HOMOPTERAN ATTENDANCE BY WASPS AND ANTS: THE STOCHASTIC NATURE OF INTERACTIONS

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Associations of Hymenoptera with Homoptera have intrigued ecologists and evolutionary biologists as model systems of mutualism. The extensive body of literature, however, tends to be skewed to the interactions between ants and homopteran trophobionts in the Aphidae or Coccoidea (e.g., Kloft et al. 1965, Nixon 1951, Way 1963, Wilson 1971). In the following account we document a web of multispecies interactions within and between trophic levels, involving a species of wasp, several species of ants, and two species of Homoptera. This account is unique in the literature on Hymenoptera-Homoptera associations because it (1) addresses observable interference between hymenopteran attendants, (2) reports behavioral preference by homopterans for certain hymenopteran attendants, and (3) describes an interaction between a polistine wasp and an aetalionid planthopper. In addition, this study has general implications about the quality of diffuse and multiple associations between Homoptera and their honeydew foragers.

MATERIALS AND METHODS

Ten aggregations of feeding *Aconophora ferruginea* Fowler (Homoptera: Membracidae) and four of *Aetalion reticulatum* (L.) (Homoptera: Aetalionidae) were located in the tropical wet forest along the Quebrada Camaronal at La Sirena, Parque Nacional de Corcovado, Osa Peninsula, Costa Rica. Both species of Homoptera are common in Costa Rica, ranging from Mexico and from Costa Rica to Brazil, respectively, and possessing wide ranges of host plants (Ballou 1935, 1936, Wood 1984). They are generally sessile, mating and depositing egg masses at the feeding site (Wood 1984).

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Parachartergus fraternus (Gribodo) (Hymenoptera: Vespidae), a major diurnal attendant, occurs from Costa Rica to Argentina and commonly nests on trees and saplings (Fig. 1a) near streams or swamps (Richards 1978). Six species of formicine and one species of myrmicine ants were also recorded among the hymenopteran attendants.

Behavioral observations were made during 15–18 August 1984 for approximately 18 hours in daylight, six at dawn or dusk, and three at night. *Parachartergus fraternus* attendants were marked to determine if the same individuals returned to the same groups of Homoptera. An extended anal tube of aetalionids allowed inspection of honeydew delivery to individual attendants. We noted the size class of droplets, and recorded the number of droplets per feeding bout and length of feeding bout for three major attendants. Common attendant Hymenoptera and Homoptera were collected for identification, and voucher specimens were deposited at the Museum of Comparative Zoology, Harvard University.

RESULTS

Two aggregations of *A. ferruginea* and two of *A. reticulatum* were tended by *P. fraternus* during daylight hours (Fig. 1b, c). Of 14 homopteran aggregations, 13 were visited by two or more species of ants. These ant species included *Camponotus abdominalis* (F.), *C. novogranadensis* Mayr, *C. sexguttatus* (F.), *C. simillimus* (F. Sm.), two unidentified *Camponotus* spp., *Zacryptocerus porrasii* (Wheeler), and a few other unidentified occasional species. One male-female pair of *A. reticulatum* was not tended during our observation period. All homopteran aggregations except one were feeding on *Piper auritum* Kunth, a common plant of forest edges and disturbed sites in moist regions from Mexico to Columbia (Burger 1971). One aggregation of *A. reticulatum* was found on balsa, *Ochroma lagopus* Swartz var. *bicolor* (Rowlee) Standl. & Steyermark.

The most explicit forms of ownership behavior (*sensu* Brown 1976) were displayed by *P. fraternus*, which tended throughout the daylight hours. During our observation period, the same individual wasps returned to the same homopteran aggregations shortly after dawn and remained there until dusk except for several short (less than 10 minutes each) breaks. The wasps constantly antennated and

Fig. 1. *Parachartergus fraternus*, a polistine wasp (ca. 13 mm): A, on the nest; B, tending nymphs of a membracid, *Aconophora ferruginea*, on *Piper auritum*; C, tending adults and nymphs of an aetalionid, *Aetalon reticulatum*, on *P. auritum*. Photographs by Jae C. Choe.

actively herded the homopterans. Whenever an aetalionid moved away from the feeding group, the wasp quickly flew over the aetalionid and assumed a stiff posture with stilt legs and elevated wings ($N = 12$). The wasp sometimes buzzed its wings and the aetalionid soon returned to its own group. The same type of behavior was observed in the wasp when attending membracid nymphs.

Parachartergus fraternus responded to any approaching animals, including ants, conspecific wasps, anole lizards, and even humans. The typical display involved a combination of the following behaviors: positioning antennae low to the dorsum, extending wings laterally, buzzing wings, chasing, making stinging movements, or biting. These activities appeared to be successful in preventing most ants from soliciting honeydew from the homopterans. On one occasion, a wasp flew at an approaching myrmicine ant and actually knocked it off the branch. Workers of *C. sexguttatus* were observed frequently (on average once every 20 seconds during three six-minute periods) to descend the branch and petiole to a point approximately 5 cm from the wasp-tended homopteran aggregation, but the mere presence of *P. fraternus* seemed to deter the ants from approaching closer. Unlike *P. fraternus*, most attendant ant species did not actively interfere with other approaching ants. One exception was *C. abdominalis*, the major nocturnal attendant, which pursued and disrupted any approaching ant of a different species.

Ants tended in groups of two or three, whereas *P. fraternus* always tended alone. *P. fraternus* also tended much larger groups of *A. reticulatum* (19 and 25 individuals) than did ants (1 and 3 individuals). For smaller membracids, however, there was no such trend; ants managed to tend groups of four to 24 individuals, while *P. fraternus* tended 12 and 13 nymphs. In wasp-tended aggregations, when a wasp was momentarily absent, ants were often quick to move in and collect honeydew. Upon the return of the wasp, however, ants always retreated.

A specialized anal tube of *A. reticulatum* enabled us to assess honeydew delivery. In response to vigorous antennation on the dorsal tip of the abdomen by wasps or ants, aetalionids protruded the anal tube and secreted droplets of honeydew often at a high rate. We counted up to 34 consecutive droplets taken from an adult aetalionid during a single feeding bout by *P. fraternus*. Aetalionid

nymphs also produced honeydew, but presented droplets on the dorsal surface about 2 mm from the tip of the abdomen. It appeared that nymphs did not have fully developed tubes.

Aetalion reticulatum appeared to discriminate between attendants. The mean number of droplets per feeding bout was significantly higher (Kruskal-Wallis test: $p < 0.001$) when *P. fraternus* was soliciting than when either *C. abdominalis*, the major nocturnal tender, or *Z. porras*i were tending (Table 1). The size of droplets from the same adults was consistently larger (about twice in diameter) when *P. fraternus* was tending. Duration of feeding bouts, however, did not differ (Table 1). In the presence of *P. fraternus*, aetalionids commonly raised a pair of legs nearest an approaching ant, kicked at it, and prevented it from collecting honeydew. Thus *A. reticulatum* appeared to play an active role in selecting an attendant.

DISCUSSION

Associations of Hymenoptera with Homoptera cover the entire range of interaction categories including predation (e.g., Evans 1968, Hook 1981), parasitism, mutualism, commensalism, and behavioral combinations such as mutualism-predation (Pontin 1958) and parasitism-predation (Gerling 1966). It is well known that wasps and bees, like ants, depend upon homopterans as sources of carbohydrates (Evans and West Eberhard 1970, Spradbery 1973); however, the behaviors associated with honeydew collection in wasps and bees have not been reviewed.

Our literature survey and field study revealed that bees and wasps exhibit nearly as great a range of interactions as do ant associates. Honeydew foraging of bees and wasps involves various types of behavior ranging from little or no contact with Homoptera to displays of active herding and guarding (Table 2). Unlike some ants (e.g., Maschwitz and Hänel 1985), however, no bees or wasps have been observed to move homopterans to favorable feeding sites. At least eight species of *Trigona* bees and ten species of polistine wasps are now known to tend and collect honeydew from various Homoptera. It is interesting to note that all hymenopteran species known to collect honeydew directly from Homoptera are meliponine bees and polistine wasps. Other social hymenopterans such as honey bees, bumble bees, and vespine wasps have been observed only to obtain

Table 1. Honeydew excretion rates of *Aetalion reticulatum* when solicited by three species of Hymenoptera.

Soliciting Hymenoptera (size, mm)	N	Drops per bout (mean $\pm$ SD)	Length of bout (mean $\pm$ SD, seconds)
Formicidae			
<i>Z. porrasii</i> (3.5)	20	2.7 $\pm$ 2.0	11.3 $\pm$ 10.0
<i>C. abdominalis</i> (6.0)	7	3.4 $\pm$ 1.0	10.6 $\pm$ 4.5
Vespidae			
<i>P. fraternus</i> (12.9)	22	8.6 $\pm$ 6.5	13.1 $\pm$ 8.9

honeydew by gleaning foliage near feeding homopterans. Furthermore, all studies, except for *Polistes fuscatus* (Barrows 1979), have been reported from tropical areas. Distinct ownership behavior has been recorded from only a few species.

Our observations on two homopteran species and their complex of hymenopteran attendants, together with those of other workers, add several facts regarding the nature of mutualism between these two groups. First, the association between Homoptera and their hymenopteran attendants is highly stochastic and often involves a multispecies complex. Most studies have focussed on a single hymenopteran species (e.g., Fritz 1982, Messina 1981), but several workers (e.g., Addicott 1979, Bradley and Hinks 1968, Bristow 1984, O'Neill and Robinson 1977) have now investigated community aspects of the relationship. An individual Homoptera may host several species of Hymenoptera during its lifetime. For instance, *A. reticulatum* has been observed to be tended by *Trigona amalthea* and *T. spinipes* along with a variety of ant species in Brazil (Brown 1976, Castro 1975, Cockerell 1920). Brown (1976) studied hymenopteran attendance of *A. reticulatum* on the Osa Peninsula, not far from our study site, and found a completely different complex of attendant species with diel shifts. An attendant hymenopteran species may also associate with more than one species of Homoptera. *Trigona amalthea* is known to tend *A. reticulatum* and at least two species of membracids (Cockerell 1920, Salt 1929, Schuster 1981). Our study also reports that *P. fraternus* readily associates with both *A. reticulatum* and *A. ferruginea*. Elements of chance due to nest distribution and nutritional need of hymenopteran attendants, and

Table 2. Activities of bees and wasps as honeydew foragers.

Gleans honeydew from foliage near feeding homopterans		
Apidae		
Apinae (Apini)		
<i>Apis mellifera</i>		Bloc et al. 1984, Kunkel & Kloft 1977, Prabucki 1972, Santas 1983
Bombinae		
<i>Bombus bifarius</i>		Wagner & Cameron 1985
Vespidae		
Vespiniae		
<i>Vespa orientalis</i>		Ikan & Ishay 1966
<i>Vespula</i> spp.		Duncan 1939, Evans & West Eberhard 1970
Obtains honeydew directly from feeding homopterans		
Apidae		
Apinae (Meliponini)		
<i>Trigona amalthea</i>		Cockerell 1920, Salt 1929, Schuster 1981
<i>Trigona cagafogo</i>		Müller 1873, 1874
<i>Trigona corvina</i>		Jiron P. & Salas D. 1975
<i>Trigona cupira</i>		Silvestri 1902
<i>Trigona hyalinata branneri</i>		Laroca & Sakakibara 1976
<i>Trigona spinipes</i> *		Castro 1975
<i>Trigona tataira</i> *		Cortopassi-Laurino 1977
<i>Trigona</i> sp.		Wood 1984
Vespidae		
Polistinae		
<i>Polistes fuscatus</i> *		Barrows 1979
<i>Parachartergus apicalis</i>		Williams 1928, Wood 1984
<i>Parachartergus fraternus</i> *		This study
<i>Parachartergus richardsi</i> *		Schremmer 1978
<i>Mischocyttarus drewseni</i>		Jeanne 1972
<i>Stelopolybia testacea</i>		Jeanne 1972
<i>Pseudopolybia compressa</i>		Brown 1976, Wood 1984
<i>Pseudopolybia vespiceps</i>		Jeanne 1972
<i>Polybia</i> sp.		Jiron P. & Salas D. 1975
<i>Brachygastra</i> sp.*		Belt 1874

*Distinct ownership behavior has been observed.

habitat heterogeneity may play a large role in determining the partnership. Recently, Law and Koptur (1986) provided an elegant theoretical argument supporting the evolution of non-specificity in mutualistic interactions.

Second hymenopteran attendants differ in tenacity of attendance. Components of these differences include fidelity and constancy of attendance, foraging strategy, and temporal activity pattern. *Parachartergus fraternus* showed high fidelity during our observation period, i.e., the same individuals tended the same homopteran groups. Similar behavior is known for *Polistes fuscatus* (Barrows 1979). In general, wasps tend to forage as individuals (Barrows 1979, Schremmer 1978, and this study), whereas social bees, like ants, more often recruit (Cortopassi-Laurino 1977, Schuster 1981). Both wasps and bees remain with homopterans for long periods interrupted only by short forays to the nest. Honeydew foraging activities of wasps and bees are always diurnal (Schremmer 1978 and this study).

Third, hymenopteran attendants also differ in quality. It is now well established that hymenopteran attendance enhances the fitness of homopterans (Bristow 1984, Fritz 1982). However, the quality of hymenopteran services varies widely in terms of the effectiveness of sanitation, enhancement of growth rate, and defense. At least in a few studies with ants and aphids (Banks and Nixon 1958, El-Ziady 1960), rapid rate of honeydew excretion indicates an increased rate of assimilation of essential nutrients, higher growth rate, and higher fecundity in homopterans. In our study, sanitation was maintained by most attendants, but wasp attendance could potentially increase the fitness of homopterans through providing better defense and enhancing growth rates. Jiron P. and Salas D. (1975), on the other hand, report no evidence that the presence of bees and wasps deter scale predators but observe benefits due to site sanitation. *Bombus bifarius* may not enhance aphid growth rates, but its leaf-gleaning activities can disrupt potential enemies (Wagner and Cameron 1985).

Fourth, homopterans may show preference for certain attendants. Benefits to homopterans from hymenopteran attendants may not be equal and certain Homoptera-Hymenoptera associations may be favored (Addicott 1979, Bristow 1984, Messina 1981). In this study, we documented differential responses of *A. reticulatum* to various hymenopteran attendants. In the presence of *P. fraternus*, aetalionids behaved defensively and provided little, if any, honeydew to soliciting ants. Furthermore, under wasp solicitation, aetalionids produced significantly larger quantities of honeydew. This

behavioral plasticity may be adaptive under conditions of variable tender quality. It may also play an important role in mediating competitive interactions within mutualistic systems.

SUMMARY

A web of multispecies interactions involving a planthopper, *Aetalion reticulatum*, and a membracid, *Aconophora ferruginea*, and their hymenopteran attendants were studied in Costa Rica. A wasp, *Parachartergus fraternus*, tended both species of Homoptera diurnally and prevented other Hymenoptera from obtaining honeydew. *Camponotus abdominalis*, a major nocturnal attendant, also showed a similar degree of "ownership" behavior. Other ant species, however, appeared to be opportunistic. Although associations were highly stochastic with regard to partnership, *A. reticulatum* showed a clear preference for *P. fraternus* over ant attendants. It provided significantly more honeydew to *P. fraternus* and in the presence of *P. fraternus* it behaved antagonistically toward any ants. The literature on associations of Homoptera with wasps and bees is also reviewed.

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