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Predatory abilities favour the success of the invasive ant *Pheidole megacephala* in an introduced area

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Abstract: The invasive African big-headed ant, *Pheidole megacephala*, is a dominant species in the many areas it has invaded. We examined whether one potential reason for its ecological success might be its predatory efficiency. We compared the density of termite nests in an area of Mexico invaded by *P. megacephala* with an adjacent area where *P. megacephala* is not present. We also compared the success of *P. megacephala* in preying on termites with that of 13 native ant species. We found that termite nest density was significantly lower in areas invaded by *P. megacephala* (0.33 vs. 1.05 nests per 30 m transect). In field trials, we established that *P. megacephala* workers were significantly more successful at capturing termite workers from termite nest fragments than even the most successful native ant species, *Dorymyrmex pyramicus*. For both *P. megacephala* and *D. pyramicus*, single scouts could trigger the mass recruitment of nestmates, but *P. megacephala* was able to recruit greater numbers of nestmates. Combined with their aggressiveness towards other ant species, their highly efficient predatory capacities help explain the ecological success of *P. megacephala* and demonstrate how it can be a major threat to invertebrate biodiversity in the areas it invades.

Key words: competition, invasive ants, Mexico, native ants, predation

1 Introduction

Of the approximately 11 500 ant species known (Bolton et al. 2006), about 150 'tramp species' have been transported and introduced to many parts of the world through human activity, but only seven have become invasive on a worldwide scale (Holway et al. 2002). Many of these invasive ants form supercolonies due to their intrinsic ability to achieve unicoloniality, which results in the absence of intraspecific territoriality over extended areas. This feature has been demonstrated for several of these invasive species (Tsutui et al. 2003; Fournier et al. 2005). The prevalence of invasive ant species in areas they have invaded has frequently been associated with their ability to utilize native food sources, including attending large numbers of hemipterans for their honeydew (Holway et al. 2002; Le Breton et al. 2005). Moreover, as arthropod diversity and abundance has been shown to decline in invaded areas, invasive ants have been assumed to be good predators (Holway et al. 2002). As much research has been done on the effect of invasive ants on native arthropod communities, it is surprising, then, to note that no study has ever specifically addressed the influence these invasive ants have had on termite abundance, even though in most humid tropics ants and termites constitute the major taxa in

terms of abundance and biomass (Wilson 1992). Here we focus on the impact of invasive ants on native termite communities to determine whether they prey on native termites or whether termites are unaffected because they have evolved several means of resistance (Hölldobler and Wilson 1990) that invasive ants are unable to overcome.

This study, conducted in Mexico, focuses on *Pheidole megacephala* (F.), an invasive ant species known to have the ability to eliminate native ants (Heterick 1997; Hoffmann et al. 1999). Like other invasive ant species, *P. megacephala* is thought to be an effective predator as arthropod abundance declines in areas it has invaded (Simmonds 1958; Zimmerman 1970; Fowler et al. 1990; Hoffmann et al. 1999). We, therefore, tested whether the density of arboreal termite nests was lower in areas *P. megacephala* has invaded compared with non-invaded areas, and whether *P. megacephala* was more successful than native species at capturing termites.

2 Materials and Methods

The present study was conducted along the Caribbean coast of Quintana Roo, Mexico, around Puerto Morelos (20°N, 86°W) where *P. megacephala* spread over several kilometres

(Drouot et al. 2002). Along this coast, a strip of land about 450 m wide separates several lagoons from the sea. The lagoons are connected to the sea by small tidal inlets. The coastal strip of land is joined to the inland in several places. Moving from the sea to the inland lagoons, four ecological zones succeed one another: the beach, dunes with shrubs and coconut trees and/or in places a wide, disturbed lower dune with sparse vegetation, and finally mangrove all along the edges of the inland lagoon.

Native to tropical Africa, *P. megacephala* has been unwittingly dispersed by human activity throughout the tropics and sub-tropics, becoming one of the most successful invasive ant species in these regions (Hölldobler and Wilson 1990; Hoffmann et al. 1999; Holway et al. 2002; Taylor 2006). The worker caste is dimorphic with no intermediary body size between the small minors (approximately 2 mm long; average 0.35 mg) and the big-headed majors (or soldiers; 3–4 mm long; average 1.65 mg); workers have an atrophied sting that they use to lay scent trails, but not to subdue prey or competitors (Wilson 2003). Colonies are found nesting in the ground, in abandoned termite nests or in the crevices of tree bark and, like most other invasive ants, *P. megacephala* is omnivorous and able to tend many hemipteran species (Dejean et al. 2005).

To assess the impact of the *P. megacephala* supercolony on the abundance of the native arboreal termite *Nasutitermes mexicanus* Light, we compared the number of termite nests found across the homogeneous mangrove located in an area occupied by *P. megacephala* ($n = 15$) and in a neighbouring area without *P. megacephala* ($n = 20$). The plots, 30 m in length, were limited to the first 5 m of mangrove (this part of the mangrove is not under water) and separated from each other by 50 m; we left a 500 m long zone between the monitored invaded area and the control (non-invaded) area. We compared the results using Student's *t*-test.

In the first series of experiments we began by isolating termite nest fragments (about 1 dm³) containing workers,

soldiers and brood from four native species (details provided in table 1). The termite workers quickly obstructed openings with dirt and secretions, so that some termite individuals were trapped outside the nest fragments and patrolled the surface. These termite nest fragments were then installed on either the territory of *P. megacephala* or on the territory of 13 native ant species. For the seven ground-nesting ant species, the termite nest fragment was placed 5 m away from nest entrances. To test the predatory abilities of the three arboreal ant species included in this study, we placed the termite nest fragments in a fork of the ant's host tree more than 2 m from the ant nests. Finally, for the three army ant species (Ecitoninae), we placed the termite nest fragments about 0.5 m from a column (but not at the front of the columns in order to reproduce a similar situation as for other ants, with discovering workers recruiting nestmates). We conducted one test at a time, with their sequence arbitrarily assigned. We verified if the ants (1) attacked, killed and retrieved some of the termites patrolling the surface of the tested termite nest fragments, (2) if all patrolling termites were captured and (3) 2 h after the beginning of the experiment when the ants had stopped patrolling the termite nest fragments in most cases, we broke them open to see whether they sheltered termites or not.

In a second series of experiments we tested whether the presence alone of chemicals produced by the termites is enough to trigger long-range recruitment in *P. megacephala* and *Dorymyrmex pyramicus* (Roger) scouts (both species were able to capture all termites in the previous test). Prior to each experiment, we placed two 'clean' sheets of A4 paper (21 × 29.7 cm) 5 m from a *P. megacephala* or *D. pyramicus* nest entrance (only one test per nest entrance), and counted the number of workers on these sheets of paper 15 min after they were discovered by a scout (pre-controls). We then placed an empty 3–4 cm³ piece of *Microcerotermes* nest at the centre of an 'experimental' sheet of paper, while we placed a piece of local dirt of the same volume at the centre of a

Table 1. Termite species mortality tested against foraging native ant species and *Pheidole megacephala* workers under natural conditions. In each experiment a standardized termite nest fragment (about 1 dm³) was deposited on the territory of a colony, or for Ecitoninae, at about 0.5 m from a column. <2h: = all termites killed in each experiment in less than two hours (no additional workers involved in patrolling the piece of termite nest; no termites recorded within the termite nest fragments). Surface: cases when the ants attacked, killed and retrieved termites patrolling on the termite nest fragments (*: all patrolling termites killed and retrieved) versus total number of cases. First column: P = Ponerinae; Et = Ectatominae; Ec = Ecitoninae (army ants); M = Myrmicinae; D = Dolichoderinae; F = Formicinae. **: arboreal-nesting ant species. ***: experiment conducted nocturnally due to the activity rhythm of the species. "-": test not conducted

Native ant species	Rhinotermitinae <i>Heterotermes</i> sp. 1 and sp. 2		Amitermitinae <i>Microcerotermes</i> sp.		Nasutitermitinae <i>Nasutitermes mexicanus</i> Light	
	<2 h	Surface	<2 h	Surface	<2 h	Surface
P <i>Anochetus emarginatus</i> (F.)	0	6*/6	–	–	1	10*/10
P <i>Pachycondyla harpax</i> (F.)	0	6*/6	0	4*/4	0	3/5
P <i>Pachycondyla stigma</i> (F.)	0	8*/8	0	4*/4	0	5/5
P <i>Pachycondyla villosa</i> (F.) **	0	5/5	–	–	0	5/5
Et <i>Ectatomma ruidum</i> Roger	0	5*/5	0	4*/4	0	5/5
Et <i>Ectatomma tuberculatum</i> Olivier	0	5/5	0	4/4	0	5/5
Ec <i>Eciton burchelli</i> (Westwood)	1	5*/5	1	4*/4	0	5/5
Ec <i>Eciton hamatum</i> (F.)	0	4/5	0	4/4	0	4/5
Ec <i>Labidus praedator</i> (F. Smith)	2	5*/5	4	4*/4	0	5/5
M <i>Solenopsis geminata</i> (F.)	0	8/8	0	4/4	0	5/5
D <i>Dolichoderus bispinosus</i> Olivier**	0	5/6	–	–	0	5/5
D <i>Dorymyrmex pyramicus</i> (Roger)	4	10*/10	3	6*/6	1	10*/10
F <i>Camponotus atriceps</i> (F.)***	0	5*/6	0	4*/4	0	3/5
Total (%)	7 (8.75)	77/80 (96.2)	8 (12.5)	64/64 (100)	2 (2.7)	70/74 (94.6)
M <i>Pheidole megacephala</i> (F.)*** (%)	7 (100)	7*/7 (100)	4 (100)	4*/4 (100)	9 (100)	9*/9 (100)

sheet of paper serving as a control ($n = 10$ in each case). We compared the results using the Kruskal–Wallis test followed by a *post hoc* test (Dunn’s test); the ‘experimental’ results between *P. megacephala* and *D. pyramicus* were compared using Student’s *t*-test (and the sequential Bonferroni-corrected multiple tests). All statistics were performed using GraphPad Prism 4.0 software.

Because we observed *P. megacephala* workers preying on newly-emerged flies, we placed five garbage cans/250-l cylindrical tanks (whose bases were pierced with numerous holes about 3 cm in diameter) with thousands of fly brood inside on the territory of a *P. megacephala* colony for several weeks and then, at night when the ants are the most active, observed their capacity to capture large numbers of prey. The workers used mass recruitment nightly to prey on flies (8 mg on average; notably they did not prey on maggots or only on a few). The number of captured flies was evaluated during a single night from 54 series of observations along the main colony trails (six observations per hour between 7:00 PM and 4:00 AM.).

3 Results

The number of *Nasutitermes* termite nests present in the first 5-m wide zone of the mangrove was significantly lower in the area occupied by the *P. megacephala* supercolony than in the control area (0.33 ± 0.13 termite nests per 30 m-long plots; $n = 15$ vs. 1.05 ± 0.15 ; $n = 20$; $t = 3.34$; d.f. = 33; $P < 0.01$).

We observed during the first series of experiments that after discovering the termite nest fragments and without ever coming into contact with the termites, the *P. megacephala* scouts returned to their nests to recruit several dozen nestmates. The recruited workers then rapidly captured and retrieved the termite workers and soldiers patrolling the surface of the termite nest fragments. A few minutes later, several recruited workers dug holes in the termite nest fragments and all the termites were captured (table 1). Most termite workers and *Nasutitermes* soldiers were captured by single *P. megacephala* individuals, rarely two, while the larger soldiers of the other termite genera were cooperatively retrieved by two to four workers. In contrast, among the native ant species only the army ants *Eciton burchelli* (Westwood) and *Labidus praedator* (F. Smith) plus *Anochetus emarginatus* (F.) and *D. pyramicus* (table 1) raided the termite nest fragments, rarely killing and retrieving all the termites. Using Fisher’s exact test we noted a significant difference between the most efficient native ant species (pooled together) and *P. megacephala* in their ability to raid native termites: *Heterotermes* (7 of 20 cases vs. 7 of 7; $P < 0.01$); *Nasutitermes mexicanus* (2 of 20 cases vs. 9 of 9; $P < 0.001$); and all termite species pooled (17 of 54 cases vs. 20 of 20; $P < 0.0001$); but not for *Microcerotermes* sp. due to low observation numbers (8 of 14 cases vs. 4 of 4; $P = 0.16$). Nevertheless, all the native ants tested attacked, killed and retrieved some of the termite individuals patrolling the outside of the termite nest fragments (although very few species captured all of them; table 1). Additionally *A. emarginatus* workers captured *Nasutitermes* individuals without triggering aggressiveness from the termite soldiers.

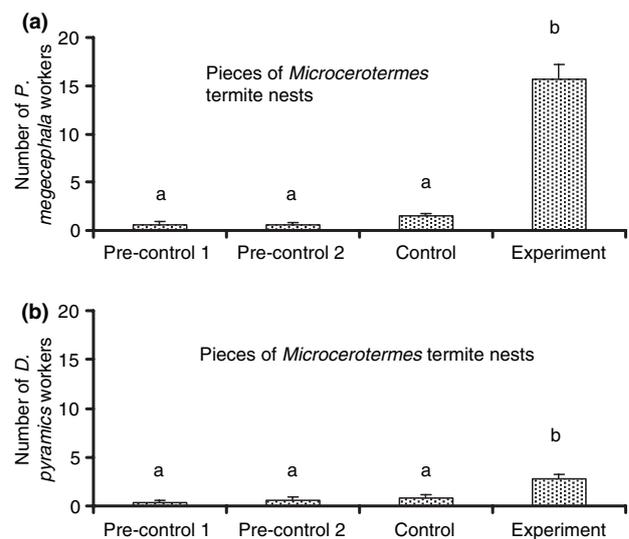


Fig. 1. Testing the influence of termite nests’ chemicals on the recruitment behavior of *Pheidole megacephala* and *Dorymyrmex pyramicus* scouts. Number of recruited individuals according to the different experiments. ‘Pre-controls’ correspond to ‘clean’ sheets of paper, ‘control cases’ to sheets of paper with a piece of dirt of about 3 cm^3 deposited at the centre of the paper, and ‘experimental cases’ to sheets of paper with a *Microcerotermes* nest fragment devoid of occupants of about 3 cm^3 ($N = 10$ in each case) deposited at the center of the paper. Global comparisons, Kruskal–Wallis tests, *P. megacephala*: $H^3_{40} = 17.8$; $P < 0.001$; *D. Pyramicus*: $H^3_{40} = 18.5$; $P < 0.001$. Post hoc comparisons, or Dunn’s test: different letters indicate significant differences ($P < 0.05$). Comparison between the two experimental lots, Student’s *t*-test: $t = 7$; $df = 18$; $P < 0.01$ (after sequential Bonferroni correction).

During the second series of experiments we observed *P. megacephala* scouts first antennated the ‘empty’ termite nest fragments, and then returned directly to their nest to recruit nestmates. Consequently, the number of *P. megacephala* workers present 15 min after the scouts discovered the sheets of paper was significantly higher on those with termite nest fragments than all control cases for which the numbers of workers were always low (fig. 1a). The same was true for *D. pyramicus*, the most efficient native species from the previous experiment, although it recruited significantly fewer workers than *P. megacephala* (fig. 1b).

Finally, *P. megacephala* workers retrieved during each 10-minute series of observations 316 ± 56 newly-emerged flies, resulting in an estimated $17\,064 \pm 3024$ flies per night (or about 130 g of fresh prey). We also observed during these raids that some workers remained immobile facing away from the trails, mandibles open, and so served as guards as do certain army ants when protecting their columns.

4 Discussion

This study demonstrates that *P. megacephala* is an efficient generalist termite predator as illustrated by

the fact that it raided all the native termite nest fragments regardless of the termite species (including *Nasutitermes* that are able to defend territories from native dominant ant species in Neotropical countries; Dejean et al. 2003). In comparison native ants were far less efficient, even though all the species observed are at least occasional termite predators (concerns termite individuals patrolling the surface of tested termite nest fragments), showing that termites may be an important protein food source for these species. It is not surprising that army ants were able to kill and retrieve all the termite individuals in some of the tested termite nest fragments (see Gotwald 1995), but the present study reveals that *A. emarginatus* and particularly *D. pyramicus* can also do the same. Several observations of columns of workers raiding arboreal termite nests confirmed that *D. pyramicus* is an effective termite predator (A.D. pers. obs.). Concerning our observations of *A. emarginatus*, it has already been noted that workers are able to patrol among *Nasutitermes* individuals without being attacked by the soldiers; a subsequent analysis of the cuticular hydrocarbons revealed the existence of a chemical mimicry between these ants and *Nasutitermes* soldiers (Dejean 1988).

The chemicals produced by termites and present on their nests serve as kairomones that triggered the recruitment of nestmates of both *D. pyramicus* and *P. megacephala* scouts, and, in this way, the individual scouts avoid termite defences and remain safe.

The raiding survey conducted on flies permitted us to verify that *P. megacephala* workers have the ability to capture large numbers of prey (see also Simmonds 1958). A similar behaviour could take place unseen in termite nest galleries with large *P. megacephala* colonies possibly destroying entire termite colonies, while most ant species specialized in termite predation only capture relatively small parts of colonies, and repeatedly prey on individual termite nests (Hölldobler and Wilson 1990).

Because termites are one of the most abundant taxa in the humid tropics (Wilson 1992) and most ant species either opportunistically or specifically prey on termites that partly or entirely satisfy their protein requirements, *P. megacephala* may be able to eliminate native ants through exploitation competition as it is a particularly efficient termite predator. Indeed, the ability of *P. megacephala* to displace native ants has been well documented (Haskins and Haskins 1965; Lieberburg et al. 1975; Majer 1985; Heterick 1997; Hoffmann et al. 1999), but this species has never before been presented as a termite predator. Rather, *P. megacephala* has always been considered to be an exotic, invasive ant species that has severely reduced native arthropod abundance when introduced both in disturbed habitats and in tropical rain forests (Zimmerman 1970; Hoffmann et al. 2002), and has been shown to have had a particularly strong, negative impact on populations of houseflies in Fiji (Simmonds 1958) and Collembolans in Queensland (Heterick 1997).

In conclusion, this is the first study to demonstrate that the predatory abilities of *P. megacephala* favour its ecological success in an area where it has been

introduced. As shown, *P. megacephala* easily captures termites, which could greatly decrease the termite populations themselves as well as populations of native termite specialists. In addition, occasional termite predators might find it difficult to satisfy their nitrogen requirements in areas where *P. megacephala* have been introduced. Taken together, these results show that *P. megacephala* is a potential threat to invertebrate diversity in areas where it has been introduced due to its ability to raid native insects with even the most well-developed defences, such as termites.

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