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Direct and Indirect Effects of Predation and Predation Risk in Old-Field Interaction Webs

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abstract: Indirect effects emerge when a change in the abundance of one species indirectly affects another by changing the abundances of intermediate species—called density-mediated indirect effects—or they arise when one species modifies how two other species interact—called trait-mediated indirect effects. I report on field experiments that evaluated how grass and herb biomass in old-field interaction webs was influenced indirectly by a spider carnivore through its interactions with a generalist and a grass-specialist grasshopper species. I manipulated interaction pathways between the spider and the plants using different combinations of the grasshopper species. I changed the modality of predator-prey interactions to isolate density-mediated from trait-mediated effects using natural spiders (predation spiders) or spiders that were prevented from subduing prey by mouthpart manipulation (risk spiders). I found that indirect effects were stronger in speciose, reticulate food webs than in linear food chains owing to a trait-mediated effect, a diet shift by herbivores in response to predation risk. Spiders alone did not have significant effects on grasshopper densities in the field experiments, removing any possibility of density-mediated indirect effects. The study illustrates that ecologists should not underestimate the importance of behavioral ecology in determining community-level interactions.

Keywords: food web interactions, indirect effects, density-mediated indirect effects, trait-mediated indirect effects, predation, old-field arthropods.

Ecologists are heavily engaged in developing a predictive theory for the dynamics of food webs (Yodzis 1988, 1996; Abrams 1992, 1993; Strong 1992; Pimm 1993; Schoener 1993; Menge 1995; Leibold 1996; Polis and Strong 1996; Schmitz 1997). Such a body of theory is crucial as it will

provide the foundation for understanding how natural ecosystems can maintain critical function in the face of natural and anthropogenic disturbances that could affect the abundances of different species in a system (Yodzis 1988, 1996; Johnson et al. 1996). Theory tells us that we may expect a variety of important indirect effects to emerge as a consequence of disturbances (perturbations) because the dynamics of particular species on which they may have an impact are often tightly linked to the dynamics of other species (Yodzis 1988, 1996; Abrams 1992, 1996; Pimm 1993; Schoener 1993; Wootton 1994; Menge 1995; Schmitz 1997). The concern, however, is that the importance of these indirect effects are not clear because two fundamental questions remain largely unanswered, empirically (Schoener 1993). To what extent does the net effect of one species on another depend on indirect effects? Are trophic interactions between species affected by the length of the interaction pathway—that is, do distant species matter? The extent to which indirect effects and distance species matter will depend on the nature of the indirect effects (Wootton 1994; Abrams et al. 1996).

Indirect effects emerge when the impact of one species on another is influenced by one or more intermediate species (Abrams 1992; Schoener 1993; Wootton 1994; Abrams et al. 1996). They can arise when a change in the abundance of one species (say species A) indirectly affects another (species B) by changing the abundance of intermediate species that interact with both species A and B (Schoener 1993; Wootton 1994; Abrams et al. 1996). This has been called a density-mediated indirect effect (Abrams et al. 1996). A trophic cascade, a classic indirect mutualism between predators and plants resulting from lethal direct effects of predators on herbivores (Schoener 1993; Menge 1995), is an example of a density-mediated indirect effect. Indirect effects may also arise when one species modifies the way two other species interact, which is called a trait-mediated indirect effect (Abrams et al. 1996). A trophic cascade arising from nonlethal direct effects such as changes in prey diet or habitat selection due to increased predation risk (e.g., Turner and Mittel-

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bach 1990; Huang and Sih 1991; McIntosh and Townsend 1996; Moran et al. 1996; Beckerman et al. 1997; Schmitz et al. 1997) is an example of a trait-mediated indirect effect.

I report here on research aimed at understanding the relative importance of density-mediated and trait-mediated indirect effects in experimental tritrophic level interaction webs (sensu Paine 1980; Menge 1995) composed of a species of spider carnivore, leaf-chewing generalist and specialist grasshoppers, and perennial grasses and herbs. I systematically manipulated the number of species in the interaction webs to alter the length of interaction pathways. I also manipulated the ability of individual predators to capture and subdue prey to change the nature of the indirect effects carnivores could propagate on species lower down in the interaction web. These manipulations enabled me to quantify how predators induced trophic cascades via direct consumption of herbivore prey (density-mediated effect) and via the induction of adaptive antipredator behavior of herbivore prey (trait-mediated effect).

Interactions among species that arise from predation and behavioral shifts involve processes at more than one organizational level (i.e., behavioral and population). The challenge is to identify how the biological processes at each level are manifest at the level of the entire interaction web. A necessary prerequisite to this understanding is a knowledge of the relevant natural history detail of the species involved in the interactions (Wootton 1993). In the following, I present the natural history relevant to the interaction webs being examined. I then develop a set of working hypotheses about direct and indirect interactions among the predator, herbivore, and plant species based on the natural history detail. Finally, I present and discuss the results of field research aimed at evaluating the predictions of the working hypotheses.

Natural History and Background

The study system is located at the Yale-Myers Research Forest in northeastern Connecticut near the town of Union. The research location is a 3,240-ha northeastern hardwood ecosystem interspersed with old fields. The fields were abandoned from farming in the late 1960s, and they currently support a variety of perennial grass and herb species, the most abundant being *Phleum pratense*, *Solidago rugosa*, *Aster novaeangliae*, *Trifolium repens*, and *Daucus carota*. The most common insect herbivores are the phytophagous grasshoppers *Melanoplus femurrubrum* and *Chorthippus curtipennis*, the goldenrod beetle *Trirhabda virgata*, the sap-feeding spittlebug *Philaenus spumarius*, and the sap-feeding plant bugs *Leptoterna dolobrata*, *Lygus lineolaris*, and *Lopidea media*. The

fields contain a variety of arthropod predators including the wolf spiders *Hogna punctulata* and *Hogna rabida*, the nursery web spider *Pisaurina mira*, the jumping spider *Phidippus rimator*, and various other small lycosids, for example, *Schizocosa* spp. and *Pirata* spp. The old fields in the research forest are attractive study systems because there is a combination of 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.

Previous research at the field site revealed that there was considerable potential for predators to exert their influence on plants via density-mediated and trait-mediated indirect effects (Beckerman et al. 1997; Rothley et al. 1997; Schmitz et al. 1997). That series of studies examined adaptive shifts in *M. femurrubrum* foraging behavior in response to predation risk induced by the nursery web spider *P. mira*. The consequences of the behavioral shifts on trophic interactions were examined by community-level experiments that manipulated the predators in ways that preserved the species composition of the experimental community but altered the functional role of predators in community dynamics. This was accomplished by rendering individual spiders incapable of subduing prey yet ensuring that they were still perceived by prey as a serious threat. The spiders' ability to capture and subdue prey was manipulated by gluing their chelicerae (feeding mouthparts) with nontoxic surgical cement. Such altered individuals were called *risk spiders*. The impacts of risk spiders on grasshopper behavior, grasshopper population densities, and trophic interactions were compared with the effects of natural spiders capable of capturing and subduing prey (termed *predation spiders*) using a series of field experiments.

At the behavioral level, individual grasshoppers moved significantly more and farther when in the presence of risk and predation spiders than when alone (Schmitz et al. 1997). More important, they did not respond differently to risk spiders than to predation spiders (Schmitz et al. 1997). Daily activity in the presence and in the absence of predators was measured on grasshoppers housed individually in terraria placed in a field. Spiders and grasshoppers were randomly assigned to either a no predator (control) or predator (predation) treatment at mean densities that matched those in the field experiments on trophic interactions (i.e., grasshoppers at 12 m⁻², spiders at 4 m⁻²). Grasshopper location in the cage was recorded every 30 min between 0700 hours and 1800 hours for 2 d. Grasshoppers were considered active if their position had changed between consecutive 1/2-h periods. Activity time was calculated by summing active 30-min periods over the 11 h of observation each day.

There was a significant 65-min (18%) reduction in grasshopper daily activity time in the presence of a spider predator (Beckerman et al. 1997). Finally, Rothley et al. (1997) found that grasshoppers exhibited significant changes in their per capita dietary proportion of grasses and herbs, from an average of 70% grass when the predator was absent to 42% grass when the predator was present, at an average density of 4 m⁻². This diet shift was consistent with predictions of theory on adaptive consumer behavior in response to predation risk (Rothley et al. 1997; Abrams and Schmitz, in press).

At the population level, risk-spider and predation-spider treatments caused a significant reduction in population densities of grasshopper nymphs relative to the no-predation control (Schmitz et al. 1997). This indicated that densities could be reduced by direct predation and indirectly perhaps via increased starvation due to reduced feeding time (McNamara and Houston 1987). There was no effect of either class of predator on adult grasshopper density, relative to a no-predator control (Beckerman et al. 1997).

At the interaction web level, both risk-spider and predation-spider treatments had a significant positive indirect effect on grass biomass and a negative indirect effect on herb biomass (Beckerman et al. 1997). These effects could be attributed largely to the grasshopper diet shift in response to predation risk described above. Consequently, the indirect effects of spiders on plants, mediated by *M. femurrubrum* grasshoppers, arose largely from trait-mediated effects of spiders on grasshoppers.

The previous research explored dynamics in a comparatively simple system, a food chain containing the generalist herbivore *M. femurrubrum*. It has been claimed that trophic cascades might simply be an artifact of the linear structure of such food chains (Strong 1992). In more species-rich interaction webs, there is a greater potential for species to interact indirectly with one another via intermediate species due to the highly interconnected nature of interaction pathways (Schoener 1993). Consequently, trophic cascades may be less likely to occur in systems in which species are highly interconnected because the effect of a single species will be differentiated among many pathways (Strong 1992; Polis and Strong 1996). Moreover, antiherbivore defenses in plants and interspecific competition within trophic levels are key interactions that tend to attenuate top-down effects of predators, especially in terrestrial systems (Strong 1992; Polis and Strong 1996). One goal of the study reported here therefore was to evaluate the role of spiders on species interactions in somewhat more complex systems with a greater variety of interaction pathways and to compare the species responses in these systems with the more simple linear food chains.

Figure 1 presents the trophic linkages among the focal species, two phytophagous insects, the generalist grasshopper *M. femurrubrum*, the specialist grasshopper *C. curtippennis*, which specializes on grass (Vickery and Kevan 1967; Helfer 1987), their grass and herb food plants, and the spider predator *P. mira*, which has a demonstrated ability to capture and subdue grasshoppers (Schmitz et al. 1997). The trophic linkages between the grasshopper species and the plant species were verified by natural history observations of the grasshopper species repeatedly feeding on these plant species in the field (O. J. Schmitz, unpublished data). The grasshopper species, as well as the plants described above, are dominant during much of the summer and fall (late June to early October).

In the experimental interaction webs, there are a variety of pathways through which the effects of spiders can pass before influencing the abundance of, say, the grass species *P. pratense* (fig. 1). The pathways in the interaction web also can be manipulated experimentally by removing one of the herbivore species. The challenge, however, is to anticipate the outcome of such experimental manipulation of interaction pathways. I now develop a set of working hypotheses, which embody the natural history and background presented above, to predict how spiders might indirectly influence grass and herb biomass via density-mediated and trait-mediated effects. Predictions are made for simple interaction webs containing only one or the other herbivore species relative to the more complex system containing both herbivores.

Hypothesized Species Interactions

According to the linkages described in figure 1, a working hypothesis of species interactions must consider the trophic (feeding) interactions between the herbivores, their predator, and their respective plant resources. The aim here was to explore only the top-down effects exerted by the predator species on interaction webs. This is a plausible starting point for identifying how predators could influence species interactions as previous research with old-field interaction webs (Schmitz 1994, 1997) indicated that the top-down effects exerted by predators tended to overpower bottom-up effects. Specifically, the approach gives an indication of the patterns in variation we may expect in field systems if the hypothesized mechanisms of trophic control by predators are having a dominant influence. If the predictions are not borne out, then alternative mechanisms must be considered (Strong 1992; Polis and Strong 1996). The advantage here, however, is that the current working hypotheses provide the basis for proposing other mechanisms. For instance, it may be hypothesized that the specialist herbivore should not have

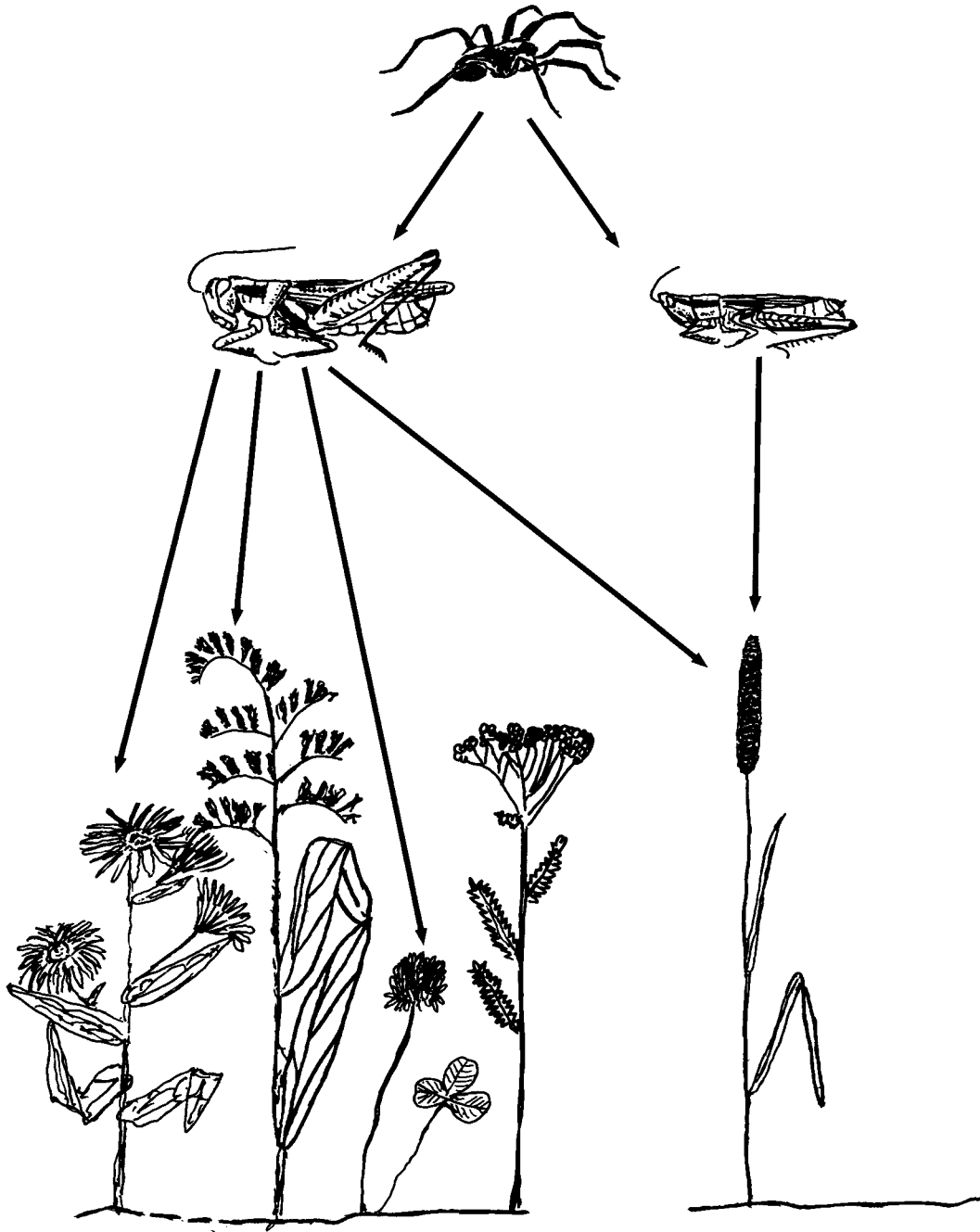


Figure 1: Trophic linkages among the hunting spider, *Pisaurina mira*, a generalist grasshopper, *Melanoplus femurrubrum*, a specialist grasshopper, *Chorthippus curtipennis*, specializing on grass, old-field perennial herbs *Aster novaeangliae*, *Solidago rugosa*, and *Trifolium repens*, and the grass *Phleum pratense* in experimental interaction webs at the Yale-Myers Research Forest study system.

an effect on herb abundance. If herb abundance changes in interaction webs containing the specialist herbivore, relative to control interaction webs without herbivores, then there is evidence of herbivore-mediated grass-herb interactions that may attenuate the top-down control ex-

erted by carnivores. The experimental design, described below, allows a test of this alternative possibility.

The effect of predators on species interactions in the experimental system depends on the nature of the predator-prey interaction. Predators can influence herbi-

vores through their direct lethal effects on prey. This interaction is embodied in classical models of trophic interactions (e.g., Rosenzweig 1973; Oksanen et al. 1981; Carpenter et al. 1986; Menge and Sutherland 1987; Leibold 1989; Schmitz 1992). In this case, predator effects on herbivores are manifest as a direct loss in herbivore numbers or biomass. Predators also can cause herbivores to reduce their feeding time or to shift their diet selection in response to predation risk (e.g., Beckerman et al. 1997; Schmitz et al. 1997). These kinds of effects are embodied in models of trophic interactions developed by Abrams (1984, 1992).

Most current models on trophic interactions focus on steady state dynamics. An important theoretical question that can be addressed by this study is, How robust are predictions from theory based on steady states for intrinsically variable systems such as arthropods and perennial plants in seasonal environments? The hope is that such steady state approximations offer some working insight, especially for comparatively simple systems such as those examined in this study. Companion studies to this one (Beckerman et al. 1997; Schmitz et al. 1997) and several other related studies on arthropod community dynamics (Ritchie and Tilman 1992; Belovsky and Slade 1993; Schmitz 1993, 1994, 1997; Chase and Belovsky 1994; Chase 1996) indicate that grasshopper densities in these systems may reach a steady state every year whereas plant abundances may continue to change. Moreover, field conditions can vary among years to alter the magnitude of interaction strengths among component species and, consequently, the exact level of the steady state (see, e.g., Joern 1992; Belovsky and Slade 1995). Thus predictions from theory may not be completely supported by the field experiments simply because steady state assumptions of current theory may not be exactly met in the field system.

In figure 2, I present the net outcomes of direct predation and antipredator behavior on plant-grasshopper interactions when interaction pathways are systematically varied, that is, simple interaction webs containing only the generalist grasshopper, only the specialist grasshopper, or a more complex interaction web containing both grasshoppers. In depicting the net effects, I assumed that plants could be assigned to two trophic groups, grasses and herbs. Grasshoppers appear to distinguish between grasses and herbs, as resources, on the basis of their relative patchy distribution in the field and differences in their net nutritional quality (Belovsky 1986; Schmitz 1997). There is the potential for grasshoppers to distinguish more finely by plant species. However, previous work (Schmitz 1997) suggests that old-field plant species within a trophic group may be treated as functionally

equivalent as they have similar nutritional contents and are consumed at similar rates by grasshoppers (Schmitz 1997).

Interaction Webs with Generalist Grasshoppers Only

Spiders should have a net positive effect on grasses and herbs in interaction webs containing only the generalist grasshopper when the effects are propagated only via density-mediated interactions (fig. 2A). This effect arises because spiders reduce the density of grasshoppers feeding on plants thereby releasing both groups of plants from herbivory. By contrast, spiders should have a net positive effect on grasses and a net negative effect on herbs when the effects are propagated only via trait-mediated interactions (fig. 2B). This effect arises because of a grasshopper diet shift favoring increased use of herbs at the expense of grass in response to predation risk (Rothley et al. 1997; Abrams and Schmitz, in press).

Interaction Webs with Specialist Grasshoppers Only

Density-mediated and trait-mediated effects of spiders on plants should be identical in interaction webs containing the specialist grasshopper (fig. 2C, D). There should be a net positive effect of spiders on grass and no effect on herbs. The positive density-mediated indirect effect of spiders on grasses results from density reductions of grasshoppers feeding on grass. At the behavioral level, specialist grasshoppers can only reduce their feeding time in response to predation risk because they have no recourse to shift their diet to another plant group. The positive indirect effect mediated through behavior results because these grasshoppers simply reduce the feeding impact on grasses.

Interaction Webs with Both Grasshoppers

Predicting the net indirect effects in interaction webs with both grasshoppers is more complicated because the effects of the spider species will depend on the form of the functional response of the spider on the two grasshoppers (Abrams 1996), whether or not there are direct interference interactions or indirect exploitative interactions between the grasshopper species and whether or not the spider can have an indirect mutualistic effect on the grasshopper species (Schoener 1993). Functional responses for multiple prey, in which carnivores, such as spiders, are limited by the time to capture and handle prey usually involve some sort of frequency-dependent prey selection (Oaten and Murdoch 1975; Kuno 1987). But in all cases this results in a density reduction in both

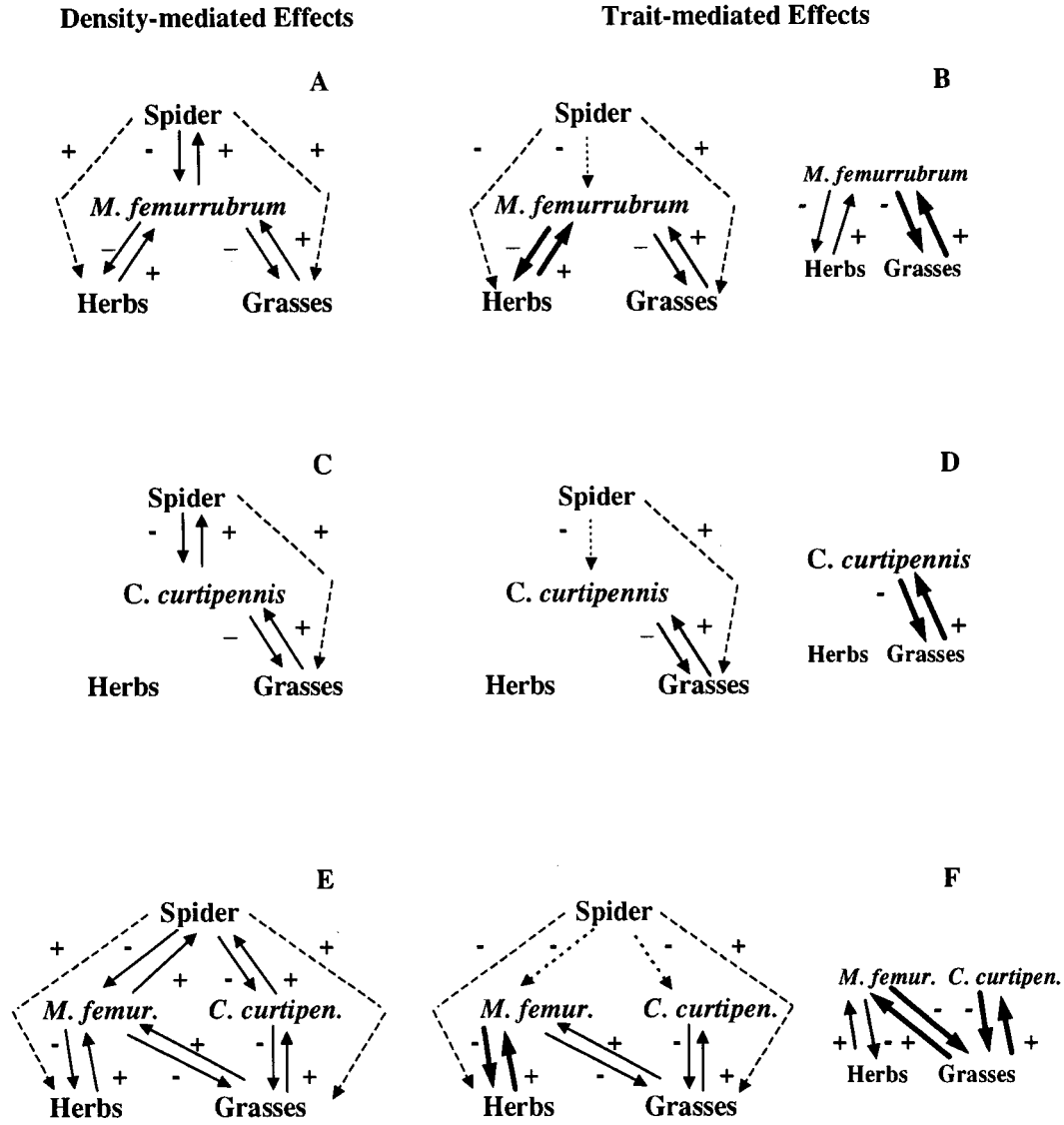


Figure 2: Hypothesized net indirect effects of spiders on plant biomass arising from lethal (density-mediated) and nonlethal (trait-mediated) direct effects of spiders on grasshoppers influencing the nature of the grasshopper-plant interactions. The solid lines indicate direct trophic (feeding) interactions. Dotted lines indicate direct behavioral modifications of prey induced by predator. Dashed lines indicate a net indirect effect of spiders on plants propagated by a density-mediated or trait-mediated interaction with grasshoppers. Arrows indicate the direction of trophic interactions and the signs of the arrows indicate the net outcome. *A, B*, Effects in interaction webs containing the generalist grasshopper. The plant-herbivore subgraph in *B* demonstrates grasshopper foraging preferences in the absence of predators (represented by the thickness of the arrows), which is shifted to the other plant category in the full tritrophic interaction web owing to adaptive shifts in grasshopper foraging. *C, D*, Effects of spiders on interaction webs containing only the grass specialist grasshopper. The diminished interaction strength between herbivores and grass in the tritrophic system relative to the plant-herbivore system (*D*) results from decreased feeding time by herbivores in response to predation risk. *E, F*, Trophic interactions in systems with both herbivore species. The net indirect effects arising from density-mediated and trait-mediated interactions in these systems should match those for interaction webs with the generalist herbivore (*A, B*) owing to the overriding effect of generalist grasshoppers in these systems.

prey species. Experiments manipulating grasshopper density and food abundance indicate that the two grasshopper species do not compete with one another at the field site (A. P. Beckerman, unpublished manuscript). Given the architecture of the two trophic-level predator-prey subweb then, and the absence of interference competition between grasshoppers, it is impossible for spiders to exert an indirect mutualistic effect on any one prey species via direct predation on the other species (Schoener 1993). Consequently, the spider species should always have a net negative direct effect on both grasshopper species via a reduction in grasshopper density. This leads to a net positive density-mediated indirect effect on grass because the net effect in this system is not different than the qualitative effects of spiders on grass in each of the single-grasshopper species systems described above (fig. 2E). There should also be a net positive effect of spiders on herbs (fig. 2E) owing to the singular direct effect of generalist grasshoppers on herbs.

At the behavioral level, spiders are expected to reduce feeding time in both grasshopper species. Qualitatively, this will lower both grasshoppers' impact on grass biomass, as shown above for both interaction webs, and cause the generalist grasshopper to increase its impact on herbs. Hence, the qualitative outcome of spiders on plants, via trait-mediated effects, is a net indirect mutualism on grass and a net indirect negative effect on herb, much like the interaction web with only the generalist grasshopper (fig. 2F).

The above predictions assume that predation or predation risk alone influence system dynamics. As such, they represent endpoints on a continuum, as natural systems will undoubtedly involve combinations of both. We only expect a tendency toward one or the other qualitative outcome if one mechanism has an overwhelming influence on dynamics. This is in fact what is observed in the field in studies deliberately aimed at evaluating the predictions. In the following, I describe the experimental protocol and results that led to this observation.

Field Experiments

Methods: Experimental Protocol

I conducted four independent randomized-block field experiments to partition and quantify the importance of density-mediated and trait-mediated effects on trophic cascades in simple and complex interaction webs. The treatments were one trophic level, two trophic levels, three trophic levels with risk spiders, and three trophic levels with predation spiders. Interaction webs were stocked with the following combination of grasshoppers in cages assigned to two trophic-level and three trophic-

level treatments: the generalist *Melanoplus femurrubrum*, the specialist *Chorthippus curtipennis*, both grasshopper species, and stocking the generalist in grass-only cages to force it to become a specialist. The experiments were conducted in 1995 and repeated in 1996 in a 50 × 50-m area within the field site using 0.25-m² × 1-m enclosure cages in which I stocked experimental interaction webs. Cages were constructed with aluminum screening and 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 approximately 1.5 m and were arrayed in a randomized block experimental design consisting of 10 blocks each year with each level of each factor represented once in each block.

All animals occurring naturally in the vegetation layer at a cage location were removed from the cages before the experimental interaction webs were stocked into the cages. This was accomplished by carefully hand sorting through the vegetation and leaf litter in each cage and capturing all insects and large spiders in the vegetation. It was not possible to remove small spiders (e.g., *Schizocosa* sp., *Pirata* sp.), which were part of the detrital food chain below the leaf litter. However, the small size of these spider species and their exclusive use of the sublitter layer precluded them from posing a predation threat on the much larger grasshoppers. Removing all insects at the beginning of the experiment also did not prevent insects from hatching within a cage during the course of the experiment and thereby altering the experimental insect community. Insects that emerged belonged to the leaf-chewing Acrididae, the non-leaf-chewing families Miridae, Cercopidae, and Cicadellidae, and the detritivorous family Gryllidae. Individuals of these families were removed from the cages whenever they were observed. Densities of the non-leaf-chewing insects averaged two to three per 0.25 m², which was much lower than the 15 per 0.25 m² observed in the field (O. J. Schmitz, unpublished data).

To evaluate the predictions for net indirect effects of carnivores on plants, I created four different interaction webs by conducting the following manipulations: (1) interaction web with the generalist grasshopper *M. femurrubrum* only (fig. 3A); (2) interaction web with the specialist grasshopper *C. curtipennis* only (fig. 3B); (3) interaction web with both types of grasshopper (fig. 3C); and (4) interaction web with grass only and the generalist grasshopper so as to force the generalist to become specialist on grass (fig. 3D). Interaction web 4 was created by placing enclosure cages over patches dominated (>90% biomass) by *Phleum pratense* and removing, by hand, all standing and emergent aboveground herb bio-

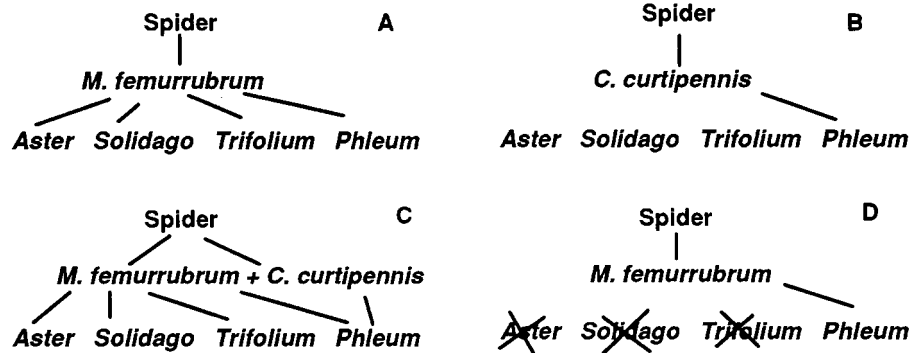


Figure 3: Experimental manipulations of interaction pathways through which the effect of spiders may pass in interaction webs containing (A) only a generalist herbivore (*Melanoplus femurrubrum*), (B) only a specialist herbivore (*Chorthippus curtipennis*), (C) both kinds of herbivore together, and (D) only the grass *Phleum pratense* to cause the generalist herbivore to become specialist.

mass during the course of the experiment. The fourth interaction web controlled for some effects of adaptive behavior as the manipulation removed any recourse for the normally generalist grasshopper to shift its diet selection toward herbs.

I created two classes of spiders, predation and risk, to change the modality of the predator-prey interactions in the experiments. The predation spiders were used to quantify density-mediated grasshopper effects on plant biomass. Risk spiders were used to quantify the trait-mediated grasshopper effects on plant biomass. I created risk spiders by gluing their chelicera with nontoxic surgical cement so that they were unable to subdue the prey, removing all chance of density-mediated effects.

I tested whether predation and risk spiders induced a trophic cascade in each of the four interaction web types by measuring responses of grasses and herbs to trophic-level manipulations. 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 the addition of carnivores (three trophic-level web) will reverse the effects of herbivore, resulting in a net increase in plant biomass from two trophic levels (Schmitz 1993; Wootton 1994; Menge 1995). For each of the four interaction web types, I tested for trophic cascades using four treatments, which varied the number of trophic levels as follows: one-level web with plants only; two-level web containing plants and grasshoppers; and three-level webs containing either plants, grasshoppers, and risk spiders or plants, grasshoppers, and predation spiders.

I stocked six late instar (fourth and fifth) grasshopper nymphs in the cages containing two trophic-level interaction webs. I stocked six grasshopper nymphs and one adult spider to the experimental cages containing three trophic-level interaction webs. Cages were stocked in early August. The spider numbers matched field densi-

ties. The exact grasshopper stocking densities was arbitrary (1.3 times higher than maximum field densities measured at the time of stocking), but grasshoppers were intentionally stocked at a higher level to allow them to decline toward density levels set by various limiting factors in each cage (i.e., food, predators, etc.) and allowed the potential to reach maximum field densities in some cages. This would not be possible if I stocked all cages at average field levels and maintained densities there. Because there was no a priori way of knowing appropriate grasshopper densities for the background conditions in each cage, I needed a pulse perturbation to avoid the possibility of artificially high resource limitation in some cages and unrealistically low levels in others. The transition time from initial grasshopper stocking density to levels determined by biotic conditions in a cage at the time of stocking tends to be short relative to the duration of the field experiment (e.g., only 4–6 d of a 60-d experiment; Belovsky and Slade 1993, 1995; Schmitz 1994). Thus, a short pulse perturbation does not have the potential to introduce artificial affects on plant biomass. Indeed, previous work demonstrated that plant biomass in three-level food chains within experimental cages was not significantly different from plant biomass in random field plots with similar three trophic-level structure (Schmitz 1994).

I censused all cages every 2 d, during midmorning when grasshoppers and spiders were most active, to monitor survivorship of grasshoppers and spiders during the field experiment. Spiders were monitored to ensure their continuous presence within a cage. If a spider was not observed in a cage after two consecutive census periods (i.e., after 4 d) it was replaced with a new individual appropriate for the specific treatment (i.e., predation spider or risk spider). The experiments ran for 60 d each year, during which time the grasshopper nymphs passed from late instars to adults. I terminated the experiments

at the onset of an insect-killing frost in October. Upon termination of the experiment, I collected all grasshoppers within each 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. There was no spider mortality during the course of the experiments, and all spiders were recovered at the end of the field experiments. Inspection of all risk spiders indicated that their chelicerae remained glued for the entire experiment.

Results: Identifying Sources of Trophic Control in Experimental Interaction Webs

Randomized-block ANOVA on data for each of the four experiments revealed that there were no significant year effects either on grass and herb biomass (all $P > .15$, $df = 1, 66$) or on grasshopper cage densities (all $P > .15$, $df = 1, 47$) owing to similar abiotic conditions in the two consecutive years. Consequently, the data were pooled for both years in all subsequent analyses.

Figure 4 presents patterns of grass biomass as a function of the number of trophic levels in an interaction web and class of predator (risk vs. predation). Randomized-block ANOVA, followed by a Tukey test, revealed that spiders had a significant net positive effect on grass in simple and complex interaction webs containing the generalist grasshopper *M. femurrubrum* (table 1). The net positive effect was marginally significant in the interaction web containing only the specialist grasshopper *C. curtippennis* (table 1). There was no significant effect of predators on grass (table 1) in interaction webs in which *M. femurrubrum* was forced to specialize on grass (table 1).

There was a net negative effect of spiders on herb biomass in interaction webs with the generalist grasshopper, as indicated by lower herb biomass in interaction webs containing spiders as opposed to those without spiders (fig. 5, table 1). There was no significant effect of spiders on herb biomass in the interaction web containing the specialist grasshopper (fig. 5, table 1). Moreover, the absence of a significant effect of the specialist grasshopper *C. curtippennis* on herb biomass, despite modest limitation of grass biomass, indicates that effects of grass on herb biomass are weak if not nonexistent. Finally, there was no significant effect of predators on grass biomass in interaction webs in which generalist grasshoppers were forced to specialize on grass (table 1).

In summary, the net positive indirect effect of spiders on grass biomass coupled with a net negative effect on herb biomass in interaction webs containing the generalist grasshopper *M. femurrubrum* was consistent with expectations of trophic control propagated by trait-

mediated effects (table 2). There was no effect of spiders on grass biomass when *M. femurrubrum* was forced to specialize on grass (table 2), indicating an absence of top-down control in this interaction web. Alternatively, the net positive effect on grass biomass and no effect on forb biomass in interaction webs with the specialist grasshopper *C. curtippennis* matches predictions of both density-mediated and trait-mediated hypotheses (table 2). In order to isolate whether the effect in interaction webs with *C. curtippennis* arose from density-mediated or trait-mediated effects, one must evaluate the effects of spiders on grasshopper density.

I compared the final densities of grasshoppers in two-level interaction webs with grasshopper densities in three-level interaction webs containing risk spiders and predation spiders using a randomized-block ANOVA (table 3). There was no significant effect of spiders on grasshopper densities in any of the interaction webs. This provides strong corroborating evidence to that presented above that the changes in plant biomass in response to spider manipulations resulted almost entirely from shifts in grasshopper behavior in response to predation risk, that is, trait-mediated effects.

Discussion

The field experiments indicate that the spider carnivore could have a strong, indirect influence on plant abundance in a terrestrial field system. Moreover, the indirect effects of the spider on plants were propagated by a trait-mediated effect rather than by a density-mediated effect. The trait-mediated effect was a shift in grasshopper foraging behavior in response to predation risk. These conclusions derive from three lines of evidence. First, the pattern of plant abundance with changes in the spider abundance was most consistent with predictions of hypotheses that embodied assumptions about the effects of predation risk on herbivore diet selection. Second, the pattern of plant abundance in interaction webs containing only risk spiders was virtually identical to the pattern of plant abundance in interaction webs containing only predation spiders. Thus, predation risk alone could explain the majority of variation in effect. Finally, there was no effect of spiders on grasshopper survivorship, as indicated by the absence of significant density differences in interaction webs with and without spiders. The results do not appear to be sensitive to departures from the assumption of steady state, which is embodied in the working hypotheses of density- and trait-mediated species interactions (fig. 2).

The lack of any measurable effect on grass biomass in the experiment in which the generalist herbivore was forced to become a specialist is a curious outcome given

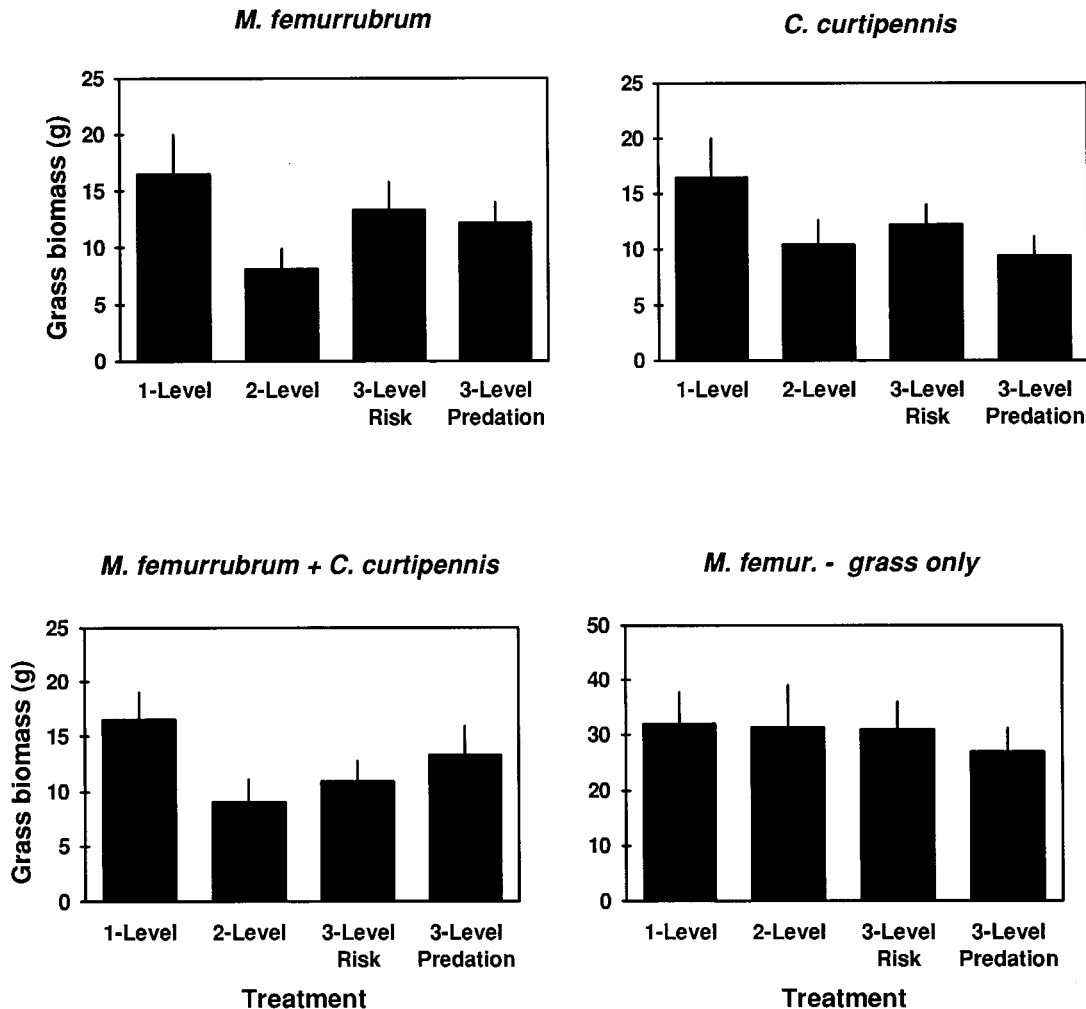


Figure 4: Effect of trophic-level manipulations on grass biomass in experimental old-field interaction webs in which the interaction pathways were manipulated by stocking different kinds of herbivores (see fig. 3). One-level webs contained plants only, two-level webs contained grasshoppers and plants, and three-level webs contained spiders, grasshoppers, and plants. In three-level webs, risk treatments contained plants, grasshoppers, and spiders that had their chelicerae glued together, and predation treatments contained plants, grasshoppers, and spiders that were not glued. Values are mean \pm SE.

the significant impact the generalist species had in the other interaction webs. Previous work in a similar study system (Schmitz 1997) may provide some clues as to why this occurred. In that system, the numerically dominant grass species *Phleum pratense* competes with numerically dominant herb species such as *Solidago* (Schmitz 1997). However, the competitive effect is asymmetrical such that *Solidago* exerts a strong negative effect on *Phleum*, but *Phleum* exerts a weak, if not nonexistent, effect on *Solidago* (Schmitz 1997). Consequently, the strong positive response of grass when spiders were added to interaction webs containing the generalist grasshopper and both grasses and herbs may have occurred, in part, because the grasshopper mediated the strong

negative effect of herbs on *Phleum* via its own response to predation risk. Accordingly, the absence of competitor plant species in enclosure cages containing grass monocultures may have allowed grass to further increase its production and perhaps compensate for losses due to herbivory, hence the lack of a measurable effect of grasshoppers on grass in this interaction web. The weak effect of *Phleum* on herbs (Schmitz 1997) may also explain why there was no measurable effect of trophic manipulations on herb biomass in interaction webs containing only the grass-specialist grasshopper species. It appears, then, that while top-down control of interaction web dynamics may be strong, the particular nature of species interactions within the plant trophic level may

Table 1: Results of field experiments evaluating the indirect effect of predator manipulations on plant biomass in interaction webs containing either generalist herbivores or specialist herbivores, or both

	<i>Generalist only</i>		<i>Specialist only</i>		<i>Both herbivores</i>		<i>Generalist with grass only</i>	
	<i>P value</i>	<i>Tukey</i>	<i>P value</i>	<i>Tukey</i>	<i>P value</i>	<i>Tukey</i>	<i>P value</i>	<i>Tukey</i>
Effect on grass	<.05	(1, 3, 4) > 2	.07	(1, 3) > (2, 4)	<.05	(1, 3*, 4) > 2	>.75	...
Effect on herb	<.05	1 > (2, 3) > 4	.69	...	<.05	1 > 2 > (3, 4)

Note: *P* values are based on ANOVA with 3, 66 df. Tukey values are a posteriori comparisons of biomass in interaction webs containing only plants (1), plants and herbivores (2), plants, herbivores, and risk spiders (3), and plants, herbivores, and predation spiders (4). Numbers in parentheses indicate no significant difference among treatment means. A trophic cascade occurs when treatment means for interaction webs with plants only are similar to treatment means for interaction webs with risk spiders or predation spiders but greater than in interaction webs with only herbivores, that is, (1, 3, 4) > 2 or (1, 3) > (2, 4). In column 6, (1, 3*, 4) > 2 indicates that treatments 1 and 4 were significantly different from treatment 2 but treatment 3 was only marginally different from 2 (*P* = .08).

explain some additional variation in the effect of trophic manipulations.

The field experiments showed that trophic cascades were more likely to occur in interaction webs with several interaction pathways rather than in linear food chains (fig. 4). At first, this observation seems to contradict Strong's (1992; see also Polis and Strong 1996) assertion that generally one should not see trophic cascades in reticulate systems. This is because in complex interaction webs the effect of predators should be differentiated among many interaction pathways and will be attenuated by a variety of interspecific interactions (e.g., interspecific competition, plant antiherbivore defenses). Trophic cascades are expected to occur in low-diversity systems only where the majority of influence comes from one or a few species along a single pathway (Strong 1992; Polis and Strong 1996). The implicit assumption in this argument, however, is that indirect effects among species emerge as a consequence of density-mediated interactions. Indirect effects resulting from trait-mediated interactions can give an entirely different perspective, namely, that top-down effects need not attenuate down the interaction web, even in speciose systems, if behavioral shifts cause some species to have overriding effects on dynamics. Indeed, the predator-induced behavioral indirect effect in the experimental interaction webs effectively caused the generalist herbivore to overpower the specialist herbivore's effect on plants. This result, therefore, is consistent with Strong's (1992) assertion that trophic cascades will only arise when one or a few species have a dominant effect on species interactions. However, the dominance arises from entirely different mechanisms than envisioned by Strong (1992).

The trophic effects did not attenuate in my system because there was no multichannel omnivory (see Strong 1992) and the potential for interspecific competition among herbivores was weaker than top-down effects of

predators. The evidence for top-down effects being stronger than interspecific interactions within a trophic level is presented in table 4, where I compare the densities of each grasshopper species when alone in an interaction web, in the presence of the other herbivore, and in the presence of both the other herbivore and predators. Comparisons of grasshopper densities in the absence of spiders indicates that some competition may be operating, but it is weak and asymmetrical. The generalist grasshopper *Melanoplus femurrubrum* caused a significant reduction in the density of the specialist grasshopper *Chorthippus curtipennis* (table 4). However, there were no significant density reductions of *M. femurrubrum* when this species coexisted with *C. curtipennis* (table 4). More intensive field research on interactions between the two grasshopper species (A. P. Beckerman, unpublished manuscript) showed that interspecific competition could not explain the patterns in grasshopper abundances.

The data in table 4 indicate that there was no significant effect of *C. curtipennis*, or both *C. curtipennis* and spiders, on *M. femurrubrum* density. However, *C. curtipennis* density was reduced when in the presence of *M. femurrubrum*, and this effect was exacerbated when predators were added to the interaction webs (table 4). This suggests that predator mediation of herbivore interactions may explain the strong negative correlations in herbivore species' densities in the experiment, and it may explain why attenuation of top-down effects was unlikely in the experimental interaction webs.

This study examined direct and indirect effects in interaction webs, defined as a set of strongly interacting species (Paine 1980; Menge 1995), in enclosure cages rather than in natural, unenclosed webs comprising the complete range of arthropod species in the field system. Studies of this nature are challenging to design because they require striking a balance between two conflicting goals. Ultimately, the objective of field ecology is to un-

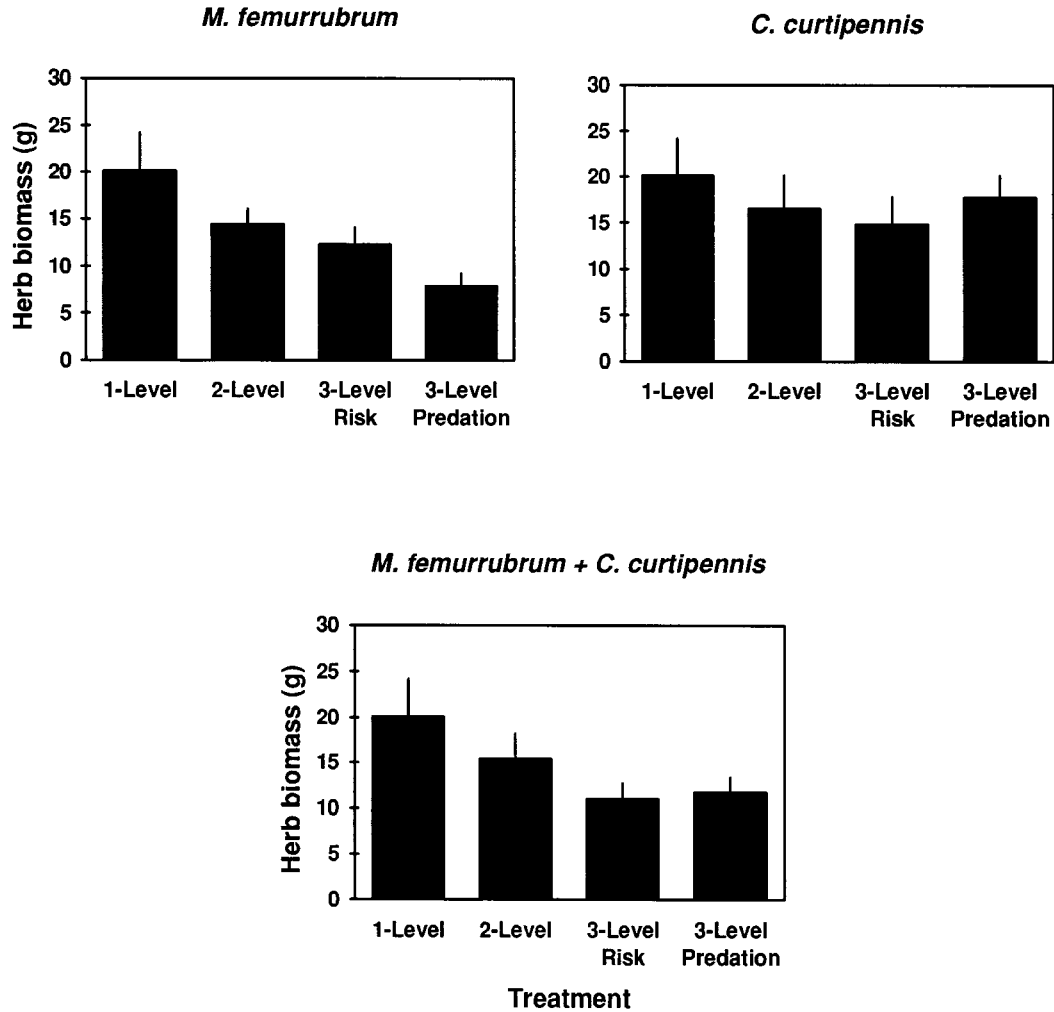


Figure 5: Effect of trophic-level manipulations on total herb biomass in experimental old-field interaction webs in which the interaction pathways were manipulated by stocking different kinds of herbivores (see fig. 3). One-level webs contained plants only, two-level webs contained grasshoppers and plants, and three-level webs contained spiders, grasshoppers, and plants. In three-level webs, risk treatments contained plants, grasshoppers, and spiders that had their chelicerae glued together, and predation treatments contained plants, grasshoppers, and spiders that were not glued. Values are mean \pm SE.

Table 2: Summary of net indirect effects of spider predators on plant biomass in interaction webs containing either generalist herbivores or specialist herbivores, or both

Interaction web type	Predicted effect				Observed effect	
	Density-mediated		Trait-mediated		Grass	Herb
	Grass	Herb	Grass	Herb		
Generalist grasshopper only	+	+	+	-	+	-
Specialist grasshopper only	+	0	+	0	+	0
Both grasshoppers	+	+	+	-	+	-
Generalist grasshopper with grass only	+	0	+	0	0	0

Table 3: Effect of predator manipulations on densities of grasshoppers in experimental interaction webs

Interaction web	Control	Risk spiders	Predation spiders	ANOVA	
				df	P
1: <i>Melanoplus femurrubrum</i>	2.9 ± .40	3.2 ± .53	3.1 ± .40	2, 57	>.70
2: <i>Chorthippus curtippennis</i>	1.9 ± .41	2.5 ± .43	2.3 ± .46	2, 57	>.70
3: <i>M. femurrubrum</i>	2.5 ± .30	2.6 ± .37	2.8 ± .41	2, 57	>.70
<i>C. curtippennis</i>	1.0 ± .22	1.1 ± .27	.5 ± .14	2, 57	.12
4: <i>M. femurrubrum</i>	3.5 ± .38	3.3 ± .32	3.3 ± .44	2, 57	>.70

Note: Values are mean and 1 SE.

derstand how natural systems function. However, understanding the range of species interactions in terrestrial systems with mobile individuals often requires a scale of resolution that is too large to quantify precisely and reliably the mechanisms and strengths of interactions among individuals (behavioral level) and among species (community level). The best one can usually hope for with a completely natural field system is to quantify the overall net trophic-level effects among component species (e.g., overall net effect of carnivores on the plant trophic level) at the expense of a detailed mechanistic understanding of the pathways through which the effects pass. Obtaining a quantitative, mechanistic understanding of how one species influences other species requires circumscribing a functional set of species and confining them in ways that allow some semblance of experimental “control” in which interaction pathways can be manipulated. Obviously, the degree to which species are confined changes the degree of realism one can assign to the outcome of an experiment.

The enclosure cage size used in this study was the largest possible to account for all individuals and still

make precise measurements of the direct and indirect interactions among the species. This cage size still may preclude the possibility of localized emigration of grasshoppers in response to the presence of predators, and therefore, the measured effects could be artificially inflated. To guard against this to the maximum extent possible, I designed the experiment so that species densities in the enclosure cages at least approximated natural field densities throughout the experiment. Although this design may not capture the full range of variability in effects one might see in a natural system, especially those arising from spatially explicit predator-prey interactions (e.g., Turner and Mittelbach 1990), it at least approximates the average response one might expect within a natural field. At the very least, this study demonstrates that the behavioral ecology of individuals can have some important manifestations at the community level.

The results present an interesting paradox for modeling predator-induced indirect effects on interaction webs. Models of predator-prey interactions involving density-mediated effects are comparatively straightforward to construct because they only require an understanding of

Table 4: Comparison of grasshopper densities in simple and complex interaction webs under different predator manipulations to evaluate the potential for predator-mediated interactions between herbivore species

Spider manipulation	Chorthippus curtippennis				Melanoplus femurrubrum			
	Alone	With <i>M. femurrubrum</i>	t-test		Alone	With <i>C. curtippennis</i>	t-test	
			df	P			df	P
Control	1.9 ± .41	1.0 ± .22	38	<.025	2.9 ± .40	2.5 ± .30	38	>.15
Risk	2.5 ± .43	1.1 ± .27	38	<.005	3.2 ± .53	2.6 ± .37	38	>.15
Predation	2.3 ± .46	.5 ± .14	38	<.0001	3.1 ± .40	2.8 ± .41	38	>.15

Note: Values are mean and 1 SE.

direct, pairwise interactions between species (Wootton 1993). Trait-mediated effects tend to be an emergent property that is contingent on the exact complement of species that are coexisting in a system. Trait-mediated effects are more difficult to model, especially in complex systems, because one must understand how species interactions are modified by examining all species involved in all possible combinations before we can specify the appropriate mathematical functions (Wootton 1993). However, once a working model is in place, it may be exceedingly difficult to predict the consequences, on interaction web dynamics, of perturbing the abundance of, say, a predator species, if the effects of that perturbation are propagated via density-mediated effects in the intermediate species (Yodzis 1988; Abrams 1992; Pimm 1993; Smith et al. 1997; but see Menge 1997; Schmitz 1997). This is because, theoretically, species farther down the chain often require long periods to adjust their population densities in response to the perturbation (e.g., Smith et al. 1997; but see Menge 1997). The indirect effects arising from behavioral responses of prey to predators may be far easier to predict because their net effects may operate on a faster timescale since they do not require density adjustments of the intermediate species (Abrams 1992, 1993). Indeed, in a companion study to this one (Rothley et al. 1997) the emergence of a behavioral-driven trophic cascade was detected within 10 d after field experiments were initiated, during which time grasshopper densities did not yet change significantly.

The important task now is to obtain a broader empirical understanding of the degree to which predator-induced indirect effects on communities are propagated by density-mediated and trait-mediated interactions, especially in more speciose systems than the ones examined here. One integral step toward this understanding is to derive theoretical models of community dynamics that embody the appropriate functions describing species interactions and that abstract biological processes at the appropriate ecological scales (Levin 1992; Abrams 1996; Yodzis 1996; Schmitz and Booth 1997). This study, in addition to previous work (Mittelbach 1986; Turner and Mittelbach 1990; Huang and Sih 1991; Rosenzweig 1991; Abrams 1992; Werner 1992; McIntosh and Townsend 1996; Moran et al. 1996; Werner and Anholt 1993; Beckerman et al. 1997; Schmitz and Booth 1997; Schmitz et al. 1997), shows that theoretical community ecology might profit by making more forceful linkages between behavioral ecology and population and community ecology. We can already draw on a substantial body of information on trade-offs made by prey when balancing foraging, habitat selection, or life-history allocation with predation hazard (Abrams 1984; Mangel and Clark 1986; McNamara and Houston 1987, 1994; Sih 1987; Dodson and Havel 1988; Crowl and Covich 1990; Lima and Dill

1990; Ludwig and Rowe 1990; Skelly and Werner 1990; Werner 1992). For modestly complex systems, such as those in this study, these trade-offs may prove to offer a reasonable approximation of interactions and thus provide a useful starting point for obtaining a broader understanding of the outcome of perturbations on species interactions.

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