

# Ant-Homoptera Interactions in a Neotropical Savanna: The Honeydew-Producing Treehopper, *Guayaquila xiphias* (Membracidae), and its Associated Ant Fauna on *Didymopanax vinosum* (Araliaceae)<sup>1</sup>

Kleber Del-Claro

Departamento de Biociências, C.P. 593, Universidade Federal do Uberlândia, 38.400-W2 Uberlândia MG, Brazil

and

Paulo S. Oliveira<sup>2</sup>

Departamento de Zoologia, C.P. 6109, Universidade Estadual de Campinas, 13.083-970 Campinas SP, Brazil

---

## ABSTRACT

We investigate the ant fauna associated with the Neotropical treehopper, *Guayaquila xiphias*, on shrubs of *Didymopanax vinosum* in the cerrado (savanna) of SE Brazil. Treehoppers infested plants at the border of the cerrado almost exclusively and preferably fed near the apical meristem. During the reproductive phase of the host plant, however, the vast majority of the treehoppers aggregated on the inflorescences. We found 21 ant species harvesting honeydew at *G. xiphias* aggregations, the most frequent being *Camponotus rufipes*, *Ectatomma edentatum*, *C. crassus*, and *C. renggeri*. Such taxonomic diversity of ants tending *G. xiphias* aggregations in the cerrado is far greater than that reported for any other ant-homopteran system. Daily turnover of ant species at a given treehopper aggregation was observed on 29 percent (64 out of 222) of the *G. xiphias* aggregations recorded on *D. vinosum* shrubs. Species replacements probably reflect distinct humidity and temperature ranges tolerated by the species, and may ultimately reduce interspecific competition at homopteran aggregations. Since predation and parasitism on *G. xiphias* can be severe, and tending ants protect the homopterans against predators and parasitoids, the round-the-clock activity by ants at *G. xiphias* aggregations is regarded as crucial for the survival of these treehoppers in the cerrado.

*Key words:* ant assemblages; ant-Homoptera interaction; ant species turnover; cerrado savanna; daily foraging schedule; *Didymopanax vinosum*; *Guayaquila xiphias*; honeydew; mutualism; plant phenology.

INTERACTIONS BETWEEN ANTS AND HONEYDEW-PRODUCING homopterans commonly have been regarded as mutualistic (Way 1963, Boucher *et al.* 1982). Tending ants harvest, the energy-rich honeydew and provide a range of benefits to homopterans, including protection from predators and parasitoids (reviewed by Buckley 1987a, b). Homopteran honeydew consists of a mixture of nutrients such as sugars, amino acids, amides, and proteins (Auclair 1963). Although its importance as a food source varies widely across different ant taxa (Hölldobler & Wilson 1990), honeydew can be a major component in the diets of many ant species (Carroll & Janzen 1973; Buckley 1987a, b; Rico-Gray 1993; Tobin 1994).

Homopterans and tending ants, however, are not totally dependent on each other for survival and development. Although ant attendance has been shown to increase significantly homopteran

survival (Bristow 1983), the latter can also do well without ant associates (Hill & Blackmore 1980). Moreover, a wide variety of ant species can tend more than one homopteran species and vice versa (Wood 1984), and protection from ants may also be mediated by ecological factors such as host plant quality, size of homopteran aggregation, and predator abundance (Cushman & Whitham 1989, 1991). Therefore, such ant-homopteran associations are generally regarded to be facultatively mutualistic (Buckley 1987a, b; Bronstein 1994).

The interest in ant-plant-homopteran interactions has increased markedly over the past 15 yr, probably because they provide good models for the study of mutualism (Messina 1981; Buckley 1987a, b; Cushman 1991; Cushman & Addicott 1989, 1991; Cushman & Beattie 1991; Bronstein 1994). However, most data on ant-homopteran interactions come from temperate areas, and only more recently have these associations been studied in Neotropical habitats (Dansa & Rocha 1992; Del-Claro & Oliveira 1993, 1996).

Ants comprise a major portion of the insect

---

<sup>1</sup> Received 15 June 1996; revision accepted 31 August 1997.

<sup>2</sup> Corresponding author.

fauna found on plant foliage in the cerrado (savanna) of Brazil (Morais 1980, Oliveira & Brandão 1991). Many species not only actively collect extrafloral nectar from a number of plant species (Oliveira & Leitio-Filho - 1987; Oliveira 1987, Oliveira *et al.* 1987, Oliveira & Brandão 1991), but also commonly associate with honeydew-producing homopterans on several plants in the cerrado (Lopes 1980). The species composition of the ant faunas at extrafloral nectaries are relatively well documented for several plants in different habitats, including cerrado areas (reviewed by Oliveira & Brandão 1991). Surprisingly, however, despite the widespread occurrence of ant-homopteran associations (Buckley 1987a, b), very little is known of ant assemblages at aggregations of honeydew-producing homopterans, especially in the tropics. The degree to which changes in plant phenology and architecture may affect host plant utilization patterns by the homopterans and their attractiveness to ants also remain poorly investigated (Bristow 1991).

This study provides a detailed field account of the ant fauna associated with the honeydew-producing treehopper, *Guayaquila xiphias* Fabr. (= *Aconophora teligera*; Dietrich & Deitz 1991). The treehopper feeds almost exclusively on *Didymopanax vinosum* March. (Araliaceae), a common shrub in the cerrados of southeast Brazil. Ant-exclusion experiments in the cerrado demonstrated that tending ants protect the treehoppers from predators such as salticid spiders and syrphid flies, and egg masses from parasitoid wasps (Del-Claro 1995). In this paper we first describe the seasonal pattern of host plant utilization by *G. xiphias*, including their location within the plant crown of *D. vinosum* shrubs at different phenological phases. In the second part we determine the species composition of the diurnal and nocturnal ant fauna associated with *G. xiphias*, and describe the daily activity patterns of the principal ant species at treehopper aggregations.

## METHODS

Field work was carried out in the cerrado reserve of the Estação Experimental do Mogi-Guaçu (22°18'S, 47°10'W). The vegetation consisted of a dense scrub of shrubs and trees, which is the cerrado *sensu stricto* of Goodland (1971). The study was undertaken along two 500 m long trails: an exposed and sunny trail at the border of the cerrado, and a more closed and shady one in the interior of the cerrado (50 m from border).

In each sift we tagged 130 shrubs of *Didymopanax vinosum* (0.5-2.0 m tall). From November 1991-October 1992, we carried out monthly censuses (0700-1100 h) of ant-*Guayaquila xiphias* associations on tagged shrubs at rash silt (apart from honeydew secreted by *G. xiphias*, there were no other sugar sources on *D. vinosum* such as extrafloral nectar or honeydew from other homopterans). Ant-treehopper associations were then monitored at 2 h intervals during a 24 h period each month, from 1400-1200 h of the next day. For each ant-treehopper association, we recorded the associated ant species and the number of tending workers, the number of nymphs and adults of *G. xiphias*, and their location within the plant crown (stem, apical meristem, or inflorescence). Occasional scout ants, not in association with the treehoppers, were not counted. Since the number of plants with ant-*G. xiphias* associations varies monthly, and the number of treehoppers and tending ants per association may also change with time, we used an "index of ant activity" (IAA) to better describe ant-treehopper interactions on tagged shrubs. The index expresses the total number of tending ants/treehopper/infested plant at 2 h intervals. Therefore, daily tending activities by ants through the whole study period will be presented using the average IAA relative to 12 monthly censuses. For example, from November 1991-October 1992, at 0200 h, we found on average  $0.77 \pm 0.1$  tending ants ( $\bar{x} \pm SE$ ;  $N = 12$ )/treehopper/infested plant (Fig. 2a).

We also took monthly data on the phenologies of 60 randomly chosen shrubs of *D. vinosum* at each site. Mean monthly records of temperature and rainfall were provided by the staff of the Estação Experimental do Mogi-Guaçu.

## RESULTS

Ant-*G. xiphias* associations were observed on only two shrubs of *D. vinosum* in the shady trail at the interior of the cerrado: in December 1991, one treehopper aggregation was tended day and night by *Camponotus rufipes*, and in September 1992, another one was tended during the day by *C. crassus* and at night by *C. renggeri*. All other ant-treehopper associations ( $N = 288$ ) occurred along the sunny trail at the border of the cerrado. nearly 50 percent of the plants in this area were flowering during the dry-season, between March and May of 1992 (Fig. 1a, c). The fruiting period peaks were, during August-September, which corresponded with the end of the dry season (Fig. 1 a, c). In the

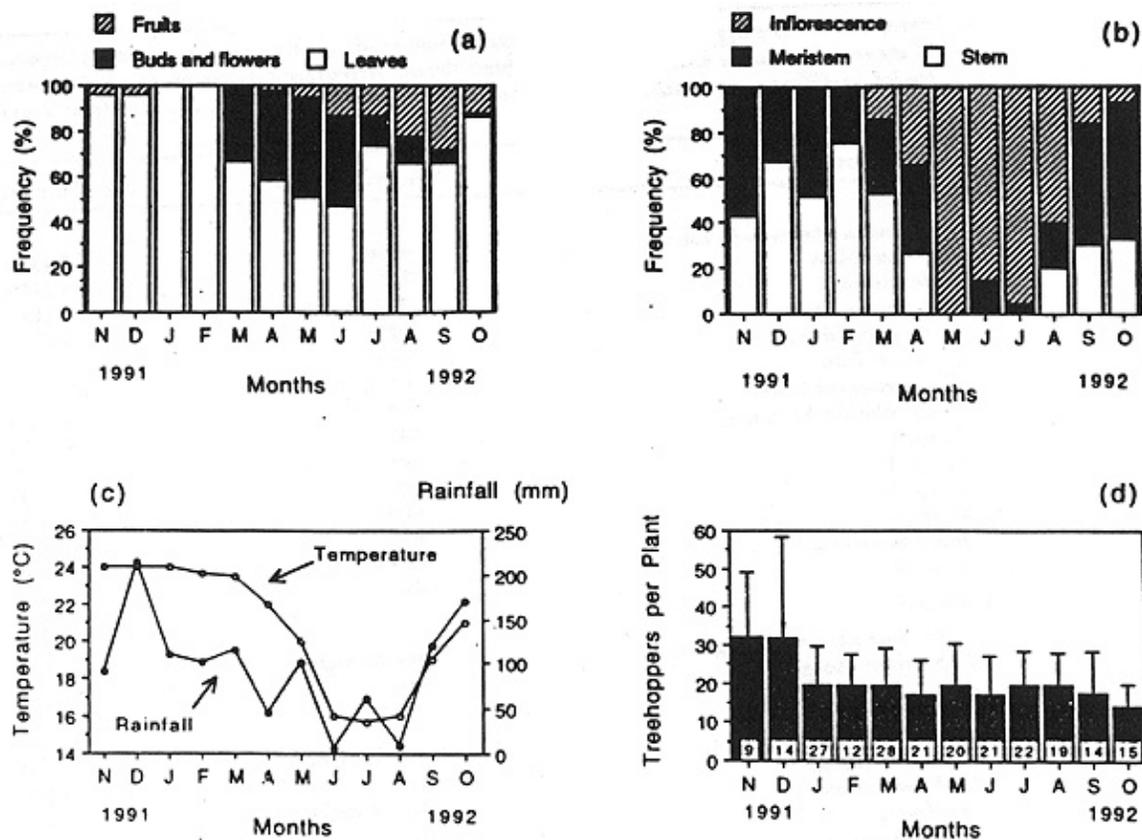


FIGURE 1. Phenology of *Didymopanax vinosum* shrubs and host plant utilization pattern by the treehopper, *Guayaquila xiphias* in the cerrado savanna of Mogi-Guaçu, SF, Brazil: (a) Frequency of plants hearing fruits, buds, and flowers, or only leaves during the study (N = 60 plants at the cerrado border); (b) Frequency of feeding sites utilized by *G. xiphias* aggregations on *D. vinosum* during di

shady area, only 10 percent of the plants flowered and produced fruit during the entire study.

We found adults, nymphs, and ovipositions of *G. xiphias* on *D. vinosum* throughout the study. Shrubs had  $2.2 \pm 1.5$  ovipositions ( $\bar{x} \pm SD$ ; N = 222), and a given treehopper aggregation could originate from two or more neighboring ovipositions at the same plant location. We never observed any treehopper aggregation untended by ants during the day or night. On two occasions we observed *C. rassus* tending ovipositions of *G. xiphias* on plants (no nymphs or adults present). On average nearly 14 percent of the *D. vinosum* shrubs (N = 130) were infested during each of the 12 censuses conducted at the border of cerrado ( $\bar{x} \pm SD = 18.3 \pm 6.0$  plants/mo). Treehopper infestation levels on host plants were similar throughout the study period (Kruskal-Wallis nonparametric ANOVA, P = 0.28; fig. 1d). Treehopper aggregations had on average  $18.8 \pm 23.6$  individuals

( $\bar{x} \pm SD$ ; N = 222), ranging from 1 female with her oviposition to 212 individuals on a single aggregation.

*Guayaquila xiphias* aggregates mainly at the apical meristems of the plants. When located on the stem, the treehoppers were usually very close to the growing meristem ( $\bar{x} \pm SD = 7.9 \pm 5.9$  cm; N = 71). We never observed treehoppers feeding on leaves, petioles, flowers, or fruits of *D. vinosum*, although they occasionally fled to that plant locations when disturbed by predators (e.g., salticid spiders) or by us. During the reproductive phase of *D. vinosum*, the treehoppers aggregated mostly on the main axis of the inflorescences (Fig. 1b), which originate from the uppermost meristematic part of the stem (a given shrub may have 13 inflorescences originating from its single reproductive branch). Mean maximum number of tending ants/treehopper was similar for aggregations located on reproductive ( $\bar{x} \pm SD = 1.5 \pm 2.5$ ; N = 87)

TABLE 1. *Ant species tending aggregations of the treehopper, Guayaquila xiphias, on shrubs of Didymopanax vinosum in the cerrado savanna of Mogi-Guaçu, southeast Brasil. Treehopper aggregations (N = 222) tended by different ant species, either simultaneously or at different periods. See also Table 2 and Figures 2 and 3*

Ant species	Activity period <sup>a</sup>	No. of records (%)
Formicinae		
<i>Camponotus abdominalis</i> Fabr.	night	10 (3.4)
<i>C. crassus</i> Mayr	day	54 (18.6)
<i>C. lespei</i> Forel	crepuscular	4 (1.4)
<i>C. pallescens</i> Mayr	night	8 (2.8)
<i>C. renggeri</i> Emery	night	43 (14.8)
<i>C. rufipes</i> Fabr.	day & night	67 (23.0)
<i>C. sericeiventris</i> Guerin	day	5 (1.7)
<i>C. aff. Blandus</i> Fr. Smith	day	5 (1.7)
<i>C. sp. 1</i>	day	3 (1.0)
<i>C. sp. 2</i>	night	1 (0.3)
<i>C. sp. 3</i>	night	1 (0.3)
<i>C. sp. 4</i>	night	3 (1.0)
<i>Brachymyrmex sp. 1</i>	day & night	6 (2.1)
<i>B. sp. 2</i>	day	1 (0.3)
Ponerinae		
<i>Ectatomma edentatum</i> Roger	day & night	66 (22.7)
<i>E planidens</i> Borgmeier	day	1 (0.3)
Myrmicinae		
<i>Zacryptocerus clypeatus</i> Farb.	day & night	7 (2.4)
<i>Z. pusillus</i> (Klug)	day	2 (0.7)
<i>Cephalotes atratus</i> L.	day & night	2 (0.7)
<i>Pheidole sp.</i>	day	1 (0.3)
<i>Crematogaster sp.</i>	day	1 (0.3)
Total no. of ant species records		291

<sup>a</sup> Diurnal activity (ca 0700-1700 h); nocturnal activity (ca 1800-0600 h).

and vegetative parts ( $\bar{x} \pm SD = 1.5 \pm 1.6$ ; N = 15) of *D. vinosum* shrubs during the flowering season (Mann-Whitney U test, P = 0.82).

We recorded a total of 21 ant species associated with *G. xiphias* aggregations (N = 222) on shrubs of *D. vinosum*. The most frequent ant species tending the treehoppers were *Camponotus rufipes*, *Ectatomma edentatum*, *C. crassus*, and *C. renggeri* (Table 1). Nine species showed a diurnal activity pattern while six others were active mostly at night. Five species were observed tending treehoppers both day and night, and one species was active mainly during dawn and dusk hours. Overall ant activity at treehopper aggregations was usually higher at night than during the day, peaking around 2240 h (Fig. 2a). Treehoppers aggregated mostly near the apical meristematic portion of the branches, and there was apparently no difference in ant species based on plant pan. The activity patterns of the four most frequent ant species tending treehoppers on *D. vinosum* are shown in fig. 2b-e. We did not find any marked seasonal shifts

in the species composition of the ant fauna at treehopper aggregations.

Daily turnover of ant species at a given treehopper aggregation was observed on 29 percent (64/222) of *G. xiphias* aggregations recorded on *D. vinosum* shrubs (Table 2). Typical diurnal ants such as *Camponotus crassus* and *C. aff. blandus* were most active at treehopper aggregations from 0800-1800 h (Fig. 2d; Table 2), after which they were sometimes replaced by predominantly nocturnal species such as *C. renggeri* and *C. abdominalis*. The tending activities of the nocturnal species extended throughout the night until early morning, when diurnal species became active again (Fig. 2e; Table, 2). A typical cast of such a turnover in ant attendants is illustrated in Figure 3a. Two ant species, *Ectatomma edentatum* and *Camponotus rufipes*, consistently tended the treehoppers both day and night (Fig. 2b, G Table 1). However, on one plant *E. edentatum* was replaced at night by *C. renggeri*. Turnover involving *C. rufipes* was observed on two plants, and in both cases tending activities at treehoppers

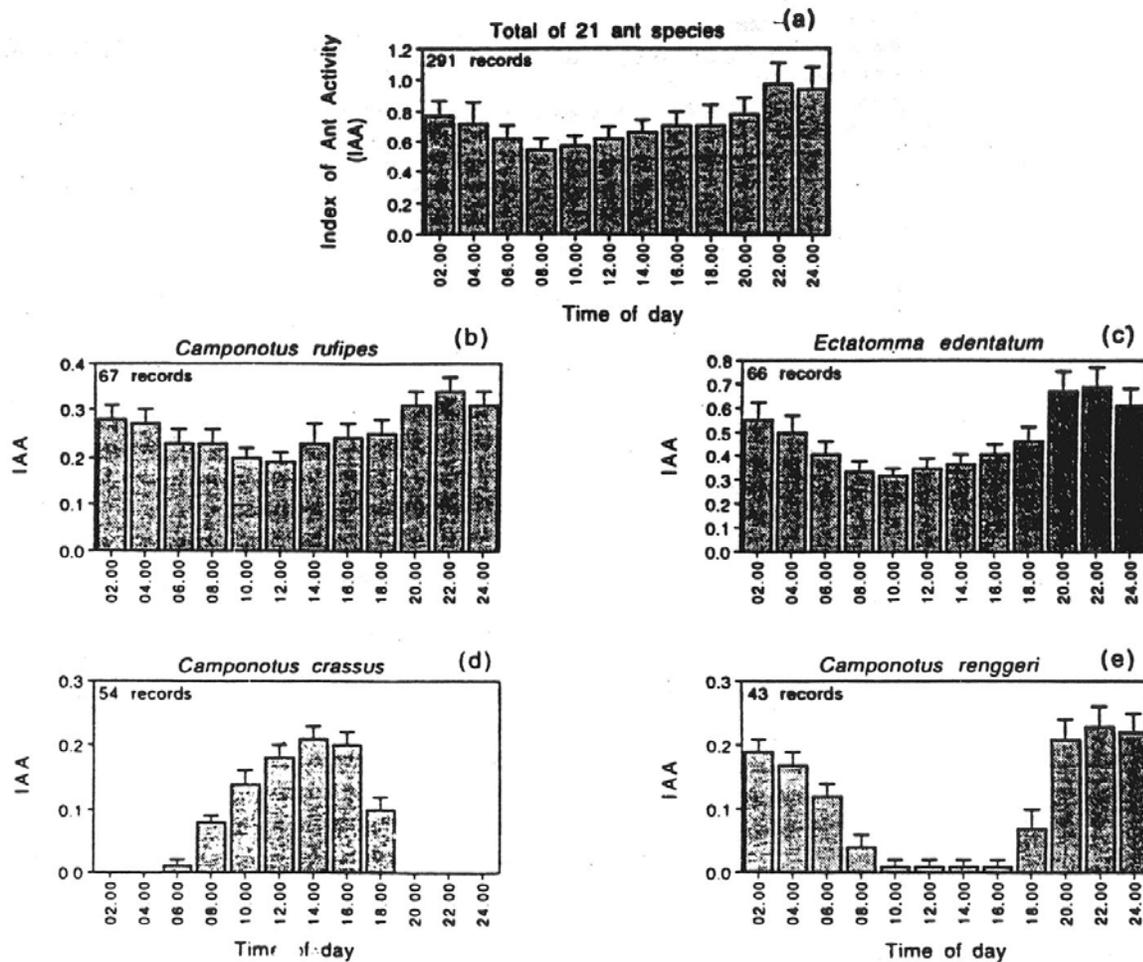


FIGURE 2. Daily tending activity by ants at *Guayaquila xiphias* aggregations (N = 222) on *Didymopanax vinosum* shrubs in the cerrado savanna of Mogi-Guaçu, SP, Brazil: (a) Overall activity by the whole associated ant fauna; and by (b) *Camponotus rufipes*, (c) *Ectatomma edentatum*, (d) *Camponotus crassus* and (e) *Camponotus renggeri* (the four most frequent ant species). Index of ant activity (IAA) is expressed as the number of tending ants/treehopper/infested plant at 2 h intervals (12 monthly censuses). Values are  $\bar{x} \pm 1$  SE. See also Table 1.

were taken over by *C. abdominalis* during the night (Table 2). We never saw interspecific aggressive interactions during ant species replacements at treehopper aggregations.

On four occasions we observed the simultaneous occurrence of the ants, *Zacryptocerus clypeatus* and *C. rufipes*, at treehopper aggregations (Fig. 3b). In every case the two species shared large treehopper aggregations (>35 individuals) during the daytime, although at night *C. rufipes* was considerably more active than *Z. clypeatus*. While ants were sharing tending activities, no agonistic interaction was ever seen between the two coexisting ant species. After harvesting honeydew from the treehoppers, *Z. clypeatus* ants occasionally shared the droplet with soliciting *C. rufipes*, with the latter

eventually collecting part of the exudate directly from the former's mandibles.

## DISCUSSION

Treehoppers are found more commonly in open and sunny areas (Havilland 1925, Funkhouser 1950, Ekkens 1972), and in cerrado vegetation these insects also tend to be more frequent on plants growing at more exposed areas (Lopes, 1984). The nutritional value of plants may vary with age and edaphic conditions, and such factors potentially can also affect plant attractiveness to phytophagous insects, including homopterans (Risebrow & Dixon 1987). That very few shrubs of *Didymopanax vinosum* produced flowers and fruits

TABLE 2. Daily turnover of ant species tending the same *Guayaquila xiphias* aggregation on shrubs of *Didymopanax vinosum* in the cerrado savanna of Mogi-guaçu, southeast Brazil. See also Table 1 and Figure 3.

Ants species active during daytime	Ant species active at night	No. of <i>G. xiphias</i> aggregations
<i>Camponotus crassus</i>	<i>Camponotus renggeri</i>	26
<i>C. crassus</i>	<i>C. abdominalis</i>	8
<i>C. crassus</i>	<i>C. pallescens</i>	6
<i>C. crassus</i>	<i>C. lespesi</i> <sup>a</sup>	3
<i>C. crassus</i>	<i>C. sp. 3</i>	2
<i>C. aff. blandus</i>	<i>C. renggeri</i>	3
<i>C. sericeiventris</i>	<i>C. renggeri</i>	4
<i>C. lespesi</i> <sup>a</sup>	<i>C. renggeri</i>	1
<i>C. sp. 1</i>	<i>C. renggeri</i>	2
<i>Pheidole sp.</i>	<i>C. renggeri</i>	1
<i>Ectatomma planides</i>	<i>C. renggeri</i>	1
<i>Brachymyrmex sp. 2</i>	<i>C. renggeri</i>	1
<i>Zacryptocerus pusillus</i>	<i>C. renggeri</i>	1
<i>Z. pusillus</i>	<i>C. abdominalis</i>	2
<i>Camponotus rufipes</i> <sup>b</sup>	<i>C. abdominalis</i>	2
<i>C. aff. Blandus</i>	<i>C. sp. 4</i>	1
Total		64

<sup>a</sup> *C. lespesi* is active at dawn and during dusk hours.

<sup>b</sup> *C. rufipes* is active both day and night.

in the interior of the cerrado at Mogi-Guaçu suggests that the plants were growing under less suitable conditions than those occurring at the cerrado border.

Plant quality may markedly affect the chemical composition and quantity of honeydew produced by homopterans (Audair 1963, Holt & Wratten 1986), and this presumably influences the recruitment behavior of tending ants and their potential beneficial effect on homopteran fitness (Cushman & Addicott 1989, 1991). Similarly, given that different plant structures are not equally valuable nutritionally (Mattson 1980), attractiveness to ants can also vary with the feeding site being exploited by the homopterans. For example, the concentration of free amino acids in homopteran honeydew may depend on the insects' feeding site on the host plant (Risebrow & Dixon 1987). Honeydew-producing homopterans are most commonly found near plant terminals such as leaf tips, inflorescences, or fruits (e.g., Wood 1984, Del-Claro & Oliveira 1993), where nitrogen concentrations and tending levels by ants are much higher [Mattson 1980, Davidson & Epstein 1989, Bristow 1991; see Baylis & Pierce (1991) on ant-tended lepidopteran larvae]. The current study showed that *Guayaquila*

*xiphias* preferably feeds near the apical meristem of *D. vinosum* shrubs, with the vast majority of the treehoppers aggregating on the inflorescences during the reproductive phase of the host plant. However, as opposed to oleander aphids which are more attractive to ants on floral rather than on leaf tips (Bristow 1991), *G. xiphias* aggregations feeding at different locations on *D. vinosum* shrubs were apparently equally attractive to tending ants, irrespective of the species. If one found nitrogen concentrations to be higher near the inflorescences of *D. vinosum*, a possible reason for the strong preference by *G. xiphias* for reproductive plant parts could be related to better development of the nymphs at this feeding site, but unfortunately, we have no data regarding this at the present.

Although we have not analyzed nutrient concentration from different plant parts, nor from plants growing in the interior or border of the cerrado, our results suggest that the infestation pattern by *G. xiphias* is strongly associated with the light conditions (shady or sunny) under which the host plant is growing, as well as with its phenological phase. Homopterans are reported to use visual, tactile, and chemical cues while selecting host plants or feeding sites within the foliage (Buckley 1987a, b, and references therein), but the degree to which plant utilization patterns by *G. xiphias* can affect ant-derived benefits in the cerrado, such as protection against natural enemies (Del-Claro 1995) has not been assessed.

Cerrado vegetation is rich in ant species that feed on homopteran honeydew and extrafloral nectar (Lopes 1984, Oliveira & Brandão 1991, Oliveira *et al.* 1995). Previous studies with *G. xiphias* in the cerrado recorded only five (Lopes 1984) and six (Dense & Rocha 1992) ant species associated with this treehopper. In the current study, the taxonomic diversity of ants tending *G. xiphias* aggregations in the cerrado (21 species) is far greater than that reported for any other ant-homopteran system (Wood 1984; Buckley 1987a, b, and references therein). Most studies on ant-homopteran interactions have focused on particular ant partners providing vital services for the homopterans, and therefore have overlooked several ant species that are either occasional attendants or whose tending activity pattern is mainly nocturnal (*cf.* Hill & Blackmore 1980). Our results from ant-*G. xiphias* associations in the cerrado demonstrate the need for more extensive round-the-clock censuses in future research dealing with ant assemblages at honeydew-producing homopterans,

The habit of harvesting honeydew from

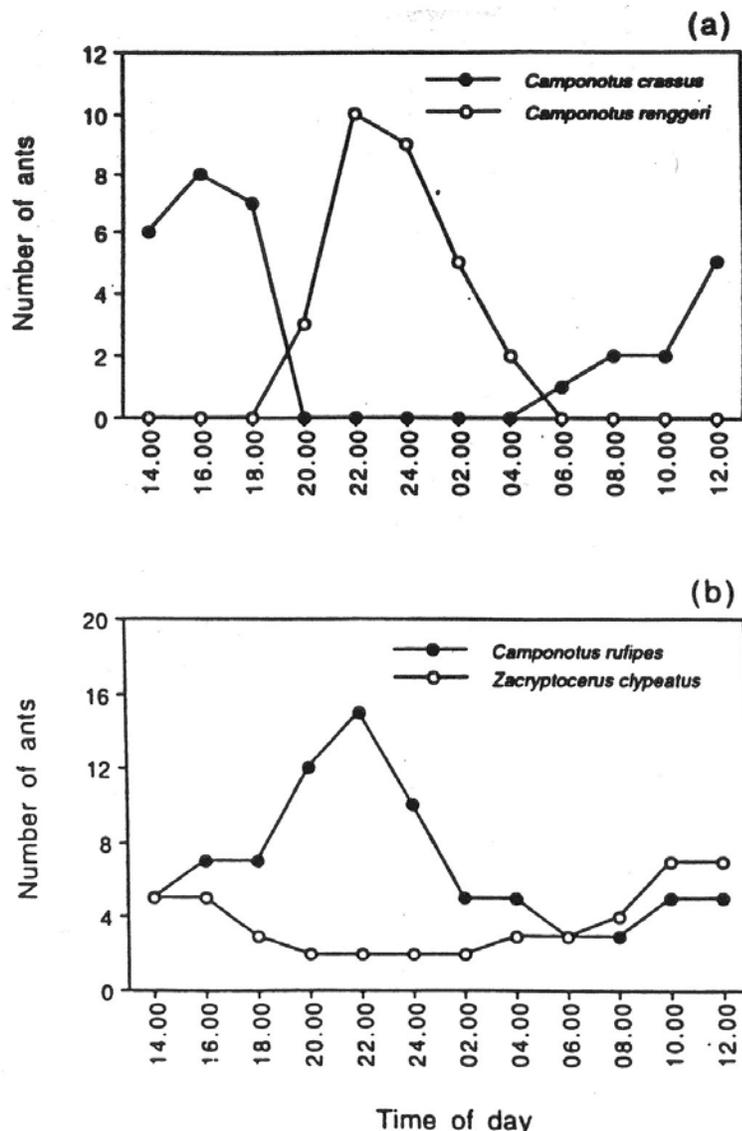


FIGURE 3. Typical cases of ant species replacement and coexistence at *Guayaquila xiphias* aggregations on *Didymopanax vinosum* shrubs in the cerrado savanna of Mogi-Guaçu, SE Brazil. (a) *Camponotus crassus* and *C. renggeri* tending an aggregation of 13 treehoppers on plant no. 103 at different times. (b) *Camponotus rufipes* and *Zacryptocerus clypeatus* sharing tending activities at an aggregation of 80 treehoppers on plant no. 68. See also Table 2.

homopterans is widespread across different ant taxa, being more developed in the subfamilies Formicinae, Myrmicinae, and Dolichoderinae (Sudd 1987, b; Hölldobler & Wilson 1990). The formicine genus, *Camponotus*, was by far the best represented at *G. xiphias* aggregations in the cerrado: 12 species accounted for 70 percent (204/291) of the ant-*G. xiphias* associations recorded on *D. vinosum* shrubs. A similar dominance by *Camponotus* also has occurred within ant assemblage at extrafloral nectaries in the cerrado and in other vegetation types in tropical and subtropical habitats (Oliveira & Brandão 1991 and reference therein),

*Camponotus* is a worldwide, dominant ant genus that usually occurs with high local abundance and large numbers of species in most zoogeographical regions (Wilson 1976, Hölldobler & Wilson 1990). In cerrado vegetation, *Camponotus* species outnumber all other ants on plant foliage, and common species like *C. rufipes*, *C. crassus*, and *C. aff. blandur* are generalized foragers of plant and homopteran exudates, fruits, carrion, and live arthropods (Luederwaldt 1926; Oliveira & Brandão 1991; Dansa & Rocha 1992; Freitas & Oliveira 1992; Oliveira *et al.* 1995; Del-Claro & Oliveira 1993, 1996).

Although ponerine ants are generally regarded as predators and scavengers, several species in this subfamily are also commonly seen harvesting extrafloral nectar, homopteran honeydew, or secretions from lepidopteran larvae (Evens & Laton 1971, Young & Hermann 1980, Hölldobler 1985, DeVries 1991; Oliveira & Brandão 1991). Indeed, *Ectatomma edentatum* was the second most common ant species at *G. xiphias* aggregations and, like the first raced *Camponotus rufipes*, extended its tending activities both day and night. In addition to homopteran honeydew, however, *E. edentatum* also captures a range of live and dead arthropods, and collects seeds and fruit matter on the cerrado floor (P. S. Oliveira, pers. obs.).

Differences in the daily foraging schedules of sympatric ant species are frequently associated with distinct humidity and temperature ranges tolerated by the species, especially in tropical habitats (Levings 1983, Torres 1984). The temporal segregation resulting from such ecophysiological differences among the ant species may ultimately reduce interspecific competition at predictable food sources (Hölldobler & Wilson 1990). Daily turnover of ant species at long-lasting food sources such as homopteran honeydew, lepidopteran secretions, and extrafloral nectaries has been well documented and strongly suggests a temporal partitioning of resources (Wilson 1971, Hill & Blackmore 1980, Klotz 1984, Hölldobler 1986, DeVries 1991, Oliveira & Brandão 1991, Oliveira *et al.* 1995).

The observed daily replacement of ant species associated with *G. xiphias* aggregations corresponds closely to others reported for ant assemblages at extrafloral nectaries in cerrado vegetation (Oliveira & Brandão 1991, Oliveira *et al.* 1995). The activity schedule exhibited by the principal ant species is roughly the same at these assemblages: a diurnal guild including common cerrado species such as *Camponotus crassus*, *C.* aff. *blandus*, and *Zacryptocerus pusillus*, and a nocturnal one formed by *C. renggeri*, *C. abdominalis*, and *G. pallescens*. However, it is worth noting that *C. rufipes*, a typical nocturnal species at extrafloral nectaries (Oliveira & Brandão 1991, Oliveira *et al.* 1995), occurs both day and night at *G. xiphias* aggregations. In fact both *C. rufipes* and *E. edentatum* (see above) seem to depend strongly on homopteran honeydew for colony maintenance and development, and are usually very aggressive near the treehoppers (Del-Claro 1995). Moreover, *G. rufipes* may occasionally build

shelters of dry grass for treehopper nymphs on the host plant (Del-Claro & Oliveira, pers. obs.).

The simultaneous exploitation of a food source by more than one ant species, as recorded for the timid *Zacryptocerus clypeatus* and aggressive *C. rufipes* at treehoppers, also has been reported for other ant taxa (Hölldobler & Wilson 1990). The food exchange between coexisting species has been interpreted as a form of appeasement aimed at dominant/aggressive ant species, being more commonly observed at attractive long-lasting food sources such as homopteran honeydew (Bhatkar 1979, 1983). Other species of *Zacryptocerus* have also been reported to share food sources with aggressive *Azteca* ants, and their acceptance by the latter is attributed to their stealthy approaching behavior and unusual body armor (Adams 1980).

In conclusion, the current account of the ant fauna harvesting honeydew at *Guayaquila xiphias* aggregations reveals the importance of this food source for ants in tropical areas, especially in the cerrado (see also Rico-Gray 1993, Tobin 1994). We never observed *G. xiphias* aggregations untended by ants during either the day or night, suggesting that ant activity on plants is high in the cerrado and/or that treehoppers are very efficient at attracting prospective tending ants (Del-Claro & Oliveira 1996). Because ant attendance significantly reduced mortality to *G. xiphias* due to predation and parasitism on *D. vinosum* shrubs (Del-Claro 1995), such round-the-clock activity by tending ants at *G. xiphias* aggregations is arguably crucial to the survival of these treehoppers in the cerrado of southeastern Brazil.

## ACKNOWLEDGMENTS

We are grateful to I. Andrade, M. R. Pie, A. T. Oliveira Filho, and A. V. Freitas for discussions and helpful suggestions on the manuscript. The final version of the manuscript was improved greatly by comments from D. W. Davidson, S. Koptur, and an anonymous referee. I. R. Leal and B. C. Lopes helped with the taxonomic identifications of the ants and treehoppers, respectively. The study was supported by the Brazilian Research Council (CNPq) through a doctoral fellowship to K. Del-Claro (140390/91-0) and research grants to P. Oliveira (300101/90-2, 400692/92-9). Fieldwork was supported by a grant from the Fundo do Apoio ao Ensino e à Pesquisa da Unicamp to P. Oliveira. We thank the Instituto de Botânica de São Paulo for permission to work in its cerrado reserve, and numerous colleagues for help in the field.

## LITERATURE CITED

- ADAMS, E. S. 1980. Interaction between the ants *Zacryptocerus maculatus* and *Azteca trigona*: interspecific parasitization of information. *Biotropica* 22: 200-206.
- AUCLAIR, J. L. 1963. Aphid feeding and nutrition. *Annu. Rev. Entomol.* 8: 439-490.
- BAYLIS, M., AND N. E. PIERCE. 1991. The effect of host-plant quality on the survival of larvae and oviposition by adults of an ant-tended lycaenid butterfly, *Jalmenus evagoras*. *Ecol. Entomol.* 16: 1-9.
- BHATKAR, A. P. 1979. Trophallactic appeasement in ants from distant colonies. *Folia Entomol. Mexicana* 41: 135-143.
- . 1983. Interspecific trophallaxis in ants, its ecological and evolutionary significance. In P. Jaisson (Ed.). *Social insects in the tropic*, Vol. 2, pp. 105-123. Université Paris-Nord, Paris, France.
- BOUCHER, D. H., S. JAMES, AND K. H. KEELER. 1982. The ecology of mutualism. *Annu. Rev. Ecol. Syst.* 13: 315-347.
- BRISTOW, C. M. 1983. Theehoppers transfer parental care to ants: a new benefit of mutualism. *Science (Wash. DC)* 220: 532-533.
- . 1991. Are ant-aphid associations a tritrophic interaction? Oleander aphids and Argentine ants. *Oecologia (Berl.)* 87: 514-521.
- BRONSTEIN, J. L. 1994. Conditional outcomes in mutualistic interactions. *Trends Ecol. Evol.* 9: 214-217.
- BUCKLEY, R. C. 1987a. Interactions involving plants, Homoptera, and ants. *Annu. Rev. Ecol. Syst.* 18: 111-138.
- . 1978b. Ant-plant-homopteran interactions. *Adv. Ecol. Res.* 16: 53-85.
- CARROLE, C. R., AND D. H. JANZEN. 1973. Ecology of foraging by ants. *Annu. Rev. Ecol. Syst.* 4: 231-257.
- CUSHMAN, J. H. 1991. Host-plant mediation of insect mutualisms: variable outcomes in herbivore-ant interactions. *Oikos* 61: 138-144.
- , AND J. F. ADDICOTT. 1989. Intra- and interspecific competition for mutualists: ants as a limited and limiting resource for aphids. *Oecologia (Berl.)* 79: 315-321.
- , AND ———. 1991. Conditional interactions in ant-plant-herbivore mutualisms. In C. R. Huxley and D. F. Cutler (Eds.). *Ant-plant interactions*, pp. 92-103. Oxford University Press, Oxford, England.
- , AND A. J. BEATHE. 1991. Mutualisms: assessing the benefits to hosts and visitors. *Trends Ecol. Evol.* 6: 193-195.
- , AND T. G. WHITHAM. 1989. Conditional mutualism in a membracid-ant association: temporal, age-specific, and density-dependent effects. *Ecology* 70: 1044-1047.
- , AND ———. 1991. Competition mediating the outcome of a mutualism: protective services of ants as a limiting resource for membracids. *Am. Nat.* 1314: 851-865.
- DANSA, C. V. A., AND C. F. D. ROCHA. 1992. An ant-membracid-plant interaction in a cerrado area of Brazil. *J. Trop. Ecol.* 8: 339-348.
- DAVIDSON, D. W., AND W. W. EPSTEIN. 1989. Epiphytic associations with ants. In U. Luttge (Ed.). *Phylogeny and ecophysiology of epiphytes*, pp. 200-233. Springer-Verlag, New York, New York.
- DEL-CLARO, K. 1995. Ecologia da interação entre formigas a *Guayaquila xiphias* (Homoptera: Membracidae) em *Didymopanax vinosum* (Araliaceae). Ph.D. Thesis, Universidade Estadual do Campinas, Sao Paulo, Brazil.
- , AND P. S. OLIVEIRA. 1993. Ant-Homoptera interaction: do alternative sugar sources distract tending ants? *Oikos* 68: 202-206.
- , AND ———. 1996. Honeydew flicking by treehoppers provides cues to potential tending ants. *Anim. Behav.* 51: 1071-1075.
- DEVRIES, P. J. 1991. Evolutionary and ecological patterns in myrmecophilous riodinid butterflies. In C. R. Huxley and D. F. Cutler (Eds.). *Ant-plant interactions*, pp. 143-156. Oxford University Press, Oxford, England.
- DIETRICH, C. H., AND L. L. DEITZ. 1991. Revision of the Neotropical treehopper tribe Aconophorini (Homoptera: Membracidae). Department of Agricultural Communications, North Carolina State University, pp. 1-134. Raleigh, North Carolina.
- EKKENS, D. 1972. Peruvian treehopper behaviour (Homoptera: Membracidae). *Entomol. News* 83: 257-271.
- EVANS, H. C., AND D. LESTON. 1971. A ponerine ant (Hym., Formicidae) associated with Homoptera on cocoa in Ghana. *Bull. Entomol. Res.* 61: 357-362.
- FREITAS, A. V. L., AND P. S. OLIVEIRA. 1992. Biology and behavior of *Eunica bechinae* (Lepidoptera: Nymphalidae) with special reference to larval defense against ant predation. *J. Res. Lepid.* 31: 1-11.
- FUNKHOUSER, W. D. 1950. Homoptera, family Membracidae. *Genera insectorum* 208: 1-383.
- GOODLAND, R. 1971. A physiognomic analysis of the cerrado vegetation of central Brazil. *J. Ecol.* 59: 411-419.
- HAVILLAND, M. D. 1925. The Membracidae of Kartabo, Bartica District, British Guiana, with descriptions of new species and binomial notes. *Zoologica N.Y.* 6: 229-290.
- HILL, M. G., AND P. J. M. BLACKMORE. 1980. Interactions between ants and the coccid *Icerya seychellarum* on Aldabra Atoll. *Oecologia (Berl.)* 45: 360-365.
- HÖLLDOBLER, B. 1985. liquid food transmission and antennation signals in ponerine ants. *Israel J. Entomol.* 19: 89-99.
- . 1986. Food robbing in ants, a form of interference competition. *Oecologia* 69: 12-15.
- , AND E. O. WILSON. 1990. *The ants*. Harvard University Press, Cambridge, Massachusetts.
- HOLT, J., AND S. D. WRATTEN. 1986. Components of resistance to *Aphis fabae* in faba bean cultivars. *Entomol. Exp. Appl.* 40: 35-40.
- KLOTZ, J. H. 1984. Diet differences in foraging in two ant species (Hymenoptera: Formicidae). *J. Kans. Entomol. Soc.* 59: 537-541.

- LEVINGS, S. C. 1983. Seasonal, annual, and among-site variation in the ground ant community of a deciduous tropical forest: sonic causes of patchy species distributions. *Font. Monogr.* 53: 435-455.
- LOPES, B. C. 1984. Aspectos da ecologia de membracideos (Insecta: Homoptera) em vegetação do cerrado do Estado de São Paulo, Brasil. M.S. Thesis, Universidade Estadual de Campinas, São Paulo, Brazil.
- LUEDERWALDT, H. 1926. Observações biológicas sobre formigas brasileiras, especialmente no Estado do São Paulo. *Revta. Mus. Paulista* 14: 186-302.
- MATESON, W. J. 1980. Herbivory in relation to plant nitrogen content. *Annu. Rev. Ecol. Syst.* 11: 119-161.
- MESSINA, F. J. 1981. Plant protection as a consequence of ant-membracid mutualism: interactions on goldenrod (*Solidago* sp.). *Ecology* 62: 1433-1440.
- MORAIS, H. C. 1980. Estrutura de uma comunidade de formigas arborícolas em vegetação de campo cerrado. M.S. Thesis. Universidade Estadual de Campinas, São Paulo, Brazil.
- OLIVEIRA, P. S. 1987. The ecological function of extrafloral nectaries: herbivore deterrence by visiting ants and reproductive output in *Caryocar brasiliense* (Caryocaraceae). *Func. Ecol.* 11: 323-330.
- , AND C. R. F. BRANDÃO. 1991. The ant community, associated with extrafloral nectaries in the Brazilian cerrados. In C. R. Huxley and D. F. Cutler (Eds.). *Ant-plant interactions*, pp. 182-212. Oxford University Press, Oxford, England.
- , AND H. F. LEITÃO-FILHO. 1987. Extrafloral nectaries: their taxonomy, distribution, and abundance in the wood flora of cerrado vegetation in southeast Brazil. *Biotropica* 19: 140-148.
- , C. KLITZKE, AND E. VIEIRA. 1995. The ant fauna associated with the extrafloral nectaries of *Qualea grandiflora* (Vochysiaceae) in an area of cerrado vegetation in central Brazil. *Entomol. Mo. Mag.* 131: 77-82.
- , A. F. DA SILVA, AND A. B. MARTINS. 1987. Ant foraging on extrafloral nectaries of *Qualea grandiflora* (Vochysiaceae) in cerrado vegetation: ants as potential antiherbivore agents. *Oecologia (Berl.)* 74: 228-230.
- RICO-GRAY, V. 1993. Use of plant-derived food resources by ants in the dry tropical lowlands of coastal Veracruz., Mexico. *Biotropica* 25: 301-315.
- RISEBROW, A., AND A. F. G. DIXON. 1987. Nutritional ecology of phloem-feeding insects. In F. Slansky, Jr., and J. G. Rodriguez (Eds.). *Nutritional ecology of insects, mites, spiders, and related invertebrates*, pp. 421-448. John Wiley & Sons, New York, New York.
- SUDD, J. H. 1987a. Ant-aphid mutualism. In A. K. Minks and P. Harrewijn (Eds.). *Aphids: their biology, natural enemies, and control*, Vol. A, pp. 355-65. Elsevier, Amsterdam, The Netherlands.
- 1987b. Ants as partners. In J. H. Sudd (Ed.). *The behavioral ecology of ants*, pp. 120-136. Chapman & Hall, New York, New York.
- TOBIN, J. F. 1994. Ants as primary consumers: diet and abundance in the Formicidae. In J. H. Hunt and C. A. Nalepa (Eds.). *Nourishment and evolution in insect societies*, pp. 279-308. Westview Press, Oxford, England.
- TORRES, J. A. 1984. Niches and coexistence of ant communities in Puerto Rico: repeated patterns. *Biotropica* 16: 284-295.
- WAY, M. J. 1963. Mutualism between ants and honeydew-producing Homoptera. *Annu. Rev. Entomol.* 8: 307-344.
- WILSON, E. O. 1971. *The insect societies*. Harvard University Press, Cambridge, Massachusetts.
- 1976. Which are the most prevalent ant genera? *Studia Entomol.* 19: 187-200.
- WOOD, T. K. 1984. Life history patterns of tropical membracids (Homoptera: Membracidae). *Sociobiology* 8: 299-344.
- YOUNG, A. M., AND H. R. HERMANN. 1980. Notes on the foraging of the giant tropical ant *Paraponera clavata* (Hymenoptera: Formicidae: Ponerinae). *J. Kans. Entomol. Soc.* 53: 35-55.