Termite raiding by the Ponerine ant *Pachycondyla analis* (Hymenoptera: Formicidae): Behavioural and Chemical Ecology

by

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Submitted in partial fulfilment of the requirements for the degree

*Philosophiae Doctor* (Entomology)

In the Faculty of Natural and Agricultural Science

University of Pretoria

Pretoria

May, 2010
Declaration

I, Abdullahi Ahmed Yusuf declare that the thesis, which I hereby submit for the degree Philosophiæ Doctor Entomology at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signature:………………………………………..

Date:………………………………………………. 
To my parents Alhaji Ahmed Rufa’i Yusufu, Hajiya Hadiza Laraba Ahmed and my lovely wife Fatima Isa Abdullahi, for the immeasurable love, care and affection. And to my daughter Khadijatul-Kubra who was born in my absence.

“Until when they came to the valley of the ants, a she ant exclaimed, “O ants, enter your houses may not Solomon and his armies crush you, unknowingly”. He therefore smiled beamingly at her speech*, and submitted, “My Lord, bestow me guidance so that I thank you for the favour which You bestowed upon me and my parents, and so that I may perform the good deeds which please You, and by Your mercy include me among Your bondmen who are worthy of Your proximity.”***(Prophet Solomon heard the voice of the she ant from far away)

[Qur’an, Chapter 27 (Al-Naml-The ant):18-19]
Acknowledgements

To my supervisors Prof. Robin Michael Crewe and Dr Christian W. W. Pirk, I express my great appreciation for the time, effort, support, patience and guidance throughout this study, for you kept your doors wide open for me. I really appreciated your knowledge and expertise in the topic and for sharing your vast experiences in the world of social insects.

My sincere appreciation goes to my supervisory team at icipe. First to Dr Ian Gordon, for it was your idea to look at the chemical ecology of P. analis, thanks for being accommodating and willing to help even at odd times. To Dr Baldwyn Torto who hosted me in his laboratory and, provided all pieces of the equipment used in this study. Indeed, you inspired me to look at insects first from the behavioural perspective, before going into the chemistry, with this approach Insect Chemical ecology became more appealing to me. You also inspired me to always think outside the box. Dr Peter Njagi, thank you for your guidance and the precious time you spent towards this project. Prof. Ahmed Hassanali, you were involved in the project at its formative stage prior to your retirement, thanks for all the knowledge you shared.

- Dr Kerstin Kruger for being the link between icipe and the University of Pretoria, and for making sure that I felt at home whenever in Pretoria.
- To Dr Ado Baba Ahmed, an extra ordinary entomologist and my former Head at Kaduna State University, for you inspired and encouraged me to take entomology this far. To Prof. A. U. Ezealor, Prof. J. Auta and Dr A. K. Adamu, all of Biological Sciences Department, ABU, Zaria. I say thanks for the support you gave me.
- Mpala Research Centre (MRC), Nanyuki Kenya, for they allowed me to use their rich ecosystem for both fieldwork and for ant collections. Raphael Erangae assisted me during the intense fieldwork and during nests location and excavation. Marcus Stüben helped with confirming the identity of P. analis, thanks for sharing your knowledge on the biology of P. analis.
- Technical help received from Mr B. O. Wanyama and Edwin Rono and all members of the Behavioural and Chemical Ecology Department (BCED), icipe is highly appreciated. Big thanks to Mr Peter Malusi of the ARCU unit icipe for looking after the ant colonies in my absence.
The German Academic Exchange Programme (DAAD) is acknowledged for providing me with the PhD fellowship through icipe, Dutch SII for funding the research at icipe, and the University of Pretoria for an International student bursary. I also express my appreciation to icipe for admitting me into its African Regional Postgraduate Programme in Insect Sciences (ARPPIS). Thanks to the CBID staff most especially, Lilian Igweta and Margaret Ochanda for being there always to help with administrative matters. Sincere appreciation goes to the library staff at icipe, most especially Eddah Wasike for her willingness to assist always.

To my ARPPIS colleagues: Drs Duna Mailafiya, Bruce Anani, David Mburu, Sabina Wachira, Benjamin Muli, Paulin Nana, Naina, Victor, Ayuka Fombong, Ernest Appiah, Tanga Mbi and Saliou Niassy, thanks for the encouraging and fruitful discussions, and for the wonderful time we spent together in the student room.

To ARPPIS class of 2006: Robert Musundire, Fikira Kimbokota, Lorna Migiro and Nigat Bekele, we rowed the boat together and we sailed through all together. Thanks for the moments we shared as one big family.

Thanks to Dr Samira Mohamed and Dr Fathiya Khamisi for becoming our second family while in Nairobi. For you were so kind to me and Fatima.

To my parents for the good upbringing, and members of my immediate family, most especially my elder brothers Abdullahi Yusuf Makarfi and Alh. Bala Umar for their immeasurable moral support.

To my better half, lovely wife and best friend Fatima Isa Abdullahi, I say thanks a million times for your patience and understanding, for I left you behind in those difficult moments when you needed my presence.

To Hajiya Hasiya Abdullahi Yusuf, I say a big thank you, for the visit you paid to us in Nairobi meant a lot.

To all friends and well wishers most especially Adamu Ibrahim (Alhazai), Engr. Ja’far Ishaq Jumare, Abdullahi S. Fada, Umar Yusuf Gidado, Mal. Bello Alkaleri, Yusuf Datti and all who kept in touch while I was away, I say a big thank you. To all those whose names I can not list due to space limitation I say NAGODE KWARAI.

Alhamdulillahi, Allahumma salli ala Muhammad (SAW) wa sahabih wa ahli baithi adayyibuna dahirun wa az-wajihi Ummahatul mumineen.
This thesis is based partly on the following publications:

Note: Chapters 1 to 4 were written as separate publications and submitted to appropriate international journals, consequently there is some overlap of information and references in the thesis.


Termite raiding by the Ponerine ant *Pachycondyla analis* (Latreille)  
(Hymenoptera: Formicidae): Behavioural and chemical Ecology

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**Abstract**

The ant *Pachycondyla analis* (formerly *Megaponera foetens*, commonly known as the Matabele ant) is a widespread ponerine in sub-Saharan Africa. It feeds solely on termites of economic importance belonging to the sub-family Macrotermitinae. These termites are captured during organised raids on their nests and galleries. Previous studies mostly concentrated on certain aspects of the raiding behaviour and trail laying pheromones in this species. Thus the detailed raiding behaviour and chemically-mediated communication between *P. analis* and its prey are virtually unknown. The aim of this study was to undertake detailed behavioural studies on termite raiding behaviour of *P. analis*, and to investigate whether *P. analis* uses olfactory cues for intra-specific communication during termite raids, and for detecting its prey.

Termite raiding behaviour of *P. analis* was monitored at Mpala, a Kenyan savannah for six months (April to September, 2007). During this period, raids were found to occur mainly in the mornings and evenings, with late night raids occurring during dry periods. *P. analis* at Mpala mainly nests under rocks and in deserted termite mounds. *Microtermes* and *Odontotermes* were the main preyed termite genera, and ant raiding behaviour was synchronised with termite prey behaviour, and was influenced by foraging costs, prey defences and rewards.

Olfactometric assays showed that *P. analis* workers used olfactory cues in their intra-specific chemical communication, with workers responding more to volatiles of
individuals of the same size class (major to major and minor to minor) than between groups. Major workers discriminated more between the volatiles of the two groups than minor workers. GC-MS analysis of volatiles from major and minor workers revealed a cocktail of 48 compounds, majority of which were hydrocarbons. Volatile compounds were colony specific and quantitative analysis showed that major and minor workers alone released 2.5 fold more volatiles than the mixed stages. This suggests that ants have the innate ability to regulate the levels of the colony odour which they make up for with higher release levels when separated from each other.

Using a Mandible Opening Response (MOR) bioassay, ants were able to distinguish between nestmates and non-nestmates based on cuticular hydrocarbon (CHC) profiles. This suggests that *P. analis* uses CHCs as short range contact recognition cues within the nest in traditional nest protection and during raids on termite species. GC-MS analyses revealed hydrocarbons of chain lengths in the range C₈-C₃₁ in the CHC profiles, comprising mainly alkanes, alkenes and methyl-branched alkanes. The CHCs were colony and individual worker specific. Nestmate recognition in *P. analis* may be encoded in the alkenes and methyl-branched alkanes.

Dual choice olfactometric assays revealed that *P. analis* uses olfactory cues in locating potential termite sources with an average of 65% of workers choosing odours against the blank (clean air). When termite odours were offered to both major and minor workers, their choices were biased towards the termite odours, with minor workers attracted more to the odours than were major workers. Although ants responded to odours from the soil obtained for the termite gallery, overall, odours from termites inside their galleries were the most attractive to ants. These results suggest that the combined odours from both the termites and gallery components (in particular soil), serves as an effective nest location cue for the ants. Comparative GC-MS analyses showed that the composition of the volatiles from the gallery soil was richer than that released by the termites. Consistent with previous studies, the volatiles of the gallery soil were found to contain hydrocarbons, naphthalene and derivatives of this compound.

In conclusion, these studies have revealed the rich diversity of chemical communication cues used by this ant species for nestmate recognition and for prey location during raids in search for its food source.
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GENERAL INTRODUCTION

Ants and termites in the terrestrial ecosystem

Ants are cosmopolitan in their distribution, but only occasionally noticed. As active participants in most of the terrestrial habitats in the world acting as premier soil turners, and channelers of energy, they are the most dominant among the insect fauna (Hölldobler and Wilson, 1990). In the Ivory Coast savannah, the density of ants is reported to be 7,000 colonies and 20 million individuals per hectare (Lévieux, 1982). Room (1971) recorded 48 genera and 128 species from 250 square metres in a cocoa farm in Ghana. Ants and termites are in the proportion of 8 million ants to 1 million termites in the Amazonian terra firme rain forest (Fittkau and Klinge, 1973). Their impact on the terrestrial environment is great as they are among the leading predators of other insects and small invertebrates (Wilson, 1971; Longhurst et al., 1978; Longhurst and Howse, 1979; Lepage, 1981; Lévieux, 1982; Hölldobler et al., 1994. and Dejean et al., 1999).

Termites are members of the order Isoptera which share almost the same habitats as ants with dual roles in the ecosystem. On the one hand they are nutrient channelers in terrestrial ecosystems and on the other; they constitute the most important of the wood-destroying insects and are responsible for heavy economic losses (Janssen, 2006). Out of more than 2900 species of termites in the world, only a small minority have negative economic effects (Culliney and Grace, 2000) since only 70 - 80 different species cause significant damage to structures (Edwards and Mill, 1986).

The biology of termites, economic importance and pest management strategies

Termites (or white ants') are medium-sized, cellulose-eating social insects that always live in communities with large numbers of individuals reaching several millions in some species (Hickin, 1971). They are placed in the order Isoptera of the class Insecta (Borror et al., 1992; Pearce et al., 1996). Recently DNA analysis has shown that members of the termite family (Isoptera) are closely related to cockroaches (Eggelton, 2001; Inward et al., 2007). Of the known termite species in the world, over 40% have at least one representative species in Africa (Borror et al., 1992; Pearce et al., 1996).
Termites are exceedingly abundant throughout the tropical and sub-tropical regions of
the world, and in some areas extend into the temperate regions (Hickin, 1971; Grace et
al., 1996; Carr, 2006). Nest densities of termites in the tropics range from 3.8 nest ha\(^{-1}\)
in Kenya (Lepage, 1981) to 2.2 - 37.5 nest ha\(^{-1}\) in Ivory Coast (Lévieux, 1982 and
Lepage, 1984).

Termites mostly live in moist subterranean and dry habitats above ground, and some
species usually construct earthen tubes between the soil and wood above ground. These
tubes are made of soil mixed with a secretion from a pore on the front of the head. In
tropical species these nests (termitaria) may reach up to 9 metre in height (Borror et al.,

The food of termites is composed of cellulosic vegetable materials, but they also feed on
the cast skins and faeces of other individuals. During their efforts to find cellulose, they
also cause extensive damage to a host of other materials. Dry wood termites mostly live
only in wood and are able to digest woody materials with the aid of colonies of
Protozoa, which secrete cellulase, an enzyme that breaks down cellulose into simpler
materials capable of being digested (Borror et al., 1992). Subterranean termites
(Macrotermes species) gather cellulosic material, chew it up and then allow it to be
partially digested by fungi before they consume it (Hickin, 1971).

Economic importance of termites

Economically, termites are seen from two broad perspectives. On the one hand, they are
beneficial because they assist in nutrient re-cycling. While on the other hand, they cause
huge economic losses worldwide as they forage for cellulose. Termites feed upon and
often destroy various wooden portions of buildings, furniture, books, utility poles, fence
posts, many fabrics and over 48 species of plants (Figure 1) (Hickin, 1971; Culliney and
Grace, 2000). Termites are said to cause damage worldwide amounting to 40 billion
USD (Janssen, 2006). An annual estimate of damage to wood and wood products
caused by termites in the United States exceeds $750 million, 95% of this is attributed
to subterranean termites (Family Rhinotermitidae) (Mauldin, 1986; Culliney and Grace,
2000). Moreover subterranean termites account for 80% of the approximately US$ 2-3
billion spent annually for termite control in the USA alone (Su, 1993 and Carr, 2006).
In Africa, the reputation of termites as pests is coupled with the presence of large mounds in agricultural fields and in forests. The greatest pest potential is mainly within the subfamily Macrotermitinae, which has a symbiotic association with termitomyces fungus. *Macrotermes*, *Odontotermes*, *Pseudacanthotermes*, *Ancistrotermes*, *Allodontotermes*, *Amitermes*, *Trinervitermes*, *Hodotermes* and *Microtermes* (Mitchell, 2002) are the genera of economic importance. Reported damage by *Microtermes subhyalinus* (Silvestri) in a savannah in the Central African Republic was between 5-15% of annual sugarcane production (Mora et al. 1996), 18% in Sudan and 28% in planted sugarcane seedlings in Nigeria (UNEP/FAO, 2000). In Kenya, foraging activities by termites are responsible for the destruction of 800-1500 kg ha⁻¹ of pasture annually (Lepage, 1981). While about 18 genera of termites are known to attack crops in Southern Africa with estimated losses of between 3-100% of annual yield with 90% of tree mortality in the forests (Mitchell, 2002). Traditionally built houses and granaries can be destroyed by termite infestation within 3-9 years if care is not taken (Pearce et al., 1996).

![Termite damage in (a) wood, (b) maize and (c) palm tree.](https://www.termite-i.com)

**Figure 1.** Termite damage in (a) wood, (b) maize and (c) palm tree.

**Termite pests Management strategies**

Termite control measures include: cultural, physical, chemical (conventional termiticides), biological control methods and the possible use of semiochemicals (Hickin, 1971; Culliney and Grace, 2000; Carr, 2006). These, are tailored towards protecting growing crops, both annual and perennial, including tree plantations and structures that are made of vulnerable cellulosic and non cellulosic materials.
The cultural control practices frequently involve variations of standard horticultural practices centred on modifying the relationships between a pest population and its natural environment (Meyer, 2006). These methods are commonly referred to as ecological control methods, and include processes like crop rotation, intercropping, and managed application of water or fertilizer, use of ash and proper sanitation (UNEP/FAO, 2000).

Distinct from that are the physical termite management strategies were commonly practiced in the 1930's and 1940's. These included, stirring up dust to suffocate the termites, use of physical barriers during building pre-construction phase. Some of the most commonly used barriers are stainless-steel wire mesh (TermiMesh ®).

Conventional termiticides comes in different formulations and packaging, some are in granular form (granules), dusts, soluble powders or wettable powders, emulsifiers, aerosols or Ultra low-Volume Concentrates (ULV) containing about eight different compounds in one formulation. Termiticides are used in soil treatment by creating a chemical barrier between termites and the soil (Jones, 2006). Some termiticides in use include bifenthrin (Talsar®), cypemethrin (Demon ®), and permethrin (Dragnet ®) (Jones, 2006).

Biological control of termites constitutes an environmentally acceptable alternative to traditional chemical control measures. When successfully implemented, it can yield permanent, cost-effective (even zero-cost) management of pest populations with minimal environmental disturbance.

Termites have a wide variety of predators, both opportunistic and specialist, ranging from invertebrates to vertebrates (New, 1991; Culliney and Grace, 2000). Ants are seen as the greatest enemies of termites in all regions of the world (Hölldobler and Wilson, 1990); because their habitats overlap (Fujiwara-Tsujii et al., 2006). A large percentage of ant species from the largest genera, *Pheidole* spp and *Componotus* spp, prey opportunistically on termites (Hölldobler and Wilson, 1990). Termite specialist ants are mostly in the subfamilies Ponerinae and Myrmicinae (Lévieux, 1966; Maschwitz and Mühlenberg, 1975; Longhurst et al., 1978; Longhurst et al., 1979; Maschwitz and Schönegge, 1983; Lepage, 1984; Corbara and Dejean, 2000).
Pachycondyla analis an ant noted for its organised raids on termites preyed upon most members of the Macrotermitinae (Longhurst et al., 1978; Lepage, 1981; Bayliss and Fielding, 2000). P. analis may make repeated raids on a termite colony until the colony is destroyed (Sheppe, 1970). Recently, studies by Cornelius et al., (1995); and Cornelius and Grace (2000), have explored the potential of semiochemicals from ants in repelling termites

The Biology of *Pachycondyla analis*

Pachycondyla analis (Latreille, 1802) is a Hymenopteran in the suborder Apocrita, superfamily Vespoidea, Family Formicidae, Sub-family Ponerinae, and Tribe Ponerini (ITIS, 2007).

P. analis nests underground, often beneath rocks, in deserted termite hills, or under trees. These nests often extend up to 0.7 m below the surface. Each colony uses a single nest where, eggs and larvae are kept together with the queen in one chamber, while the cocoons are often placed in the sun outside the nest entrance (Lepage, 1981; Villet, 1990). Colonies of P. analis consist of between 442-1400 members with a polymorphic worker caste (Longhurst and Howse, 1979; Lepage, 1981). Workers have been regarded as dimorphic by taxonomists, but measurements of head width versus head length indicated that rather than being dimorphic, this species exhibit monophasic allometry (Crewe et al., 1984). These termitophagous ponerine ants are widely distributed in Africa (Sheppe, 1970; Longhurst et al., 1978; Lepage, 1984; Bayliss and Fielding 2002, and Taylor, 2006). The size of workers varies between 5-18 mm (Rödel and Braun, 1999), the morphology of the queen is convergent with that of the workers, and like in other social insects the biology of the males is different from the workers (Villet, 1990).

Morphological differentiation is exhibited among workers in terms of size. Larger workers (Figure 2) have a fine pubescence, which is much reduced in smaller workers with an interocular width less than 1.12 mm. Smaller workers are black and shiny. Mated workers are absent in the colonies of P. analis, with reproduction being exclusively the role of the queen (Villet, 1990).
Figure 2 Major workers of *Pachycondyla analis*

**Termite predation by *P. analis***

Livingstone (1857) was the first to describe the hunting raids of the African Ponerinae ant *P. analis*. Later a great number of entomologists became interested in the hunting behaviour of this species, which is known to feed exclusively on termites, mostly Macrotermitinae, and to forage by group predation. Sheppe (1970) reported *P. analis* as one of the frequent and specialised predators of termites. He further observed that *P. analis* organises two types of raids on termites, i.e. quick raids by hundreds of ants on underground nests or solitary raids by single ants on termites on the surface.

The organised raids as described by Longhurst et al., (1978), start with single major workers (scout ants), emerging from the nest in search for foraging termites. During the searching phase a scout ant moves slowly (ca 3.0 cm s⁻¹) (Longhurst and Howse, 1979) actively palpating the litter and any termite soil sheeting with their antennae, searching through litter and under wood. This searching phase can last for an hour and can cover an area of up to 95 metres from the nest. If the scout ant is not successful, it generally returns to the nest by a circuitous route, but its behaviour changes for the return journey if potential termite sources were found. The stimulus for the behavioural change is attributed to chemicals from termites incorporated into the soil sheeting (Longhurst and Howse, 1977). *P. analis* detects termites using kairomones of its prey, which are
believed to act as pheromones (see page 17 for details on semiochemical classes) within
the termite colony (New, 1991). After locating the prey the scout ant returns to the nest
laying a chemical trail that is used to recruit a column of worker ants to the termites
nest/gallery. On the return journey to the colony the scout ant moves more rapidly (ca.
4.5 cms\(^{-1}\)) (Longhurst and Howse, 1979) with its gaster bent downwards and the sting
partially extruded, the antennae held upwards and away from the soil surface. Return
journeys to the nest are more direct than the outward journeys (Longhurst, et al, 1978).
However, it has been suggested that if termite nests are abundant this process of
recruitment by scout ants could be absent (Lévieux, 1966).

If recruitment is successful, a column of ants, comprising of all worker caste, emerges
from the nest in about 60-300 seconds (Sheppe, 1970; Longhurst and Howse, 1979)
after the return of the scout ant, which leads them, accompanied by 5-12 other major
workers. Foraging parties follow the same route used by the scout ant on return from
scouting with each ant bending its gaster downwards.

During the raids, the ants spread out and break open the soil sheeting constructed by
termite to cover their food and dig into the termite galleries. Sister workers are
attracted to points where single ants are digging and assist them even when they are not
in direct line-of-sight with the attracted ants, suggesting non-visual cues. When the raid
has been completed, worker ants, predominantly majors, pick up a number of termites
(2-10) in their mandibles and the column of ants returns to the nest along the same trail
usually keeping close formation with a column width of 3-5 ants wide in close ranks
(Sheppe, 1970; Longhurst et al., 1978; Longhurst and Howse, 1979). When ants are
disturbed either during outward or return journeys, they make audible stridulatory
sounds. Hölldobler et al., (1994) showed that stridulation signals made by P. analis do
not serve any intraspecific communication, but serve as a warning to potential predators
such as birds and mammals of the powerful sting a P. analis worker can administer.

Raids by P. analis are reported to occur twice in a day, during the first two hours after
sunrise and the last two hours before sunset (morning and evening, Sheppe, 1970;
Longhurst and Howse, 1977; Longhurst et al., 1978; Longhurst and Howse, 1979).
Lepage (1981) also reported a third peak of activity in Kajiado a Kenyan semi-arid
ecosystem. Morning raids are most frequent between 0700 to 0930hr and the evening
raids between 1630 to 1830 hr. The termite species preyed upon by *P. analis* mainly belong to the genus *Macrotermes* (Longhurst *et al.*, 1978) which are of great economic importance mostly in sub-Saharan Africa (see section on the economic importance of termites).

**Semiochemicals**

A generally accepted terminology has evolved to classify the functional chemical substances in insect communication (see Figure 3 for a schematic of semiochemical groupings). A *semiochemical* or *infochemical* is any chemical compound used in communication, whether between species (as in symbioses) or between members of the same species (Hölldobler and Wilson, 1990; Meyer, 2006). The signals transmitted between individuals of different species are called *allelochemicals*, while those mediating behaviour between individuals of the same species are known as *pheromones*. Pheromones are usually glandular secretions which when released by one individual trigger a behavioural response from other individuals upon tasting or smelling it (Hölldobler and Wilson, 1990; Howse *et al.*, 1998; Torto, 2004).

**Figure.3** Schematic diagram showing the classification of semiochemicals

*Allelochemicals* are those chemicals used between species. Allelochemicals are further subdivided into three broad classes: *allomones*, *kairomones* and *synomones* (Nordlund, 1981; Hölldobler and Wilson, 1990; Torto, 2004). Allomones are signals that benefit the emitter while being of negative or no significance to the receiver, e.g. a
lure used by a predator to attract a prey. Kairomones are signals which are of benefit to the receiver by either evoking a behavioural or physiological reaction e.g. chemicals used by insect pests to locate a potential host plant. While synomones benefit both the emitter as well as the receiver, e.g. floral odours from plants which attract pollinators.

Chemical Communication in Ants
Ants communicate in various ways, including; tapping, stridulation, stroking, grasping, nudging, atenations, as well as tasting, puffing or streaking of chemicals that induce responses ranging from recognition to recruitment and alarm (Hölldobler and Wilson, 1990).

Chemicals used in communication by ant societies contain complex mixtures of substances which vary in molecular composition and in their relative proportions (Hölldobler and Wilson, 1990). These multicomponent signals are either produced in single exocrine glands or can be blends composed of secretions from several glands (Hölldobler and Wilson, 1990). Chemical signals can be combined with cues of other sensory origin, such as vibrational or tactile stimuli (Hölldobler, 1995).

The role of odours in behaviour of ants
The ambient atmosphere contains complex mixtures of millions of volatile compounds, that makes it difficult to understand how organisms distinguish and discriminate between certain odours. Olfaction is said to be a universal sense that permits all animals to find food, identify con-specific mating partners, and avoid predators (Keller and Vosshall, 2003; Bruyne and Baker, 2008). Blends of volatile organic chemicals that differ in size, shape, charge, and functional groups are said to make up the stimuli that control olfactory-driven behaviours (Keller and Vosshall, 2003). The puzzle of how the brain processes complex and often contradictory blends of odorant chemicals from the environment into meaningful odour stimuli is still not clearly understood (Keller and Vosshall, 2003). Recently Bruyne and Baker (2008), attributed the detection and encoding of odours in insects to volatile codes encoded in the olfactory receptor neurons (ORN).

According to Malnic et al., (2004), the stimulus spectrum which the olfactory system has to deal with is very different from that of other senses i.e. touch and taste. Light and sound stimuli occur (in very limited dimensions) in contrast to odour molecules, which
are multi-dimensional in nature with different chain lengths, chiralities and functional groups. While the visual system functions with a lower number of photoreceptors, the olfactory receptors (ORs) constitute the largest gene family in the human genome, made up of approximately 300 functional genes (Malnic et al., 2004), with 170 Or genes (Robertson and Wanner, 2006) annotated in the honeybee. Yet the human sense of smell is surpassed by that of other animals (Keller and Vosshall, 2003). Insects have a large number of olfactory receptors on a given organ e.g. the antenna, and have developed an extreme sensitivity to certain odours (Keller and Vosshall, 2003). Many insects rely almost exclusively on odour cues in their search for food, nest and mates and in the detection and avoidance of their natural enemies.

What do we know about chemical communication in *P. analis*?

The raiding behaviour of *P. analis* has attracted entomologists and myrmecologists to study it and try to look at the coordinated way in which it is organised. Studies like those of Longhurst et al., (1979) and subsequently those of Hölldobler et al., (1994) and Janssen et al., (1995) did try to understand the use of trail pheromones and their sources in *P. analis*.

Longhurst et al., (1979) identified the Dufour’s and mandibular glands as the sources of trail pheromones in *P. analis*. The active compounds identified in the Dufour’s gland were \( n \)-undecane and \( n \)-tridecane. While they identified dimethyl disulfide, dimethyltrisulfide from the secretions of the mandibular glands as those responsible for attraction and digging by sister worker ants during raids.

Hölldobler et al., (1994) discovered other sources of trail pheromones in *P. analis*, as the pygidial glands. Janssen et al., (1995) using microreaction techniques with GC-MS identified \( N, N \)-dimethyluracil, and actinidine as the volatiles in the poison gland. Using the same techniques and approach to identify the chemical components of extracts from the pygidial gland proved futile. They attributed this to the volatility of the components as suggested in Hölldobler et al., (1994).

Thesis organisation

The aim of this study was to undertake detailed behavioural studies on the raiding behaviour of *Pachycondyla analis* in order to determine the ant’s ecology, prey
preferences and factors affecting prey choices in the study area (Mpala, Kenya) for comparison with other habitats. Also *P. analis* seemed to be a potential candidate for use in pest control strategies aimed at termites, however, little is known about its intraspecific chemical communication apart from studies on its trail pheromones. On the other hand, there is no literature that clearly shows how or what cues *P. analis* uses in detecting its termite prey. It is also of considerable interest to understand this interaction between ants and termites from the perspective of co-evolutionary arms race since ants are said to have co-evolved with termites for over 100 million years ago (Hölldobler and Wilson, 1990).

Each chapter in this thesis is presented as a research article

**Chapter one** investigates the detailed behavioural studies of the interactions between *P. analis* and its termite prey in the field. It examines the nesting habits, raiding dynamics, prey preference based on prey capture and abundance of prey species and possible factors determining prey choice by *P. analis*. **Chapter two** asks the question whether olfactory cues are used by *P. analis* to determine the presence of nestmates either inside or outside the nest during raids when workers are not in line of sight. This chapter also analysed and identified chemicals in the volatile emissions of *P. analis* workers within a colony. GC-MS was used to see whether the volatile profiles differed between different worker groups when they were together and when they were separated. **Chapter three** asks the question if *P. analis* uses contact chemical cues in nestmate and non-nestmate discrimination within and outside the colony. This was tested using a mandible opening response bioassay with ant cuticular hydrocarbons as chemical cues. Also, the chemical composition of the cuticular hydrocarbons (CHCs) from different colonies of *P. analis* were identified using GC-MS. **Chapter four** looks at detection of termite prey by *P. analis*. Olfactometric bioassays were conducted to investigate if ants detect potential food sources using olfactory cues from termites. Chemical composition of the volatiles emitted by termite galleries and termites were also identified by GC-MS. The **General conclusion** looked at the findings from all the chapters and proposed ideas for future research.
References


