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Non-consumptive interactions between grasshoppers (Orthoptera: Acrididae) and wolf spiders (Lycosidae) produce trophic cascades in an old-field ecosystem

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Abstract

Top-down control by spider predators on grasshopper herbivores can produce trophic cascades, which may enhance plant biomass and alter plant community composition. These trophic level effects may be the result of either predator reduction in prey numbers (*i.e.*, consumptive effects) or decreased prey foraging time in response to predator presence (*i.e.*, non-consumptive effects). However, predator-prey interactions can be context dependent and do not always affect the plant trophic level. We conducted a field and laboratory experiment in a Northern Wisconsin (USA) old field ecosystem to uncover whether consumptive or non-consumptive effects of spider predation on grasshopper herbivores result in a trophic cascade, and if so to determine the underlying mechanisms that drive these trophic cascades. In a field experiment, four treatments examined the effects of multiple trophic-level interactions on plant biomass: 1) control treatment of vegetation only, 2) a two trophic-level interaction (grasshoppers and vegetation), and two different three trophic-level interactions: 3) the presence of "predator spiders" to examine consumptive effects, and 4) "risk spiders" with their chelicerae disarmed with beeswax to examine non-consumptive effects. In addition, a lab experiment was conducted to examine behavioral responses by grasshoppers in the presence of both an armed-spider predator and a risk spider to assess whether food quality (high *vs* low C:N ratios) had an effect on this interaction. Both risk and predator spiders decreased the impact of grasshoppers on plant biomass in the field experiment, and equally reduced overall grasshopper survival, indicating a non-consumptive effect. At the behavioral level, grasshoppers exhibited anti-predator behavior at the expense of reduced food intake. Food quality had no effect on the survival of grasshoppers as foraging was sacrificed for predator avoidance. Taken together, our results indicate that the resulting trophic cascade was the result of non-consumptive effects and that spider presence alone may reduce grasshopper herbivory rates.

Key words

ecology of fear, grasshopper, wolf spider, tri-trophic interactions, trophic cascade, predator-prey interaction

Introduction

Grasshoppers (Orthoptera: Acrididae) are important herbivores in grassland ecosystems, altering nutrient cycling processes in some instances, and providing important food resources for grassland birds (Belovsky & Slade 2000, Joern 1986, McEwen & DeWeese 1987). Despite their positive role in the ecosystem, some grasshopper species have negative effects as well. Grasshoppers in rangeland can outbreak to large numbers that then cause widespread economic damage and reduced plant productivity (Branson *et al.* 2006). Therefore, understanding grasshopper population dynamics is crucial for the successful management of pest grasshopper species (Belovsky & Joern 1995).

Since grasshoppers can reduce plant biomass and productivity, research often focuses on food web dynamics to better understand how these effects are mediated (Belovsky & Joern 1995, Chase 1996, Schmitz *et al.* 1997, Oedekoven & Joern 2000, Danner & Joern 2003a). Studies of food web dynamics help ecologists better understand natural species interactions, and document the regulation of energy flow from one trophic level to the next via exploitation. Trophic interactions can directly affect plant biomass through the regulation of herbivore populations (Laws & Joern 2013). Predators can directly reduce prey abundance via predation (*i.e.*, consumptive effects), or indirectly through non-consumptive effects such as "fear", where predators alter prey time budgets and foraging activity leading to reduced time spent foraging and reduced plant tissue eaten (Danner & Joern 2003b, Schmitz *et al.* 1997). Consequently, plant biomass may increase as predators reduce prey densities or foraging time. Both direct and indirect effects of spider predators on grasshoppers can lead to trophic cascades in old-field ecosystems (Schmitz *et al.* 1997, Schmitz 1998).

Many studies document that spiders can have important trophic level effects on grasshoppers through these direct and indirect interactions (Schmitz *et al.* 1997, Oedekoven & Joern 2000, Danner & Joern 2003b, Rothley & Dutton 2006, Laws & Joern 2013). Interestingly, nonlethal effects of spiders in the presence of a grasshopper can be just as effective in reducing herbivory rates as consumptive predation itself (Schmitz 1998). These changes in prey behavior, known as risk effects or non-consumptive effects, result from altering behavior by prey as a trade-off to avoid predation (Schmitz *et al.* 2004, Rothley & Dutton 2006). However, this behavioral shift may also increase the likelihood of grasshopper starvation; a detrimental trade-off (Belovsky *et al.* 2011, McNamara & Houston 1987). The effect of the predator on the grasshopper's host plants through a non-consumptive effect is known as a trait-mediated indirect interaction. The trade-off induced by the predator can involve a habitat shift to poor-quality resources for shelter at the expense of high-resource intake in risky habitats (Schmitz *et al.* 2004). Predation risk causes grasshoppers to shift the plants they choose to forage on, often forgoing more nutritious plants for "safer" plants that have a more complex structure which in turn reduces predation risk. In turn, plant community dynamics may shift over time as grasshoppers switch from feeding on preferred grass species that provide little protection from spiders to less nutritious forbs that provide

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grasshoppers refuge. For example, grasshoppers may abstain from eating grass and seek refuge from wolf spiders in forb species in an old field, causing high amounts of damage to the forbs, reducing their abundance relative to grass species (Schmitz 2003, Beckerman *et al.* 1997). Therefore, food quality plays an important role in grasshopper foraging preferences (Jonas & Joern 2013, Joern & Behmer 1997). If high quality food is readily available in the presence of spiders, grasshoppers may still obtain sufficient nutrients to support survival, even if less food is eaten. More nutrients can be consumed in a shorter amount of time, limiting exposure time to predation (Danner & Joern 2004). If only low quality food is present, survivorship decreases (Oedekoven & Joern 2000). Since high quality plants often have elevated protein concentrations relative to carbohydrates (Behmer & Joern 2012), and thus have a low C:N ratio (*i.e.*, high nitrogen compared to low carbon); (Strengborn *et al.* 2008), plant quality can be readily elevated above ambient levels by fertilizer applications (Danner & Joern 2004, Belovsky & Slade 1995, Oedekoven & Joern 2000).

While both consumptive and non-consumptive effects are well documented across geographically isolated spider-grasshopper food webs (Schmitz 1994, Schmitz *et al.* 1997, Rothley & Dutton 2006, Laws & Joern 2013), the magnitude of this top-down control varies both spatially and temporally. For instance, spider mediated trophic cascades do not occur regularly in the intermountain prairies of western Montana where grasshoppers are the dominant herbivore (Belovsky & Slade 1993, Chase 1996). In contrast, spiders in old fields often have strong effects on plant communities by altering grasshopper foraging behavior – a non-consumptive effect (Schmitz 1994, Schmitz *et al.* 1997, Schmitz 2003, Rothley & Dutton 2006).

In this study, we tested 1) whether wolf spiders (Lycosidae) induced a consumptive or non-consumptive mediated trophic cascade in a field experiment, and 2) whether food quality affects prey foraging decisions in a lab experiment. Given that we used a widely roaming active predator spider in our field experiment, we expected a consumptive effect to occur, even though this experiment takes place in an old field where non-consumptive effects typically arise (Schmitz *et al.* 2004). Alternatively, if grasshoppers can effectively seek shelter in the low quality forbs, then grass biomass should increase at the expense of the forb community. Such a plant community shift would be the result of a non-consumptive effect given that spider predation is reduced as grasshoppers seek shelter in the less nutritious forbs. In the laboratory experiment, grasshoppers should increase their consumption rates when presented low quality food to avoid starvation/malnutrition, thereby increasing their risk of predation. In contrast, laboratory grasshoppers fed high quality food should exhibit decreased consumption rates since they would need to consume less food to survive. In turn, these well fed grasshoppers should spend more time avoiding spiders than those fed low quality food.

Methods

Study site and organisms.—This study was conducted at the University of Notre Dame Environmental Research Center in Northern Wisconsin (46° 13′ N, 89° 32′ W). The field experiment took place in an old field that was clear-cut for dairy cattle grazing over 70 years ago. The site is not actively managed and has persisted as an old field environment. This site is dominated by the grass, *Phleum pratense*. Common forbs include *Achillea millefolium*, *Solidago* spp. and *Asclepias speciosa* (Laws & Belovsky 2010). *Melanoplus borealis* (Fieber) and *Melanoplus dawsoni* (Scudder) (Acrididae: Melanoplinae) were captured in the wild and utilized as study species due to their local abundance and close taxonomic affinity. *M. borealis* were used in the field experiment, and *M. dawsoni* were used in the feeding trials. This was done because the field and lab experiments started at different times, and the earlier emerging species (*M. borealis*) grew too large for use in the laboratory experiment. Both species are univoltine, generalist feeders, consuming both grasses and forbs (Pfadt 1994). First to third instar nymphs were used due to their small size; wolf spiders generally cannot subdue larger developmental stages. Forest wolf spiders (*Hogna frondicola*) were used as predators since they primarily comprised the ground-dwelling spider community (Laws *et al.* 2009). All experimental wolf spiders (≤ 20mm, abdomen length) were collected with pitfall traps.

Field Experiment.—A field experiment was conducted in July 2014. Aluminum screen cages were placed over similar natural vegetation (basal area = 0.35 m^2, height = 1 m), and each cage had aluminum flashing attached to the base which allowed it to be buried in the ground to prevent organisms from entering and leaving the cage. The cage was secured to the ground by wire tied to wooden stakes to prevent deformation and wind damage. The cage tops were folded over and secured by binder clips, which allowed easy access, but prevented grasshoppers from escaping. Cages were spaced ~ 1m apart (Kistner & Belovsky 2014). Prior to the beginning of the experiment, all cages were carefully examined and any invertebrates inside the enclosures were removed. We employed a completely randomized design with five replicate cages for each treatment for a total of twenty cages. Field cages were randomly assigned one of four treatments: 1) enclosures with only vegetation, where all herbivorous insects were actively excluded to serve as a control, 2) grasshoppers and vegetation, 3) vegetation, grasshoppers and spiders, and 4) vegetation, grasshoppers, and spiders with their chelicerae glued with beeswax to prevent them from subduing prey and only acting as intimidating factors. This experimental design enabled us to test whether spiders induced consumptive or non-consumptive effects on grasshoppers in our system (Schmitz *et al.* 1997). Chelicerae were sealed by applying melted beeswax to the mouthparts with a small paintbrush. The enclosures were stocked with 10 grasshoppers and 1 spider depending on the treatment. Caged grasshoppers were counted every 2-4 days to quantify survivorship for 23 days. Living vegetation (green) was clipped at ground level after 3 weeks. The vegetation was sorted into grasses and forbs, dried at 60°C for 48 hours, and weighed to estimate aboveground plant biomass.

Feeding trials.—Lab-based feeding trials consisted of three treatments of grasshoppers and spiders: 1) grasshoppers only as a control, 2) grasshoppers and predator spiders, and 3) grasshoppers and risk spiders with their chelicerae glued, again to prevent lethal consumptive interactions. These three treatments were included with two different qualities of food, and replicated three times. A high quality food source was acquired from a 3×3m plot of grass fertilized previously with Miracle Gro N-P-K (The Scott Company LCC, Marysville, OH) at 6g of nitrogen per m^2, and a low quality food source from the same size plot of short grass growing in poor quality rocky soil. Past studies have shown that fertilizer treatments increase foliar-N levels (Joern & Mole 2005, Laws & Joern 2013). Grass was clipped at ground level, dried and then weighed. Six ten-gallon aquaria were used for the experiment. Aquaria consisted of three sticks for structure, and the grass was presented in a pile. The aquaria were stocked at a density of ten grasshoppers to one spider. Grasshoppers were starved for twelve hours prior to tests, and were then presented with one gram of either fertilized or unfertilized grass. Feeding trials lasted six hours. Prior to the end of the experiment,

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both grasshopper position in the cage (number of grasshoppers on the sides, ceiling, structure, and base of aquaria), and the number of grasshoppers actively foraging were recorded. After trials, the remaining food was re-weighed to determine the amount eaten in the presence or absence of a risk or predator spider.

Statistical analysis.—Before analysis, the homogeneity of the variances was checked using Shapiro-Wilk's test. If the variances were not homogeneous, they were subjected to log or arcsine transformations to remove heteroscedasticity (Zar 1999). For the field experiment, a repeated measures ANOVA was used to analyze grasshopper survivorship followed by Tukey's post-hoc analysis to examine if significant differences were detected between trophic level treatments. Biomass for both grasses and forbs were analyzed using a one-way ANOVA followed by Tukey's post-hoc analysis. For laboratory feeding trials, we employed a two-way ANOVA to assess the effects of 1) fertilizer application (*i.e.*, food quality) and 2) spider treatment (none, predator or risk) on grass biomass consumed during the feeding trails. Pearson's chi-square tests were performed on the grasshopper behavioral counts across spider treatments in both fertilized and unfertilized grass fed grasshoppers. All analyses were conducted in R 3.0.1 (R Development Core Team 2013).

Results

Field experiment.—Grasshopper survivorship decreased over time across all trophic level treatments ($F_{6,104}$ = 114.0, P < 0.001; Fig. 1) and overall survival differed across experimental trophic levels ($F_{12,\ 104}$ = 4.46, P = 0.014). Grasshopper survival was lower in the two treatments that received spiders compared to the treatment with grasshoppers alone (Tukey HSD, P < 0.05), but did not differ between treatments with predatory and risk spiders (Tukey HSD, P > 0.05). The time × treatment interaction was not significant ($F_{12,104}$ = 0.724, P = 0.723). Grass biomass was significantly lower in all three treatments with grasshoppers compared to the control (Tukey HSD, P <0.05; Fig. 2). Grass biomass was higher in the two treatments that received spiders compared to the treatment with grasshoppers alone (Tukey HSD, P < 0.05), but did not differ between treatments with predatory and risk spiders (Tukey HSD, P > 0.05). Forb biomass did not vary across trophic level treatments ($F_{3,16}$ = 1.57, P = 0.24; Fig. 2).

Feeding trials.—Fertilizer treatments did not affect grasshopper consumption rates ($F_{2,18}$ = 1.83, P = 0.19). However, more grass biomass remained in the spider treatments than in treatments with only grasshoppers ($F_{2,18}$ = 9.98 , P = 0.001). The fertilizer × spider treatment interaction was not significant ($F_{2,18}$ = 0.38, P = 0.62). Grasshoppers exposed to either the risk or predatory spider consumed 76% less grass biomass compared with grasshoppers housed alone (Tukey HSD, P < 0.002), but consumption rates did not differ between the predatory and risk spider exposed grasshoppers (Tukey HSD, P = 0.99; Fig. 3). Grasshoppers housed with spiders avoided the ground where the spider was typically found, but were frequently observed on the sides or ceilings of the aquaria when offered unfertilized (χ^2 = 27.87, df = 8, P < 0.001) and fertilized grass (χ^2 = 31.51, df = 8, P < 0.001; Fig. 4). A total of 9 grasshoppers were subdued by predatory spiders during these behavioral experiments.

Discussion

In this study, the presence of spiders decreased grasshopper foraging time, resulting in increased grass biomass in a northern Wis-

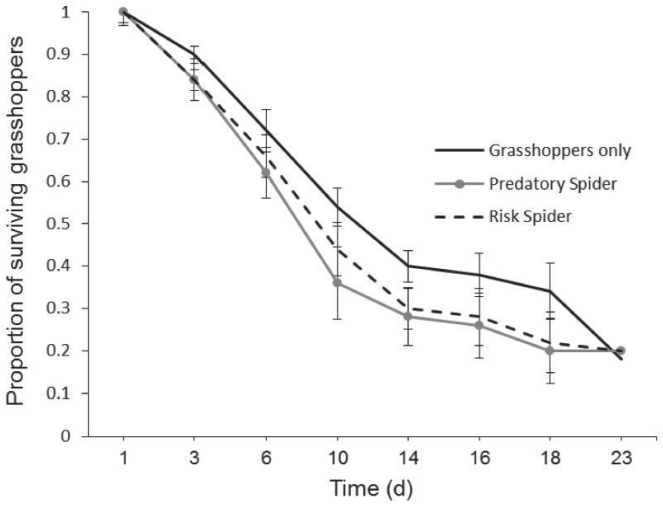


Fig. 1. Cumulative survival of grasshoppers (n=10) in caged populations across spider and grasshopper treatments over time (± SE).

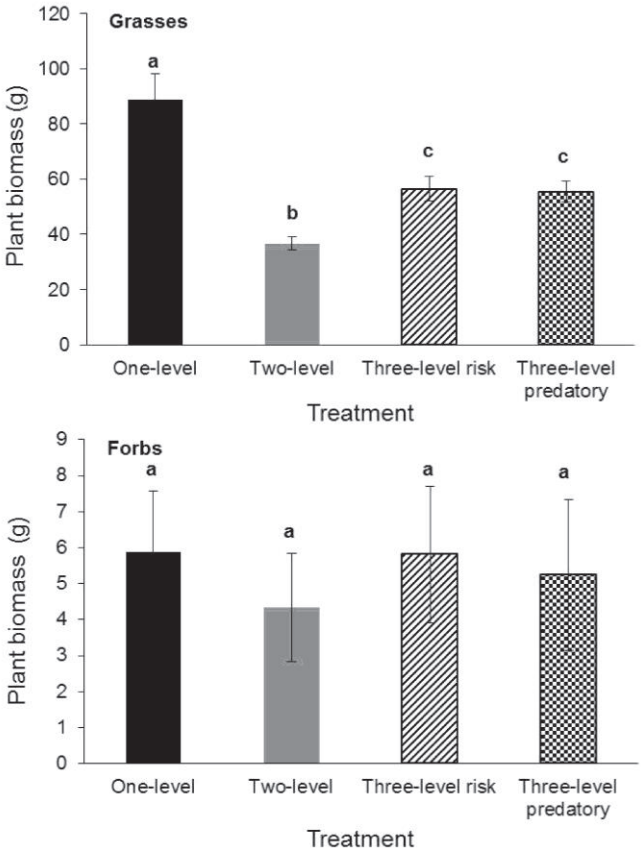


Fig. 2. Mean grass (top) and forb (bottom) biomass across trophic level treatments after the experiment was terminated (±SE). One-level treatment contains only plants; two-level treatment contains grasshopper nymphs and plants; and three-level treatment contains spiders, grasshopper nymphs, and plants. Columns bearing the same letter were not significantly different within treatments (Tukey HSD test, P > 0.05).

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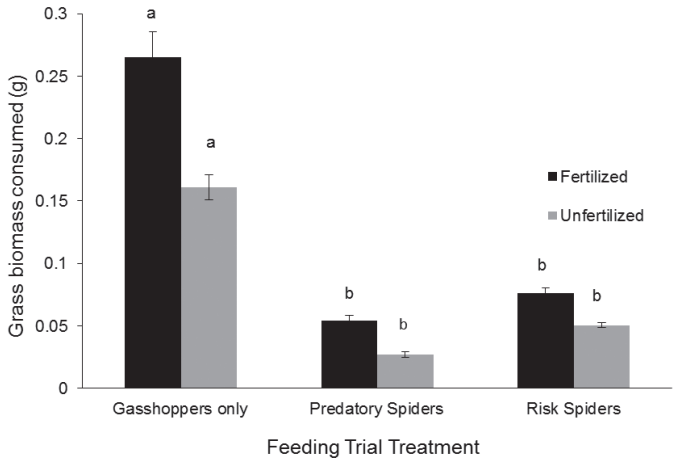


Fig. 3. Mean grass biomass consumed (± SE) in feeding trials across fertilization and spider exposure treatment combinations. Columns bearing the same letter were not significantly different within treatments (Tukey HSD test, $P > 0.05$).

consin old field. Although spider reduction of grasshopper survival was moderate, grass biomass in cages with spiders (both predator and risk types) was 35% higher compared to grasshopper-only field cages. In lab feeding studies, grasshopper nymphs consistently kept their distance from spiders and consumed less grass biomass compared to grasshoppers housed alone. Overall, our results indicate that spiders can limit grasshopper herbivory because of predator avoidance activity and may enhance primary productivity in old-field ecosystems. However, there is still considerable debate about the strength, nature, and significance of these interactions (Shurin *et al.* 2002).

We found no evidence of consumptive effects given that grasshopper survival did not differ between predatory versus risk exposed grasshopper populations. Therefore, the increase in grass biomass in the three-level web treatments was likely the result of reduced foraging time in the presence of a spider (Schmitz 1998). As the nymphs reach 4^{th}-5^{th} instar stages, spider predation rates drop as larger instars are harder to subdue (Oedekoven & Joern 1998). Yet, larger grasshopper nymphs at a lower risk of predation still respond behaviorally in a fearful manner in the presence of spiders (Danner & Joern 2004). Our results are indicative of this behavioral response since cages with both the predator and risk spider treatments resulted in similar amounts of remaining grass biomass (Fig. 2). Schmitz *et al.* (1997) also found similar effects on trophic dynamics in response to risk and predator spiders, and Beckerman *et al.* (1997) documented that grasshopper behavior was the same in the presence of a risk and predator spider. This suggests that in our experiment, the effects of a risk and predator on grass biomass were equivalent.

The remaining forb biomass in cages did not vary across trophic level treatments, which is consistent with similar studies conducted in a Connecticut old field (Schmitz 1994, Schmitz *et al.* 1997). The generalist grasshoppers in this system did not shift their diet from grasses to forbs, leading to a reduction of forb biomass. There are several possible explanations for this grass over forb preference. First, it is plausible that there was no observed diet shift because the forbs in our system may have been chemically defended whereas grasses are not (Joern 1979). Second, grasshoppers will sometimes shift their foraging to ingest more digestible carbohydrates under stress for more energy, and this may even be a limiting resource for them in some instances along with nitrogen (Hawlena & Schmitz 2010). Finally, grass and forb biomass may have also been biased because initial weights were unknown and were assumed to be somewhat equal by arbitrarily placing the cages over "similar" vegetation.

While we did find evidence of a trophic cascade at our site, its magnitude was much weaker than spider-grasshopper trophic cascades observed at other old-field sites (Schmitz 1994, Schmitz 1997, Rothley & Dutton 2006). We suspect that grasshopper ectoparasites may have weakened observed spider-grasshopper interactions. Throughout the field experiment, a substantial number of *M. borealis* became infected with two different ectoparasitic mites. *Eutrombidium locustarum* are red mites that commonly parasitize grasshoppers and attach to the wings and body, feeding on their hemolymph (Branson 2003). Another type of mite was much more abundant on *M. borealis*, is not formally named, and attaches to the appendages of grasshoppers (Belovsky *et al.* 1998). These mites were not present when the grasshoppers were stocked in experimental cages. Nevertheless, all surviving grasshoppers were infected with mites by the end of the experiment. The severity of infection ranged from mild to severe, with some individuals having over 60 mites on the appendages alone. Mites can decrease grasshopper survivorship (Belovsky *et al.* 1998), which may explain why spider reduction of grasshopper survival was relatively moderate. In addition, parasitized grasshoppers may increase their rate of food consumption to compensate for the loss of resources due to parasitism (Branson 2003). Thus, grasshopper consumption rates across all treatments may have been altered by parasitism.

The results of the laboratory feeding trials provide supplemental evidence that the trophic cascade observed in our field experiment was a result of non-consumptive interactions. Experimental grasshopper nymphs responded strongly to the presence of both risk and predatory spider. Grasshoppers housed with spiders consistently avoided the base of the aquarium where the food was placed. In the presence of spiders, grasshopper nymphs spent the majority of time on the sides and ceiling in the aquaria when a spider was present (Fig. 4). In the two trophic-level treatments, there was an 80% increase in the number of grasshoppers observed on the base of the cage compared to the three trophic-level system. Interestingly, food quality had no effect on grasshopper consumption rates in both the risk and predatory spider treatments. However, significantly less grass was eaten by grasshoppers housed with spiders in both the fertilized and unfertilized treatments compared to the amount of grass consumed by grasshoppers housed alone (Fig. 3). These results are tentative, given that the 12 hour starvation period may have not been long enough to properly induce hunger in our experimental grasshoppers. The short 6 hour duration of the feeding trial also may have been too short for food quality to have any effect on grass biomass consumed. Therefore, this experiment should be viewed as a supplement to the field experiment, showing the effects of spiders on the feeding behavior of grasshoppers. To adequately address grasshopper responses to food quality, future studies should starve experimental grasshoppers for longer periods of time and calculate behavior as a proportion over time rather than a count per each cage.

Taken together, our results indicate that predatory spiders can benefit plant communities by reducing grasshopper herbivory through fear alone. Our results are consistent with previous food web research conducted in old fields (Schmitz 1994, Schmitz *et al.* 1997, Schmitz 2003, Rothley & Dutton 2006). However, our results should be approached with some caution as grasshopper-spider interactions vary both spatially and temporally. This study specifically

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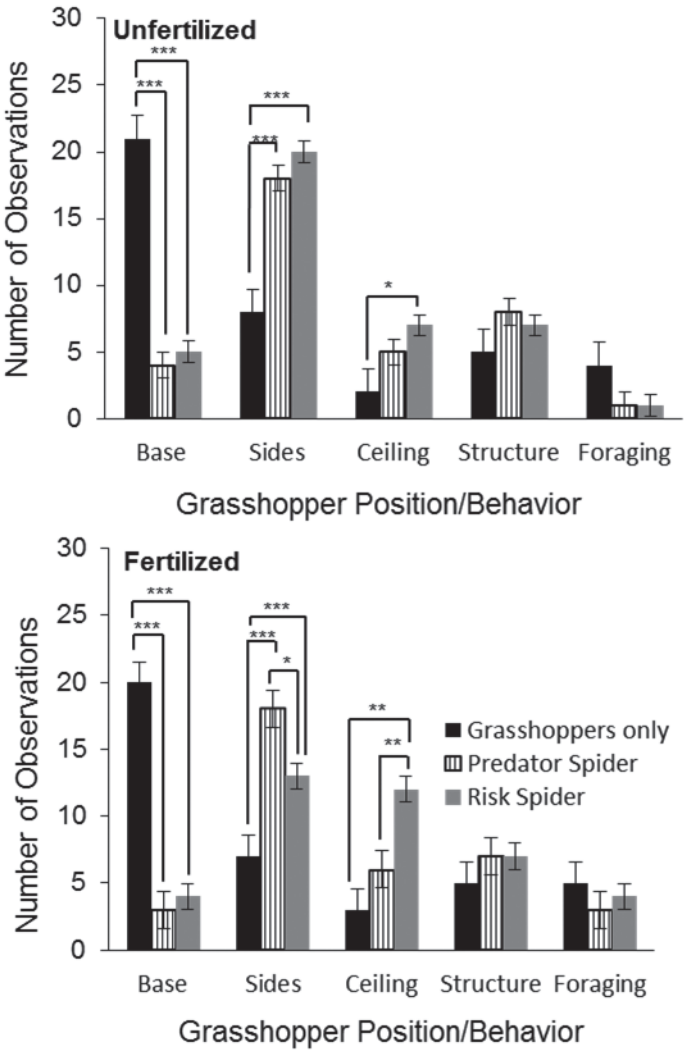


Fig. 4. Number of grasshopper observations (± SE) in unfertilized (top) and fertilized (bottom) food treatments with the presence of a risk or predator spider, or the absence of a spider. "Base, sides, ceiling, and structure" indicate a grasshopper's position in the cage, and "foraging" indicates a behavior. Grasshopper nymphs and spiders were housed in aquaria with a small branch (*i.e.*, structure) and offered one gram of fertilized or unfertilized grass. Asterisks indicate significant differences.

focused on the juvenile stages of two grasshopper species, but the strengths of these trophic interactions involving grasshoppers may be life stage dependent due to the variety of predators that feed on grasshoppers throughout their life cycle (Belovsky & Slade 1993). While grasshoppers outgrow significant predation pressure from spiders, adults experience intense predation from birds (Belovsky & Slade 1993, Joern 1986, Oedekoven & Joern 1997). Future studies should examine old-field food web dynamics over multiple years, and examine the effects of multiple predators on all grasshopper life stages. The dynamic, coupled oscillation that defines predator-prey populations and their functional responses should also be more closely examined to see if spider predators have this lagged effect on grasshopper population densities.

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