to the different food forms and colony needs that have to be taken into account. The function of the larvae is not just limited to the digestion of solid foods but goes way beyond that. Larvae play an important role in regulating the distribution of food within the colony (Børgesen, 1989). Børgesen (2000) even stated that the fecundity of *Monomorium pharaonis* (Linnaeus) was dependent on the transfer of food between the larvae and the queen. This may be due to larval secretions that contain high concentrations of amino acids and proteins (Maschwitz, 1966) which are crucial for brood development. The fat bodies in larvae and workers act as food storage (Lim et al., 2005). In temperate countries, some ants will ensure the continuous supply of food to the colony by storing large amounts of lipids in their bodies by the time the winter season comes (Ricks & Vinson, 1972; Rosengren, 1971). Ant larvae contain large amounts of lipids and proteins, small portions of inedible cuticular structures and can withstand longer starvation periods, thus making them ideal food storage devices (Jander, 1963; Lim et al., 2005). In some species of ants, the workers lay eggs which are not viable, called trophic eggs. These eggs serve primarily as a protein rich food source (Wilson, 1963b; Abbott, 1978) and are fed to the queens and larvae (Freeland, 1958; Markin, 1970).

The feeding behaviour of ants is influenced by many factors. Intrinsic factors include the caste composition, feeding history, satiation, colony age, presence and stages of brood. On the other hand, extrinsic factors include: different food forms, food quality, food abundance and weather (Stein et al., 1990). For example, in temperate countries, in order to ensure optimum development of their brood, ants will usually forage for more proteinaceous food during spring and summer. Foraging at a higher rate for lipids and proteins happens when the colony is in a reproductive stage (Stradling, 1978). Brood cannibalization has been recorded many times in the laboratory when colonies were under stress (Markin, 1970; Wilson, 1971), the larvae/worker ratio was too high or when foraging became too dangerous (Nonacs, 1991). However, even under conditions where food is available *ad libitum*, larvae may still be cannibalized in some ant species (Sorensen et al., 1983; Hunt, 1988 as cited by Nonacs, 1991). Amount and size of the broods that are present may reflect the current availability of nutrients and their perceived future availability (Nonacs, 1991). It is believed that colonies that have access to more protein tend to produce workers of higher quality and with an intrinsically longer life-span (Calabi & Porter, 1989 as cited by Nonacs, 1991). Ants show extremes of dietary specialisation and generalisation. They still tend to forage for foods with a higher protein and carbohydrate content even when the diet is rich or comprehensive (Stradling, 1978) in order to maximize the net rate of energy delivery to the nest (Davidson, 1978). Alternation of food is crucial to ensure the colony receives a more balanced diet (Edwards & Abraham, 1990) and also to avoid satiation (Lee & Tan, 2004). Most species of ants prefer liquid food (Howard & Tschinkel, 1981). For example, the foragers of *Formica rufa* (Linnaeus) carried back 81% of their food in liquid form compared to only 19% of the food intake that was in solid form (Stradling, 1978).

2.4 Foraging behaviour

The proportion of foragers in a colony varies greatly between species (Mackay, 1985; Porter & Jorgenson, 1981 as cited by Traniello, 1989). However, according to Petal (1978), only around 10-20% of the workers are allocated for foraging. These foragers are usually the older and more experience workers in the colony (Mirinda & Vinson, 1981). Age alone cannot be the only factor that is used to determine the foraging status of a worker but the stimuli and information on the nutritional level and needs of the nest and the status of other colony members are also taken into account (Traniello, 1989).

Basically ants forage for food as individuals or as a group. Individual foragers are usually seen in species which practice a well coordinated mass recruitment, for example, *Solenopsis saevissima* (Smith) and these ants will lay chemical trails behind while searching for food (Wilson, 1962b). This trail system is very important to help the foragers return to a permanent resource (Hölldobler, 1976a) or avoid repeated searching within the same area (Carroll & Janzen, 1973) and also to prevent them from entering into the territory of other colonies (Ryti & Case, 1986; Hölldobler, 1976a). Only a small portion of ant species which come mainly from subfamilies of Ecitoninae, Dorylinae and Ponerinae are considered as group foragers

(Carroll & Janzen, 1973). These ants will form an aggressive foraging group and raid over certain areas.

When foragers encounter a food source, the ants will gather or transfer back the food to their nest in different ways depending on the form of the food. If it is in liquid form, the ants will ingest and bring it back in their crop. As for small particles or fragments of food, workers may consume them directly at the site and digest them so that nutrients can be carried in the crop. However if the food items are too large or heavy for one or two workers to carry them back to the nest, the foragers will lay some short-lived pheromone trails in order to call for group or even mass recruiting (Sudd, 1967; Wilson, 1971). Mass recruitment means that the workers will gradually arrive at the food until the numbers saturate at a certain level. The number of workers that are being recruited will increase if the trail signal gets "stronger" which is also determined by the quality and the abundance of the food (Wilson, 1963a). This strategy is commonly used by large colonies with many small workers (*Paratrechina, Monomorium, Pheidole, Solenopsis* and *Crematogaster spp.*etc). There are a few benefits and biological circumstances which encourage the colony response for mass recruitment. Due to the huge number of workers available in a colony, deploying the mass recruitment method would not deplete the nest population. Besides that, with a large number of workers attending to the food, it will warn off other competitors and help protect the resource (Carroll & Janzen, 1973). An odour trail laid by one worker is weak and would not be effective enough to communicate over a distance and so multiple workers are required to produce a longer and with stronger signal trail (Wilson, 1963a). As for the group recruiting strategy, it is widely used by species with large colonies but with a proportionally smaller number of larger sized workers such as in *Camponotus* and *Pogonomyrmex spp.* In thes species, a group of foragers will arrive at the food items but there tend to be few or no other workers that follow the initial recruitment at later times. Hölldobler (1971) who analysed this strategy in *Camponotus socius* (Roger) pointed out that when a worker finds a large food source, it will return back and lay a trail. After that, other workers will follow the old trail back to the food and again lay some additional markers (formic acid from the sting gland and also some hind gut material) for other ants to follow. He observed that only around 30 workers arrived at the food and this may be due to the fast evaporation of the chemical trail. The larger castes are also more likely to be involved in transportation as well as prey dissection. There is another type of recruitment called "tandem running". According to Wilson (1959), a pair of workers involved in carrying back a food item which is only slightly difficult to handle by one worker. This behaviour is usually seen in *Camponotus* and *Cardiocondyla spp.* (Sudd, 1967; Wilson, 1959).

The foraging behaviour of ants is greatly influenced by circadian rhythms and every species has their very own daily foraging schedule (Hölldobler & Wilson, 1990). McClusky and Soong (1979) successfully recorded the foraging activity of some species in southern California. *Pogonomyrmex californicus* (Buckley) and *P. rugosus* usually forage actively from early midday until afternoon while *Messor andrei* (Mayr) and *Messor pergandei* (Mayr), will slow down towards midday before becoming active again during the late afternoon and through dusk. However, sometimes the rhythms can be affected by environmental factors such as temperature and humidity (Traniello, 1989). In order to adapt to changes in the physical environment and to promote thermoregulation, desert ants will change their foraging pattern from nocturnal in summer to diurnal in winter. This is a very common phenomenon and has been widely reported in different species of *Atta* (Mintzer, 1979b), *Pheidole* (Hölldobler & Möglich, 1980) and *Pogonomyrmex* (Hölldobler, 1976a). Risk factors such as predators and competitors will also influence the foraging decision by the workers to some extent. There have been some reports that *Pogonomyrmex spp.* will change their foraging patterns and directions if they encounter competitors from nearby colonies (Hölldobler, 1976a). A similar avoidance has been noted between *Lasius pallitarsus* (Provancher) and *Formica subnuda* (Emery) workers. Foragers of *L. pallitarsus* will stay away from *F. submuda* and forage in a safer site even though the resources available there are of lower quality (Nonacs & Dill, 1988 as quoted in Traniello, 1989).

There has always been a debate between maximizing energy and minimizing time which is crucial when it comes to decision making in foraging. Oster and Wilson (1978) stated that if the production of new queens is directly related to the amount of energy (or nutrition) harvested, ant colonies will try to increase the net energy return to the nest. By increasing the distance between the seed patches and the nest, the foragers of *P. rugosus* and *P. barbatus*, foragers will show more specialization in their diet (Davidson, 1978). Moreover, some observations made on tropical leaf-cutting ants also found that around 70% of colonies choose to cut plants which are closer to their nest but will choose higher quality tree species if the distance from nest increases. In *Solenopsis geminata* (Fabricius) more workers were recruited to higher concentration of sucrose patches which were also nearer to the nest (Taylor, 1977). The foraging procedures of ants tend to follow models of energy maximization more than time minimization.

2.5 Aggressive behaviour

Ants communicate in various ways, from simple tactile stimuli such as antennation, grasping, stroking, stridulation and nudging to a more complex system which involves numerous semiochemical substances. All of these modes of communications among the colony members enable the coordination out of the diverse tasks such as foraging, recruitment, trophallaxis, grooming, mating, raising of alarm when threatened and also kin recognition. Chemical signals or pheromones are believed to be the dominant cue behind the behaviour of ants (Hölldobler & Wilson, 1990).

Kin recognition is very important in eusocial insects to maintain the integrity of the societies. Ants basically distinguish between nestmates and intruders by using different chemical cues based on four main strategies which are spatial distribution, allelic recognition, recognition through association and phenotype matching (Hölldobler & Wilson, 1990). If the ants detect any alien workers or species within their territory, alarm substances will be emitted to warn off or to recruit other colony members to defend the nest. According to Howse (1983), pheromones consist of multiple components and are multifunctional and different species have different behavioural threshold responses to different quantities of a given secretion. For example, *Pogonomyrmex badius* (Latreille) will exhibit circular running alarm behaviour and aggressive posturing when exposed to higher concentrations of pheromones. When exposed for longer periods, it will stimulate directional digging by the workers.

There are several major exocrine glands involved in alarm communication which serve to alert, attract and even evoke aggression. However, different glands secrete different pheromones depending on circumstances and the caste (Howse, 1983). For example, the Dufour's gland is usually involved in alarm, recruitment and sexual attraction. As for the pygidial gland, in Nothomyrmeciinae, Aneuretinae, Dolichoderinae and Myrmicinae, it appears to produce alarm and defensive substances. However, in the Ponerinae, it was reported to function as stimuli in recruitment or sexual attraction (Jenssen et al., 1979; Hölldobler & Engel, 1978). In contrast, the primary function of the poison gland is to produce formic acid (in the Formicinae) or venom (in the Ponerinae, Dorylinae etc.) which is used for defence or killing prey (Hölldobler & Wilson, 1990).

Ants employ a wide range of defensive behaviours and methods of attack for protecting their territory and food sources. Their weapons for attack include big mandibles, stings with venom, repellents and poisonous secretions. Sabre-shaped or hatchet-shaped mandibles are effective weapons used by slave-making ants (*Harpagoxenus, Polyergus* and *Strongylognathus*) to cut through enemy bodies (Buschinger, 1986). By comparison, some members of the subfamily Myrmicinae, for example, *S. geminata*, usually paralyse their prey using a sting (Brian, 1983). In some species, ants will spray or emit toxic substances into the air or wipe them onto the enemy's body to repel any intruders (Blum & Hermann, 1978a,b; Buschinger & Maschwitz, 1984). Ants from the subfamily of Formicinae are not equipped with any stings and they often bite or spray poisonous secretion towards alien species when under threat. For example, *Paratrechina longicornis* (Latreille) will twist its gaster forward to spray formic acid towards its opponents. Other defensive techniques include closing the nest when being under attack such as in *Myrmecocystus sp.* (Hölldobler, 1981). Other species (*Pheidole, Pogonomyrmex, Formica, Solenopsis* etc.) will execute rapid and organised evacuation when escaping from enemy raids or from floods (Hölldobler, 1976a; Buschinger & Maschwitz, 1984; Wilson, 1986).

The territories of ants can be divided into two types: absolute and spatiotemporal. Ants will control and defend a certain area, i.e. the absolute territory, at any given time regardless of the availability of food resources or nests. In the case of spatiotemporal territories, ants will only defend an area for the duration that resources are available (Hölldobler & Wilson, 1990). Competition between colonies to establish territories and territorial defence will usually result in casualties due to the overtly aggressive behaviour shown during warfare. The aggression of workers patrolling territories or the foraging area is not just species specific, but also depends on factors such as season, colony status and needs. *Formica spp.* workers were reported to be more aggressive towards intruders in early spring because of the development of brood which increases the colonies protein demands (Brian, 1955; Elton, 1933). However, less aggression towards other colonies was observed during summer and any aggression involved more of a ritualized combat (De Bruyn & Mabelis, 1972). When the food resources are rich, colonies may get bigger and their foraging area becomes comparatively smaller. All of these factors may lead to more frequent overlapping of territories. Under such conditions, ants will be more aggressive during territorial defence and competition among species may increase or even result in displacements (Carroll & Janzen, 1973).

Dominant species are usually characterized by large aggressive colonies that can gain absolute control of a territory. When competition occurs among ant colonies, the dominant species will stand out from the crowd. An example would be *Lasius neoniger* (Emery) getting displaced by large numbers of more dominant imported fire ants. The results of conflict will usually lead to colony destruction and the brood being consumed (Bhatkar et al., 1972). In a local community, dominant species are the core species. Other ants have to comply or adapt to the daily rhythms of the dominant species; their foraging times and space they occupy in order to survive. Such was the case studied by Greenslade (1979) in South Australia. He pointed out that *Iridomyrmex spp.* is very competitive and dominant in that area. Ants like *Melophorus sp.* and *Camponotus sp.* will usually only forage at times when *Iridomyrmex spp.* are inactive. They even nest far from the *Iridomyrmex* colony. Changing dominance between species may also occur through time. However, changes from one species to another will also involve alterations of the ant community which is associated with that dominant species. Such phenomenon has been observed at a site in Australia where within two years, the community shifted from three dominant species of *Iridomyrmex spp.* to only two of those species (*Iridomyrmex spp.*) and *Tapinoma minutum* (Mayr). Almost all of the dolichoderines had been replaced and the overall ant diversity was affected (Fox & Fox, 1982).

Interference among colonies of the same species also plays an important role in the coexistence of different species within an area or community. It is because such interference will help to regulate and control the population size (Hölldobler & Wilson, 1990). Pontin (1961) had reported that the newly mated queens of *Lasius spp.* if placed too near to the mature colonies were attacked and eventually killed by workers which belong to same species. Besides that, niche differentiation will also increase the chances of competing species coexisting (Klotz, 1984). This includes having a flexible foraging time when in the presence of other species. For example, *Tetramorium aculeatum* (Mayr) have been observed changing their foraging schedule from diurnal to nocturnal when more aggressive species such as *Oecophylla longinoda* (Latreille) occurred (Majer, 1976).

2.6 General biology and behaviour of *Paratrechina longicornis*

Paratrechina longicornis (Figure 2.1) is a member of the subfamily Formicinae. The common name for this species is crazy ant (Smith, 1965) due to the rapid and erratic movements displayed when they are disturbed. Other common names include long-horned ant and hairy ant (Naumann, 1993). In addition, it was also known as “black crazy ants” (Wetterer, 2008). The workers are monomorphic and relatively small (2.3-3.0mm). They have extremely long legs and long 12 segmented antennae without a club. The length of the antennae is at least 1.5 times as long as head including closed mandibles. Each mandible has five teeth. The ants are dark brown to black in colour and the body often has a faint bluish iridescence (Creighton, 1950). This species does not have a sting but it does bite and spray formic acid from their acidopores to paralyse or kill prey.

P. longicornis is believed to have originated from Africa (Wilson & Taylor, 1967) and Asia (Smith, 1965) and has been introduced to many other regions across the world with about 181 areas have been reported for the occurrence of this species (Wetterer, 2008). However, based with the distribution of its closely related species to, Wetterer (2008) suggested that *P. longicornis* was native to Melanesia and Southeast Asia. The crazy ant may have become one of the most widely distributed

Figure 2.1 Worker ant of *Paratrechina longicornis*.

tramp ant species in the world due to their high adaptability to a wide range of environments (Wetterer, 2008). This species can nest in diverse locations from dry to moist sites such as in trash, refuse, cracks and crevices, cavities in plants or trees, under the rocks or objects and even rotten wood (Smith, 1965). In areas with cooler climates, these ants are found in glass houses and centrally heated buildings (Naumann, 1994).

The workers are opportunistic omnivores and feed on almost everything, from insects, honeydew and fruits to many of our daily household foods such as meat, sweets, liquids, and grease. Crazy ants obtain honeydew by tending mealy bugs, aphids and soft scale insects (Smith, 1965). These ants prefer protein diets during summer and refuse to feed on honey or sugar baits (Trager, 1984). They can forage up to 25 m from the nest (Jaffe, 1993). They are usually the first to arrive at a newly developed area and also quick to discover food (Lee, 2002) but are often displaced by other more dominant ants (Bank & Williams, 1989).

In a single colony, there can be up to 2000 workers with multiple queens (polygyne) (Passera, 1994). In the tropics and subtropics, reproductives can be produced continuously throughout the year but not in cooler climates. A colony may change its nest location, especially after disturbance (Trager, 1984). According to Lim et al. (2003), this species will exhibit strong aggression towards individuals from distant sites but not individuals from colonies that come from same location. Findings have also shown that the colony signature is obtained through the diet and it is this factor which influences the intra-specific aggression and not the queens.

P. longicornis has become a major pest ant in urban areas (Lee, 2002). In United States, these ants have become pest and often been found in apartment buildings in New York, flats and hotels in Boston and hotel kitchens in San Francisco (Nickerson & Barbara, 2000). In Brazil, they are known as mechanical vectors which transport pathogenic bacteria in hospitals (Fowler et al., 1993).

In Penang, Lee (2002) reported that crazy ant was one of the most common ants being sampled in buildings and often first to arrive in newly developed structures. This species can occur abundantly both indoors and outdoors which make them a great nuisance. Crazy ants also create problems in agriculture as they tend to protect and distribute hemipteran pests such as aphids, mealy bugs and scale insects which plague the industry (Wetterer, 2008). There were reports about the difficulties in controlling this ant as they show limited response to the current commercially available baits (Hedges, 1996a, b; Lee, 2002) and they can forage far from the nest, a feature that adds to the difficulty in managing this pest (Nickerson & Barbara, 2000). Therefore, more efforts and research on crazy ants has to be carried out especially on their foraging ecology and feeding behaviour in order to establish effective management methods.

2.7 Management of ants

Invasive species such as *P. longicornis*, *Linepithema humile* (Mayr), *S. invicta*, *M. pharaonis* and *Tapinoma melanocephalum* (Fabricius) have spread around the world due to advancements in logistics and transportation systems. Besides that, they are highly adaptable to the urban and suburban areas (Passera 1994; McGlynn, 1999). Tramp ants are usually a nuisance and may also affect human health (Hölldobler & Wilson, 1990; Lee, 2002). In the USA, ants are considered one of the most important pests by the pest control industry. Estimates show that around 1.7 billion dollars is spent annually for their control (Curl, 2005).

Achieving colony eradication is the main objective of ant management programmes but it is hard to accomplish such a task (Hedges, 1998). The most ideal method is direct treatment or direct removal of the nest. However, it is hard to locate the source of the infestation as the nest may be located far away from the foraging area or have multiple entrances. Moreover, only about 5% to 10% of the entire ant population are visible foragers (Haack & Granovsky, 1990; Adams et al., 1999). Methods that are commonly used to control ants are residual insecticide treatment and baiting (Lee, 2003). Besides that, combinations of both methods have also been reported (Vail & Bailey, 2002). Residual insecticide treatments for ant control, especially repellent insecticides, are ineffective because they only kill the foraging workers but not the reproductive members (Lee & Chong, 2003). However, repellent insecticides are crucial as perimeter treatment to create a protective barrier surrounding the structure (Vega & Rust, 2001; Rust et al., 2003). At the same time, they can also prevent ants from escaping within the structure and result in extra treatments (Rust et al., 1996; Gulmahamad, 1997). Use of repellent products may promote budding (sociotomy) of ant colonies which would create a larger area of infestation and would make control efforts even more difficult (Loke, 2005). Under such circumstances, non-repellent insecticides such as fipronil, chlorfenapyr and imidacloprid can provide effective perimeter treatment against ants.

Baiting as a control method is getting more popular. It is more effective in managing many urban pest ant species (Knight & Rust, 1991; Lee, 2000; Lee, 2007).