

Benefits of Ant Attendance for Aphid Colonies of Varying Density

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Abstract

Benefits between species engaged in mutualistic interactions are often dependent on ecological context. For instance, in mutualisms in which aphids exchange food for ant protection from predators, the degree of benefit that aphids receive from ants depends on the presence of other arthropod predators. In this study I examined the influence of aphid density on the benefits that aphids (*Artemisaphus artemisicola*) receive from ants (*Formica obscuripes*). Treatments of ant presence and starting aphid density (N=5, 10, or 15) were factorially crossed on individual sagebrush stems in a field experiment. A significant increase in aphid per capita growth rate was found in the intermediate density treatment with ants present. Mirroring this relationship, the abundance of predators was highest when ants were excluded and aphid populations started at an intermediate density. No ant exclusion treatments managed to establish successful aphid colonies. These results reveal a strong benefit of ant attendance for aphids that is dependent on aphid density, likely reflecting changes in the balance of costs and benefits of the mutualism across aphid densities.

Introduction

Mutualistic interactions between organisms are interactions in which both species gain a net benefit (Bronstein 1994). These interactions are important to understand because they can have wide-reaching effects on the communities of which they are a part (Grinath et al. 2012). Though they are generally positive in outcome, mutualisms can be hard to understand because they are conditionally dependent on the balance of benefits and costs that each partner species incurs (Bronstein 1994).

A mutualism in which the benefits are well-studied is that between ants and aphids. Many ant species provide aphids with protection from predators while the aphids provide ants with honeydew as a sugar-rich food source (Breton & Addicott 1992a, Yao et al. 2000, Stadler et al. 2001). Ant attendance has also been found to increase lifetime reproductive success of aphids and allow them to generate larger populations (Stadler et al. 2001). These benefits, together, with dependence on ecological contexts, contribute to variability in the outcome of the interaction (Stadler et al. 2001). Some ecological contexts found to be important in this interaction are ant tending intensity (Yoo & Holway 2011), ant resource availability (Offenberg 2001), distance of

the host plant from ant mounds (Wimp & Whitman 2001, Domisch et al. 2011), and host plant quality (Breton & Addicott 1992b, Wimp & Whitman 2001, Reithel & Campbell 2008).

Several studies have also demonstrated that aphid density may be important for determining the magnitude of benefits in these mutualisms (Breton & Addicott 1992a, Harmon & Andow 2007, Reithel & Campbell 2008). These studies suggest that the benefits of ant attendance decrease with increasing aphid density; however, they either completely excluded aphid predators or manipulated their presence in such a way that the study systems were unrepresentative of the natural environment (Breton & Addicott 1992a, Harmon & Andow 2007). There has been little study considering the effects of aphid density on the benefits for aphids in a natural environment exposed to all potential predators.

Considering that protection from predators is one of the primary benefits that ants provide in this mutualism, evaluating the benefits of ant attendance on aphid population growth rate across varying aphid densities in a natural setting could increase our understanding of the importance of density as an ecological context. In this study I evaluated the benefits of ants for aphids across aphid densities. Using a field experiment in a natural setting, I assessed the effects of ant presence and aphid density on aphid growth rate, ant tending, and arthropod predator abundance.

Methods

This study took place in a sagebrush meadow in the Almont Wildlife Management Area, CO in the summer of 2013 (research meadow size = approx. 2 ha, elevation = 2769 m, latitude = 38.719, longitude = -106.816). Treatments of ant presence and starting aphid density (N=5, 10, or 15) were factorially crossed on individual sagebrush stems. Each set of treatments was arranged on one sagebrush plant to control for plant quality. On each plant 6 relatively equally

sized branches were randomly assigned one of the 6 treatments after all aphids, ants, and predators were removed. Aphids were removed and added to branches using a small paintbrush. These aphid transfers occurred at the same time that many aphid aggregations were establishing on sagebrush, thereby mimicking newly established colonies. Ants were excluded from ant-free treatments by applying Tanglefoot (Tanglefoot Company, Grand Rapids, MI, USA) to a ring of tape at the base of branches and trimming surrounding vegetation that could be used by ants to access the branches. Rings of tape were applied to non-exclusion treatments as well. These treatments were replicated on 15 different sagebrush plants, each within 3 meters of an ant nest to ensure ant visitation.

Counts of aphids, ants, and predators on each sagebrush stem were performed 10 days after the manipulations had been implemented and then once more 7 days later. Aphid per capita growth rate was calculated as the number of aphids in each count divided by the starting density of aphids. Non-parametric analyses of means, using a bootstrap procedure to find confidence intervals for the differences in means, were performed on the data from the first survey to analyze effects of aphid density and ant presence on predator abundance, aphid per capita growth rate, and ant tending rate. In each analysis, the difference in means between treatment groups was compared to a null distribution of the difference in means in randomly re-sampled datasets ($N = 10,000$). Significant differences between treatment groups were identified when the actual difference in means was outside the 95% confidence interval of the null distribution (Fig. 1). Too few aphids survived to perform bootstrap analyses for data from the second survey.

Results

Ants were beneficial for aphids in a density dependent manner. Aphids had significantly higher per capita growth rates when they started at the intermediate density and when ants were

present ($p < 0.05$, Fig. 2). All other treatment groups had lower aphid growth rates. One treatment group had an intermediate response, when starting aphid density was small and ants were present. The treatment with high starting aphid density and ants did not have aphid growth rates different than any of the ant exclusion treatments, of which almost none had surviving aphids at the time of the first survey. By the second survey, no aphids survived when ants were absent. No difference in ant tending per aphid was found across treatments on which ants had access (Fig. 3).

Because ant benefits often vary depending on other arthropod predators (Wimp & Whitman 2001), I tracked predator abundances across the experiment. However, more predators (lady beetles, hunting spiders, and hemipteran bugs) occurred on plants without ants and predator abundance was greatest when aphids started at intermediate densities and ants were absent ($p < 0.05$). Mirroring the trends in aphid growth rates, this was true for comparisons with all treatments except when initial aphid density was small and ants were excluded, which was not significantly different from any other treatment group (Fig. 4).

Discussion

In this system, ants provide aphids with significant benefits that are density dependent. My results suggest that the aphid, *Artemisaphus artemisicola*, requires ant tending to successfully initiate the formation of a colony. No aphid populations in ant exclusion treatments managed to increase from their initial size or survive to the time of the second survey. This is likely due to consumption by predators as more predators were found on ant exclusion treatments. My findings also suggest that there is an ideal density for colony initiation in these aphids at around 10 individuals. Larger aphid populations may be more easily detected by predators and could explain why the largest starting aphid populations had the lowest growth

rates. At this population size, predators could have been more efficient at finding aphids than ants. Alternatively, ants could have shown more predatory behavior towards aphids at higher densities, as in similar systems (Offenberg 2001). Aphid populations at the smallest starting density also had low growth rates, and may have taken longer for ants to find, allowing predators more time to forage on these branches. It seems clear that ants provide significant benefits for aphids by deterring predators and allowing successful aphid colonization of new plant stems.

The trends in arthropod predator abundances mirror the aphid growth rates and suggest that predators are hunting on stems that have the greatest potential aphid growth rates. This lends support to the finding that the intermediate starting density is the most ideal for aphid population growth as predators should be inclined to attack larger food sources more frequently. It also suggests that the intermediate density may have been the most successful on ant exclusion treatments until predators arrived, though more frequent surveys would have been required for this conclusion.

Though the benefits of ants for aphids have been well studied under semi-natural conditions (Breton & Addicot 1992a, Harmon & Andow 2007), I show here that ants provide density dependent benefits for aphids in a natural setting. My findings are consistent with previous studies that identify protection from predators as a substantial benefit for aphids (Stadler et al. 2001). They are also consistent with findings that the benefits of ant tending decrease as aphid density increases (Breton & Addicot 1992a), though that study excluded predators. My study confirms those findings in a more natural setting though my results were less linear and I observed no decrease in ant tending per aphid across density treatments. There seem to be strong indirect costs for aphids, which occur in the absence of ants but are still attributable to the relationship with ants. These aphids were unable to survive without ant

protection in this system. Other studies have found similar indirect costs in systems of ant-aphid interactions (Stadler et al. 2001).

Mutualisms produce a net positive outcome for both participating species based on a balance of costs and benefits. Future studies could further our understanding of density-dependence by analyzing the costs as well as the benefits. Understanding the contexts that affect the costs and benefits of mutualisms such as that between ants and aphids is important for breaking down what factors are most relevant in these relationships. Identifying which of these contexts have the greatest effects on the interactions between organisms can only add to our knowledge regarding the often tight balance between the costs and benefits that drive mutualisms. Mutualisms often have significant effects on the ecological communities that they inhabit, thus, knowledge of the balance of mutualisms across ecological contexts is important for understanding the role of mutualisms in their communities.

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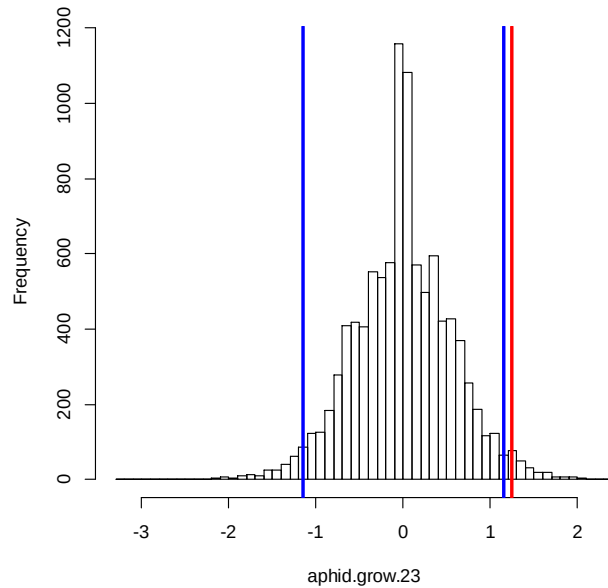


Figure 1: An example of a bootstrap procedure comparing the means between experimental treatment groups. Blue lines indicate the 95% confidence interval for bootstrapped data and the red line indicates the actual difference in means between treatment groups. Treatment groups are significantly different ($\alpha=0.05$) if the red line is outside of the blue lines.

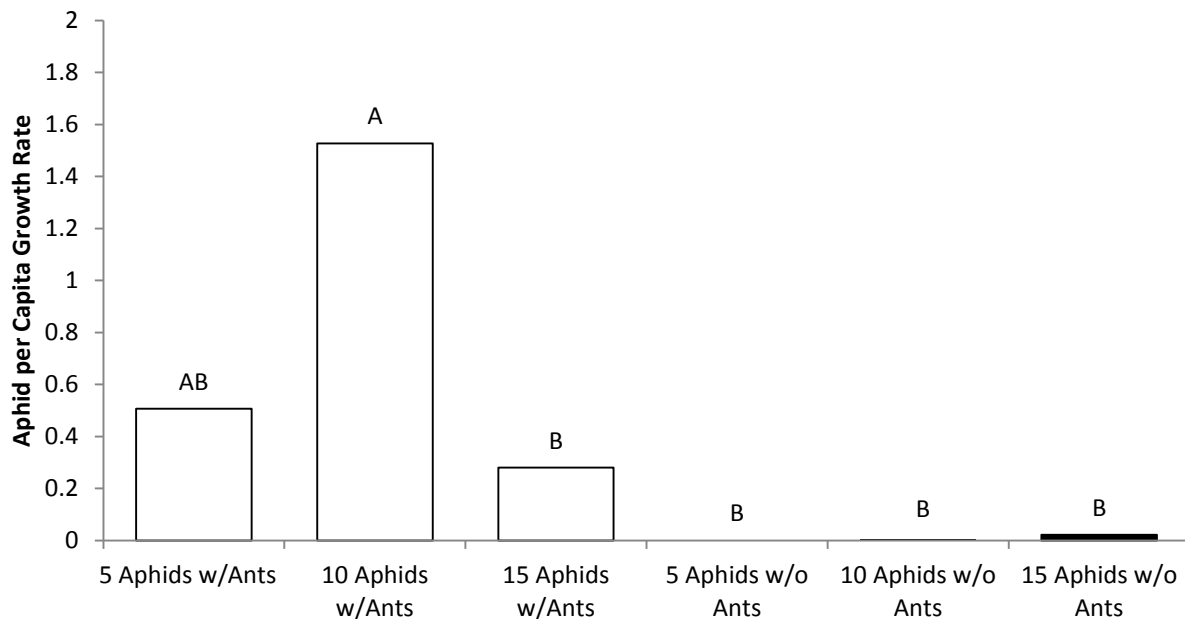


Figure 2: Mean aphid per capita growth rate, calculated by dividing the number of aphids present at the time of the first survey by the starting density, plotted by treatment. Numbers in treatments refer to starting density. Black bars represent treatments which excluded ants while white bars represent treatments which allowed ants. Letters above bars represent significance where bars with different letters are significantly different and bars with the same letters are not significantly different.

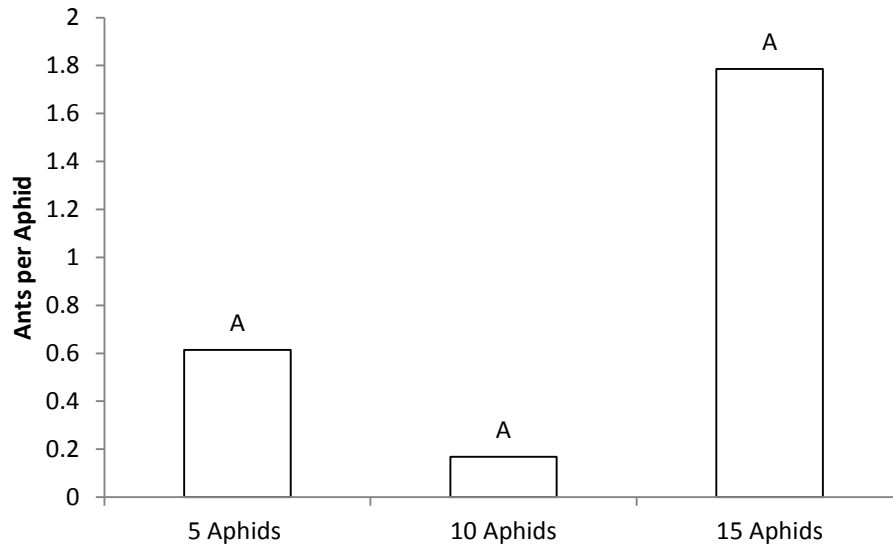


Figure 3: Mean ants per aphid found on each treatment allowing ants at the time of the first survey. Numbers in treatments refer to starting density. Letters above bars represent significance where bars with different letters are significantly different and bars with the same letters are not significantly different.

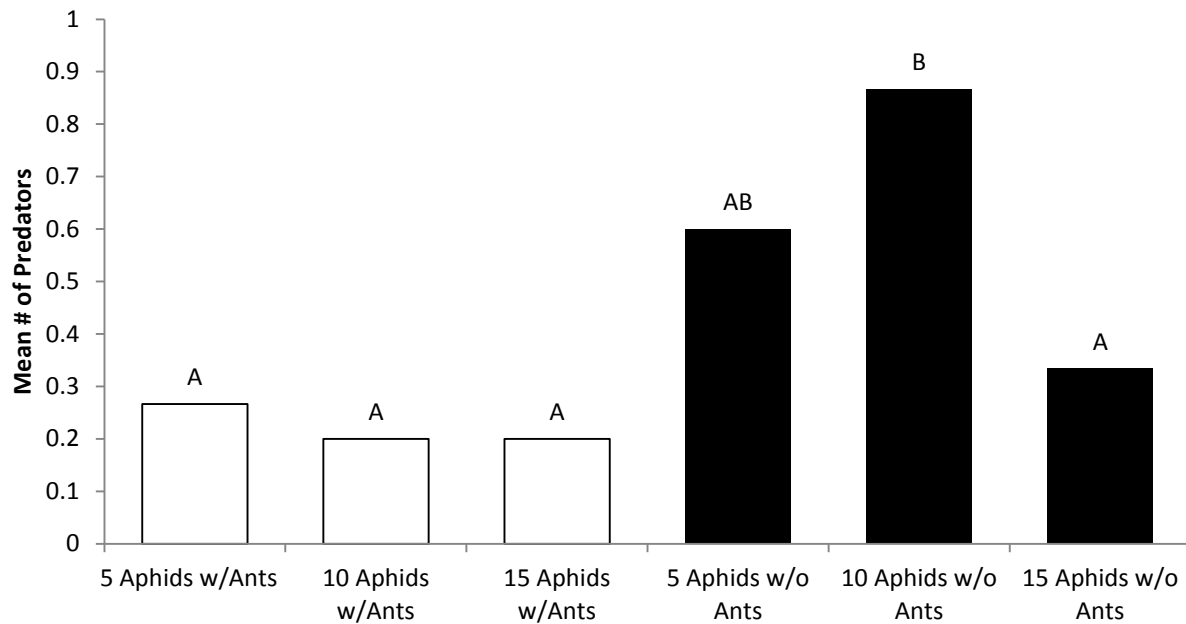


Figure 4: Mean number of active predators found on each treatment at the time of the first survey. Numbers in treatments refer to starting density. Black bars represent treatments which excluded ants while white bars represent treatments which allowed ants. Letters above bars represent significance where bars with different letters are significantly different and bars with the same letters are not significantly different.

