

Ant Defense of *Euphyonarthex phyllostoma* (Homoptera: Tettigometridae) during Trophobiotic Associations¹

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ABSTRACT

During a five-year field study, we made observations and conducted experiments to demonstrate unequivocally that *Euphyonarthex phyllostoma* (Fulgoromorpha: Tettigometridae) is a myrmecophile. Isolated adults and colonies always were found in association with ants. Colonies were associated only with *Camponotus brutus* or *C. acvapimensis* (Formicinae), whereas isolated adults were attended by ants belonging to several species of Formicinae, Dolichoderinae, and Myrmicinae. The size of the planthopper colonies reached higher levels when attended by *C. brutus* than by *C. acvapimensis*. Experiments using ant exclusion showed that both ant species protected egg masses against parasitic wasps, but egg masses were less parasitized on trees occupied by *C. brutus* than on those occupied by *C. acvapimensis* ($P = 0.0052$). The production of egg masses by female hoppers was recorded only when *C. brutus*, *C. acvapimensis*, or the myrmicine ant *Myrmecaria opaciventris* attended the hopper. In both former cases, the presence of ants influenced the aggregation of the nymphs as they dispersed when ants were excluded. The aggregation of the nymphs ensured that they were properly attended. Parental care by the females was reduced to their presence above or close to the egg masses. In fact, specialized workers of the attending ant species protected the egg masses as well as nymphs.

Key words: ant–Homoptera mutualism; *Camponotus*; *Euphyonarthex phyllostoma*; insect–plant relationships; Tettigometridae.

PLANTS OF ECONOMIC INTEREST IMPORTED TO AFRICA are attacked frequently by endemic phytophagous insects; among them, homopterans often are associated with ants. There is currently a debate to determine if ant-tended species provide indirect protection to their host plant against further herbivory through their associated ants, or alternatively, if the ant–homopteran association results in a proliferation of the homopteran, increasing the damage caused to the plant (Beccera & Venable 1989, Buckley *et al.* 1990, Fiala 1990, Del-Claro & Oliveira 1993). Such damage is particularly likely when the homopteran is a vector of plant disease, as is the case for numerous Auchenorrhyncha (Harris 1983). An example can be found in the family Tettigometridae, with the ant–*Hilda patruelis* association benefiting the natural host plant, *Ficus sur* (Compton & Robertson 1991), whereas this planthopper is an economic pest of the groundnut (Weaving 1980).

The trophobiotic relationships between ants and homopterans seem to be well known (Beattie 1985, Hölldobler & Wilson 1990, Jolivet 1996), but studies principally have concerned the Sternorrhyncha (*e.g.*, aphids and coccids). Among the Auchenorrhyncha, membracids, Eurymelid, and aethalionids of the Cicadomorpha group have been the most studied. Few studies have looked at the trophobiosis between ants and members of the Fulgoromorpha group, although several cases of association with ants have been reported (Bourgoïn 1997, Dejean, Ngnegueu *et al.* 1997). Nevertheless, Silvestri (1903) made the first detailed observations and noted that workers of *Tapinoma* sp. antennate the glandular areas of two species of *Tettigometra*, and Bourgoïn (1985, 1986) has hypothesized that the secretions of these glands could be chemical mediators in ant–Tettigometridae relationships. Recently, Dejean, Bourgoïn *et al.* (1997) showed that due to their territoriality, ants attending *Hilda undata* protect figs against attacks from other ants.

We present the results of field research on the

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ant protection of *Euphyonarthex phyllostoma* Schmidt (Fulgoromorpha: Tettigometridae: Hildinae) during trophobiotic associations. This hopper, recently known to be attended by ants on *Bridelia* spp. (Euphorbiaceae) in nature, is a parasite of quinquina, coffee, and cocoa (Fennah 1957; Dejean & Bourgoïn 1998; the collection at the National Museum of Natural History in Paris).

MATERIALS AND METHODS

STUDY SITE.—This study was conducted during five years (1991–1995) in Mvolié and Nkolbisson, two suburbs of Yaoundé, Cameroon.

EFFECT OF THE ATTENDING ANT SPECIES ON THE HOPPER POPULATION.—We followed the dynamics of populations descended from adults of *E. phyllostoma* as a function of the attending ant species on 17 supporting *Bridelia micrantha* of 1.9 to 2.1 m in height and oriented similarly. We counted adults and nymphs six times during nine months: the week when we found them, one and two months later, and then every two months. We also marked 100 adults of the hopper on trees occupied by *Camponotus brutus* (Formicinae) with a spot of enamel paint placed on the thorax, which permitted us to verify if they migrated later to other *B. micrantha*.

We selected 15 other *B. micrantha* attacked by *E. phyllostoma* because 10 of them were situated on the territory of *C. brutus* colonies and the 5 others were on the territory of *C. acvapimensis* colonies. Five of the former lot served as an experimental sample because ants were excluded through the use of a sticky barrier (an 8-cm band encircling the base of the trees, brushed over with birdlime each week). Adults and nymphs were counted on the 15 trees the first day of the experiment, then one month after. Using a magnifying glass, we also counted the number of parasitized versus unparasitized eggs out of 100 hatched eggs chosen at random on each tree (four egg masses per tree). Parasitized eggs were recognizable due to the small emergence holes that had been pierced by the wasps, whereas unparasitized eggs obviously had been opened by the hatching first instars. On the five *B. micrantha* in the experimental lot, we counted the number of nymphal aggregations before and then two days after the application of the sticky barrier (at 0800 h in both cases). Statistical analyses were performed using repeated measures ANOVA from Statistica software and Fisher's exact test from StatXact software; error bars reported in the figures

are ± 1 SE. Voucher specimens of ants and parasitic wasps were deposited at the Museum of Natural History in London.

BEHAVIORAL CHARACTERISTICS OF THE TROPHOBIOSIS.—Observations were conducted on 20 *B. micrantha* occupied respectively by *C. brutus* (10 trees) and *C. acvapimensis* (10 trees).

We noted: (1) if the ants had built rough carton pavilions to shelter the hopper; (2) whether the females of the hopper laid eggs or not as a function of the tending ant species; (3) the number of eggs in 32 egg masses taken at random and the presence of clumping on 20 *B. micrantha* situated in the territories of colonies of *C. brutus* (16 trees <2 m in height; 4 trees >3 m tall); (4) the number of branches per tree; (5) the number of branches with egg masses; (6) the number of egg masses on these branches; and (7) if the workers of *C. brutus* and *C. acvapimensis* chased or captured female parasitic wasps (Chalcidoidea: Encyrtidae: *Ooencyrtus* sp.) that tried to lay their own eggs on the eggs of the hoppers.

To evaluate the number of female wasps killed daily per egg mass by *C. brutus* workers, we observed five egg masses situated on five nonadjacent trees for one-half hour four times daily (ca 0900, 1200, 1500, and 1700 h).

RESULTS

INFLUENCE OF THE ATTENDING ANT SPECIES ON THE POPULATION SIZE OF THE HOPPER.—We recorded *E. phyllostoma* individuals or clusters on 163 trees of the genus *Bridelia*, particularly *B. micrantha* (87.1% of the cases). Ants always attended both isolated adults and colonies of the hopper (Fig. 1). Although we observed adult individuals tended by several ant species belonging to the subfamilies Formicinae, Dolichoderinae, and Myrmicinae, adults attended by ants other than *C. brutus* and *C. acvapimensis* never developed colonies. Nevertheless, we noted that on a large *B. micrantha*, workers of the myrmicine ant *Myrmecaria opaciventris* attended non-aggregated nymphs and two egg masses of the hopper. Hopper populations developed only when associated with *C. brutus* and *C. acvapimensis*, but reached significantly higher levels during associations with the former (Fig. 2). Numerous adults left the trees on which they were produced; 42 of the 100 individuals marked with enamel paint were recorded on adjacent *B. micrantha*.

Evidence of a protective action against enemies was obtained from experiments using ant exclusion.

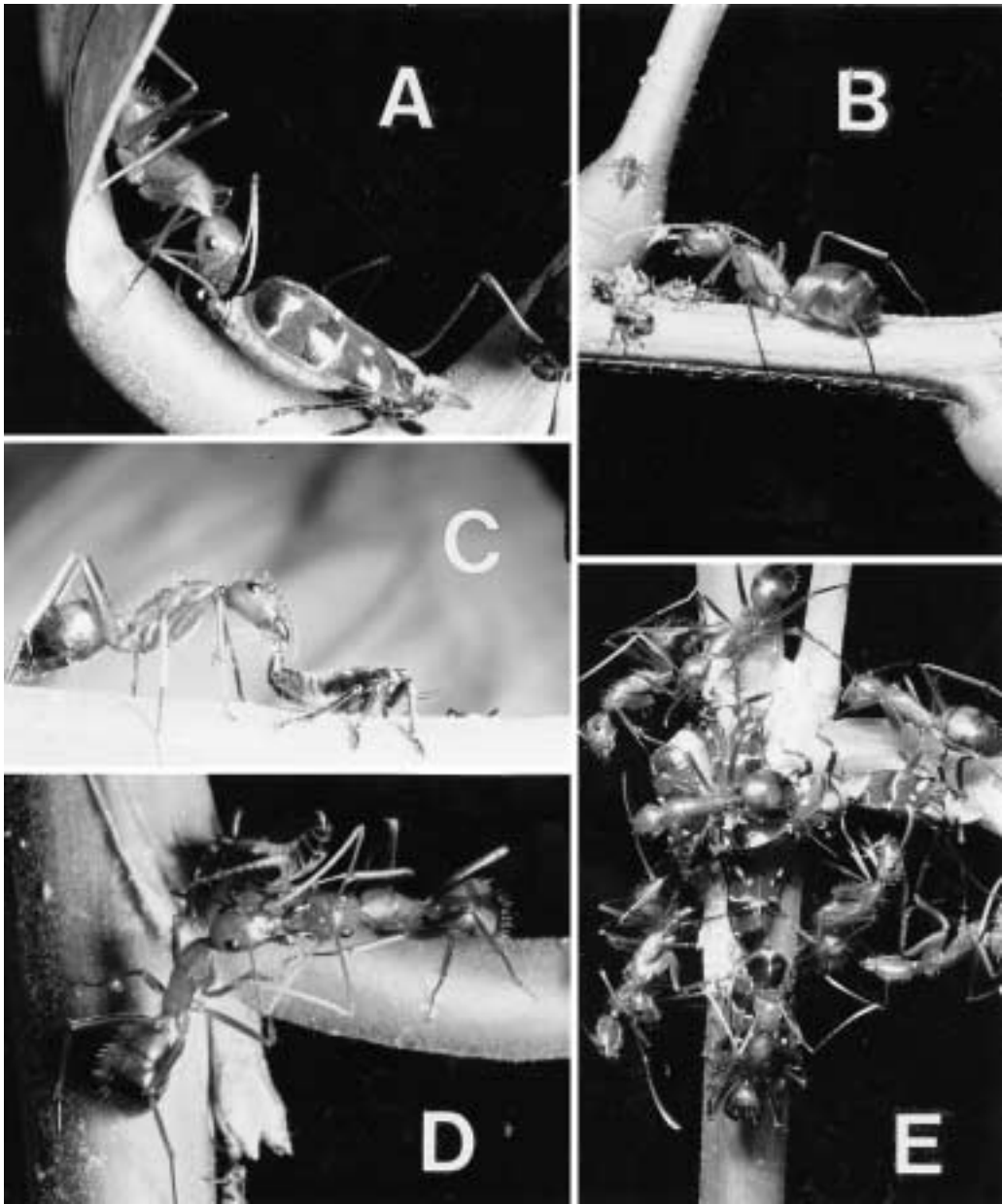


FIGURE 1. *Euphyonarthex phyllostoma* attended by workers of *Camponotus brutus*. (A) A worker folds its antennae to palpate the apex of the abdomen of an adult *E. phyllostoma* excreting a droplet of honeydew. (B) First instars attended by a worker with its crop full of honeydew. (C) A worker, antennae folded, receives honeydew from a last instar. (D) Trophallaxis between a donor worker (right) which remains near a last instar of the hopper for hours (site allegiance), and the receiving worker (left) specialized in this task. When its crop is full after receiving honeydew from different donors, it will return to the nest. (E) Group of workers around adults of the hopper and their egg masses. Some of them attend the adults for honeydew while others serve as guards.

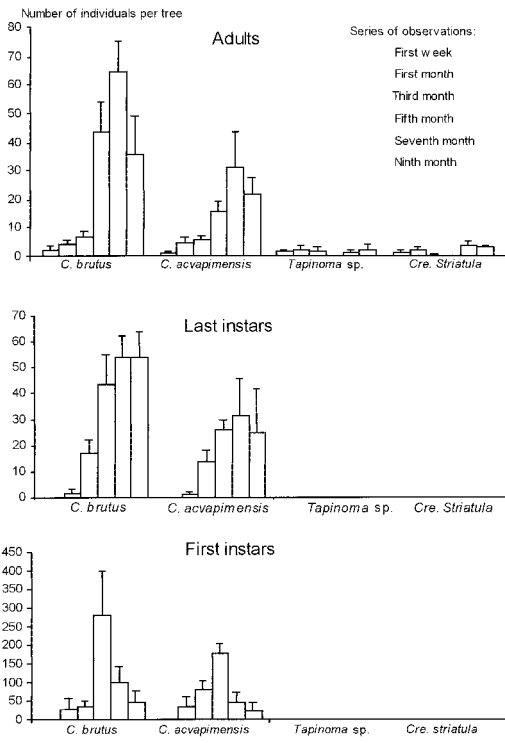


FIGURE 2. Influence of the attending ant species on the populations of adults and larvae of *E. phyllostoma* during nine months (*C. brutus* and *C. acvapimensis*: 5 trees; *Tapinoma* sp., and *Cre. striatula*: 3 trees). Statistical comparisons (ANOVA). *C. brutus* × *C. Acvapimensis*: $df_1 = 1$; $df_2 = 8$; adults: $F = 23.28$; $P < 0.01$; last instars: $F = 18.11$; $P < 0.01$; first instars: $F = 6.66$; $P < 0.05$; other comparisons concern only adults; $df_1 = 1$; $df_2 = 6$: *C. brutus* × *Tapinoma* sp.: $F = 72.27$; $P < 0.001$; *C. brutus* × *Cre. striatula*: $F = 76.63$; $P < 0.001$; *C. acvapimensis* × *Tapinoma* sp.: $F = 36.87$; $P < 0.001$; *C. acvapimensis* × *Cre. striatula*: $F = 44.47$; $P < 0.001$; *Tapinoma* sp. × *Cre. striatula*: $df_1 = 1$; $df_2 = 4$; $F = 0.43$; $P = 0.54$ (interactions among factors were significant in all cases except the last).

The hopper populations of the control lot (hopper colonies attended by *C. brutus*) were significantly higher than those of the experimental lot (ants excluded) after one month (Fig. 3). Moreover, both ant species protected the egg masses against parasitic wasps, as the rate of eggs parasitized was significantly higher in the experimental lot than in the controls (Fig. 4). Note that the egg masses were parasitized less on trees occupied by *C. brutus* than on those occupied by *C. acvapimensis*.

BEHAVIOR OF ANTS DURING PROTECTION OF THE HOPPER.—We never recorded *E. phyllostoma* attended in shelters; yet *Camponotus* spp. frequently attend-

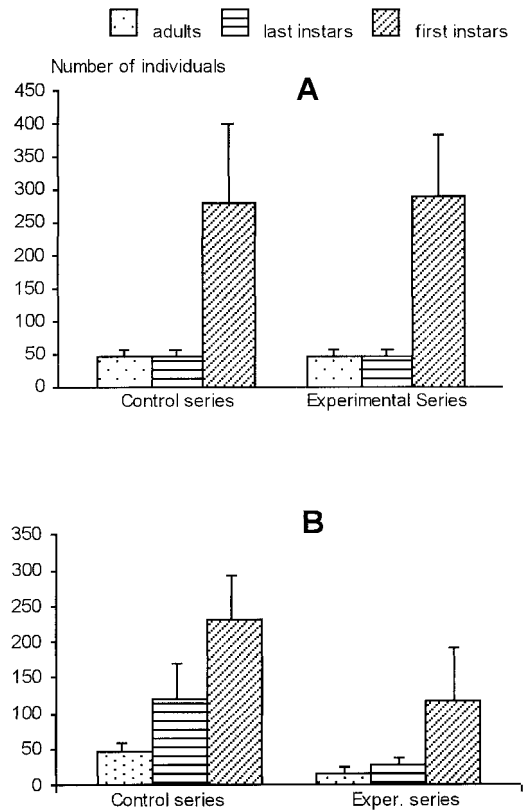


FIGURE 3. Comparison of the *E. phyllostoma* population between a control series (the workers of *C. brutus* attended the hoppers during the survey; five *B. micrantha*) and an experimental series (workers of *C. brutus* excluded; five other *B. micrantha*). (A) Before the experiment, the hoppers were attended by *C. brutus* in both series (compositions were similar; ANOVA: $df = 4$ in all situations; adults: $F = 1.88$; $P = 0.24$; last instars: $F = 0.23$; $P = 0.65$; first instars: $F = 0.029$; $P = 0.87$). (B) After one month, the two series were significantly different (adults: $F = 54.7$; $P < 0.01$; last instars: $F = 15.21$; $P < 0.05$; first instars: $F = 68.9$; $P < 0.01$).

ed other kinds of homopterans in shelters. *C. brutus* and *C. acvapimensis* protected adults, nymphs, and eggs of the hopper against any approaching insects, regardless of their size; they attacked all insects that tried to settle on their tree, including dipterans and social wasps, which covet the honeydew of their trophobionts (Dejean & Turillazzi 1992). We did not observe any attempt to capture the intruders, but the workers chased them and at times flexed their gasters and sprayed venom.

In reaction to the tiny female parasitic wasps flying around the extremities of the branches for hours and attempting to lay on the egg masses of the hopper, certain workers became specialized as

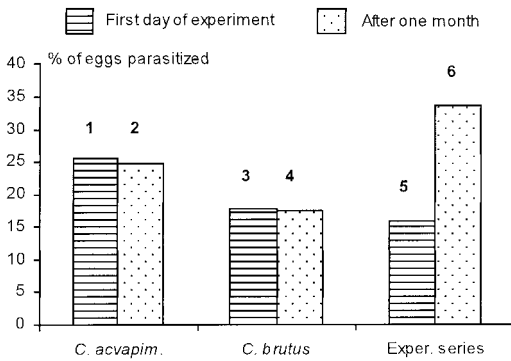


FIGURE 4. Evidence of the protective action of attending ants on the eggs of *E. phyllostoma*. Comparison between egg masses guarded by ants or not (ants excluded). Each series corresponds to five *B. micrantha* trees; the evaluation was undertaken on 100 unhatched eggs per tree. Statistical comparisons (Fisher's exact test). (1) Controls. The rate of eggs parasitized the first day was similar to that recorded one month later on the same trees, either when occupied by *C. acvapimensis* (1 vs. 2: $P = 0.88$) or *C. brutus* (3 vs. 4: $P = 1$). The rate of eggs parasitized on trees occupied by *C. brutus* was similar between trees chosen as a control and trees of the experimental series on the first day of the experiment (3 vs. 5: $P = 0.55$), as well as on trees chosen as a control, one month later (4 vs. 5: $P = 0.61$). (2) The egg masses were parasitized more on trees occupied by *C. acvapimensis* than on those by *C. brutus* (1 vs. 3: $P = 0.0034$; 2 vs. 4: $P = 0.0052$), and also on the experimental trees after one month without ants (5 vs. 6: $P = 1 \times 10^{-10}$; 2 vs. 6: $P = 0.0028$; 4 vs. 6: $P = 5 \times 10^{-9}$).

guards and stayed on the egg masses, antennae apart (Fig. 1). The marking of these workers (20 workers for each species) with a spot of enamel paint of different colors permitted us to note that 2–10 workers guarded each egg mass and that the same workers remained on the same egg mass for at least six consecutive days. There was therefore a daylong challenge between the workers that guarded the egg masses and the female wasps that tried to lay their own eggs. Workers of *C. brutus* and *C. acvapimensis* disturbed the ovipositing parasitoids and were even able to seize and kill them. For example, in the case of *C. brutus*, we noted 11 seizures for 150 attempts (7.3%) during 30 minutes. The survey counting female wasps killed by the workers on five egg masses resulted in 11.65 ± 3.08 female wasps killed per half hour ($N = 20$; min. = 7; max. = 18) and 233 ± 61.6 female wasps killed daily per egg mass.

ORIGIN OF THE FORMATION OF *E. PHYLLOSTOMA*.—Parental care by the female hoppers was restricted to egg guarding. After laying, they stayed above or

in direct proximity to the egg masses, but did not respond when wasps attempted to parasitize their eggs. Therefore, egg protection by ants was greater than that of the females, while nymph guarding was completely reserved to ants.

The egg masses of *E. phyllostoma* (103.5 ± 24.3 eggs per mass in our sampling; $N = 32$) were clumped on the extremities of certain tree branches. On the 16 trees <2.5 m high (total of 105 branches; 96 egg masses on 25 branches), egg masses were distributed over a small volume of foliage corresponding to the extremity of one to three adjacent branches ($\bar{x} = 1.5 \pm 0.63$), while the number of branches per tree varied from five to eight ($\bar{x} = 6.56 \pm 0.89$). On larger trees (4 trees with 267 branches having 63 egg masses on 10 branches), egg masses were also distributed over small zones of foliage corresponding to the extremity of one to three branches; however, on one tree we noted two such zones. In this case, the mean number of branches per tree was 66.75 ± 15.09 , while the mean number of branches with egg masses was 2.5 ± 1.3 . The comparisons between the number of branches with egg masses and a random distribution of the egg masses resulted in significant differences (Fisher's exact test: $P = 7 \times 10^{-25}$ and $P = 7 \times 10^{-12}$).

Moreover, the nymphs had a tendency to disperse when attending ants were excluded. Two days after the application of the sticky barrier on the five experimental *B. micrantha*, the number of nymphal aggregations decreased significantly (6.8 ± 2.6 vs. 3.8 ± 1.9 ; $df_1 = 4$; $df_2 = 4$; $F = 14.98$; $P < 0.05$). As a consequence, the number of individuals per aggregation was obviously lower, and we even recorded isolated individuals.

DISCUSSION

The relationships between *E. phyllostoma* and both *C. brutus* and *C. acvapimensis* are therefore beneficial for the hopper since it receives protection in exchange for honeydew, as do other ant-attended honeydew-producing homopterans (McEvoy 1979, Bristow 1984, Buckley 1987, Sudd 1987, Bach 1991, Buckley & Gullan 1991, Bristow 1991, Gullan *et al.* 1993, Jiggins *et al.* 1993, Rozario *et al.* 1993) and lycaenid lepidopterans (Pierce & Mead 1981, Takada & Yashimoto 1985, Baylis & Pierce 1992, Cushman *et al.* 1994, DeVries 1997). Because of chemical mimicry, certain parasitic wasps undermine ant efficiency in trophobiont protection (Liepert & Dettner 1993, Brodeur & Vet 1994, Fiedler *et al.* 1995).

Concerning *E. phyllostoma*, ant protection benefits the nymphs, the adults, and even the egg masses, due to specialized workers remaining at the same site. This territorial fidelity, or "site allegiance," was observed in specialized *Formica* and *Camponotus* workers that were observed repeatedly at the same site for several months, attending homopteran nymphs or adults but never guarding the eggs (Cosens & Toussaint 1985, Tilles & Wood 1986). During the guarding of egg masses, territorial fidelity and trophobiont protection is independent of a "reward" in the form of honeydew, so that the existence of an allomone on the eggs is suspected. As a result, entire colonies of *E. phyllostoma* were protected from the egg stage.

Therefore, egg protection by ants surpassed that of the female hoppers, while nymph guarding was completely reserved to the ants. These behaviors can be compared to those of ant-attended Membracidae, such as *Entilia bactriana* (parental care is restricted to egg guarding and protection of first instars while associated ants guard first and later instars; Wood 1977) and *Publilia reticulata*, which abdicate parental care to the ants (Bristow 1983).

It seems likely that a kind of feedback has developed between *E. phyllostoma* and attending ants; egg mass clumping favors nymphal aggregation and, as a consequence, ant attendance, while the presence of workers of *C. brutus* or *C. acvapimensis* seems necessary for nymphal aggregation. Wood (1982) demonstrated that for ant-attended Membracidae, the clumping of egg masses promotes offspring aggregations. Furthermore, the survival of nymphs depends on the number of individuals in

the aggregations because larger groups of nymphs appear to be located sooner by ants and are properly attended.

Ant attendance may reduce dispersal and increase survivorship and growth, while decreasing the development time of the hopper; however, these effects vary with the tending ant species (Bristow 1983). For *E. phyllostoma*, the differential development of colonies as a function of the tending ant species (*C. brutus* vs. *C. acvapimensis*) is firstly due to differences in efficiency during the protection of the hopper's eggs against parasitoids (aggressiveness also was noted as playing an important role in certain cases; Buckley & Gullan 1991). Differences in size and in the behavior of the workers also can play a role in dispersal. *C. acvapimensis* workers, smaller than *C. brutus*, are obliged to alternate between solicitation and honeydew absorption and have livelier movements; thus individuals of the hopper have a tendency to move (Dejean & Bourgoïn 1998). Adult hoppers themselves apparently select their associated ants by leaving trees occupied by "non-suitable" ants and staying on trees occupied by *C. brutus* or *C. acvapimensis* (Dejean & Bourgoïn 1998). Nevertheless, the mechanism that might explain these differences between tending ants remains unknown.

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