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An asymmetrical relationship between an arboreal ponerine ant and a trash-basket epiphyte (Araceae)

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The relationship between ants and *Philodendron insigne*, a trash-basket epiphyte abundant along streams, was studied in French Guiana. Only a few (3%) of the young plants sheltered ants, whereas 90% of the mature individuals did. The most frequent associate was *Odontomachus hastatus* (Fabricius), an arboreal ponerine ant, and its nests were almost entirely (94.4%) located in *P. insigne* root clusters. Experimental choice tests conducted on *O. hastatus* workers confirmed their preference for *P. insigne*. We propose that the interactions between *P. insigne* and ants may be intermediate between non-obligatory, reward-based interactions and obligatory, specific ant–myrmecophyte interactions because (1) almost all mature *P. insigne* individuals are associated with ants; (2) *O. hastatus* is the most frequent when diverse ants nest in its root clusters; (3) ants colonize mature *P. insigne*, but rarely young individuals; (4) ants, particularly *O. hastatus*, protect the foliage of their host; and (5) at least one ant species, *O. hastatus*, prefers *P. insigne* over other host plants. The latter relationship is asymmetrical because *P. insigne* is inhabited by diverse ants whereas *O. hastatus* nests almost exclusively in *P. insigne*. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, **91**, 341–346.

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INTRODUCTION

Ant–plant mutualisms are important components of tropical communities, and their diversity, associated with a similar global pattern of interactions, makes them a useful tool for understanding the origin and evolution of mutualisms. They range along a continuum from opportunistic and facultative interactions to specific and obligatory associations between specialized partners (Heil & McKey, 2003). At one end of this continuum are non-obligatory, reward-based interactions involving a large diversity of partners (Blüthgen *et al.*, 2000b; Apple & Feener, 2001; Hossaert-McKey *et al.*, 2001). These interactions mostly involve the indirect protection provided to plants through the predatory activity of ants that, in return, obtain food rewards (e.g. from plant's extrafloral nectaries; EFNs). At the other end of the continuum, myrmecophytic plants have developed specialized hollow structures (e.g. domatia) inhabited by only one or a few specialist ant species (Yu & Davidson, 1997; Gaume & McKey, 1999; Murase *et al.*, 2002). Most previous studies of ant–plant associations have focused on cases of interactions representing both extremes of the continuum (Benzing, 1990; Jolivet, 1996; Blüthgen *et al.*, 2000a, b). Epiphytes and hemi-epiphytes are included among the types of plants with which ants interact in this continuum. These plants influence the structure of ant communities in many Neotropical forests because they accommodate the nests of abundant nondominant ants and/or provide them with EFNs. To understand the middle ground between these two extreme types of associations, intermediary cases need to be examined.

In the present study, we investigate the nature of the relationships between ants and the aroid *Philodendron insigne* (Schott), a trash-basket epiphyte (e.g.

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*Corresponding author. E-mail: dejean@cict.fr an epiphyte that creates its own rooting medium by intercepting falling litter) whose young leaves bear active EFNs (Croat, 1997; Bastien & Belin-Depoux, 1998). We addressed the following questions: (1) how diverse is the ant community associated with *P. insigne*; (2) do preferential associations emerge from the community between one or few ant species and this epiphyte; and (3) do these preferential associations follow the classic pattern of ant–plant mutualism (food and/or shelter vs. protection)?

MATERIAL AND METHODS

This study was conducted between February 1995 and March 2003 in French Guiana at Petit Saut (5°03′N, 53°02′W) and Paracou (5°15′N, 52°56′W), two forest stations close to the city of Sinnamary. The root clusters of 124 young (small individuals that have not yet produced inflorescences) and 481 mature *P. insigne* located between 1.5 and 6 m in height were opened *in situ* using pruning scissors to collect ant and termite colonies present. The nesting habits (ground-nesting vs. arboreal-nesting) of the different species collected were defined through data from the current literature (Longino & Nadkarni, 1990; Dejean, Olmstead & Snelling, 1995; Orivel *et al*., 1998) and our own unpublished observations (J. Delabie & A. Dejean, unpubl. data). Voucher specimens for the ants are deposited in the Laboratório de Mirmecologia, Itabuna, Bahia, Brazil; *Philodendron* specimens are deposited at the Marie-Victorin Herbarium, Montreal (Specimen numbers: *P. insigne*: *Barabé 129*; *Philodendron linnaei*: *Barabé 130*). We used chi-square tests (Statistix, 1994) to compare rates of ant occupation between young and mature *P. insigne*. The arboreal-nesting ponerine ant, *Odontomachus hastatus* (Fabricius), was frequently associated with *P. insigne*. Consequently, we searched for colonies of this species associated with other epiphytes growing up to 6 m high on all trees situated along 4.5 km of streams.

NEST SITE SELECTION

To test whether *O. hastatus* individuals are differentially attracted to *P. insigne*, we conducted preference tests according to the protocol used by Djiéto-Lordon & Dejean (1999a). We compared *P. insigne* with co-occurring and closely related *P. linnaei* (Kunth), an EFN-bearing hemi-epiphytic vine that accumulates almost no litter (Croat, 1997; D. Barabé, pers. observ.). *Odontomachus hastatus* workers were allowed to choose between tubular shelters made from the rolled leaves of *P. insigne* or *P. linnaei* (2 cm in diameter and 6 cm in length with only one opening) in plastic boxes (50 × 50 × 10 cm) that were cleaned with alcohol, then with detergent, after each experiment. Each plastic box contained four shelters (two per plant species) forming an 'X' with their openings orientated toward the centre of the boxes where four *O. hastatus* workers and six cocoons were placed. The boxes were then covered and set aside for 12 h, permitting the ants to install themselves and their cocoons in one shelter (rarely two). Fifty tests were conducted with *O. hastatus* workers taken from six colonies established on trees that did not support *P. insigne* or *P. linnaei*. Nests were located among the tangled roots of *Cyclanthus* sp. (Cyclanthaceae) and *Vriesea splendens* (Brongn.) Lem (Bromeliaceae). Two control experiments were conducted. We used *O. hastatus* workers originating from (1) five colonies associated with *P. insigne* (50 choice tests) and (2) from one colony associated with *P. linnaei* (only 14 choice tests). Ant choices of shelter (*P. insigne* or *P. linnaei*) were compared with a binomial distribution ($N = 14$ or 50 cases; $P = 0.5$) using Statistix software, version 4.1. Note that, in nature, *P. linnaei* can on rare occasions shelter *O. hastatus* colonies and attract various ants to its EFNs, precluding the possibility that this epiphyte repelled *O. hastatus* foragers during the choice tests.

PLANT PROTECTION

Three surveys were conducted (in 2000, 2001, and 2003) to examine the protection from defoliators provided to *P. insigne* by ants. The number of damaged leaves (e.g. with more than 10% of their surface destroyed) out of the six youngest was noted for each sampled plant (for details, see Dejean *et al*., 2004). We compared three groups of *P. insigne* individuals: (1) occupied by an *O. hastatus* colony ($N = 25$, 20, and 25 in 2000, 2001, and 2003, respectively); (2) occupied by a colony other than *O. hastatus* ($N = 19$, 24, and 39); and (3) unoccupied by ants ($N = 24$, 21, and 28). The numbers of damaged leaves per plant were normalized by a square-root transformation prior to analysis of variance (Systat, 1998). For multiple comparisons, we performed a post-hoc test for pairwise mean differences with a Bonferroni adjustment.

RESULTS

RELATIONSHIP BETWEEN *PHILODENDRON INSIGNE* AND ANTS

Of the 481 mature *P. insigne* sampled, 90.2% sheltered an ant colony, whereas only four out of the 124 juvenile individuals (3.2%) did so ($\chi^2 = 373$, d.f. = 1, $P < 0.001$). A founding *O. hastatus* queen was recorded from one these latter four plants, whereas the three others were associated with *Azteca chartifex* Forel, a dominant ant species that also occupied the entire supporting tree.

We noted 44 ant species belonging to four subfamilies, as well as several termite species associated with mature *P. insigne* (Table 1), with 82% of the plants sheltering only one ant species. The infrequent (38 cases; 8%) co-occurrence of two or more ant species involved mostly parabiotic associations (e.g. associations between ant species within a same nest; Forel, 1898) between *Crematogaster levior* Forel and *Camponotus femoratus* Fabricius (21 cases), and between *Crematogaster carinata* Mayr and *Odontomachus mayi* Mann (nine cases). The ant colonies recorded nested in the litter accumulated between the leaf bases or in the root clusters, and no carton nests were observed under the leaves.

The Myrmicinae was the most species-rich subfamily (20 species) associated with *P. insigne*, whereas subfamily Ponerinae (seven species) represented 55.5% of the colonies recorded (240 cases for Ponerinae vs. 192 for all other ant subfamilies; Table 1). The two most abundant species were *O. hastatus* followed by *O. mayi* (36.8% and 10.8% of the sampled *P. insigne*, respectively). Both arboreal and ground-nesting ant species were similarly represented (almost 40% of the species). Except for *O. hastatus*, *Dolichoderus imitator* (Emery) a ground-dwelling species, *Camponotus atriceps* (F. Smith), and *Cephalotes atratus* (L.), all the other arboreal ant species recorded are able to build their own carton nests, although they did not when associated with *P. insigne*.

NEST SITE SELECTION BY ODONTOMACHUS HASTATUS

We noted 184 *O. hastatus* stream-side colonies out of 195 (94.4%) nested in association with *P. insigne*; 179 with this aroid only and the five others with clusters of epiphytes that included *P. insigne* [the other epiphytes or hemi-epiphytes present were *Philodendron squamiferum* (Poepp.), *Codonanthe calcarata* (Miq.) Hanst. (Gesneriaceae), *Clusia* sp. (Clusiaceae), *Peperomia macrostachya* (Vahl) A. Dietr. (Piperaceae), and an unidentified fern]. Eleven colonies were not associated with *P. insigne*. Eight were located in root clusters of groups of epiphytes including *Vriesia splendens*, *Guzmania* sp. (Bromeliaceae) and *Cyclanthus* sp. (230 clusters examined). The three remaining colonies were located in ant gardens composed of *Aechmea mertensii* (G. mey.) Schult. f. (Bromeliaceae), *Anthurium gracile* (Rudge) Lindl. (Araceae), and *Codonanthe crassifolia* (Focke) Morton (460 ant gardens examined).

During the choice tests, *O. hastatus* workers mostly chose shelter tubes made from *P. insigne* rather than *P. linnaei* leaves. For 'naive' workers from colonies nesting in epiphytes other than *P. insigne* and *P. linnaei*, in 41 cases, the ants sheltered in tubes made from *P. insigne* leaves vs. nine in tubes made from *P. linnaei* leaves [*Bin* (9; 50; 0.5); $P < 0.00001$]. The same choice tests resulted in 48 vs. two cases [*Bin* (2; 50; 0.5), $P < 0.00001$] for workers taken from colonies associated with *P. insigne*, and nine vs. five cases [*Bin* (5; 14; 0.5); $P = 0.21$] for workers originating from colonies located on *P. linnaei*.

PLANT PROTECTION BY ANTS

A comparison of the numbers of damaged leaves between the three groups of *P. insigne* individuals (e.g. sheltering an *O. hastatus* colony, a colony of another ant species, or without ants) were significantly different regardless of the sampling period (2000, 2001 or 2003; $F_{2,216} = 66.1$, $P < 0.0001$). Because we did not record differences from one sampling period to the next, regardless of the group considered (year × group; $F_{4,216} = 0.78$, $P < 0.53$; year: $F_{2,216} = 1.96$, $P = 0.14$), the numbers of damaged leaves per plant were pooled for the three years of study as they concerned different plant individuals (Fig. 1). *Philodendron* sheltering an *O. hastatus* colony were significantly less damaged than those sheltering another ant species or those without ants (Fig. 1).

DISCUSSION

RELATIONSHIPS BETWEEN *PHILODENDRON INSIGNE* AND ANTS

Although they lack the domatia characterizing myrmecophytic epiphytes, the root clusters of mature *P. insigne* can be inhabited by ant colonies. Because young individuals seldom shelter ants, we deduce that ants colonize this epiphyte as it grows. Due to the dearth of suitable shelters, arboreal ants that are unable to build their own nests tend to utilize many kinds of existing sites, such as the roots beneath the large leaves of trash-basket epiphytes, as noted in *Platycerium* ferns (Jolivet, 1996; Djiéto-Lordon *et al.*, 2006). The same is true for mature *P. insigne* individuals sheltering diverse ant species, including some ground-dwellers species (plus termites; see also Longino & Nadkarni, 1990; Nadkarni & Longino, 1990; Blüthgen *et al.*, 2000b), and even opportunistic ant-garden ants (e.g. *Cr. carinata*; *Cr. levior*, *Ca. femoratus*, and *O. mayi*). Nevertheless, although we recorded a total of 44 ant species associated with *P. insigne*, *O. hastatus* was by far the most frequent associate. The relationship between this ant and *P. insigne* is asymmetrical because 94.4% of the *O. hastatus* colonies were associated with *P. insigne*, whereas only 36.8% of the *P. insigne* individuals were occupied by an *O. hastatus* colony. The remaining *O. hastatus* colonies were associated with other epiphytes whereas, in the understory (where *P. insigne* is absent), censuses of fauna inhabiting the litter

Table 1. Numbers of ant and termite species recorded in 481 *Philodendron insigne* root clusters and the percentages of *P. insigne* individuals occupied by each species

Subfamily	Species	Nesting habits	Number of plants	%
Ponerinae	*Odontomachus hastatus* (Fabricius)	Arboreal	177	36.8
	Odontomachus mayi (Mann)	Arboreal	52	10.8
	Odontomachus haematodus (L.)	Opportunist	1	0.2
	Pachycondyla inversa (F. Smith)	Arboreal	2	0.4
	Pachycondyla constricta (Mayr)	Ground-dwelling	2	0.4
	Pachycondyla harpax (Fabricius)	Ground-dwelling	3	0.6
	Pachycondyla stigma (Fabricius)	Ground-dwelling	1	0.2
Ectatomminae	*Ectatomma tuberculatum* (Olivier)	Ground-nesting	2	0.4
Myrmicinae	*Acromyrmex hystrix* (Latreille)	Ground-dwelling	3	0.6
	Atta cephalotes (L.)	Ground-dwelling	4	0.8
	Basiceros singularis (F. Smith)	Ground-dwelling	1	0.2
	*Cyphomyrmex trans*vs. (Emery)	Ground-dwelling	5	1
	Myrmicocrypta sp. 1	Ground-dwelling	10	2.1
	Rogeria subarmata (Kempf)	Ground-dwelling	1	0.2
	Solenopsis saevissima (F. Smith)	Ground-dwelling	4	0.8
	Wasmannia auropunctata (Roger)	Opportunist	5	1
	Cephalotes atratus (L.)	Arboreal	1	0.2
	Crematogaster carinata (Mayr)	Arboreal	9	1.9
	Crematogaster levior (Forel)	Arboreal	21	4.4
	Crematogaster sumichrasti (Forel)	Arboreal	1	0.2
	Crematogaster longispina (Emery)	Arboreal	4	0.8
	Crematogaster sp. 1	Arboreal	5	1
	Crematogaster sp. 2	Arboreal	3	0.6
	Crematogaster sp. 3	Arboreal	3	0.6
	Pheidole sp. FG4	Unknown	6	1.2
	Pheidole sp. 1	Unknown	6	1.2
	Pheidole sp.5	Unknown	5	1
	Pheidole sp. 14	Unknown	6	1.2
Dolichoderinae	*Azteca chartifex* (Forel)	Arboreal	7	1.5
	Azteca sp.	Arboreal	4	0.8
	Azteca sp. FG1	Arboreal	2	0.4
	Azteca sp. FG2	Arboreal	5	1
	Azteca sp. FG3	Arboreal	6	1.2
	Dolichoderus attelaboides (Fabricius)	Arboreal	6	1.2
	Dolichoderus bispinosus (Olivier)	Arboreal	2	0.4
	Dolichoderus imitator (Emery)	Ground-dwelling	5	1
Formicinae	*Camponotus atriceps* (Fr. Smith)	Opportunist	8	1.7
	Camponotus femoratus (Fabricius)	Arboreal	21	4.4
	Camponotus mocsaryi (Forel)	Unknown	2	0.4
	Camponotus rapax (Fabricius)	Ground-dwelling	1	0.2
	Camponotus renggeri (Emery)	Arboreal	2	0.4
	Camponotus crassus (Mayr)	Opportunist	2	0.4
	Camponotus sp.	Ground-dwelling	1	0.2
	Camponotus sp.	Unknown	3	0.6
Termites	*Nasutitermes arborum* (Noirot)	Arboreal	18	3.8
	Other termites	Ground-dwelling	18	3.8
	No ants nor termites		47	9.8

As presented, the sum of the percentages is higher than 100% due to cases of two or more species sharing the same plant.

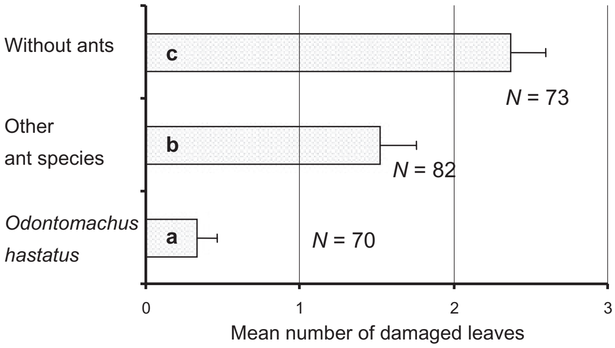

Figure 1. For the six youngest leaves of each plant, a comparison is shown of the number (mean and standard error) of leaves damaged by defoliating insects, among three groups of *Philodendron insigne* individuals: (1) without ants; (2) occupied by ants other than *Odontomachus hastatus*; and (3) occupied by *O. hastatus*. Individuals sheltering an *O. hastatus* colony were significantly better protected. Bars with different letters have significantly different means ($P < 0.0001$).

accumulated between the fronds of young palm trees resulted in 12 *O. hastatus* colonies recorded out of 338 palm trees sampled (3.5%; A. Dejean & J. Lebreton, unpubl. data).

NEST SITE SELECTION BY *ODONTOMACHUS HASTATUS*

The remarkable specificity of certain ant species for a single myrmecophyte species reflects host plant selection by founding queens (Yu & Davidson, 1997; Fiala *et al.*, 1999; Murase *et al.*, 2002). In 'generalist' arboreal ants, the selection of host plants by winged females (dissemination of colonies) and workers (colony budding) results from an inherently (e.g. genetically) determined attraction toward certain plant species and a familiarization process (contact with plants during development) (Djiéto-Lordon & Dejean, 1999a). On the other hand, the attraction of the plant-ant *Tetraponera aethiops* F. Smith (Pseudomyrmecinae), obligatory associated with myrmecophytic *Barteria fistulosa* (Mast.) (Passifloraceae), is a inherently determined, regardless of any familiarization processes (Djiéto-Lordon & Dejean, 1999b). The choice test results reported in the present study, although limited to only two plant species, suggest that familiarization with a plant for *O. hastatus* does not supersede its inherently determined attraction for *P. insigne*, confirming the ecological data presented above.

PLANT PROTECTION BY ANTS

Because herbivores can kill epiphytes (Schmidt & Zotz, 2000), their biotic protection by ants is particularly important; however, certain ant species are more efficacious against defoliators than others (Heil & McKey, 2003). *Philodendron insigne* individuals sheltering no ants were more damaged than those associated with a colony inhabiting the root cluster. However *O. hastatus* was by far the most efficacious protector, highlighting the importance of this ant species for *P. insigne*.

In conclusion, although *P. insigne* individuals can shelter a wide range of ant species in their root clusters in non-obligatory associations. However, one ant species, *O. hastatus*, greatly predominates and is the most efficacious antidefoliator agent, illustrating an intermediary step between diffuse and specific associations. Therefore, the case of *P. insigne* parallels that of myrmecophytic epiphytes by the high percentage of adult, but not juvenile, individuals that are associated with ant colonies attracting preferentially one ant species (*O. hastatus*), and being protected from defoliators by the ants that it shelters. The observed preferential attraction of *O. hastatus* towards *P. insigne* may result from a local adaptation, and further studies in different populations should confirm such a pattern.

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