

Species Interactions in Arthropod Communities: Density
Dependence and Ant Interactions on Aphid Per Capita
Population Growth

Mitchell Lopez

Kailen Mooney

23 June 2010

The Rocky Mountain Biological Laboratory

Abstract

Ant and aphid interactions are often assumed to be mutualistic, with both participating parties receiving a benefit that outweighs the cost. Yet this interaction can range between mutualistic and antagonistic due to factors that alter this ratio of cost and benefit. Some factors that can affect the cost-benefit ratio are the abundance of predators, aphid population density, availability of alternative nutrients for the ants, and host plant quality. This study investigated the effects of ants, plant sex, and aphid density on aphid per capita population growth of *Aphis valerianae* feeding on the host plant *Valeriana edulis* and tended by several ant species (*Formica podzolica*, *Tapinoma sessile*, and *Lasius neoniger*). In addition to monitoring aphid population size, predator density and aphid emigration were observed to determine what mechanisms were responsible for the effects observed. It was found that per capita population growth was effected by population density due to a combination of intra-specific competition and predator recruitment. Contrary to other studies, we found that ants negatively affected per capita population growth and did not differ with a change in density. As well the effect of ants negatively effected aphid colony survival, but there was no effect of initial density. Ant tending did differ between plant sexes, in that there was less tending on male plants. This resulted in no effect of ants on aphid per capital population growth on male plants, regardless of density, which is unlike studies that have been done previously.

Introduction

Species interactions are a continuum of positive to negative effects and have a large impact on those individuals that are involved, as well the community that the individuals exist in. An interaction that increases fitness and exceeds the cost of the interaction for both parties is considered a mutualism (Cushman and Addicott 1989). These interspecific relations can be conditional upon the benefit that an individual will receive, which can vary depending on the physical and biological context (Cushman and Whitham 1989). Once the cost exceeds the benefit, the relationship becomes antagonistic such as a predation, parasitism, and herbivory.

Ants and aphid interactions often vary from mutualistic to antagonistic. Protection in exchange for food, or trophobiosis, is a behavior trait that is present in 41% of ant genera, and 40% of all aphid species are tended by ants (Ness et al. 2009). Aphids consume the phloem sap from the host plant, which is mostly sugar, and excrete it on demand for the ants. Ants will tend to aphids and harvest the sweet honeydew, which is a source of energy for the ant colony. Ants that are omnivorous, and that prey on other arthropods, will not attack their mutualist partner. The benefit of the ant to the aphid is protection from predators, reduction of competing herbivores, and cleaning up honeydew deposits that cause fungal outbreaks and otherwise interfere with aphid phloem sap consumption (Ness et al. 2009). Though this interaction can be beneficial for the aphid, provisioning ants with honeydew can become costly to the aphid.

Whether or not ant tending is beneficial for an aphid depends on the biotic and abiotic environment. It has been shown that aphid density can have an effect on whether the interaction will be positive or negative for the aphids (Cushman and Addicott 1992). The benefit of ant tending decreases at relatively high aphid densities and is most beneficial at low densities (Cushman and Addicott 1992). When predator abundance is low, then the cost of producing honeydew for ants remains the same but the benefit decrease and be unfavorable for the

aphids. This could result in fewer resources for the aphids which could be used for reproduction and growth (Ness et al.2009). As well, ants will ignore or prey upon aphids if carbohydrates are not a limiting factor for ants, due either to the availability of other resources and ant nutritional needs (Petry and Mooney 2009).

Plant quality can also alter the cost-benefit ratios in ant-aphid interactions. Mooney and Agrawal (2008) showed that host plant genotype variation can alter ant-aphid interactions from mutualistic to antagonistic, and speculated that such effects occurred due to variation in phloem sap quality. Plant quality can differ between plant sexes in dioecious plants (Cornelissen and Stiling 2005) and this has been shown to influence ant tending of aphids in the dioecious plant *Valeriana edulis*; ants preferred to tend aphids on female plants rather than male plants (Perry and Mooney 2009). These studies show that ant-aphid interactions are contextual on such factors as plant sex and genotype.

This study investigated how the direction and magnitude of the interaction between local ant species and *Aphis valerianae* is influenced by aphid density and plant sex on the host-plant *Valeriana edulis*. Specifically, we tested if aphid per capita population growth is affected by aphid density, the presence of ants, and how such effects vary based upon whether they occur on male or female plants. To investigate possible mechanisms that might govern aphid per capita population growth, we investigated how ant tending, predation, and aphid emigration differed based upon aphid density, ant presence/absence and plant sex. Overall this study will increase the understanding of the conditions that effect species interactions and the cost-benefit of the interaction.

Methods

Study Species

The perennial dioecious dicot *V. edulis* var. *edulis* is found throughout much of western North America where it blooms in early summer. The aphid *Aphis valerianae* (Cowen) is a specialist herbivore of *V. edulis* and the ants commonly seen tending *A. valerianae* at our field site in the Colorado Rocky Mountains are *Tapinoma sessile* (Say), *Formica podzolica* (Francoeur) and *Lasius neoniger* (Emery). Ants have been observed to tend aphids that live on female plants more than male plants (Perry and Mooney 2009).

Experimental Design

The location of the study was in Gothic, CO (2895.6 m). We located 30 females and 20 males of *V. edulis* from an open meadow that had aphids and that were tended by ants. Within each sex two plants were either in treatments of ant access (15 control plants for females, 10 for males) or ant exclusion (15 plants for females, 10 for males). The female plants were then randomly assigned one of three aphid population densities (low, medium, and high), and the male plants were divided into two groups (low and high). Each plant was randomly assigned to an aphid density and ant access treatment. Aphid densities of *A. valerinea* were established by removal or transplantation to a terminal inflorescence at approximately 1 m in height to create initial densities of approximately 20, 170, and >250 (range 267-1990) aphids for the low, medium, and high densities, respectively. The different levels of densities were determined from a survey of the natural aphid abundance for that time, of that year.

Ants were excluded by use of a sticky paste (Tangle Foot, Contech Enterprises, Inc, Victoria, BC) on a piece of tape on the bottom section of the stalk. The paste was placed on the tape to avoid any possible effects on plant quality. The aphids were allowed to establish for 2 to 5 days, over which time some aphid populations were thinned out as to achieve the appropriate density before the ants were excluded.

Data Collection

We observed the number of all arthropods on female plants for two days/week from the 16th of July, 2010 until the 6th of August and on the male plants from the 21st of July until the 6th of August. As well five additional surveys were taken of the abundance of ants and predators for each female plant at the moment of arrival at the plant. This was conducted to determine the relative number of ants and predators in relation to aphid density. Because the female and male plants were studied over different time intervals, they were treated as a separate experiment in our analyses. The number of tending ants and the density of natural enemies (parasitoid wasps and predators such as ladybird beetles [Coccinellidae], and syrphid flies) were censused two days per week for three weeks for the female plants and were not determined for the male plants. All counts of aphids, natural enemies and ants were taken at the moment of arrival to a plant subject.

Data Analysis

We calculated the per capita daily growth of aphid populations (hereafter population growth) as $\frac{[\log(N_{t-x}) - \log(N_{t-0})]}{(t-x) - (t-0)}$, where N_{t-0} is the initial density, N_{t-x} is the density at time x , $t-x$ is the date at time x , and $t-0$ is the initial date. For each experiment (plant sex), a mixed model ANOVA was used with the MIXED procedure in SAS 9.2 (SAS Institute, 2008) to analyze the interactions between ant treatment, initial density, time, and all 2-way interactions (fixed effects) on population growth, with subject included as a random effect. We removed all terms that had $P > 0.15$ with the exception that where terms were significant in a 2-way interaction terms for the main effects were kept regardless of their level of significance. Plant sex effects could not be directly compared because they were conducted at different time intervals so they will be compared individually. Survivorship of aphid colonies at the conclusion of the experiment was analyzed as a function of ant treatment, initial density and their interaction with logistic regression using the LOGISTIC procedure of SAS 9.2 (SAS Institute, 2008). As stated above, all factors that did not have $P > 0.15$ were removed from the model.

Because predator observations were low for any single observations, predator density was analyzed as the total number of predators observed across all censuses. Effects of ants and aphid density were measured on predator density with the GLM procedure in SAS 9.2 (SAS Institute, 2008). These data were log +1 transformed to meet assumptions of normality distributions. A model was created comparing initial density, ant treatment, and as previously stated, all factors that did not have $P > 0.15$ were removed from the model.

Results

For female plants, aphid population growth was significantly influenced by ant treatment (Figure 1A, $F_{1,80} = 4.08$, $P = 0.0468$), initial density (Figure 2A, $F_{1,80} = 6.48$, $P = 0.0128$) and the interactions between date and initial density ($F_{3,80} = 5.32$, $P = .0021$). All other factors were not significant ($P > 0.15$). Population growth rates were higher in ants exclusion than control (Figure 1A). Population growth rates were initially positive at low initial densities but negative for mid and high densities (Figure 2A). Yet as the experiment progressed, population growth rates also fell for low density populations.

For male plants, aphid population growth was significantly influenced by date alone ($F_{2,35} = 4.90$, $P = 0.0133$). Although the effect of ants was not significant, but showed a similar trend of being lower when ants are present (Figure 1B). Similarly, initial density was not significant, but showed a similar trend as the female plants in that there was a positive growth for the low densities and a negative growth for the high densities (Figure 2B).

For female plants, aphid colony survival was only influenced by ant exclusion (Figure 4, $\chi^2_1 = 3.85$, $P = 0.497$). There was no significance for ant treatment on male plants Figure 4, $\chi^2_1 = 1.60$, $P = 0.21$.

Predator abundance on female plants was compared between ant treatment, initial density, and the interaction between them. There was no significant effect of ant exclusion (Figure 5, $F_{1,27}=0.76$, $P=0.39$) or the aphids density ($F_{1,27}=1.51$, $P=0.23$).

Discussion

This study found that ants have a negative effect on the per capita population growth in aphids though there is no density dependence of the effects of ants. There is density dependence for population growth, in that populations at lower densities have a positive growth rate and the mid and high density have negative growth rates. Ants did not have a significant effect on the abundance of predators, though there was an effect of ants on aphid colony survival. Ants negatively impacted the survival of the aphid colony.

The negative impact of ants on aphid population growth is opposite of our hypothesis that aphids that ants would increase aphid per capita population growth by protecting the aphids from predators. This is congruent with other studies that found that mutualistic interactions only occur in years that had high predation (Cushman and Whitham 1989). They accounted for this when the amount of salticid spiders were in high abundance. In this system there was no difference between the amount of predators when ants were present or absent. Thus provisioning ants with honeydew will exceed the benefit of protection due to ants not protecting the colonies. This might not be true for every year or even location. Further studies can conclude the sufficient predator abundance levels that would induce a mutualistic interaction between ants and aphids.

Aphid population growth was density dependent in that higher densities of aphids have a smaller per capita daily population growth rate. This effect can be accounted for by intra-specific competition at higher densities. This is apparent from the first time point, where low densities do better than mid densities which do better than high densities. This changes over time, which is

due to predation, though not by ants. It was never observed that ants were preying on aphids nor was it observed that aphids were walking of the plant. The decline in populations was not due to emigration or predation by ants but rather predation by other arthropods.

Ants negatively effected the survival of the aphid colony. For aphid colonies that had ants there was a lower survival rate compared to when ants were absent (Figure 5). Aphid colony survival was density independent and was only observed on male plants. Why there was an effect of ants and not density is still undetermined, though this is not due to a difference in the abundance of predators. Ants are not protecting aphids from predation and are also obtaining honeydew which is lowering the fitness of the aphid population, and having a significant effect on the population.

There was no effect of density on the interaction between ants and aphids. Previous studies have found that as the population of aphids increases the net affect of ants decreases (Brenton and Addicott 1992). Ants will only recruit a discrete amount of workers to a specific resource, and if the aphid colony becomes too large then the ratio of ants to aphids decreases until the effect of ants on aphids becomes insignificant. The effect of ants was the same through out the treatments, though we would expect to see a positive growth of aphids at higher densities due to the negative impact that ant have on these specific aphids. At the higher densities the effect of ants decreases, but then as the population increases so does the intraspecific competition. Because of this we don't see a difference in the effect of ants between densities.

Though there was no significant effect of density or ants on the male plants, we do see similar trends between male and female plants. The lower densities do much better than higher densities and the effect of ants was negative for aphid growth. The mean densities of aphids on male plants was much lower then female plants, it could be that there is less intraspecific

competition between aphids on male plants. A study done in the previous year found that there is far less tending on male plants than female plants (Perry and Mooney 2009). Thus the overall effect of ants is similar for males and females, it is not significant for male plants because of the lack of tending by ants. This could also account for the difference in survivorship of aphid colonies on male plants, in that there was no effect of ants or density.

The species interaction between ants and aphids has been found to be contextual for this system as well as others depending on the biotic and abiotic factor that the individuals exist in (Cushman and Whitham 1989, Brenton and Addicott 1992). To understand the context of an interaction one must consider the cost and benefit of the interaction and how this affects the overall fitness of the individuals involved. Contrary to our original hypothesis ants negatively affected the growth of aphid colonies for females, but not for males. Density had no effect on the interaction between aphids and ants for both males and females, though the effects of density on aphid growth were significantly different for females. These factors, as well as the abundance of predators, can have a significant effect on the interactions between ants and aphids and even determine the direction and magnitude of the interaction. Thus the behavior of the individuals and the environment that they exist in can determine the context of their interaction.

Literature Cited

Breton, L. and Addicott, J.F. 1992. Density-dependent Mutualism in an Aphid-Ant Interaction. *Ecology*. 73: 2175-2180

- Bronstein, J.L. 2001. The Exploitation of Mutualisms. *Letters in Ecology*. Vol. 4, 3:277-287
- Cornelissen, T. Stilling, P. 2005. Sex Biased Herbivory: a Meta-Data Analysis of Effects of Gender on Plant-Herbivore Interactions. *Oikos*. 111:488-500
- Cushman, J.H. and Addicott, J.F. 1989. Intra- and Interspecific Competition For Mutualists: Ants as a Limited and Limiting Resource for Aphids. *Oecologia*. 79:315-321
- Cushman, J.H. and Whitham, T.G. Conditional Mutualism in a Membracid-Ant Association: Temporal, Age-Specific, and Density Dependent Effects. *Ecology*, Vol. 70, No. 4 1040-1047
- Mooney, K.A. and Agrawal, A.A. 2007. Phenotypic Plasticity in Plant-Herbivore Interactions. Book chapter in *Specialization, Speciation, and Radiation*, Kelly Tillmon Ed. Univ. California Press. Pp. 43-59.
- Mooney K.A. and Agrawal, A.A. 2008. Plant Genotype Shapes Ant-Aphid Interactions: Implications for Community Structure and Indirect Plant Defense. *American Naturalist*. E195-E205 (E-only)
- Ness et al. 2009. Ants as Mutualists. *Ant Ecology*. 97-114
- Perry K.I. and Mooney, K.A. 2009. Variation in Host Plant Sex Mediates Ant-Aphid Interactions. REU paper
- Petry, W.K. Perry, K.I. Mooney, K.A. A Balanced Diet: Ant Colony Nutritional Status Affects Interactions with Plants, Aphids, and Aphid Population Dynamics in the Field.
- SAS Institute. 2008. Sas version 9.2. SAS Institute, Cary, N.C.
- Styrsky, J.D. and Eubanks, M.D. 2007. Ecological Consequences of Interactions Between

Ants and Honeydew-Producing Insects. The Royal Society. 274: 151-164

FIGURES

Figure 1A: Average daily growth with ants 0.04666 (0.01688 1SE). Average daily growth without ants 0.01571 (0.01518 1SE). Log-transformed per capita daily population growth rates for aphids on female plants with and without ants on four sampling dates.

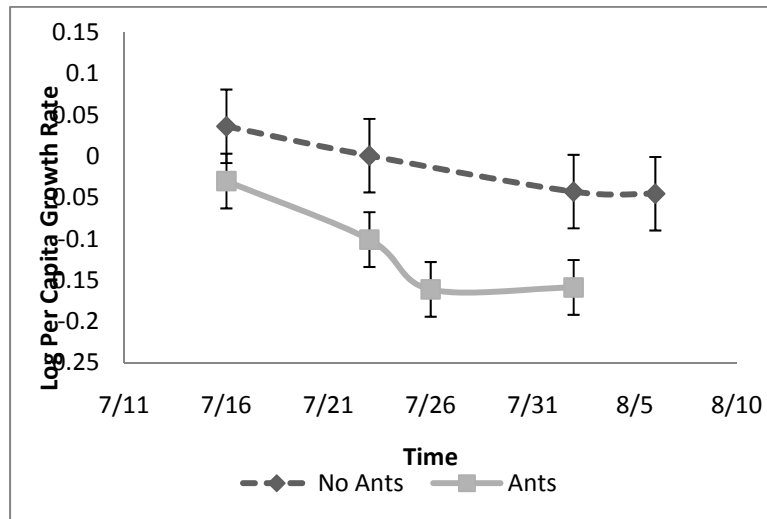


Figure 1B: Average daily growth with ants 0.03329 (0.04034 1SE). Average day growth without ants -0.03969 (-0.06726 1 SE). Log-transformed per capita daily population growth rates for aphids on male plants with and without ants on three sampling dates.

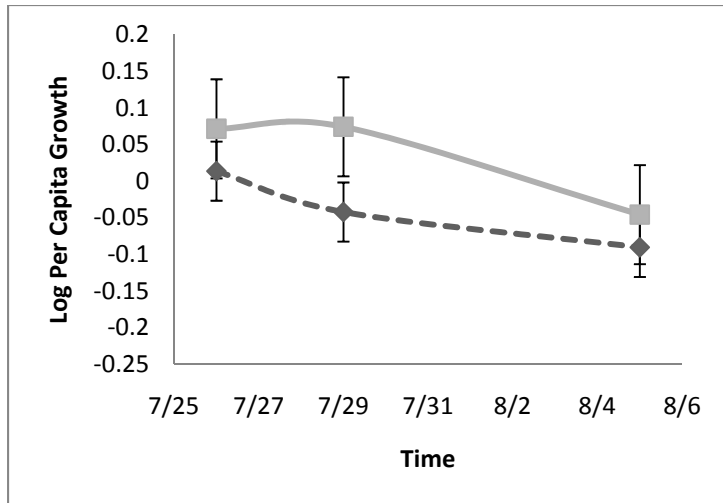


Figure 2A: Average growth rate for Low density .04036 (0.0328 SE), Mid density -0.14127 (.0552 SE), and High density -0.1064 (0.0387 SE). Log transformed per capita daily growth rate for aphids on female plants over four sampling dates for three initial aphid densities (low= 20, medium=170, high= >250).

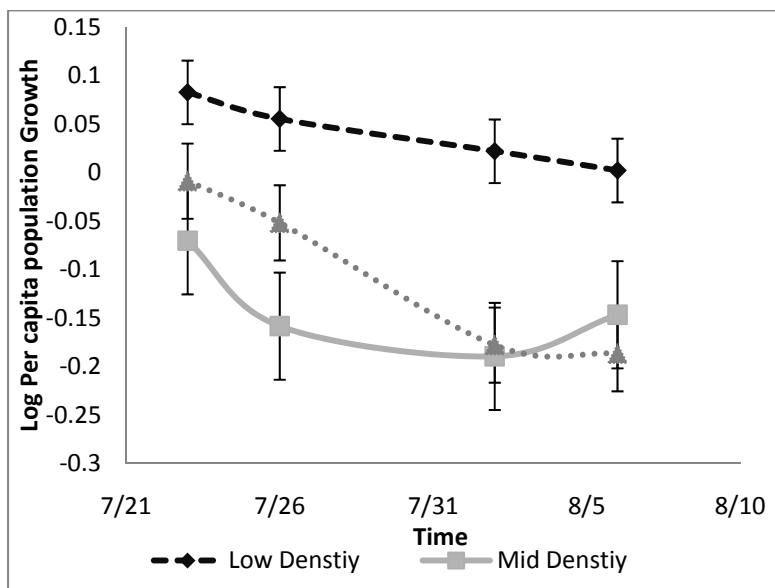


Figure 2B: Average growth rates for Low density 0.037263 (0.0527 SE), and High density -0.05269 (0.0350 SE). Log transformed per capita daily growth rate for aphids on male plants over three sampling dates for two initial aphid densities (low= 20, high= >250).

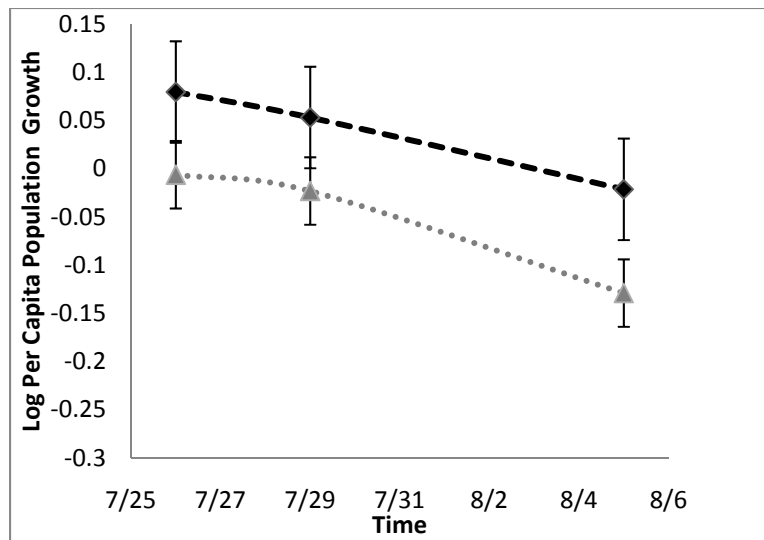


Figure 4: Effects of ants on colony survival for male and female plants. Ants significantly reduced colony survival on female but not males.

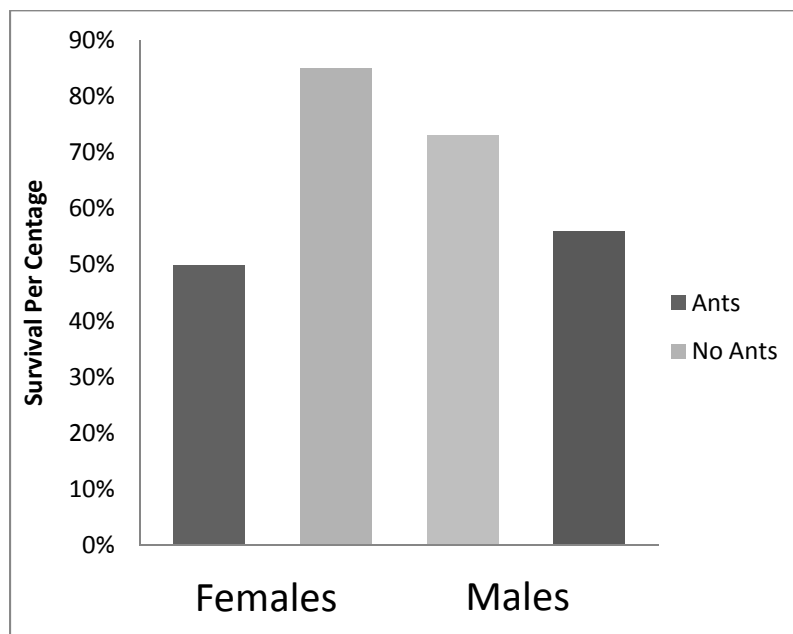


Figure 5: Effects of ants on mean ($\pm$ 1SE) predator abundance on female plants. Ant exclusion did not significantly alter predator abundance.

