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Trophobiotic relationships between ants (Hymenoptera: Formicidae) and Tettigometridae (Hemiptera: Fulgoromorpha) in the grey dunes of Belgium

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Abstract. We recorded the association between the planthopper *Tettigometra laetus* Herrich-Schäffer, 1835 (Hemiptera: Fulgoromorpha: Tettigometridae) and three ant species belonging to the subfamilies Myrmicinae and Formicinae in a coastal dune area of Flanders (Belgium). *Lasius psammophilus* Seifert, *Tetramorium caespitum* L. and *Formica cunicularia* Latreille were observed attending and palpating the dorsal glandular area of this planthopper, taking honeydew directly from its anus, herding them and carrying them into their nests when disturbed. The planthopper was rarely found in the absence of ants and probably develops within ant nests, which may provide protection against predation and adverse weather conditions. The natural history of temperate ant-hemipteran relationships is discussed.

INTRODUCTION

The trophobiotic relationship between ants and Hemiptera is well known (Hölldobler & Wilson, 1990). Ants profit by enriching their diet with carbohydrate-rich honeydew, spending less time in a search for food and, depending on the availability of honeydew, eating some of the Hemiptera. Hemiptera are believed to benefit not only from protection against predators and competitors but also from either direct (e.g. ants keep plant surfaces honeydew- and fungus-free) or indirect advantages of ant attendance (e.g. more space, or shelter from adverse weather conditions) (Way, 1963; Itioka & Inoue, 1996; Dejean et al., 1996; Moya-Ragoza & Nault, 2000). The survival and fitness of Hemiptera thus increase when ant-attended (Way, 1963; Bristow, 1983, 1984; Buckley, 1987).

Studies of ant-hemipteran relationships principally focus on Sternorrhyncha: Aphidae (e.g. Stadler & Dixon, 1999) and Coccidae (e.g. Itioka & Inoue, 1996) (for an overview, see Way, 1963; Buckley, 1987; Hölldobler & Wilson, 1990). Among the Auchenorrhyncha, Membracidae (Messina, 1981; Fritz, 1982; Del-Claro & Oliveira, 1996, 1999; Wetterer et al., 2000; Cocroft, 2003), Eurymelidae (Rozario et al., 1993) and Aethalionidae (Brown, 1976) of the Cicadomorpha group are the most studied. Some records mention the association of ants with honeydew producing Cicadellidae (Cicadomopha; Larsen & Nault, 1994; Hruska & Peralta, 1997; Moya-Ragoza & Nault, 2000; Larsen et al., 2001; Blüthgen & Fiedler, 2002). However, the trophobioses between ants and members of the Fulgoromorpha are rarely documented (but see Compton & Robertson, 1988; Dejean et al., 2000b, and others).

The (non-aphid) hemipteran-ant trophobiosis is well-known in tropical and subtropical regions, but uncommon in temperate regions, or at least largely overlooked (but see Bourgoin, 1985; Schlick-Steiner & Steiner, pers. com.). Delabie (2001) states that trophobiotic interactions between tettigometrid planthoppers and ants is rather rare and reports such interactions in the Ethiopian region. The skewness of research towards the tropics is because of the economic importance of plant diseases transmitted by Hemiptera, which are often tended by ants (Way, 1963; Dejean et al., 1996, 1997a, b; Buckley et al., 1990; Delabie, 2001). Auchenorrhyncha-ant associations are recorded from Australia (Blüthgen & Fiedler, 2002), Cameroon (Dejean & Bourgoin, 1998; Dejean et al., 1996, 1997a, b, 2000a, b), Zimbabwe (Weaving, 1980) and South-Africa (Compton & Robertson, 1988; Bourgoin & Pajor, 2000).

In this paper, we document a new trophobiotic relationship between planthoppers and ants in temperate regions based on observations made on grey dunes in Belgium. Ecological and ethological observations are discussed.

MATERIAL AND METHODS

Study site

The research was done on the coastal dunes of Ter Yde (Oostduinkerke, Western-Flanders, Belgium; 51°07'N, 2°43'E), in three geologically identical sites of 62.3, 76.4 and 47.6 ha, respectively (see Lehouck et al., 2004 for details). Grey dunes and dense grasslands on lime-rich sandy soils dominate the vegetation. Coastal "grey dune" dominant vegetation includes moss as well as grassland (with a distinct organic soil layer) belonging to the *Cladonio-Koelerietalia* (Provoost et al., 2002). On the moss dunes, species such as *Tortula ruralis* or, in more fixed conditions, *Hypnum cupressiforme*, are dominant and accompanied by the therophytes (e.g. *Crepis capillaris*, *Leontodon saxatilis*). Grasslands, which have a distinct soil development, are dominated by herbs (e.g. *Asperula cynanchica*,

Potentilla erecta, *Thymus pulegioides*, *Galium verum*) and grasses (*Festuca rubra*, *Avenula pubescens*).

Fieldwork

During July – September 2001, ant nests were mapped in 59 3×3 m² plots, laid out around randomly chosen ant nests. In each plot, all plant rosettes where mapped, identified and measured (diameter). Ants and trophobiont Hemiptera were searched for under at least five plant rosettes in each plot.

When trophobionts were found under ant-attended rosettes, an equal number of "control" rosettes of the same species and size, but lacking ant nests were sampled within the same plot. Only when ants tended all the rosettes within a plot could no control rosettes be sampled. Ant and hopper behaviour was observed and noted. At least three workers of the ant species, were collected and identified using the keys of Seifert (1988a, b and 1996). All planthoppers were collected and identified using the keys of Haupt (1935), Ribaut (1936, 1952), Le Quesne (1960, 1965), Ossiannilsson (1979, 1983), Della Giustina et al. (1989) and Remane & Wachman (1993). Voucher specimens of ants and hoppers are deposited in the collection of the Royal Belgian Institute of Natural Sciences in Brussels.

Statistical analyses

Because the ant-nests (Lehouck et al., 2004) and associated planthoppers show an aggregated distribution, the rosette preference (with/without ants) of the planthopper within each plot was tested using a sign test. Other analyses of the association of the planthopper with the ants were conducted at the plot-level using a non-parametrical Mann-Whitney U-test. All analyses were performed using Statistica 6.0 (Statsoft 1994).

RESULTS

General results

A total of 438 nests were found (14 ant species), 7617 rosettes mapped (28 plant species) and 560 of them inspected for the presence of trophobionts. On 43 of these rosettes, planthoppers were present. The most frequent ant species in the study area were *Lasius psammophilus* Seifert, 1992 (57.6% of the study plots), *Tetramorium caespitum* L. (44.1%), *Formica cunicularia* Latreille, 1798 (30.1%) and *Myrmica sabuleti* Meinert, 1860 (28.8%).

There were five planthopper species (Table 1), with *Tettigometra laetus* Herrich-Schäffer, 1835 (Hemiptera: Fulgoromorpha: Tettigometridae) the most common (51 nest records, with 43 records of planthoppers associated with rosettes and the remaining 8 in ant nests not under rosettes). The planthoppers were more common under rosettes with than without ants (Sign test; number of nonties = 17; % v < V = 88.24; Z = 25.910; $p < 0.001$). Most tettigometrids normally live in short xerophilous vegetation (Remane & Wachman, 1993). *T. laetus* is not host specific and was found under grass tussocks as well as rosettes of different plant species (Table 2; see also Nickel & Remane 2002). The species was not more common in moss dune vegetation than grassland (Mann-Whitney-U-test; U = 311.800; Z = –0.630; $p = 0.529$). The planthopper was found both above ground (on the leaves of rosettes, n = 3) and below ground (on the roots, n = 40) (Chi-Square-test; $\chi^2 = 31.8$; df = 1; $p < 0.001$).

All other hopper species, belonging to the Cicadellidae, were only occasionally found in ant nests (6 times in 125 ant nests) (see also Table 1 for presence in plots). In none of these cases was communication with ants observed. In addition, all these species were frequently observed on bare soil, not associated with ants or rosettes.

TABLE 1. The species of planthopper and frequency with which they were found with ants (between brackets: number of plots where planthoppers were present/total number of ant nests inspected).

Planthopper species (family)	Ant species and frequency of presence in plots
Tettigometra laetus (Herrich-Schäffer, 1835) (Tettigometridae)	*F. cunicularia* (1/2) *L. psammophilus* (10/24) *T. caespitum* (3/15) Without ants (4/31)
Anaceratagallia sp. (Cicadellidae)	*M. sabuleti* (1) *L. psammophilus* (1) Without ants (1)
Megalophthalmus sp. (Cicadellidae)	*L. psammophilus* (1) Without ants (3)
Aphrodes sp. (Cicadellidae)	*T. caespitum* (1) *L. psammophilus* (1) Without ants (4)
Psammotettix sp. (Cicadellidae)	*M. sabuleti* (1) Without ants (2)

Observations of ant-hemipteran relationships in Flemish grey-dunes

The planthopper *T. laetus* was found in nests of *L. psammophilus*, *T. caespitum* and *F. cunicularia* (Table 1, Fig. 1), indicating a nonspecific association with ants. However, our observations indicate a certain degree of specificity between *T. laetus* and *L. psammophilus*, and to a lesser degree between *T. caespitum* and *F. cunicularia* (Fig. 1). *Myrmica*-species (mainly *M. sabuleti*) were never observed with hoppers in the 59 plots (n = 6, where n = numbers of *Myrmica*-nests inspected). The association is hence asymmetric and facultative for all ant partners, since more plots occupied by ants were recorded without the planthopper. This contrasts to the significant preference of *T. laetus* for ant nests (see further).

Co-occurrence with other trophobionts

On nine rosettes (five plots), aphids were found both above and below ground, together with *T. laetus* in the same nest (Fig. 2a). In these plots, planthoppers were present under all the plant rosettes tended by ants, whereas

TABLE 2. The species and numbers of plants infested with the planthopper *T. laetus*.

Plant species	No. of tussocks/rosettes infested with *T. laetus*	No. of rosettes examined
Koeleria macrantha	2	82
Crepis capillaris	28	217
Hieracium umbellatum	3	5
Erodium glutinosum	1	7
Leontodon saxatilis	2	82
Senecio jacobaea	6	79
Oenothera sp.	1	9

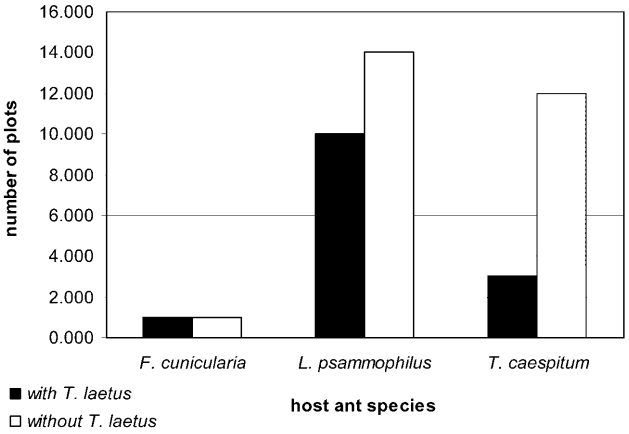

Fig 1. Frequency with which *T. laetus* was found in the nests of the ants *F. cunicularia*, *L. psammophilus* and *T. caespitum*. The number of plots in which the ants were found in the presence (black) or in absence (dotted) of the planthopper is shown. Ant species that did not host *T. laetus* are not indicated.

root aphids were only present beneath 28.6% of these rosettes and 5.8% of the rosettes not tended by ants. Hence, different trophobionts can coexist in ant shelters. However, different aphid species were not observed together in one ant nest (1394 plant rosettes inspected for the presence of aphids).

Behavioural aspects of the ant-hopper association

The behaviour of ants in the vicinity of planthoppers (both colonies and single individuals) is remarkable and indicate them communicate with one another. Usually one worker tended one hopper and positioned itself behind it. Often, more workers were located behind and at the sides of a single hopper. The workers palpated the dorsal regions of the abdomen of adult planthoppers with their antennae (Fig. 2), which stimulated them to produce droplets of energy rich honeydew. Several times we observed ant workers controlling several planthoppers at a time, their antennae continuously moving above the hoppers. The conditions did not always permit a detailed study of this behaviour, since the planthoppers (especially the nymphs) were often in underground cavities or along on roots of the plants (Fig. 2a).

When ant nests were disturbed by opening them to inspect for the presence of endogeic invertebrates, one or several ant workers tapped the abdomens of the adult planthoppers with their antennae. Planthoppers were then driven forward by the ant workers, and disappeared into the ants' nest.

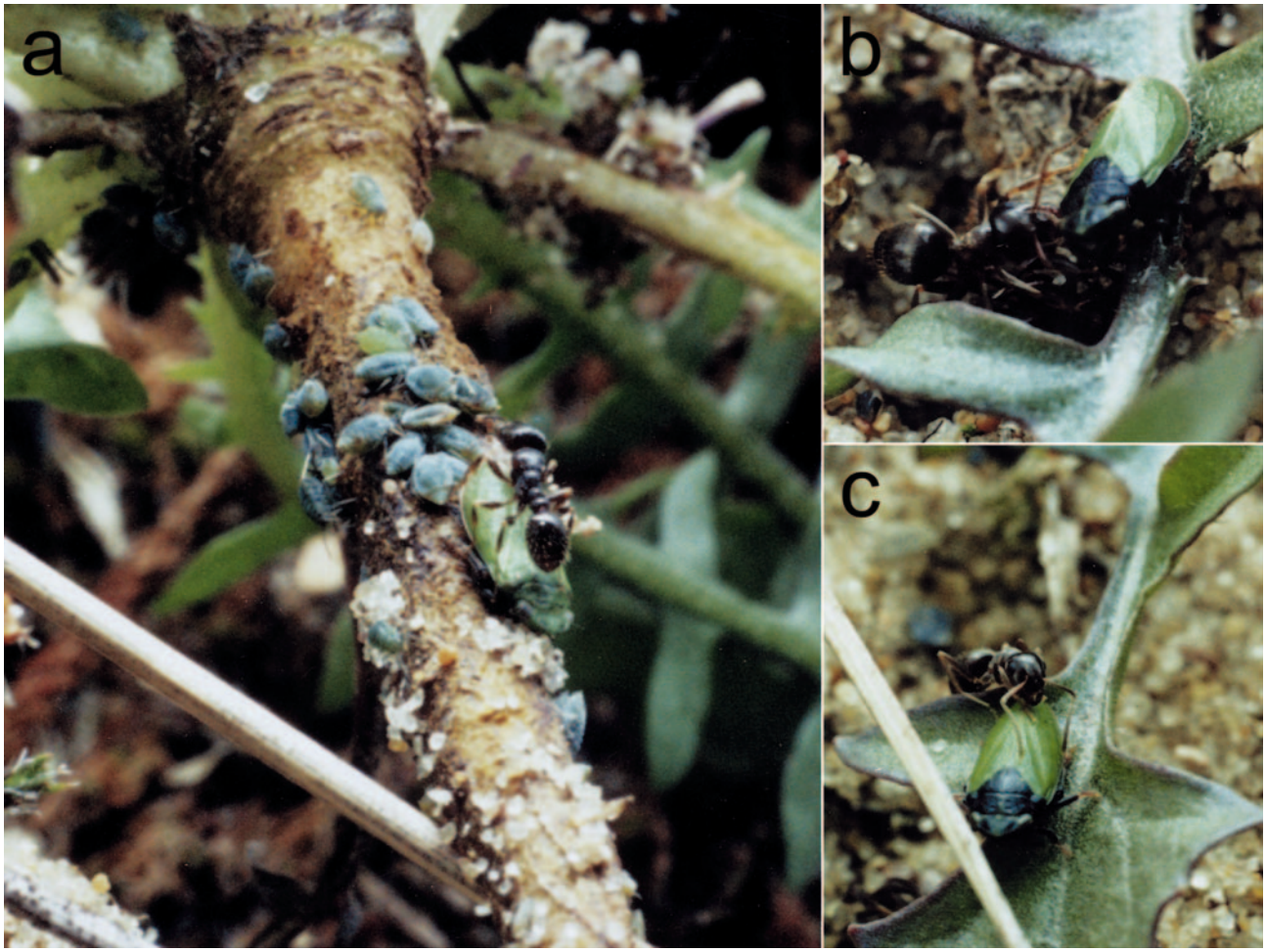

Fig 2. Photographs of worker ants of (a) *T. caespitum*; (b) and (c) *L. psammophilus* tending the planthopper *Tettigometra laetus* (Tettigometridae). In picture (a) there are also other Homoptera (aphids) tended by the ants and present in the same nest.

The black larvae of *T. laetus* were found in ant nests up to July 21st end then up to the end of September, only adults. Larvae were never found outside ant nests. On four occasions, ants were seen carrying larvae into their nest by holding them between their mandibles. Adults were also observed being carried in this way by ants into a nest when disturbed, although adults were more frequently "herded".

DISCUSSION

Records of ant-hopper associations in temperate regions are rare and only based on co-occurrence, without further evidence of trophobiont behavioural interactions (e.g. observations by Bourgoin (1985) in France and Schlick-Steiner & Steiner, pers. com., in Austria). The trophobiotic association between the planthopper *Tettigometra laetus* and three ant species in the coastal dunes of Flanders (Belgium) reported here is therefore remarkable. Until now, most research on ant-hemipteran mutualisms in temperate regions was on aphid-ant interactions. Previous studies on ant-Fulgoromorpha relationships are rare and concern Delphacidae (Dejean et al., 1996, 1997a, 2000a) or Tettigometridae (Weaving, 1980; Bourgoin, 1985, 1986; Compton & Robertson, 1988; Dejean et al., 1997b; Dejean & Bourgoin, 1998; Bourgoin & Pajor, 2000; Dejean et al., 2000b) in the tropics.

Trophobiotic relationships

Among the Fulgoromorpha, ant-mutualisms are only documented in a few species of Cixiidae (Myers, 1929; Thompson, 1984), Delphacidae (Dejean et al., 1996, 1997a, 2000a), Hypochthonellidae (China & Fennah, 1952, in Bourgoin, 1997) and mainly in species of Tettigometridae (Bourgoin, 1985, 1986; Bourgoin & Pajor, 2000; Compton & Robertson, 1988; Dejean & Bourgoin, 1998; Dejean et al., 2000b), which make up more than 70% of the records from Fulgoromorpha. Morphological or behavioural adaptations resembling those described for aphids, favouring or limiting ant-associations, probably account for this dominance (Bourgoin, 1997).

The association of ants and Tettigometridae was recorded in the 19th century, first by Lichtenstein (1870). According to Lesne (1905), the genus *Tettigometra* is the most frequently attended of all Fulgoromorpha in Europe and North-Africa. More recently, Bourgoin (1985) reported another two planthopper species, *Tettigometra sulfurea* Mulsant & Rey and *T. impressifrons* Mulsant & Rey attended by *Tetramorium* spp., *Camponotus aethiops* Latreille, *Tapinoma* spp. and *Formica rufibarbis* F. in France. The trophobiotic relationship between ants and *Tettigometra sulfurea* was never previously recorded. Tettigometridae have previously been observed underground attended by ants [e.g. Bellevoye (1870) in Lesne 1905], which even led to the suggestion that tettigometrid nymphs typically feed on plant roots, although most nymphs and adult tettigometrids live above ground [see Bourgoin (1997) for a discussion of possible habitats and their historical significance]. In our study, however, hoppers were found mostly within ant nests and rarely above ground. Bourgoin (1997) documents that all durable Fulgoromorphan-ant associations are observed when hoppers are either (i) unable to escape (underground in ant galleries or under a shelter) or sessile (non-jumping) or (ii) forced into gregariousness or subsocial (see also Delabie, 2001). Dietrich & McKamey (1990) noted that all Membracoidea and Cicadelloidea attended by ants above ground are sessile and exhibit subsocial behaviour. Although tettigometrids are usually described as sessile, *T. laetus* can jump (Lehouck, pers. observ.) but is held immobile in ant nests [see Myers (1929) and Thompson (1984) for other examples of hoppers found in ant nests].

A monospecific trophobiotic relationship most commonly occurs among Hemiptera associated with tropical arboricolous ants, which permanently live among the brood within the ant nests and receive continuous protection and attention (Way, 1963). In contrast, Delpino [cited in Lesne (1905)] found that *Tettigometra virescens* Latr. is able to live with three different ant species and individuals can change from one host species to another. As recorded in this study, most ant-hemipteran associations are not monospecific (Way, 1963).

The association of *T. laetus* with ants seems to be obligate since adults of this hopper were rarely observed without ants. In three cases when not ant attended, they were close to other *T. laetus* present under or on ant-attended plant rosettes. In a fourth plot, the planthopper colony was in the immediate vicinity of an ant nest (10 cm). Five other nests within the plot hosted *T. laetus* and a few hours (2–34 h) after the initial observation, hoppers became associated with ants or left the plant rosette, probably for other rosettes, attended by workers. These observations indicate that the planthopper colony was possibly too large to be entirely and simultaneously tended, as noticed by Dejean & Bourgoin (1998). Most ant species are omnivorous and combine predation or scavenging with the collecting of plant foods and honeydew (Alonso, 2000). It is generally accepted that predation and scavenging provide protein while carbohydrates are largely obtained by collecting honeydew (Way, 1963). This facultative relationship from an ants' point of view enables them to change their foraging tactics according to changes in resource (honeydew) abundance and distribution (abundance and distribution of honeydew-producing Hemiptera) and so optimise their foraging efficiency or intake (Way, 1963; Itioka & Inoue, 1996; Traniello, 1989; Hölldobler & Wilson, 1990; Wilby & Shachak, 2000). Ant visiting frequency and attendance time indicate ants prefer dense aggregations of Hemipteran (Henderson & Jeanne, 1992). This may account for the varying interest of particular ant species for different species or colonies of Hemiptera.

Behavioural aspects

The same dorsal regions of the planthoppers are palpated by ants during our observations as recorded in other ant-Tettigometridae (Hemiptera; Dejean & Bourgoin, 1998) and ant-Plataspidae associations (Heteroptera; Dejean et al., 2000c). Bourgoin (1986) described glands peculiar to these areas (the prothorax and pleural regions of the abdomen) and hypothesized that their secretions

might chemically mediate ant-Tettigometridae relationships. In the trophobiotic relationship between *Dalbulus quinquenotatus* (Hemiptera, Cicadellidae) and *T. caespitum*, Larsen et al. (1992) indicate that the leafhopper responds to ant antennation by excreting and holding honeydew droplets until these are removed by ants, whereas non-attended species avoid contact with ants and expel droplets from the anal tube immediately after they are formed. Dejean & Bourgoin (1998) found the position of the workers differs depending on the size of the nymphs of the hopper and that the ants show a distinctive behaviour towards nymphs. Due to the often secretive and endogeic way of life of the nymphs we were unable to observe this behaviour.

The curious "herding" and "driving" behaviour of the ants is also recorded by Lesne (1905) for Tettigometridae and Ledoux (1950, in Way, 1963) for larval and adult Membracidae, and seems to be a modification of brood care behaviour. Forel (1890, in Lesne 1905) records the ant *Tapinoma nigerrimum* Nyl., carrying larvae of *Tettigometra* sp. into their nests. According to Way (1963) ants indeed show brood care behaviour towards the Hemiptera they attend. In many ways the behaviour ants, such as *Lasius flavus* F., show towards their attended aphids is similar to that towards their brood: they transport them to brood chambers in spring and remove them when disturbed. When taken into ant nests, some Hemiptera hibernate there and are in this way protected against fungi, excessive moisture, low temperatures (Pontin, 1960; Way, 1963) and enemies (Way, 1963; Dejaen et al., 1996). In our study, the ants *Lasius psammophilus*, *Tetramorium caespitum* and *Formica cunicularia* communicated with the planthoppers by palpating the dorsal glandular area, taking honeydew directly from their anus and herding or carrying them into the nest when disturbed. These planthoppers were rarely found in the absence of ants and probably develop within ant nests, which may provide protection against predators, parasites and adverse weather. Our findings additionally indicate that ants benefit from the honeydew produced by *T. laetus*, since they stay with the hopper colonies, but that this diet is not essential for their survival. However, it is highly likely there is a trophobiotic relationship between *T. laetus* and ants.

Furthermore, the association between *Tettigometra laetus* and ants could be an important mechanism structuring intra- and interspecific competition. As documented by Dejean et al. (1997b), the activity of the ant *Camponotus brutus* changed dramatically in the presence of *Hilda undata* (Hemiptera: Fulgoromopha: Tettigometridae) and *Caternaultiella rugosa* (Heteroptera: Plataspidae; Dejean et al., 2000c). *C. brutus* variates its rhythm of activity and shows an increase in behavioural flexibility, such as territoriality and aggressiveness, when tending leaf hoppers. Although not documented, trophobiotic interactions between ants and Hemiptera can potentially influence the outcome of inter- and intraspecific interactions.

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