

How predators affect the behavior and foraging of nymph *Melanoplus femurrubrum*
grasshoppers in a prairie system

Practicum in Field Biology: BIOS 35503-01

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2008

ABSTRACT

Predators can indirectly affect populations of organisms many trophic levels away in top down systems. These effects can be driven by direct predation on prey or indirect predation effects in which prey exhibit potentially lethal antipredatory behaviors. Often the latter indirect effects can have a greater influence on the community. The perception of predators is also important in such systems as clues of a predator trigger these antipredatory responses. In this study I looked at the effect of direct and indirect predator threats on a dry prairie food chain of spiders, grasshoppers, and plants. Using a combination of field, lab, and behavioral experiments, I hypothesized that direct predation would cause as much an influence on the grasshopper community as indirect predation threats and that grasshopper prey respond more to chemical cues of predators rather than visual cues. Experimental food webs in the lab supported this hypothesis suggesting that indirect effects do play as large a role on grasshopper communities as direct predation. However due to issues with the field experiment, no conclusions can be drawn about whether indirect effects influence a top down trophic cascade or if the grasshoppers are too food limited and experience bottom up control. In the lab experiment replicating one done on crickets (Kortet & Hendrick 2004), while it was found that grasshoppers and crickets exhibit different antipredator behaviors, no conclusions can be made about whether visual and/or chemical cues initiate an antipredatory response in grasshoppers.

INTRODUCTION

Predators play a major role in biological systems. They often determine how a community is structured and can influence organisms through multiple trophic levels. This is especially seen in trophic cascades in which the foraging habits of predators indirectly influence organisms with which they have no direct association. Carpenter et al. (1985) famously introduced this concept when talking about limnetic systems. They found the addition of more top predators had a negative effect on the next trophic level, which had a positive effect on the following trophic level and so on until ultimately nutrient levels were positively affected. Since the publication of that study, researchers have expanded on this concept and have found that it applies to many other systems and have found that predators can have profound indirect influences on the community structure.

There are two schools of thought that attempt to describe what drives trophic cascades. The first, coined by Menge (1995) as the interaction web approach, claims that predators affect prey populations through direct predation and lethal interaction by actively killing and decreasing prey populations creating direct and indirect influences down the food web (Leibold 1989, Spiller and Schoener 1990, Schmitz 1994, Menge 1995). The second examines indirect effects of predators on their prey. These are the prey's adaptive shifts in behavior either in foraging, development, or placement in the presence of predators to prevent from being preyed upon. Such prey behaviors are known as "risk effects" and can be lethal, causing starvation or stress on the prey organism or nonlethal by resulting in a change of the prey's habitat selection or diet (Abrams 1984, McNamara and Houston 1987, Ludwig and Rowe 1990, Danner and Joern 2003).

While these two schools of thought are somewhat independent, there is a call to integrate them to gain a more complete view of predators' roles in communities as conventional models of communities often do not take into account these indirect risk effects resulting from the presence of predators (Schmitz et al. 1997, Adams 1984). For example, many models look at predators indirectly increasing plant growth by directly consuming herbivores. However, most predators only consume one herbivore at a time. When looking at indirect predator prey effects, the presence of one predator can affect the behavior and foraging habits of many more herbivores, perhaps benefiting the plants even more than a singular direct lethal interaction (Schmitz et al. 1997, Hlivko and Rypstra 2003).

A vital aspect to indirect risk effects on prey in communities is how prey detect the presence of a predator. In aquatic systems, predators are often detected by chemical cues, especially when the predator has previously fed upon another individual of the same or similar species (Mathis and Smith 1992). Chemical cues left behind in the excreta of terrestrial predators have also been shown to affect terrestrial prey (Kortet and Hendrick 2004). Sight can also be a form of predator detection causing immediate responses (flight, hiding, defense mechanisms, ect.). Other forms of predator detection include but are not limited to sound and/or vibration, tactile clues, and warning signals from other prey.

I present here my study testing the direct and indirect interactions between grasshoppers, their predators and the vegetation on which grasshoppers feed, conducted in an open prairie. Grasshoppers are known to have different types of predators and therefore different

predator avoidance strategies at different stages of their development (Belovsky and Slade 1993, Schultz 1981, Belovsky et al. 1990, Schmitz et al 1997, Danner and Joern 2003). While grasshopper populations are mostly food limited and predation at all levels on grasshoppers is known to be compensatory, grasshoppers are still known to exhibit antipredator behavior (Schmitz et al 1997, Belovsky and Slade 1993, Danner and Joern 2003, Oedekoven and Joern 2000). Therefore, although the direct predation of grasshoppers themselves is compensatory, the presence of predators in a grasshopper community and the indirect effects they cause on the grasshoppers still have the potential to influence the trophic cascade of the community.

I studied a predator/prey relationship between invertebrate predators, *Rabidosa rabida* spiders, and herbivorous prey, *Melanoplus femurrubrum* nymph grasshoppers, in a palouse prairie environment and the trophic cascade involved with their relationship. I used a caged field experiment and a paralleling lab experiment to see if indirect effects of spiders on grasshoppers cascaded down to benefit the plants as much as the lethal direct effects of spiders on grasshoppers. This included exposing grasshoppers to “risk” predators in which the predators were rendered unable to directly kill their prey. In a laboratory experiment I also observed the behavior of grasshopper nymphs to see if they reacted to chemical, visual, or some other unknown factor to see how grasshopper nymphs are able to detect the presence of their predators.

Second, I tested how these grasshoppers were able to detect the presence of a predator. As with many animals, scent plays a large role in grasshopper foraging habits (Szentesi et al. 1996). A study by Kortet and Hendrick (2004) on field crickets, a close relative to the grasshopper, found that crickets use scent for predator detection and avoidance, especially if the predator had recently fed upon a cricket. Grasshopper eyesight, rather, appears to be less developed and relatively simple as literature suggests grasshoppers responding mostly to vertical lines (Bailey and Harris 1991, Szentesi et al. 1996). While this may be useful for avoiding larger vertebrate predators, it is likely useless for the detection of smaller invertebrate predators.

Because previous studies have suggested that grasshoppers have predator avoidance behaviors that affect their foraging (Schmitz et al. 1997, Belovsky and Slade 1993, Danner and Joern 2003, Oedekoven and Joern 2000), I expect to find the presence of spider predators to have an indirect negative effect on the grasshoppers thereby having a positive effect on their vegetative food. Also since spider predation on grasshoppers is compensatory, I expect to find no difference in the ultimate population numbers in the caged enclosures between those with

grasshoppers alone and with predators. However since the predators cannot kill some of the population in order to provide more food for the surviving individuals, I expect to find the lowest numbers of grasshoppers in the risk treatments because of higher resource limits. I also expect grasshoppers to respond more to chemical cues left behind from spiders than to the sight of them because literature suggests a more developed sense of smell than sight in grasshoppers.

MATERIALS & METHODS

Study Site

The field portion of this study was carried out in July of 2008 in the Palouse prairie environment at the National Bison Range, Montana (Sanders and Lake counties). This study site is fully described by Belovsky et al. (1990). The site is dominated by grasses; *Bromus spp.* and *Elymus spp.* are the most abundant types of grass and *Achillea millefolium*, *Aster falcatus*, and *Erigeron sp.* are the most abundant species of forb (Belovsky 1993).

Many species of grasshopper have been observed here in the past 20 years. *Melanoplus femurrubrum* and *Melanoplus sanguinipes* are the most common averaging about 82% of all individuals (Belovsky 1993). The most common predatory spiders for grasshoppers in the area belong to the families Aranea and Lycosidae.

Experimental organisms

I used *Melanoplus femurrubrum* grasshopper nymphs in this study because of their abundance in the field and because their small size make them easy prey for predators. There have also been previous studies with *M. femurrubrum* indicating they are a good candidate for caged experiments (Belovsky 1993, Schmitz et al. 1997). *M. femurrubrum* are also grass and forb generalists (Vicery and Kevan 1967, Helfer 1987, Schmitz et al. 1997). Nymphs (instars II-IV) were used because preliminary observations showed that spiders had difficulty overcoming and subduing 5th instar nymphs and adults. Grasshoppers were initially caught at a site a few miles away from the study site (because of higher densities of nymphs at this area) but because of a high death rate in the cages likely due to a high handling time and stresses involved with moving to a new environment, cages were restocked with nymphs collected from the study site. At the second stocking, special care was taken to reduce handling time.

The predatory spiders used in this experiment were female *Rabidosa rabida* (Rabid wolf spider) of the family Lycosidae. Females were used because their larger size makes them more

likely to prey on grasshoppers. Spiders were caught using pitfall traps around the field study site and were kept in plastic containers with a saturated paper towel until needed for experimentation. In some of the experiments “risk” spiders (spiders rendered unable to catch and kill prey) were needed. Risk spiders were created by gluing chelicerae shut with cyanoacrylic glue as described in Schmitz et al. (1997). Such a treatment is not known to affect hunting behavior (Schmitz et al. 1997).

Field Study

I created experimental food webs in order to study the population and trophic level effects of spiders upon grasshopper populations and plant biomass in this system. Using the protocol described in Belovsky (1993), I constructed cages $\sim 0.1\text{m}^2$ by 0.8m high, made aluminum screening fastened at the base to a 126 x 10 cm strip of aluminum sheet metal. The bases of the cages were sunk into the ground to prevent the escape and entry of organisms. All insects and arachnids were cleared from the area prior to burying the cages in the ground. The cages were secured with stakes to give them stability and the tops were folded and clipped shut to allow easy access in the cages. I placed 32 cages on a grid $\sim 1.5\text{m}$ apart from each other and I laid the cages out in a randomized block design of 8 blocks each with four treatments. The four treatments were different experimental food webs: 1. one trophic level with only plants; 2. two trophic levels with plants and herbivores (grasshopper nymphs); 3. three trophic levels with plants, herbivores, and predators (spiders); and 4. three trophic levels with plants, herbivores, and risk predators (spiders with glued chelicerae).

I stocked 10 *M. femurrubrum* grasshopper nymphs (II, III, IV instars) into the cages and 2 *R. rabida* spiders of their respective treatments (risk and predation) to the cages according to their assigned trophic levels. Both the spider numbers and grasshopper numbers were well above field densities. Grasshopper numbers were stocked above the field densities of the area in order to create a pulse perturbation in the cages. The prairie study site had patches with higher and lower densities of the grasshopper depending on multiple biotic and abiotic factors. The pulse perturbation was created so that the grasshopper population could steadily decline to the level that the environment in each cage was able to support. This is so that there was no artificially high or unrealistically low resource limitation in the cages. Such a pulse perturbation is not known to artificially affect the plant biomass in the cages (Schmitz 1994). I stocked cages with artificially high numbers of spiders because I was time limited in running the experiment

and I wanted to increase the level of predation or predation risk in each of the cages so that the effects of the predation could be seen in a shorter time period.

Cages were stocked with grasshoppers and spiders and the experiment was allowed to run for 15 days. The cages were checked every day and the numbers of grasshoppers found in each cage were counted. Because of an initial high death rate (more than 95% dead after 3 days), grasshoppers were restocked to their initial levels of 10 per cage on the 6th day. Also at this time, spiders of their respective treatments were added to cages where no spiders were visible. After 15 days, the grasshoppers were released and all standing plant growth from that year in the cages was clipped, dried for 48 hours and weighed.

Laboratory Experiment

I carried out a laboratory experiment to parallel the field experiment. The set up of this experiment was very similar to the field. I created four different treatments of a food web in eight 1000mL, 14cm high clear plastic containers. Two containers had just plants, two had plants and grasshoppers, two had plants, grasshoppers, and predation spiders, and two had plants, grasshoppers, and risk spiders. About 2g of freshly picked dandelion leaves were weighed and placed in each container, 5 grasshoppers and 1 spider of each treatment were then added to their respective containers. Insect screening covered the top of each container. After letting the experiment run for 24 hours, the grasshoppers and spiders were taken out of the containers and the plant matter left was cleaned off of all feces and silk and weighed. I ran this experiment over 7 days resulting in 14 reps/treatment. I recorded if a grasshopper was killed or died in each jar.

To account for moisture lost from the leaves during the 24 hours each block ran, the ratio of after/before weight was averaged from the two “control” treatments of one trophic level and this mean was used as the percentage of moisture lost from the dandelion leaves during each block’s run. I used this percentage to calculate the amount of moisture the leaves in the other containers should have lost during the 24 hour incubation period and subtracted this from the original weight of the leaves in each of the containers. The final weight was then subtracted from this value to calculate the total consumed biomass in each of the containers.

Behavioral Study

To test which aspect of a predator’s presence affects grasshopper behavior, three different treatments were tested: smell, sight, and the predator itself. A 29 x 23cm arena was set up in which a treatment and a control were placed 17cm from one another at the center of the arena.

Three sets of ten repetitions were tested for each treatment; 10 grasshoppers were tested 3 times in each set. In each repetition, a *M. femurrubrum* grasshopper nymph was placed in the center of the arena and a glass dish the size of the arena and 5 cm deep at its maximum was placed over the arena. After 5 minutes, the distance of the grasshopper from the control and the treatment circle were each measured. If the grasshopper was on either of the circles, then the distance to that circle was measured as “0.”

For the smell treatment, a spider was fed a grasshopper and placed on a 6cm diameter piece of filter paper for at least 48 hours to collect its excrement, excretions, and silk. The filter paper with spider excreta was placed on the treatment circle, and a blank piece of filter paper was placed on the control circle. Clean forceps were used during the transfer of filter paper in order to ensue that no oils or smells from my hand that may affect results would contact with the paper. For the sight treatment, a spider was placed under an inverted 1 x 6cm diameter Petri dish on the treatment circle and an empty inverted Petri dish was placed on the control circle. For the final treatment, a spider was glued with cyanoacrylic glue to a 3 cm thread tether on its abdomen and a 3 cm piece of thread was fastened to the center of the control circle. In each treatment a fresh spider or filter paper was used for each replicate except in the final predation treatment, the same spider was used since gluing the tether to the spider was so traumatic for the spiders that I did not want to increase the possible mortality of my lab spiders by gluing more than one. Also only two sets of 10 repetitions were carried out in this final treatment for the same reasons mentioned above.

Statistical Testing

A repeated measure ANOVA test was used to analyze the population of grasshoppers in the cages over the run of the experiment. Because the cages were restocked on the 6th day, the test was done only on days 7-15. An ANOVA test was used to analyze the biomass clippings from each cage. For the laboratory experiment, a GLM Estimate model was used to analyze the biomass eaten by the grasshoppers with days acting as a block. An ANOVA was also used to compare the biomass in the jars where a grasshopper died or was killed in a predation treatment and the biomass in the jars where none died. I used both paired t-tests and ANOVA tests to analyze the behavioral data. Paired t-tests were used to compare the distances between control and distances from the source within each treatment; an ANOVA test was used to compare the distances from the control and from the source sites across the treatments.

RESULTS

There were no significant differences between the biomass consumed within any of the treatments in the field experiment (Figure 1); varying trophic levels had no effect on biomass. While grasshopper numbers did significantly change between the days the field experiment ran, there were no significant trends or differences in grasshopper survival within any of the treatments across the days the experiment ran (Figure 2).

In the lab experiment, the average biomass consumed by the grasshoppers in the two trophic level treatment was significantly higher than both of the three trophic level treatments (predation and risk predation) (figure 3). There were no significant differences in biomass consumed between the predation and risk predation treatments. Because of the short time span of each experimental run and the low mortality of grasshoppers throughout the experiment, the risk predation and predation treatments should be looked at on the same scale. There, however, was no significant difference in the average biomass consumed by grasshoppers in predation treatments in which a grasshopper was killed or died and when all five survived the 24 hour period (figure 4).

In the predator cue avoidance experiment, when comparing the distance the grasshopper traveled from the spider cue source and the control source there were no significant differences between any of the treatments (figure 5). There appears to be a trend that grasshoppers avoided predators when they could see them but the average difference between the two is highly non significant. There was no significant difference between any of the treatments when comparing the distances traveled from the spider cue source ($F=0.802$, $p_{df=2}=0.452$) or when comparing the distances traveled from the control source ($F=0.300$, $p_{df=2}=0.741$).

DISCUSSION

In this study, I tested whether predatory spiders have an indirect effect upon grasshoppers and if these potential indirect effects influence a trophic cascade. Results from the lab experiment show that spiders indeed do have an indirect effect upon grasshopper feeding habits. Grasshoppers that were in containers with foraging spiders and those with risk spiders ate less than grasshoppers that were in containers with no predators. In the presence of spiders, grasshoppers will perform anti-predator behavior and forage less. This experiment also suggests

that spiders are at the top of a trophic cascade in this system and their predation indirectly aids plants. The fact that there were no significant differences between biomass consumed in containers with spiders that had a grasshopper death and those with no deaths suggests that the indirect effects of predation drives the trophic cascade more than the direct effects of predation. This goes along with conclusions made in previous studies which also found that indirect predation effects on grasshopper prey creates a trophic cascade, positively affecting the primary producers (Schmitz 1997).

The lab results indicate a true trophic cascade due to indirect effects of predator presence. However, these results are likely to change under field conditions where there are many variable environmental factors. Biotic factors such as the first trophic level were much different in the lab than in the field (dandelions are uncommon in prairie habitats) and other abiotic factors were not recreated in the lab (temperatures, UV radiation). For wider inference, the presence of a trophic cascade in the laboratory must be tested and supported by data collected in the field. Unfortunately, the data from the field experiment are inconclusive due to the unexpectedly high mortality of grasshoppers in the enclosures. The fact that there were no differences in the average biomasses remaining after the end of the experiment between the one trophic level cages and the two trophic level cages (Figure 1) is likely due to the overall high mortality of grasshoppers early in the experiment. Since mortality was so high in the experiment no accurate conclusions can be drawn about the spiders' influences on grasshopper populations. This is indicated by the high grasshopper mortality rate even in cages without predator influence, along with the fact that there were no differences in rate of grasshopper die off between the treatments (figure 2). It should be noted that the high mortality rates in the cages are unexplained and unexpected since studies of a similar manner have been previously carried out at the same site with the same organisms (Belovsky & Slade 1993).

In cooler, wetter environments trophic cascades relating to spiders and grasshoppers have been observed, (Schmitz 1997). However, previous studies done in dryer, warmer, prairie habitats have suggested that there is no trophic cascade found with the simple spider-grasshopper-vegetation food chain (Chase 1996, Schmitz 1992). They found grasshoppers are food limited in the grassland environment and therefore bottom up control has more impact than top down pressures. Then why is there evidence of a top down trophic cascade in this food chain in the lab experiment? Chase (1996) found that abiotic factors in the environment, such as

temperature, can alter the direct and indirect relationships. He demonstrated that this spider-grasshopper-vegetation food chain can be changed from a bottom-up, food-limited system to a predator-limited, trophic cascade by reducing the temperature and sunlight in the environment. Lower temperatures cause grasshoppers to forage less, become more susceptible to prey, and rearrange the order of the system. This demonstrates that the indirect relationships between the same two organisms in a warmer environment can be entirely different between those in a cooler environment. The results of the laboratory experiment are therefore logical since the abiotic conditions of the lab did not match those of the field (cooler temperature in lab and no direct sunlight). Also the lab experiments provided the grasshoppers with an unlimited amount of food so if the grasshopper populations are food-limited in the prairie environment, it would not show in the lab experiment.

The second part of this study attempted to determine how prey become aware of a predator threat. Since there were no significant changes in behavior (figure 5), and since the lab experiment showed that there was an antipredator response, no conclusions can be drawn on which predator cue grasshoppers respond to. This experiment was a replicate of one done by Kortet and Hendrick (2004) in which a nymph field cricket detected chemical cues from a spider predator. Since grasshoppers and crickets are in the same order, Odonata, it was assumed that the experimental design of this study would apply to grasshopper nymphs as well. However, that grasshoppers and crickets likely have different predator avoidance strategies. A cricket may run away and avoid areas where a predator is detected while a grasshopper may lie still and attempt to camouflage when a predator is detected. Since in every run, a predator cue was always present, perhaps the grasshopper was exhibiting its antipredator behavior during the experiment. A few “control” sets were set up in which a grasshopper was placed in the arena alone to see if there was any change in its behavior without predator cues. The grasshoppers in these control runs exhibited the same behavior of nonmovement as in the experimental runs. There were other factors that could have also affected the results of this experiment. For example, perhaps five minutes was not enough for the grasshopper to recover from my handling of it and was still exhibiting antipredatory behavior because it still perceived me as a predator risk. To improve this experiment, observations would initially need to be made on predator avoidance strategies of *M. femurrubrum* nymphs and then an experiment should be designed so that that predator avoidance behavior can be quantified when in and out of the presence of a predator. This

experiment has indicated that grasshoppers and crickets react differently in the presence of predators or predator cues. Perhaps in a more comfortable environment with more cover and with more time, an antipredator behavior to various cues can be better quantified.

In conclusion, this study showed that there are indirect predator effects on grasshopper populations as much or more than direct predation. However, due to mysterious complications with the field experiment, whether this indirect predation drives a trophic cascade in the grassland habitat or whether grasshoppers are food limited driving a bottom up effect is inconclusive. However, no conclusions can be drawn on which aspect of a predator's presence triggers an antipredatory response in *M. femurrubrum* nymphs as no significant changes in behavior were observed that related to the presence of various predator cues. (figure 5).

ACKNOWLEDGEMENTS

I would like to thank Notre Dame and the University of Notre Dame Environmental Research Center for providing me with funding and the opportunity to carry out this experiment. Also to Dr. Gretchen Gerrish and Dr. Gary Belovsky for their aid in the design and guidance throughout the study. I would really like to thank Stephanie Dorries, Kelly Collins, and Veronica Velez for their long hours in helping me with the set-up of the study. And finally to the rest of the 2008 UNDRC West class for keeping me sane (or insane) the entire summer.

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TABLES AND FIGURES

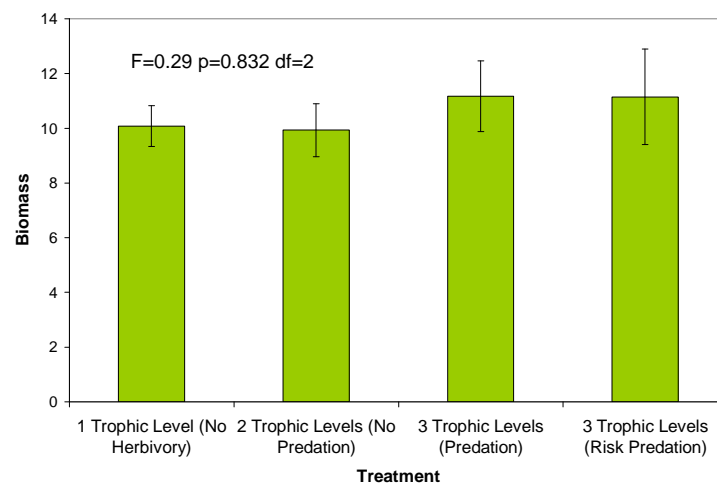


Figure 1: Biomass remaining in cages after field experiment. Bars represent differences between foraging occurring with the multiple trophic level treatments.

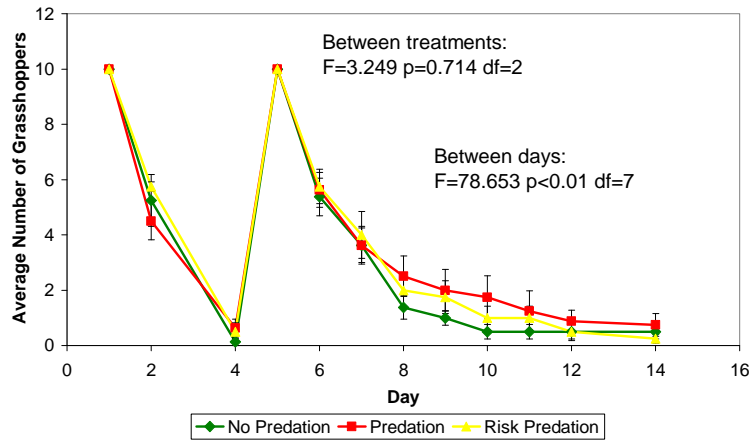


Figure 2: The effect of time on grasshopper populations in various trophic treatments. The spike in numbers on the 5th day is due to restocking after initially high mortality rates. Grasshoppers were in the presence of spiders in the predation and risk predation treatments but the spiders were rendered unable to kill in the risk predation treatment.

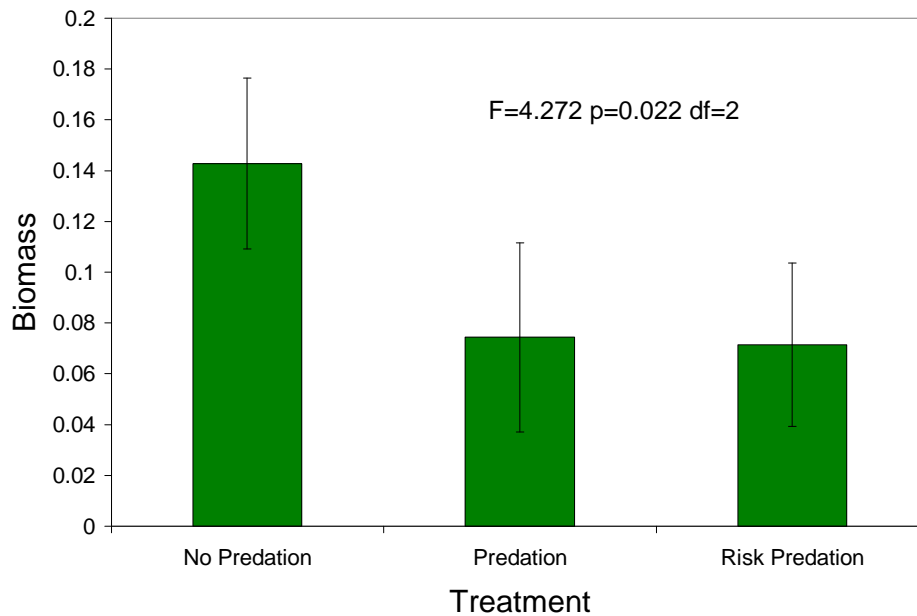


Figure 3: Effect of predation types on biomass consumed by grasshoppers. Bars represent treatments; grasshoppers were in the presence of spiders in the predation and risk predation treatments but the spiders were rendered unable to kill in the risk predation treatment.

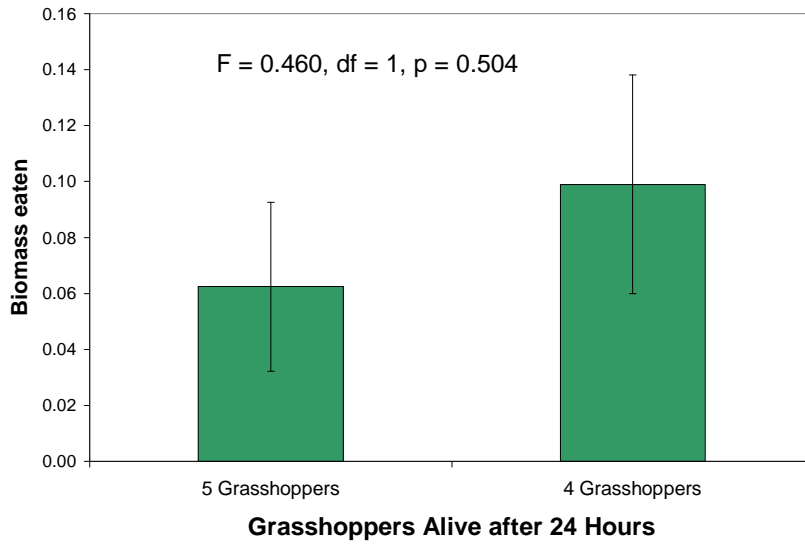


Figure 4: Effect of direct and indirect predation on grasshopper foraging. “5 Grasshoppers” treatment were exposed to spiders with no fatalities; “4 Grasshopper” treatments were grasshoppers exposed to spiders with at least one fatality.

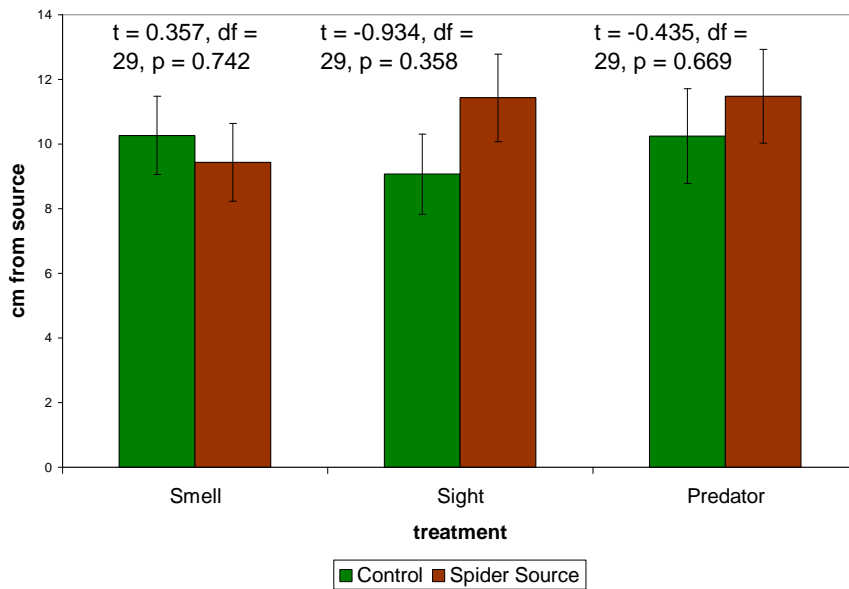


Figure 5: Grasshopper avoidance of predatory spider cues. Bars represent differences in the distance a grasshopper traveled from each source. A tethered spider was used for the “Predator” treatment.