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BEHAVIORALLY MEDIATED TROPHIC CASCADES: EFFECTS OF PREDATION RISK ON FOOD WEB INTERACTIONS

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Abstract. Trophic cascades are regarded as important signals for top-down control of food web dynamics. Although there is clear evidence supporting the existence of trophic cascades, the mechanisms driving this important dynamic are less clear. Trophic cascades could arise through direct population-level effects, in which predators prey on herbivores, thereby decreasing the abundance of herbivores that impact plant trophic levels. Trophic cascades could also arise through indirect behavioral-level effects, in which herbivore prey shift their foraging behavior in response to predation risk. Such behavioral shifts can result in reduced feeding time and increased starvation risk, again lowering the impact of herbivores on plants. We evaluated the relative importance of these two mechanisms, using field experiments in an old-field system composed of herbaceous plants, grasshopper herbivores, and spider predators. We created two treatments, Risk spiders that had their chelicerae glued, and Predation spiders that remained unmanipulated. We then systematically evaluated the impacts of these predator manipulations at behavioral, population, and food web scales in experimental mesocosms. At the behavioral level, grasshoppers did not distinguish between Risk spiders and Predation spiders. Grasshoppers exhibited significant shifts in feeding-time budget in the presence of spiders vs. when alone. At the grasshopper population level, Risk spider and Predation spider treatments caused the same level of grasshopper mortality, which was significantly higher than mortality in a control without spiders, indicating that the predation effects were compensatory to risk effects. At the food web level, Risk spider and Predation spider treatments decreased the impact grasshoppers had on grass biomass, supporting the existence of a trophic cascade. Moreover, Risk spider and Predation spider treatments produced statistically similar effects, again indicating that predation effects on trophic dynamics were compensatory to risk effects. We conclude that indirect effects resulting from antipredator behavior can produce trophic-level effects that are similar in form and strength to those generated by direct predation events.

Key words: lethal direct effect; lethal indirect effect; Melanoplus femurrubrum; *old-field food web;* Pisurina mira; *predation risk; predator–prey interactions; top-down control; trophic cascade.*

INTRODUCTION

There is an overwhelming body of evidence in the ecological literature demonstrating that predators can have a tremendous influence on community structure and dynamics. This evidence comes from two independent, yet complementary, lines of research that examine the effects of predation at different organizational levels within natural systems. The first line of research, known conventionally as an interaction web approach (Menge 1995), examines the *lethal direct effects* of predators on prey populations, and determines how those direct effects pass along the entire network of direct and indirect pathways linking species in a community (e.g., Sih et al. 1985, Leibold 1989, Schoener 1989, Spiller and Schoener 1990, Jenkins et al. 1992, Paine 1992, Wootton 1992, 1994*a*, Menge et al. 1994, Schmitz 1994, De Ruiter et al. 1995, Menge 1995, Winemiller 1996). The second line of research examines how predators cause adaptive shifts in prey behavior or life history allocation. Changes in prey behavior, caused by predator presence, are known as risk effects. Risk effects are most commonly treated as a trade-off in which any attempt by prey to reduce predation hazard comes at the expense either of foraging time and, hence, increased mortality due to the risk of starvation, i.e., *lethal indirect effects* (Abrams 1984, Mangel and Clark 1986, McNamara and Houston 1987, 1994, Lima and Dill 1990, Ludwig and Rowe 1990, Hik 1995), or of altered life history schedules or habitat selection, i.e., *nonlethal indirect effects* (Sih 1987, Dodson and Havel 1988, Crowl and Covich 1990, Huang and Sih 1990, Ludwig and Rowe 1990, Skelly and Werner 1990, Rowe and Ludwig 1991, Werner 1991).

There is now increasing recognition these two independent lines of research must be integrated in order to evaluate the importance of behavioral- and population-level effects of predators on community dynamics (Abrams 1984, 1992, Mittelbach 1986, Mittelbach et al. 1988, Huang and Sih 1990, 1991, Turner and Mittelbach 1990, Werner 1992, Wissinger and Mc-

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Grady 1993, Werner and Anholt 1996). This integration is critical to the development of a complete understanding of predator impacts on communities. If predators have stronger effects on communities by altering prey behavior than by consuming prey, ecologists may have considerable difficulty explaining interactions within communities using conventional models of community dynamics that do not account for the behavioral indirect effects (Abrams 1984, 1992, 1996, Schoener 1993, Werner and Anholt 1996).

For example, many current models of trophic interactions (e.g., Hairston et al. 1960, Rosenzweig 1973, Oksanen et al. 1981, Carpenter et al. 1985, Menge and Sutherland 1987, Leibold 1989, Schmitz 1992) predict that predators indirectly benefit plants by reducing the abundances of herbivores eating the plants, i.e., cascading trophic effects (Paine 1980, Carpenter et al. 1985, Power 1992, Menge 1995; for empirical examples see Kajak et al. 1968, Power 1990, Spiller and Schoener 1990, Vanni and Findlay 1990, Huang and Sih 1991, Wootton and Power 1993, Schmitz 1994, Carter and Rypstra 1995, Hartvigsen et al. 1995). However, each predation event only influences a single herbivore prey per unit time, whereas the risk introduced by the mere presence of a predator could have more widespread effects, in that same time period, by causing many prey individuals to alter their foraging behavior.

Altered behavior can influence trophic interactions in several ways. For example, herbivores could move to different patches or plants to feed in response to risk. In this case, total herbivory per unit area may be the same as without predators, but localized impacts will be modified due to spatially explicit effects that are dependent on predator movement (e.g., Turner and Mittelbach 1990, Schmitz and Booth, *in press*). Alternatively, we may see a reduction in herbivore foraging activity, which translates into reduced impacts on the plant trophic level via two mechanisms (Abrams 1992). First, herbivores spend less time feeding on plants. Second, the increased starvation mortality reduces the number of herbivores feeding on plants.

The challenge now is to derive an empirical understanding of the relative contribution of predator effects on community dynamics arising indirectly through the effects of predation risk and directly via predation events (Turner and Mittelbach 1990, Huang and Sih 1991, Abrams et al. 1996, Werner and Anholt 1996). Such a research question requires research programs that manipulate predators in ways that preserve the species composition of natural communities, but alter the functional role of predators in community dynamics. One way to do this is to render predators incapable of subduing prey, yet ensure that the predators still are perceived by prey as a serious threat (e.g., Wissinger and McGrady 1993, Werner and Anholt 1996).

We present here the results of field experiments in an old-field system, composed of herbaceous perennial plants, phytophagous grasshoppers, and insectivorous spiders, in which the spiders' ability to capture grasshopper prey was manipulated. Old fields containing phytophagous grasshoppers are good candidates for studies on direct and indirect effects of predators, because grasshoppers are consumed by a wide range of predators (Lavigne and Pfadt 1966, Kajak et al. 1968, Joern and Rudd 1982, Joern 1986, 1992, Belovsky et al. 1990, Hurd and Eisenberg 1990, Fowler et al. 1991, Bock et al. 1992), their population dynamics can be strongly influenced by predation (Kajak et al. 1968, Joern 1986, 1992, Belovsky and Slade 1993, Schmitz 1993, 1994), and they are known to exhibit adaptive antipredator behavior (Schultz 1981). Our experiments were designed to evaluate the relative importance of two mechanisms by which predators could exert an indirect mutualistic effect on plants (i.e., trophic cascade) through their effects on herbivores (Fig. 1). First, an indirect mutualism between spiders and plants could be propagated largely by the consumption of grasshoppers by spiders, a direct predator–prey interaction (Fig. 1a). An indirect mutualism could also arise largely from changes in herbivore feeding activity and survival resulting from grasshopper antipredator behavior in the presence of spiders, a nonlethal predator–prey interaction (Fig. 1b) that could cause increased starvation mortality.

Our hypothesis of cascading trophic effects caused by predators rests on the assumption that the system exhibits top-down control (Schoener 1989, Power 1992, Schmitz 1992, 1993). This assumption is supported by previous work in a similar system (Schmitz 1994, 1997). We also assume that plants cannot be treated as a single trophic group or trophospecies (sensu Yodzis 1996) in our assessment of trophic interactions. We divided plants into two trophic groups, grasses and forbs. Grasshoppers appear to distinguish between grasses and forbs, as resources, on the basis of their relative patchy distribution in the field and differences in their net nutritional quality (Belovsky 1986*a*, *b*, Schmitz 1997). Grasshoppers potentially may distinguish more finely by plant species. However, previous work (Schmitz 1997) suggests that old-field plant species within a trophic group are functionally equivalent, since they have similar nutritional contents and are consumed at similar rates by grasshoppers (Schmitz 1997).

The multiscale nature of our research question dictated that we systematically evaluate the impacts of predators at morphological, behavioral, population, and food web scales. At the morphological level, we examined herbivore prey size selection by carnivores to determine the sizes of prey most vulnerable to predation by the spiders used in this study. At the behavioral level, we examined changes in herbivore vigilance and activity budgets induced by predators. At the population level, we independently investigated the effects of direct predation and predation risk on population dynamics of herbivore prey. Finally, at the entire food

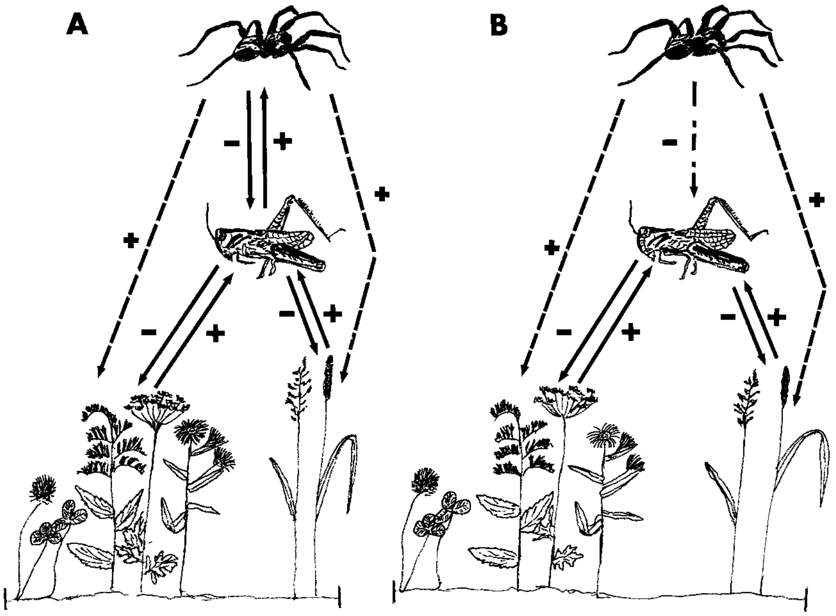

FIG. 1. Hypothesized mechanisms driving trophic cascades in the experimental old-field system composed of spiders, grasshopper nymphs, and herbaceous vegetation (forbs and grasses). Solid lines represent direct consumer–resource interactions (+/−). Dashed lines represent indirect interactions. The dash-dotted line represents a nonlethal effect or behavioral modification. In (A), trophic cascades are brought about by the direct lethal effects of spiders on grasshopper nymphs. In (B), trophic cascades are induced indirectly by spiders causing shifts in grasshopper foraging behavior and increasing starvation risk.

web level, we quantified the extent to which three-level trophic interactions are influenced directly by predation on herbivores and indirectly via responses of herbivores to predation risk.

METHODS

Study area and natural history

The study was conducted at the Yale-Myers Research Forest, in northeastern Connecticut near the town of Union. The research location is a 3240-ha northeastern hardwood ecosystem interspersed with old fields. Our research fields were abandoned from subsistence farming in the late 1960s, and currently support a variety of grass and forb species, the most abundant being *Phleum pratense, Solidago rugosa, Poa pratensis, Aster novaeangliae, Trifolium repens,* and *Daucus carota.* The most common phytophagous insect herbivores are the grasshoppers *Melanoplus femurrubrum,* a grass and forb generalist, and *Eritettix simplex,* a grass specialist (Vickery and Kevan 1967, Helfer 1987). The most common arthropod predators include wolf spiders (Lycosidae) and nursery web spiders (Pisuridae). Old fields in the research forest are attractive study systems because they combine moderate species richness and small-statured organisms. The small stature, in particular, allows us to include a representation of the entire community within experimental units when evaluating species interactions. Moreover, the comparatively low species richness of plants and phytophagous insect herbivores keeps evaluations of species interactions among trophic levels quite tractable (e.g., see Schmitz 1994, 1997).

Here, we report the effects of predation and predation risk caused by the nursery web spider, *Pisurina mira,* on nymphs (instar stages II–IV) of the most common grasshopper, *M. femurrubrum.* Trophic dynamics in grasshoppers, as in many size- or age-structured populations, are dependent on stage of the life cycle, with which vulnerability to particular predators varies (Lavigne and Pfadt 1966, Kajak et al. 1968, Joern and Rudd 1982, Joern 1986, 1992, Belovsky et al. 1990, Hurd and Eisenberg 1990, Fowler et al. 1991, Bock et al. 1992). Because of logistical limitations, we have not yet had the opportunity to replicate adequately systems involving adult grasshoppers at densities that match natural field conditions. Therefore, we cannot report on the results of experiments with adults. Nevertheless, our detailed, mechanistic examination of trophic interactions involving grasshopper nymphs illustrates the kinds of impacts that predators may have on trophic interactions, when the effects of predation and predation risk can be isolated and quantified using experimental methods that preserve the natural community structure and natural field densities.

We conducted our experiments between early July and mid-August, a time that is representative of the period during which consumers impact the field system through trophic interactions. In the study system, the key plant species are perennials (Britton and Brown 1970), which dominate the community from May until

November, when they begin to senesce. Grasshopper nymphs emerge in late June to early July, become adults in mid-to-late August, and begin to die off in late September following breeding. The nymphs are abundant during an ≈40-d period in which they develop through various instar stages at densities of 20–45 nymphs/m^2. At this same time, adult nursery web spiders co-occur with grasshopper nymphs at densities of 8–10 adults/m^2.

Morphological-level effects

Our morphological-level assessment focused on defining size classes of grasshoppers that could be consumed by the spider predators used in the field experiments. We sampled different life cycle stages of grasshoppers in the field to quantify their body length and body mass. Melanopline grasshoppers pass through five instar stages before becoming adults (Vickery et al. 1981). The specific instar stage of nymphs can be determined by the number of antennal segments (beginning with 13 and increasing by approximately three segments with each instar), and by the size and orientation of the wing buds (see Vickery et al. 1981). Adults have fully developed wings. Individual grasshoppers were caught in the field with a sweep net and were then held in outdoor terraria for subsequent measurements in the lab. In the lab, we used vernier calipers to measure the length of each individual from the head to the distal part of the last abdominal segment. We then measured body mass using an electronic balance.

Following the protocol in Schmitz (1993), we conducted a series of spider feeding trials, using all instar stages of grasshopper nymphs to identify which prey size classes were vulnerable to adult *Pisurina mira* spiders of a size that matched the sizes of spiders used in our field experiments on trophic interactions. Individual grasshoppers of known body size were placed with spiders of known body length (measured using vernier calipers) in a 0.6 × 0.6 × 0.6 m terraria made of aluminum screen. We placed small sticks, bark, and a piece of sponge saturated with water in each cage to provide spiders with a refuge from potentially lethal (dehydrating) conditions. The cages were lined up in a field setting, such that all terraria had the same exposure to sunlight. We presented each spider with a single fresh, field-caught grasshopper for a 24–48 h period, and monitored the cages every 2 h during daylight. In all cases, we were able to confirm that grasshopper mortality was due to spider predation, because the spiders were observed holding the grasshoppers with their chelicerae.

Behavioral-level effects

In order to render spiders ineffective at subduing prey, we glued together the chelicerae (mouthparts used to subdue prey) of adult *Pisurina mira* spiders. Chelicerae were glued by holding the spiders with foam-padded forceps under a stereoscopic microscope and then applying a nontoxic surgical cement to the mouthparts with a small paintbrush. One concern was that such physical manipulation would traumatize the spiders and, therefore, cause them to alter their predatory behavior. Second, we were concerned that our manipulations would cause spiders to behave in ways such that grasshopper prey would no longer perceive them as a threat. Therefore, we conducted behavioral observations on spiders and grasshoppers to evaluate the effect of gluing spider chelicerae.

Evaluating the effects of manipulating spiders.—We used the screen terraria to evaluate the response of grasshoppers to glued vs. nonglued spiders and to assess the effect of gluing on spider behavior. Our assessment was based on mobility of both spiders and grasshoppers in the terraria. We drew a 2 × 2 cm grid on each side of each terrarium to quantify movement in three-dimensional space. We placed small sticks, bark, and a piece of water-saturated sponge in each cage to provide spiders with a refuge from dehydrating conditions. The cages were placed in a field setting and arrayed linearly as previously described. We conducted two different trials in which individual spiders and/or grasshoppers were placed in a cage. Trial 1 compared movements of spiders that had glued chelicerae (Risk spiders) with those that were not glued (Predation spiders). Trial 2 quantified the movement, after placement at a random starting point, of grasshoppers (1) alone, (2) with Risk spiders, (3) with Predation spiders, and (4) with a fake spider (a child's novelty toy). Behavioral observations were made on eight individual grasshoppers, glued spiders, and nonglued spiders. In all trials, individuals were observed at six time periods (4-h intervals) over 24 h. At each time period, individuals in all cages were observed for 1 h and movements were quantified at 10-min intervals within each hour. The 10-min values were averaged for each hour. Because the activity level of ectotherms such as grasshoppers and spiders is sensitive to thermal conditions, we examined behavior during three different 24-h periods with different thermal environments to obtain a representative average for activity.

Evaluating grasshopper responses to predators.—We used the screen terraria to quantify feeding-time budgets of the grasshoppers. Each of 10 terraria was randomly assigned to one of two treatments: no predator or predator. The terraria were placed in a field setting in a line, with uniform exposure to the sun. We placed a 40-cm^2 piece of fresh, watered sod containing a mixture of forbs and grass 25–30 cm tall in each terrarium. Four fourth-instar *Melanoplus femurrubrum* grasshoppers were assigned to each terrarium. Each terrarium designated as a predator treatment was assigned a single, nonglued *P. mira* spider predator.

The plants and animals were placed in the terraria in the afternoon prior to the day of observations to allow the grasshoppers and spiders time to acclimatize to the enclosures. On the morning of each observation day, the grasshoppers and spiders were counted to ensure that four nymphs were present for the observation period (i.e., no natural or predation deaths had occurred overnight). Each of the 10 cages was observed at 20-min intervals from 0600 to 2000. We examined behavior during three different days with different thermal environments (e.g., overcast vs. clear conditions, hot vs. cool temperatures) to obtain a representative average time budget.

We measured grasshopper daily activity budgets, in the absence and presence of spiders, using feeding as an index of activity. We examined the interior of each cage to determine whether the grasshoppers were feeding during a sampling period, and if so, how many. We attempted to minimize the impact of our shadow and air disturbance on the grasshopper in each cage during this observation by crawling quietly next to each cage. If the grasshoppers were feeding when the observation was made, they were assumed to be active for the entire 20-min period.

Population- and trophic-level effects

We followed the protocol described in Schmitz (1993, 1994, 1997) to create experimental food webs in which to assess the herbivore population-level and trophic-level effects of predators. The experiment was designed to partition and quantify the indirect effects of predation risk and the direct effects of predation (Fig. 1) at the herbivore population level and at the entire food web level. At the herbivore population level, we monitored grasshopper survival under different predator manipulations. At the trophic level, we analyzed the changes in plant abundance brought about by interactions between carnivores and herbivores, relative to a control in which spiders and grasshoppers were absent.

The experiment was conducted in 1994 and repeated in 1995 in a 50 × 50 m area within the field site, using 0.1 $m^2 \times 1$ m exclosure cages (Ritchie and Tilman, 1992, Belovsky and Slade 1993, 1995, Schmitz 1993, 1994, 1997). Cages were constructed with aluminum screening and were fastened at the base to a 126 × 10 cm strip of aluminum sheet metal. Cages were secured by sinking the sheet metal beneath the soil surface and by fastening the sides of the cages to wooden stakes. The cages were separated by ≈1.5 m and were arrayed in a randomized block experimental design consisting of eight blocks (1994) or 10 blocks (1995), with four treatments (trophic-level manipulations) replicated once per block. In the enclosure cages, we assembled experimental food webs (treatments) composed of one trophic level (plants), two trophic levels (plants plus *Melanoplus femurrubrum* nymphs), or three trophic levels (plants, grasshopper nymphs, and adult *Pisurina mira* spiders). In addition, we physically manipulated spiders, using the gluing method previously described, to create two different predation treatments for the three trophic-level food webs: (1) Risk spider treatment (glued spiders), and (2) Predation spider treatment (nonglued spiders). Gluing the chelicerae did not result in starvation of the spiders during the course of the study, as all individuals were recovered at the end of the field experiment. Moreover, the chelicerae remained glued together on all individuals. Table 1 summarizes the treatments and number of replicates in each of two years of the study.

TABLE 1. Design of the field experiment to test population and food web level effects of predation and predation risk in the Yale-Myers Research Forest study system. Values are the number of experimental replicates.

	Treatment			
			Three trophic levels	
Year	One trophic level†	Two trophic levels‡	Risk spiders	Predation spiders
1994	8	8	8	8
1995	10	10	10	10

† Control for experiments evaluating the trophic-level effects of predation risk and predation.

‡ Control for experiments evaluating grasshopper population level effects of predation risk and predation.

We stocked 10 early (II and III) instar grasshopper nymphs or 10 nymphs and one adult spider to experimental cages. The spider numbers matched field densities. The exact grasshopper stocking density was arbitrary (1.3 times higher than maximum field densities measured at the time of stocking). However, grasshoppers were intentionally stocked at a higher level to produce a pulse perturbation that would cause their densities to decline toward a steady state set by various limiting factors in each cage (i.e., food, predators, etc.), and that would allow the potential to reach maximum field densities in some cages. This would not be possible if we were to stock all cages at average field levels and maintain densities there. Because there was no a priori way of knowing appropriate grasshopper densities for the background conditions in each cage, we needed a pulse perturbation to avoid the possibility of artificially high resource limitation in some cages and unrealistically low levels in others. The pulse perturbation has no artificially adverse affects on plant biomass, as previous food web experiments (Schmitz 1994) revealed no differences in plant abundance between cages and random field plots, each with three trophic levels. It was also important to ensure that we reached a steady state, because our predictions of food web interactions assume a steady-state system.

All caged grasshoppers were censused every 2 d to monitor natural survivorship over the course of the field experiment, during which the grasshopper nymphs passed from early-instar (II and III) to late-instar (V) stages. The experiments ran for 30 d each year. We terminated the experiments when the grasshopper nymphs began to molt into adults, because the feeding trials indicated that adult *P. mira* spiders were incapable of subduing adult grasshoppers. Upon termina-

TABLE 2. Morphometric characteristics of the different stages in the life cycle of *Melanoplus femurrubrum* grasshoppers at the Yale-Myers Research Forest.

		Body mass (g)		Body length (mm)	
Stage of life cycle	*n*	$\bar{X}$	1 SE	$\bar{X}$	1 SE
Early nymphs (instars I–III)	20	0.050	0.001	9.4	0.3
Late nymphs (instars IV–V)					
Females	20	0.216	0.020	20.9	2.3
Males	20	0.169	0.015	18.1	1.8
Adults					
Females	20	0.515	0.016	24.2	1.1
Males	20	0.285	0.009	20.0	0.9

tion of the experiment, we collected all nymphs by cage and preserved them in 70% alcohol. All aboveground live plant material within each cage was clipped at the soil surface, sorted to species, dried at 60°C for 48 h, and weighed.

RESULTS

Morphological-level effect

The morphometric characteristics of different stages in the grasshopper lifecycle are presented in Table 2. Given that specific stages were similar in body size, we grouped the grasshoppers according to three distinct size classes: early (I–III) instar nymphs, late (IV–V) instar nymphs, and adults.

The range of grasshopper sizes presented to, and eaten by, different-sized *Pisurina mira* spiders is presented in Fig. 2. There was an increase in the size range of prey eaten with increasing spider body size. However, the feeding trials indicate that there were upper limits to the size of prey that could be consumed by a predator of a certain body size. The largest spiders (16–18 mm) used in our studies would be capable of subduing a grasshopper up to a maximum size of 19 mm (Fig. 2). This range would include all early-instar nymphs, and most late-instar nymphs, but not adults (Table 2).

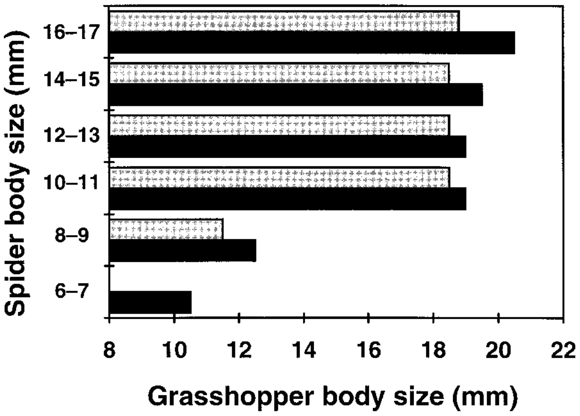

FIG. 2. Range of grasshopper body sizes presented to (solid bars) and eaten by (shaded bars) adult *Pisurina mira* spiders of different body size classes in spider feeding trials. The size range of grasshoppers eaten increases with spider body size. Grasshopper body sizes include all early-instar and most late-instar nymphs, but not adults, indicating that *P. mira* spiders are unable to subdue adult grasshoppers.

Behavioral-level effects

Evaluating the effects of manipulating spiders.—A *t* test revealed that there was no significant difference ($P > 0.50$; Fig. 3) in movement between Risk spiders

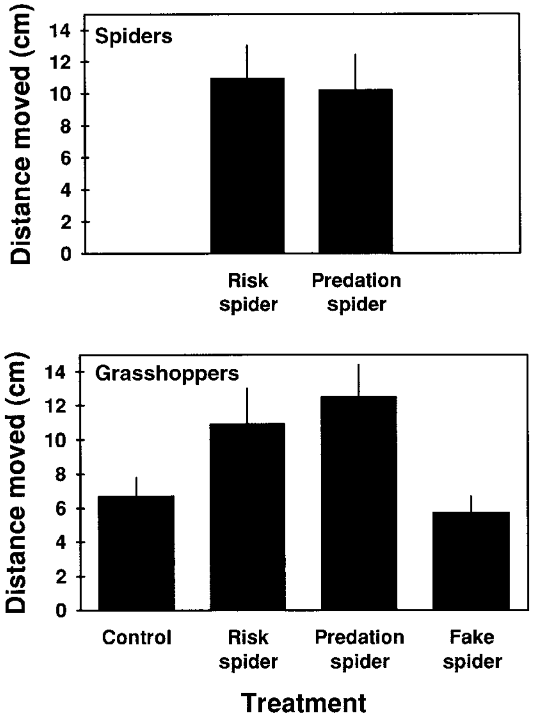

FIG. 3. Movement distances of spiders and grasshoppers in experimental terrraria placed in a field setting. Spider movement experiments were conducted to determine if gluing spider chelicerae (Risk spider treatment) altered their behavior relative to spiders with chelicerae not glued (Predation spider treatment). Grasshopper movement experiments were conducted to evaluate whether grasshoppers could distinguish between real and fake spiders, and whether or not they perceived Risk spiders and Predation spiders as equally threatening. Values are mean + 1 SE.

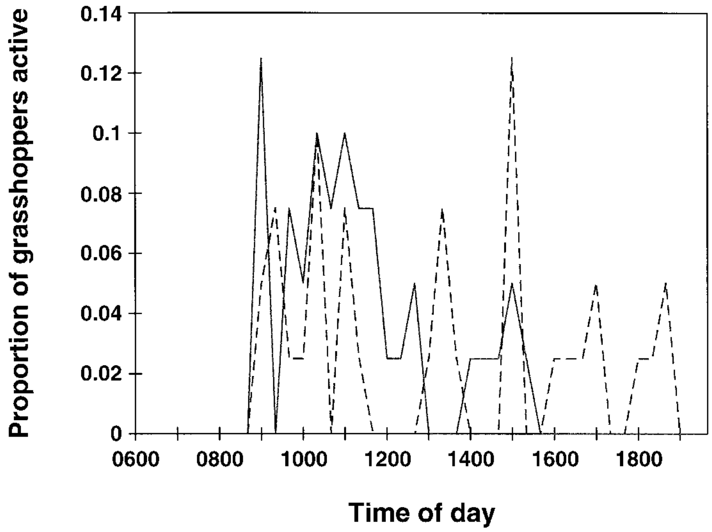

FIG. 4. Feeding-time budgets of grasshopper nymphs in the absence (dashed line) and presence (solid line) of spider predators. Time budgets were measured in terraria placed in a field setting.

(chelicerae glued) and Predation spiders (chelicerae not glued), suggesting that our manipulations did not alter the movement and hunting behavior of the spiders. ANOVA revealed a significant pattern ($F = 3.47$; df $= 3, 28$; $P = 0.03$) in grasshopper movement behavior (Fig. 3). A Tukey test indicated that grasshoppers (1) exhibited significant differences in movement when in the presence of real spiders vs. when alone ($P < 0.05$); (2) were able to distinguish between real and fake spiders ($P < 0.05$); and (3) did not distinguish between Risk spiders and Predation spiders ($P > 0.25$).

Evaluating grasshopper responses to predators.—A two-way contingency table analysis revealed that grasshoppers exhibited significantly different ($\chi^2 = 44.3$, df $= 30$, $P < 0.05$) activity budgets under predation vs. no predation treatments (Fig. 4). Activity in the presence of spiders was concentrated between 1000 and 1300 (Fig. 4), which tends to be the hotter part of the day when spiders are least active (O. J. Schmitz and A. P. Beckerman, *unpublished data*).

Population-level effects

We compared the final densities of grasshoppers in two-level food webs vs. three-level food webs with Risk spider and Predation spider treatments (Fig. 5), using a random complete block ANOVA, followed by a Tukey test. The ANOVA table and Tukey probabilities are presented in Table 3.

ANOVA revealed that there was a significant treatment (spider abundance) effect on grasshopper density. There was no significant year effect, indicating that the pattern in grasshopper densities was consistent between years. There also were no significant block effects or year × treatment interactions.

A Tukey test (Table 3) revealed a significant differ-

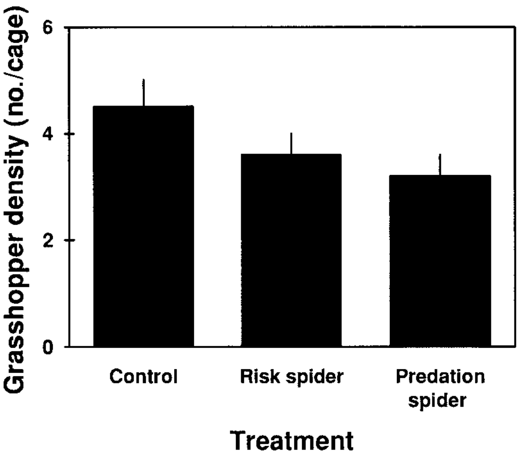

FIG. 5. Effects of predation risk (Risk spiders) and predation (Predation spiders) relative to a control (no spiders) on densities of grasshopper nymphs in experimental old-field food webs. Values are mean + 1 SE.

TABLE 3. Results of the randomized-block ANOVA and Tukey test for the experiment testing the effects of predation risk and predation by spiders on grasshopper population density in the Yale-Myers Research Forest study system. Treatments are predation risk and predation relative to a control that excluded predators.

Randomized-block ANOVA

Source of variation	df	F	P
Treatment	2	3.30	0.05
Year	1	2.27	0.117
Block	9	1.40	0.253
Treatment × year	2	1.445	0.634
Error	39		

Tukey test probabilities (H_0)†

	Control	Risk spiders
Risk spiders	0.07	
Predation spiders	0.05	0.80

† Treatment differences are due to random chance.

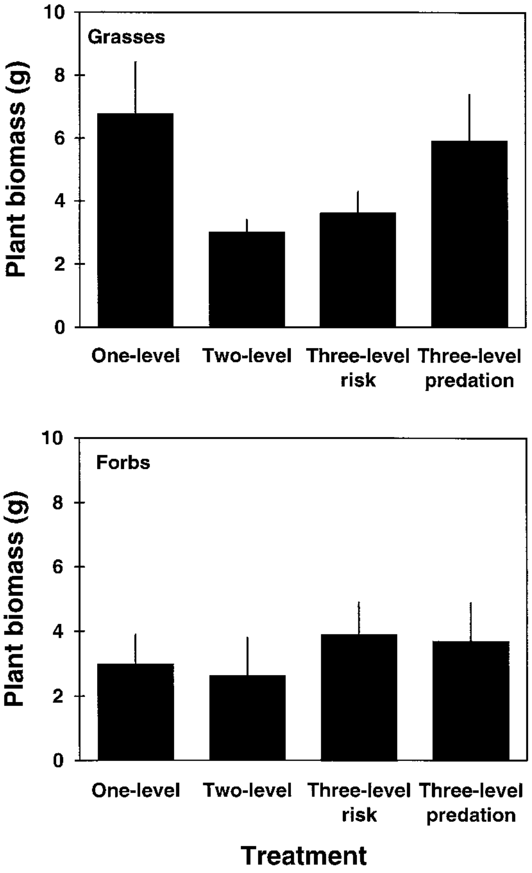

FIG. 6. Effect of trophic-level manipulations on grass and forb biomass in experimental old-field food webs. One-level webs contain plants only; two-level webs contain grasshopper nymphs and plants; and three-level webs contain spiders, grasshopper nymphs, and plants. In three-level webs, Risk treatments contained spiders that had their chelicerae glued together; Predation treatments contained spiders that were not glued. Values are mean + 1 SE.

ence between the Predation spider treatment and the control (no spiders), and a marginally significant difference between the Risk spider treatment and the control. Indeed, there was an average 20% reduction in grasshopper densities in the risk-only treatment relative to the control, and a 29% reduction in density in the risk-plus-predation treatment. The difference in grasshopper density between Risk spider and Predation spider treatments was not significant (Table 3), indicating that the risk effects were similar in magnitude to the predation effects. A power analysis revealed a 10% chance of committing a Type II error (i.e., concluding that there was no treatment effect when there really was), given $\alpha = 0.05$ and $n = 18$ replicates.

Trophic-level effects

Based on the working hypothesis for trophic interactions (Fig. 1), we tested for the existence of a trophic cascade in grasses and forbs separately. The signature for a trophic cascade at the plant level is that the addition of herbivores (two-trophic-level web) will cause a reduction in plant biomass from its initially high level (one-trophic-level web), and that the addition of carnivores (three-trophic-level web) will reverse the effects of herbivores, resulting in a net increase in plant biomass from two-trophic levels (Schmitz 1993, Wootton 1994*b*, Menge 1995). We compared the biomass of grasses and forbs in one-level food webs (plants only) with biomasses in two-level food webs and three-level food webs with Risk spider and Predation spider treatments (Fig. 6). We used a random complete block ANOVA, followed by a Tukey test whenever there was a significant difference.

TABLE 4. Results of a randomized-block ANOVA and Tukey test for the experiment testing the effects of predation risk and predation on grass biomass, mediated through the herbivore trophic level in the Yale-Myers Research Forest study system. Treatments are the different numbers of consumer trophic levels in the experimental food webs, relative to a control containing plants alone (one-level food web).

Randomized-block ANOVA

Source of variation	df	*F*	*P*
Treatment	3	3.91	0.013
Year	1	0.585	0.448
Block	9	0.741	0.670
Treatment × year	3	1.810	0.325
Error	55		

Tukey test probabilities (H_0)†

	One level	Two levels	Three levels (Risk spiders)
Two levels	0.01		
Three levels (Risk spiders)	0.10	0.08	
Three levels (Predation spiders)	0.80	0.05	0.45

† Treatment differences are due to random chance.

ANOVA revealed that there was a significant treatment effect (Table 4) on grass biomass (Fig. 6). There was no significant year effect or treatment × year interaction, indicating that the trophic-level pattern was consistent between years. There also was no significant block effect.

A Tukey test (Table 4) revealed that the difference between the plant-only control (one-level food web) and the herbivore treatment (two-level web) was significant. The differences between the Risk spider treatment vs. control and the Predation treatment vs. control (Fig. 6) were not significant (Table 4). However, the difference in grass biomass between the Risk spider treatment and the two-level web was marginally significant (Table 4), and the difference between the Predation treatment and the two-level web was significant (Table 4). These comparisons support the conclusion that a trophic cascade exists in grass biomass (Fig. 6). Grasshoppers caused a significant reduction in grass biomass, and spiders significantly reduced the impact of grasshoppers on grass biomass. Moreover, the difference between the Risk spider and Predation spider treatments was not significant (Table 4), indicating that the risk effects on trophic dynamics were similar to predation effects. A power analysis revealed that that there was a 10% chance of committing a Type II error (i.e., concluding that there was no trophic cascade when there really was), given $\alpha = 0.013$ and $n = 18$ replicates.

ANOVA revealed that there was no significant treatment effect ($P = 0.835$) on forb biomass (Fig. 5).

DISCUSSION

A trophic cascade, the propagation of an indirect mutualism between nonadjacent trophic levels by a predator–prey interaction between adjacent trophic levels, is regarded as an important signal for top-down control in food webs (Schoener 1993, Menge 1995). Although trophic cascades have been demonstrated experimentally in many systems (e.g., Kajak et al. 1968, Power 1990, Spiller and Schoener 1990, Vanni and Findlay 1990, Huang and Sih 1991, Strong 1992, Wootton and Power 1993, Schmitz 1994, Carter and Rypstra 1995, Hartvigsen et al. 1995), our understanding about the mechanisms driving this pattern is still limited (Turner and Mittelbach 1990). In this study, we experimentally evaluated the relative importance of two mechanisms thought to be responsible for inducing trophic cascades. First, carnivores could indirectly benefit plants through their direct, lethal effects on herbivore prey. This mechanism is embodied in conventional theory on trophic interactions (Rosenzweig 1973, Oksanen et al. 1981, Carpenter et al. 1985, Menge and Sutherland 1987, Leibold 1989, Schmitz 1992, Schoener 1993, Menge 1995). Second, carnivores could indirectly benefit plants by causing shifts in the behavior of individual herbivores that result in reduced feeding time and increased risk of starvation within herbivore populations. This second mechanism is embodied in more contemporary theory on trophic interactions (Abrams 1984, 1992, 1996). Our study indicates that a predator-induced, indirect behavioral effect in herbivores is the underlying mechanism driving a trophic cascade in our experimental old-field system. This conclusion is based on measured changes in grasshopper behavior and diet selection, with effects manifest at three organizational levels: behavior, population, and food web.

We found that grasshoppers shifted their daily activity time when in the presence of predators (Fig. 4.). A detailed, complementary foraging study on this system showed that grasshoppers also exhibited a significant diet shift when they were exposed to the same levels of predation risk as in this study (K. D. Rothley and O. J. Schmitz, *unpublished data*). The altered activity time, coupled with the diet shift, translates into an estimated 25% reduction in daily energy intake. Moreover, most of the grasshopper foraging activity under predation risk was concentrated between 1000 and 1300. (Fig. 4), which tends to be the hotter part of the day when spiders are least active (O. J. Schmitz, A. P. Beckerman, and K. M. O'Brien, *unpublished data*). Although there may be a reduction in predation risk by such a time budget shift, the reduced risk of predation may be partially offset by the increased risk of mortality resulting from coping with increased heat loads (Chappell and Whitman 1990). Prolonged exposure of grasshoppers to higher temperatures could induce heat stress. Such heat stress not only entails significant energetic costs (Chappell and Whitman 1990), but also can result in heat torpor and uncoordinated locomotion (Chappell 1983, Chappell and Whitman 1990). This could increase the vulnerability of grasshoppers to predation during later time periods if the heat load is not dissipated rapidly.

We observed a 20% reduction in grasshopper abundance when grasshoppers were faced with predation risk only (Risk spider treatment). By comparison, the Predation spider treatment caused a 29% reduction in grasshopper abundance. Moreover, grasshopper abundances in both treatments were not significantly different. It appears, then, that mortality from direct predation is largely compensatory to indirect mortality from risk effects.

We observed a trophic cascade in the spider–grasshopper–grass pathway of the food web (Fig. 1). The cause of this cascade can be traced directly to changes in herbivore foraging behavior that result from predation risk. In the absence of predators, grasshoppers in this system selected a diet composed almost entirely of grass (91 ± 11%, mean ± 1 SE; $n = 20$ grasshopper nymphs [K. D. Rothley and O. J. Schmitz, *unpublished data*]). This accounts for the significant reduction in grass biomass, and lack of significant change in forb biomass, in the experimental two-trophic-level food webs relative to the one-level controls (Fig. 6). When faced with predation risk, grasshoppers reduced dramatically the percentage of grass in the diet (32.5 ± 6.5 %, mean ± 1 SE; $n = 20$ grasshopper nymphs [K. D. Rothley and O. J. Schmitz, *unpublished data*]). This diet shift, combined with decreased feeding time and lower grasshopper abundances brought about by predation risk, can account for the decreased impact of grasshoppers on grass biomass in three-level food webs relative to two-level webs in ways that are consistent with assumptions of contemporary theory on indirect, behavioral effects of predators on food web dynamics (Abrams 1984, 1992). Hence, the effects of predation risk on grasshopper diet selection and survival seem to explain the emergence of a trophic cascade in grass biomass. It is uncertain why forb biomass did not decrease when grasshoppers shifted their diet to that resource in three-level food webs. Insight from previous work with similar old-field plants (Schmitz 1994, 1997) suggests that herbivore mediation of plant–plant competitive interactions may not be simply linear, i.e., forb abundance is not expected to compensate exactly for changes in grass abundance.

Our conclusion, that risk effects could account for the majority of variation in grasshopper density and could be the driving force behind the trophic cascade, implies that the Risk spider treatments were more similar to the Predation spider treatments than to other treatments. This is open to subjective interpretation. We claimed that the effects of Risk spider treatments on grasshopper population density and grasshopper impacts on grass biomass were marginally significant (i.e., $0.08 < \alpha < 0.05$; Tables 3 and 4), whereas the effects of Predation spider treatments were significant (i.e., $\alpha = 0.05$). We feel justified in concluding that there was a sigificant Risk effect for two reasons. First, the Tukey test, used to discriminate the source of significant effects at the population level, revealed that there was an order of magnitude greater likelihood that grasshopper abundances in Risk spider treatments were more similar to abundances in the Predation spider treatments than to the control (Table 3). The Tukey test also revealed that grass biomass in Risk spider treatments was more similar (by a factor of sixfold) to grass biomass in Predation spider treatments than to grasshopper-only treatments. Second, the power analysis, based on the differences between treatments with the closest means (i.e., three-level, Risk spider vs. two-level treatment) indicated that there was a strong likelihood (90%) that we are detecting a trophic cascade, given our level of replication. This implies that a larger number of replications is unlikely to change our interpretation.

This study focused specifically on the juvenile stage of *Melanoplus femurrubrum* grasshoppers, their plant resources, and their predators. This represents one portion of the entire grasshopper life cycle in which detailed mechanistic observations can be made at a spatial scale that matches natural field conditions (Schmitz 1993, 1994). The strengths of trophic interactions involving grasshoppers tend to be dependent on stage of the life cycle, because the kinds of predators feeding on grasshoppers vary with the life cycle of the grasshoppers (Onsager 1983, Belovsky et al. 1990, Belovsky and Slade 1993, Schmitz 1993). Thus, it would not be appropriate at this time to extrapolate our findings to the adult grasshopper stage. However, we have begun to evaluate experimentally the importance of risk vs. predation effects on trophic interactions involving adult grasshoppers, at a spatial scale more representative of natural field conditions when adult grasshoppers exist in the system. We do not yet have adequate replication to present the results of experiments involving adult grasshoppers. Nevertheless, the current study indicates that, for certain stages of the life cycle, antipredator behavior can produce trophic-level effects that are similar in form and strength to those generated by direct predation events.

The distinction between predation risk and predation is well established in theoretical and empirical research on predator–prey interactions. However, the implications of this distinction on the dynamics and structure of larger food chains or food webs have remained largely theoretical. Our research demonstrates that indirect effects at the behavioral level, in populations that comprise the food webs, are potentially responsible for community level, indirect patterns such as trophic cascades. In our study, herbivore time budget and diet shifts in response to predation risk, rather than direct mortality due to predation, seem to be the most parsimonious explanations of the trophic cascade. Whether or not this is true in general remains to be determined. It would be worthwhile to begin considering the behavioral responses induced by predator presence, as well as accounting for classic consumption interactions, when investigating the source and outcome of indirect trophic-level effects.

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