



Animal biology and pathology/Biologie et pathologie animales

A mimetic nesting association between a timid social wasp and an aggressive arboreal ant[☆]

Une guêpe sociale discrète dont le nid mime celui de fourmis associées agressives

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ABSTRACT

In French Guiana, the arboreal nests of the swarm-founding social wasp *Protopolybia emortualis* (Polistinae) are generally found near those of the arboreal dolichoderine ant *Dolichoderus bidens*. These wasp nests are typically protected by an envelope, which in turn is covered by an additional carton 'shelter' with structure resembling the *D. bidens* nests. A few wasps constantly guard their nest to keep *D. bidens* workers from approaching. When alarmed by a strong disturbance, the ants invade the host tree foliage whereas the wasps retreat into their nest. Notably, there is no chemical convergence in the cuticular profiles of the wasps and ants sharing a tree. The aggressiveness of *D. bidens* likely protects the wasps from army ant raids, but the ants do not benefit from the presence of the wasps; therefore, this relationship corresponds to a kind of commensalism.

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RÉSUMÉ

En Guyane française, les nids de la guêpe *Protopolybia emortualis* (Polistinae) se trouvent généralement à proximité de ceux de la fourmi arboricole *Dolichoderus bidens* (Dolichoderinae). Ces nids de guêpes sont typiquement protégés par une enveloppe de carton, elle-même recouverte d'une autre enveloppe formant un abri qui ressemble aux nids de carton de *D. bidens*. Quelques guêpes gardent leur nid en permanence afin de tenir à distance les ouvrières *D. bidens*. Alarmées par une forte perturbation, les fourmis envahissent tout le feuillage de leur arbre support alors que les guêpes se réfugient dans leur nid. Il n'y a pas de convergence chimique entre les profils cuticulaires des guêpes et ceux des fourmis associées. Il est très probable que les *P. emortualis* bénéficient d'une

[☆] This paper is dedicated to the memory of Philippe Cerdan (1959–2018), a dear friend and colleague.

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protection contre les fourmis légionnaires grâce à l'agressivité des *D. bidens*, mais il n'y a pas réciprocité, de sorte que cette relation correspond à une forme de commensalisme.

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1. Introduction

Social wasps, which very often have arboreal nesting habits, are regularly confronted with patrolling ants, so that, in the Neotropics, the predatory pressure exerted by ants has been considered the main driving force behind the evolution of wasp nest architecture [1–4]. Thus, to protect their colonies, non-swarming Polistinae build a nest with a pedicel onto which the workers deposit substances repellent to ants, while most swarming species build an envelope to protect the combs, facilitating the defence of the nest [5]. Furthermore, social wasps rely on active vigilance and physical removal to prevent ant intrusion [6,7] and select sites where attacks by ants are unlikely or more difficult (e.g., man-made structures, attaching their nests to the long thorns of palm trees that serve as easily-defended 'pedicels' [1,8,9]).

Whereas these defences seem effective against many ant species, they are futile against columns of army ants that force wasps to abscond and build a new nest elsewhere [10,11]. As a suitable defence mechanism against army ants, some wasp species install their nests in the vicinity of certain arboreal ant nests, the workers of which tolerate them, whereas they are very aggressive towards intruders. For instance, *Polybia rejecta* generally nests in close vicinity to large arboreal nests of *Azteca chartifex* [9,12] whose workers can defend the access to their host tree by attacking army ants at its base, causing the columns to deviate [13,14]. Such nest associations, well known throughout the Neotropics, concern a relatively limited number of social wasps species [9,13,15–18]. Although they benefit from protection by their associated ants, these wasps must nevertheless avoid attacks by the latter.

In French Guiana, the nests of *Protopolybia emortualis* de Saussure are systematically installed on trees sheltering colonies of the arboreal ant *Dolichoderus bidens* (L.) [9]. We therefore aimed to assess the level of specificity of this relationship by revisiting a corpus of field data collected during studies spreading over 20 years where all cases of associations between these wasps and arboreal ants were noted. To better understand the characteristics of the links between *P. emortualis* and *D. bidens*, we evaluated the opportunities for contact between the two species by comparing their respective rhythms of activity, studied the characteristics of the *P. emortualis* nest architecture and verified if a chemical mimicry exists between the wasps and the ants (see [16,19]) by comparing the cuticular hydrocarbons of *P. emortualis* and *D. bidens* individuals sharing the same trees.

2. Materials and methods

2.1. Study sites

These studies took place in the Sinnamary district, French Guiana, in a 30 km radius around the Petit-Saut

dam (5°03'39"N, 53°02'36"W), mostly along dirt road corridors. The climate of the area studied is moist tropical with 3400 mm of yearly precipitation typically recorded at Petit-Saut. The maximum and minimum monthly temperatures average 33.5 °C and 20.5 °C, respectively. The dry season occurs between July and November and the rainy season between December and June with a marked decrease in precipitation during March.

2.2. Ant and wasp species

The arboreal ant *D. bidens* is abundant in pioneer formations, secondary forests and plantations [20]. The colonies, of up to a few thousand workers, are polydomous (i.e. multiple nests) with each carton nest built under a host tree leaf. The external part of the nests cover part or all of the adaxial surface of a single leaf or envelop two to a few contiguous leaves [11]. This is an aggressive, territorially dominant arboreal species active 24/7 that hunts insect prey in tree crowns [21]; consequently workers defend the access to their host tree by leaf-cutter ants and army ants at its base (AD, pers. obs.; see [13,14] for *Az. chartifex*).

Social wasps of the recently revised genus *Protopolybia* [22] are characterized by very different nest architectures, including transparent envelope made predominantly of chitin that is secreted orally in some species [23–25]. Diversification in female aggressiveness is seen in this genus, from very docile females in *P. chartergoides*, to extremely aggressive ones and a hemolytic venom in *P. exigua* [26,27]. *Protopolybia emortualis* is a swarming polistine species known to nest in close contact with *D. bidens* societies [28,29]; the workers of both species are approximately the same size.

2.3. Nesting association occurrences

In a previous field survey [9], wasp nests were looked for along forest edges and in secondary formations, noting, each time we encountered a wasp nest, whether or not it shared its host tree with arboreal ants. Because *P. emortualis* nests are difficult to detect, a complementary survey was conducted where we inspected 750 arboreal ant nests to verify whether their supporting trees also sheltered nests of this social wasp species (survey occurring from 2006 to 2016). Voucher specimens of *P. emortualis* and *D. bidens* were deposited in the American Museum of Natural History (New York) and the *Laboratório de Mirmecologia* (CEPEC-CEPLAC, Itabuna, Bahia, Brazil), respectively.

2.4. Rhythm of activity

We recorded the rhythms of activity of both the wasps and the ants living on nests installed on a *Vismia sessilifolia*

(Clusiaceae) tree. The tree sheltered 42 nests of a *D. bidens* colony and one of *P. emortualis*. Due to frequent rainfall, observations were spread over one week in order to complete a 24-hour-day cycle. For each hour of the contiguous 24 h period, during 10 minutes we recorded:

- the number of wasps leaving or returning to their nest;
- those resting on the wasp nest;
- the number of *D. bidens* workers patrolling on the wasp nest (i.e. on its “external envelope” or “shelter”) and on the three closest ant nests;
- the number of ants on the main foraging trail running along the trunk of the tree;
- the number of ants in two distinct foraging areas where they attended Hemiptera.

2.5. Gas-chromatography analysis

For the analysis of cuticular substances, we used three *P. emortualis* nests associated with two *D. bidens* colonies (i.e. two wasp nests associated with the same ant colony). Each ant and wasp sample (i.e. workers, larvae, and pupae) was prepared using the combined cuticular substances from five individuals killed by freezing and immersed in 1 mL of hexane for 5 min. The extracts were then evaporated under nitrogen and redissolved in 200 μ L of hexane for *D. bidens* and *P. emortualis* workers and 50 μ L for *P. emortualis* larvae and pupae and *D. bidens* larvae, pupae and queens (see Table 1). A sample of 2 μ L of these solutions was analyzed with a Hewlett-Packard 5890 Series II gas chromatograph equipped with a split-splitless injector, a flame ionization detector, and a nonpolar fused-silica capillary column (HT-5, 25 m \times 0.22 mm ID \times 0.1 μ m film thickness). Sample injections were performed in splitless mode using helium as the carrier gas with injector and detector temperatures at 300 °C and 320 °C, respectively. The oven temperature program was as follows:

- 100 °C to 180 °C at a rate of 15 °C/min;
- increased to 250 °C at 5 °C/min;
- increased to 320 °C at 3 °C/min;
- isothermal (320 °C) for 15 min.

Integrations were performed with Millennium 2.15 software (Waters). To estimate the similarities of the profiles, we converted the data into binary values (i.e.

presence/absence) and used Ochiai's resemblance coefficient, which takes the same value as Nei's distance when binary data are used [30].

3. Results

3.1. Occurrences

During this survey, we recorded 45 active *P. emortualis* nests; one was associated with a *Dolichoderus omacanthus* colony and the 44 others with 40 *D. bidens* colonies out of the 147 noted (27.2%) among the ca. one thousand arboreal ant colonies surveyed. Moreover, three *D. bidens* colonies were associated with two *P. emortualis* nests, another with three *P. emortualis* nests (see [9] for other ant species).

3.2. Nest architecture

The *P. emortualis* nests were generally composed of one comb, rarely two (six cases out of 45) or three (two cases); each comb was protected by an envelope typical of swarm-founding wasps. This envelope started at the margins of a pedicellate comb as has generally been reported for *Protopolybia* [3]. For *P. emortualis*, the combs were hidden by an external carton envelope, or ‘shelter’, perfectly duplicating the envelope covering the ant nests; as for the latter, their envelopes sometimes enveloped two to four contiguous leaves. In most cases, the shelter margins were attached to the margins of the protecting leaf that acted as an umbrella. This carton shelter was connected to the comb envelope by several pillars that look like the pedicels attaching the combs to the leaf, which, as reported by Carpenter and Wenzel [31], seem to be made using salivary secretions. The nest entrances, located between the shelter and the supporting leaf margins, are often very narrow (ca. 2 mm in diameter), hence easy to defend by the resident wasps. So, access to these nests is difficult or impossible for *D. bidens* workers (Figs. 1, S1). In five cases, the *P. emortualis* nests were devoid of any shelter, which indicates that the latter are built after the comb and its envelope are constructed, although we never observed nest building.

3.3. Rhythm of activity and alarm behavior

The foraging activities of *P. emortualis* workers were strictly diurnal (not represented here), while one to six individuals patrolled their nest shelter day and night

Table 1

Average Ochiai's resemblance coefficient (mean \pm SE) as a measure of similarity in the cuticular profiles between *D. bidens* and *P. emortualis* larvae, pupae and adults (workers and queens for *D. bidens*). Ochiai's resemblance coefficient was calculated from binary values (i.e. presence/absence) in each recorded peak and vary between 0 (totally different) and 1 (identical).

	<i>D. bidens</i> larvae	<i>D. bidens</i> pupae	<i>D. bidens</i> workers	<i>D. bidens</i> Queens	<i>P. emortualis</i> larvae	<i>P. emortualis</i> pupae	<i>P. emortualis</i> adults
<i>D. bidens</i> larvae	0.90 \pm 0.05	0.92 \pm 0.05	0.90 \pm 0.02	0.80 \pm 0.05	0.68 \pm 0.07	0.69 \pm 0.07	0.68 \pm 0.08
<i>D. bidens</i> pupae	–	0.96 \pm 0.03	0.87 \pm 0.02	0.83 \pm 0.02	0.70 \pm 0.05	0.70 \pm 0.05	0.70 \pm 0.07
<i>D. bidens</i> workers	–	–	0.97 \pm 0.01	0.78 \pm 0.02	0.66 \pm 0.05	0.69 \pm 0.05	0.64 \pm 0.07
<i>D. bidens</i> queens	–	–	–	0.95	0.65 \pm 0.01	0.69 \pm 0.05	0.66 \pm 0.06
<i>P. emortualis</i> larvae	–	–	–	–	0.89 \pm 0.10	0.78 \pm 0.06	0.75 \pm 0.08
<i>P. emortualis</i> pupae	–	–	–	–	–	0.86 \pm 0.11	0.80 \pm 0.11
<i>P. emortualis</i> adults	–	–	–	–	–	–	0.83 \pm 0.13

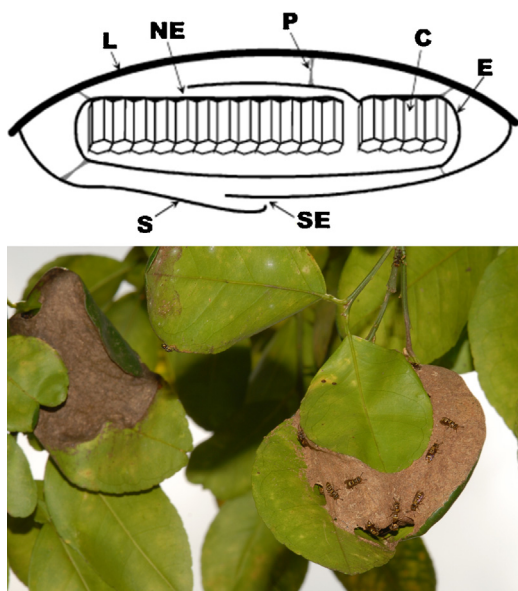


Fig. 1. A. Diagram of a transverse section of one single-combed *Protopolybia emortualis* nest (C: comb; E: wasp-nest envelope; L: leaf; NE: *P. emortualis* nest entrance; P: pedicel; S: shelter; SE: shelter entrance). B. *P. emortualis* nest (on the right) near a *D. bidens* nest (on the left). The slightly opened shelter of the wasp nest allows to see the underlying envelope.

(Fig. 2A). *Dolichoderus bidens* workers were active day and night, with nest patrolling mainly nocturnal (Fig. 2B, C). Despite the proximity of the respective nests (as close as 4 cm as the nests were located under adjacent leaves), the ants rarely climbed onto the wasp nests (only seven cases observed in 24 h). The *D. bidens* workers that approached the wasp nest entrance were immediately confronted with wasp guards with their mandibles open. This was enough to cause these ants to flee. Very rarely, *P. emortualis*

workers landed on the *D. bidens* territory at close proximity to their own nests. They were not attacked by *D. bidens* workers as they avoided contact and immediately returned to their own nest (N = 14 observations). Short agonistic interactions with ants occurred only when the latter stepped onto the wasp nest and were reduced to a wasp approaching the ant intruder with the mandibles wide open; this was sufficient as the ant workers fled in all cases.

When we simulated a disturbance by tapping the twig supporting the nests with a stick (N = 10), the *D. bidens* workers reacted with a typical alarm behavior consisting of drumming the abdomen on the branch, leaf or their nest surface (producing a sound similar to raindrops). This caused numerous nestmates to rush out of their nests ready to attack any intruder. On the contrary and simultaneously, *P. emortualis* wasps flew inside their nests, avoiding any contact with ants, while their nest entrance was blocked by the head of a wasp individual.

3.4. Gas-chromatography analysis

The analysis of the cuticular substances of *D. bidens* and *P. emortualis* workers and brood did not bring to light any congruence in the patterns (Fig. 3). Qualitative comparisons of the cuticular profiles using Ochiai's resemblance coefficient demonstrated that individuals were closer to their conspecifics (i.e. larvae, pupae or workers) than to the associated species (Table 1). Furthermore, the lowest qualitative similarity in the cuticular profiles corresponded to *D. bidens* and *P. emortualis* workers (i.e. those individuals that are likely to encounter each other).

4. Discussion

Despite a high level of sampling effort during this study, *P. emortualis* was found only once out of 45 cases in the absence of *D. bidens* and this was with a congeneric species,

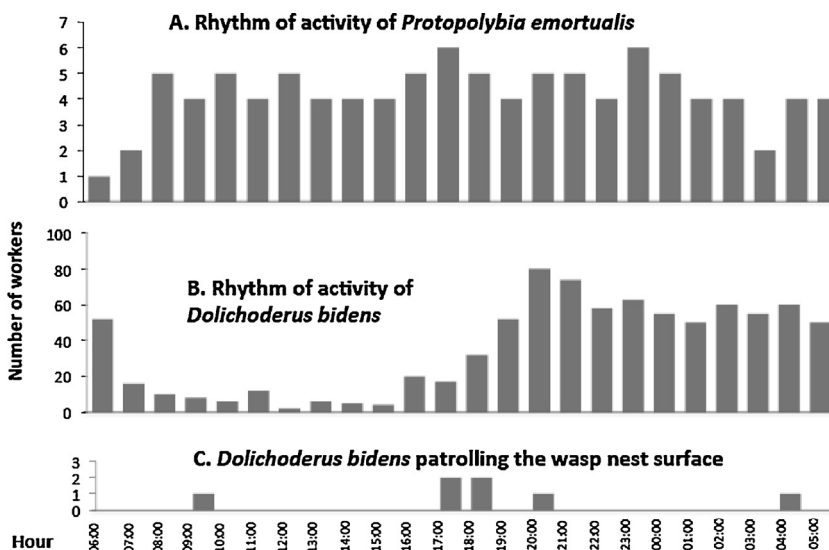


Fig. 2. A. Rhythm of activity of *Protopolybia emortualis* workers on their nest's surface. B. Rhythm of activity of *Dolichoderus bidens* on three nests of their colony. C. Number of *D. bidens* workers patrolling the wasp nest surface.

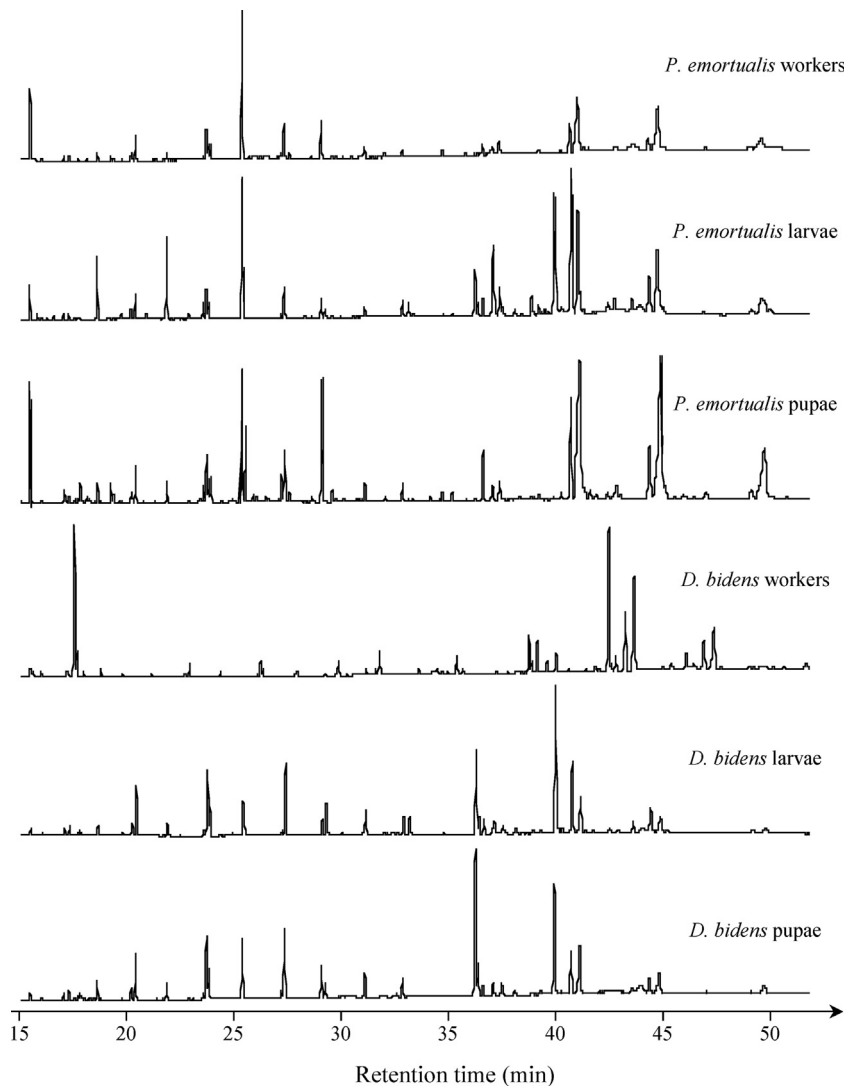


Fig. 3. Comparisons of the cuticular profiles between developmental stages of *Protopolybia emortualis* and *Dolichoderus bidens* (i.e. workers, pupae, and larvae).

whereas 27.2% of the inspected *D. bidens* colonies shared their host tree with one to three *P. emortualis* nest(s). Thus, *P. emortualis* swarms likely selects trees hosting *D. bidens* colonies for their installation (see also [9]).

Although *P. emortualis* and *D. bidens* workers do not tolerate contact with one another, the wasp nests are generally installed very close to an ant nest. Tolerance of the wasps by *D. bidens* workers and *vice versa* is not reflected by a convergence in the cuticular profiles of workers from the two species (chemical mimicry or camouflage) as is known for *Parachartergus apicalis* wasps nesting on myrmecophytic *Vachellia* spp. sheltering *Pseudomyrmex* ant colonies [16] (see also the case for several myrmecophiles [19,32–34]). Rather, such a scenario is reminiscent of the parabiotic associations between two ant species sharing the same nest in ant gardens, each species having its own colony odor. Thus, individuals are able to learn the chemical profile of both the parabiotic species and their colony mates [20].

Consequently, whereas their foraging activities are diurnal (as for most other wasp species), *P. emortualis* workers patrol the outer surface of their nest day and night, preventing *D. bidens* worker access. By very rarely venturing beyond their nest surface, *P. emortualis* wasps avoid physical contact with *D. bidens* workers, so that such contacts were rare. When an alarm was triggered in the ant colony, the wasps immediately took shelter in their nest, only protecting its small entrance (see also [28]). More generally, the wariness of *P. emortualis* enables them to mostly avoid *D. bidens* workers and thus contributes to the peaceful cohabitation. This is comparable to the way territorially-dominant arboreal ant species (*D. bidens* belongs to this group) tolerate non-dominant ant species (which have small colonies) on their territory that they would aggressively defend against other dominant ants [35,36].

The peculiarity of building an external supplementary envelope we called the ‘shelter’ in their nests constitutes

the main novelty of *P. emortualis*. First, the shelters resembles the *D. bidens* nests (see also [37]: p 144) confusing predators such as birds. As far as we know, this is the only case of ant nest-mimicking construction in a social wasp species. This is reminiscent of the quite perfect camouflage of the greenish envelope of *Leipomeles dorsata* also displayed under a leaf [38]. Second, the presence of the ‘shelter’, hence a double envelope, renders access to the nest’s interior more difficult for any intruder as it furnishes additional protection for the brood. Thus, the *P. emortualis* colonies benefit from two lines of defence where, in both cases, intruders need to gain access through a small entrance hole easy to defend by a single wasp (one of the guards). This situation is a strong protection from ant raids whose strategy is based on the *Square Law* of the *Lanchester theory of combat* predicting that when combatants can mix freely, numerical superiority is the deciding factor. Here, the wasp guards need to defend a narrow entrance, a situation corresponding to the *Linear Law* where fighting ability contributes more toward victory than the number of combatants. This is known for several ant species defending their nest entrances from army ant raid attacks (see [14] and papers cited therein). Thus, this double envelope can be useful when the *D. bidens* workers are excited by a strong external disturbance. However, it is very improbable that this strategy allows the tiny *P. emortualis* to resist any army ant raid.

Therefore, the main potential enemies of *P. emortualis* are birds, even tiny birds, detecting wasp nests by sight and striking them, making the wasps abscond (and to swarm to create a new nest), so that these birds can freely feed on the wasp larvae from the stricken nest [39]. Yet, thanks to their mimetism with *D. bidens* nests, *P. emortualis* nests are undetectable by birds. Furthermore, because *D. bidens* workers are particularly aggressive and bite en masse all animals that venture on their host tree (AD, BC pers. com. [21]), a bird landing on such a tree is immediately attacked by hundreds of workers and instantly flies away. Note that the situation differs from that of *Az. chartifex* that are preyed upon by birds, but defended by associated aggressive social wasps [18].

In conclusion, the spatial nesting association between *P. emortualis* and *D. bidens* is asymmetrical with a minimum level of tolerance by the ants towards the presence of wasps. The wasp nesting behavior is based on:

- an appropriate nest site selection (*i.e.* branches sheltering a *D. bidens* colony) permitting them to benefit from protection against army ant raids;
- a nest architecture including a supernumerary envelope, the ‘shelter’, making the wasp nest indistinguishable from neighboring ant nests, hence the wasps benefit from a double line of defense from the *D. bidens*;
- behavioral wariness which facilitates the cohabitation with *D. bidens* workers.

Disclosure of interest

The authors declare that they have no competing interest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.crvi.2018.01.006>.

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