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Predatory and trophobiont-tending ants respond differently to fig and fig wasp volatiles

Yuvaraj Ranganathan, Renee M. Borges*

Centre for Ecological Sciences, Indian Institute of Science

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The interaction between figs and their pollinating or parasitic fig wasps is mediated largely by chemical communication. These fig wasps are often preyed upon by predatory ants. In this study, we found that predatory ants (*Oecophylla smaragdina*) patrolling *Ficus racemosa* trees were attracted to the odour from fig syconia at different developmental phases, as well as to the odours of fig wasps, whereas other predatory ants (*Technomyrmex albipes*) responded only to odours of syconia from which fig wasps were dispersing and to fig wasp odour. However, trophobiont-tending ants (*Myrmicaria brunnea*) patrolling the same trees and exposed to the same volatiles were unresponsive to fig or fig wasp odours. The predatory ants demonstrated a concentration-dependent response towards volatiles from figs receptive to pollinators and those from which wasps were dispersing while the trophobiont-tending ants were unresponsive to such odours at all concentrations. Naïve predatory ants failed to respond to the volatiles to which the experienced predatory ants responded, indicating that the response to fig-related odours is learned. We suggest that predatory ants could use fig-associated volatiles to enhance their probability of wasp encounter and can eavesdrop on signals meant for pollinators.

Figs (*Ficus* spp., Moraceae) have an obligate mutualism with pollinating fig wasps (Hymenoptera, Agaonidae). This 90-million-year-old nursery pollination mutualism (Machado et al. 2001), in which pollinators breed within fig syconia, is largely mediated by chemical communication via volatiles produced by the fig syconia (Hossaert-McKey et al. 1994; Gibernau et al. 1998; Grison-Pigé et al. 2002). The mutualistic interaction between figs and their pollinating wasps is susceptible to exploitation by parasites. The parasitic (nonpollinating) fig wasps use chemical cues emanating from fig syconia (Proffit et al. 2007) and oviposit from the exterior into the fig syconium through the syconial wall, thereby deriving benefits from having their offspring develop at the expense of a potential fig seed or pollinator. Fig trees are also occupied by many nonagaonid insects including sap-sucking trophobionts and ants (Compton & Robertson 1988). Predatory ants patrolling fig trees could function as indirect mutualists of the fig–wasp interaction by capturing parasitic wasps (Schatz et al. 2006), while the sap-sucking insects are often brought into fig trees by trophobiont-tending ants which cultivate them for the honeydew that they produce (Compton & Robertson 1991).

Perception of odours emanating from host plants, host animals and prey is of fundamental importance to many insects (Mustaparta 1984). Use of volatile infochemicals has been proven to be important in locating food and shelter by many insect species (Vet & Dicke 1992; Vos et al. 2006). Ants involved in an obligate mutualistic interaction with plants have been shown to respond to the volatiles emitted from their host plants (Fiala & Maschwitz 1990; Brouat et al. 2000; Edwards et al. 2006, 2007; Jurgens et al. 2006). In the case of seed dispersal mutualisms involving ants (myrmecochory), the mutualistic ant partner responds to seed odours (Sheridana et al. 1996; Youngsteadt et al. 2008) or to compounds present in seed-associated structures (elaiosomes; Gammans et al. 2006; Fischer et al. 2008). Even in facultative interactions between ants and plants, ants respond to herbivore damage-induced volatiles (Agrawal 1998; Agrawal & Rutter 1998; Agrawal & Dubin-Thaler 1999; Bruna & Vasconcelos 2003), indicating that the ability to respond to particular compounds could equip certain ants to form symbiotic interactions with plants.

Since fig syconia produce different volatile signatures at different stages in their developmental cycle (Borges et al. 2008; Proffit et al. 2008), it is possible that predators of fig wasps such as ants may use these phase-specific odours to locate syconia that are attracting fig wasps or from which wasps are dispersing (Bronstein 1988). For example, predatory ants have been shown to be present

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* Correspondence: R. M. Borges, Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India.

E-mail address: renee@ces.iisc.ernet.in (R.M. Borges).

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in greater numbers on male trees in dioecious fig species (Schatz et al. 2008), since in dioecious species it is only the male trees in which wasps (pollinators and parasites) breed and from which they exit. Furthermore, *Crematogaster scutellaris* ants were better at capturing pollinating wasps rather than parasitic wasps in the dioecious *Ficus carica* (Schatz & Hossaert-McKey 2003). Behavioural choice experiments on *C. scutellaris* using fig and fig wasp odours demonstrated that these predatory ants patrolling fig trees were significantly attracted only to odours emitted by pollinating fig wasps either alone or in association with odours of male figs releasing wasps (Schatz et al. 2003). Therefore, whether predatory ants can be attracted by odours from figs alone is not known. Furthermore, ants may vary in their exposure to fig volatiles, depending on whether or not they forage or nest in fig trees. Naïve *C. scutellaris*, that is, those that did not patrol fig trees, were not attracted to fig wasp odours (Schatz et al. 2003). Also, fig trees may be occupied by trophobiont-tending nonpredatory ant species that may be exposed to fig and/or wasp odours, but may be unresponsive to them since fig wasps are not a food source for these ants. Learning of relevant cues by ants may be crucial in governing the potential for net positive or negative interactions between ants and fig trees.

In this study, we addressed the following questions. (1) Do predatory and trophobiont-tending ants on fig trees respond to fig and fig wasp volatiles? (2) Does this response vary with the fig syconium cycle? (3) Is there a difference between experienced and naïve predatory ants in their response to fig and/or fig wasp odours?

METHODS

Study System and Study Site

Ficus racemosa Linn., a monoecious fig species, is pollinated by the wasp *Ceratosolen fusciceps* Mayr. *Ficus racemosa* produces cauliflorous syconia (i.e. borne on the trunk) throughout the year, and one fruiting crop cycle takes approximately 60 days to complete. Each cycle can be partitioned into distinct phases depending on the developmental phase of the syconia, namely (1) prereceptive: production of new flush of syconia; (2) receptive: female flowers inside the syconia are ready to receive pollen brought by the pollinating fig wasps that enter the syconia through the open ostiole, with simultaneous oviposition in some flowers; (3) interfloral: fig seeds and fig wasp larvae develop; (4) wasp dispersal: fully developed female pollinators collect pollen and exit the syconia through the exit hole made by the male pollinators; and (5) fruit dispersal: syconia become attractive to frugivores which aid in seed dispersal (Galil & Eisikowitch 1968). Externally ovipositing (nonpollinating) fig wasps arrive at different times from the prereceptive to the mid-interfloral phase of the syconium developmental cycle, while the internally ovipositing pollinating wasps are present in large numbers only at the receptive and wasp dispersal stages. The trunk, main branches and syconia of *F. racemosa* are patrolled by many species of ants, but each *F. racemosa* tree is occupied by a single dominant ant species (Y. Ranganathan, M. Ghara & R. M. Borges, unpublished data). The location of the cauliflorous syconia facilitates interactions with ants. Syconia, fig wasps and associated ant species from *F. racemosa* trees were collected from within the campus of the Indian Institute of Science, Bangalore, India (12°58′N, 77°35′E), where the behavioural experiments were also conducted.

Odour Sources

As odour sources, we used, from several trees, fig wasps and *Ficus racemosa* syconia in distinctly different developmental phases: prereceptive (at least 5 days before pollen receptivity), receptive, interfloral, wasp dispersal (after the fig wasps have exited). Thirty freshly harvested syconia of each phase were used for the initial choice experiments ($N = 48$ trials for each odour and for each ant species). If the odour of 30 figs did not elicit a significant response, we increased the number of figs for that odour source to 50, 70 and 90 ($N = 16$ trials for each odour and for each ant species) to determine a concentration-dependent response, if any. To determine the lower limit of the sensitivity of the ants towards odours of figs in the wasp dispersal phase, we reduced the odour concentration by decreasing the number of figs in this phase from 30 to 10 and four ($N = 16$ for each group). For choice experiments with fig wasps as the odour source, we used live wasps that emerged from 10 wasp dispersal phase syconia. The numbers of these wasps varied but on average 70–100 wasps emerged from each wasp dispersal phase syconium. The dispersal phase syconia, from which wasps were collected for use in the wasp odour experiments, were not used as dispersal phase odour sources. For the dispersal phase trials, separate syconia were collected.

Ants of the Fig Community

Ficus racemosa trees at this site were patrolled by three dominant species of ants: *Oecophylla smaragdina* (Fabricius) (Formicinae), *Technomyrmex albipes* (Smith) (Dolichoderinae) and *Myrmicaria brunnea* Saunders (Myrmicinae). Several other species of ants were also observed to patrol the trunks, but these were limited in their presence either temporally (seen only for a few days) or spatially (localized to a small region of a trunk). These ‘minor’ ant species were: *Solenopsis* sp., *Tapinoma melanocephalum*, *Camponotus pariah*, *Paratrechina* sp. and *Crematogaster subnuda*. *Oecophylla smaragdina* is an aggressive ant with huge arboreal colonies often spanning several branches, and with multiple nests within fig trees. It is largely predatory, but also scavenges. *Technomyrmex albipes*, although much smaller than *O. smaragdina*, is also a predatory ant species. Although this ant has smaller arboreal colonies than *O. smaragdina*, quick recruitment facilitates efficient monopoly of ephemeral food resources. *Myrmicaria brunnea* is predominantly a honeydew-feeder and scavenger, and builds underground nests.

Behavioural Experiments

We used a Y-tube glass olfactometer (arms 13 cm long and stem regions of 4.5 cm in diameter) to conduct volatile choice experiments. Odourless polyethylene terephthalate bags (Nalophan) contained the odour source (fig syconia or fig wasps). Air was allowed to flow (20 ml/min flow rate) through a bag containing the odour source to one arm of the olfactometer (odour arm), while the other arm (no-odour arm) received air at the same flow rate from an empty bag. Air was drawn from the basal arm with the same flow rate to avoid backdraught of volatiles. The odour sources were kept 0.8 m below the plane of the olfactometer, which ensured that no visual cues were available to the test ants. Furthermore, the ends of the Y-tube were closed with fine cloth mesh that ensured laminar air flow but prevented wasps from entering the olfactometer. Each trial consisted of an ant forager being singly introduced into the basal arm of the olfactometer, and lasted 5 min. To control for directional bias, the odour arm was reversed between left and right sides of the Y-tube, in successive trials. Additionally, control trials with blank air were conducted, to examine directional bias if any ($N = 16$ trials for each odour and for each ant species). The olfactometer was rinsed with water, followed by 70% ethanol, and air dried between trials. All the choice experiments were done from 0900 to 1300 hours which corresponded with the peak activity of the ants. Freshly collected ants were used every hour of the experimental duration, to minimize the effect on the ants of being separated from the colony. All experimental ants were major workers, and were collected as required from trails near their colonies which were either on or below fig trees (experienced ants) or far away, that is, at least 300 m from fig trees. The latter ants were unlikely to have experienced fig odours, and were thus considered naïve ants, that is, naïve to fig odours. Since buildings on campus separate the widely dispersed fig trees, the probability that a colony of ants far away from a fig tree had experienced fig odours was remote.

Analysis of Behavioural Data

Different parameters such as the ‘first choice’ made by the test subject after introduction into the chamber, the final choice made after a stipulated amount of time, the number of times the subject visited each arm of the chamber, and time spent in each arm are frequently used as measures of response shown by insects in an olfactometer set-up. The choice of a particular parameter, however, depends heavily on the type of interaction being tested and on the test species. For instance, in our olfactometer set-up the highly mobile ants made no significant ‘first choice’ for the odour arm. There was no difference in the number of visits made to each arm of the chamber since searching behaviour ensured that all arms were visited equally. Furthermore, in generalist predatory or trophobiont-tending ants, all-or-none responses are not expected. Therefore, only the total time spent in the odour arm and the control (no-odour) arm were analysed as in several other hymenopteran studies (De Jong & Kaiser 1991; Colazza et al. 1997; Lo Bue et al. 2004; Villagra et al. 2005) besides those in other taxa (Kaldonski et al. 2007; Perrot-Minnot et al. 2007). The time spent in the stem of the olfactometer was excluded from the analysis. The time (out of each 5 min trial) spent by the ant in the odour arm was divided by the total time spent in the odour and no-odour arms. This proportion of time spent in the odour arm was evaluated using the nonparametric one-sample Wilcoxon signed-ranks test with median = 0.5 as the null expectation. The medians and nonparametric 95% confidence intervals generated by this test are plotted in the figures. Nonparametric tests were used as the data could not be rendered normal by any transformation procedure. Two-tailed tests were used. All statistical analyses were performed using the software package R version 2.7.2 (R Development Core Team 2008).

RESULTS

Response to Fig and Fig Wasp Odours

The control trials showed no significant difference in the mean time spent by the ants in each arm indicating that the apparatus or lighting conditions were not biasing their choice (results not shown). *Oecophylla smaragdina* ants spent a significantly greater proportion of time in the odour arm when exposed to receptive (with increased fig numbers: see next section), wasp dispersal phase ($V = 791$, $P = 0.037$) and fig wasp volatiles ($V = 869.5$, $P = 0.004$; Figs 1, 2). However, *O. smaragdina* showed an indifferent response towards prereceptive ($V = 699.5$, $P = 0.15$; Fig. 1) and interfloral phase volatiles ($V = 641$, $P = 0.59$; Fig. 1) which did not reverse when tested with an increased number of figs (prereceptive: 50 figs: $V = 60$, $P = 0.70$; 70 figs: $V = 18$, $P = 0.99$; 90 figs: $V = 72$, $P = 0.86$; interfloral: 50 figs: $V = 63$, $P = 0.82$; 70 figs: $V = 61$, $P = 0.74$; 90 figs: $V = 69$, $P = 0.98$; Fig. 2). *Technomyrmex albipes* responded significantly only to fig wasp-associated fig volatiles, that is, wasp dispersal phase fig volatiles ($V = 785$, $P = 0.043$) and fig wasp odour ($V = 884$, $P = 0.002$; Figs 1, 2). *Myrmicaria brunnea* did not respond to any of the tested volatiles even after we increased odour concentration (Figs 1, 3).

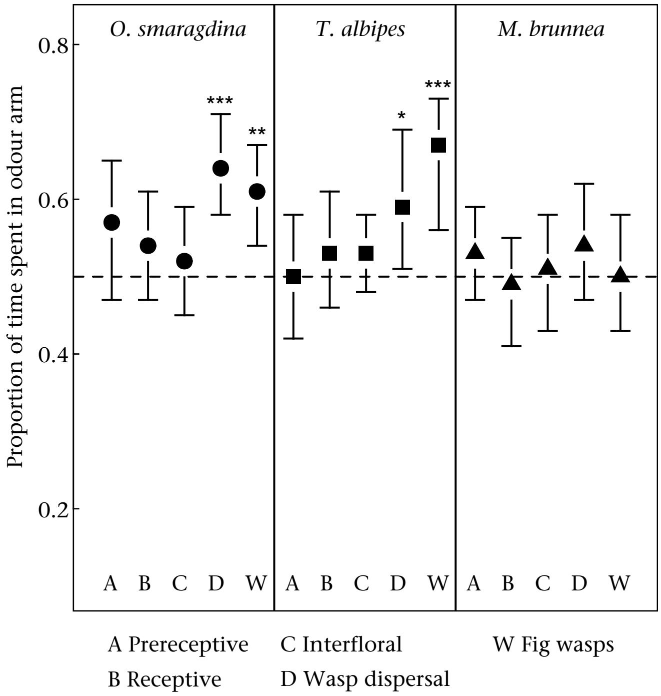

Figure 1. Behavioural responses of *O. smaragdina*, *T. albipes* and *M. brunnea* exposed to fig syconium and fig wasp odours using a Y-tube olfactometer. Bars represent medians and 95% confidence intervals of proportion of time spent in the odour arm. $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, as tested using a one-sample Wilcoxon signed-ranks test with median = 0.5 as the null expectation. $N = 48$ trials in all cases.

Concentration-dependent Response to Fig and Fig Wasp Odours

While *O. smaragdina* did not respond to the receptive-phase fig volatiles of 30 figs ($V = 699$, $P = 0.26$), its response was positive and significant when an increased number of receptive fig syconia

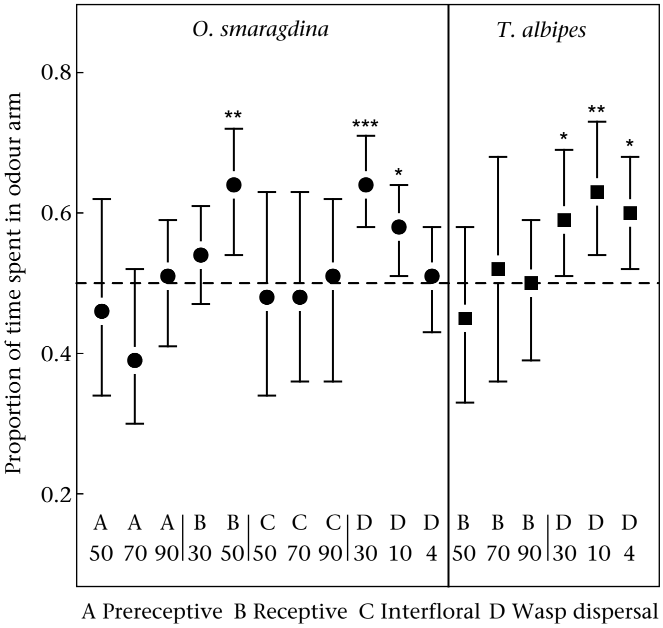

Figure 2. Concentration-dependent response of the predatory ant species *O. smaragdina* and *T. albipes* to fig syconium odours using a Y-tube olfactometer. Description of data representation and analysis as in Fig. 1. Numbers below the fig stage indicate syconium numbers used in the experiment. $N = 16$ trials in all cases, except for responses with 30 syconia where $N = 48$.

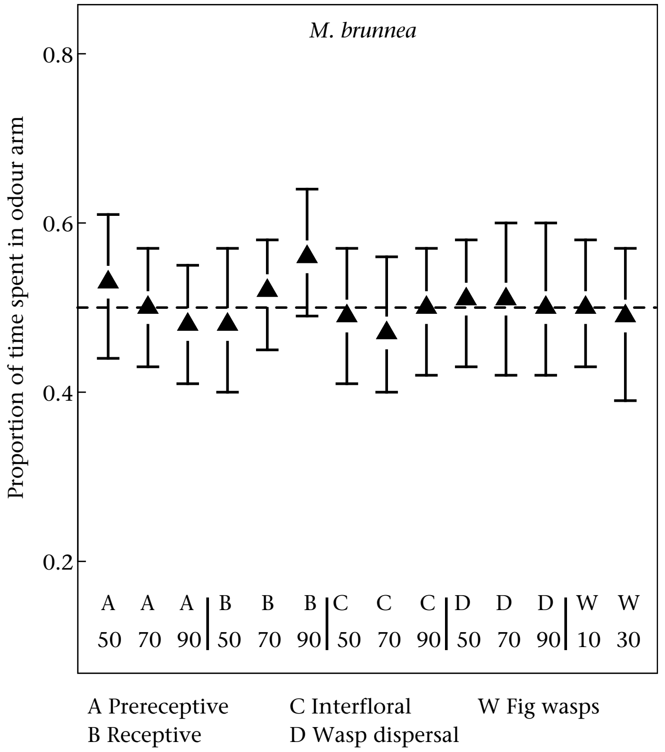

Figure 3. The response shown by *M. brunnea* to fig syconium and fig wasp odours using a Y-tube olfactometer. Description of data representation and analysis as in Fig. 1. Numbers below the fig stage indicate syconium numbers used in the experiment. All values were nonsignificant. $N = 48$ trials in all cases.

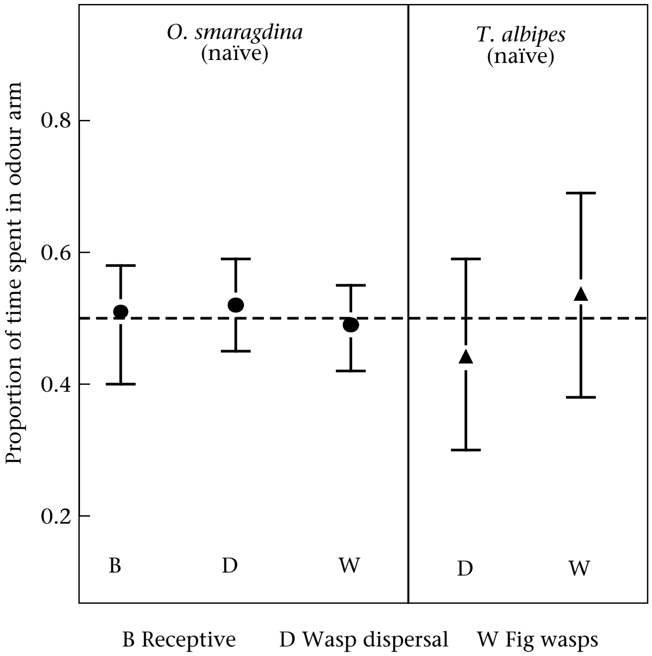

Figure 4. Behavioural responses of naïve (patrolling nonfig trees) predatory ants *O. smaragdina* and *T. albipes* exposed to fig syconium and fig wasp odours using a Y-tube olfactometer. Description of data representation and analysis as in Fig. 1. All values were nonsignificant. $N = 48$ trials in all cases.

($N = 50$ figs) were used as the odour source ($V = 408$, $P = 0.006$; Fig. 2). Also, the positive response of *O. smaragdina* shown towards the volatiles of 30 wasp dispersal phase figs ($V = 900$, $P = 0.0004$) did not change when 10 wasp dispersal phase figs were used ($V = 791$, $P = 0.037$), while the positive response was lost when only four wasp dispersal figs were used as the odour source ($V = 584$, $P = 0.84$; Fig. 2) indicating a declining response with lower concentration as with receptive figs. Unlike in *O. smaragdina*, the nonsignificant response of *T. albipes* towards receptive-phase fig volatiles was not reversed when increased numbers of fig syconia ($N = 50$, 70 and 90 figs) were used as the odour source ($P = 0.43$, 0.90, 0.98, respectively; Fig. 2). Moreover, unlike *O. smaragdina*, *T. albipes* responded positively to all reduced concentrations of wasp dispersal phase volatiles tested (10 figs: $V = 118$, $P = 0.008$; four figs: $V = 114$, $P = 0.015$; Fig. 2).

Response of Naïve Ants to Fig Volatiles

While ant foragers patrolling fig trees responded to fig volatiles of certain syconial developmental stages, the same species of ants that patrolled nonfig trees failed to show any response (Fig. 4). This pattern was consistent with both predatory ant species *O. smaragdina* and *T. albipes*. Thus, naïve *O. smaragdina* tested with the odour of 50 receptive figs, 30 wasp dispersal figs (the minimum tested concentration at which the familiar ants had responded; Figs 1, 2) and that of wasps from 10 figs showed a nonsignificant response (receptive figs: $V = 276$, $P = 0.83$; wasp dispersal figs: $V = 640$, $P = 0.60$; fig wasps: $V = 539$, $P = 0.62$; Fig. 4). The naïve *T. albipes* ants tested with volatiles from 30 wasp dispersal figs (the maximum tested concentration at which the familiar ants had responded; Fig. 2) demonstrated no response ($V = 47$, $P = 0.30$; Fig. 4). A test of naïve *T. albipes* ants with a lower concentration (10 wasp dispersal figs) also yielded nonsignificant results ($V = 53$, $P = 0.78$). Naïve *M. brunnea* were not used for this experiment, since *M. brunnea* tending trophobionts on fig trees had not responded to fig or fig wasp volatiles (Fig. 3).

DISCUSSION

The predatory *O. smaragdina* and *T. albipes* responded to fig-associated volatiles. However, trophobiont-tending *M. brunnea* failed to respond to fig or fig wasp volatiles, even after exposure to increasing concentrations. A successful hunting strategy for predatory ants on fig trees is to anticipate an abundance of prey at times when the syconia are attracting wasps or wasps are dispersing from them (Bronstein 1988). It would thus be advantageous for *O. smaragdina* and *T. albipes*, being permanent residents of this semiurban habitat in which *F. racemosa* trees are abundant, to exploit ephemeral prey resources that arrive at fig trees in temporally separated pulses. These pulses of prey occur mostly at the following times: (1) parasitic wasps arriving during the prereceptive phase, (2) pollinating and parasitic wasps arriving during the receptive phase, and (3) pollinating and parasitic wasps exiting during the wasp dispersal phase. Furthermore, after the fruit dispersal phase, the trees enter a gap phase, lasting for as long as 1 month, during which no syconia of any phase are available (Y. Ranganathan & M. Ghara, personal observation). It would therefore benefit predatory ants to use prereceptive or receptive syconial volatiles as a signal for the renewed availability of syconia on these trees and thereby the impending arrival of the wasps. This might be especially relevant for ants that nest in the arboreal stratum since they can move their nests into fig trees, as occurs in *O. smaragdina*.

Response to Plant Volatile Types and Concentrations

Oecophylla smaragdina responded to the odour of receptive figs indicating that this ant can sense components of the syconium signal that is meant for pollinating wasp attraction (Gibernau et al. 1998; Grison-Pigé et al. 2002). This response could ensure their presence at the syconia when wasps are numerous, and since ants respond to signals that are meant only for pollinating fig wasps, this response can be considered as an example of eavesdropping. The response of both predatory ant species to fig wasp odours and to those of wasp dispersal figs, however, is an example of direct response to prey cues and was also shown previously in *C. scutellaris* (Schatz et al. 2003).

The concentration-dependent response of both predatory ant species, albeit less marked in *T. albipes* (Fig. 2), is possibly an attribute of the sensitivity of their olfactory sensillae, which so far has been examined only for leaf-cutting ants (López-Riquelme et al. 2006; Kleineidam et al. 2007). A concentration-dependent response towards seed extracts was also observed in *Camponotus femoratus* ants (Youngsteadt et al. 2008). Although *O. smaragdina* responded to volatiles from receptive figs only at higher concentrations (50 figs; Fig. 2), since bunches of cauliflorous syconia of *F. racemosa* on the tree trunks usually contain numerous figs (30–50 per bunch), a single ant on a fig tree could easily be exposed to cues emanating from more than 50 figs at any given time. Thus, the limitation of sensitivity of the ant's olfactory system would be readily overcome under natural conditions. *Technomyrmex albipes* showed a higher sensitivity towards odour of wasp dispersal figs than *O. smaragdina* (Fig. 2), although they are much smaller ants. Also, *O. smaragdina* occupied 43% of 21 *F. racemosa* trees on campus while *T. albipes* occupied only 24% of the trees, the rest being occupied by *M. brunnea*. Yet, while *O. smaragdina* is a well-known ferocious predatory ant (Offenberg et al. 2004; Tsuji et al. 2004; Schatz et al. 2006), *T. albipes* can also be an effective predator, since on the ant-plant *Humboldtia brunonis* in India, it is the ant that provides the greatest protection from herbivores (Gaume et al. 2005; Shenoy 2008).

The sensitivity of the ants to receptive phase volatiles seems to be much lower than that of the fig wasps in which only a few fig syconia are sufficient to elicit a response in an olfactometer (e.g. Proffit et al. 2007). It is possible that ants that use local prey resources, and also possibly visual cues, may not need such high sensitivity to fig volatiles, while pollinating wasps that arrive at fig trees from distances of 5–100 km (Nason et al. 1998; Compton 2002; Harrison 2003; Harrison & Rasplus 2006) may require much greater sensitivity to find the right fig species and the right phenological stage. This is probably why female pollinating wasps, which live for only 24 h (Kjellberg et al. 1988; Dunn et al. 2008), have evolved elongate and multiporate sensillae on their antennae (Ware & Compton 1992; Kjellberg et al. 2005); the sensillae of ants, however, have scarcely been investigated. The lack of response by ants to interfloral phase fig volatiles may not be the result of a quantitative decline in volatiles which occurs in the dioecious *F. hispida* (Proffit et al. 2008), since the quantity of volatile production per fig syconium actually increases in the interfloral phase in *F. racemosa* (Y. Ranganathan, unpublished data). This indifferent response is likely to be caused either by the smaller available prey base or by an inappropriate volatile signature for this stage. Our study thus emphasizes that odour concentration must be taken into consideration while conducting bioassays with ants under natural conditions. Such an approach would provide important insights into the integrated interactions between figs and their mutualistic and parasitic insects. Also, the fact that *F. racemosa* displays a degree of asynchrony within trees at the study site (A. Krishnan, unpublished data) such that syconia of different phases may at times be present on the same tree indicates that ants also need to be responsive at small spatial scales to syconial volatiles.

Associative Learning of Prey Cues

Naïve ants of both predatory species did not respond to fig syconial odours indicating that there are no specific volatiles within these odours that are innately attractive to ants as has been found in some cases (Djiéto-Lordon & Dejean 1999a, b). The positive response of experienced ants towards fig syconium and wasp odours therefore indicates the phenomenon of associative learning, specifically olfactory learning, as in other ant species (Roces 1990, 1994; Schatz et al. 1994; Dupuy et al. 2006). *Oecophylla longinoda* in Africa, for example, imprints on the chemical signatures of natal trees (Djiéto-Lordon & Dejean 1999b). This learned association between volatile cue and reward can thus trigger the behavioural response. Furthermore, our study is the first report of predatory ants responding to odours emanating from fig syconia alone, even in the absence of odours of fig wasps. Although *O. smaragdina* is a generalist predator and a scavenger, such associative learning could increase its fitness, and was predicted to occur in the interactions of fig wasps with their ant predators (Bronstein 1988). While ants involved in specialized obligate mutualisms with plants respond to specific plant compounds (Seidel et al. 1990; Brouat et al. 2000; Inui et al. 2001; Youngsteadt et al. 2008), it is important for generalist predatory ants to learn to use temporally fluctuating, local cues, as indicators of the likelihood of prey presence. Furthermore, in the ant response to volatiles from wasp dispersal stage fig syconia, there may be chemical cues left by the wasps themselves, although female wasps at least had exited. Experiments using solely seed-bearing (not wasp-producing) monoecious fig syconia to determine the response of ants to cues emitted only by syconia and not by the developing wasps would resolve this issue, and are underway.

The lack of response by *M. brunnea* to syconium-associated volatiles, even at elevated concentrations (Fig. 3), could either mean that these ants are not sensitive to these volatiles, or that while their antennae are sensitive, since fig wasps are not their food source, no association is formed. For example, trophobiont-tending ants respond to surface chemicals of their trophobionts, which in some cases may reduce aggression in the tending ants (Choe & Rust 2006). Similarly, only mutualistic ants responded to chemicals from seed elaiosomes, whereas nonmutualistic (granivorous) ants were unresponsive (Gammans et al. 2006). While other species of *Myrmicaria* are known to be highly predatory (Kenne et al. 2000), *M. brunnea* mostly tends trophobionts on *F. racemosa*, or is a scavenger in the study site. Also, in another ant–plant interaction, *M. brunnea*, although abundant on the semimyrmecophyte *H. brunonis*, and feeding extensively on its extrafloral nectar, provided little protection from herbivory (Gaume et al. 2005; Shenoy 2008). Yet, the proximate reasons for the lack of responsiveness of *M. brunnea* to syconium-related volatiles can only be evaluated by electroantennogram studies which are planned for the future.

Predatory or trophobiont-tending ant species may have traits that could equip them to form net positive or negative interactions with fig trees. These biological traits have traditionally included ecological and behavioural parameters such as (1) arboreal versus terrestrial nesting, (2) colony size, (3) aggressiveness and (4) recruitment ability, but should now also include traits such as (5) responsiveness to volatiles as we have shown in this study. Such traits will have important implications for the mutualism between figs and fig wasps. Much more comparative work is needed to understand chemical and behavioural correlates of fig and ant interactions.

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