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Ant-Homoptera interaction: do alternative sugar sources distract tending ants?

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In the resent study we tested whether ants *(Camponotus* spp.) would stop tending honeytew-producing membracids *(Guayaquila xiphias) when* an alternative sugar source was available on the host plant *(Didymopanax vinosum).* Results show that the discovery of an alternate sugar source (simulated extrafloral nectaries) did not provoke desertion by ants. Instead, tending of *Guayaquila* aggregations continued nearly the same as ant visitation to the honey solution increased steadily within the same period. An increase in the honeydew flow rate by *Guayaquila* aggregations probably explains why ant tending levels remained unchanged in the presence of an alternate sugar source. The current experimental study and available field evidence from cerrado vegetation do not support the prediction that ants would neglect honeydew-producing homopterans in the presence of extrafloral nectaries.

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Many ant species commonly tend Homoptera (mostly aphids, membracids and scales) and feed on their energy-rich honeydew. Through ant tending, homopterans frequently receive a wide range of beneficial services, including protection from predators and parasitoids (reviewed by Way 1963, Buckley 1987a, b, Cushman and Beattie 1991, Cushman and Addicott 1991). Although homopterans can be regarded as major pests to many plant species, ant-tended homopterans may indirectly benefit their plant hosts through ant protection against external herbivores whose damage to the plant outweighs the cost of homopteran infestation (Messina 1981, Buckley 1987a, b, Compton and Robertson 1988, but see also Fritz 1983).

A wide variety of ant taxa complement their diets by visiting plants with extrafloral nectaries (EFNs) for their sugary secretions (reviewed by Oliveira and Brandão 1991). In the last two decades, a series of experimental field studies have shown that ant visitors to EFNs can defend the plant against several types of herbivores (Bentley 1977a, Beattie 1985, Hölldobler and Wilson 1990, and citations therein). Several other studies, however, have also shown that visiting ants may not benefit plants with EFNs (e.g., O'Dowd and Catchpole 1983, Heads 1986, Rashbrook et al. 1992).

Recently, Becerra and Venable (1989) proposed that EFNs may function to defend plants against ant-Homoptera mutualisms by supplying ants with extrafloral nectar which would distract them from honeydew-producing homopterans. As a result of being abandoned by their tending ants, homopterans would suffer higher mortality rates (due to predation and parasitism) and their damage to the plant would be either reduced or eliminated. In short, according to Becerra and Venable (1989: 278), "the main fitness benefit of EFN's is the reduction of homopteran damage". In a subsequent comment Fiala (1990) presented evidence against this hypothesis, and questioned the supposed superiority of extrafloral nectar to honeydew in being highly predictable in space, time and quality (as viewed by Becerra

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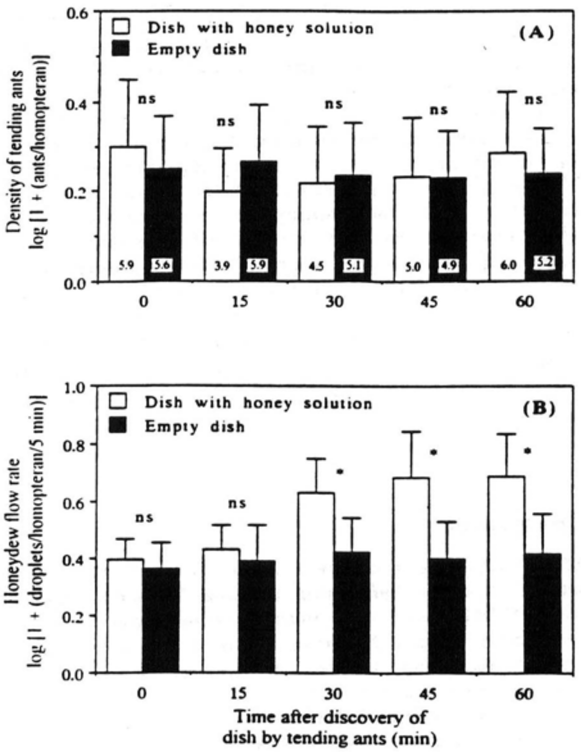

Fig. 1. Ant tending and honeydew production in aggregations of *Guayaquila xiphias* on treated (white bars) and control (black bars) shrubs of *Didymopanax vinosum*. (A) the discovery of the sugar solution does no lead to deesrtion by tending ants, and aggregations on both plant categories remains equally tended after 1 h. Values inside the bars refer to mean number of tending ants per homopteran aggregation. (B) After 30 min. the honeydew production by aggregations on treated plants becomes significantly higher than on control ones. Values are means ± 1 SD: N =l0 plants in each group. Significance levels of *t* tests: ns = not significant; *P < 0,001. See text tear further details.

and Venable 1989). Although it is known that ants can drop lower quality resources from their diets as higher quality ones become available, some of the studies cited by Becerra and Venable (1989) in support of the "ant-distraction hypothesis" either do not corroborate it, or actually show the opposite (see Addicott 1978, 1979, Sudd and Sudd 1985). In fact, existing information suggest that ants switch from visiting a plant's EFN to visiting honeydew-producing homopterans (Buckley 1983. Sudd and Sudd 1985, but see also Way 1954). Becerra and Venable (1989, 1991) suggested that well designed experiments were needed before a firm conclusion on the subject could be drawn. More recently, Rashbrook et al. (1992) experimentally showed that the foliar nectaries of bracken do not reduce tending levels of homopterans, and ants strongly prefer homopteran honeydew to foliar nectar.

In the present study, we quantified ant tending of aggregations of the honeydew-producing treehopper *Guayaquila xiphias* (Membracidae) on shrubs of *Didomopanax vinosum* (Araliaceae). Although this plant species lacks EFNS, controlled field experiments enabled us to assess the effects of alternative sugar sources (simulated EFNs) on the behavior of tending ants and membracids.

Methods

Field work was carried out during April-May 1992 in an area of cerrado (savanna-like vegetation) near the town of Mogi Guaçu (22°18'S. 47°13'W)- State of São Paulo, SE Brazil. The vegetation consists of a dense scrub of shrubs and trees, which corresponds to the cerrado sensu stricto of Goodland (1971). *Didyinopanax vinosum* is an abundant shrub in the study area, and its stems frequently host aggregations of the treehopper *Guayaquila xiphias* which are invariably tended by ants (Lopes 1984).

We tagged 10 experimental pairs of *D. vinosum* shrubs (0.7 to 1.9 m tall), all of which were growing under similar light conditions in the study area. Each experimental shrub hosted one aggregation of *G. xiphias* at the apical portion (near the growing meristem) of its principal stem. Plants in a given pair were at least 2 m apart from each other, had their leaves and growing meristem in the same phenological state, were approximately the same height, and had equal numbers of leaves and stems. Membracid aggregations of a given experimental plant pair were in the same developmental stage, contained approximately the same number of nymphs, and were tended by ants of the same species (but from different colonies), We only utilized *G. xiphias* colonies being tended by *Camponotus* ants (Formicinae): seven plant pairs had aggregations being tended by *C. rufipes*, while three others were tended by *C. crassus*.

To evaluate how an alternative sugar source would affect ant tending of *G. xiphias* aggregations on shrubs of *D. vinosum*, we used round transparent plastic dishes (0.5 cm diameter. 0. 1 cm high) containing 50% diluted honey as simulated EFNS. This sugar concentration was higher than that generally found in homopteran honeydew (cf., Auclair 1963). Each of the four nearest leaves to the ant-tended *G. xiphias* aggregations received one dish at the basal portion of the petiole (1 cm from the stem; petiole length ≈ 10 cm), totaling four dishes per plant. Dishes were glued to plants with a fast-drying adhesive (Super Bonder®, Loctite Brasil Ltda) which apparently had no effect on ant behavior. One hour after the placement of the dishes on the plants, each *D.*

Table 1. Honeydew production by ant-tended *Guayaquila xiphias* aggregatoins on *Didymopanax vinosum* in the presence of an alternate sugar source (treated shrub) or distilled water (control shrub) over 6 h of observation. Numbers in the parenthesis refer to number of tending ants. See text for further details.

Time after discovery of dish (hours)	Honeydew flow rate (droplets/homopteran per 5 min)	
	control shrub (dish with water)	treated shrub (dish with honey solution)
0	0.33 (3)	0.33 (1)
1	0.00 (6)	1.67 (2)
3	2.00 (4)	6.67 (3)
4	1.67 (5)	8.33 (3)
6	1.33 (4)	7.67 (4)

vinosum shrub of a given pair was randomly assigned by the flip of a coin as either a treatment or control plant. Dishes on treated plants received one droplet of honey solution, those on control ones remained empty. We began recording behavioral data after the first dish had been discovered by a patrolling ant. Behavioral data on ants and membracids were gathered simultaneously for both plants of a pair during one hour. Within this period, the number of ants tending the membracids, or visiting the dishes, was recorded at 15 min intervals (treated dishes were occasionally refilled with honey solution after depletion by ants). Production of honeydew by ant-tended membracids was estimated by focusing, on a selected group of similar-sized nymphs (3rd or 4th instar) which we could easily locate visually. During 5 min. at every 15 min interval, we counted the number of honeydew droplets being produced by the same selected Group of ant-tended nymphs. The honeydew flow rate was therefore expressed as the number of droplets/ nymph per 5 min. On a separate experimental pair, we used control dishes filled with distilled water and gathered the same type data over a period of 6 h. All field data were taken on sunny days between 11930 and 1530 hours, under warm and humid climate conditions.

Results

The results of ant tending and honeydew production by *Guayaquilas xiphias* aggregations on treated (alternative sugar source present) and control (no alternative sugar source) shrubs of *Didymopanax vinosum* are summarized in Fig. 1. At the time the first dish was discovered by a patrolling ant, both the density of tending ants and honeydew production by *G. xiphias* aggregations did not differ significantly between treatment and control plants. Our experimental data over 1 h revealed no difference in ant tending between control and treated plants after the discovery of the honey solution by the ants (Fig. 1). On the other hand. within the same period, ant visitation to the honey solution increased steadily to 2.8 ± 2.7 ants on treated plants ($\bar{X}$ ± SD. N = 16). Empty dishes were never revisited after being discovered by patrolling ants on control plants.

Although honeydew production by *G. xiphias* colonies did not differ between plant categories during the first 15 min, it was consistently higher on treated plants 30 min after the discovery of diluted honey by tending ants (Fig. 1). In factt, honeydew production by *G. xiphias* aggregations on some treated plants was sometimes five times higher than by their counterparts on control plants. This difference was maintained for over 6 h on a separate experimental plant pair (Table 1). We did not notice any major variation in the size of the honeydew droplets (≈ 0.7 mm diameter) being produced by *G. xiphias* during the course of our observations.

Discussion

After supplying a honey solution to one established colony of *Oecophylla* ants tending *Saissetia* coccids. Way (1954) noted that many tending ants not only switched to collect the honey solution but a few major workers also began to prey on the coccids. Our results with *Camponotus* ants and *Guayaquila* membracids. however. are quite different from those obtained by Way. The discovery of an alternate sugar source on *Didymopanax* shrubs did not provoke desertion by tending ants. Instead, ant tending of membracids continued nearly the same as ant visitation to the honey solution increased steadily within the same period. In general, the number of ants collecting extrafloral nectar from a plant, or honeydew from a homopteran aggregation, is proportional to the productivity of the plant or aggregation (e.g.. Bentley 1977b, O'Dowd 1979, Dreisig 1988, Cushman 1991). Therefore the discovery of a new food source by tending ants on *Didymopanax* justifies an increase of recruited workers for better use (and protection) of this resource.

Ant tending may provoke higher production rates of honeydew by aphids (Takeda et al. 1982). We believe that the increased ant activity on *Didymopanax* shrubs due to the new sugar source, and the resulting greater excitement of tending ants, might have provoked the observed increase in the honeydew flow rate by *Guayaquila* aggregations. It is known that an aphid is significantly more likely to produce a droplet of honeydew a few seconds after an ant made contact with it than at other times (Douglas and Sudd 1980). Although we did not quantify ant-membracid contacts, we did note that excited *Camponotus* ants moved more rapidly within the aggregation. possibly contacting more membracids per unit time. The greater honeydew production by *Guayaquila* aggregations probably explains why ant tending remained unchanged in the presence of honey solution. The vidence from observation over 6 hours suggests that this high level of honeydew secretion can be maintained for longer periods. We observed that the honeydew production within a *Guayaquila* aggregation is maintained by several individuals (nymphs and adults) which are constantly replacing each other in the provision of exudates for tending ants. As also observed by Douglas and Sudd (1980) with *Formica* ants and *Symydobius* aphids, *Camponotus* ants did not remain stationary at a single *Guayaquila* membracid, but frequently moved from one to another. This behavior probably allows high honeydew flow rates by *Guayaquila* aggregations for extended periods.

According to Becerra and Venable (1989, 1991) many plant species bear EFNs on predictable anatomical positions and this can be advantageous to attract ant visitors. However many ant-tended homopterans are also predictable with respect to their location on host plants, being commonly found on the apical meristem, leaf axis and inflorescences (Wood 1984, Bristow 1991). For example, *Guayaquila* aggregations are invariably found near the apical meristem of the principal stem of *Didymopanax* shrubs. We monitored more that 100 *Guayaquila* aggregations on *Didymopanax* shrubs in the study area, and we never observed the membracids untended by ants. Moreover we observed that honey dew droplets occasionally fell on lower leaves and/or ground and may have served as cues to foraging ants, who climbed on *Didymopanax* and eventually found *Guayaquila* aggregations. It is possible that gravid females of *Guayaquila* use this tactic to attract ants before initiating oviposition (see also Kiss 1981).

Becerra and Venable (1991: 106) argue that extrafloral nectar "does not require extensive ant husbandry in order to be maintained". Ants are known to exhibit ownership behavior near the nest and at rich food sources (Way 1963)., and some species can be remarkably aggressive toward any object approaching a nectary (Bentley 1977b). We recently found that use of extrafloral nectar by different ant species on *Urena lo*hrua (Malvaceae) is largely regulated by interspecific aggression: the most aggressive species monopolizes for longer periods the most productive glands within the plant (Del-Claro et al. unpubl. manuscript). Therefore the defense of a productive nectar source against competitors could he as costly for visiting ants as the maintenance of an homopteran aggregation.

Plant species hearing EFNs are common in the Brazilian cerrados and ant-homopteran associations can be found on several plant genera with EFNS. such as *Qualea, . Tocoyena, Bauhinia, Arrabidaea* and *Ouratea* (Lopes 1984, Oliveira and Leitão-Filho 1987, Oliveira and Oliveira-Filho 1991). Although ants are observed visiting the EFNs on these plants, they often seem to prefer homopteran honeydew. Therefore the available evidence from the literature (Fiala 1990, Buckley 1983, Sudd and Sudd 1985, Rashbrook et al. 1992). and the current experimental study with *Camponotus* ants and *Guayaquilla* membracids in cerrado vegetation, contradict Becerra and Venable's (1989, 1991) prediction that ants would neglect homopterans in the presence of EFNS. On the contrary, EFN-bearing plants may even indirectly benefit homopteran aggregations by attracting more would-be tending ants than plants lacking these glands (see Buckley 1987b, Compton and Robertson 1988, Cushman and Addicott 1991). Evidence from myrrnecophilous butterfly larvae possessing ant-organs also suggests that caterpillars are more attractive to ants than EFNs (DeVries and Baker 1989).

We agree with Becerra and Venable (1991) in that any generalization about the superiority of honeydew or extrafloral nectar as food source for ants would perhaps be simplistic and premature. Both food types can be major components in the diet of many ants. and their superiority to one another may depend largely on the plant and insects involved, as well as on several other ecological factors. Thus more effort should be made toward controlled experiments before any firm conclusion can be reached on the relative benefits/costs of these food types for an ant colony.

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References

Addicott, J. F. 1978. Competition for mutualists: aphids and ants. - Can. J. Zool. 56: 2093-2096.

- 1979. A multispecies aphid-ant association: densitv-de. pendence and and species-specific effects. - Can. J. Zool. 57: 558-569.

Auclair, J. L. 1963. Aphid feeding and nutrition. - Annu. Rev. Ent. 8: 439-490.

Beattie, A. 1985. The evolutionary ecology of ant-plant mutualisms. - Cambridge Univ. Press. New York.

Becerra, J. X. and Venable, D. L. 1989. Extrafloral nectaries: a defense against ant-Homoptera mutualisms? - Oikos 55: 276-280.

- and Venable, D. L. 1991. The role of ant-Homoptera mutualisms in the evolution of extrafloral nectaries. - Oikos 60: 105-106.

Bentley, B. L. 1977a. Extrafloral nectaries and protection by pugnacious bodyguards. - Annu. Rev. Ecol. Syst. 8: 407-427.

- 1977b. The protective function of ants visiting the extrafloral nectaries of *Bixa orellana* L. (Bixaceae). - J. Ecol. 65: 27-38.

Bristow, C. M. 1991. Are ant-aphid associations a tritrophic interaction? Oleander aphids and Argentine ants. - Oecologia 87: 514-521.

Buckley, R. 1983. Interaction between ants and membracid hugs decreases growth and seed set of host plant bearing extrafloral nectaries. - Oecologia 58: 132-136.

- 1987a. Interactions involving plants, Homoptera, and ants.
- Annu. Rev. Ecol. Syst. 18: 111-138.

- 1997h. Ant-plant-homopteran interactions. - Adv. Ecol. Res. 16: 53-85.

Compton, S. G and Robertson, H. G. 1988. Complex interactions between mutualisms: ants tending homopterans protect fig seeds and pollinators. - Ecology 69: 1302-1305.

Cushman, J. H. 1991. Host-plant mediation of insect mutualisms: variable outcomes in herbivore-ant interactions. - Oikos 61: 138,-144.

- and Addicott. J. F. 1991. Conditional interactions in ant-plant-herbivore mutualisms. - In: Huxicy, C. R. and Cutler, D. F. (eds). Ant-plant interactions. Oxford Univ. Press. Oxford. pp. 92-103.

- and Beattie. A. 1991. Mutalisms: Assessing the benefits to host.s and visitors. - Trends Ecol. Evol. 6: 193-195.

De\/ries, P. J. and Baker, I. 1989. Butterfly exploitation of an ant-plant mutualism: adding insult to herbivory. - J. New York Ent. Soc. 97: 332-340.

Douglas, J. M. and Sudd, J. H. 1980. Behavioural coordination between an aphis (*Symydobius ablongus* yon Heyden; Hemiptera: Callaphidae) and the ant that attends it (*Formica lugubris* Zetterstedt: Hymenoptera: Formicidae): an ethological study. - Anim. Behav. 28: 1127-1139.

Dreisig, H. 1988. Foraging rate of ants collecting honeydew or extrafloral nectar, and some possible constraints. - Ecol. Entomol. 13: 143-154.

Fiala, B. 1990. Extrafloral nectaries versus ant-Homoptera mutualisms: a comment on Becerra and Venable. - Oikos 59: 281-282.

Fritz, R. S. 1983. Ant protection of a host plant's defoliator: consequence of an ant-membracid mutualism. - Ecology 64: 789-797.

Goodland. R. 1971. A physiognomic analysis of the cerrado vegetation of central Brazil. - J. Ecol. 59: 411-419.

Heads, P. A. 1986. Bracken, ants and extrafloral-nectaries. IV. Do wood ants (*Formica lugubris*) protect the plant against insect herbivores? - J. Anim. Ecol. 55: 795-809.

Hölldobler, B. and Wilson, E. 0. 1990. The ants. - Harvard Univ. Press. Cambridge. MA.

Kis, A. 1981. Melezitose, aphids and ants. - Oikos 37: 382.

Lopes, B. C. 198.1. Aspectos da ecologia de membracídeos (Insecta: Homoptera) em vegetação de cerrado do Estado de São Paulo, Brasil. Master's Thesis. Universidade Estadual de Campinas, São Paulo.

Messina, F. J. 1981. Plant protection as a consequence of ant-membracid mutualism: Interactions on Goldenrod (*Solidago* sp.). - Ecology 62: 1433-1440.

O'Dowd, D. J. 1979. Foliar nectar production and ant activity on a neotropical tree. *Ochroma pyramidale*. - Oecologia 43: 233-248.

- and Catchpole, E. A. 1983. Ants and extrafloral nectaries: no evidence for plant protection in *Helichrysum* spp.-ant interactions. - Oecologia 59: 191-200.

Oliveira, P. S. and Brandio, C. R. F. 1991. The ant community associated with extrafloral nectaries in the Brazilian cerrados. - In: Huxley, C. R. and Cutler, D. F. (eds). Ant-plant interactions. Oxford Univ. Press. Oxford. pp. 198-212.

- and Leitão-Filho, H. F. 1987. Extrafloral nectaries: Their taxonomic distribution and abundance in the woody flora of cerrado vegetation in Southeast Brazil. - Biotropica 19: 140-148.

- and Oliveira-Filho, A. T. 1991. Distribution of extrafloral nectaries in the woody flora of tropical communities in Western Brazil. - In: Price, P. W., Lewinsohn. T. M., Fernandes, G. W. and Benson, W. W. (eds). Plant-animal interactions: evolutionary ecology in tropical and tem. perate Tegions. Wiley. New YOTK. pp. 163-175.

Rashbrook, V. K., Compton, S. G. and Lawton, J. H. 1992. Ant-herbivore interactions: reasons for the absence of benefits to a fern with foliar nectaries. - Ecology 73: 2167-2174.

Sudd, J. H. and Sudd, M. E. 1985. Seasonal changes in the response of wood-ants (*Formica lugubris*) to sucrose baits. - Ecol. Entomol. 10: 89-97.

Takeda, S., Kinomura, K. and Sakurai, H. 1982. Effects of ant attendance on the honeydew excretion and larviposition of the cowpea aphid. - Appl. Entomol. Zool. 17: 133-135.

Way, M. J. 1954. Studies on the association of the ant *Oecophylla longinoda* (Lat.) with the scale insect *Saisseria zanzibarensis* Williams (Coccoidae). - Bull. Entomol. Res. 45: 113-134.

- 1963. Mutualism between ants and honeydew-producing Homoptera. - Annu. Rev. Entomol 8: 307-344.

Wood, T. K. 1984. Life history patterns of tropical membracids (Homoptera: Membracidae). - Sociobiology 8: 299-344.