Diel Shifts in Treehopper-Tending by Ants and Wasps in Costa Rica (Hymenoptera)

by

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ABSTRACT

We examined the activity pattern of seven ant species (Hymenoptera: Formicidae; *Brachymyrmex* sp., *Camponotus atriceps*, *Camponotus integellus*, *Camponotus* sp., *Crematogaster nigropilosa*, *Pheidole biconstricta*, and *Pheidole* sp.) and one wasp species (Hymenoptera: Vespidae; *Parachartergus apicalis*) tending two treehopper species (Homoptera: Membracidae; *Antianthes* sp. and *Cerosa* sp.) on *Acnistus arborescens* trees (Solanales: Solanaceae) at San Luis Biological Station in Costa Rica. We observed hymenopteran attendants at 61 of 67 treehopper aggregations. All eight hymenopteran species tended treehoppers during the day, but only three of the ant species (*C. atriceps*, *C. nigropilosa*, and *P. biconstricta*) also tended at night. Whereas 23 treehopper aggregations had the same species of ant tending during both day and night, 19 aggregations had two different attendant species, one diurnal and one nocturnal. In all 19 cases, the nocturnal tender was *Camponotus atriceps*, a large carpenter ant. Several earlier studies have reported a diel shift in species tending homopterans. In all cases, the nocturnal tender was a species of *Camponotus*. A possible cause for this diel shift relates to the relatively large body size of *Camponotus* workers, which may allow them to displace smaller ants at night, but may be a disadvantage during the day because it makes *Camponotus* workers a preferred target for diurnal parasites and predators.

Key words: ants, *Camponotus*, Costa Rica, diel shifts; Homoptera, Membracidae, myrmecophily, mutualism, *Parachartergus*, wasp

INTRODUCTION

One of the best known mutualisms between animal species is the association between plant-feeding bugs (Homoptera) and their attendant ants (Hymenoptera: Formicidae) (Buckley 1987). Homopterans

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feed on the phloem liquid of plants and produce a sugary waste excretion called honeydew. Ants commonly feed on honeydew and protect homopterans from attack by predators and parasites (Wood 1977, Tilles & Wood 1982, Adenuga & Adeboyeku 1983, Cushman & Whitham 1989, Buckley & Gullan 1991, Novak 1994, Murdoch *et al.* 1995, Huebner & Voelkl 1996, Itioka & Inoue 1996, Stechmann *et al.* 1996). Homopteran honeydew appears to be a very important source of food for many ant species (Tilles & Wood 1982, Tobin 1994). Due to the tremendous economic impact of homopterans in agricultural systems, a vast literature exists on the relationship between a wide range of homopterans and their attendant ants (reviewed in Hölldobler & Wilson 1990). Although not commonly reported, other insects also feed on homopteran honeydew (reviewed in Hölldobler & Wilson 1990). For example, earlier studies have recorded eight species of *Trigona* bees (Hymenoptera: Trigonidae) and twelve species of polistine wasp (Hymenoptera: Vespidae, subfamily Polistinae) feeding on honeydew (Letourneau & Choe 1987; Harris *et al.* 1994).

The present study was motivated by our June 1996 observation of ants and wasps tending aggregations of treehoppers (Homoptera: Membracidae) at San Luis Biological Station in Costa Rica. We noted that some treehopper aggregations were tended by wasps during the day and by ants at night. In January 1997, we surveyed treehopper aggregations to document this diel shift in tending activity.

METHODS

We conducted this study on the grounds of San Luis Biological Station (10° 17' N, 84° 48' W; elevation 1100m) during June 1996 (wet season) and January 1997 (dry season). In June 1996, we first noted treehoppers being tended by both ants and wasps on an *Acnistus arborescens* tree (Solenaceae). We searched for treehoppers on 100 *A. arborescens* trees in the abandoned pasture areas on the station grounds and marked all aggregations of treehoppers we found using flagging tape. At each tree, we estimated the number of treehoppers in each aggregation. In January 1997, we returned to San Luis and made a similar search for aggregations of treehoppers on approximately 150 *A. arborescens* trees. We visited each treehopper aggregation twice per day (between 1100 and 1800h and again between 1900 and 2300h) for three days, and recorded the presence or absence of attending ants and wasps.

RESULTS

In June 1996, we found 35 aggregations of unidentified treehoppers

(ave. ~50 per aggregation) on seven small *Acnistus arborescens* trees. We also noted two *Parachartergus apicalis* wasps tending treehopper aggregations on two adjacent trees during the day. At night, *Camponotus atriceps* ants tended these same two aggregations. We noted several other ant species, including both *Camponotus atriceps* and *Camponotus integellus*, tending the homopterans on other trees during the day.

In January 1997, we found 67 aggregations of two treehopper species (*Antianthes* sp. and *Cerosa* sp.) on 29 *A. arborescens* trees. In total, we observed attendants on at least one occasion at 61 of the 67 treehopper aggregations. Because we used spot surveys rather than continuous observation, it is possible, and even likely, that some treehopper aggregations where we did not observe attendants were actually being infrequently tended.

Camponotus atriceps, a large species of carpenter ant, was the most widespread attendant, tending at 41 treehopper aggregations (Table 1). In addition to *Camponotus atriceps*, six other ant species (two *Camponotus*, two *Pheidole*, one *Brachymyrmex*, and one *Crematogaster*) tended treehoppers during the day, but only two of these ant species also tended at night (Table 1). For 23 treehopper aggregations, the same species of ant tended during both day and night.

We found individual *P. apicalis* wasps tending seven treehopper aggregations. The wasps spent little time during the daylight hours away from their aggregation, but left at dusk. The wasps seemed unperturbed by our presence, by our disturbances to the branches on

TABLE 1. *Hymenopteran attendants at 67 aggregations of treehoppers during the day and night.*

	Night Attendant				
Day Attendant	*C. atriceps*	*C. nigropilosa*	*P. biconstricta*	None	Total
Parachartergus apicalis	6*	0	0	1	7
Brachymyrmex sp.	1*	0	0	1	2
Camponotus atriceps	13	0	0	0	13
Camponotus integellus	2*	0	0	0	2
Camponotus sp.	1*	0	0	0	1
Crematogaster nigropilosa	8*	2	0	7	17
Pheidole biconstricta	0	0	8	0	8
Pheidole sp.	1*	0	0	1	2
None	9	0	0	6	15
Total	41	2	8	16	67

Underlined = same species tended both day and night. * = two species tended in diel shifts.

which they perched, or by close-up flash photography. In the absence of the wasps at night, *Camponotus atriceps* tended six of these seven aggregations. Thirteen other treehopper aggregations had two different species of ant attendants, one diurnal and one nocturnal. In all cases, the nocturnal tender was *Camponotus atriceps* (Table 1). The only species that was never replaced at night by *Camponotus atriceps* was *Pheidole biconstricta*, which always tended both day and night in large numbers.

Camponotus atriceps workers were quick moving and easily alarmed, frequently dropping to the ground when their branch was disturbed. We did not notice such extreme skittishness in any other species tending homopterans.

On several occasions we observed *C. atriceps* workers during the day in the vicinity of treehopper aggregations tended by wasps and other ant species. Once we witnessed a *P. apicalis* wasp attack a *C. atriceps* worker that was near the treehopper aggregation she was tending.

DISCUSSION

Our observations on wasps and ants tending homopterans corroborate and extend the findings of several earlier studies. Two earlier studies (Williams 1928, Wood 1984) documented *Parachartergus apicalis* wasps tending homopterans. In addition, Fallas & Hije (1985) observed a wasp identified as *Parachartergus* near *apicalis* tending homopterans. Fallas & Hije (1985) noted aggressive interactions between these wasps and *Camponotus abdominalis* ants tending the same species of homopterans. Fallas & Hije (1985) found that *C. abdominalis* tended homopterans primarily at night, but did not record what time of day the wasps tended homopterans and interacted with *C. abdominalis*.

The behaviors that we observed in *P. apicalis* appear to be similar to those described for a closely related species, *Parachartergus fraternus*, tending treehoppers and planthoppers (Homoptera, Aetalionidae) in Corcovado National Park, Costa Rica (Letourneau & Choe 1987). Letourneau & Choe (1987) found that *P. fraternus* tended homopterans only during daylight hours. Individual wasps were loyal to one aggregation of homopterans, arriving shortly after dawn and staying until dusk, with only short breaks of less than ten minutes. Letourneau & Choe (1987) noted that the wasps were aggressive towards other animals, including ants. When any ants approached, the wasps would attack them, preventing them from contacting the homopterans. When the wasp was temporarily absent, ants would rush in and take the opportunity to collect honeydew. Letourneau & Choe (1987) observed seven ant species (six *Camponotus* species and *Zacryptocerus porrasi*)

tending the same homopteran species. Letourneau & Choe (1987) also observed a diel shift in tending. *Parachartergus fraternus* wasps tending homopteran aggregations during the day were commonly replaced at night by *Camponotus abdominalis* ants.

Several earlier studies noted diel shifts in homopteran attendance with two different species of ants, one diurnal and one nocturnal, tending the same aggregations of homopterans. Greaves & Hughes (1974) observed the ant *Iridomyrmex purpureus* tending homopterans during the day and *Camponotus consobrinus* or *Camponotus perthiana* tending the same aggregations at night. Swain (1977, cited in Hölldobler & Wilson 1990) found that *Monacis bispinosa* ants tended scale insects during the day, but were aggressively displaced by a large yellow *Camponotus* species at night. Del-Claro & Oliveira (1999) studied a large guild of ants tending a treehopper species in Brazil and found diel shifts in the ant species tending 64 of 222 (29%) aggregations (compared with 19 of 67 or 28% in our study). In all 64 cases, the nocturnal tender was one of six species of *Camponotus*.

In all published studies that we found describing two different species tending the same homopteran aggregations, one by day and the other by night, the nocturnal tender was always a species of *Camponotus*. This is not entirely surprising because many *Camponotus* species commonly tend homopterans and many are primarily nocturnal (*e.g.*, Pfeiffer & Linsenmair 1998). It is puzzling, however, why *Camponotus* workers tend some homopteran aggregations both day and night, and tend others only at night. Perhaps the relatively large body size of *Camponotus* workers allows them to aggressively displace smaller ants, but the advantage of large size is sometimes offset during the day because it also makes *Camponotus* workers a preferred target for diurnal parasites and predators. Numerous studies have indicated that the presence of a natural enemy, such as parasitic phorids, can influence diel shifts in ant foraging activity (Feener 1988, Wetterer 1990, Orr 1992, Orr *et al.* 1995, Feener & Brown 1992) and alter the competitive balance between two ant species foraging on the same resource (Feener 1981, Orr & Seike 1998). *Camponotus* workers are the host of numerous parasitic phorid flies (Disney 1981, Brown & Feener 1993, Gadau & Disney 1996, Disney *et al.* 1998) and prey of insectivorous birds (Clark & Giezentanner 1978).

The skittishness we observed in *Camponotus atriceps* workers may relate to high vulnerability to parasitism and predation. Wetterer (1991, 1993) observed similar skittishness in the foragers of some leaf-cutting ant species but not in others. In non-skittish species, such as *Atta cephalotes*, small workers accompany the large foragers outside the

nest and protect them from attack by parasitic phorid flies (Orr 1992). In skittish species, such as *Acromyrmex octospinosus* and *Acromyrmex volcanus*, small workers do not accompany the foragers, leaving them more vulnerable to attack (Wetterer 1991, 1993).

Our study identifies the principal players in what appears to be a complex system involving many levels of intra- and interspecific interactions, both positive and negative. The hymenopteran species appear to have a mutualistic relationship with the homopterans, feeding on honeydew produced by aggregations of homopterans and guarding the homopterans against attack by predators and parasites. However, hymenopterans appear to compete with other hymenopterans for access to homopterans, and may expose themselves to their own predators and parasites in the process of tending. Homopterans have direct negative effects on plants, both by feeding on them and by spreading plant pathogens. However, if the homopterans are tended by hymenopterans that also keep away other herbivores, the presence of the homopterans and their attendants may have a net benefit for the plants (see Messina 1981, Compton & Robertson 1988). Finally, homopterans may compete with other homopterans both for feeding sites on plants and for attention of hymenopteran attendants (Addicott 1978), though it is possible that homopteran aggregations are beneficial to each other by attracting proportionally more attendants to the plant. Certainly this complex system, particularly the costs and benefits accrued by the different participants, deserves further attention.

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