

Causes of Predation Intensity in an Ant/Aphid Mutualist System

Student: Daniel V. DeSantiago

Mentor: Josh Grinath (Bear)

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Introduction

Trophic cascades are common in many ecosystems, but we still do not understand what causes strong cascades, especially in terrestrial environments. A trophic cascade is defined as the propagation of impacts by consumers on their prey downward through food webs (Estes et al. 2011). These impacts are dependent on bottom up effects at lower trophic levels. Understanding the mechanisms that drive cascading effects is important because strong cascades can cause dramatic effects on entire systems. For example, sea otters in the Aleutian archipelago enhance kelp production by limiting herbivorous sea urchins (Estes et al. 2011). The cascade from sea otters to kelp has myriad effects on other species and ecological processes (Estes et al. 2011); for instance, enhanced kelp production in the presence of otters increases particulate organic carbon production in coastal ocean waters, which increases the growth rate of filter feeding mussels (Estes et al. 2011). The sea otters presence can drastically change species evenness and abundance, which can alter the feeding regimes of other species such as bald eagles and gulls (Estes et al. 2011). The most compelling examples of cascades come from aquatic systems; several authors have proposed that cascades are more prevalent and stronger in water than on land (Shurin et al. 2002). The differences between cascades in aquatic and terrestrial ecosystems may be due to a number of factors, including limited availability of

nutrients in terrestrial systems (Hall et al. 2007). As anthropogenic pollutants enrich ecosystems with nitrogen, phosphorus and other nutrients, there is growing interest in understanding how these nutrient additions affect cascade dynamics, specifically predation strength. The food quality hypothesis states that an increase in food quality at any trophic level will increase the strength of cascades (Hall et al. 2007). This mechanism for determining cascade strength has yet to be shown in the field.

Predation on herbivores is an important link in trophic cascades; and top predators may be an important, overlooked determinant of plant diversity and productivity in terrestrial systems (Schmitz 2003). The strength of predation depends on several factors, including the nutritional value of prey, whether the predator is a specialist or generalist, and the strategic behaviors that predators employ to access food. For example, a study conducted on insect herbivory on willows found that the plant's compensatory regrowth response to herbivory had positive effects on the abundance and performance of herbivorous insects via increasing food quality and/or quantity (Utsumi et al. 2009). Schmitz' (2003) studies on top predator control suggest the effects of antipredator behavior of herbivores, which is typically assumed to be short term and to attenuate on the time scale of ecosystem dynamics, may indeed have cumulative longer-term impacts on community structure. We need studies that evaluate the different factors influencing the strength of predation in order to understand how trophic cascades are propagated.

Many studies of predator effects on herbivores use functional classes of predators, separating them into broad categories of specialist and generalist species (ex. Snyder & Ives 2003); however, important differences may exist among predator species within

these classes. In Almont, Colorado, there are two common generalist arthropod predators of an ant/aphid mutualism system: the seven-spotted lady beetle (*Coccinella septempunctata*) and the brown crab spider (Thomisidae). These two predators commonly prey on the same aphid (*Artemisaphis artemisicola*) on sagebrush (*Artemisia tridentata*), but with different predatory mechanisms. This aphid species is protected by ants (*Formica obscuripes*) that feed on aphid honeydew, and would-be predators must avoid ant attacks to access their food. Through our observation, the ladybeetle strictly ignores the ants and retreats off the plant if being attacked, whereas the crab spider avoids ants by being more cryptic and faster. The 7-spotted lady-beetle is an exotic species that was brought to the U.S. as biological control for agricultural systems (Finlayson et al. 2009). This beetle has taken over vast expansions of territory of their native counter parts in many states, which may be due to the non-native lady-beetle species outcompeting native species for food (Finlayson et al. 2009). A number of studies on ladybeetles have shown that the 7-spotted ladybeetle and other exotic species are more efficient predators compared to native species (Gardiner et al. 2009). The crab spider is a native intraguild predator (IGP) that will feed on aphids and the ants that protect the aphids. The spider's cryptic color and agility aids in its efficiency as a predator (Huseynov 2007). In a study conducted on predation by crab spiders (*Thomisus onustus*), over half of the large prey exceeded the length of their captors more than twice (Huseynov 2007). These crab spiders were found to have the highest feeding rate reported for any cursorial (do not use silk for prey capture) spider and ants are their most abundant Hymenopteran prey (42.8%) (Huseynov 2007). To most cursorial spiders, worker ants possess effective defensive equipment (strong mandibles, formic acid, hard cuticle), are not palatable, and

are avoided, but the high percentage of ants in crab spider diets indicates that these spiders are competent ant predators (Huseynov 2007) and that they may be well-adapted for targeting on ant-protected prey.

In this study, I investigated several factors that may influence the strength of predation in a system composed of predatory ladybeetles and crab spiders, their aphid prey and the honeydew-tending ants that protect the aphids. I had two primary questions: 1. How does food quality and quantity affect the strength of predation on ant-tended aphids? 2. How does the identity of two common generalist predators affect the strength of predation on aphids? I hypothesized that: 1. Greater food quality/quantity will increase predation strength. 2. Crab spiders will reduce ant-tended aphid abundance more than seven-spotted lady beetles because spiders avoid ant harassment.

Methods

The study was conducted in a sagebrush scrub community in Almont, Colorado. I used a nested factorial design to test for the affect of food quality/quantity and predator identity on predation intensity. A plant level treatment was nested within plot level treatments. The plot level independent factors tested for the effects of food quality and quantity on the strength of predation. The plant level treatment tested how predation strength depends on predator identity. At the plot level, I crossed a high and low aphid abundance treatment (initial aggregation sizes were either 10 or 30 individuals) with a nutrient addition treatment in the form of a slow release ammonium nitrate fertilizer applied in two applications of 0.5g/m². I expected the nitrogen addition to result in higher quality plant food for aphids, which would increase the nutritional quality of aphids for

predators. Each five meter diameter plot consists of an ant mound surrounded by natural vegetation. I replicated each plot-level treatment combination nine times for a total of 36 plots. Nested within these plots, I randomly chose three great basin sage plants (*Artemisia tridentata*), to which I applied the plant level treatment. I manipulated aphid aggregations on sage stems to create three kinds of communities: 1. the control, consisting of only ants and an aphid population, 2. 7-spotted ladybeetles, ants and aphids, 3. brown crab spiders, ants and aphids. A total of 108 experimental sage plants were used for this experiment. Each plant had a mesh bag placed over it that still allowed air and moisture flow and access for ants to tend aphids, but it limited predator access. The experiment lasted three weeks. At the beginning of each week, ladybeetles and spiders were collected by sweep netting and one predator was added to predator addition plants. To measure the response to these treatments, I surveyed the abundances of aphids, ants, ladybeetles and crab spiders still present on the plants at the end of the third week. I used a nested ANOVA to test for the interactive effects of food quality, quantity, and predation (Hypothesis 1), with the predator treatment and ant mound identity nested as factors within the crossed honeydew-producer abundance and nutrient addition factors. I used a one-way ANOVA to specifically test for the effects of predator identity on aphid and ant abundances (Hypothesis 2). Welch's 2-sample t-tests were used to compare treatment combinations within the ANOVAs; all statistical analyses were performed in R 2.12.1 (R Development Core Team 2011).

Results

Food quality (nitrogen to host plants) and quantity (honeydew-producer initial abundances) did not interact with predation on aphids (Nested ANOVA: $F=0.965$,

P=0.471; Table 1(A), Figure 1). However, food quality and quantity significantly interacted with each other ($F=5.291$, $P=0.025$; Table 1(A), Figure 1) and with ant nest identity to determine aphid numbers ($F=1.674$, $P=0.040$; Table 1, Figure 1). The highest abundances of aphids were found on plants with low nutrients and when aphid aggregations were initially small. Food quality and quantity also interacted to determine the abundances of tending ants. Tending ant abundances were highest when aphid aggregations were large, in the low honeydew and low nitrogen group (Nested ANOVA: $F=3.816$, $P<0.001$; Table 1(B), Figure 2), but this pattern depended on ant mound identity (provide the nested result for ant mound identity effect on ants).

The two predator species differed in their ability to reduce aphid and tending ant abundances. Significantly fewer aphids were surveyed when ladybeetles were present (provide t-test result), whereas spiders did not significantly reduce aphid numbers compared to plants without predators (t-test result; Table 3, Figure 3). However, crab spiders did moderately reduce aphid abundances, indicated by there being no significant difference between the effect of spiders and ladybeetles on aphids (t-test result). There were no effects on tending ant abundances on plants (Table 3, Figure 4), though one dead ant was observed being carried by a spider. A total of eight dead ladybeetles were found in the surveys, where-as no dead crab spiders were observed.

Discussion

Effects of Food Quality and Quantity

The results show that my first hypothesis, greater food quality and quantity will increase predation strength, was rejected. Nitrogen additions and larger initial aphid aggregation sizes did not interact with the predator manipulation, though these bottom-up factors did have effects on aphid and tending ant abundances, which in turn will affect predation. Interestingly, the results show that lower food quality and quantity resulted in the highest aphid numbers later in the summer. Perhaps the lower food quality and quantity made aphids less desirable to predators, compared to other available groups of more nutritious and abundant aphids, which would give the small, nutrient poor population a greater chance of increasing. However, we would have expected to see an interaction between food quality/quantity treatments and the predator treatment if this was the case. An alternative explanation is that host plants used the added nitrogen for herbivore-defensive mechanisms (physical and/or chemical) instead of growth, which would depress aphid populations on fertilized plants (Chen et al. 2010) and mean that the unfertilized plants were higher quality food for the aphids. The transfer of nutritional quality from plants to herbivores is important for determining the nutritional quality of herbivores for predators, and host plant quality deserves additional study to explain the patterns observed here.

Additionally, a significant effect of ant mound replicate indicates that other factors could be driving the patterns in the effects of food quality and quantity. One such factor is black bear attacks on ant mounds, which has been frequent this summer. Other factors could include pathogens of ants or differences in the honeydew-producer communities that feed the ants.

Effects of Predator Identity

My second hypothesis, that crab spiders will reduce ant-tended aphid abundances more than 7-spotted ladybeetles because spiders avoid ant harassment, was not supported. Seven-spotted ladybeetles were the effective predator, even though they are less cryptic than spiders and are often killed by ants. The ladybeetles possibly have higher consumption rates compared to spiders. These results suggest that trade-offs exist in foraging strategies, where more aggressive behavior results in greater foraging, but at the cost of higher mortality. Also, the lack of an effect of crab spiders on aphids may be explained if sagebrush aphids are not a preferred prey source for the crab spider; the experimental spiders may prefer treehoppers, other aphids, or additional insects in their diets. It is also possible that the crab spiders may prefer a different host plant than the one chosen for the experiment. When sweep netting was performed to catch predators for experimental manipulations, I found that brown crab spiders were most abundant on rabbitbush (*Chrysothamnus viscidiflorus*) and not sage.

Conclusions

Apex predators in food webs are commonly not recognized as important components that alter and shape ecosystems (Estes et al. 2011). Apex predators' effects on ecosystems can reverberate through all the trophic levels and have profound effects on species productivity, evenness, and biodiversity (Estes et al. 2011). Yet, these cascading effects are reciprocal, and food quality and quantity at lower trophic levels (bottom-up effects) are important determinants of the strength of cascades at the predator level. In this study, I found that both bottom-up and top-down effects had large influences on aphid abundances, which can reverberate

through other trophic levels. Although my hypotheses were rejected, the results show that the nutritional value and quantity of food and the hunting strategies used by predators will extensively shape the strength of predation and cascading effects on lower trophic levels.

Table 1. Nested ANOVA results for the effects of the predator treatment (predator manipulation) and ant mound identity (ant mound replicate) nested within the plot level factors initial honeydew-producer abundances (H-producer) and nitrogen addition (N) on A. aphid abundances and B. tending ant abundances. H=Honeydew, N=Nitrogen.

A Aphids			
Treatment Factors	Df	F value	P value
H-producer	1	1.130	0.292
N	1	0.083	0.775
H-producer&N	1	5.291	0.025*
H-producer&N& predator manipulation	32	0.965	0.471
H-producer&N&ant mound replicate	64	1.674	0.040*
B Ants			
H-Producer	1	12.451	0.001*
N	1	0.602	0.441
H-producer&N	1	7.961	0.001*
H-producer&N& predator	8	0.956	0.478

manipulation			
H-producer&N&ant mound replicate	32	4.025	0.001

Table 2. Welch's Two Sample t-tests comparing the effects of different treatments combinations at the plot level A. aphid and B. tending ant abundances, with H denoting the honeydew-producer abundance treatment and N indicating the nitrogen addition.

A Aphid (Comparison of treatments)	Df	T value	P value
Low H&Low N vs. High H&Low N	51.981	2.158	0.0356
Low H&Low N vs. Low H&High N	51.943	0.86	0.3937
Low H&Low N vs. High H&High N	51.94	0.86	0.394
High H&Low N vs. Low H&High N	51.86	-0.506	0.615
High H&Low N vs. High H&High N	51.988	-1.270	0.210
Low H&High N vs. High H&High N	51.768	-0.800	0.427
B Ants (comparison of treatments)	Df	T value	P value
Low H&Low N vs. High H&Low N	50.09	3.307	0.002
Low H&Low N vs. Low H&High N	51.99	1.702	0.095
Low H&Low N vs. High H&High N	51.35	2.163	0.035
High H&Low N vs. Low H&High N	49.831	-1.422	0.161
High H&Low N vs. High H&High N	51.631	-1.136	0.261
Low H&High N vs. High H&High N	51.183	0.353	0.261

Table 3: One-way ANOVA results of predator treatment effects on aphid and tending ant abundances.

Dependent Factor	Df	F value	P value
Aphids	2	2.312	0.104
Ants	2	1.175	0.313

Table 4: Welch's Two Sample t-test comparisons of groups in the predator treatment and effects on aphid and tending ant abundances.

Aphid (reaction to predators)	Df	T value	P value
No pred vs. LB	69.679	2.033	0.046
No pred vs. S	69.896	0.408	0.685
LB vs. S	69.94	-1.601	0.114
Ants (reaction to predators)	Df	T stat	P value
No pred vs. LB	69.989	1.279	0.205
No pred vs. S	69.986	-0.078	0.938
LB vs. S	69.95	-1.365	0.938

Food quality & quantity effect on aphids

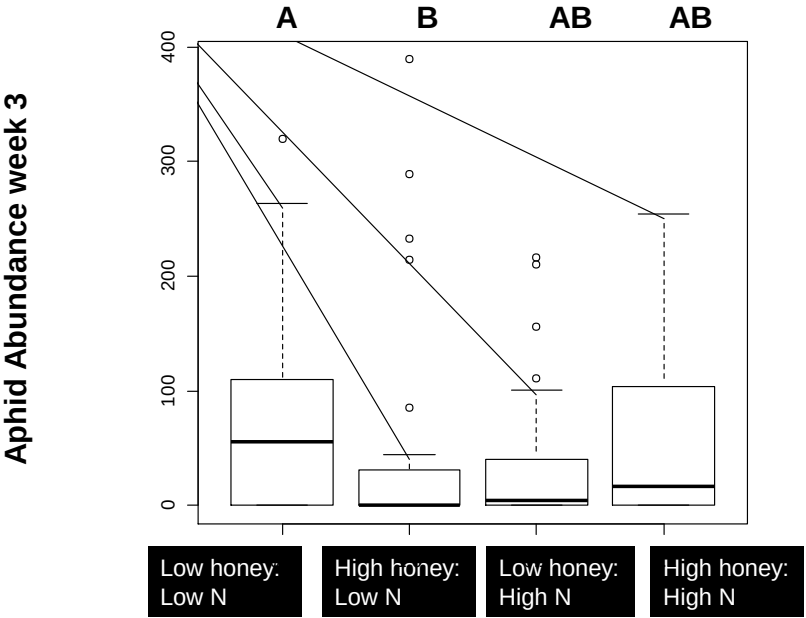


Figure1. Boxplots of the effects of food quality (nitrogen addition = N) and quantity (initial aphid abundances = honey) on final aphid abundances. A's and B's denote significantly different groups according to Welch's two sample t-tests (Table 2).

Food quality & quantity effect on ants

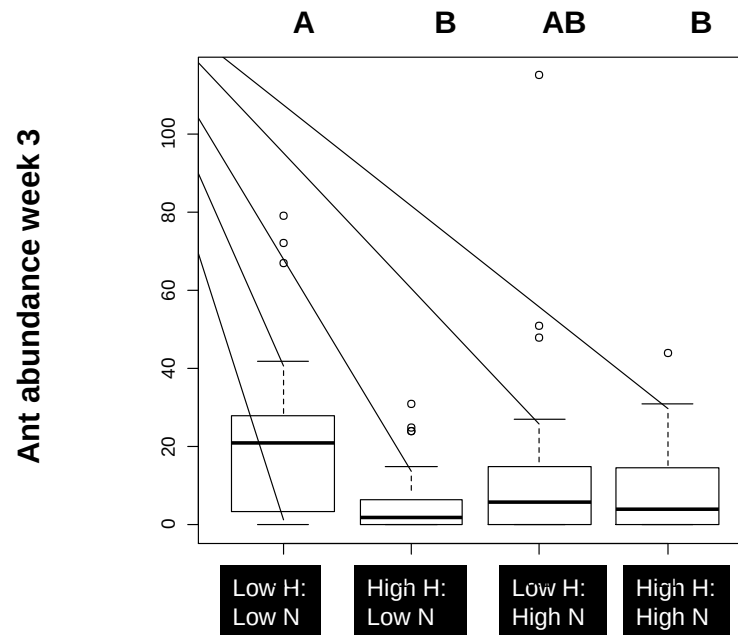


Figure2. Boxplots of the effects of food quality (nitrogen addition = N) and quantity (initial aphid abundances = honey) on final tending ant abundances. A's and B's denote significantly different groups according to Welch's two sample t-tests (Table 2).

Predator identity differences:

One-way ANOVA & Welch Two Sample t-test

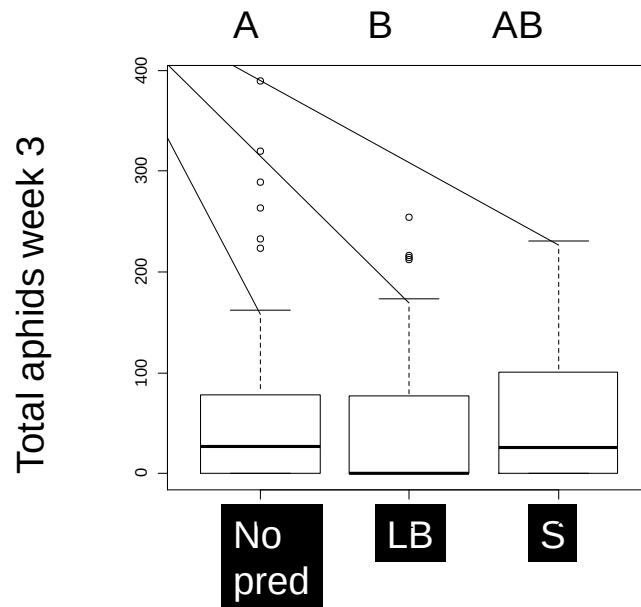


Figure3. Boxplots of the effects of predator identity (control = No Pred, ladybeetle addition = LB, brown crab spider addition = S) on final aphid abundances. A's and B's denote significantly different groups according to Welch's two sample t-tests (Table 2).

Ants interactions to predators

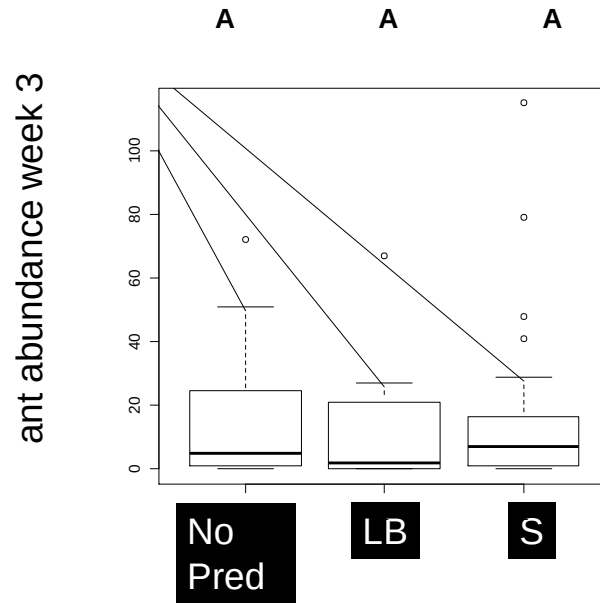


Figure4. Boxplots of the effects of predator identity (control = No Pred, ladybeetle addition = LB, brown crab spider addition = S) on final tending ant abundances. No significant differences were detected.

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