Ant–Aphid Interactions: Are Ants Friends, Enemies, or Both?

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ABSTRACT Interactions between ants and aphids range from mutualistic to antagonistic. Understanding the ecological basis for such interactions requires understanding the costs and benefits to the aphids of ant-tending. Such an analysis is not simple, because ants can simultaneously have positive and negative effects upon aphids. The aphids *Pleotrichophorus utensis* Pack & Knowlton and *Uroleucon escalantii* Knowlton (both Hemiptera: Aphididae) are occasionally tended by *Formica obscuripes* Forel (Hymenoptera: Formicidae) at field sites in central Colorado. To compare the relative effects of protection and predation by ants on aphid abundance, we experimentally crossed the presence of the ants and other predators on host plants on which one or both aphids occur. Within a week of the start of the experiment, ants had a strong negative impact on aphid numbers that lasted the course of the experiment. Nonant predators initially had a weak negative effect on aphids, but by the end of the experiment, the negative effect of nonant predators was similar in magnitude to the effect of the ants. The negative effect of ants and other enemies on aphids was nonadditive; simultaneous predation by ants and other enemies was not as strong as expected from estimates of predation rates by only ants or only other enemies. This study suggests that ants simultaneously protect and prey upon aphids. We suggest selection to appease ants and to gain protection from ants can both be important forces generating ant–aphid mutualisms.

KEY WORDS ant–aphid interactions, mutualisms, predation

Among mutualisms, ant–aphid interactions are among the most variable in terms of their outcomes (Bristow 1991); whether or not the ant–aphid interaction is beneficial to the aphids often depends upon both the spatial and ecological context (Stadler and Dixon 2005). Indeed, there is little evidence that phylogeny constrains the evolution or maintenance of mutualisms; the characteristic of being ant-tended is evolutionary labile, with numerous gains and losses in clades with ant-tended species (Stadler et al. 2001, Shingleton and Stern 2003). Thus, over both ecological and evolutionary scales, ant–aphid interactions often exhibit extreme conditionality in outcomes, varying between antagonism and mutualism: given the right set of circumstances the presence of ants could have an overall positive effect on the aphids, or the net effect can be negative (Stadler and Dixon 2005).

One approach to understand this variability in the outcomes of relationships between ants and aphids is to examine the various costs and benefits of ant-tending. Reflecting the evolutionary variability seen in ant–aphid interactions, ecological studies have revealed a range of outcomes and patterns in the interaction (Stadler and Dixon 2005). Ants have a positive effect on growth rates in some aphid species (e.g., Flatt and Weisser 2000, Stadler et al. 2001) and negative effects in others (Yao et al. 2000, Fischer and Shingleton 2001). In a recent review, Stadler and Dixon (2005) argue that the variety of studies showing both positive and negative effects on the strength of ant–aphid interactions is not an artifact of differences in experimental design and conditions, but rather it is an accurate representation of the diversity of factors that shape these mutualisms. They suggest a more dynamic approach, in which experimental studies on the costs and benefits of ant–aphid interactions explicitly address the relative importance of combinations of factors that predispose partners toward mutualism (beneficial effects) or antagonism (costly effects).

Here, we study the combined effects of ants and predators on aphid abundance. Complicating efforts to understand the costs and benefits of ant-tending, ants can have multiple and sometimes opposing effects upon aphids that make it difficult to discriminate antagonism from mutualism. Although a clear benefit of ant-tending for some aphid species is protection from predators (Stadler and Dixon 1998, Fischer et al. 2001, Stadler et al. 2001, Stadler 2004), ants may occasionally or even mostly eat rather than tend aphids (Stadler and Dixon 1999, Delabie 2001, Fischer et al. 2001). Consequently, the extent to which the interaction between ants and aphids is a net benefit for aphids may depend upon the presence of other enemies. To date,

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no work has been done to quantify the relative effects of ant predation, predation by other arthropods, and ant protection on aphid abundance. Indeed, although understanding how multiple ecological factors interact to affect ant–aphid interactions is critical to understanding the evolution of mutualisms, decisive field experiments are largely lacking (Stadler and Dixon 2005).

In this study, we directly manipulated the presence of ants and other potential enemies of aphids in a field environment to determine whether the interaction between two facultatively tended aphid species, *Pleotrichophorus utensis* Pack & Knowlton (Hemiptera: Aphididae) and *Uroleucon escalantii* Knowlton (Hemiptera: Aphididae), and the ant species, *Formica obscuripes* Forel (Hymenoptera: Formicidae), was dependent upon the presence of nonant predators. This experiment allowed us to ask the following questions: 1) Does *F. obscuripes* prey upon these aphid species?; 2) Even in the presence of ant predation, do ants protect aphids from other predators?; and 3) What is the relative importance of ant predation and ant protection to aphid numbers?

Materials and Methods

This study was conducted in the Almont Triangle of the Gunnison National Forest ≈25 km north of Gunnison, Gunnison County, CO. We used an open meadow at an elevation of ≈2,600–2,700 m. *Chrysothamnus viscidiflorus* (Hooker) Nuttall (Asteraceae) plants at this site are hosts to three sap-feeding hemipterans: the membracid *Publilia modesta* Uhler (Hemiptera: Membracidae) and aphids *P. utensis* and *U. escalantii.* Both aphid species are found occasionally, usually in small numbers (tens of individuals).

The primary tending ant of the hemipterans at this site is *F. obscuripes.* The ants are largely seen tending the membracids, although ants also are occasionally seen associating with the aphids, particularly when aphid densities on a plant are high. Although these aphids are not obligately ant-tended, related species are known to have more specialized ant interactions: at least one species of *Uroleucon* has been reported to associate with ants (Fagundes et al. 2005), and ants also tend at least one aphid species in the genus *Capitophorus* (Jones 1929), a genus closely related to *Pleotrichophorus* and for which little is known. A review by Bristow (1991) indicated that close to 50% of aphid genera have at least one species that associates with ants, with ant-tending being a labile trait at the level of the subtribe and genus. This is consistent with more detailed phylogenetic work by Shingleton and Stern (2003) that indicates mutualisms can be highly labile even below the level of genera. Thus, there seem to be no phylogenetic impediments that constrain the evolution of a mutualism for either of the two aphid species.

Experimental Design. Beginning 22 June 2004, we set up a two-way analysis of variance (ANOVA) design in which the presence or absence of ants and nonant predators was fully crossed with 30 plants per treatment. We set up a fifth group of plants that were left unmanipulated and that we used to assess the extent to which our results were an artifact of the experimental design. We started the experiment by choosing 150 plants with membracids. Plants were randomly assigned to the five different treatments.

The ubiquity of membracids at the site means that ant colonies naturally have ready access to membracids. The availability of alternative honeydew sources can affect ant–aphid interactions (Offenberg 2001). The foraging decisions individual workers make are a function of colony nutritional status (Pierce et al. 1991). Because ant colonies in the experiment were confined to enclosures, we provided colonies access to both aphids and membracids to mimic food availability under natural circumstances.

For all the treatments except the unmanipulated controls, we erected 25-cm-tall aluminum cylinders ≈2 m in circumference around each individual host plant, and we nailed them into the ground. In the center of each was a 103-cm wooden stake. We attached netting (generic bridal veil; 25 holes per cm^2) to the cylinders with Velcro (2.54 cm [1 in.] in width), and we gathered and tied the netting to the stake to close the cage, which sealed the plants and excluded nonant predators but allowed light into the cages. In the treatments with nonant predators, we covered the southern side of the cage with bridal veil, which controlled for any netting effect.

For treatments in which ants were present, we built artificial ant colonies inside the cages. We dug up *F. obscuripes* colony fragments of several hundred workers, brood, and nest material, and we placed them in 11.3-liter tubs (17 by 24 by 32 cm, Rubbermaid Incorporated, Wooster, OH). Tubs were placed inside the cylinders. For treatments in which ants were absent, we filled Rubbermaid tubs with dirt and placed them inside the cylinders. We trimmed vegetation around cylinders to prevent ants from accessing cages over the vegetation in treatments that were open to nonant predators. As a control, vegetation also was trimmed in treatments closed to nonant predators. Once the treatments were applied, we searched cages in the no-ant treatment for ants and cages in the no-predator treatment for nonant predators, and we removed ants and nonant predators from the two treatments, respectively. We applied Tanglefoot (Tanglefoot Company, Grand Rapids, MI) to the inside rim of all cylinders and the outside rim of all open cages to keep colony fragments in and other ants out. Treatments were maintained once per week. All treatments were fully set up by 5 July.

We counted the numbers of aphids within the cages during the weeks of 12 July (week 1 after initiation of the experiment) and 9 August (week 5). To determine whether treatments were working, we surveyed nonant predators and ants the weeks of 12 July, 19 July, 26 July, 2 August, and August 9. We collected aphids, but we were unable to confidently distinguish between species in the field, so aphid numbers reported refer to both species. When aphid aggregations were very large, we estimated aphid number by counting a plant

bud that seemed to have a representative number of aphids on it, and then we multiplied this number by the number of buds with aphids present. This method introduced error, but there were few plants that had large numbers of aphids, and this method sufficed to rank order the data.

Statistical Analyses. To determine whether there was an "enclosure" effect we performed a Mann–Whitney *U* test comparing aphid numbers on the completely unmanipulated plants to aphid numbers on plants within cages where both ants and nonant predators were allowed (the experimental controls).

To determine whether the full veil reduced predators relative to the half veil, we performed a repeated measures ANOVA on predators. In a similar manner, we performed a repeated measures ANOVA on the number of ants to determine whether the absence of colonies reduced the number of ants.

To test the effects of ants and predators on aphid numbers, we examined the data in the four manipulated treatments (ants/full veils, ants/half veils, no ants/full veils, and no ants/half veils). Because of the number of plants that had zero aphids in our surveys, the data had a lognormal distribution, and there was no transformation that could normalize the residuals. Consequently, we could use neither ANOVA nor repeated measures ANOVA to analyze the data. To evaluate the effect of treatments on aphid numbers, we used a sampled randomization test (Sokal and Rohlf 1995) to conduct a nonparametric two-way ANOVA to analyze the number of aphids at the beginning and end of the experiment.

We performed the randomization analysis by using ranks of the values. Plants with fewer aphids were assigned lower ranks. We assigned ranks by ordering plants from 1 to 120, starting with plants that had the fewest aphids. Following Sokal and Rohlf (1995), in case of ties, we assigned each plant that had the same number of aphids the average value for that group (e.g., if there were four plants with zero aphids they were each given the rank of 2.5). After ranking the data, we calculated the *F* values for the two main effects, ants and nonant predators, along with the interaction. We used a randomization program written in True Basic to estimate *P* values associated with the calculated *F* values. Data were randomly swapped among treatments, and the *F* values recalculated 1,000 times; the *P* values were the percentage of times the *F* values from the randomizations exceeded the observed *F* values.

Results

Ten of 30 of the unmanipulated plants had aphids during both surveys, with a range of zero to 24 aphids per plant (12 July) and zero to seven aphids per plant (9 August) (see Table 1 for a summary of the raw data). There was no significant difference between the unmanipulated plants and the cages with nonant predators and ants with respect to the number of aphids on the plants (12 July: tied z-value = -1.3, $P = 0.18$; 9 August: tied z-value = -0.17, $P = 0.86$), indicating that the effects of ants and nonant predators within the enclosures did not differ significantly from the effects of ants and nonant predators outside the enclosures.

Table 1. Frequency distribution of the number of cages with different numbers of aphids

Date	Treatment	No. aphids				
		0	1–10	10–100	100–1,000	>1,000
12 July	No predator/no ants	19	6	4	1	0
	Predators/no ants	20	7	3	0	0
	No predators/ants	28	1	1	0	0
	Predators/ants	25	4	1	0	0
	Unmanipulated	20	9	1	0	0
9 Aug.	No predator/no ants	13	7	6	3	1
	Predators/no ants	21	4	4	1	0
	No predators/ants	21	5	3	1	0
	Predators/ants	22	1	6	1	0
	Unmanipulated	20	10	0	0	0

Aphid distributions were roughly log normally distributed, and most cages did not have any aphids.

The ant manipulations were very effective in controlling the number of ants, with 42.55 ants/enclosure with colonies present compared with 0.31 ants/enclosure with colonies absent (ant treatment: $F_{1,118} = 144$, $P < 0.0001$; time: $F_{4,115} = 11.9$, $P < 0.0001$; treatment × time: $F_{4,115} = 12.0$, $P < 0.0001$). The predator treatments were also effective. Both time and treatment (veils versus half-veils) affected the number of predators (predator treatment: $F_{1,118} = 21.2$, $P < 0.0001$; time: $F_{4,115} = 2.92$, $P < 0.02$) with half-veils having >3 times as many predators (0.324 predators/enclosure versus 0.096). There was no time × treatment interaction ($F_{4,115} = 0.79$, $P = 0.50$). The magnitude of reduction of the predators was very similar to levels reported in Morales (2000), another study that also included the same nonant predator removal treatment.

Both treatments affected aphid numbers. During July, nonant predators reduced the number of aphids on plants (Fig. 1; $F = 0.19$, $P = 0.058$). Ants strongly reduced aphid numbers (Fig. 1; $F = 11.2$, $P < 0.001$), and the ants and nonant predators interacted such that their simultaneous presence did not reduce numbers as much as was expected from the main effects (Fig. 1; $F = 0.81$, $P = 0.004$). On 9 August, both nonant predators and ants strongly reduced aphid numbers (Fig. 1; ants: $F = 3.09$, $P < 0.001$; nonant predators: $F = 2.93$, $P = 0.005$). There was also a significant nonant predator × ant interaction (Fig. 1; $F = 2.96$, $P = 0.001$): having both nonant predators and ants present did not reduce aphid numbers below levels seen when either ants or nonant predators were present.

Discussion

Both ants and other nonant predators had negative effects on aphid numbers. *F. obscuripes* had a strong

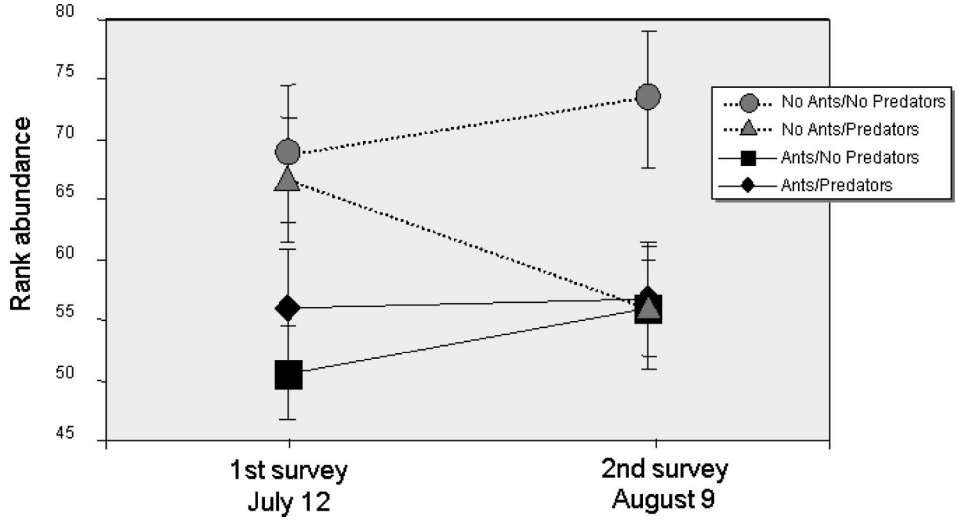

Fig. 1. Effect of the treatments on the rank of aphid numbers (±1 SE). There were 30 plants in each treatment. Ants had a strong negative effect on aphid numbers throughout the experiment. Nonant predators initially had a weak negative effect on aphids, but by the end of the experiment the effects of nonant predators and ants were of similar magnitudes. The presence of both nonant predators and ants did not reduce aphid densities below the effect of ants or nonant predators alone. Aphid distributions were strongly lognormal, so we portray the data by using ranks rather than with means. We used a randomization approach to analyze the data because the data were strongly non-normal (see Materials and Methods).

negative effect on the densities of *P. utensis* and *U. escalantii* (Fig. 1) that manifested itself by the first survey, and it was still evident almost 1 mo later. The effect of *F. obscuripes* on aphid numbers was likely due to predation, although our experimental design did not permit us to distinguish between direct predation and other negative effects. For example, the ants also may have had an effect on aphid reproductive rates: ants may cause aphids to move more and feed less or to even drop off plants (Stadler 1997). Nonant predators had a substantially smaller effect on aphids compared with ants at the beginning of the experiment, but they had nearly an identical effect as ants by the end of the experiment (Fig. 1). We note that although the nonant predator removal treatment was not effective enough to remove all nonant predators, it was sufficiently effective to produce a treatment effect on aphid numbers. However, our results demonstrate unequivocally that both ants and nonant predators reduce aphid numbers.

Previous research demonstrating an overall negative effect on aphid densities is limited. Although some studies have demonstrated a negative effect of ants on aphids (Sakata 1994, Stadler and Dixon 1998, Stadler and Dixon 1999, Yao et al. 2000, Fischer et al. 2001, Offenberg 2001, Mooney and Tillberg 2005), these negative effects are commonly assumed to be the costs of engaging in the mutualism, with a net overall benefit of ant-tending (e.g., Fischer et al. 2001). The best evidence that ants have an overall negative effect on aphids comes from field studies under natural conditions (Addicott 1979, Skinner and Whittaker 1981, Andersen 1991). Our results support previous work that ants can have a strong negative effect on aphid densities.

The second main finding of this study is that the ants seemed to simultaneously prey upon and reduce aphid predation. We detected a significant ant × nonant predator interaction. By the end of the experiment, it was clear that although individually both ants and other enemies had strong negative effects on aphids, the simultaneous presence of both was no worse for aphids than the presence of only one of these factors (Fig. 1). One possible explanation for such an interaction is that one or the other had such a strong negative effect alone that it was impossible to reduce aphid densities much lower when the two were both present. However, scrutiny of aphid numbers (Table 1) indicates this explanation is unlikely: almost one third of the plants with both ants and other enemies still had aphids on them. The most likely explanation for the significant interaction is that ants provided protection to aphids, either by preying upon other enemies of the aphids or because those other enemies actively avoided ants, even as the ants preyed upon aphids themselves. Whether this protection was simply an incidental by-product of ant presence or whether it was the result of specific ant protective behaviors is uncertain.

These results have several implications for understanding the selective pressures of ants on aphids. First, they indicate that if nonant enemies such as salticid spiders and coccinelid beetles are a natural part of the aphid's environment, then adding or subtracting ants may have little effect on aphid numbers. When ants encounter the aphids, the negative effect of ants on aphids is largely balanced by the protection the ants provide from other aphid enemies, so that one source of predation is simply replaced by another. We also can say that the substantial cost of ants we mea-

sured implies that the need to mitigate the antagonistic effects of ants could be equal to or more important than any initial beneficial advantages of ant association. Thus, there may be strong selection on aphids to offer high-quality honeydew to avoid predation, not just to receive protective services from the ants (Sakata 1995). Stadler and Dixon (2005) argue that aphids are such a poor resource for ants that ant predation was unlikely to be an important selective force on aphids. However, this study clearly demonstrates that ant predation has very strong effects for some aphid species. For these species, ant-tending may essentially offer a "double benefit," requiring adaptations to appease ants that are rewarded by reductions in both ant and nonant predation. For aphid species that are not tended (the majority) and that are intensely exploited by ants for food, evolutionary transitions to more derived mutualistic interactions may initially arise out of largely antagonistic precursors such as those described herein. Indeed, pollination mutualisms also are thought to have started within the context of a predatory relationship (Crepet et al. 1991), suggesting that predation may be an important starting point for a diverse set of mutualisms.

As with any field experiment, we must ask to whether the results are an artifact of the experimental design. Was there anything about the artificial conditions within the cages that somehow skewed our results? The lack of a difference between the unmanipulated control and the experimental control (ants and nonant predators both present) suggested that the use of cages and artificial colonies did not create effects on the aphids noticeably different than real-world pressures. The presence of membracids on the plants undoubtedly influenced our results. Work on the same aphid species at a different location in which other honeydew sources were absent might have generated different results. However, at least locally, the membracids are ubiquitous on the host plants of the aphids. Consequently, the membracids are simply a common feature of the biotic environment at the research site. However, there is now recognition that the interaction between two species is often contingent upon the community context (Billick and Case 1994), and this set of interactions is not different. The extent to which variation in the distribution of the membracids generates variability in the interaction between ants and aphids is an open, interesting question.

The final issue we address is our inability to distinguish between the two aphid species. We do not know whether ants and nonant predators had different effects on the two species. However, as it turned out, given the substantial decreases in total aphid species, the combined mortality factors affected both species negatively, or alternatively, one of the aphid species was present in such low numbers as to have nonappreciable effects on the experiment. Either way, the magnitude of the effect indicates that ants are clearly significant predators on one, and likely both, species. There has been no previous field study that teases apart the predator and beneficial effects of ants on aphids and the finding that ants can be significant predators while simultaneously providing protection is an important result, even if we were not able to distinguish between the two species.

Our results indicate that ants are an important selective force on the aphids. Why then do these aphids not successfully appease the ants and avoid predation? This is a central problem, and our results add to the puzzling nature of these interactions. Ant-tending can reduce growth rates (Stadler and Dixon 1999, Yao et al. 2000), and it can have other costly physiological effects on the aphids (Stadler and Dixon 1998). Ant-tending also is associated with high rates of honeydew production (Fischer et al. 2002), which may attract predators or facilitate fungal infections (Bristow 1991). If ant availability is limited (Bristow 1991), the costs of engaging in the mutualism may outweigh the benefits (Stadler et al. 2001). Alternatively, spatial variability in the benefit of the mutualism combined with gene flow may prevent the local buildup of adaptations promoting ant appeasement and mutualism (Thompson 1999). However, in keeping with the work of Stadler and Dixon (2005)), for care in invoking single explanations for the diversity of outcomes in ant–aphid interactions, substantially more empirical work will need to be done to directly address how various factors work together to determine the pathways by which some aphid–ant interactions become mutualistic, whereas others remain or revert to trophic interactions.

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