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# The antipredatory behaviours of Neotropical ants towards army ant raids (Hymenoptera: Formicidae)

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**Abstract**

Group hunting, nomadism, wingless queens and colony fission characterize army ants, allowing them to have become the main tropical arthropod predators, mostly of other social insects. We studied the reactions of different ant species to the New World army ants *Eciton burchellii* (WESTWOOD, 1842) and *E. hamatum* (FABRICIUS, 1782) (Ecitoninae). We compiled our results with those already known in a synthetic appendix. A wide range of ant species react to the approach of army ant raids by evacuating their nests with several workers transporting brood. The *Eciton* plunder a large part of the brood but rarely kill workers or queens, so that the latter return to their nest and resume colony activity. One exception is *Paratrechina longicornis* (LATREILLE, 1802) colonies that quickly evacuate their nest, so that the entire colony can generally escape a raid. Another is *Leptogenys mexicana* (MAYR, 1870) that leave their nests in columns while some nestmates resist the attack; they therefore lose only a few larvae. We noted that colonies can avoid being raided if the army ants ignore them (*Atta cephalotes* (LINNAEUS, 1758)), or if the workers produce a repellent substance (*Azteca* associated with myrmecophytic *Cecropia*) or are repellent themselves (*Pachycondyla villosa* (FABRICIUS, 1804), *Ectatomma* spp.). In the other cases, a part of the brood is lost. When an *Eciton* raid approached the base of their host-tree trunk, *Azteca andreae* GUERRERO, DELABIE & DEJEAN, 2010 workers dropped a part of their brood on the ground. While numerous *Eciton* workers were gathering up this brood, the front of the column advanced, so that the *Azteca andreae* nests were not plundered. *Pheidole megacephala* (FABRICIUS, 1793) nests were partly plundered as the workers reacted aggressively, blocking the *Eciton* inside their nests during a long time. When the latter returned toward their bivouac, they were attacked and killed by their nestmates whether or not they had retrieved *Pheidole* brood. Consequently, the front of the column turned away from the *Pheidole* nest.

**Key words:** Army ants, Ecitoninae, prey-ant species, antipredatory behaviour.

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## Introduction

Army ants belong to the dorylomorph section of the Formicidae for which four of the six subfamilies constitute a monophyletic group where the Aenictinae, Aenictogitoninae and Dorylinae make up the Old World army ants and the Ecitoninae the New World army ants (BRADY 2003, MOREAU & al. 2006, KRONAUER 2009). Species from these four subfamilies are characterized by large colonies (up to 10 million individuals for *Dorylus*), nomadism, dichtadiiform queens (i.e., extremely physogastric and without wings, ocelli and often eyes), reproduction through colony-fission and obligate group predation (GOTWALD 1995, KRONAUER 2009).

Old world *Dorylus* army ants are known to be generalist predators able to attack termites; certain species are even specialized in termite predation (GOTWALD 1995, SCHÖNING & MOFFETT 2007). If *Dorylus* have rarely been noted as preying on other ant species (but see BERGHOFF & al. 2003, BECK & KUNZ 2007), *Aenictus* species are specialist ant predators (HIROSAWA & al. 2000). All New World army ants, on the other hand, prey mostly on other ants even when they are generalist predators, while they are only rarely termitophagous (BORGMEIER 1955, PULLEN 1963, MIRENDA & al. 1980, RETTENMEYER & al. 1983, GOTWALD 1995, SOUZA & MOURA 2008). Certain ecito-

nine are specifically predators of ants, some of them to the point of specializing in a particular genus (PERFECTO 1992, GOTWALD 1995, LAPOLLA & al. 2002, POWELL & CLARK 2004, POWELL & FRANKS 2006, LE BRETON & al. 2007). When they successfully raid a colony, most ecitonine only collect the brood and callow workers. Because they are not injured, the older workers and queens later reestablish the colony (RETTENMEYER & al. 1983, GOTWALD 1995, LE BRETON & al. 2007).

Because potential prey colonies need to limit the impact of the army ant raids, their workers must be able to recognize the aggressor in order to elicit a "defence response" starting with the emission of an alarm pheromone. The notion of enemy specification (WILSON 1975) is based on the recognition of cues for species presenting a high degree of threat. Indeed, prey-ants can detect the pheromone emitted by army ant workers detecting a potential prey from a distance since the group hunting strategy of army ants requires the rapid recruitment of nestmates to overwhelm large or grouped arthropods. Contact can also permit the recognition of species-specific cuticular substances by prey-ants (HÖLLDOBLER & WILSON 1990, GOTWALD 1995, LALOR & HUGHES 2011). When detecting army ant presence, prey-ants emit alarm pheromones produced in the mandibular gland, triggering a rapid but short-lived behavioural stimulus (HÖLLDOBLER & WILSON 1990). WILSON & REGNIER (1971) broadly categorized alarm responses according to the size and vulnerability of the colonies. Small or vulnerable colonies typically exhibit "panic" responses in which individuals run away from the stimulus, either back into the nest or away from the nest, carrying brood. Like for slavemaking ants that emit a "propaganda" substance produced by the Dufour's gland (LENOIR & al. 2001), this panic can be due to an allomone released by the army ants (LE BRETON & al. 2007).

The threat of an army ant raid can be limited by reducing the probability of being detected as do *Pheidole* spp. which make their nest entrance difficult to discern (MIRENDA & al. 1980) and *Stenamma* which build elevated nest entrances or close them with a pebble (LONGINO 2005). Even if detected, workers of the leaf-cutting ants *Atta cephalotes* (LINNAEUS, 1758) and *Atta colombica* (GUÉRIN-MÉNEVILLE, 1844) plug their nest entrances with soil and organic debris, including pieces of leaves (SWARTZ 1998, POWELL & CLARK 2004), while in *Pheidole obtusospinosa* PERGANDE, 1896 super majors block the nest entrance with their heads (HUANG 2010).

Another way of defending against army ants is found in chemical-based protection. *Eciton* spp. avoid certain species of *Crematogaster*, *Myrmecocystus*, *Forelius*, and *Acromyrmex* (RETTENMEYER & al. 1983, SAN JUAN 2002) and they do not climb up myrmecophytes (i.e., plants housing specific ants in hollow structures) as they are likely repelled by territorial markings on these plants by the resident plant-ants (BEQUAERT & WHEELER 1922, HERRE & al. 1986, DEJEAN & al. 2001). Also, chemical repellency can be associated with aggressiveness toward the army ants as has been noted for *Azteca* with large colonies such as *Azteca chartifex* (FOREL, 1896) and *Azteca instabilis* (F. SMITH, 1862) whose workers attack *E. burchellii* (WESTWOOD, 1842) or *E. hamatum* (FABRICIUS, 1782) raids at the base of their trees (CHADAB-CREPET & RETTENMEYER 1982, WILD 2011, ANTWEB 2012). When they detect a *Neivamyrmex nigrescens* (CRESSON, 1872) raid, *Pogonomyrmex barbatus* F. SMITH, 1858 workers even form a group and walk into the column scattering the army ants in all directions (MIRENDA & al. 1980).

Counter-offensives have also been reported. When *Nomamyrmex esenbeckii* (WESTWOOD, 1842) columns raid mature *Atta colombica* or *Atta cephalotes* colonies, teams of both major (fighting ability) and small *Atta* workers (numerous individuals) counterattack outside their nests (POWELL & CLARK 2004; see the Lanchester theory of combat in FRANKS & PARTRIDGE 1993). Indeed, the worker caste of *Atta* spp., which is composed of several million individuals, is highly polymorphic and colony defence is enhanced by the presence of large-headed majors equipped with powerful mandibles (HÖLLDOBLER & WILSON 1990). The attacked *Atta* colonies are generally raided if they are immature with fewer workers and an absence of majors (SWARTZ 1998, SANCHEZ-PENA & MUELLER 2002, POWELL & CLARK 2004, SOUZA & MOURA 2008, LONGINO 2012).

One might wonder what happens when two army ant columns meet. In the Neotropics, *Eciton burchellii* colonies never fight each other and separate from one another when the fronts of columns come into contact (FRANKS & BOSSERT 1983, RETTENMEYER & al. 1983, WILLSON & al. 2011). Also, colony mergers with queenless colonies can occur (SCHNEIRLA 1971).

The aim of this study, which takes a "bottom-up" approach (see TSCHINKEL 2011), was to look for new cases of prey-ant reactions when raided by *Eciton burchellii* and *E. hamatum* and to compile these cases along with those previously known into a wider classification including other New World army ants (Appendix 1, as digital supplementary material to this article on the journal's web pages).

## Materials and Methods

**Study areas:** This study was partly conducted along the Caribbean coast of Quintana Roo, Mexico, between Puerto Morelos (20° 51' 00" N; 86° 52' 00" W) and the Sian Ka'an Biosphere Reserve (20° 7' 40" N; 87° 27' 56" W). Along this coast, strips of land about 450 m wide separate fossil lagoons from the sea. The lagoons are connected to the sea by small tidal inlets. The coastal strip is made up of dune vegetation and mangroves where, from the sea to the inland fossil lagoons, there is a succession of three ecological zones: sandy beach, dunes with shrubs and coconut trees and occasional low vegetation, and then mangrove all along the inland lagoon. The *Eciton* colonies set up their bivouacs almost exclusively in the mangrove (DUROU & al. 2002). During the two years (1989 - 1990) that we lived and worked in the area, we had frequent opportunities to witness *E. burchellii* and *E. hamatum* raids due to their high density (0.71 colonies per hectare versus 0.033 in Panama, 0.49 in Peru and 0.057 in Costa Rica; FRANKS 1982, DUROU & al. 2002, VIDAL-RIGGS & CHAVES-CAMPOS 2008, WILLSON & al. 2011). Arboreal ants were mostly present in the mangrove, while ground-nesting species occurred in the other areas (DUROU & al. 2002). Another part of the study was conducted in the mature forest situated around the Petit Saut biological station in Sinnamary, French Guiana (05° 03' 30" N; 52° 58' 34.6" W). Numerous myrmecophytic *Cecropia obtusa* TRÉCUL, 1847 trees grow along

the paved road leading to the station and along dirt roads, permitting us to note the reactions of their associated plant-ants when an *Eciton* raid occurred at the base of their host trees (1996 - 2012).

**The army ants studied:** *Eciton burchellii* lives in colonies of 300,000 to 650,000 individuals that reproduce by fission (FRANKS 1985). During the 20 days of the "statary" phase of its typical 35-day-long cycle of activity, a colony resides in a fixed bivouac made up of numerous workers using their claws to link their legs and bodies together, with the queen and brood at the centre. The physogastric queen may lay ca. 100,000 eggs that hatch into larvae at the end of this phase. To be able to pass through their five larval instars before pupating, the larvae trigger an increased demand for prey, so that the colony enters its 15-day nomadic phase during which a new bivouac is formed nearly daily at dusk. Each morning a new raid forms; the queen, no longer physogastric, joins in the nightly emigrations. As the larvae pupate, a new statary phase begins with the pupae emerging into callow workers at the end of this phase. Large colonies rear a sexual brood resulting in numerous males and a few gynes. Note that *E. hamatum* has a very similar lifestyle (HÖLLDOBLER & WILSON 1990, GOTWALD 1995, KRONAUER 2009).

During the statary phase, the raids radiate away from the bivouac like the spokes of a wheel from the hub; colonies avoid foraging twice over the same area thanks to successive raids at a mean angle of 129.3° (WILLSON & al. 2011). Throughout the nomadic phase, the colonies follow a relatively straight path from one day to the next, maximizing the distance between the positions of the successive statary bivouacs. Indeed, the values of the angles between foraging bouts from one day to the next, 56.4° to 67.6°, are oriented in the opposite direction (WILLSON & al. 2011, but see CALIFANO & CHAVES-CAMPOS 2011). In their raids, *Eciton burchellii* workers follow a main column whose front widens, forming a "carpet" of workers that fans out to a width of up to 20 m; in this way, they may capture ca. 30,000 prey items per day (BOSWELL & al. 1998). *Eciton hamatum* is a column raider whose workers branch out along each side of the main column in small foraging groups; they can capture 15,000 to 40,000 prey items per day and sometimes up to 90,000 items (RETTENMEYER & al. 1983). In both cases, when the workers reach the front of the column, they return to the bivouac even if unsuccessful at capturing a prey, so that the trunks of the columns are formed by workers running in both directions. This fact is particularly important as it determines if an area (or a tree) will be thoroughly explored (if a worker finds a prey, it emits a pheromone that attracts nestmates); the workers concentrate their efforts on areas where prey is plentiful. The raids of these two species are epigaeic and mostly diurnal. They also climb trees to attack arboreal insects, particularly ants and wasps whose brood represents more than 50% of *E. burchellii* prey and most of the *E. hamatum* diet (TELES DA SILVA 1977a,b, 1982, RETTENMEYER & al. 1983, GOTWALD 1995, POWELL & FRANKS 2006).

## Results and discussion

### Ant species that evacuate their nest

**Species in which the queens remain inside the nest:** Just before being raided by army ants, *Camponotus atriceps* (F. SMITH, 1858), *Camponotus planatus* (ROGER, 1863), *Pheidole* sp. (*flavens* group) and *Solenopsis geminata* (FABRICIUS, 1804) workers evacuated their nests, many workers carrying brood (Tab. 1). They climbed on the nearby vegetation, rocks and walls. Groups of five to 20 *S. geminata* workers, most of them transporting a pupa or a larva, formed and stayed in the same spot during three to five hours, then returned to their nests all at once. Note that when present, male and winged female *C. atriceps* and *C. planatus* participated in the nest evacuation. In the same situation, *Pachycondyla harpax* (FABRICIUS, 1804) workers, which apparently cannot climb trees or walls, evacuated their nest in a column carrying pupae and large larvae (Tab. 1). They continued until they found a hole in the ground in which they sheltered. All of these colonies, particularly *Pheidole* sp., lost a part of their brood.

Nest evacuation by workers transporting brood was frequently noted when different species of *Camponotus* and *Pheidole* were raided by *Eciton burchellii*, *E. hamatum* or *Neivamyrmex nigrescens* (MIRENDA & al. 1980, DROUAL & TOPOFF 1981, LAMON & TOPOFF 1981, TELES DA SILVA 1982, DROUAL 1983, 1984, RETTENMEYER & al. 1983). Yet, other *Camponotus* and *Pheidole* species resist by recruiting major workers that plug the nest entrance (LAMON & TOPOFF 1981). When raided by *Labidus coecus* (LATREILLE, 1802), *Solenopsis geminata* workers also evacuate their nests and transport brood (PERFECTO 1992).

**Species in which the entire colony evacuates the nest, queen included:** Thanks to the alarm pheromone emitted by returning foraging workers, *Paratrechina longicornis* (LATREILLE, 1802) evacuated their nest long before an *Eciton burchellii* raid reached them. The entire *Paratrechina* colony quickly formed a concentric group with the queens at the centre surrounded by workers transporting nymphs, then larvae or eggs, all surrounded by workers not transporting brood. At the extreme periphery were the *Paratrechina* workers that zigzagged at high speed along loops 20 - 50 cm in diameter, joining the migrating colony from time to time. They were likely scouts able to gather information on the location of the front of the *E. burchellii* column they encountered during their swift movements. The *E. burchellii* workers never tried to attack these *Paratrechina* workers or to locate the migrating group, while, in the same situation, *E. hamatum* workers did try to attack. The *E. hamatum* workers likely emitted a pheromone as nestmates situated in a radius of 30 - 40 cm increased their speed, taking the direction of the migrating *Paratrechina* colony. Yet, they seemed disarmed by the very fast, zigzagging *Paratrechina* workers and ended the pursuit as, in the meantime, other prey were found (Tab. 1).

Exceptionally, a *Paratrechina* colony nesting at the base of the wall of a house was not alerted before their nest was raided by *Eciton hamatum*. The *Paratrechina* queens and workers, some of the latter carrying brood, escaped quickly from several holes and cracks in the ground, scattering in all directions. Then, several groups formed, climbed the wall and took refuge in the roof. This time, the *E. hamatum* workers successfully plundered some *Paratrechina* larvae (Tab. 1).

**Species that display slight resistance while nestmates evacuate the nest in a column:** *Leptogenys mexicana* (MAYR, 1870) workers carrying brood evacuated their nests from one opening while some nestmates resisted an *Eciton*

Tab. 1: Reactions of different ant species when faced with *Eciton burchellii* or *E. hamatum* raids.

| Raided ant species | Subfamily | Army ant species | Number of encounters noted | Number of colonies invaded | Country |
|---|---|---|---|---|---|
| **Avoided by army ants** | | | | | |
| *Atta cephalotes* | Myrmicinae | *Eciton burchellii* | 4 | 0 | Mexico |
| **Plant-ants having a repulsive effect on army ants** | | | | | |
| *Azteca alfari*, *Azteca ovaticeps* | Dolichoderinae | *Eciton burchellii* | 6 | 0 | French Guiana |
| **Workers guard the nest entrance; they are avoided by army ants** | | | | | |
| *Pseudomyrmex gracilis* | Pseudomyrmecinae | *Eciton burchellii* | 5 | 0 | Mexico |
| *Pachycondyla villosa* | Ponerinae | *Eciton burchellii* | 5 | 0 | Mexico |
| *Ectatomma brunneum* | Ectatomminae | *Eciton burchellii* | 4 | 0 | French Guiana |
| *Ectatomma ruidum* | Ectatomminae | *Eciton burchellii* | 4 | 0 | Mexico |
| *Ectatomma tuberculatum* | Ectatomminae | *Eciton burchellii* | 7 | 0 | Mexico |
| **Sacrificed a part of the brood** | | | | | |
| *Azteca andreae* | Dolichoderinae | *Eciton burchellii* | 4 | 0 | French Guiana |
| **Nest evacuation, workers transported brood** | | | | | |
| *Solenopsis geminata* | Myrmicinae | *Eciton burchellii* | 5 | 5 | Mexico |
| | | *Eciton hamatum* | 1 | 1 | Mexico |
| *Pheidole* sp. (*flavans* group) | Myrmicinae | *Eciton burchellii* | 4 | 4 | Mexico |
| | | *Eciton hamatum* | 3 | 3 | Mexico |
| *Camponotus atriceps* | Formicinae | *Eciton burchellii* | 39 | 39 | Mexico |
| | | *Eciton hamatum* | 12 | 12 | Mexico |
| *Camponotus planatus* | Formicinae | *Eciton burchellii* | 29 | 29 | Mexico |
| | | *Eciton hamatum* | 31 | 31 | Mexico |
| *Pachycondyla harpax* | Ponerinae | *Eciton burchellii* | 3 | 3 | Mexico |
| *Leptogenys mexicana* | Ponerinae | *Eciton burchellii* | 7 | 7 | Mexico |
| *Paratrechina longicornis* | Formicinae | *Eciton burchellii* | 12 | 1 | Mexico |
| | | *Eciton hamatum* | 2 | 0 | Mexico |
| **Reacted by fighting, blocked the army ants inside their nests for a long time, partly plundered** | | | | | |
| *Pheidole megacephala* | Myrmicinae | *Eciton burchellii* | 24 | 24 | Mexico |
| | | *Eciton hamatum* | 11 | 11 | Mexico |
| **Attacked the army ants** | | | | | |
| *Dolichoderus bispinosus* | Dolichoderinae | *Eciton burchellii* | 4 | 0 | Mexico |
| *Dorymyrmex pyramicus* | Dolichoderinae | *Eciton burchellii* | 22 | 0 | Mexico |
| | Dolichoderinae | *Eciton hamatum* | 8 | 0 | Mexico |

*burchellii* raid at the other entrance. During contact with the *Eciton*, the defending *Leptogenys mexicana* workers were very rarely bitten; if they were, their well-sclerotized cuticle permitted them not to be injured. During the nest evacuation, they lost only a few small larvae and maybe some eggs. Each time, they formed a column and took refuge in a rotten log more than 100 m away (Tab. 1).

Cases of prey-ants evacuating their nests early enough to avoid being raided have rarely been noted (some cases for *Pheidole desertorum* WHEELER, 1906 and *Pheidole hyatti* EMERY, 1895, see MIRENDA & al. 1980), while this was almost always the case in this study for *Paratrechina longicornis* and *Leptogenys mexicana* that lost only a few larvae.

### Ant species that are ignored or avoided

We observed five encounters between *Atta cephalotes* and *Eciton burchellii* and never noted aggressiveness between the workers, even when a raid traversed a part of an *Atta* nest (Tab. 1). This is in keeping with findings by RETTENMEYER (1963) who observed that *Atta cephalotes* and *E. burchellii* or *E. hamatum* workers typically ignore one another during encounters in nature. Yet, *Eciton quadriglume*

(HALIDAY, 1836) and *Nomamyrmex* spp. can raid *Atta* nests (RETTENMEYER 1963, SWARTZ 1998, POWELL & CLARK 2004, LONGINO 2012).

*Pseudomyrmex gracilis* (FABRICIUS, 1804) colonies nest in myrmecophytic acacia or in dry, hollow twigs; their nests are not attacked although the *Eciton burchellii* workers from the raids thoroughly explore the shrubs in the area. One worker plugs the nest entrance with its head even in the absence of an army ant raid. Thanks to their hypertrophied eyes, foraging workers detect the *Eciton* by sight at a distance of more than 15 cm. They easily avoid them and are too fast to be seized (Tab. 1). Also, *E. burchellii* workers ignore *Pseudomyrmex ferruginea* F. SMITH, 1877, a plant-ant typically associated with myrmecophytic acacia (DEJEAN & al. 2001), yet *Pseudomyrmex* spp. can be raided by *Neivamyrmex pseudops* (FOREL, 1909) and *N. diana* (FOREL, 1912) (see RETTENMEYER & al. 1983).

Because we had previously observed that *Eciton burchellii* workers surrounding the base of myrmecophytic *Cecropia obtusa* trees sheltering a colony of *Azteca alfari* EMERY, 1893 or *Azteca ovaticeps* FOREL, 1904 did not climb up these trees even though they invaded the low vegetation all around them, we followed three fronts of columns along a dirt road. We noted that the *E. burchellii* workers did not invade the six inhabited *Cecropia obtusa* they encountered, while this was the case for 57 out of 60 trees of other species whose trunk diameters were similar (Fisher's exact-test: $P < 0.0001$; see also Tab. 1). Because no fighting occurred, it is probable that *E. burchellii* workers are repelled by a substance deposited by the *Azteca* as has been noted for other ant-myrmecophyte associations (HERRE & al. 1986, DEJEAN & al. 2001). Also, it has been noted that *E. vagans* (BEQUAERT & WHEELER 1922) and even leaf-cutting *Atta* ants (VASCONCELOS & CASIMIRO 1997) avoid *Cecropia* inhabited by *Azteca alfari*. Because wasp brood are preyed upon by both *E. burchellii* and *E. hamatum*, many wasp species have adapted by nesting on myrmecophytes whose associated plant-ants repel army ants (CHADAB-CREPET & RETTENMEYER 1982, TELES DA SILVA 1982, HERRE & al. 1986, DEJEAN & al. 2001, 2012, CORBARA & al. 2009).

**Ant species that defend the nest entrance so that colonies are not raided**

*Pachycondyla villosa* (FABRICIUS, 1804) colonies shelter in the amphora-shaped central leaf of the bromeliad *Aechmea bracteata* (SWARTZ) GRISEBACH 1864, in the pseudobulbs of the orchid *Myrmecophila christinae* CARNEVALI & GÓMEZ-JUÁREZ 2001, or in the hollow branches of mangrove trees (see DEJEAN & OLMSTED 1997, DUROU & al. 2002). In this study, although *Eciton burchellii* raids reached the vegetation where the colonies were located, they never plundered these ants although some contact occurred at the entrance to the nests. In all cases, one or several large *Pachycondyla villosa* workers plugged the nest entrance with their head, mandibles wide open. Some of them bent their gasters under their alitrunk and oriented their devaginated sting forward. The *E. burchellii* workers very rarely tried to attack by biting a *Pachycondyla villosa* guard or trying to pull it backward to have access to the rest of the nest. The *Pachycondyla villosa* guards remained passive although they are able to cut the army ants into pieces with their large mandibles, but all of the *Eciton* workers that came into contact with their devaginated stings were immobilized and then died in less than 10 minutes. They had likely received a drop of venom that acted topically as no attempt at stinging them was noted. Because *Pachycondyla villosa* colonies were never plundered nor did they evacuate their nests at the approach of a raid, it is likely that the *E. burchellii* workers were repelled (Tab. 1).

*Ectatomma ruidum* (ROGER, 1860) and *Ectatomma brunneum* F. SMITH, 1858 have small nest entrances flush with the ground that are plugged by a guard worker so that none of the *Eciton* raids that passed above these nests resulted in an attack (Tab. 1). The nest structure also plays a role in their resistance to enemies as the entrances and nest chambers communicate through relatively long, narrow vertical tunnels that the workers defend easily. *Ectatomma tuberculatum* (OLIVIER, 1792) also nests below ground at the base of a tree trunk up the side of which workers construct a characteristic "chimney" made of plant fibres that serves as the nest entrance. Due to the relatively wide diameter of the chimney (ca. 2 cm in diameter and up to 1 m tall), several workers are necessary to guard the nest entrance to prevent the *Eciton* from entering, but the latter seem to be repelled as we never noted an attack (Tab. 1). It is likely that here, too, the defence of the nest entrances was helped by a kind of repellency vis-à-vis *E. burchellii* because *Eciton mexicanum* ROGER, 1863 can capture *Ectatomma* spp. (RETTENMEYER & al. 1983). Indeed, similar cases of repellency were noted when *Neivamyrmex nigrescens* raids avoided *Myrmecocystus* spp. nests and even palpated the ants; the *Myrmecocystus* workers did not noticeably react to these encounters (MIRENDA & al. 1980).

**Ant species that defend the colony, which is partly plundered**

*Pheidole megacephala* (FABRICIUS, 1793) is a tramp species originally from Africa which is frequent in coastal areas of Quintana Roo where it forms large colonies (DUROU & al. 2002, see also WETTERER 2012). Both *Eciton burchellii* and *E. hamatum* successfully raided these nests, plundering a part of the brood. Although they were involved in a fierce battle with the *Pheidole* workers that spread-eagled many of them, most of the *Eciton* were able to escape. Consequently, each *Eciton* worker that entered the *Pheidole* nest took a long time before returning to its bivouac with or without a *Pheidole* larva between its mandibles. During their return trip, those nestmates that were going toward the *Pheidole* nest attacked and killed them, retrieving both their booty and their corpses. Consequently, little by little the front of the column turned away from the *Pheidole* nest which was no longer attacked (Tab. 1). Therefore, the *Pheidole* lost a part of their brood, but the core of the nest was spared. A similar situation was triggered during an experiment using *Pseudomyrmex ferruginea* (DEJEAN & al. 2001). We hypothesized that the heterospecific compounds from the prey-ant were passed onto the cuticle of these *Eciton* workers during the combat so that they were not recognized by their nestmates (see the water-based experiment conducted by ROUX & al. 2009).

**Ant species that sacrifice a part of their brood**

When an *Eciton burchellii* raid reached the base of a *Cecropia obtusa* tree sheltering a colony of the carton-building *Azteca andreae* GUERRERO, DELABIE & DEJEAN, 2010 on

the upper part of the tree trunk (DEJEAN & al. 2010), the first *Azteca* workers that detected the presence of the raiders triggered an alarm for their nestmates. Dozens of the latter left their nest carrying small larvae that they dropped on the ground. All of the *Eciton* that arrived at the base of the tree stopped when they found this "manna", each gathering and retrieving an *Azteca* larva. The raiders did not climb the *Cecropia* tree (or only a few workers over less than 60 cm) because there was no recruitment toward the tree trunk due to the presence of the dropped young larvae at its base. Meanwhile, the front of the raid moved forward so that the core of the *Azteca* colony was preserved (Tab. 1; see illustration in COLLET 2003).

**Ant species able to repel and attack *Eciton* raids**

*Dolichoderus bispinosus*, like *Pachycondyla villosa*, can shelter in the amphora-shaped central leaf of *Aechmea bracteata* or can build spherical carton nests in the vegetation (DUROU & al. 2002). In both cases, when a foraging *Dolichoderus bispinosus* worker detected an *E. burchellii* raid in its host plant foliage, it likely emitted an alarm pheromone as several nestmates left their nests. The *Eciton* workers always avoided them and no attack occurred (Tab. 1). Not all *Dolichoderus* species are avoided; for instance, *E. hamatum* can attack *Dolichoderus rugosus* that evacuate their nests; even the odour of a crushed *E. hamatum* triggers a nest evacuation (RETTENMEYER & al. 1983). Workers attacking army ant raids have been noted for *Azteca* spp. with large nests, *Aphaenogaster cockerelli*, and *Pogonomyrmex barbatus* (MIRENDA & al. 1980, CHADAB-CREPET & RETTENMEYER 1982).

*Dorymyrmex pyramicus nigrus* ROGER, 1863 build their very deep (up to 1.8 m) nests in sandy zones with the nest connected to the opening by a long, thin vertical tunnel that is easy to defend from intruders. Yet, when an *Eciton burchellii* raid or column was detected by a *Dorymyrmex* forager, the latter, mandibles open, rushed toward the intruders and likely emitted an alarm pheromone. Indeed, all of the other foragers situated in a radius of 50 - 60 cm changed their behaviour, visibly increasing their speed, most of them running toward the individual that discovered the *Eciton*. Meanwhile, a group of *Dorymyrmex* workers left their nest, most of them running in the same direction. The *E. burchellii* workers, seemingly panicked, avoided any contact with the *Dorymyrmex* and scattered in all directions. The *E. burchellii* column re-formed half an hour later, leaving a large space between them and the *Dorymyrmex* foraging area (and nest) (Tab. 1). Here a single *Dorymyrmex* worker, although small, can attack an *E. burchellii* column whose workers panic; this time there is a "propaganda"-like effect, but it is initiated by the raided species (Appendix 1). Similarly, if a *Neivamyrmex nigrescens* column "trespasses" on their mound, small groups of comparatively large *Pogonomyrmex barbatus* workers walk into the column scattering army ants in all directions. The column re-forms later, over a new route that gives the mound a wide berth. Not a single *Pogonomyrmex barbatus* worker is killed during such an encounter (MIRENDA & al. 1980). Yet, *Dorymyrmex insana* can be raided by *Neivamyrmex nigrescens*, whereas the workers of the latter species avoid *Forelius pruniosus* (ROGER, 1863) nests, another dolichoderine species, whose workers can even climb over the raiders (MIRENDA & al. 1980).

**Encounters between *Eciton* raids**

The high density of *Eciton burchellii* in the study area in Quintana Roo permitted us to observe 12 intraspecific encounters between swarms. In all cases, the workers avoided each other; they even retreated before physical contact. In the two cases noted of an encounter between *E. burchellii* and *E. hamatum* columns, major workers were recruited, but no battle occurred. The opponents placed their antennae backward (as do *Pachycondyla* workers when encountering termite soldiers; see DEJEAN & al. 1990) likely to avoid being bitten by media workers. Indeed, in some cases, a media worker seized an opponent's leg or antenna but it released its grip a few seconds later. In both cases, the swarms ended up by separating from each other, each taking a different direction.

In conclusion, although predation in *Eciton burchellii* and *E. hamatum* has previously been studied, the present study contributes to this information by providing new examples. Nest evacuations as well organized as those by *Paratrechina longicornis*, whose colonies escape sufficiently early to avoid the raids, were previously unknown. Among the new facts reported in this study, *Azteca andreae* sacrifice a part of their brood (mostly small larvae), to prevent the *Eciton* from recruiting nestmates to their nest, and, through intense fighting, *Pheidole megacephala* likely soak the *Eciton* raiders with chemicals, so that the latter are not recognized by their nestmates that then attack and kill them. If workers attacking army ant raids have been noted, the case of *Dorymyrmex pyramicus* is notable as a single worker, although small, is able to cause panic in an *Eciton* column through a propaganda-like effect. Nonetheless, although dolichoderine ants seem to be involved in several cases of defence and to be more repellent than other prey-ants, we did not record any trend in the reactions at the subfamily level.

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