Ethology / Éthologie

The raiding success of *Pheidole megacephala* on other ants in both its native and introduced ranges

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Abstract

We studied the behaviour of the invasive African myrmicine ant, *Pheidole megacephala*, when confronted with colonies of other common ant species in Cameroon, a part of its native range, and in Mexico, where it has been introduced. *P. megacephala* raided the nests of the other ants in both cases. Eleven species out of 12 put up a rather strong resistance to raiding *P. megacephala* workers in Cameroon compared to only three species out of 11 in Mexico, where only colonies of *Solenopsis geminata*, *Dorymyrmex pyramicus* and *Dolichoderus bispinosus* resisted these raids. We conclude that *P. megacephala*'s heightened ability to successfully raid colonies of competing ants may help explain its success and the decline of native ants in areas where it has been introduced. *To cite this article: A. Dejean et al., C. R. Biologies 331 (2008).*
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Résumé

Succès des raids de *Pheidole megacephala* contre d'autres fourmis en zone d'origine ou d'introduction. Nous avons étudié le comportement de la fourmi envahissante *Pheidole megacephala* confrontée avec des colonies d'autres fourmis du Cameroun, faisant partie de son aire d'origine, et du Mexique où elle a été introduite. Au Cameroun, 11 espèces sur 12 ont montré une résistance plutôt forte aux raids de *P. megacephala* en comparaison de trois espèces sur 11 au Mexique, où les colonies de *Solenopsis geminata*, *Dorymyrmex pyramicus* et *Dolichoderus bispinosus* ont bien résisté aux raids. Nous concluons que la capacité de *P. megacephala* de piller les nids des autres fourmis peut expliquer en partie son succès et le déclin des espèces natives dans les zones où elle a été introduite. *Pour citer cet article : A. Dejean et al., C. R. Biologies 331 (2008).*
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Mots-clés : Fourmis envahissantes ; Prédation ; Pillage d'autres colonies ; Recrutement

1. Introduction

The success of invasive, introduced species depends on several characteristics, including their own biology,

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the recipient community, and the abiotic conditions that together are known as a 'niche opportunity' [1]. Consequently, it is a challenge to identify the factors that regulate these species in their native range and those factors that allow such species to become invasive once introduced into a new area.

Invasive ants offer a good model for exploring this issue. Out of the 12,431 ant species known [2], about 150 so-called 'tramp species' have been transported and introduced into many parts of the world through human activity. Although the impact of many introduced ant species is limited to human settlements, some species have also become invasive, penetrating into many habitats in introduced regions where they seriously affect agricultural production and native biodiversity in part due to their ability to form huge supercolonies [3,4]. Invasive species share four characteristics generally noted as making this possible. First, the species must possess the intrinsic ability to shift from a multi-colonial social structure (i.e., several independent colonies) in their native range to unicoloniality (i.e., populations do not have colonial boundaries resulting in the absence of intraspecific territoriality over extended areas) in the introduced range. This genetically-based feature has been demonstrated in several species [5–8]. Second, separation from co-evolved parasites, predators and competitors (known as the 'enemy release' hypothesis) allows invasive species to allocate more energy and workers to tasks other than colony protection [4]. Third, the ability to have a mutualistic association with hemipterans permits invasive ants to tend native as well as introduced hemipterans [4,9,10]. Fourth, the success of most invasive ants is associated with the monopolization of resources in part due to mass recruitment and a high level of aggressiveness towards native ants that are either displaced or eliminated through competition [4,9, 11,12].

Once their colonies have reached a relatively high density, invasive ants lower native ant abundance and diversity by eliminating native species and by altering the community organization among those species that survive their invasion [4,13,14]. Thus, invasive ants directly or indirectly affect all other organisms, so that they have become known as 'pests' and are considered to be one of the greatest causes of lowering biodiversity in the world [1,4].

Although invasive ants have been the focus of numerous studies in areas where they have been introduced, little is known about their behaviour in their native range [4]. We felt, then, that the best way to understand the mechanisms leading to these ants' invasive success was to see whether, in their native range, these ants already possessed certain characteristics that may allow some of them to become invasive once introduced into other areas [1,15]. To that end, we focused this study on the activity of one species, *P. megacephala*, when confronted with other ants both in Cameroon, a part of its native range, and in Mexico where the species has been introduced.

2. Materials and methods

This study was conducted on four *P. megacephala* colonies in Cameroon (on the campus of Yaoundé University, 3°50′N, 11°30′E), and in Mexico (Puerto Morelos, Quintana Roo; 20°N, 86°W) on a huge colony whose territory has spread over several kilometres along the Caribbean coast [16]. The colonies we studied in Yaoundé very likely correspond to the *P. megacephala* colonies referred to as 'Cameroon 109' in Taylor [17] as they were found in the same areas (although these colonies extended for hundreds of meters along the road side, different colony recognition was observed, as workers from different regions will fight each other during confrontation tests; A.D. pers. obs.).

Pheidole megacephala is native to tropical Africa and has become pantropical [18] after having been unwittingly dispersed by human commerce throughout the tropics and sub-tropics. Because it is able to produce dominant supercolonies in introduced areas [3,4,17], it is one of the invasive ants that has most successfully and severely reduced native arthropod abundance both in disturbed habitats and in tropical rain forests [9,19].

As it is the case for most species in this genus, the worker caste is dimorphic, with no intermediary body size between the small minors (approximately 2 mm long) and the big-headed majors (or soldiers; 3–4 mm long). Also, workers have an atrophied sting that they use to lay scent trails, but not to subdue prey or competitors [20]. This species nests in the ground, in termite mounds or in the crevices of tree bark and, like most other invasive ants, is omnivorous. It has always been assumed that *P. megacephala* is a good predator, because arthropod abundance and diversity decline in areas where it has been introduced [3,17,21,22]; however, this has also recently been demonstrated in its native range [23,24].

To examine *P. megacephala*'s response to potential competing ant species, we reared colonies of the most frequently encountered species in Cameroon, and in a non-invaded area in Mexico adjacent to the invasion zone. The ants tested were reared in the laboratory in 22×2.5 cm test tubes supplied with a water source and opening into hunting arenas composed of wooden

Table 1

Ant species tested against *Pheidole megacephala* workers foraging under natural conditions (the tested ant colonies were in captivity). A: all individuals were killed in less than one hour; B: all individuals were killed in over one hour; C: only some individuals were killed; D: none of the individuals were killed. We defined four scores of species' resistance to *P. megacephala* raids as follow: (1) low resistance to *P. megacephala* (A, B or AB), (2) average resistance (medium: ABC or BC), (3) rather high resistance (BCD), and (4) high resistance (C, CD or D). Statistical comparison based on scores (frequency at which species resisted *P. megacephala* raids) between Cameroon and Mexico: *Chi*-square test for trends, $\chi^2 = 5.59$; 1df; $P = 0.018$

Native range: Cameroon (12 species)		No of cases	A	B	C	D	Score
Ponerinae	*Leptogenys* sp.A	4	2	2			Low
	Odontomachus troglodytes Santschi	4		1	3		Medium
	Plectroctena minor Emery	11		1	6	4	Rather high
	Pachycondyla analis (Latreille)	3			3		High
	Pachycondyla soror (Emery)	12			11	1	High
	Pachycondyla tarsata (Fabricius)	8			5	3	High
Cerapachyinae	*Cerapachys* sp.A	3			3		High
Myrmicinae	*Crematogaster striatula* Emery	5		1	2	2	Rather high
	Myrmicaria opaciventris Emery	6			2	4	High
	Tetramorium bicolor Viehmeyer	6		1	4	1	Rather high
Formicinae	*Anoplolepis tenella* Sanstchi	2			2		High
	Camponotus brutus Forel	5			5		High
	Total	69	2	6	45	15	
Invaded area: Mexico (11 species)							
Ponerinae	*Leptogenys mexicana* (Mayr)	3	3				Low
	Odontomachus brunneus (Patton)	5	2	3			Low
	Pachycondyla harpax Fabricius	8	3	5			Low
	Pachycondyla obscuricornis Emery	4	3	1			Low
	Pachycondyla villosa (Fabricius)	4		4			Low
Ectatomminae	*Ectatomma tuberculatum* (Olivier)	4	1	2	1		Medium
Myrmicinae	*Crematogaster* sp.A	5		2	3		Medium
	Solenopsis geminata (Fabricius)	2			2		High
Dolichoderinae	*Dolichoderus bispinosus* (Olivier)	5			5		High
	Dorymyrmex pyramicus (Roger)	8				8	High
Formicinae	*Camponotus planatus* (Roger)	6	1	3	2		Medium
	Total	54	13	20	13	8	

boxes (50 × 30 × 7 cm) covered with a plate of glass (see Table 1 for the list of species reared). Depending on the size of the workers from the tested species, one to three test tubes were connected to the hunting area. The mouths of the tubes were stopped with a cork pierced with a hole permitting the reared ants to pass through. One side of each hunting arena was pierced with small holes permitting the *P. megacephala* workers and soldiers to enter (these holes were plugged with cotton prior to the field experiments). Each time 200–250 workers plus brood (or entire colonies for certain species) were reared for three days prior to the experiments.

For each experiment, we placed one box plus the connected test tubes in the field, on the natural territory of a *P. megacephala* colony, 3–4 m from a nest entrance (several nest entrance sites were tested in both Cameroon and Mexico). We then monitored *P. megacephala* workers for two hours following the installation of the introduced ant colonies, or less if the time required for *P. megacephala* to find and completely de-

stroy the ant colonies was under two hours. The encounters between *P. megacephala* and workers from colonies of the tested species therefore occurred in the hunting arenas. We observed and scored the four following situations. A: All of the individuals of the tested colony were killed in less than one hour following the discovery of the introduced nest by a *P. megacephala* scout; B: the same result in between the first and second hour; C: only some of the individuals were killed during the total duration of the experiment (monitoring of each introduced colony for two hours); or D: none of the individuals were killed. Then, a statistical comparison between the results found in Cameroon and Mexico was conducted on the frequency at which species resisted *P. megacephala* raids from both localities using a contingency table and the *Chi*-square test for trends (GraphPad Prism 4.0 software).

3. Results

In all tested cases, the experimental device/colony was discovered in less than 20 min by *P. megacephala*

scout workers (only minor workers) in both study sites. In Cameroon, when these scouts discovered the experimental devices, they entered the hunting arenas and then immediately returned to their nest to recruit nestmates in all cases. Recruited *P. megacephala* individuals gathered and retrieved refuse from the competing species' nests (prey debris and dead workers deposited in a corner of the foraging arena). In Cameroon, seven species out of twelve resisted the raids without losing a worker (*High* in Table 1); three others resisted well overall, but in some instances their colonies were killed in more than an hour (*Rather high* in Table 1). *Leptogenys* sp. A was the most vulnerable species tested and the only species in the native range with all of its colonies killed, sometimes in less than one hour.

In Mexico, the colonies of eight species out of 11 were always (*Low* in Table 1; $n = 5$) or often killed (*Medium* in Table 1; $n = 3$) by *P. megacephala*. In contrast, only *Dorymyrmex pyramicus*, *Dolichoderus bispinosus* and *Solenopsis geminata* always resisted the raid with little or no loss of life.

It so happens that in both Cameroon and Mexico, the guards of the colonies of some species were ineffectual when faced with small *P. megacephala* workers, and hardly reacted when the latter entered the hunting arena or even the mouths of the test tubes (i.e., their nest entrance). On the contrary, species that resisted well first counter-attacked, and then stayed just behind the holes pierced on one side of the hunting arena, ready to bite any intruder. Even, *D. pyramicus* workers, which are relatively small, sometimes exited the hunting arena to attack the intruders outside of the nest.

The overall result is a significant difference between Cameroon and Mexico concerning the frequency at which species resisted *P. megacephala* raids (Table 1).

4. Discussion

The negative impact on native species by invasive ants in areas where they have been introduced is hypothesized to be related to a high level of aggressiveness, because the invaders come from species-rich environments where heightened aggressiveness is adaptive [4,9,11,12]. Indeed, in central Africa, *P. megacephala* colonies can compete with territorially dominant arboreal ants such as *Crematogaster africana* and *Oecophylla longinoda* in the low canopies of cocoa tree plantations [10,17]. In addition, the success of invasive species is facilitated when they are able to take advantage of a 'niche opportunity', or the combination of a so-called 'escape opportunity' and a 'resource opportunity' [1]. An 'escape opportunity' arises when native

species do not abound or are not effective in keeping out introduced species, a situation that is generally true for islands, but not for the Mexican study site, which is species-rich, at least in ants, and has one of the highest densities of army ants ever noted [16]. A 'resource opportunity' arises when the resources that a species needs are highly available, a situation difficult to apply to the Mexican study site as numerous food sources and nesting sites, if not all, were exploited by native ants before *P. megacephala* was introduced, as shown by a study conducted in an adjacent non-invaded area [16]. It is therefore probable that the *P. megacephala* colony first successfully invaded the disturbed habitat of the small harbour of Puerto Morelos, far from competition with native ants or predation by army ants, before spreading into the village of Puerto Morelos, and then over a wider, natural, undisturbed area.

The present results highlight the capacity of *P. megacephala* to raid other ant colonies in both its native and introduced ranges, a behaviour also noted in *Linepithema humile* and *Solenopsis invicta* in their introduced range [4,25]. It is likely that, in addition to its ability to achieve unicoloniality, raiding other ants constitutes a prerequisite for *P. megacephala* for becoming an 'ecologically dominant' species in areas where it is introduced. This is particularly true on islands where organisms (including ants) offer only little resistance to invasive species due to their high taxonomic endemism [1,4,7,26,27]. Furthermore, invasive species not only eliminate native species, but also disassemble their communities where each species occupies and maintains its position after a long co-evolutionary process [28]. Comparing these situations for *P. megacephala*'s in both the native and introduced range has given us new insight into 'how' disassembling ant communities can initially occur: in its native range, the ant community is structured in large part due to numerous species that are able to resist raids, a trait that we have now shown is reduced or absent in a number of species in the introduced range.

During successful *P. megacephala* raids in the native and introduced range, the guards of the attacked colonies seem stunned, even when the *P. megacephala* workers do not come directly into contact with them. Since the same thing has been noted for non-ant prey, it has been suggested that the workers release a secretion from their mandibular glands [24], but secretions from the pygidial gland could also be involved [29]. The size of the attacked workers does not play a role, as relatively large Poneromorphs workers are inefficient guards when confronted with *P. megacephala* raiders.

Moreover, the efficacy of *P. megacephala* scout workers is enhanced by the fact that they recruit nestmates when they discover the landmarks of competing ant colonies, avoiding actually having to come into contact with alien workers, and potentially being attacked and even killed; the same is also true when they perceive termite scents [23,24].

In conclusion, this study suggests that *P. megacephala*'s heightened ability to raid the colonies of most of the ant species it encounters in its introduced range permits it to very rapidly destabilize the native ant communities that constitute a first bulwark of defence against invasive ants.

Acknowledgements

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