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Conditional outcomes in a neotropical treehopper-ant association: temporal and species-specific variation in ant protection and homopteran fecundity

Abstract We studied the association between the honey-dew-producing membracid *Guayaquila xiphias* and its tending ants in the cerrado savanna of Brazil, during 1992 and 1993. Results showed that ants attack potential enemies of *G. xiphias*, and that increased ant density near the treehoppers affects the spatial distribution of parasitoid wasps on the host plant, keeping them away from brood-guarding *G. xiphias* females. Controlled ant-exclusion experiments revealed that ant presence (seven species) reduces the abundance of *G. xiphias*' natural enemies (salticid spiders, syrphid flies, and parasitoid wasps) on the host plant. The data further showed that ant-tending not only increased homopteran survival, but also conferred a direct reproductive benefit to *G. xiphias* females, which may abandon the first brood to ants and lay an additional clutch next to the original brood. Two years of experimental manipulations, however, showed that the degree of protection conferred by tending ants varies yearly, and that at initially high abundance of natural enemies the ant species differ in their effects on treehopper survival. Ant effects on treehopper fecundity also varied with time, and with shifts in the abundance of natural enemies. This is the first study to simultaneously demonstrate conditionality in ant-derived benefits related to both protection and fecundity in an ant-tended Membracidae, and the first to show the combined action of these effects in the same system.

Key words Ants · Conditional mutualism · *Guayaquila xiphias* · Species-specific effects · Treehopper-ant association

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Introduction

The outcomes of mutualistic interactions are strongly dependent upon the ecological settings in which they occur (Thompson 1982, 1988; Bronstein 1994). During the past few years a number of studies have shown that the results of ant-plant and ant-herbivore mutualisms can vary with several factors (reviewed by Cushman and Addicott 1991; Koptur 1992; Bronstein 1994, 1998). For example, ant-derived benefits to plants bearing extrafloral nectaries may vary with the species of visiting ant (Koptur 1984; Rico-Gray and Thien 1989), rate of ant visitation to the plant (Inouye and Taylor 1979; Rashbrook et al. 1992; Oliveira et al. 1999), local abundance of ants and herbivores (Barton 1986), as well as with the capacity of specialized herbivores to circumvent the ants' deterrent traits (Horvitz and Schemske 1984). Similarly, ant-derived protection against natural enemies of honeydew-producing homopterans was demonstrated to vary with factors such as the species of tending ant (Addicott 1979; Bristow 1984), size of homopteran aggregation (Cushman and Whitham 1989; Breton and Addicott 1992), developmental stage of homopterans and predator abundance (Cushman and Whitham 1989), as well as competition among homopteran aggregations for the services of ant mutualists (Addicott 1978; Cushman and Addicott 1989; Cushman and Whitham 1991). It became clear from these recent findings that ant-plant-herbivore mutualisms are inherently variable, and therefore studying the factors that mediate their possible outcomes should provide a more precise picture of the ecological dynamics of interspecific associations in nature (Cushman 1991; Cushman and Addicott 1991; Bronstein 1994, 1998).

In the present paper we focus on the association between the honeydew-producing treehopper *Guayaquila xiphias* (Membracidae) and its tending ants on shrubs of *Didymopanax vinosum* (Araliaceae), in the cerrado (savanna-like) vegetation of Brazil. We used the data from a 2-year study to address the following questions:

1. Do tending ants behave aggressively towards other organisms (i.e. potential enemies of *G. xiphias*) on the

host plants, and is aggression more pronounced near *G. xiphias* aggregations?

2. Does the foraging pattern of tending ants affect the spatial distribution of parasitoid wasps on the host plants?
3. Do tending ants affect the abundance of *G. xiphias*'s natural enemies on the host plant?
4. Does ant-tending affect homopteran survival, and the fecundity of *G. xiphias* females?
5. Do ant-derived benefits to *G. xiphias* present temporal and species-specific variation?

Study organisms

G. xiphias commonly infests shrubs of *D. vinosum* in the cerrado vegetation of Brazil (Del-Claro and Oliveira 1993, 1999). Ovipositions, nymphs and adults of *G. xiphias* occur on host plants through the whole year, and infestation levels may range from one female with her oviposition to 212 individuals in a single aggregation (mean±SD=18.8±23.6; *n*=222). Nymphs complete development in 20–23 days, after which newly emerged adults begin to disperse from natal aggregations. The treehoppers preferentially feed near the apical meristem of the host plant, but during the reproductive phase of *D. vinosum* (March–September) they most frequently aggregate on the inflorescence at the uppermost meristematic part of the single reproductive branch (Del-Claro and Oliveira 1999). Aggregations of *G. xiphias* have never been seen untended by ants in the cerrado. Recent field experiments have demonstrated that the flicking of accumulated honeydew by the treehoppers serves as a cue to ground-dwelling ants, that climb onto the host plant upon finding honeydew droplets beneath the host plant, and start tending activity (Del-Claro and Oliveira 1996). Tending levels by ants, as expressed by the mean maximum number of ants per treehopper, are similar for aggregations located on vegetative and reproductive plant parts (1.5 ants/treehopper; Del-Claro and Oliveira 1999). As reported for other treehopper species (Beamer 1930), females of *G. xiphias* exhibit parental care by remaining with their egg masses and young nymphs. In the presence of ants, however, some *G. xiphias* females may abandon the first brood to tending ants and produce an additional clutch on the same stem, 4–6 cm from the original brood (Del-Claro 1995; see also Wood 1977; McEvoy 1979; Bristow 1983).

Aggregations of *G. xiphias* are tended day and night by a total of 21 honeydew-harvesting ant species; the most frequent ones are *Camponotus rufipes*, *Camponotus crassus*, *Camponotus renggeri* (Formicinae) and *Ectatomma edentatum* (Ponerinae). Round-the-clock censuses at treehopper aggregations revealed that the species composition of tending ants changes markedly from day to night. A detailed account of the ant fauna associated with *G. xiphias* is given by Del-Claro and Oliveira (1999).

Aggregations of *G. xiphias* are attacked by three main types of natural enemies on shrubs of *D. vinosum*. Both day and night salticid spiders (15 species) may prey on nymphs, and more rarely on agile and sclerotized adult *G. xiphias*. Larvae of the dipteran *Ocyptamus arx* (Syrphidae) prey on both nymphs and adults of *G. xiphias*, and suck empty the entire body content of the treehoppers. Syrphid larvae may also occasionally feed on ovipositions when no nymph or adult treehoppers are present on the plant. Both larvae and adult *O. arx* are active during the day. The diurnal parasitoid wasp *Gonatocerus* sp. (Myrmaridae) oviposits on the white egg masses of *G. xiphias*, and parasitized ovipositions are easily identified by their brownish appearance. No other natural enemies were commonly seen with *G. xiphias* during this study.

Materials and methods

Field work was carried out during March 1992 and 1993, in the cerrado reserve of the Estação Experimental de Mogi-Guaçu (22°18′S, 47°10′W), State of São Paulo, southeast Brazil. The vegetation of the study area consists of a dense scrub of shrubs and trees, which corresponds to the cerrado sensu stricto of Goodland (1971). The climate of the region is characterized by a dry/cold season (April–September) and a rainy/warm season (October–March).

In March 1992 and 1993 we tagged 22 experimental pairs of *D. vinosum* at the border of the cerrado reserve, where *G. xiphias*-ant associations most commonly occur (Del-Claro and Oliveira 1999). Plants in a given pair were approximately the same height (1–2 m tall) and in the same phenological state, had similar numbers of leaves and stems, and were 4 m apart from each other. Experimental plants were infested by similar-sized ant-tended treehopper aggregations, which were usually located on the apex of the principal stem of *D. vinosum* shrubs. Each experimental plant had only one incipient aggregation formed by the female and her brood (egg mass and nymphs). We randomly designated each shrub in a given pair as a control (ants present) or treatment plant (ants excluded) by the flip of a coin. Ants were excluded from treatment plants by applying a sticky barrier of tree Tanglefoot (Tanglefoot company, Grand Rapids, Mich.) to the base of their trunks every 10 days. Neighbouring grass bridges providing aerial access of ants to the trunk of treated plants were regularly pruned. Ants had free access to control plants, and the species composition of tending ants was similar during both years of study (Table 1). In both 1992 and 1993 there was no statistically significant difference in the initial size of control and treatment treehopper aggregations (1992, *U*=247.5, *P*=0.897, *n*=22; 1993, *U*=303.5, *P*=0.148, *n*=22; Mann-Whitney *U*-tests).

We censused the treehoppers and their natural enemies (spiders, syrphid flies, and parasitic wasps) every 2–3 days on both control and treatment plants during a period of 16 days. The production of an additional brood by the resident female was also recorded. The location of parasitoid wasps within the plant crown was categorized as "near the homopteran oviposition" if the wasp was seen at the apical meristem <5 cm from the egg-guarding female, or "on foliage" if the wasp was seen on leaves. The number of ants tending the homopterans on control plants was also recorded in each census. Organisms were censused during sunny days between 0800 and 1600 hours. Given that newly-emerged adult treehoppers begin to disperse from natal aggregations ca. 20 days after hatching from eggs (see above), the 16-day duration of the ant-exclusion experiments was a priori considered suitable for the evaluation of ant-derived effects on *Guayaquila* aggregations.

To investigate if ant-derived effects on treehoppers would vary with ant species, both in 1992 and 1993 treehopper aggregations of control plants were divided into three groups, as follows: (1) tended by *C. rufipes*; (2) tended by *Camponotus* spp. (*C. crassus*,

Table 1 Species composition of the ant faunas tending experimental aggregations of the treehopper *Guayaquila xiphias* in the cerrado of Mogi-Guaçu, Southeast Brazil, during 1992 and 1993

Ant species active in daytime	Ant species active at night	No. of treehopper aggregations
1992		
Camponotus rufipes	*C. rufipes*	6
Camponotus crassus	*Camponotus renggeri*	5
Camponotus sp.	*C. renggeri*	2
Ectatomma edentatum	*E. edentatum*	9
Total no. of aggregations		22
1993		
C. rufipes	*C. rufipes*	6
C. crassus	*C. renggeri*	3
Camponotus aff. *blandus*	*C. renggeri*	4
E. edentatum	*E. edentatum*	8
Ectatomma planidens	*C. renggeri*	1
Total no. of aggregations		22

C. renggeri, *C.* aff. *blandus*, or *C.* sp.); (3) tended by *E. edentatum* and/or *E. planidens* (in one treehopper aggregation tending activity by *E. planidens* was taken over by *C. renggeri* during the night period; see Table 1). In both years initial homopteran densities did not differ among groups of tending ants (1992, $H_{adjusted}=1.13$, $P=0.568$, $df=2$; 1993, $H_{adjusted}=4.433$, $P=0.109$, $df=2$; Kruskal-Wallis tests).

The foraging pattern of tending ants within the crown of *D. vinosum* shrubs, and their aggressiveness towards other organisms (i.e. potential enemies of *G. xiphias*) on the host plant, were evaluated by using live workers of the termite *Armitermes euamighnathus* SILVESTRI (Termitidae) as baits for ants. Live baits have already been used to investigate patterns of ant predation, or ant aggressiveness, on ant-visited plants (e.g. Jeanne 1979; Barton 1986; Oliveira et al. 1987; Freitas and Oliveira 1996). Baiting experiments were performed on *D. vinosum* shrubs different from the ones tagged for the ant-exclusion experiment (see above). Two classes of *D. vinosum* shrubs were used for the tests – plants with a *G. xiphias*-ant association, and plants without the association (only occasional ant scouts present). In each test on a given plant, one live termite was placed either near the apical meristem, or on the upper surface of the first leaf below the meristem (≈10 cm from the apex). On plants with a *G. xiphias*-ant association, the live termite at the apical meristem was ≈10 cm from the treehoppers. Termites were glued by the dorsum (agitated legs upwards) with a fast-drying adhesive (PVAc plastic glue, 3M; Brasil) which apparently had no effect on the behaviour of the ants or treehoppers. A given plant was used only once in the same week, and no plant was tested more than twice. *D. vinosum* shrubs with ant-tended treehoppers were baited with a total of 103 termites on the meristem, and 99 on the leaf blade. Shrubs without the association received 43 termites on either plant location. Attacks on termites by ants from different species groups (see above) were recorded during a 20-min period for each plant. Baiting tests were performed during sunny days between 0800 and 1600 hours.

Abundance data of treehoppers and natural enemies were analysed performing repeated-measures ANOVAs, with ant treatment as the grouping factor and time as the repeated measure. We performed square-root transformations on the data to stabilize treatment variances for the statistical analyses. We present untransformed data in the figures. We performed χ^2 tests to analyse the spatial distribution of ant attacks on termites, and of parasitoid wasps within the host plant, as well as the number of control and treatment plants with an additional treehopper oviposition.

Results

Ant foraging pattern on host plants

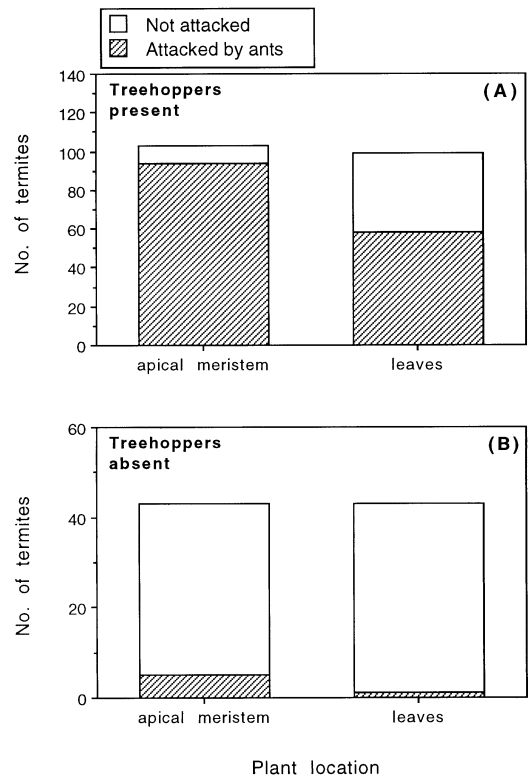Tending ants behaved aggressively towards organisms other than treehoppers found on *D. vinosum* shrubs, as ex-

Fig. 1A, B Ant predation on live termites placed at the apical meristem and on leaves (≈10 cm from apex) of *Didymopanax vinosum* shrubs. On plants infested by *Guayaquila xiphias* (**A**) predation by ants is significantly higher near the treehoppers at the apical meristem than on leaves ($P=0.0001$), whereas on uninfested plants (**B**) ant predation does not vary with plant location ($P=0.20$, χ^2 tests)

pressed by the attacks on live termites placed on the host plants. The spatial distribution of ant attacks within the plant's crown indicated that the presence of treehoppers near the apical meristem results in increased numbers of termites being attacked at this location than on the leaf surface ($\chi^2=27.21$, $P=0.0001$, $df=1$; Fig. 1A). On plants without treehoppers, however, ant predation did not vary with plant location ($\chi^2=1.61$, $P=0.20$, $df=1$; Fig. 1B). The proportions of termites attacked did not differ among *C. rufi*-
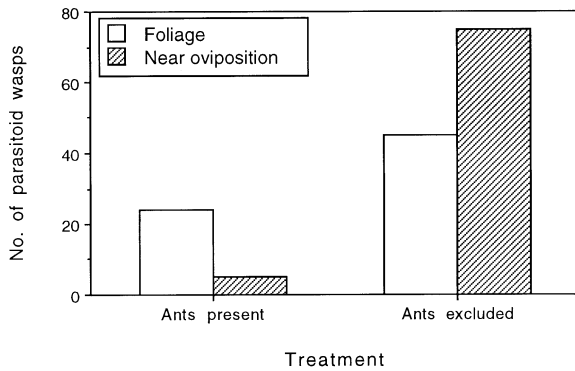
Fig. 2 Spatial distribution of *Gonatocerus* parasitoid wasps within the crown of *Guayaquila*-infested shrubs of *Didymopanax* as a function of the presence (*n*=22 plants) or absence (*n*=22 plants) of tending ants. Parasitoid distribution is significantly affected by ant activity near brood-guarding *Guayaquila* females (*P*=0.0001, χ^2 test)

Table 2 Repeated-measure ANOVAs performed on the no. of *G. xiphias* per plant through time, for the ant-exclusion experiments of 1992 and 1993. Analyses were performed on square-root-transformed data. *SS* Sums of squares, *MS* mean square

Year source	SS	df	MS	F	P
1992					
Ant treatment	79.23	1	79.23	2.35	0.133
Time	78.87	7	11.27	8.96	0.0001
Treatment×time	38.09	7	5.44	4.33	0.0001
Error	369.58	294	1.26		
1993					
Ant treatment	192.71	1	192.71	3.58	0.065
Time	158.40	7	22.63	9.47	0.0001
Treatment×time	18.57	7	2.65	1.11	0.3566
Error	702.63	294	2.39		

toid wasps on the host plant. The exclusion of ants from homopteran-infested plants made the wasps more successful at approaching the homopteran oviposition on the apical meristem (χ^2=17.46, *P*=0.0001, *df*=1; Fig. 2, see below).

Behavioural interactions

Predation on treehoppers by salticid spiders was observed on nine occasions, all on ant-excluded plants. The salticids conspicuously avoided encounters with tending ants near the apical meristem, and were usually warded off from the vicinity of the treehoppers by large tending ants such as *C. rufipes* and *E. edentatum*. The spiders were seen jumping off the plants after attacks by *C. rufipes* and *E. edentatum*. The fast-moving *C. rufipes* were particularly aggressive towards intruding predators, and one worker was once seen killing a spider near the homopterans.

Predation on *Guayaquila* treehoppers by larvae of the syrphid fly *O. arx* was seen in the field on 18 occasions, both on ant-excluded (11 cases) and control plants (seven cases; tending ant always *C. crassus*). Syrphid larvae generally approached the treehopper from beneath, and sucked empty the body contents of the victim through its anterior portion. Syrphid larvae consumed untended *Guayaquila* ovipositions on two occasions. We never saw tending ants attacking syrphid eggs or larvae on the plants. On four occasions, however, we observed adult syrphids being attacked by ants near treehopper aggregations attended by *C. rufipes* and *E. edentatum*.

In the absence of tending ants, the *Guayaquila* female protects her brood from *Gonatocerus* parasitoid wasps by sitting on the egg mass, and by vigorously kicking away approaching wasps with the third pair of legs. In this study, after a few attempts, however, the wasps usually succeeded in parasitizing the egg mass. If tended by ants, the treehopper female normally remained motionless over her brood as the wasps were warded off to nearby leaves by ants (Fig. 2). A total of 80 successful parasitization events were seen in the field, 75 of which
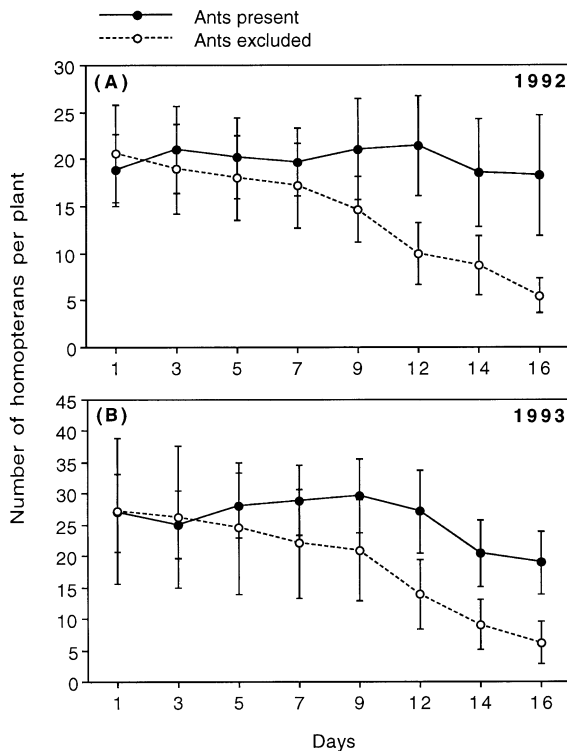

Fig. 3 Number of *G. xiphias* membracids per *Didymopanax* shrub through time as a function of the presence (*n*=22 plants) or absence (*n*=22 plants) of tending ants, during experiments carried out in March 1992 (**A**) and 1993 (**B**). Ants had a significant, positive impact on treehopper survival in 1992, but not in 1993. Values are means±1 SE. See also Table 2

pes (72 of 108), *Camponotus* spp. (39 of 52) and *E. edentatum* (29 of 42) (χ^2=0.204, *P*=0.903, *df*=2). The three groups of tending ants also presented the same tendency to attack the termites in increased proportions (66–69%) near the apical meristem (χ^2=1.873, *P*=0.396, *df*=2).

The increased ant density near the treehoppers strongly affected the spatial distribution of *Gonatocerus* parasi-

Fig. 4 Number of *G. xiphias* membracids per *Didymopanax* shrub through time as a function of the species of tending ants, during experiments carried out in March 1992 (**A**) and 1993 (**B**). In 1992 all tending ants were equally beneficial to *Guayaquila*, whereas in 1993 the ants differed significantly in their impact on treehopper survival. Values are means. See also Tables 1 and 3
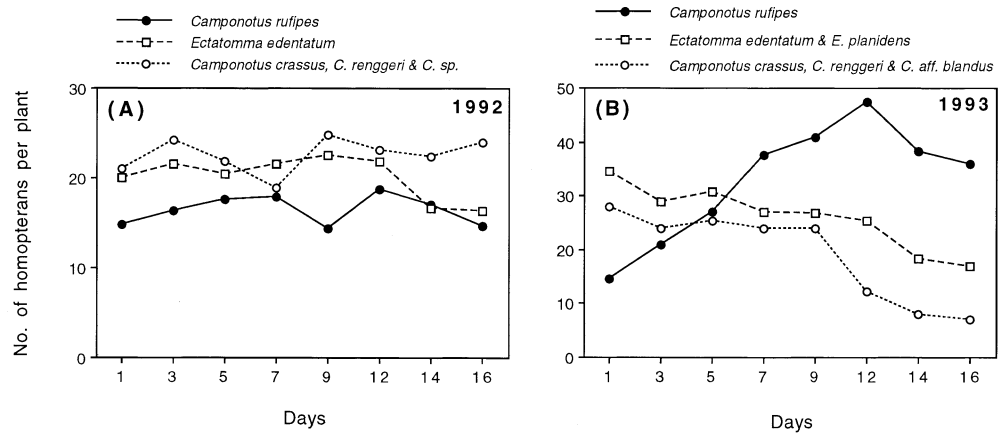

Table 3 Repeated-measure ANOVAs performed on the no. of *G. xiphias* being tended by different ant species through time, during the censuses of 1992 and 1993 on control plants (*n*=22 in each year). Aggregations of *G. xiphias* were grouped according to tending ants, as follows. 1992: group 1, *C. rufipes* (*n*=6); group 2, *C. crassus*, *C. renggeri*, and *Camponotus* sp. (*n*=7); group 3, *E. edentatum* (*n*=9). 1993: group 1, *C. rufipes* (*n*=6); group 2, *C. crassus*, *C.* aff. *blandus*, and *C. renggeri* (*n*=7); group 3, *E. edentatum* and *E. planidens* (*n*=9). Daytime tending activities by *E. planidens* at one treehopper aggregation in 1993 was taken over by *C. renggeri* during the night period. Analyses were performed on square-root-transformed data. See also Table 1 and Fig. 4

Year source	SS	*df*	MS	*F*	*P*
1992					
Ants	8.96	2	4.48	0.12	0.8869
Time	7.62	7	1.09	0.89	0.5195
Ants×time	8.60	14	0.61	0.5	0.9298
Error	163.45	133	1.23		
1993					
Ants	33.83	2	16.91	0.38	0.6913
Time	53.88	7	7.70	5.32	0.0001
Ants×time	113.76	14	8.13	5.16	0.0001
Error	192.46	133	1.45		

Fig. 5 Number of aggregations of *G. xiphias* membracids with an additional oviposition as a function of the presence (*n*=22 plants) or absence (*n*=22 plants) of tending ants, during experiments carried out in March 1992 and 1993. Plants in each category had one brood-guarding *Guayaquila* female. Ants had a significant positive impact on treehopper fecundity in 1992 (*P*=0.018), but not in 1993 (*P*=0.164, χ^2 tests)

were directed toward treehopper ovipositions on ant-excluded plants. Successful attacks by parasitoid wasps on control plants were observed on ovipositions tended by *C. crassus* and *C.* aff. *blandus*.

Ant-exclusion experiments, and ant-derived benefits to treehoppers

Although ant-tending positively affected the survival of *Guayaquila* membracids in 1992, we were unable to detect a significant benefit of ants on treehoppers in 1993 (Fig. 3; Table 2). We also found a species-specific effect in the impact of ants on the membracids. In 1992 all groups of tending ants (see Table 1) were equally beneficial to *Guayaquila*, while in 1993 the ant species differed in their effects on treehopper survival (Fig. 4; Table 3).

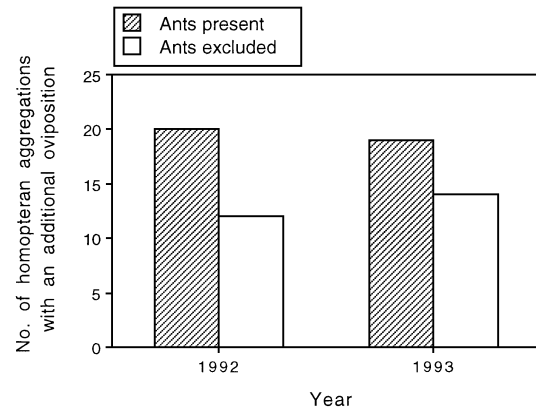We detected yearly variation in the effect of tending ants on the fecundity of *Guayaquila* females. A positive

effect of ants was detected only in 1992, when the production of an additional brood by the resident female was more frequent among ant-tended membracid aggregations than among ant-excluded ones (1992, χ^2=5.61, *P*=0.018, *df*=1; 1993, χ^2=1.94, *P*=0.164, *df*=1; see Fig. 5). In both 1992 and 1993 we found no species-specific effect of ant-tending on treehopper fecundity, as expressed by the number of aggregations with an additional brood (1992, χ^2=0.873, *P*=0.646, *df*=2; 1993, χ^2=5.018, *P*=0.081, *df*=2).

Abundance of natural enemies

In both 1992 and 1993 the exclusion of ants resulted in an overall increase in the abundance of the natural enemies of *Guayaquila* treehoppers on their host plants (Fig. 6; Table 4). Except for predatory syrphid dipterans which were significantly affected by ants only in 1993, predatory spiders and parasitoid wasps were significantly more abundant on ant-excluded plants in both 1992 and 1993. The combined abundance of the three types of nat-

Fig. 6A–H Number of *G. xiphias'* natural enemies per *Didymopanax* shrub through time as a function of the presence (*n*=22 plants) or absence (*n*=22 plants) of tending ants, during experiments carried out in March 1992 and 1993. Data are presented separately for salticid spiders (**A, E**), syrphid dipterans (**B, F**), and parasitoid wasps (**C, G**), as well as for all three combined (**D, H**). Except for dipterans in 1992, in all other cases the abundance of natural enemies was significantly greater on ant-excluded *Guayaquila*-infested plants than on plants with ants. Values are means+1 SE. See also Table 4
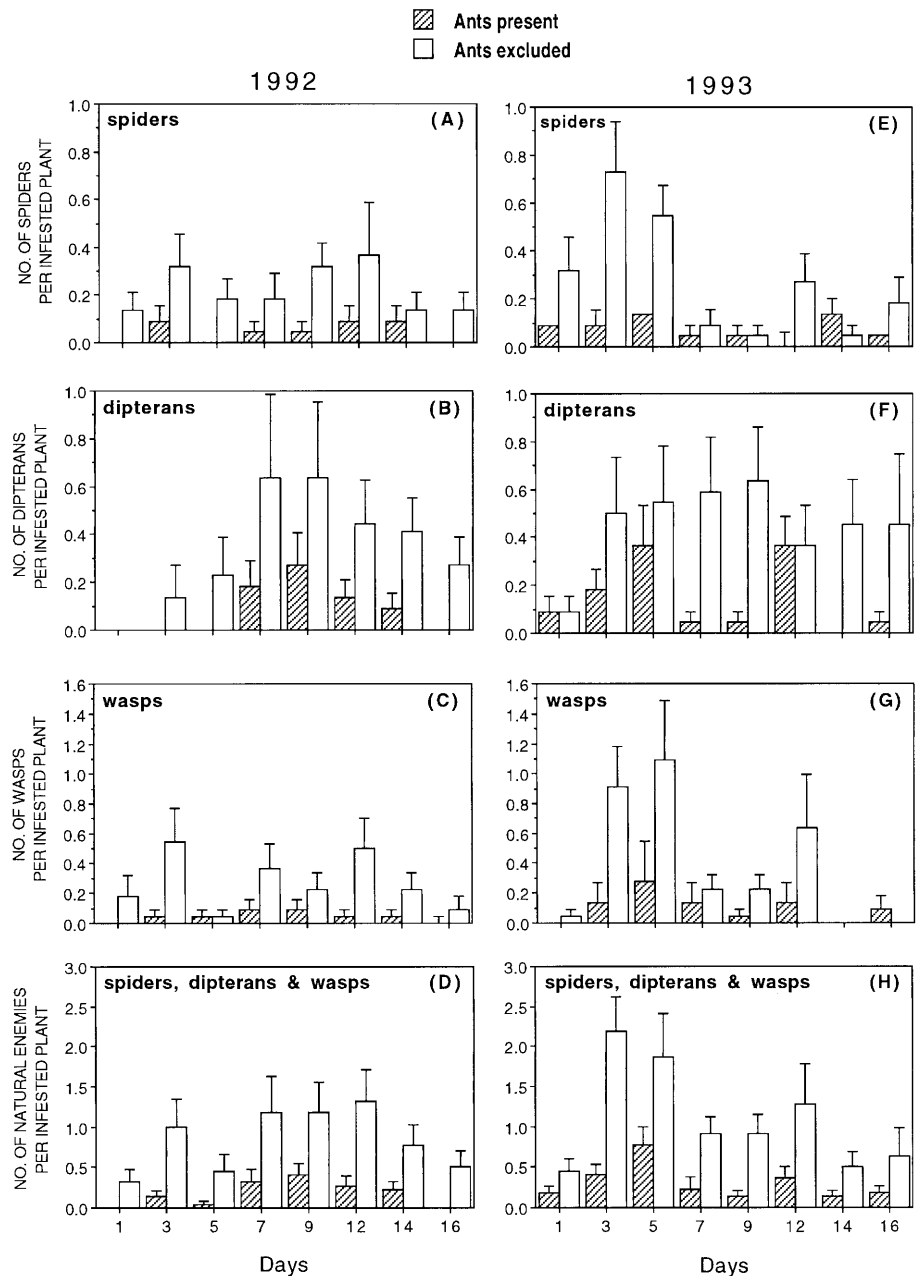
ural enemies, however, was higher on ant-excluded plants than on plants with ants in both years of the study (Fig. 6D,H; Table 4).

A significant interaction between ant treatment and time was detected for all natural enemies in 1993, but not in 1992 (Table 4). In fact, the abundance of natural enemies in 1993 was high in the first week and then decreased toward the end of the experiment (Fig. 6H).

Discussion

The field experiments and observations on the association between *G. xiphias* and tending ants revealed that:

1. Ants attack potential enemies of the treehopper on the host plant, and aggression is more pronounced near the homopteran aggregation.
2. Increased ant density near the treehoppers affects the spatial distribution of parasitoid wasps on the host plant, keeping them away from brood-guarding *Guayaquila* females.
3. The presence of ants reduces the abundance of *Guayaquila*'s natural enemies on the host plant.
4. Ant-tending increases homopteran survival and fecundity.
5. Ant-derived benefits to treehoppers can vary with time and/or species of ant partner.

Although some of these findings have already been reported for temperate ant-homopteran systems (see

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Table 4 Repeated-measure
ANOVAs performed on the no.
of natural enemies (spiders,
wasps, and dipterans) per
Guayaquila-infested plant
through time, for the ant-
exclusion experiments of 1992
and 1993. Analyses were
performed on square-root-
transformed data. See also
Fig. 6

Year source	SS	df	MS	F	P
1992					
a. Spiders					
Ant treatment	1.92	1	1.92	11.13	0.0018
Time	0.66	7	0.09	0.87	0.5348
Treatment×time	0.33	7	0.04	0.44	0.8779
Error	31.85	294	0.11		
b. Dipterans					
Ant treatment	2.14	1	2.14	3.09	0.0861
Time	3.62	7	0.52	4.70	0.0001
Treatment×time	0.59	7	0.09	0.76	0.6179
Error	32.36	294	0.11		
c. Wasps					
Ant treatment	2.35	1	2.35	8.00	0.0071
Time	1.68	7	0.24	2.14	0.0393
Treatment×time	1.09	7	0.16	1.40	0.2063
Error	32.84	294	0.11		
d. Spiders, dipterans and wasps					
Ant treatment	13.45	1	13.45	11.54	0.0015
Time	8.50	7	1.22	5.41	0.0001
Treatment×time	1.16	7	0.17	0.74	0.6397
Error	65.96	294	0.22		
1993					
a. Spiders					
Ant treatment	2.37	1	2.37	10.59	0.0022
Time	3.66	7	0.52	4.35	0.0001
Treatment×time	2.67	7	0.38	3.17	0.003
Error	35.35	294	0.12		
b. Dipterans					
Ant treatment	3.92	1	3.92	6.29	0.0161
Time	9.10	7	1.3	8.93	0.0001
Treatment×time	3.23	7	0.46	3.17	0.003
Error	42.82	294	0.15		
c. Wasps					
Ant treatment	2.42	1	2.42	5.39	0.0252
Time	8.95	7	1.28	8.92	0.0001
Treatment×time	3.00	7	0.43	2.99	0.0048
Error	42.13	294	0.14		
d. Spiders, dipterans and wasps					
Ant treatment	15.35	1	15.35	11.51	0.0015
Time	13.93	7	1.99	7.42	0.0001
Treatment×time	4.03	7	0.58	2.15	0.0387
Error	78.86	294	0.27		

Bristow 1983, 1984; Cushman and Whitham 1989; Cushman and Addicott 1991), to our knowledge this is the first study to simultaneously demonstrate conditionality in ant-derived benefits related to both protection and fecundity of an ant-tended membracid. Moreover, the combined action of these effects is shown for the first time in the same ant-Homoptera system.

In many membracid species, the egg-guarding female can effectively defend herself and the offspring from predators and parasitoids (Havilland 1925; Beamer 1930; Hinton 1977; Wood 1978, 1984). Our field observations with *G. xiphias*, however, indicated that this species depends strongly on ant-tending for protection against its natural enemies. The experiments with live termite baits showed that honeydew-gathering activity by ants resulted in many more termites being attacked near the treehoppers (apical meristem) than on leaves (Fig. 1). Aggression by ants towards intruding organisms is expected to be more pronounced near the nest and at a food source, and is referred to as

"ownership behaviour" (Way 1963). The data obtained with termite baits, as well as the behavioural interactions between tending ants and *G. xiphias*' natural enemies, corroborate other studies in which increased ant activity and aggression have been correlated with the spatial distribution of food rewards on plant foliage (Bentley 1977; Pierce and Mead 1981; Fritz 1982; McKey 1984; Koptur 1984; Völkl 1992; Oliveira 1997). Our results also showed unequivocally that increased ant density near *G. xiphias* can markedly affect the spatial distribution of parasitoid wasps on the host plant (Fig. 2). As opposed to ant-excluded plants where foraging wasps were more frequently seen near *G. xiphias* ovipositions at the apical meristem, on control plants the parasitoids were more common on leaves due to aggression by tending ants near the treehoppers. Similar results were recently reported by Völkl and Kroupa (1997) for an ant-aphid association in which the foraging behaviour of aphid parasitoid wasps was also shown to be markedly affected by aggression from tending ants.

Our behavioural observations and experimental data are in accordance with several other studies showing that species of ants can differ greatly in their deterrent abilities against the natural enemies of ant-tended homopterans (Addicott 1979; Messina 1981; Bristow 1984; Takada and Hashimoto 1985; Buckley 1987; Buckley and Gullan 1991) (see also DeVries 1991; Wagner 1993; Fiedler et al. 1996 on ant-tended butterfly larvae). Protection of homopterans can vary with species-specific traits of tending ants which are associated with their deterrent capacity, such as size, alertness toward intruders and promptness to attack, running speed, structural and chemical weapons, and recruitment communication (see Addicott 1979; Buckley and Gullan 1991). The effectiveness of these ant traits as deterrents against homopterans' natural enemies can vary widely among different ant-homopteran systems (see Takada and Hashimoto 1985; Bristow 1984; Bach 1991; Völkl and Mackauer 1993).

Although different groups of tending ants attacked equal numbers of live termite baits on *Didymopanax* shrubs, this result does not necessarily imply similar deterrent abilities of the ants, since the termites were prevented from fighting back or escaping. Indeed, our behavioural observations indicate that *C. rufipes* and *E. edentatum* are perhaps the best-equipped ants to deter the treehoppers' natural enemies (see above). As opposed to the other ants which are active only during the day or at night, *C. rufipes* and *E. edentatum* seem to be highly dependent on homopteran honeydew and extend their tending activities for 24 h (Table 1; see Del-Claro and Oliveira 1999). Moreover, *C. rufipes* frequently builds satellite nests at the base of plants to house *G. xiphias* nymphs, as also reported by Cushman and Whitham (1989) for the ant *Formica altipetens* and the membracid *Publilia modesta*.

The experimental manipulations with *G. xiphias* showed that the degree of protection by tending ants varied from 1992 to 1993 (Fig. 3), and that at an initially high abundance of natural enemies the ant species differ in their impacts on treehopper survival (experiment of 1993; Fig. 4). *C. rufipes* tends the treehoppers on a round-the-clock basis (Del-Claro and Oliveira 1999), and our field data showed that it was much more aggressive toward intruding organisms than the other "part-time" *Camponotus* species. The method of liquid food sharing employed by *Ectatomma* ants, on the other hand, may limit their deterrent abilities near the treehoppers if natural enemies are abundant. As opposed to *Camponotus*, which stores liquid food in the forager's crop ("social stomach") before passing it to nestmates, *Ectatomma* transports the liquid as droplets between the mandibles and shares it in the nest with other ants (Hölldobler and Wilson 1990). By having their mandibles loaded with honeydew, tending *Ectatomma* may become less prompt in chasing the treehoppers' enemies than the more agile *C. rufipes* whose mandibles are free for aggression. This difference between tending ants can be crucial for *G. xiphias*' survival if its natural enemies become abundant.

The experimental data have revealed that ant-tending may also confer a direct reproductive benefit to *G. xiphias* females, which may abandon the first brood to ants and lay an additional clutch next to the original brood. A similar benefit was demonstrated by Bristow (1983) for the ant-tended membracid *P. reticulata* in New Jersey (see also Wood 1977; McEvoy 1979). Two years of experimental manipulations with brood-guarding *G. xiphias*, however, have further shown that such a positive impact of ants on treehopper fecundity also varies with time, and with shifts in the abundance of natural enemies (Figs. 5, 6; Table 4). It is possible that at increased mortality risks from predation and parasitization, females refrain from deserting their first brood. The proximate mechanisms underlying female desertion is not known, and her decision could be mediated by mechanical and/or chemical stimulation from tending ants, and/or by information about mortality risks (number of encounters with natural enemies).

In conclusion, homopteran honeydew is an important promoter of ant activity on plant foliage in the cerrado savanna, as expressed by the taxonomically diverse ant assemblage attracted to *G. xiphias* aggregations both day and night (Del-Claro and Oliveira 1999). We have demonstrated elsewhere that the treehoppers are able to attract potential tending ants through the flicking of honeydew beneath the host plant (Del-Claro and Oliveira 1996), and the results from the current study have shown that ant attendance can increase *G. xiphias* survival and fecundity. Finally, regardless of the mechanisms involved, our results have also demonstrated that ant-derived benefits to *G. xiphias* are conditional, and may vary with time and/or ant partner. Although conditionality has already been demonstrated for other ant-homopteran systems (Bristow 1984; Cushman and Whitham 1989, 1991; Breton and Addicott 1992), this is the first study to simultaneously demonstrate variation in ant-derived benefits related to both protection and fecundity in an ant-tended membracid species, and the first to show such combined effects in the same system. Although most studies on such interactions have focused on the benefits afforded to homopterans by honeydew-gathering ants, recent work has demonstrated that there is also an associated cost for aphids resulting from ant-tending (Stadler and Dixon 1998). The study of ant-plant-herbivore mutualisms and the detection of their complexity can provide an important bridge between general theories and experimental research on mutualism. As stressed by several authors (Thompson 1982, 1988; Cushman and Addicott 1991; Bronstein 1994, 1998), only by considering how and why the intensity of mutualisms vary in space and time can we form a more realistic picture of the dynamics of interspecific associations, and a better understanding of their ecology and evolution.

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