CHAPTER FOUR

Behavioural evidence of olfactory detection of prey by the termite raiding ant *Pachycondyla analis* (Hymenoptera: Formicidae)

Abstract

There exists a co-evolutionary arms race between termites and predatory ants, both of which occupy and share the same habitats. Over time, these two different groups of insects developed several predatory and counter predatory strategies against each other to enable them survive in these shared habitats. The African termite raiding ant *Pachycondyla analis* organises raids on colonies of Macrotemitinae which are responsible for a certain degree of losses in agricultural production in sub-Saharan Africa. Here we asked whether ants chemically detect their potential termite prey before and during raids in order to reveal the possible cues involved. Using Y-tube olfactometric assays, we tested the responses of ants to odours emitted from termites alone, termite gallery soil and termites inside their galleries. We demonstrate for the first time that *P. analis* detects odours of both termites and those of their galleries; but odours from termites inside their galleries were more attractive to both minor and major workers. GC-MS analysis was used to identify the composition of the volatiles. While the volatiles from termite gallery soils were compositionally richer, those from the termites alone were quantitatively richer, releasing about six times more volatiles than gallery soil. Most of the compounds in the volatiles were identified are hydrocarbons. Naphthalene previously identified as an insect repellent was also identified as a component of the volatiles of the gallery soil. In conclusion, these results suggest that odours play an important role in prey detection by *P. analis*.

Introduction

Termites are economically important from two different perspectives. On the one hand, they assist in nutrient re-cycling (beneficial), while on the other hand, they destroy cellulose containing materials (destructive) in their quest to acquire cellulose (Culliney and Grace, 2000). As a result of this behaviour, termites cause damage estimated at many billions of dollars worldwide, and in Africa alone they account for between 15-100 % loss of crops (both on farm and in storage) and in tree production (Janssen, 2006).

Ants (Hymenoptera) are said to be the greatest predators of termites (Isoptera) worldwide (Hölldobler and Wilson, 1990). They both share the same habitats and are abundant in terms of biomass and density (Fujiwara-Tsujii *et al*., 2006). During their 100 million years of coexistence, ants and termites are said to have engaged in a co-evolutionary arms race, with ants on the one hand developing several predatory tactics and termites on the other hand responding with several defensive strategies (Deligne *et al*, 1981; Mill, 1983; Hölldobler and Wilson, 1990;). Despite these counteracting strategies from termites, most ant-termite interactions are antagonistic with the well armed ants wining the battles against the soft bodied termites. Among ants there exist specialists as well as opportunistic predators of termites. Ants that prey opportunistically on termites are members belonging to two of the largest genera *Pheidole spp* and *Componotus spp* (Hölldobler and Wilson, 1990). The most specialised predatory ant species are concentrated in the sub-families 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).

A lot of energy and time is used by virtually all animals in search for food regardless of their social organisation (Bell, 1991). For a colony of ants, foraging is energetically expensive but in the long run it is beneficial by an increase in the probability of retrieving more food items (Lighton *et al*., 1987). In ants, scouts have the ability to learn and recognise prey characteristics such as their spatial distribution and availability (Hölldobler and Wilson, 1990; Schatz *et al*., 1999) or their specific odours or kairomones (Durou *et al*., 2000); this has the potential to increase their foraging efficiency. Since termite availability is determined by their complex spatial and temporal presence (foraging and nesting habits), their exploitation as prey requires some synchronisation on the part of the predators as observed in the raiding behaviour of *P. analis* (AAY, unpublished data).

Pachycondyla analis (Latreille) is a specialised termite predator, which is widely distributed in sub-Saharan Africa (Lévieux, 1966). This ant species, commonly referred to as 'Matabele ants', organizes group raids on termite species which mainly belong to the sub-family Macrotermitinae (Longhurst *et al.*, 1978). These raids are initiated when a scout ant detects a potential food source (Longhurst *et al.*, 1978, Lepage, 1981) and it then recruits nest mates using trail pheromones (Longhurst *et al.,* 1979). Upon arrival at the food source, the ants spread out, break open the termite galleries and then invade them to raid the termites. *P. analis* capture termites by stinging, which paralyses them after which they carry them out of the galleries to a place near the gallery entrance and then return to continue hunting. After gathering enough termites they stop hunting, re-group in columns and start the return journey back to their nest (Longhurst *et al.,* 1978). A major worker can grasp up to seven termites between its mandibles, while a minor can grasp up to three termites (AAY personal observation). Some do not carry any termites but lead the columns of nest mates on the return journey back to the nest (Longhurst *et al.*, 1978). The raids last between 4-50 min depending upon the foraging distance and the termite species being raided.

However, the cues involved in the detection of prey by *P. analis* have not been well studied. Previous studies by Longhurst and Howse (1978) reported that *P. analis* scouts either use chemical or mechanical cues of termite origin to detect potential termite prey. However, New (1991) was of a different opinion; that *P. analis* detects termites using termite pheromones, which serve as kairomones for *P. analis*. These suggestions have not been supported by any experimental evidence that documented the cues used by *P. analis* while foraging for termites.

These gaps in our knowledge of this specific interaction prompted us to investigate whether olfactory cues mediate the detection of prey by *P. analis*. To investigate this, we tested the responses of worker ants to the odours of termites, termite galleries and termites inside their galleries. We also compared the composition of the volatiles from these odour sources by GC-MS.

Materials and methods

Study insects

Colonies of *P. analis* with all representative individuals (queen, workers, males, brood and eggs) were excavated from Mpala Research Centre (0°17’N, 37°52’E) Central Kenya, 250 Km north of Nairobi. The ant colonies were kept in artificial nests boxes (20 cm × 20 cm × 20 cm) made of aluminium that were connected to foraging arenas (1.5 × 1.0 m) made of Perspex. The nests were maintained at 25 ± 1 °C, with about 50-60% relative humidity and a 12L: 12D photoperiod. Ants were fed on live termites (mainly from the subfamily Macrotermitinae) collected twice daily around the Duduville campus of *icipe* in Nairobi, Kenya.

Termites (*Odontotermes sp*) and gallery soils were obtained from termite foraging galleries in and around the Duduville campus of *icipe* in Kasarani Nairobi, Kenya.

Bioassays

The olfactory responses of major and minor workers of *P. analis* to odours were tested in a Y-tube olfactometer. The odour source consisted of: (a) 40 workers and 10 soldiers (termites only), (b), 250g gallery soil (termite gallery soil only), (c) a combination of (a) and (b) offered as choices. The bioassays were conducted at room temperature (24 ±1°C) and 50-60 % RH. In order to simulate ants foraging and raiding behaviour as observed in the field, all bioassays were carried out in the mornings (0700-1000 hr) and evenings (1600-1730 hr) local time over a number of days using ants from different colonies.

Y-tube olfactometer set-up

The olfactometer set-up consisted of a glass Y-tube (base 7.5 cm long; Y-arms 7.5 cm long; internal tube diameter 10 mm), as described in Chapter two Figure 2.3. Each arm was extended by fitting it with a small piece of stiff Teflon tube which was connected to a long flexible Teflon hose that entered directly into the odour source. The base tube was also extended with a piece of stiff Teflon tube to a further flexible Teflon hose, leading to a vacuum pump. Air coming from the pump was directed outdoors to avoid contamination of the indoor air. At each end of the Y-tube, a wire mesh was placed to prevent a test ant from getting out of the base or any of the Y-arms. Odour sources were placed in 200 ml glass jars (odour chambers) with screw tops containing inlets and outlets for air entering and odour exiting through the Y-tube. Each jar was connected to an air supply via flexible Teflon hoses. Charcoal-purified air was passed into the odour chambers at a flow rate of 250 ml/min. One of the Y-arms was connected to an odour source while the other was connected to an empty jar with only clean air (blank) when comparing odours with blank. When comparing odours with each other, each arm was provided with a different odour source. The odours were extracted through the base arm at 500 ml/min by a vacuum pump to prevent odours from building up in the Y-tube. A score line was drawn on the two arms of the olfactometer at 2 cm from the joint.

Test ants were introduced individually into the apparatus by disconnecting the Y-tube at its base and allowing the ant to walk into the olfactometer. Subsequently, the tube was reconnected to re-establish the airflow from the odour sources through the arms and out at the base towards the vacuum pump. An ant was allowed to settle down for 5 min, after which its behaviour was monitored. A choice was recorded when an ant stayed for at least 1 min in an arm, or when it frequently visited an arm. No-choice was recorded when the ant remained in the base arm for more than 5 min. Each test was terminated after 10 min from the introduction of the ant into the Y-tube. Sixty ants were used for each treatment (30 minor and 30 major workers). To avoid positional bias, odour chambers were rotated for every replicate. A clean Y-tube was used for each ant test in order to avoid carryover of odours. Parts between the Y-tube, vacuum and odour sources were changed or cleaned with soapy water, rinsed with dicholoromethane and acetone after each bioassay to remove traces of odours or contaminants. Glassware was cleaned with Teepol® laboratory detergent, rinsed with acetone and dried for five hours at 160°C in an oven. Teflon parts were rinsed with acetone and water to remove volatiles and then flushed with a stream of nitrogen to dry them.

Extraction of compounds and chemical analyses

Termite galleries: ~2g of termite gallery soil was weighed into a clean 2 ml glass vial, and to this 1 ml of *n*-pentane was added. The sample was vortexed for about 10 min, and then extracted for 2 hrs at room temperature, after which the supernatant was filtered through solvent-cleaned glass wool and concentrated under charcoal-purified nitrogen to about 100 µl. If samples were not analysed immediately, they were stored in the freezer at -20°C until used.

Ten whole bodied termites which were previously killed on ice were extracted in 1 ml of *n*-pentane kept in ice for 2 hrs. After extraction the extracts were filtered through glass wool and the filtrate concentrated under nitrogen to 100µl. Extracts were either analysed immediately or stored at -20°C until used.

GC analysis

Gas chromatographic (GC) analysis was carried out on a HP 5890 Series II gas chromatograph equipped with a flame ionisation detector (FID) and a HP-5 column (30 m × 0.25mm ID × 0.25µm film thickness). Nitrogen was used as a carrier gas with a column pressure of 46 psi and injection temperature of 250°C. One µl of sample was injected in the splitless mode, with the oven temperature programmed at 60°C for 5 min and at 10°C/min to 250°C, and held at this temperature for 13 min. GC-MS analysis was carried on an Agilent Technologies 7890A gas chromatograph equipped with a capillary column HP-5 MS (30 m × 0.25mm ID × 0.25µm film thickness) and coupled to a 5795C mass spectrometer. One µl of each sample was injected in the splitless mode, and helium was used as the carrier gas at 1.0 ml min^{-1}. The oven temperature was 35°C held for 5 min, increased to 250°C at 10°C min^{-1}, and then held at this temperature for 15 min. The analysis was carried out at 70eV in the electron impact ionization mode. Compounds were identified tentatively based on a comparison of their mass spectra with published MS spectra and retention indices.

Statistical analyses: Data analysis was carried out using SAS version 9.2 (SAS Institute, 2002). Data obtained using the Y-tube olfactometer assays were analysed using a chi-square test to test whether odours were more attractive to ants than the control (blank). Ants that did not make a choice were not included in the analysis. Since the olfactometer assays were performed under the same conditions, individual assays were pooled to evaluate the differences in attractiveness of the three odour sources by the major and minor workers. A logistic regression model was fitted to the data using PROC GENMOD (SAS Institute Inc., 2008).

Results

Bioassays: In general, significantly more ants (65%) responded to the treatment odours than to the control (clean air). Responses of both major and minor workers to termite gallery soil were significantly higher than the control (Figure 4 1A). In particular, 21 majors, representing 81%, responded to the gallery soil odour as compared to only 19%

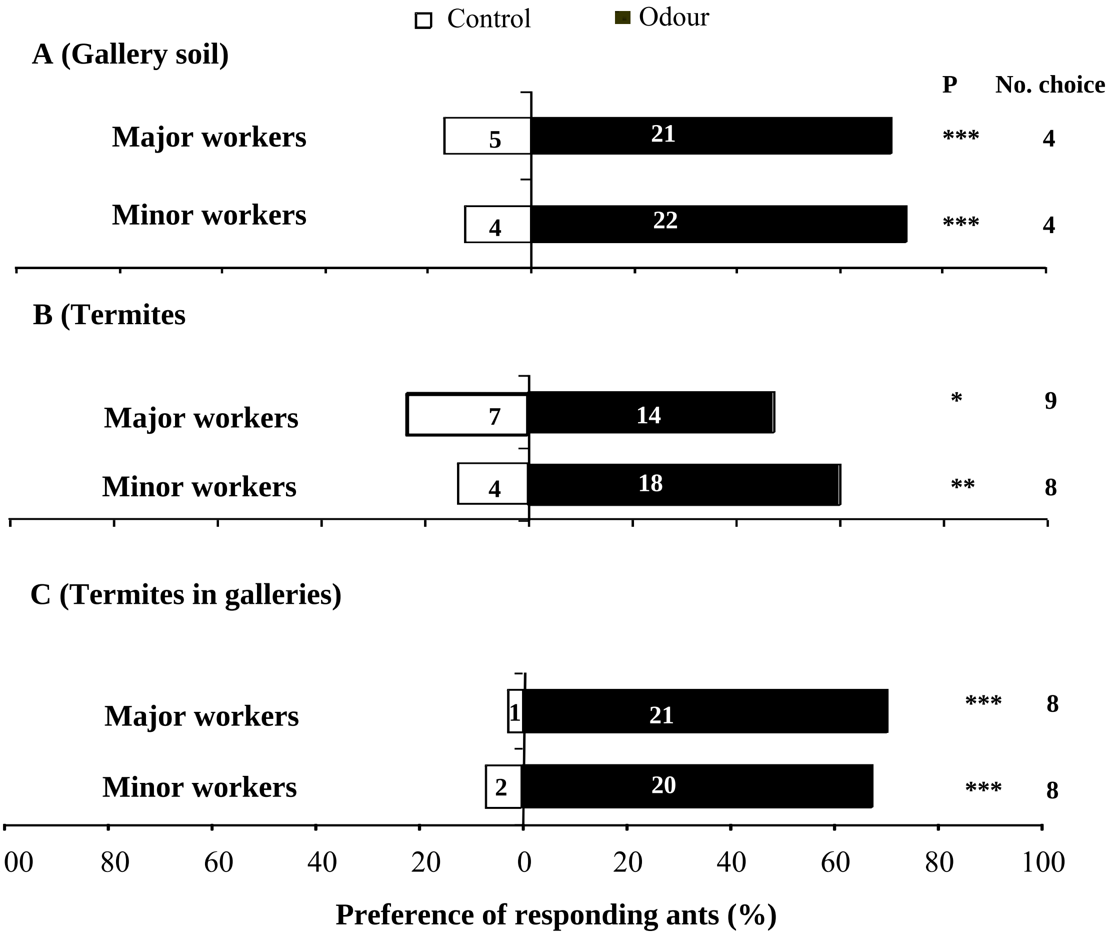

Figure 4.1 Preferences of *Pachycondyla analis* major and minor workers for odours from (A) *Odontotermes sp.* gallery soil, (B) *Odontotermes sp.* workers and soldiers and (C) *Odontotermes sp.* and gallery soil when presented alongside clean air. Black bars represent response to odours, while white bars represent response to the control. Numbers within bars refer to the number of ants making a choice, while numbers outside bars refer to ants that made no choice (*N*= 30 each for major and minor workers in each test, **= significant at $P < 0.05$ and ***= significant at $P < 0.001$).

response to the control ($\chi^2 = 11.56$, $P < 0.001$, n = 26). In the case of minors, 85% chose the gallery soil compared to 15% to the control ($\chi^2 = 12.46$, $P < 0.001$, n = 26). Minors (82% vs. 18% controls; $\chi^2 = 8.90$, $P < 0.01$, n = 22) were more responsive to termite odours than majors (67% treatment vs. 33% control; $\chi^2 = 4.33$, $P < 0.05$, n = 21) (Figure 4.1B). Both majors (95% vs. 5% control $\chi^2 = 18.18$, $P < 0.001$, n = 22) and minors (91% vs. 9%; $\chi^2 = 14.72$, $P < 0.001$, n = 22) were highly attracted to the odours from termite galleries, (Figure 4 1C).

Given a choice between odours from termite only and termites in the gallery soil, the difference in the response of both major and minor workers to these odours were not statistically significant (Majors, $\chi^2 = 0.33$, $P = 0.54$, n = 25, Minors, $\chi^2 = 11.56$, $P = 0.67$, n = 27) (Figure 4.2).

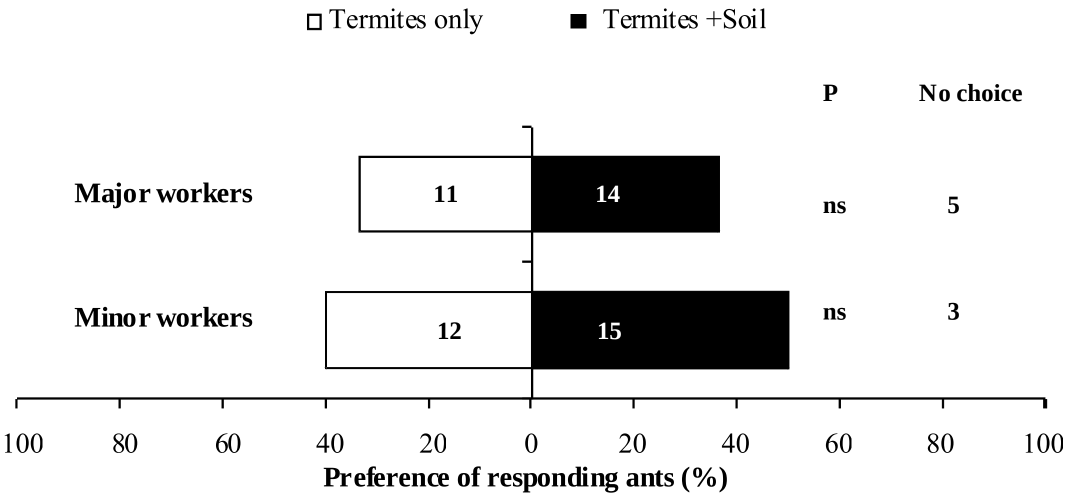

Figure 4.2 Preferences of *Pachycondyla analis* major and minor workers to odours from *Odontotermes sp.* (workers and soldiers), against odours from *Odontotermes sp.* in gallery soil. Black bars represent response to odours from termites in gallery soil, while white bars represent response to odours from termites only. Numbers within bars refer to the number of ants making a choice, while numbers outside bars refer to ants that made no choice. *N* = 30 each for major and minor workers in each treatment, ns= Not statistically significant at α = 0.05.

When the responses of both major and minor workers were pooled for all the odours tested, the response of workers to the odours from the gallery soil and those from the gallery with termites inside was not significantly different ($P = 0.54$). However, responses of the ants to odours from termites and to the combined odours from termites and gallery were significantly different (*P* = 0.04), with no differences between the responses of major and minor workers, respectively (*P* = 0.84).

Identification of chemicals

Using GC-MS a total of seventeen components were tentatively from the odours of the termite gallery soil and the termites only (Figure 4.3). These components were mainly hydrocarbons and esters. The volatile from the termite gallery was compositionally richer, with thirteen components compared to nine in the volatile profile of termites (Figure 4.3).

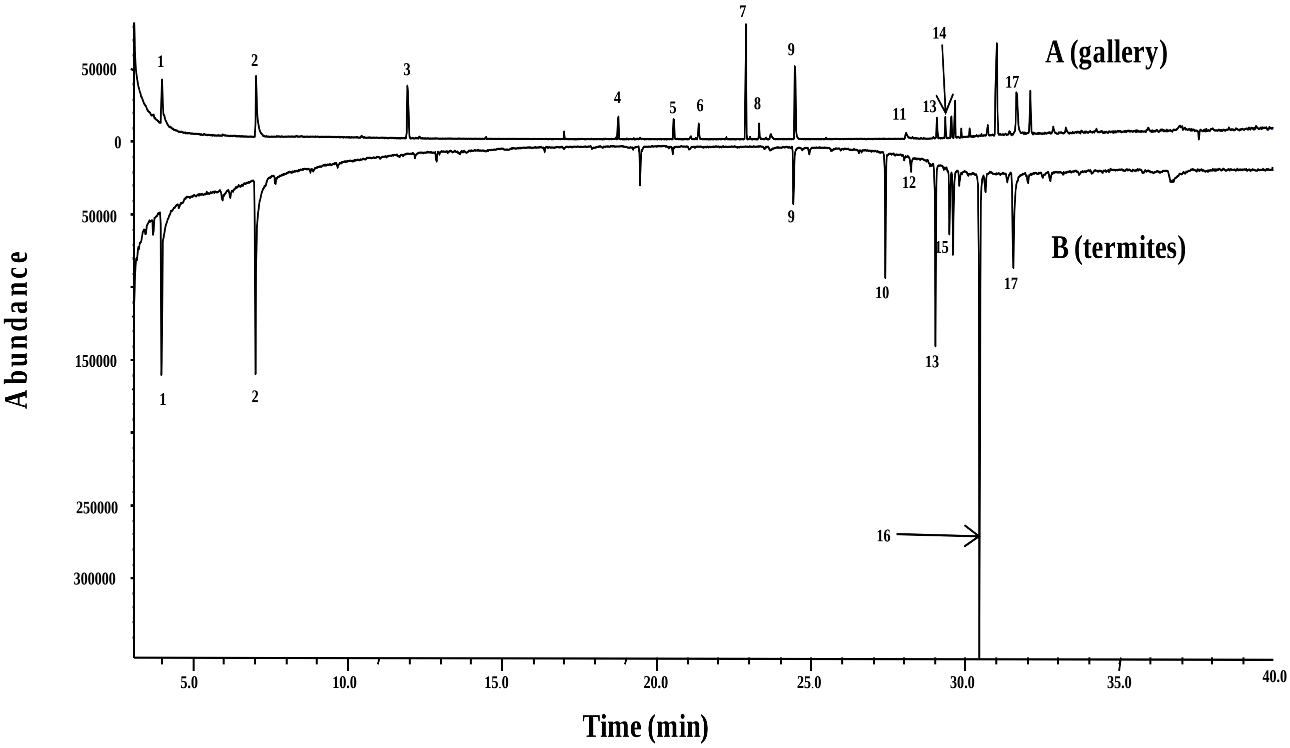

Figure 4.3 GC-MS trace of chemical compounds extracted from (A) ~2g of *Odontotermes* sp. gallery soil and (B) 10 *Odontotermes* sp. workers. Labelled peaks are: 1) *n*-heptane; 2) *n*-octane; 3) α-Phallendrene; 4) naphthalene; 5) Butanoic acid-tridecyl-ester; 6) 2-Napthalenemethanol; 7) Methyl-carbinol; 8) *n*-heptadecane; 9) *n*-eicosane; 10) *n*-tetracosane; 11) *n*-pentacosane; 12) hexylpentadecane; 13) 13-undecylpentacosane,; 14) *n*-octacosane; 15) 1-Nonadecene; 16) Oxalic acid, hexyl pentadecyl ester; 17) squalene.

Discussion

The results from the Y-tube olfactometer bioassays showed that workers of *P. analis* use olfactory cues associated with both termite and termite galleries in prey location. The combined odours from termites plus galleries were most attractive to both major and minor workers (Figure 4.1C). It appeared that, major workers were more sensitive to detecting these odours than minors. This differential sensitivity may be associated with the fact that the majors are frequently engaged in scouting for food and possibly an innate ability to also detect these food sources for the colony. Their specialisation in locating potential food sources accurately was observed in the field during raids. Out of total 330 raids observed in the field, only 5 were unsuccessful.

Longhurst and Howse (1978), performed behavioural assays with scout ants (major workers) in the field and found that they responded more to dry soil sheeting containing live termites (suggesting response to mechanical cues i.e. vibrations from termites) than soils without termites. However, in bioassays involving extracts of fresh soil sheeting, old soil sheeting, top soil and extract from head and thorax of termites, extract from whole termites and fresh soil sheeting Longhurst and Howse (1978) discovered that ants responded differently to these extracts. In the present study, field observations showed no raids by ants on fresh termite soil. As such this type of soil was not included in the study, and furthermore, in preliminary assays ants did not discriminate between odours from wet soil sheeting and the blank. The results from these studies reveal that *P. analis* workers use olfactory cues to locate termites prey accurately in the absence of visual or mechanical cues, which adds a new dimension to host location by *P. analis*.

Comparatively, minor workers were more responsive to odours from termite and termite galleries only than major workers (Figure 4.1A and B). These slight differences were not apparent when odours of the termites in the galleries were offered to different worker groups against a blank. These differential responses may be associated to the type of task minor workers undertake most especially during raids. During raids, the smaller body size of minor workers, unlike that of majors, allow them to enter deep inside the termite galleries to seek, paralyse and carry prey from the galleries. We observed a similar sensitivity to olfactory cues of chemical origin by minor workers in assays we carried out on volatile cues from conspecific *P. analis* workers.

In choice tests with termite odours only and those from termites in galleries, both worker ants responded more to the termites in galleries odours than to odours from termites alone (Figure 4.2). Although the results were not statistically significant, behaviourally it showed that ants could use cues from the galleries as long range cues or as first guides to potential termite sources. The ability of *P. analis* workers to detect odour cues coming from termites only can be used by workers to detect the presence of termite species like *Hodotermes mossambicus* which does not utilise soil sheeting (Longhurst and Howse, 1979). However, for a scout to make a decision to label that source as a potential food source; the scout has to detect the presence of termite prey inside by the use of chemical or mechanical cues from termites.

Although this is the first time olfactory cues in detecting prey by *P. analis* has been demonstrated, a previous study had reported similar detection mechanism in Myrmicinae ant *Crematogaster scutellaris* that uses olfactory cues to detect its fig wasp prey (Schatz *et al.,* 2003). The use of allomones in detecting termites has also been described for the larva of *Lomamyia latipennis* (Johnson and Hagen, 1981).

In the present study, chemical profiles of gallery soils and those of *Odontotermes sp* (termites) were found to be different. Except for 5 hydrocarbons (*n*-heptane, *n*-octane, *n*-eicosane, *n*-pentacosane and squalene) common to the profiles of these two ant attractive sources (Figure 4.3). The composition of the gallery soil was qualitatively richer than that of the termites. However, with respect to quantity, about six-fold more volatiles were released by the termites (Figure 4.3) with a major component of the latter being oxalic acid (not present in the gallery soil). To the best of our knowledge, this is the first time the potential chemical cues from both termites and their galleries had been identified in relation to the raiding behaviour of *P. analis*. The presence of naphthalene and its derivative 2-naphthalene-methanol in the volatiles of the galleries, which are known insect repellents, has previously been reported for subterranean termites (McLaughin, 2004). Termites use naphthalene and related compounds as a repellent to other insects, especially against ant predators. Naphthalene and a naphthalene derivative of plant origin (2-acetonaphthone) have also been reported as repellents for termites (Henderson *et al*., 2007). The chemicals in the termite soil galleries are believed to come from intestinal secretions of workers who mix them with soil particles and their saliva (Briunsma and Leuthold, 1977). These chemical components of termite origin embedded in the galleries are used by *P. analis* scouts as an indicator of the presence of termites before detecting other cues associated with the termites themselves. The ability of *P. analis* to be attracted to odours from the galleries that include the presence of known ant repellents shows that this ant could have adopted the use of naphthalene and its derivatives of termite origin as possible kairomones along with other components from the cues.

To conclude, this study tested the roles of olfactory cues in the detection of termite prey by the termite-specific ant *P. analis*. Ant scouts initially detect chemical cues from termite galleries and then use a combination of the cues of termite origin and those of the galleries to identify a potential food source in order to initiate a raid. Both major and minor workers of *P. analis* detect these chemical cues. However, there is the need to identify the behaviourally active components, either singly or in a blend contributing to the detection of the termite food source.

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