Relationships Between Ants (Hymenoptera: Formicidae) and *Euphyonarthex phyllostoma* (Hemiptera: Tettigometridae)

by

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ABSTRACT

During a five-year field study we noted that *Euphyonarthex phyllostoma* (Fulgoromorpha, Tettigometridae) was always associated with plants of the genus *Bridelia* (Euphorbiaceae), particularly with *B. micrantha*. Moreover, we gathered arguments permitting us to unequivocally demonstrate that this plant hopper is a myrmecophile. Isolated adults were attended by ants belonging to 17 species and three subfamilies, while colonies were only associated with *Camponotus brutus* or *C. acvapimensis* (Formicinae). The behavior of the workers of *C. brutus* during the solicitation of honeydew was studied in detail. The position of the workers varies as a function of the size of the nymphs of the hopper. The workers place themselves at the side of clusters of small first instar nymphs, moving their antennae slowly above the nymphs. The workers antennate the extremity of the abdomen of the nymphs which begin to produce honeydew. This antennation continues during the entire period of honeydew excretion. In contrast, generally only one worker attends one last instar nymph or one adult and places itself behind the hopper. The worker antennates the dorsal regions of the abdomen and the thorax of the hopper in broad prolonged movements. A hopper ready to secrete honeydew raises its body; in response, the worker folds back the antennae and palpates the apex of the hopper's abdomen, all the while absorbing the excreted droplets. If an attending worker is not in the proper position when the hopper is ready to excrete honeydew, the latter attracts the ant by alternating the extrusion and withdrawal of the first droplet. All other arboreal ant species tested under laboratory conditions (*B. micrantha* cultivated in planters) were able to get honeydew from both adults and nymphs, even those not recorded as being associated with the hopper in nature. Behavior varied with the workers' size, but the same body areas of the hopper were palpated.

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INTRODUCTION

Although the trophobiotic relationships between ants and homoptera seem to be well known, few studies are concerned with the Fulgoromorpha group. Nevertheless, Silvestri (1903) made the first detailed ethological observations and noted that workers of *Tapinoma* sp. antennate the dorsal areas of two species of Tettigometra and Bourgoin (1985, 1986a, b, 1997a), who described glands peculiar to these areas, hypothesized that their secretions could be chemical mediators during ant-Tettigometridae relationships. Recently, Dejean *et al.* (1997) showed that ant attended *Hilda undata* protect figs against other ants.

Endemic phytophagous insects frequently attack the plants of economic interest imported into Africa, so that it is very important to know the biology of these insects and their natural association with plants, because these associations can be the source of crop infestation (see Dejean & Matile-Férêro 1997) It was with this in mind that we studied the natural associations of *Euphyonarthex phyllostoma* Schmidt (Fulgoromorpha; Tettigometridae; Hildinae) with plants and ants during field research. This hopper which is distributed in the Congo basin is found in nature on *Bridelia* sp. (Euphorbiaceae) and has been recorded as a parasite of quinquina, coffee, and cocoa, three imported plants belonging to the families Rubiaceae and Sterculiaceae (see Fennah 1957, Bourgoin 1986a, and the collection at the National Museum of Natural History in Paris).

MATERIALS AND METHODS

Research of the associated plant and ant species

This work was conducted in southern Cameroon. During a detailed survey conducted in the secondary forest at Matomb and in the forest reserve of Campo at Ebodié (more than three centuries old) we worked both at the canopy level and along the forest edges. We had access to the canopy thanks to the "treetop raft" and the "canopy sled" (Hallé & Pascal 1992) at Ebodié and at Matomb, the forest had just been cut down by farmers. At the forest edge (3m wide) we recorded plants, ants and attended homoptera on a series of 5m lengths along 1000m (Matomb) and 500m (Ebodié) on both sides of dirt roads crossing the forests. During an extensive survey consisting of 270 outings in the field, two to six researchers noted each time they encountered *E. phyllostoma*: the associated plant and ant species; if on the same tree

the hopper is attended by one or several ant species; and the presence or absence of nymphs and eggs of the hopper.

Behavioral characteristics of the trophobiosis

Observations were conducted in nature on 28 *B. micrantha* occupied respectively by *C. brutus*, *C. acvapimensis*, *Tapinoma* sp., *Crematogaster striatula*, *Myrmicaria opaciventris*, and *Pheidole megacephala* and on *B. micrantha* cultivated in planters in the territory of colonies of *C. brutus* (control), *C. flavomarginatus*, *C. melanocnemis*, *Oecophylla longinoda*, *Polyrhachis laboriosa*, *Cr. depressa*, and *Tetramorium aculeatum*. For studies in planters we installed 10 adults, 10 last instars and 10 first instars of *E. phyllostoma* on each tree and we observed the reactions of workers. We noted: 1- if the workers palpated the dorsal glandular area of the hopper (see Silvestri 1903; Bourgoin 1986b) to get honeydew and if they palpated other areas of the body of the hopper; 2- the reactions of the hopper when a worker was not ready to imbibe the honeydew that it began to extrude; and 3- the number of cases when adult individuals or last nymphal instars left versus remained in place during a series of 10 minute observations when attended by workers of *C. brutus* or *C. acvapimensis* (observations performed during three consecutive days in January 1993, between 8 and 10 a.m.).

For comparisons of percentages we used the Fisher exact test (StatXact software). Voucher specimens of the ants were deposited in the Museum of Natural History, London.

RESULTS AND DISCUSSION

Relationships between *E. phyllostoma* and plants

We never recorded *E. phyllostoma* in the canopy of the forests (old forest: sampling on 167 trees belonging to 63 species and 29 families and 20 vines belonging to 8 species and 7 families; old secondary forest: 41 trees belonging to 22 species and 18 families), but another Tettigometridae (*Hilda rubrospersa*), always attended by *C. brutus*, was recorded on 25 *Musanga cecropioides* (Cecropiaceae) growing around the sampled parcel. Along the forest edges, *E. phyllostoma* was recorded only on *B. micrantha* (old forest: sampling on 378 plants belonging to 58 species and 30 families, *B. micrantha* represents 1% of the plants; secondary forest: 343 plants belonging to 15 species and 10 families, B. micrantha represents 4.3% of the plants). In the savanna of Batchenga we recorded *E. phyllostoma* only on *B. ferruginea* (sampling on 655 plants belonging to 22 species and 14 families, *B. ferruginea* represents 7.9% of the plants). Another Tettigometridae, (*H. undata*), attended by *C. brutus*, or by *C. acvapimensis*, was recorded on *Ficus valis-choudae*

(Moraceae) (11.1% of the plants; see also Dejean *et al.* 1997).

During the extensive survey, *E. phyllostoma* individuals or clusters were recorded on 163 trees belonging to the genus *Bridelia* (we therefore confirm the observations of Fennah 1957), along the forest edges on *B. micrantha* (87.1%) or on *B. grandis* (5.5%), and in the savanna of Batchenga on *B. ferruginea* (7.4%) (Table 1).

Although we systematically searched at the bases of the trunks or on the roots of the trees, we never recorded *E. phyllostoma* adults or nymphs at these levels, but we recorded numerous associations between *C. brutus* and *Leptocentrus* sp. (Membracidae) or *Caternaultiella rugosa* (Heteroptera; Plataspidae).

The relationship between *B. micrantha* and *E. phyllostoma*, which is the most frequent, corresponds to a relatively narrow specificity. We never recorded *E. phyllostoma* on other Euphorbiaceae such as *Alchornea cordifolia* and *Macaranga* spp., very frequent in the forest edges (Dejean *et al.* 1994), or on endemic Rubiaceae or Sterculiaceae, although it is able to attack quinquina, coffee and cocoa trees (see the collections of the MNHN, Paris). Bourgoin (1985) cites the case of a paleartic tettigometrid (*Tettigometra sulphurea*) only recorded on an *Onopordon* (Composeae) while associated with several ant species. The nymphs and the adults are found more frequently at the base of the petiole of the leaves but egg laying usually occurs at the collar of the plant (Bourgoin, pers. obs.). By contrast, *H. patruelis* can be found on the aerial as well as the underground parts of numerous plants from diverse families (Rose 1962; Weaving 1980).

Ant species associated with *E. phyllostoma*

As previously recorded for other Tettigometridae (Jerath 1968; Weaving 1980; Compton & Robertson 1988, 1991; Bourgoin 1997b) trophobiosis can occur with several ant species but colonies of this hopper were only observed when attended by *C. brutus* or *C. acvapimensis* (respectively 49.1% and 15.9% of the associations; Table 1). Nevertheless, on a large *B. micrantha* workers of *M. opaciventris* attended non-aggregated nymphs of the hopper.

Isolated adults of the hopper were rarely observed without ant attendance or, if so, a few hours after the initial observation they were associated with ants or they had left the tree. They generally did not remain more than one week on the same tree when attended by ants other than *C. brutus* or *C. acvapimensis*. Note that *Oecophylla longinoda* and *Tetramorium aculeatum*, the most frequent ant species recorded along the forest edges (Dejean *et al.* 1994) and on tree crop plantations (Majer 1976; Taylor 1977; Dejean *et al.* 1991), were not recorded as

Table 1. List of different ant species which tend *E. phyllostoma* on *Bridelia* spp. (each case corresponds to one tree; 163 cases in total).

Ant species attending colonies of *E. phyllostoma*	No of cases	Ant species attending only *E. phyllostoma* individuals	No of cases
1- On *Bridelia micrantha*			
Formicinae			
Camponotus brutus	68	*Camponotus chrysurus*	3
Camponotus acvapimensis	18	*Camponotus* sp.1	14
		Camponotus flavomarginatus	2
		Paratrechina sp.	2
Dolichoderinae			
		Tapinoma melanocephala	4
		Tapinoma sp.	2
		Technomyrmex sp.	2
Myrmicinae		*Crematogaster clariventris*	1
		Crematogaster sp.1	4
		Crematogaster striatula	4
		Monomorium sp.	1
		Myrmicaria opaciventris	3
		Pheidole megacephala	2
		Pheidole sp.	12
2- On *Bridelia grandis*			
Camponotus brutus	8	*Crematogaster striatula*	1
3- On *Bridelia ferruginea*			
Camponotus brutus	4		
Camponotus acvapimensis	8		
TOTAL	106		57

attending *E. phyllostoma*.

Large trees can support several colonies of *E. phyllostoma* that are attended by only one ant colony. Exceptionally, on one tree, workers of *C. brutus* attended two colonies of the hopper while workers of *C. chrysurus* attended some adult individuals.

These results permit us to assert that there is a certain degree of specificity between *E. phyllostoma* and *C. brutus*, and to a lesser degree with *C. acvapimensis*, since they follow *E. phyllostoma* along a succession of complete cycles of development while other ant species do not. The same kind of situation has been observed for certain Membracidae (Bristow 1984).

Shelter closing by ants

It is known that the shelters built by ants provide protection for homoptera from weather and enemies (Way 1963; Beattie 1985; Maschwitz *et al.* 1985; Dejean *et al.* 1996; Bourgoin 1997a). We never

recorded *E. phyllostoma* attended in shelters, yet *C. brutus* frequently attends Membracidae and Plataspidae in shelters at the bases of the trunks of *B. micrantha*. *Crematogaster* spp., *M. opaciventris* and *Pheidole* spp. were also observed attending Coccidae, Stictococcidae and even Delphacidae in shelters built on different plants. It seems therefore that *E. phyllostoma* does not trigger shelter building by ants, corroborating Bourgoin (1997a) who classified Tettigometrids as "long-time attendance with no shelter" in his description of the main types of ant-attendance in Fulgoromorpha.

The solicitation of honeydew by *C. brutus* workers

The workers located at the side of the clusters of first instar nymphs slowly moved their antennae above the nymphs in a wide sweeping movement permitting them to detect when a nymph began to excrete honeydew. The tips of the antennae also frequently touched the nymphs at the level of the apex of the abdomen. The contact with antennae, labial and maxillary palps, and even the legs of the ant triggered the release of honeydew by nymphs ready to excrete. When a nymph produced its droplets of honeydew, the worker advances in order to absorb them. During this absorption the ant palpated the extremity of the nymph's abdomen, antennae completely folded back.

In contact with last instars and adults, the workers generally placed themselves behind one hopper, sometimes two or three. The size of the workers, clearly superior to that of the hoppers, allowed them to palpate the entire body of the trophobionts without needing to move. We recorded two types of antennal movements. Broad, prolonged movements, the antennae slightly bent, correspond to the palpation of the pleural regions of the abdomen (the tegminas for the adults) and the lateral-dorsal regions of the thorax. Once the hoppers prepared to secrete, they raised their body, so that in some cases their hindlegs left the substratum. In response, the ants folded their antennae back and palpated the apex of the hoppers' abdomen with feverish movements, all the while absorbing the excreted droplets. In certain cases, labial and maxillary palps can be used in addition to or in place of simple antennal palpations.

If a worker was not in the proper position when the hopper was ready to excrete its honeydew, it repeated the alternate extrusion and withdrawal of the first honeydew droplet; this signal immediately attracting the ant.

Variations in the behavior of the ants as a function of their size and response of the attended *E. phyllostoma*

The behavior of workers of more than 10 mm in length (i.e. *C. brutus*;

C. flavomarginatus; *C. melanocnemis*; and majors of *O. longinoda*) attending last instars and adults of the hopper was the same as previously described. The two types of antennal movements were also observed for ants 0.6 to 0.8 mm in length (i.e. *C. acvapimensis* and minors of *O. longinoda*). In this case, the workers placed themselves on one side of the hoppers during the broad, prolonged movements of the antennae. They quickly moved behind the hoppers ready to excrete honeydew. Then they palpated the extremity of the hoppers' abdomen with feverish movements as they absorbed the honeydew. For ants of less than 0.5 mm (i.e. *Crematogaster* spp.; *P. megacephala*; *Tapinoma* sp.) the behavior was different. Generally, one to six workers placed themselves behind one hopper to wait for the excretion of honeydew, while one to three others placed itself/themselves on the sides of the hoppers and antennated their thorax and abdomen (tegminas for the adults). Sometimes anal antennation of the hopper occurred.

The pleural regions of the abdomen and the lateral-dorsal regions of the thorax of the hopper, contain several types of glands and, in particular, glands where the voluminous basal ampulla is bound to the exterior by a short cuticular canal (Bourgoin 1986b). Therefore, the hypothesis of a trophobiotic action by these glands secreting chemical mediators playing a role in interspecific ant-Tettigometridae relationships (Bourgoin 1986a) can thus be corroborated. These secretions attracted all ant species tested (even those that were not recorded as associated with the hopper), and triggered the same behavior as a function of their size. As they offer an adaptive advantage both to the issuer (protected at least at the individual level) as well as the receiver (supplied), they should be considered as synomones (Philogène 1992). Adult females can therefore install themselves in any *Bridelia* as they are attractive to all arboreal ants (most frequent species in nature) tested, until they find a tree within the territory of a *C. brutus* or a *C. acvamimensis* colony.

Reactions of *E. phyllostoma* to antennal palpations of *C. brutus* versus *C. acvapimensis*

During a series of 10 minute observations, 66% of the adults (N = 50) left when attended by *C. acvapimensis* versus 10.7% (N = 75) when attended by *C. brutus* (Fisher exact test: $P < 10^{-3}$); for last instars, we recorded 62% (N = 100) versus 20% (N = 60; $P < 10^{-3}$). When attended by *C. brutus*, certain adults or nymphs of the hopper can remain exactly in the same place all day, a reaction never registered with *C. acvapimensis*. The responsive departure of the hoppers when attended by *C. acvapimensis* is probably due to the livelier movements of the workers

of this ant species, that are moreover obliged to move during trophobiosis because of their smaller size. As a consequence, nymphs and adults disperse themselves on the tree instead of being well aggregated and are thus more exposed to predation or parasitism (see also Wood 1982). These differences may be the origin of a certain degree of specificity between *E. phyllostoma* and *C. brutus* at the expense of other ant species, including *C. acvapimensis*.

Reaction of the nymphs and adults to the different attending ant species

On *B. micrantha* cultivated in planters, the nymphs of different instars developed until they reached imaginal moult when attended by *C. brutus* (control) as well as *C. flavomarginatus*, *C. lacnocnemis*, *O. longinoda*, and *P. laboriosa*. Nevertheless, the adults (present at the beginning of the experiment as well as those developing from nymphs) remained on the trees long enough to lay egg masses only when attended by *C. brutus*. When attended by small ant species, such as *Cr. depressa*, *Cr. striatula*, *P. megacephala*, *T. aculeatum*, and *Tapinoma* sp., nymphs were attended and could develop, but most of them left the trees, as did the adults. Not one egg was recorded when *E. phyllostoma* was associated with these small ant species, while we recorded an egg mass on one of the two trees occupied by *M. opaciventris* workers that then attended the offspring. It seems therefore that both the adults and nymphs of the hopper play a role in the selection of their associated ant species.

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