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Unadapted behaviour of native, dominant ant species during the colonization of an aggressive, invasive ant

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Abstract Among the factors driving the invasive success of non-indigenous species, the “escape opportunity” or “enemy release” hypothesis argues that an invader’s success may result partly from less resistance from the new competitors found in its introduced range. In this study, we examined competitive interactions between the little fire ant *Wasmannia auropunctata* (Roger) and ant species of the genus *Pheidole* in places where both are native (French Guiana) and in places where only species of *Pheidole* are native (New Caledonia). The experimental introduction of *W. auropunctata* at food resources monopolized by the *Pheidole* species induced the recruitment of major workers only for the Guianian *Pheidole* species, which were very effective at killing *Wasmannia* competitors. In contrast, an overall decrease in the number of *Pheidole* workers and no recruitment of major workers were observed for the New Caledonian species, although the latter were the only ones able to kill the *Wasmannia* workers. These results emphasize the inappropriate response of native dominant New Caledonian species to *W. auropunctata* and, thus, the importance of enemy recognition and specification in the organization of ant communities. This factor could explain how invasive animal species, particularly ants, may be able to successfully invade species-rich communities.

Keywords Biological invasions · Competition · Enemy recognition · *Pheidole* · *Wasmannia auropunctata*

Introduction

The success of invasive alien species relies on numerous interconnected factors, including their own characteristics, the recipient community, the abiotic conditions and the relationship among these variables (Holway 1998; Naeem et al. 2000; Gabriel et al. 2001). In an effort to consider all of these issues jointly, Shea and Chesson (2002) developed a theoretical framework known as ‘niche opportunity’. A niche opportunity is the potential for alien species to increase their population densities thanks to conditions found in their introduced area. This might be a “resource opportunity”, an “escape opportunity” or a combination of both. A “resource opportunity” arises when the resources that a species needs are highly available, while an “escape opportunity” occurs when native species do not abound or are not effective against introduced species. An “escape opportunity” may be compared to the “enemy release hypothesis (ERH)”, which argues that the success of an invader results from fewer attacks by enemies native to invaded areas and, as a consequence, exotic pests reach much higher densities than normally occur in their native habitats (Shea and Chesson 2002). “Enemy” most often means pathogens, parasitoids and predators, while very aggressive competitors can also be considered as enemies since aggressive encounters often lead to the death of one or both of the opponents (Colautti et al. 2004). As a result, the success of invaders is multifactorial, including characteristics intrinsic to the invaders, and the relative importance of each factor may fluctuate during the consecutive phases of biological invasions (Colautti and MacIsaac 2004; Colautti et al. 2004).

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It is therefore a challenge to identify the factors that allow such species to become invasive once introduced into a new area and those that regulate non-indigenous species in their native range. In this context, invasive unicolonial ant species offer a good model for exploring this issue. Generally ants coexist in well-organized communities through effective interactions such as competition and predation at both the intra- and inter-specific level (Hölldobler and Wilson 1990). In contrast, unicolonial species typically form spatially vast and competitively dominant supercolonies that lack territorial boundaries; they are polygynous and reproduce by colony budding (Holway et al. 2002). Due to their huge populations they are among the most devastating invaders in the animal kingdom, with major consequences for the structure of other animal communities and the functioning of ecosystems (Holway et al. 2002; O'Dowd et al. 2003). According to Human and Gordon (1999), the numerical advantage gained through their unicoloniality is the main factor explaining the success of invasive ants. Indeed, in introduced areas, once an invasion has begun, exotic unicolonial ants are often more successful in obtaining resources such as territory and food than any native species. Nevertheless, during the colonization process, the numerical advantage of alien ants over native species at the onset of an invasion is unlikely, so that other mechanisms may take over.

The behavioural mechanisms involved in the proximate factors contributing to an ant invader's success have received considerable attention from researchers, but much remains to be learned about the factors governing colonization success. To date, the competitive abilities of exotic ants have often been assessed in introduced areas but poorly studied in their native range, although the comparison of both situations is essential to the understanding of the mechanisms leading to invasion success (Holway et al. 2002).

In order to partly explain these factors, we hypothesize that native dominant ant species do not adopt appropriate responses towards alien ants during encounters. We therefore examined competitive interactions between the little fire ant *Wasmannia auropunctata* (Roger) and ant species of the genus *Pheidole* in places where both are native (French Guiana) and in places where only species of *Pheidole* are native (New Caledonia). Native to the New World, this tiny myrmicine ant (body length of workers: 1.4 mm) is one of the most widespread, abundant and destructive invasive ants (Holway et al. 2002; Wetterer and Porter 2003). On several Pacific islands, *W. auropunctata* has invaded a wide array of habitats causing the disruption of local ant and even vertebrate communities such as reptiles (Clark et al. 1982; Jourdan et al. 2001; Le Breton et al. 2003, 2005). We assessed the ability of the different *Pheidole* workers to defend food resources against *W. auropunctata* by studying their responses at both collective and individual levels.

Materials and methods

Study sites and the place of *W. auropunctata*

This study was carried out in the rainforest of the Rivière Bleue Natural Park (22°04'S, 166°36'E), a 9,000-ha reserve located in southern New Caledonia, and in the proximity of the Petit Saut hydroelectric dam in French Guiana (4°5'N, 53°0'W).

In New Caledonia, *W. auropunctata* was formerly confined to human-modified ecosystems, although it has now spread over a wide range of natural habitats and occurs throughout most lowlands (Jourdan et al. 2001; Le Breton et al. 2003). This species was first detected in the Rivière Bleue Natural Park in 1997 and has now invaded several areas where it has excluded native ants, including *Pheidole* species (Le Breton et al. 2002, 2003). In non-invaded areas, the *Pheidole* species are numerically dominant and common on the ground but not on vegetation (Wilson 1976a; Le Breton et al. 2003, 2005).

In French Guiana as well as in other areas of its home range, *W. auropunctata* is a common species regarded as dominant in disturbed areas but rarely in undisturbed areas such as the rainforest (Tennant 1994; Majer and Delabie 1999; Armbrecht and Ulloa-Chacón 2003).

Choice of taxa

The *Pheidole* genus (subfamily Myrmicinae) is an abundant and often the most prevailing ant genus in most of the warm climates of the world (Wilson 2003). The worker caste of most *Pheidole* species is dimorphic with relatively slender minors and more robust, conspicuously large-headed majors, so-called "soldiers". The minors take care of most of the daily tasks of the colony, while the majors are specialized in seed milling, abdominal food storage, nest and food resource defence, or some combination of these functions (Wilson 2003). Through this dimorphism, we can easily compare the relative involvement of each worker caste during inter-specific competition.

Some South American ant species of the genera *Pheidole*, *Solenopsis*, *Crematogaster* and *Azteca* compete successfully against *W. auropunctata* and may help keep its population densities low (Tennant 1994; Majer and Delabie 1999; McGlynn and Kirksey 2000; Armbrecht et al. 2001). Nevertheless, the genus *Pheidole* provides a richer source of comparative material than perhaps any other genera because it is well represented in the New Caledonian rainforest litter ant community (Wilson 1976a; Le Breton et al. 2002, 2003).

We studied four *Pheidole* species, two from New Caledonia, and two others from French Guiana. Given the poor state of taxonomic knowledge of New Caledonian ants, *Pheidole* species were designated as mor-

phospecies. *Pheidole* sp. NC1 (body length of minors 2.1 mm; majors 3.5 mm) and *Pheidole* sp. NC2 (body length of minors 1.9 mm; majors 3.5 mm), which appeared to be common in the study site, were tested in areas totally devoid of *W. auropunctata* in order to observe the reaction of colonies that never had contact with this invading species before the experimental encounters of this study. Among the French Guianian species, *P. embolopyx* (body length of minors 2.3 mm; majors 3.5 mm) is commonly found in the deep forest, while *P. fallax* (body length of minors 3.2 mm; majors 5.8 mm) is common at the edges of the rainforest, in open grasslands and in crop plantations (Perfecto 1994; Perfecto and Snelling 1995).

Voucher specimens of *W. auropunctata* and the two Guianian *Pheidole* species were deposited in the ant collection at the *Centro de Pesquisas do Cacau*, Ceplac, Itabuna, Brazil (CPDC), while voucher specimens of New Caledonian *Pheidole* morphospecies were deposited with a code in the IRD collection in Nouméa.

Food resource defence experiments

In the laboratory, we reared *W. auropunctata* colonies, each containing several queens, brood and more than 1,000 workers, in artificial nests (10×10×10 cm closed plastic boxes) purveyed with test tubes half-filled with water and plugged with cotton. The boxes were held in large trays the walls of which were coated with Fluon. A flexible plastic tube connected to each box allowed the ants to exploit food sources placed in the tray. The colonies were starved for 3 days prior to field-based experiments and the plastic tubes were plugged with cotton during their transfer to the field. In the field, we staged interactions between these colonies and *Pheidole* colonies using the same method as Human and Gordon (1996) and Holway (1999) during their studies on the Argentine ant. Each laboratory *W. auropunctata* colony and field *Pheidole* colony was used only once.

During a preliminary stage, baits consisting of a mixture of tinned tuna in oil, cookie crumbs and honey (a source of proteins, lipids and carbohydrates) were deposited on white plastic disks (12 cm in diameter) placed on the ground within 50–100 cm of the nest entrance to each *Pheidole* colony. Once resident *Pheidole* workers had discovered the baits and recruited a stable number of nest mates, a threshold reached after about 45 min, the *W. auropunctata* nests were placed 5 cm away from the baits, and the supple plastic tubes were unplugged. The mouth of the tube was placed at the edge of the white plastic disk. The *W. auropunctata* foragers exited and explored near the baits where they were rapidly detected by the *Pheidole* workers. We monitored the interactions between *Pheidole* and *W. auropunctata* workers for 20 min, and then we removed the *W. auropunctata* workers using an aspirator. This experiment was repeated 15–20 times according to the different *Pheidole* species.

Number of *Pheidole* workers before, during and after the introduction of *W. auropunctata*

We monitored the number of *Pheidole* workers (minors and majors) present at the baits before (Pre.), 20 min after the introduction of *W. auropunctata* (Dur.), and 30 min after the removal of the *W. auropunctata* workers (Post.). The number of workers present at the baits before the introduction (Pre.) of the four *Pheidole* species was compared using a one-way analysis of variance (ANOVA). Then, separately for each *Pheidole* species, we compared the number of workers at the baits before, during and after the introduction of the *W. auropunctata* by applying a paired *t*-test, corrected for three comparisons, using the Bonferroni method.

The number of *Pheidole* majors recruited was registered every 5 min for 20 min from the introduction of the *W. auropunctata*. The number of majors before the introduction of the *W. auropunctata* was compared among the *Pheidole* species using a Kruskal–Wallis one-way ANOVA on ranks. In order to separate out differences among species, we subsequently performed a post-hoc multiple comparison test for non-parametric data (Dunn's method). Secondly, we compared for each species the number of majors at the baits for each time period by applying a one-way ANOVA from transformed square-root data. In order to separate out differences between time periods, we subsequently performed a post-hoc multiple comparison test (Student–Newman–Keuls).

Behavioural data during one-on-one interactions

For each experiment, we observed no more than five interactions between *Pheidole* workers and *W. auropunctata*. The observations were separated by at least 2 min. For each interaction, we noted the initiator, the mechanisms employed by both species (i.e. biting, stinging), the outcome (i.e. win or lose) and the caste of the *Pheidole* worker involved (i.e. minor or major).

For data analysis, these observations were pooled across replicates for each *Pheidole* species. To determine whether it was the *Pheidole* species or the little fire ants that initiated most of the interactions, we compared the proportions of all the interactions that were initiated by each species using Chi-square tests. We performed the same statistical analysis to determine whether *Pheidole* species or *W. auropunctata* won most of the interactions.

Laboratory mortality experiments

These experiments were performed to evaluate the workers' ability to (1) kill and (2) resist the enemy. Ten *Pheidole* workers and 10 *W. auropunctata* workers were placed for 30 min in a glass arena (4.5 cm diameter; 1 cm high), whose walls were coated with Fluon. Then, we counted the number of dead workers from each

species. For each *Pheidole* species, we performed ten separate experiments for each caste (minor and major). The results were compared among workers from each *Pheidole* species by applying a Kruskal–Wallis analysis of variance on ranks. In order to separate out differences among workers, we subsequently performed a post-hoc multiple comparison test for non-parametric data (Dunn's method).

All statistical tests were performed using SigmaStat software.

Results

Number of *Pheidole* workers before and after the introduction of *W. auropunctata*

The introduction of *W. auropunctata* did not affect the number of *Pheidole* workers present at the baits for the Guianian species, although it triggered a decrease in the number of New Caledonian species (Fig. 1). After the removal of the *W. auropunctata* workers from the baits, the number of *Pheidole* workers (Post.) significantly decreased in French Guiana while it returned to its initial value in New Caledonian species (Fig. 1). Note that there were fewer workers of the *P. embolopyx* species at the baits than of the three other species that were present in equivalent numbers (Fig. 1).

Recruitment of major *Pheidole* workers

The number of majors present at the baits differed significantly among the *Pheidole* species before the introduction of *W. auropunctata* (Kruskal–Wallis: df 3; $H=22.129$; $P<0.001$), with the lowest number noted for *Pheidole* sp.NC1 when compared with *P. fallax*; the two other *Pheidole* species had an intermediate number of majors at the baits (Fig. 2).

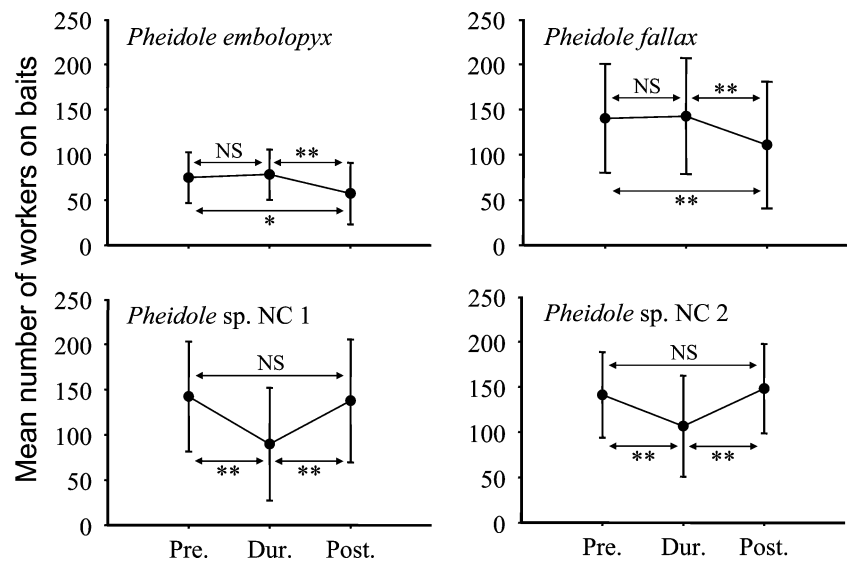
During the 20 min following the introduction of *W. auropunctata*, the number of majors at the baits significantly increased in French Guiana (Fig. 2). The recruited majors of the Guianian *Pheidole* species were immediately directed to the mouth of the flexible plastic tube where they intercepted and killed most of the *W. auropunctata* workers (Fig. 3). In contrast, the number of majors at the baits did not significantly differ in New Caledonia (Fig. 2).

Results of confrontations between *W. auropunctata* and *Pheidole* workers

In French Guiana, *P. embolopyx* workers initiated more interactions than *W. auropunctata*, while no differences were observed between the latter and *P. fallax* workers (Table 1). In New Caledonia, *W. auropunctata* initiated the majority of the interactions (Table 1). The main difference between the encounters observed in the two compared geographical areas concerns the proportion of *Pheidole* majors that initiated the interactions (Table 1). For Guianian species, in which minors avoid *W. auropunctata* and recruit majors, the latter initiated more interactions than the minors, while the contrary was true for the New Caledonian species.

Both Guianian and New Caledonian minor and major *Pheidole* workers attacked *W. auropunctata* workers by biting them. The *W. auropunctata* workers were pinioned but not disabled by minor *Pheidole* workers, while large-headed majors have mandibles sufficiently powerful to crush them. When *W. auropunctata* workers attacked, they first bit the legs or antennae of their opponent and immediately after tried to sting them between two segments. In encounters involving minor *Pheidole*, they often successfully stung their opponent, although they were rapidly crushed and killed by majors before being able to sting them. It clearly appeared that *W. auropunctata* workers attack in

Fig. 1 Comparisons of the number of workers from the tested *Pheidole* species (mean \pm SE) before laboratory colonies of *Wasmannia auropunctata* were introduced (Pre.), 20 min after introduction (Dur.), and 30 min subsequent to removal (Post.) (paired t -test corrected for multiple comparisons using the Bonferroni method; NS $P>0.05$; * $P<0.05$; ** $P<0.001$)



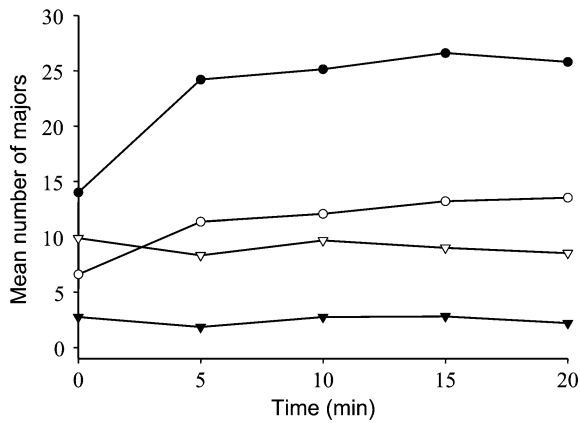


Fig. 2 Average number of majors present on baits during the 20 min following the introduction of a laboratory colony of the little fire ant. Species tested in French Guiana are represented by circles. *Pheidole embolopyx* (white circle one-way ANOVA $F_{4,130}=2.91$; $P=0.05$), *Pheidole fallax* (black circle one-way ANOVA $F_{4,123}=5.78$; $P=0.001$). Species tested in New Caledonia are represented by triangles. *Pheidole* sp. NC1 (black triangle one-way ANOVA: $F_{4,175}=0.656$; $P=0.624$), *Pheidole* sp. NC2 (white triangle one-way ANOVA $F_{4,130}=0.084$; $P=0.987$)



Fig. 3 Illustration, in French Guiana, of recruited *Pheidole fallax* soldiers positioned around the opening of the plastic tube permitting the *Wasmannia auropunctata* to leave their nest in order to forage. Note that the soldiers have their mandibles wide open, ready to crush any *W. auropunctata* that attempts to leave the tube

order to kill their opponent, acting more as predators than as competitors. We also observed that in New Caledonia the corpses of the numerous *Pheidole* workers that were killed were rapidly transported to the nests.

Workers from Guianian *Pheidole* species won significantly more interactions than did *W. auropunctata* workers, while the opposite was true for New Caledonian *Pheidole* species (Table 1). Nevertheless, the outcomes of the interactions appear to depend on which *Pheidole* caste is involved. Against minors, *W. auropunctata* workers won the interactions, while they generally lost against majors. So, the differences in the outcomes of the interactions observed between Guianian and New Caledonian *Pheidole* species were mostly due to the proportion of minors and majors involved. These results are corroborated by laboratory mortality experiments (Fig. 4). Among the minors, this ability did not significantly differ; nevertheless, only minor *P. fallax* workers were able to kill *W. auropunctata* workers, probably due to their relatively large size (Fig. 4a). Except for *Pheidole* sp. NC2, the majors from the other species killed significantly more *W. auropunctata* than the minors (Fig. 4). The major workers from the Guianian species killed more *W. auropunctata* than those from the New Caledonian species, but the difference was significant only for *P. fallax*, again probably due to their relatively large size (Fig. 4b).

Discussion

By highlighting the unadapted behaviour of native dominant species when they face an aggressive invasive species, our study provides an additional explanation as to how the ERH might operate during the colonization process (Shea and Chesson 2002). Moreover, this factor could partly explain how invasive animal species may be able to successfully invade species-rich communities. In fact, most successful ant invasions are probably due to the inability of native dominant species to adopt an efficient behaviour during the prime encounters occurring at the onset of an invasion event.

We have demonstrated in our experiments that South American *Pheidole* species have adopted a more appropriate response to encounters with *W. auropunctata* than have New Caledonian species. Considering the

Table 1 Tendency of *Wasmannia auropunctata* (*Wasm*) or *Pheidole* (*Pheid*) workers to initiate encounters and to win during interactions by killing the antagonist (between parenthesis: part initiated by *Pheidole* majors)

<i>Pheidole</i> species	Location	No. of encounters	Species initiating interactions			Killed the antagonist		
			<i>Wasm</i>	<i>Pheid</i>	<i>P</i>	<i>Wasm</i>	<i>Pheid</i>	<i>P</i>
<i>P. embolopyx</i>	French Guiana	75	17	58 (57)	**	1	74 (74)	**
<i>P. fallax</i>	French Guiana	75	31	44 (42)	NS	16	59 (59)	**
<i>Pheidole</i> sp. NC1	New Caledonia	100	60	40 (12)	*	83	17 (14)	**
<i>Pheidole</i> sp. NC2	New Caledonia	80	51	29 (0)	*	79	1 (0)	**
Total encounters		330	159	171		179	151	

Chi-square tests * $P < 0.05$; ** $P < 0.01$

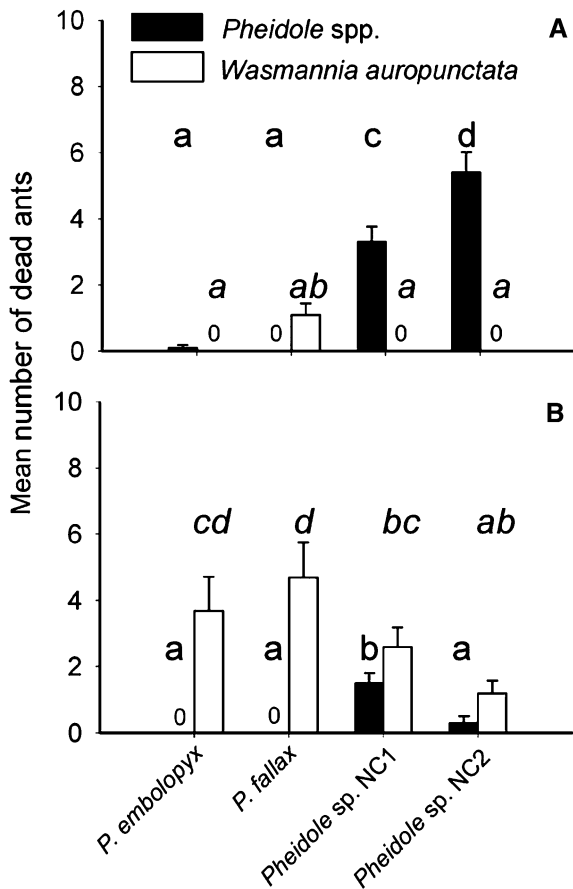


Fig. 4 Results of mortality experiments during group confrontations conducted under laboratory conditions between ten *Wasmannia auropunctata* and ten minor (a) or ten major (b) *Pheidole* workers (ten experiments for each confrontation; mean \pm SE). The *Pheidole* mortality rate differs significantly among the species and the castes involved (Kruskal–Wallis $H_{7,72} = 66.71$; $P < 0.001$) as does the rate of *W. auropunctata* mortality (Kruskal–Wallis $H_{7,72} = 46.32$; $P < 0.001$). The bars bearing the same letters indicate values that are not significantly different at the 5% level of significance [Kruskal–Wallis analysis of variance on rank followed by a Dunn’s post-hoc test; a separate analysis was conducted for rates of *Pheidole* mortality (roman letters) and *W. auropunctata* mortality (italic letters)]

tremendous ability of *W. auropunctata* to rapidly perform mass recruitment, it is to the advantage of the *Pheidole* colonies to strike hard and fast when little fire ant scouts are encountered. Indeed, *P. embolopyx* and *P. fallax* minor workers recruited majors and avoided initiating direct conflicts with *W. auropunctata* since they are inefficient at killing them. The majors were rapidly directed to the mouth of the plastic tubes, where they attacked and killed most of the *W. auropunctata* they encountered. This mode of food defence displayed against *W. auropunctata* is reminiscent of that described between *Pheidole dentata* and different *Solenopsis* species (Wilson 1975).

If the *Pheidole* workers do not eliminate the *W. auropunctata* scouts encountered in the vicinity of a resource, the scouts will rapidly recruit a large number of

nest mates, resulting in a double loss for the *Pheidole* colonies: the resource will be lost and most of the workers present at the resource will likely be killed during the fighting. This occurred when minor workers of New Caledonian *Pheidole* species encountered *W. auropunctata* at the baits and initiated more interactions that mostly led them to their death. Nevertheless, mortality experiments revealed that majors were able to kill the *W. auropunctata* workers, which indicates that they do have the potential to change the outcome of competition events with *W. auropunctata*; however, they were not recruited.

Our results suggest some factors that regulate populations of *W. auropunctata* in its native range and allow it to become invasive when introduced into a new area. In undisturbed natural ecosystems of its native range, *W. auropunctata* is an integral part of the ant community. As long as there is no disturbance, this potential pest ant appears to be regulated by competition, predation and parasitism, and its population is kept under a threshold that does not allow this species to dominate this community. When disturbance does occur, *W. auropunctata* outbreaks may be observed, such that this ant species is considered to be a disturbance specialist in its native range (Majer and Delabie 1999). In contrast, on the scale of New Caledonia, numerous favourable conditions often combine to allow for the huge success of *W. auropunctata*. During the colonization phase, too few native species are able to compete with *W. auropunctata* at the onset of an invasion. Then, during the proliferation phase, the unicoloniality of *W. auropunctata* allows it to develop huge populations (Le Breton et al. 2004). Moreover, *W. auropunctata* promotes the development of native hemiptera that in return provide them with a valuable and constant food resource (Le Breton et al. 2005). In due course, the invading species completely monopolizes available resources and saturates the area leading to the displacement of many native ant species (Le Breton et al. 2003) and, in the case of New Caledonia, one of the worst ecological threats to a highly bio-diversified hotspot.

Two main hypotheses can explain the different behaviours expressed by Guianian and New Caledonian *Pheidole* species. On one hand, New Caledonian *Pheidole* species have evolved in an isolated insular environment where they did not have to adopt such aggressive collective behaviours as Guianian *Pheidole* species. In New Caledonia, the ant species diversity is relatively low, around 130 species (Le Breton 2003) when compared with that found in French Guiana where the total number is estimated at 1,000 species (J.H.C. Delabie, personal communication). The naiveté of island arthropods toward aggressive invaders has often been advanced as an important argument to explain why introduced species have a disproportionate impact on island communities (Gillespie 1999).

Another factor, non-antagonistic to the former, could be advanced. Even if the New Caledonian native dom-

inant *Pheidole* species have the intrinsic ability to adopt an effective defence behaviour, the encounter with *W. auropunctata* did not necessarily trigger an aggressive or defensive reaction. When they are introduced into an area, invasive species are confronted with native species they never encountered during their evolution, and vice-versa. Native species have no benchmark to recognize introduced species as dangerous competitors or enemies; and it is unlikely that they adopt appropriate responses towards introduced species during encounters. A general rule in community ecology is that the ability to recognize competitors or predators and to assess their fighting ability may help to reduce cost of fighting (Grostal and Dicke 2000; Lopez and Martin 2001; Magalhães et al. 2002). In ants, the perception of the potential competitors or enemies can be relatively precise and appears primordial in the issue of many competitive interactions (Wilson 1976b; Feener 1987; Langen et al. 2000). Moreover, it has been shown that in some *Pheidole* species, workers are able to discriminate different species of enemy ants and modify their defensive actions accordingly (Wilson 1976b; Feener 1987; Langen et al. 2000).

In conclusion, our results emphasize the importance of enemy recognition and specification in the organization of ant communities where different species coexist while they have to respond to their natural competitors, predators and parasites with specific aggressive or defensive actions.

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