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Reciprocal protection from natural enemies in an ant-wasp association

Protection réciproque contre des ennemis naturels dans une association guêpes-fourmis

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ABSTRACT

We show that in French Guiana the large carton nests of *Azteca chartifex*, a territorially-dominant arboreal dolichoderine ant, are protected from bird attacks when this ant lives in association with *Polybia rejecta*, an epiponine social wasp. Because *A. chartifex* colonies are well known for their ability to divert army ant raids from the base of their host tree so that they protect their associated wasps from these raids, there is a reciprocal benefit for these two partners, permitting us to call this association a mutualism. We also show that *P. rejecta* nests are significantly less often attacked by birds than are those of two compared epiponine social wasp species. Furthermore, experimentation using a standardized protocol demonstrated the significantly higher aggressiveness of *P. rejecta* compared to seven other wasp species. We conclude that the efficacious protection of its associated ant nests is likely due to the extreme aggressiveness of *P. rejecta*.

Mots clés :
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RÉSUMÉ

Nous avons montré qu'en Guyane française les grands nids en carton de la fourmi arboricole *Azteca chartifex* (Dolichoderinae) ne sont pas attaqués par des oiseaux lorsqu'un nid de la guêpe *Polybia rejecta* (Epiponinae) est situé dans leur voisinage immédiat. Les colonies d'*A. chartifex* étant connues pour leur aptitude à détourner les colonnes de fourmis légionnaires, et par-là, indirectement, pour protéger les nids de guêpes associés, il y a donc bénéfice réciproque dans ce partenariat, qui peut être considéré comme une association mutualiste. Les nids de *P. rejecta* sont significativement moins attaqués par les oiseaux que

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ceux de deux autres Epiponinae de taille équivalente, sans doute en relation avec l'agressivité particulièrement importante de cette espèce en comparaison de celles de sept autres espèces de guêpes. Cette forte agressivité est vraisemblablement à la base de la bonne protection des nids d'*A. chartifex* par *P. rejecta*.

1. Introduction

Mutualisms are interspecific interactions involving two or more species where each partner obtains a benefit with positive implications for its fitness. Two main groups of arboreal ants (i.e. arboreal-nesting and -foraging species and ground-nesting, arboreal-foraging species) have evolved mutualistic associations with plants where each partner derives benefits [1]:

- in the obligate mutualism involving myrmecophytes, the latter shelter specialized plant-ants in preformed cavities and usually provide them with food such as extrafloral nectar and/or food bodies. In return, plant-ants protect their host myrmecophyte from herbivores, competitors, encroaching vines and fungal pathogens;
- territorially-dominant arboreal species (TDAs; e.g., weaver and carpenter ants plus carton-builders) have very populous colonies with large and/or polydomous nests, and defend territories both intra- and interspecifically from other TDAs.

Through their predatory behavior and aggressiveness, they protect their host trees from herbivorous insects. TDA colonies nest on certain tree species rather than others and, as for plant-ants, workers recruit nestmates in areas where host tree leaves are wounded by herbivores (induced defense), proving that the association is narrow [2,3].

The territoriality of both plant-ants and TDAs, particularly in the genus *Azteca*, prevents leaf-cutting ants and army ants from climbing up the trunks of their host trees ([4,5] and papers cited therein). Indeed, arboreal ants, including the TDA *Azteca chartifex*, can divert army ant columns from the base of their host trees by attacking them [5,6] or by depositing repellent compounds [7].

This anti-army ant behavior is thought to be exploited by social wasps that install their nest near the nests of plant-ants or TDAs [7–10]. Among them, the epiponine wasp, *Polybia rejecta*, has frequently been noted as associated with the large carton nests of *A. chartifex*. Generally, the nests are less than 50 cm from each other, but they can be in contact in certain cases; also, it can happen that several wasp nests surround an *A. chartifex* nest [10–13] (Fig. 1a). Thus, it is a challenge to know if this social wasp species is only an "exploiter" (i.e. a species obtaining a benefit from an association and that does not reciprocate), or, on the contrary, if it protects *A. chartifex* nests from vertebrate predation, mostly birds, something frequently asserted but never demonstrated.

On the other hand, it is recognized that birds are predators of arboreal ants and social wasps [14–16]. Certain bird species strike wasp nests to cause the workers to abscond (i.e. abandon their nest) [17,18]. In the other cases, one can easily see the damage caused by the birds in gathering ant or social wasp brood: the opened thorns of myrmecophytic *Acacia* [19]; holes pierced in *Cecropia* trunks [20] or bamboo internodes [21] or directly in the walls of *Azteca* spp. carton nests or through the envelope of epiponine wasp nests (Fig. 1b).

Our aim was three-fold:

- to verify, through a field survey, if the presence of *P. rejecta* protects *A. chartifex* colonies from bird predation as the damage can be extremely great;

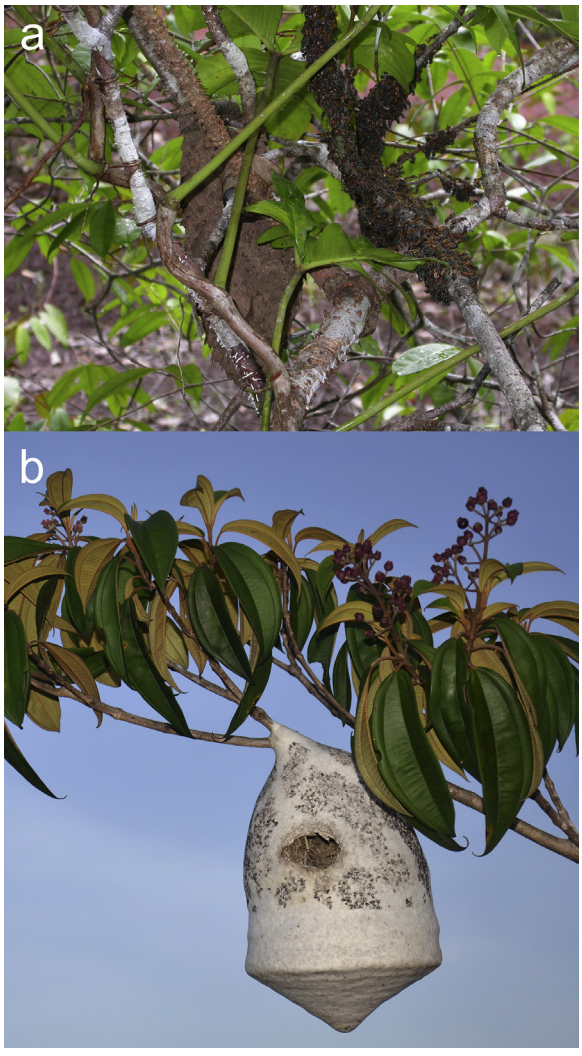

Fig. 1. (Color online.) a: a *Polybia rejecta* swarm close to an *Azteca chartifex* carton nest illustrating that the wasps arrive after the ants; b: a *Chartergus artifex* nest after being attacked by birds.