

Are ant-aphid associations a tritrophic interaction? Oleander aphids and Argentine ants

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Summary. Oleander aphids, (*Aphis nerii*), which are sporadically tended by ants, were used as a model system to examine whether host plant factors associated with feeding site influenced the formation of ant-aphid associations. Seasonal patterns of host plant utilization and association with attendant ants were examined through bi-weekly censuses of the aphid population feeding on thirty ornamental oleander plants (*Nerium oleander*) in northern California in 1985 and 1986. Colonies occurred on both developing and senescing plant terminals, including leaf tips, floral structures, and pods. Aphids preferentially colonized leaf terminals early in the season, but showed no preference for feeding site during later periods. Argentine ants (*Iridomyrmex humilis*) occasionally tended aphid colonies. Colonies on floral tips were three to four times more likely to attract ants than colonies on leaf tips, even though the latter frequently contained more aphids. Ants showed a positive recruitment response to colonies on floral tips, with a significant correlation between colony size and number of ants. There was no recruitment response to colonies on leaf tips. These patterns were reproducible over two years despite large fluctuations in both aphid population density and ant activity. In a laboratory bioassay of aphid palatability, the generalist predator, *Hippodamia convergens*, took significantly more aphids reared on floral tips compared to those reared on leaf tips. The patterns reported here support the hypothesis that tritrophic factors may be important in modifying higher level arthropod mutualisms.

Key words: Ant-aphid association – Tritrophic interaction – Oleander – Argentine ants – *Aphis nerii*

The associations between ants and honeydew-producing Homoptera such as aphids and scale insects have been widely studied as textbook examples of mutualisms (see reviews in Nixon 1951; Way 1963; Buckley 1987). Although these studies have increased appreciation of the

importance of these interactions for specific cases, we still have very little information regarding their distribution in nature. In a recent survey of ant-aphid associations of the Rocky Mountain region, Bristow (1991) documented the presence or absence of myrmecophily for 479 aphid species. Only about one-fourth of those aphids had been recorded with ant attendants. Since aphids produce honeydew – the substance collected by ants – as a waste product of their mode of feeding on phloem sap (Klingauf 1987), and since omnivorous ant species occur in virtually every habitat that supports aphids (Holldobler and Wilson 1990), this observation generated the question – why are so few aphids ant-tended?

One hypothesis is that ant-aphid interactions may reflect a tritrophic relationship: the host plant may determine whether the aphids will be able to attract ants. The impact of host plants on higher trophic levels has received considerable attention (Price et al. 1980; Barbosa and Letourneau 1988). Demonstrated plant effects on higher trophic levels include attractants and repellents (Altieri et al. 1983; Nordlund et al. 1985; Smiley et al. 1985); structural refuges (Hawkins et al. 1987); interference with search (Hua et al. 1987); and toxic effects (Brower et al. 1982; McLain and Shure 1985; Thorpe and Barbosa 1986). That such effects could also be transmitted via honeydew or other excretory products has recently received empirical support. Secondary chemicals have been documented in a number of Homopteran honeydews, Molyneux et al. (1990) detected a variety of host-derived secondary chemicals in the honeydews of a diverse array of Homoptera. In addition, the honeydew of *M. persicae* fed on *Brassica nigra* contains glucosinolates which may be host derived (S. Merritt, pers. comm.) Despite increased interest in tritrophic interactions, the effect of host plants on mutualistic or commensal interactions among higher trophic levels has received little attention.

Several studies suggest that host quality may influence ant attendance, both in Homoptera and in other insects. Lycaenid butterfly larvae produce a secretion which is highly attractive to ants (Hinton 1951). Lycaenids appear

to choose host plants and feeding sites within plants which are high in nitrogen thus assuring a high amino acid concentration in the secretion which attracts ants (Pierce and Elgar 1985; Holldobler and Wilson 1990). The only recorded instance of host-associated effects on ant attendance in aphids involved several species of *Cinara* aphids which were tended by *Formica lugubris* Zett. when feeding on *Pinus silvestris* but not when feeding on *P. contorta* (Sudd 1983). Although the mechanism for this shift was not explicitly determined, Sudd suggested that it might simply reflect reduced feeding by the aphids on the non-preferred host. Data from the Rocky Mountain survey (Bristow 1991) indicate that some host plants support a high proportion of ant-tended species, while other hosts supporting an equally rich aphid fauna have relatively few myrmecophilous species. Thus there is some empirical evidence to justify further examination of the host permissiveness hypothesis. To examine this idea explicitly in the field, a sporadically ant-associated plant – aphid system was used to address 1) the circumstances under which aphids attract ants, and 2) whether patterns of ant association correlated with changes in host quality.

Species studied

Nerium oleander L. The host plant used in the study was the ornamental oleander, *N. oleander*, an evergreen shrub (Apocynaceae). Oleander is native to the Mediterranean region; because of its profuse production of showy flower clusters, coupled with high drought and pest resistance, however, it is widely planted as an ornamental in many warmer regions of the world (Hall and Ehler 1980; Fuller and McClintock 1986). In northern California, where the study was conducted, oleander's flowering season is prolonged from mid-spring through late summer.

Oleanders are highly toxic to many herbivores due to their high concentration of glycosides, particularly oleandrin and neriin (Aplin 1976). The distribution of cardenolides within the plant is not well-known, but they are presumed to be translocatable since cicadas feeding on oleander sap suffer high mortality (Janzen 1978).

Aphis nerii Fonscolombe. The oleander aphid, *A. nerii*, is a small, conspicuous yellow aphid infesting species of the Apocynaceae and Asclepidaceae throughout the world (Bodenheimer and Swirski 1957). In California, it attacks both native milkweeds and oleanders, however it overwinters on oleander (Hall and Ehler 1980; Groeters 1989). Although oleanders appear to be less preferred than milkweeds in some regions (Malcolm 1990), in northern California *N. oleander* supports vigorous populations of aphids (pers. obs.; Hall and Ehler 1980; Groeters 1989). Populations show a characteristic seasonally bimodal distribution both in northern California and in Israel (Bodenheimer and Swirski 1957; Groeters 1989). In the Davis area, the first population peak gives rise to numerous alates that colonize both oleander and other suitable wild host plants. A population crash fol-

lows, due to emigration, predation, and parasitism by the braconid parasitoid, *Lysiphlebus testaceipes* Cresson (Hall and Ehler 1980). A larger and more protracted population peak occurs in July and August but it also precipitously declines due to natural enemies and emigration. Although *A. nerii* can overwinter as parthenogenetic adults on green inner stems, all visible activity ceased at the study site by mid-October.

Colonies are initiated by immigrant alates which settle on the current season's tender branch tips. Secondary colonization may occur as apterous females move to adjacent terminals. In the study site, as elsewhere, colonies were confined to the distal portion of infested branches (Ismail and Swailem 1971; pers. obs.). Oleander aphids feed preferentially on the abaxial phloem tissues of growing plant terminals and, to a lesser degree, on adaxial phloem tissue of older leaves (Botha et al. 1975). The aphids sequester and excrete a variety of host plant cardenolides (Rothschild et al. 1970; Malcolm 1986, 1990), which render them unpalatable to many arthropod predators.

Iridomyrmex humilis (Mayr). The Argentine ant, *I. humilis*, is widely distributed in California, particularly in disturbed habitats (Ward 1987), where it often forms associations with honeydew producing Homoptera (Smith and Armitage 1931; Flanders 1951). During this study, *I. humilis* was the only ant associated with the oleander aphid. The ants became active with the onset of warm weather, and could be found foraging at baits in March, when the ambient temperature exceeded 15° C (Ward 1987). Some ant activity was observed in every census from early April until October. The Argentine ant shows a recruitment behavior typical of many ant species (Deneubourg et al. 1990). Individual workers, or scouts, forage randomly in the environment. When a worker encounters a food item too large to retrieve, she recruits nestmate assistance by means of a pheromone trail (Cavill et al. 1979). Thus a large number of workers can be concentrated at profitable resource sites in a short time.

Methods

Censuses: Most of the data were collected from a repeated survey of oleander plants on the campus of the University of California, Davis, California conducted from April through October of 1985 and 1986. The study site supported several hundred oleander plants and a mix of varieties. The most common varieties were Sister Agnes, Hardy Red, and Jannoch. Initially 30 plants from across the campus were selected without reference to variety or location. The 1.5 m to 5 m plants were pruned during the winter, but were not otherwise fertilized or treated with pesticides. Plants were examined biweekly throughout both years of the study. On each date, fifty haphazardly selected terminals per plant (1500 terminals per census) were examined for aphids, ants or predators. Terminals were defined as the meristem plus leaf or floral structures plus the stem down to the first mature leaves. Where several structures occurred on the same tip – as with late buds and flowers co-occurring, the tip was classified as the most mature structure present. Six categories were identified:

1. *leaf tips:* the new season's growth including the developing meristem and the terminal whorl of three full (expanded) leaves.

2. *early buds*: tips recognizable as developing flower structures, but lacking floral pigmentation.

3. *late buds*: tips maturing into flower buds. This class included any clusters of buds where the color of the mature flower was distinguishable.

4. *flowers*: tips or floral clusters with at least one open flower.

5. *senescent flowers*: tips with only dried flowers or floral structures.

6. *Pods*: distinguishable seed-pods.

This report focuses on leaf and floral tips since these accounted for 70% or more of the aphid-infested terminals. Leaf tips included all tips lacking floral differentiation. Floral tips included pooled observations from late buds and flowers. Early buds, being transitional between leaf and floral tips, presented a potential source of error in classification and thus were not treated in this analysis. Similarly, senescent flowers and pods, because they supported only a small fraction of aphid colonies and only occurred late in the season, were also excluded. Census data for each aphid colony included: feeding site, colony size, and the number of associated ants. No attempt was made to distinguish instars and/or adults. Alate adults were enumerated, but will not be treated further in this study. In addition to ant-aphid associations, census data provided information on the overall abundance of classes of feeding sites as well as the presence and location of scout ants. Scouts were defined as individual ants on any terminal that did not support aphids or any other apparent food source.

Data analyses were performed using SYSTAT® and SAS (MDCTA). Data were tested for normality and homogeneity of variance prior to analysis. Where assumptions of normality were met, parametric tests were employed (Sokal and Rohlf 1969). Where data did not support parametric assumptions, a nonparametric test was employed (Siegel 1956).

Results

Seasonal distribution and utilization of plant resources

Availability of feeding sites. Plant growth commences with the onset of warmer weather in the early spring and can therefore vary from year to year. When the surveys began in early April, leaf meristems were well-initiated and some differentiation of floral tips was observed. Figure 1 shows, for the 30 census plants, the pooled number of plant tips in each developmental category over time. The patterns were similar between years, although 1986 was slightly warmer, and flowering commenced and peaked somewhat earlier. As differentiation progressed, the proportion of the major classes of resources available to the aphids also changed. The numbers of terminals available and colonized during the peak early and late census periods are given in Table 1. Leaf terminals were always the most abundant feeding site available, comprising from 48% to 72% of tips. Floral terminals provided between 15% and 27% of the available feeding sites.

Aphid seasonal dynamics and host utilization. In 1985 the overall infestation rate for leaf tips was 18.1% (1998 colonies on 11,009 tips examined). For floral tips the rate was 20.6% (812 colonies on 3949 tips). In 1986, aphids were much more abundant. Leaf infestation was 34.0% (3793 colonies on 11,168 tips) and floral infestation was 25.5% (1344 colonies on 5,274 tips). Table 1 shows the numbers of infested tips on the four specific dates coin-

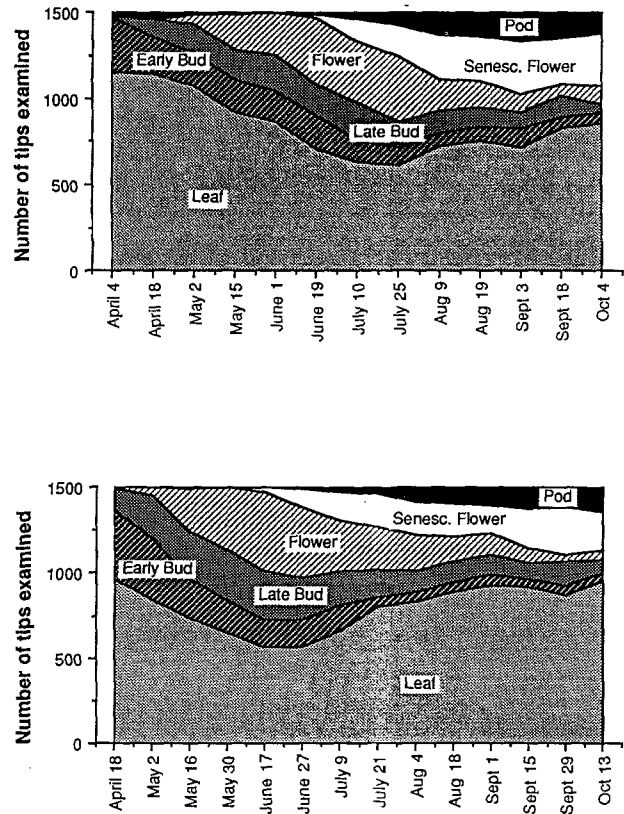


Fig. 1. Seasonal patterns of availability of feeding sites for *Aphis nerii* in (a) 1985 and (b) 1986. Cumulative total of 1500 tips examined per census

Table 1. Availability and utilization of feeding sites by *A. nerii* for censuses with peak population density

Year	Census	Terminal		Tips with aphids	Tips without aphids
1985	May 2	Leaf	<i>n</i> 370 (%) (34.3%)	709 (65.7%)	
		Floral	<i>n</i> 38 (%) (16.9%)	187 (83.1%)	
		Other	<i>n</i> 54 (%) (27.6%)	142 (72.4%)	
	August 9	Leaf	<i>n</i> 347 (%) (47.7%)	381 (52.3%)	
		Floral	<i>n</i> 155 (%) (49.5%)	158 (50.5%)	
		Other	<i>n</i> 225 (%) (49.0%)	234 (51.0%)	
1986	May 2	Leaf	<i>n</i> 458 (%) (54.7%)	379 (45.3%)	
		Floral	<i>n</i> 77 (%) (26.2%)	217 (73.8%)	
		Other	<i>n</i> 187 (%) (50.7%)	182 (49.3%)	
	July 21	Leaf	<i>n</i> 468 (%) (58.2%)	336 (41.8%)	
		Floral	<i>n</i> 204 (%) (49.8%)	206 (50.2%)	
		Other	<i>n</i> 131 (%) (45.8%)	155 (54.2%)	

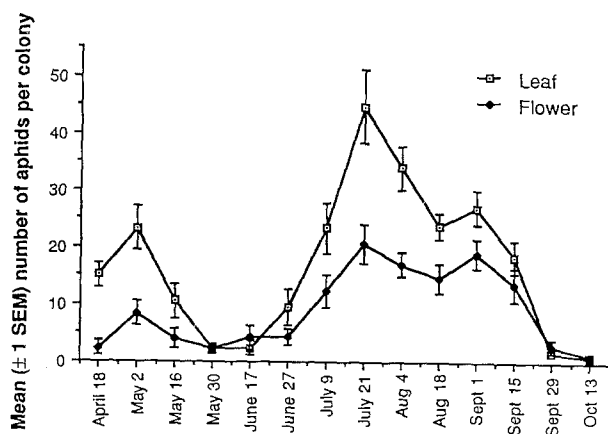
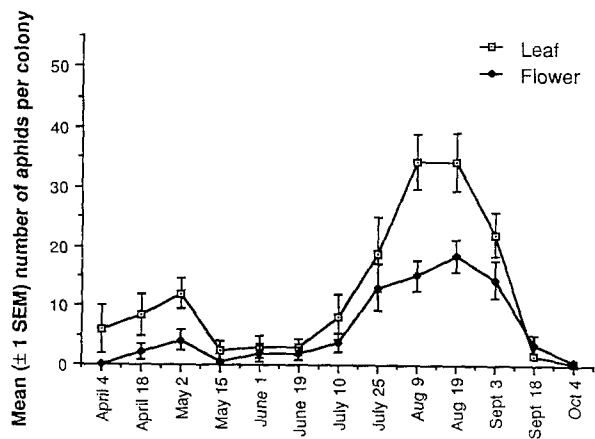


Fig. 2. Mean number of aphids per colony infesting leaf tips and flower tips for census dates in (a) 1985 and (b) 1986. Bars indicate ± 1 SEM. Based on mean colony size per plant for 30 sample plants

ciding with peak aphid populations. A Multidimensional Contingency Table Analysis (Bishop et al. 1977) was performed to test the effects of year, season, and feeding site on occupation of terminals by aphids. The best fit model showed significant effects due to year ($\chi^2 = 81.88$; $df = 1$; $p < 0.001$), season ($\chi^2 = 109.33$; $df = 1$; $p < 0.001$), and site ($\chi^2 = 68.62$; $df = 2$; $p < 0.001$) as well as a highly significant interaction between season and site ($\chi^2 = 40.04$; $df = 2$; $p < 0.001$), reflecting the observed tendency for aphids to avoid floral terminals early in the season, but not late in the season.

The mean size of colonies found on leaf tips was consistently larger than that of colonies found on floral tips (Fig. 2). In addition, the seasonal bimodality of the aphid population is clearly observed in both leaf and floral colonies, although the peaks are significantly earlier in the second year. (Three factor repeated measure ANOVA on log-transformed data: Year effect: $F = 30.33$; $df = 1$; $p < 0.001$; feeding site effect, $F = 33.07$; $df = 1$; $p < 0.001$; there was no significant interaction between year and feeding site: $F = 0.729$; $df = 1$; $p > 0.05$.)

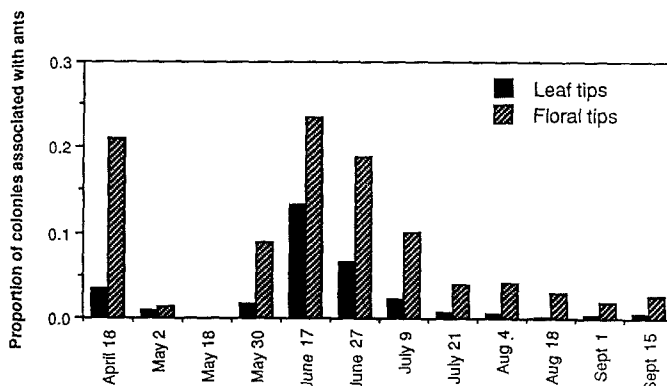
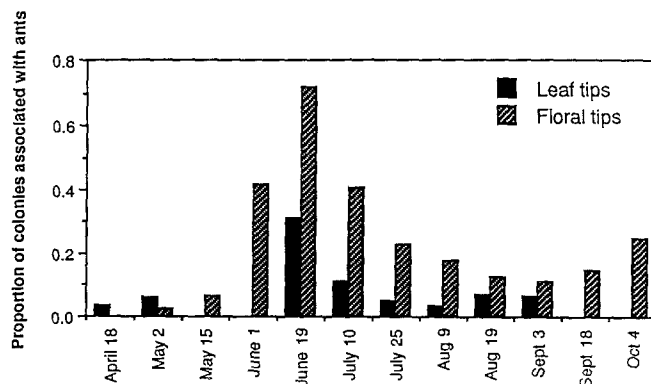


Fig. 3. Proportion of all ant-tended aphid colonies on leaf tips vs. floral tips for (a) 1985 and (b) 1986

Association with ants. The seasonal association of ants with colonies of *A. nerii* on leaf and floral feeding sites is shown in Fig. 3. The overall proportion of colonies that attracted ants was relatively low. In 1985, 5.9% of leaf colonies and 18.8% of floral colonies were anttended. In 1986, the associations were reduced to 1.1% of leaf colonies and 5.1% of floral colonies. A plant by plant comparison showed that floral colonies were significantly more likely to attract ants than were leaf colonies ($p < 0.02$; Wilcoxon Matched Pairs Signed-ranks test). The decrease in tending rate in 1986 does not solely reflect a dilution caused by twice as many aphids being tended by the same number of ants. There was also a decrease in the absolute number of ants scouting (62 in 1985 vs. 17 in 1986) and ants tending aphids (712 in 1985 vs. 224 in 1986). The reason for the observed difference in ant activity between years is not known, but may reflect either switching to an unidentified but preferred food source or the loss of some ant colonies through mortality or emigration.

Further details of the association of ants with aphid colonies, and with plant structures in the absence of aphids, are given in Table 2. Scout ants were found on floral tips somewhat more frequently than on leaf tips, however MDCTA indicated that only the difference between years was significant ($\chi^2 = 43.19$; $df = 1$; $p < 0.001$) while there was no difference in scouting effort in response to feeding site ($\chi^2 = 3.07$; $df = 1$; $p > 0.05$).

Table 2. Association of ants with oleander and oleander aphids

	1985		1986	
	Leaf	Floral	Leaf	Floral
Ant-plant association				
Scout ants				
-total scout ants	37	25	8	9
-scouting effort (ants/1000 tips)	4.11	4.29	1.08	2.29
Ant-aphid association				
Tended colonies				
- n	117	153	42	68
- mean # of aphids	25.9	25.7	32.2	25.5
aphids				
- (SEM) tending effort (ants/1000 aphids)	(2.6) 15	(3.0) 44	(5.3) 2	(3.0) 10

Overall, leaf colonies tended to be larger than floral colonies, (see Fig. 2); however, a comparison of tended colonies showed no significant difference in colony size either in response to variation between years or due to feeding sites (Table 2; Two-way ANOVA on log-transformed data. year effect, $F = 1.048$; $df = 1$; $p > 0.05$; feeding site effect, $F = 1.33$, $df = 1$; $p > 0.05$).

Ant recruitment response. On census plants, aphids in floral colonies were consistently associated with more tending ants than were aphids feeding on leaf structures (Table 2). The ratio of tending ants per aphid was three to five times higher for floral colonies compared to leaf colonies.

An additional set of observations were conducted specifically to determine whether ants responded to increasing aphid colony size by recruiting more nestmates. Five non-census plants were selected from those that 1) showed significant ant activity, defined as visible trails of ants going up and down the lower trunk of the shrub, and 2) had approximately equal numbers of leaf and floral tips. For each of the five selected plants, randomly-selected terminals were examined. The analysis included the first ten leaf terminals and the first ten floral terminals located that supported aphids. The numbers of aphids and ants were recorded. In one plant, only nine floral colonies were found. All data were collected on July 10, 1985 between 10:00 am and noon. The results of this set of observations supported the patterns noted during the census. There was no significant ant response due to plant, but there was a highly significant effect due to feeding site (2-way Analysis of Variance: Plant effect, $F = 1.615$; $df = 4$; $p > 0.05$; Feeding site effect: $F = 44.93$; $df = 1$; $p < 0.001$.) The correlation between aphid colony size and number of ants is shown in Fig. 4. There is no significant correlation for leaf colonies ($r^2 = 0.107$; $p > 0.05$) however the correlation between number of aphids and number of ants is significant for floral colonies ($r^2 = 0.446$; $p < 0.01$).

Predator bioassay. The census results suggested that honeydew produced by leaf-feeding aphids was less pal-

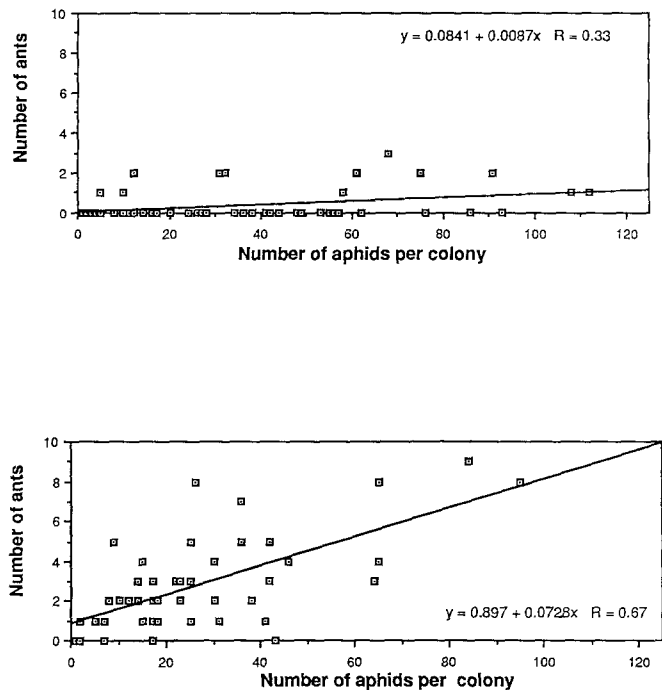


Fig. 4. Recruitment response of ants to aphid colonies on different plant parts. Number of ants associated with aphid colonies of different sizes on (a) leaf tips and (b) floral tips plotted against the size of the aphid colony. Based on observations taken July 5, 1985 (10:00 am to noon) on five plants (10 leaf and 10 floral colonies per plant.)

atable to ants than honeydew from floral colonies. Based on these observations, I postulated that aphids feeding on leaf tissues would be less palatable to other species in higher trophic levels. To test this, a simple bioassay was conducted using the generalist coccinellid predator, *Hippodamia convergens* Guerin-Meneville. Several hundred adult ladybeetles, collected from overwintering aggregations, were purchased from a garden supply source. Preliminary trials indicated that these beetles readily fed on a variety of aphid species under the experimental conditions. Observations were conducted as follows: field collected aphid colonies from a variety of oleander plants were brought into the laboratory. Twenty aphids from either a leaf colony or a floral colony – including a mix of all instars – were offered to a randomly selected beetle in a 14 cm covered petri dish arena for 15 min. The number of aphids wholly or partially eaten was recorded. Observations were repeated for 50 beetles for each treatment.

Convergent ladybeetles preferred aphids from floral colonies over those from leaf colonies. When offered aphids from leaf sources, beetles consumed from 0 to 2 prey, with a mean of 0.68 prey (± 0.10) per trial. The fifty beetles offered floral aphids consumed from 0 to 4 prey, with a mean of 1.10 (± 0.16) aphids taken in 15 min. These differences are significant (unpaired t-test (one-tailed), $df = 98$; $t = 2.151$; $p < 0.02$). Even when predation occurred on leaf aphids, the beetles often failed to consume the prey entirely, and spent from one to 10 minutes cleaning their mouthparts after each attack.

Discussion

This report presents observational and experimental data indicating that feeding site on the host plant alters the interaction between oleander aphids and ants. First, ant associations are always more common for colonies on floral tips than leaf tips, even though the latter tend to be larger and more numerous. This pattern is reproducible regardless of high fluctuations in aphid abundance over the season or between years, and regardless of great differences in overall ant activity. Secondly, ants respond to changes in colony size on floral tips but not on leaf tips. This recruitment response leads to an increase in the number of tending ants in response to increases in the colony size. There is no recruitment response to colonies on leaf tips. Although scout ants are more likely to be found on floral tips, it is unlikely that the bias in tending response solely reflects a fortuitous association between flower-visiting ants and aphids that happen to be on those shoots. There was little evidence that oleander flowers are visited by ants in their own right. Of approximately 9,000 uninfested floral stems examined, fewer than 30 had ants present. Of the 2148 floral stems that supported aphids, however, 221 also had ants present. Finally, an experimental bioassay of aphids reared on the different feeding sites indicated that their attractiveness to general predators paralleled their attractiveness to ants. This study provides the first field evidence supporting the hypothesis that ant-aphid associations may represent a tritrophic interaction.

Ant-aphid associations are among the most facultative and variable mutualistic interactions. Coevolutionary interactions are diffuse, with associations reflecting opportunistic responses among ants to shifting resource requirements and availability (McNeil et al. 1977). The degree of mutualism vs. commensalism may shift depending on the species and number of attendant ants (Bristow 1984), the presence of competitor aphids (Addicott 1978; Cushman and Addicott 1989), or the degree of pressure from predators (Cushman and Whitham 1989). In the case of the oleander aphid presented here, it is unlikely that the ants provide significant protection, in part because the tending rate is so low, and in part because the major natural enemy in the study area – a braconid parasitoid, *Lysiphlebus testaceipes* Cresson – oviposits very rapidly and is not deterred by ants (Hall and Ehler 1980; R. W. Hall, pers. comm.) On other host plants, such as *Asclepias eriocarpa* Benth. and *A. syriaca* L., ant association is much more common (pers. obs.), and may provide more consistent benefit to the aphids. A further analysis of the cardenolide contents of both aphids and honeydew from the different feeding sites is needed to assess the tradeoffs in the value of different defenses. Such analysis could also help clarify the pattern of aphid preference for leaf sites both in terms of proportion of tips colonized and size achieved by those colonies.

The mechanism generating the observed variation in aphid attractiveness to ants is not known. Different plant structures may vary significantly in terms of nutritional value (Mattson 1980), or chemical or physical defenses (Hall and Langenheim 1986), which may in turn directly

affect the herbivore (Greene 1989) and/or higher trophic levels (Price et al. 1980). Changes in host quality could affect the quantity or quality of honeydew available to ants. For *A. nerii*, the most likely explanation for differential attractiveness is through its use of host defensive chemistry for its own defense. Rothschild et al. (1970) and more recently, Malcolm (1986, 1990) have shown that *A. nerii* sequesters host cardenolides which provide it with some defense against many generalist predators. In an extensive study of *A. nerii* feeding on a milkweed, *A. curassavica* L., Malcolm identified 25 cardenolides in the host plant, of which 17 appeared in the aphids, and 20 were detected in the aphids' honeydew. The honeydew excreted by *A. nerii* feeding on this plant was 46% cardenolide. Malcolm's analysis also provides interesting anecdotal support that feeding site may affect cardenolides. Although almost all of these honeydew samples came from aphids feeding on leaves, the one analysis from aphids feeding on a pod contained both the lowest cardenolide concentration for the aphids, and one of the lowest concentrations for the plants sampled. Although there are no further data on chemical variability in feeding sites for oleander, Yamauchi et al. (1983) have documented differences in the cardenolide profiles and content of different varieties of oleander.

The host plant appears to modify the potential for aphids to attract ants in the case of *Aphis nerii* on oleander; however, this is not always the case. Cushman and Addicott (1989), using plant height as a correlate of host quality for aphids on fireweed, found no significant plant effect on tending. Ewart and Metcalf (1956) comment that, on citrus, the Argentine ant readily sought out honeydew from colonies of the brown soft scale (*Coccus hesperidum* L.) but not the citricola scale (*C. pseudomagnoliarum* (Kuwana)). Since both scales feed on citrus, and their honeydews contain qualitatively similar sugars and amino acids, this might provide an interesting system to address questions regarding differential attractiveness to ants. Similarly, Dixon (1985) detailed a fascinating case of the aphid, *A. urticata* Gmelin, on nettle. In the spring, *A. urticata* colonies are composed of dark-green individuals, often ant tended, which cluster on the growing tips of nettles. The summer form which is not ant tended is comprised of small, yellow individuals which feed spaced out across mature nettle leaves. The forms are so different that they were initially placed in different genera. As these examples illustrate, a considerable amount of work remains to be done in elucidating the factors which underlie the formation of ant associations with Homoptera. The relative importance of nutrients vs. plant defensive chemistry needs to be taken into account, as does the quantity of honeydew produced. Since honeydew is attractive to many natural enemies as well as to ants (Krombein 1951; Zoebelen 1956 a, b, 1957), aphids may truly be caught "between the devil and the deep blue sea" (Lawton and McNeill 1979), and the presence and types of predators may prove to be an important factor as well. Extending our focus of tritrophic interactions to include the potential contribution of the host plants to the attraction of mutualists may well be necessary before we fully understand these interactions.

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