

EFFECTS OF TOP PREDATOR SPECIES ON DIRECT AND INDIRECT INTERACTIONS IN A FOOD WEB

OSWALD J. SCHMITZ¹ AND K. BLAKE SUTTLE²

Yale University, School of Forestry and Environmental Studies and
Department of Ecology and Evolutionary Biology, New Haven, Connecticut 06511 USA

Abstract. Current theory on trophic interactions in food webs assumes that ecologically similar species can be treated collectively as a single functional unit such as a guild or trophic level. This theory implies that all species within that unit transmit identical direct and indirect effects throughout the community. We evaluated this assumption by conducting experiments to compare the direct and indirect effects of three top-predator species, belonging to the same hunting spider guild, on the same species of grasshopper and on old-field grasses and herbs. Observations under field conditions revealed that each spider species exhibited different hunting behavior (i.e., sit-and-wait, sit-and-pursue, and active hunting) and occupied different locations within the vegetation canopy. These differences resulted in different direct effects on grasshopper prey. Grasshoppers demonstrated significant behavioral (diet) shifts in the presence of sit-and-wait and sit-and-pursue species but not when faced with actively hunting species. Grasshopper density was significantly reduced by spider species that occupied lower parts of the vegetation canopy (sit-and-pursue and actively hunting species), but it was not significantly reduced by the sit-and-wait spider species that occupied the upper parts of the canopy. These direct effects manifested themselves differently in the plant trophic level. The sit-and-wait spider caused indirect effects on plants by changing grasshopper foraging behavior (a trait-mediated effect). The sit-and-pursue spider caused indirect effects by reducing grasshopper density (density-mediated effects); the effects of changes in grasshopper behavior were thus not reflected in the plant trophic level. The actively hunting spiders had strictly density-mediated indirect effects on plants. The study offers mechanistic insight into how predator species within the same guild can have very different trophic effects in food webs. Thus classical modeling approaches that treat all predator species as a single functional unit may not adequately capture biologically relevant details that influence community dynamics.

Key words: antipredator behavior; density-mediated indirect effects; direct and indirect effects; food webs; grasshopper herbivores; old-field interaction webs; predation and predation risk; hunting spiders; top-down effects of predators; trait-mediated indirect effects; trophic interactions and cascading effects.

INTRODUCTION

In community ecology, most current models of trophic interactions are based on the assumption that groups of species can be treated collectively as distinct functional units, such as guilds or trophic levels (Rosenzweig 1973, Oksanen et al. 1981, Carpenter et al. 1985, Menge and Sutherland 1987, Leibold 1989, Schmitz 1992). This necessarily implies that species within the same functional unit (e.g., top carnivores) have identical effects on lower levels in the food web. Such a conceptualization, however, tends to abstract important mechanistic details about the effects of individual species in food webs (Polis and Strong 1996, Janssen et al. 1998, McPeck 1998, Schmitz 1998, Persson 1999). For example, predator species within the same guild may be segregated by habitat or foraging

periodicity and they may have differential abilities to capture and subdue prey (McPeck 1998, McIntosh and Peckarsky 1999, Persson 1999). Also, predator species can both reduce prey-species density and cause prey to change their behavior to avoid risks of predation (Sih 1980, Mangel and Clark 1986, Lima and Dill 1990, Houston et al. 1993).

The nature of the direct effects of top predator species on prey also can have a profound influence on the kind of indirect effects transmitted throughout a community. Community ecologists recognize two broad classes of indirect effect (Abrams 1995, Abrams et al. 1996, Werner and Anholt 1996). The first, called *density-mediated indirect effects*, arise when one species (A) indirectly affects another species (B) by changing the abundance of intermediate species that interact with both species A and B (Abrams 1995, Abrams et al. 1996, Werner and Anholt 1996). Cascading trophic effects predicted by most current theory (Rosenzweig 1973, Oksanen et al. 1981, Carpenter et al. 1985, Menge and Sutherland 1987, Leibold 1989, Schmitz 1992) are examples of density-mediated indirect effects. The

Manuscript received 30 August 1999; revised 9 May 2000; accepted 5 June 2000; final version received 13 July 2000.

¹ E-mail: oswald.schmitz@yale.edu

² Present address: Department of Integrative Biology, University of California, Berkeley, California 94720-3140 USA.

second, called *trait-mediated indirect effects*, arise when one species (A) modifies the way two other species (B and C) interact by causing changes in the behavior or life history of the intervening species (B) (Abrams 1995, Abrams et al. 1996, Werner and Anholt 1996). Cascading effects arising from changes in prey diet or habitat selection in response to increased predation risk represent examples of trait-mediated indirect effects (e.g., Messina 1981, Power et al. 1985, Turner and Mittelbach 1990, Huang and Sih 1991, McIntosh and Townsend 1996, Moran et al. 1996, Peacor and Werner 1997, Beckerman et al. 1997, Janssen et al. 1998, Turner et al. 1999).

In order to develop a general theory of natural community structure and dynamics, we need to understand the mechanisms of direct and indirect effects of different species. One way to gain this insight is through experimental studies that systematically compare the effects of individual species occupying similar trophic positions in food webs (e.g., McPeck 1998, McIntosh and Peckarsky 1999, Turner et al. 1999). To this end, we report on laboratory and field experiments that examined the direct effects of three species of spider predators on a common grasshopper prey species. We also illustrate how the nature of the predator-prey interaction influenced the indirect effects of the spider species on grasses and herbs in experimental old-field food webs.

The predators belong to the same guild, viz. hunting spiders, but they come from three different families (Pisauridae, Lycosidae, and Salticidae). Spiders in this guild have long been recognized as common and important natural predators of many insect herbivore species, including grasshoppers (Lavigne and Pfadt 1966, Kajak et al. 1968, Watt 1968, Bristowe 1971, Cherrill and Begon 1989, Belovsky et al. 1990, Wise 1993, Oedekoven and Joern 2000). Because of their ubiquity among terrestrial grassland and old-field systems (Wise 1993), these predators can be used to create model experimental systems that may provide generalizable insights about the structure and dynamics of food webs containing terrestrial arthropods.

Previous work on this system examined the nature of direct and indirect effects of one species of spider predator (*Pisaurina mira*, Fam. Pisauridae) on its grasshopper prey and on species of perennial grasses and herbs (Beckerman et al. 1997, Rothley et al. 1997, Schmitz et al. 1997, Schmitz 1998). That research demonstrated that the indirect effects of spiders on grass and herb resource selection by a generalist grasshopper, *Melanoplus femurrubrum*, in response to predation risk—a trait-mediated indirect effect.

This study expands on previous work by comparing the direct and indirect effects of the three spider species on the same species of grasshopper and plants in the old-field system. We made detailed measurements on the effects of each spider species on *M. femurrubrum*

foraging behavior and density, and on plant biomass. The effects were evaluated using observational studies and experiments with three primary goals: (1) to quantify spider species habitat selection and behavioral observations, and verify that each species hunts grasshoppers in the field; (2) to quantify the feeding behavior of the grasshoppers in the presence and absence of each spider species; and (3) to quantify the effects of each spider species on grasshopper population density and plant biomass.

NATURAL HISTORY

The study was conducted at the Yale-Myers Research Forest in northeastern Connecticut (USA), near the town of Union (Schmitz et al. 1997, Schmitz 1998). The research location is a 3240-ha northeastern hardwood ecosystem interspersed with old-fields supporting a variety of perennial grasses and herbs. Most fields at the Yale-Myers Forest, including the one used for this study, are in early to mid-successional state. The particular field used for this study was dominated by the grass *Phleum pratense*, and the herbs *Solidago rugosa*, *Aster novaeangliae*, and *Daucus carota*. Collectively, those species comprised ~95% of the total plant biomass in the study field (O. J. Schmitz, *unpublished data*).

Two distinct herbivore-insect feeding guilds are present each year and tend to be temporally segregated. The sap-feeding guild predominates during early June to mid-July; the leaf-chewing guild predominates in late July and persists into late September. The leaf-chewing guild, which is the focus of this study, is comprised of the specialist grasshopper *Chorthippus curtipennis* and the generalist grasshopper *Melanoplus femurrubrum*.

Top-down effects are transmitted from the spiders to plants through the leaf-chewing guild in fields of different ages at the Yale-Myers forest (Beckerman et al. 1997, Schmitz et al. 1997, Schmitz 1998, Uriarte and Schmitz 1998). Top-down effects are transmitted through the sap-feeding guild, but only in the few fields where the plant community has reached a mid-successional state, i.e., dominated by the herbs *Solidago rugosa*, *Rhumbekia hirta*, and *Asclepias syriaca*, and the grass *Poa pratensis* (Uriarte and Schmitz 1998, O. J. Schmitz, *unpublished data*). Because of the preponderance of earlier-successional fields at Yale-Myers Forest, this study focused on top-down effects transmitted through the leaf-chewing guild.

Hunting-spider predators of the leaf-chewing guild include the salticid spider *Phidippus rimator*, the pisaurid spider *Pisaurina mira*, and the lycosid spider *Hogna rabida*. Previous work (Schmitz 1993, Beckerman et al. 1997, Schmitz et al. 1997) indicated that lycosid and pisaurid hunting spiders could capture and subdue prey up to 1.3 times their own body size. Thus, *Hogna* can capture and subdue individuals from each life-cycle stage of the generalist grasshopper. *Pisaurina*

TABLE 1. Morphometric characteristics of grasshoppers and hunting spiders used in field experiments (at the Yale-Myers forest, Connecticut, USA) examining effects of spider species on direct and indirect effects in interaction webs.

Species	Life-cycle stage	Body mass (g)		<i>n</i>
		\bar{X}	1 SE	
Grasshopper				
<i>Melanoplus femurrubrum</i>	Adult	0.374	0.011	24
	5th instar	0.210	0.019	24
	4th instar	0.150	0.014	18
Spider				
<i>Pisaurina mira</i>	Adult	0.147	0.015	20
<i>Hogna rabida</i>	Adult	0.529	0.042	14
<i>Phidippus rimator</i>	Adult	0.151	0.016	10

and *Phidippus* should easily capture 4th- and 5th-instar grasshoppers but may have some difficulty preying on adults (Table 1). We verified the ability of each spider species to subdue different life-cycle stages of grasshopper by presenting them as prey to individual spiders in 0.5-L glass jars. In these trials, 8 of 8 *Hogna* captured and consumed individual 4th- and 5th-instars and adult *M. femurrubrum* within a 10-d period. Seven of 12 *Pisaurina* killed 4th-instar grasshoppers, 5 of 12 *Pisaurina* killed 5th-instar grasshoppers and 1 of the 12 *Pisaurina* killed an adult grasshopper within a 10-d period. Finally, 6 of 6 *Phidippus* killed 4th-instar grasshoppers, 4 of 6 *Phidippus* killed 5th-instar grasshoppers and 1 of 6 *Phidippus* killed adult grasshoppers within a 3-d period.

Previous research demonstrated that *M. femurrubrum* grasshoppers selected plant categories (grass and herb) as resources rather than individual plant species (Schmitz et al. 1997). Grasshoppers decreased their per capita dietary proportion of nutritious grass in favor of less nutritious herbs after *Pisaurina* spiders were experimentally introduced into enclosures at average field densities (Rothley et al. 1997). We hypothesized that the increased preference for herbs was a predation risk-foraging trade-off. Grasshoppers may be seeking refuge from predation in structurally more complex herbs, which tend to be spatially segregated from grasses in the field system (Beckerman et al. 1997).

METHODS

This study included three parts. First we observed spider hunting behavior in the field to compare the location and movement of each species within the vegetation canopy. Then we conducted a laboratory experiment to compare the direct effects of each spider species on *Melanoplus femurrubrum* diet (trait), which could ultimately influence the grasshopper effects on plants (Rothley et al. 1997, Schmitz et al. 1997). Third, we conducted a field experiment to compare the direct effects of each spider species on populations of *M. femurrubrum* prey (mortality rate and density). In this experiment, we also compared the indirect effects of each spider species on the abundance of grasses and

herbs via grasshopper diet shifts in response to predation risk (trait-mediated effect) relative to grasshopper density reductions due to predation (density-mediated effect). Specifically, we focused on the generalist *M. femurrubrum* rather than both the specialist and generalist grasshoppers for two reasons. First, the generalist displays both density- and trait-based responses to predators; the specialist does not (Schmitz 1998). Second, the effects of the generalist species on plants is much stronger than the effects of the specialist (Schmitz 1998). Thus, measuring top-down effects via the generalist species had the highest probability of providing insight into impacts of the leaf-chewing guild on plants (Schmitz 1998).

Field observations: spider species hunting and habitat use

Study design.—During summer 1997 and 1998 we observed the hunting behavior and habitat use of each spider species under natural conditions. Prior to gathering data, we observed spiders in the field to familiarize ourselves with the daily activity budget, behavioral repertoire (hunting and non-hunting behavior), and minimum observation distance (the distance beyond which individual spiders would no longer react to the observer's presence) of each species. We observed *Pisaurina* and *Phidippus* at minimum distances of 1.5 m. *Hogna* retreated to the litter whenever an observer was within 1.5 m. We therefore dusted individual *Hogna* with fluorescent powder and observed them from 2–2.5 m using binoculars. We observed *Hogna* inside circular 2 m² × 20 cm high aluminum sheet metal enclosures sunk 3 cm into the soil layer. We observed *Pisaurina* and *Phidippus* between 0800 and 1600. We observed *Hogna* throughout the day, but most activity occurred between 1700 and 2200. Behavior of a focal individual, including all predation attempts, was recorded continuously. We quantified the horizontal and vertical distances traveled by individuals every 5 min until an individual spider reacted to the presence of the observer (50 min–6 h), after which the observation was terminated.

Statistical analysis.—We estimated the mean (\pm 1

TABLE 2. Initial relative abundance (proportion of area covered by a species) of the four dominant grass and herb species at the Yale-Myers Forest study field in cages allocated to each treatment.

Plant species	Initial conditions by treatment				
	1-level web†	2-level web‡	3-level web§		
			<i>Pisaurina</i>	<i>Hogna</i>	<i>Phidippus</i>
<i>Phleum pratense</i>	0.35 ± 0.09	0.43 ± 0.08	0.45 ± 0.08	0.36 ± 0.07	0.29 ± 0.10
<i>Solidago rugosa</i>	0.19 ± 0.04	0.19 ± 0.05	0.25 ± 0.05	0.29 ± 0.06	0.36 ± 0.06
<i>Daucus carota</i>	0.02 ± 0.07	0.02 ± 0.07	0.01 ± 0.05	0.01 ± 0.01	0.02 ± 0.08
<i>Aster novaeangliae</i>	0.02 ± 0.01	0.01 ± 0.006	0.01 ± 0.006	0.02 ± 0.008	0.01 ± 0.01

Note: Data are means ± 1 SE ($n = 10$ replicate cages).

† Plants only.

‡ Plants and grasshoppers.

§ Plants, grasshoppers, and one spider.

SE) in both time moving and distance moved for each spider species by averaging the mean time and distance that each individual of a species moved per 5-min interval. Since we observed individual spiders for different lengths of time, we weighted each individual mean by the total number of 5-min intervals that we observed that individual. The sizes of independent samples for the analysis were 14 *Pisaurina*, 10 *Phidippus*, and 24 *Hogna*. We compared horizontal and vertical movement of spider species in the vegetation canopy by estimating and plotting the 95% confidence ellipse for each species.

Laboratory experiment: spider effects on grasshopper diet

Experimental design.—During August 1998 we observed individual *M. femurrubrum* feeding in six rectangular 2 m² × 1 m high screen terraria that were filled with pieces of sod cut from the same fields in which we conducted the spider behavioral observations and trophic interaction experiments (see *Field experiment: direct and indirect effects* . . . , below). The terraria were small enough to observe grasshopper feeding yet large enough for grasshoppers to escape predators by whatever natural means they chose (e.g., crawling, hopping, or flying). The terraria were placed in a field, exposed to ambient light, temperature, and moisture.

We included four treatments: (1) 10 adult grasshoppers alone; (2) 10 grasshoppers with 4 *Pisaurina*; (3) 10 grasshoppers with 4 *Hogna*; and (4) 10 grasshoppers with 4 *Phidippus*. While densities of predators and prey were lower than natural field densities at the time of observation, we used the highest densities that we could monitor during 30-min observation periods. Grasshoppers were collected with sweep nets and added to the terraria one day before observations. Field-collected spiders were stocked at dawn on the day of observation. To obtain independent estimates of grasshopper behavior we collected and stocked new individual grasshoppers and spiders for each day. Tops of terraria were sealed with wire so that grasshoppers and spiders could not escape. Because we were constrained by the number of terraria, we conducted trials over five

days with the same ambient temperatures and cloud cover. Treatments were randomly assigned to observation days and terraria with at least six replicates of each treatment.

We observed grasshoppers every 30 min from 0700 until darkness and recorded the behavior of each individual (i.e., feeding, resting, moving). If a grasshopper was feeding, we recorded whether it was feeding on grasses or herbs.

Statistical analysis.—We estimated the mean proportion of grasshoppers observed feeding on grass in 0.5-h observation periods to estimate diet selection for a treatment. We compared proportions between treatments using a Kruskal-Wallis test because the data could not be normalized by a transformation. For $k > 3$ treatments, the Kruskal-Wallis test statistic has a chi-square distribution with $k - 1$ degrees of freedom (Siegel 1956).

Field experiment: direct and indirect effects of spiders

Experimental design.—During summer 1997 we conducted an experiment using field cages to compare the direct effects of each spider species on grasshopper populations and the indirect effects on plants. We used standard enclosures made of aluminum screening (Beckerman et al. 1997, Schmitz 1998), into which we stocked grasshoppers and spiders. Our goal was to evaluate the effects of each spider species on lower levels in the food web independently of interactions among predators. We used smaller (0.25 m² × 1 m high) cages than in the behavioral trials in order to stock one spider to a cage while matching natural field densities. To determine whether there were differences in the initial abundance of plant species among cages allocated to different treatments, we estimated the percentage of area covered by each plant species. MANOVA on arcsine-square-root-transformed data of the four dominant species (Table 2) revealed no significant difference ($P > 0.29$, $df = 12, 108$) in initial relative abundance among treatments.

We arrayed the cages in a randomized-block design consisting of 10 blocks with each treatment randomly

allocated to one cage in each block. Cages were separated by 1.5 m. Most naturally occurring animals were removed from the cages prior to stocking by careful hand-sorting of the vegetation and leaf litter in each cage. We were unable to remove small spiders (e.g., *Schizocosa* sp., *Pirata* sp.) that use the sub-litter layer but do not eat grasshoppers.

We compared the direct effects of hunting spiders on grasshopper mortality rate and density and compared the indirect effects of spider species on plant biomass. Treatments included: (1) 1-level web with plants only; (2) 2-level web containing plants and grasshoppers; and (3) 3-level webs containing plants, grasshoppers, and one spider (either *Pisaurina*, *Hogna*, or *Phidippus*).

In early August we stocked eight 4th-instar grasshopper nymphs in the cages containing two-trophic-level and three-trophic-level interaction webs. The stocked grasshopper density was 1.5 times higher than natural field levels at the time of stocking. This stocking protocol allows grasshopper populations to undergo exponential decline in density to the levels set by biotic conditions within each cage (Belovsky and Slade 1993, 1995, Schmitz 1993, 1997, Oedokoven and Joern 2000). We censused all cages every 2 d for the first week to ensure that grasshopper populations did not go extinct. Thereafter, cages were censused every 6 d. The experiment ran for 54 d, during which time grasshoppers passed from late instars (4th to 5th) to adults. We ended the experiment at the onset of an insect-killing frost in October. All above-ground, live plant material within each cage was clipped at the soil surface, sorted to grass or herb, dried at 60°C for 48 h, and weighed. In two instances (one replicate of the *Hogna* and the *Phidippus* treatments), the grasshopper populations went extinct before 54 d. For these cases, all vegetation was clipped, sorted to species, and dried within 2 d after the last census. Data from these cases were used to estimate grasshopper mortality rate and plant biomass, but not grasshopper density.

Statistical analysis.—We calculated the mortality rate (m) of grasshoppers under different treatments using nonlinear regression to fit the negative exponential function $N_t = N_0 e^{-mt}$ for each cage independently (N_t = density at time t , N_0 = starting density (8 grasshoppers) and t = time). We estimated final density of grasshoppers on day 54, except for cases where the grasshoppers went extinct. Populations in all treatments remained in steady state for at least 18 d before the end of the experiment. We tested for significant treatment and block effects on mortality rate and density using MANOVA followed by separate ANOVAs for mortality rate and density when a significant overall effect was detected. For significant ANOVAs we used Tukey tests to identify which spider species had significant effects on mortality rate and grasshopper density.

We tested for indirect effects of spider species on plants by comparing the biomass of grasses and herbs

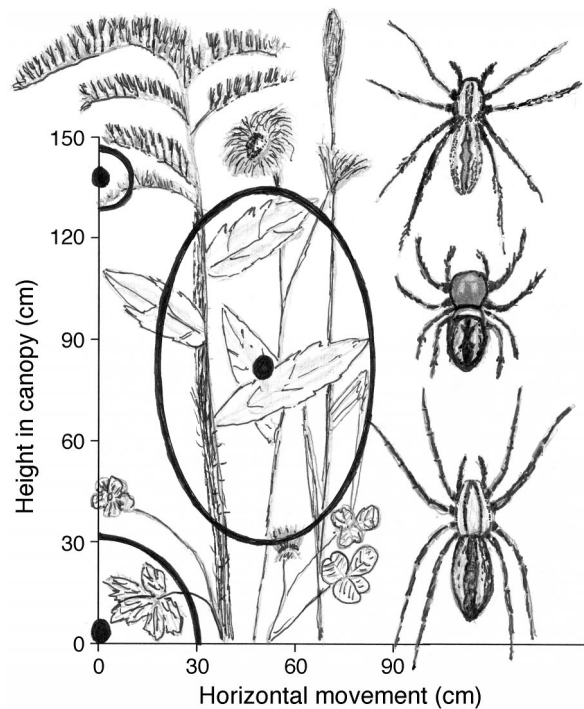


FIG. 1. Horizontal and vertical distance traveled per hour (cm/h) by spiders hunting under natural field conditions at the Yale-Myers study site (Connecticut, USA). The solid circles represent the mean vertical height of and mean horizontal distance traveled by individual spiders in the vegetation canopy. The ellipses represent 95% confidence limits in height location and horizontal movement in the canopy. Data are for the nursery web spider *Pisaurina mira* (top), the jumping spider *Phidippus rimator* (middle), and the wolf spider *Hogna rabida* (bottom). Spiders are drawn to relative size scale. A vertical profile of the vegetation canopy is drawn for reference.

in 1-level interaction webs (plants only) with biomass in 2-level interaction webs and 3-level food interaction webs using a MANOVA, followed by separate ANOVAs for grasses and herbs when MANOVAs were significant. For significant ANOVAs, Tukey tests were used to identify which treatments significantly altered grass or herb biomass.

RESULTS

Field observations: spider species hunting and habitat use

Pisaurina resided in the upper canopy within or immediately below the flower heads of plants (Fig. 1). *Hogna* remained in fixed locations primarily in the ground litter layer (Fig. 1). Both species moved comparatively infrequently (2 ± 0.4 seconds per 5-min sampling period [mean \pm 1 SE], $n = 14$ *Pisaurina* spiders and 3 ± 0.3 s/5-min interval $n = 24$ *Hogna* spiders). *Phidippus* moved more frequently (49 ± 4.5 s/5-min interval $n = 10$ spiders) and moved throughout the canopy (Fig. 1).

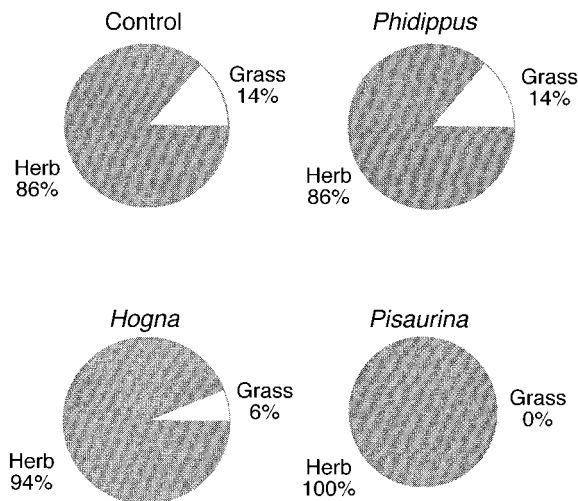


FIG. 2. Grasshopper diet selection in the absence of predators (control) and in the presence of different species of hunting spider. Diet selection is measured as the average daily proportion of grasshoppers feeding on grass and herb.

Pisaurina was a classic sit-and-wait predator, pouncing only when prey were within striking distance. We observed 17 predation attempts on a variety of prey; two attempts resulted in the capture of a late-instar grasshopper nymph and an adult grasshopper. *Hogna* waited until prey moved to within several centimeters proximity and then ran and attacked the prey. This sit-and-pursue hunting behavior has been observed in several other lycosid species (Schoener 1969, Ford 1977, 1978, Wagner and Wise 1997, Uetz 1979). We observed three different *Hogna* consuming grasshoppers during our field observations. *Phidippus* stalked prey throughout the canopy and pounced on them. This active hunting behavior is similar to other salticid spider species (Gardner 1964, Forster 1977, 1982, Givens 1978, Johnson 1996). We observed 35 predation attempts on a variety of prey species. Three of thirteen attempts on *Melanoplus femurrubrum* nymphs resulted in successful captures.

Laboratory experiment: spider species effects on grasshopper diet

Grasshoppers exhibited significant diet shifts from grass to herbs (Kruskal-Wallis test, $P < 0.01$, $df = 3$) when they were in the presence of the comparatively sedentary species (the smaller *Pisaurina* and the larger *Hogna*) compared to controls without spiders (Fig. 2). Grasshoppers in the presence of the smaller and comparatively more active *Phidippus* spiders, however, did not alter their diet selection when compared to control (Fig. 2).

Field experiment: direct and indirect effects of spiders

Populations of grasshoppers underwent exponential decline in density, eventually reaching a steady state

toward the end of the field experiment (Fig. 3a). Mean grasshopper mortality rate and steady-state density varied significantly (MANOVA: $F = 8.12$, $df = 6, 52$, $P < 0.001$) with spider species (Fig. 3b and c). Block effects were not significant (MANOVA: $F = 1.07$, $df = 18, 52$, $P > 0.33$). The effect of spider species on grasshopper mortality rate was significant (ANOVA: $F = 7.18$, $df = 3, 27$, $P < 0.01$) due to higher mortality rates in treatments with *Hogna* and *Phidippus* relative to the control (Tukey test, both $P < 0.01$) but not by *Pisaurina* (Tukey test, $P > 0.60$). The effect of spider species on grasshopper density was also significant (ANOVA: $F = 18.94$, $df = 3, 25$, $P < 0.001$), again due to significant reductions in grasshopper density by *Hogna* and *Phidippus* (Tukey test, both $P < 0.001$) but not by *Pisaurina* ($P = 0.78$).

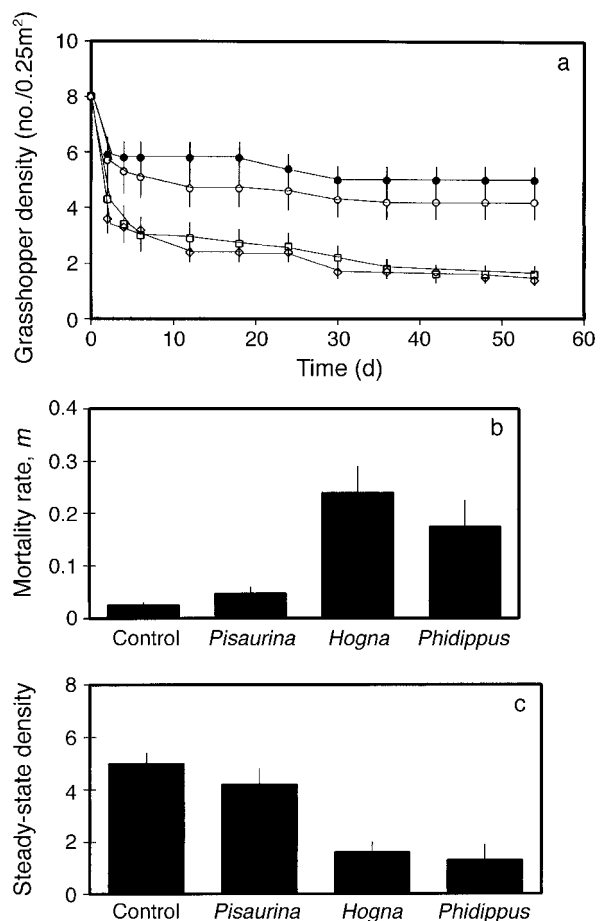


FIG. 3. Effects of spider species on grasshopper populations in enclosures. (a) Time series of grasshopper cage densities; ● = grasshoppers alone (control), ○ = grasshoppers with *Pisaurina*, □ = grasshoppers with *Hogna*, and ◇ = grasshoppers with *Phidippus*. (b) Mortality rates of grasshoppers in different spider species treatments, estimated by fitting negative exponential functions to the time series for each cage. (c) Grasshopper density at the end of the experiment (day 54). Values are means ± 1 SE for (a) and means ± 1 SE for (b) and (c) ($n = 10$ replicate cages).

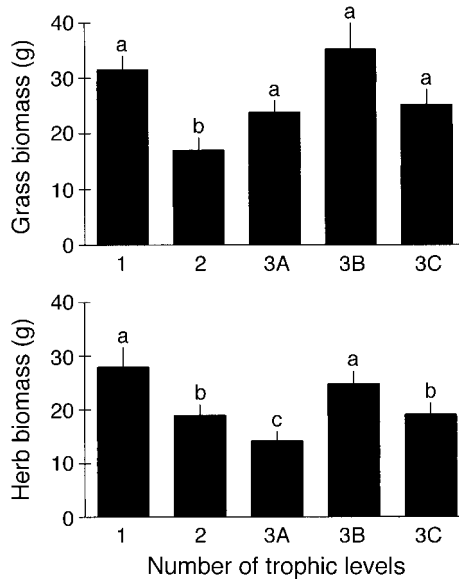


FIG. 4. Effect of trophic-level manipulations on grass and herb biomass in experimental 0.25-m² old-field enclosures. Trophic-level key: 1 = enclosures containing plants only, 2 = enclosures containing grasshoppers and plants, 3 = cages with plants, grasshopper, and natural field densities of one spider species; 3A, 3B, and 3C are 3-level webs containing, respectively, *Pisaurina*, *Hogna*, and *Phidippus*. Bars with different lowercase letters identify treatments that are statistically significantly different at the $P < 0.05$ level. Values shown are means and 1 SE ($n = 10$, replicate cages).

There were also significant treatment effects on grass and herb biomass (MANOVA: $F = 6.582$, $df = 8, 70$, $P < 0.001$), but there were no significant block effects (MANOVA: $F = 1.32$, $df = 18, 70$, $P > 0.30$). Grasshoppers caused significant reductions in both grass and herb biomass (Fig. 4, Table 3). All three spider species had a similar net effect on grass biomass, a positive indirect effect (Fig. 4), while causing different net effects on herbs. *Pisaurina* had a significant negative effect on herb biomass, *Hogna* had a significant positive indirect effect on herb biomass, and *Phidippus* had no significant effect on herb biomass (Fig. 4, Table 3).

DISCUSSION

This study compared the food-web effects of different species of top predators that belong to the same guild. The motivation for doing this study was to evaluate the assumption that aggregating species that have putatively similar functional roles into the same guild (e.g., cursorial hunting spiders) is a reasonable starting point for purposes of modeling complex food webs (e.g., Yodzis 1996). Counter to this intuition, however, we found that the spider species that would normally be assigned to the same guild had different effects on food webs. These differences arose because differences in predator-species habitat use and hunting behavior altered the nature of the direct effects on grasshopper prey and consequently the indirect effects on plants.

The three spider species were segregated vertically within the vegetation canopy (Fig. 1). The comparatively sedentary species (sit-and-wait *Pisaurina* and sit-and-pursue *Hogna*) were located in the upper canopy on flower heads of grasses and herbs and in the lower one quarter of the canopy and the ground story, respectively. The more active *Phidippus* roamed on grasses and herbs throughout the canopy. The differences in spider mobility and habitat use may have influenced the use of different plants in the community by grasshoppers. Grasshoppers consumed a higher proportion of herbs when in the presence of the sit-and-wait *Pisaurina* and the sit-and-pursue *Hogna* than in the presence of the actively hunting *Phidippus* and without predators. We present three possible explanations for the presence or absence of a diet shift. First, herbs are more structurally complex than grasses, so they may offer some refuge from predation by the more sedentary spider species (Beckerman et al. 1997). However, switching to herbs may not protect grasshoppers from *Phidippus*, which hunts on grasses and herbs throughout the canopy. Second, when grasshoppers are faced with conflicting demands of feeding and vigilance, adaptive foraging theory (Abrams and Schmitz 1999) predicts that they should shift their diet to eat those foods that fill the gut faster thereby reducing time exposed to predators. The diet shift toward herbs is

TABLE 3. Results of ANOVA and Tukey test for the experiment testing the effects of trophic-level manipulation and spider species on plant biomass in experimental cages in the Yale-Myers Research Forest study system.

Spider species (hunting style)	Plant group	df	<i>F</i>	<i>P</i>	Tukey test†
<i>Pisaurina mira</i> (sit-and-wait)	grass	3, 27	6.48	<0.01	(1,3)>2
	herb	3, 27	6.06	<0.01	1>2>3
<i>Hogna rabida</i> (sit-and-pursue)	grass	3, 27	4.08	<0.05	(1,3)>2
	herb	3, 27	2.89	0.056	(1,3)>2
<i>Phidippus rimator</i> (actively hunting)	grass	3, 27	6.32	<0.01	(1,3)>2
	herb	3, 27	3.23	<0.05	1>(2,3)

† Comparing plant biomass in interaction webs containing (1) only plants, (2) plants and herbivores, (3) plants, herbivores, and spiders. Numbers in parentheses indicate no significant difference between treatment means. A positive indirect effect of spiders occurs when (1,3)>2. A negative indirect effect occurs when 1 > 2 > 3.

TABLE 4. Summary of direct and indirect effects of spider species on experimental old-field food webs at the Yale-Myers study system.

Spider species (hunting style)	Direct effect on grasshoppers			Indirect effect on plants		Net food-web effect†
	Density	Consumption of		Grass	Herb	
		Grass	Herb			
<i>Pisaurina mira</i> (sit-and-wait)	0	↓	↑	+	-	TMI
<i>Hogna rabida</i> (sit-and-pursue)	-	↓	↑	+	+	DMI>TMI
<i>Phidippus rimator</i> (actively hunting)	-	0	0	+	0	DMI

† TMI = trait-mediated indirect effect; DMI = density-mediated indirect effect.

consistent with this prediction. Herbs fill the gut faster because of higher water content than that of grass (Rothley et al. 1997). The cost of this diet shift, however, is that herbs have a lower digestible nitrogen content than grasses, resulting in lower net nutrient intake (Rothley et al. 1997, Schmitz 1997). Third, the strength of predator-avoidance behavior by prey may be related to the amount of information prey have about predator presence (Bouskila and Blumstein 1992, Sih 1992). For example, *Pisaurina* and *Hogna*, which do not move far in a day, may provide a persistent visual cue to grasshoppers in those locations where they hunt (i.e., upper canopy and lower one quarter of the canopy and ground litter layer). Actively hunting *Phidippus*, on the other hand, may only provide infrequent and unpredictable visual cues.

The direct effect of spiders on grasshopper mortality rate and density also varied with spider species (Fig. 3) but not in the same way as the behavioral shifts. The sit-and-wait *Pisaurina* did not have a significant effect on grasshopper mortality and density, consistent with findings from previous field experiments (Beckerman et al. 1997, Schmitz 1998). The lack of an effect could have been an artifact of using late-instar and adult grasshoppers in the experiment. With earlier instars we might have seen greater mortality effects because those stages may be more vulnerable to predation. However, previous experiments on early instars found that most of the variation in trophic effects between *Pisaurina* and grasshoppers was also due to behavioral shifts rather than density reductions (Schmitz et al. 1997). Alternatively, *Pisaurina* may not have reduced grasshopper density if grasshoppers were able to avoid prolonged contact with the predators by feeding in the middle canopy. However, this shift in use of the canopy may involve a trade-off because the most nutritious parts of a plant tend to occur in the uppermost part of the canopy that receives the greatest sunlight (Pitt 1999).

In contrast to *Pisaurina*, the other two spider species had significant effects on mortality of grasshoppers. *Hogna* most effectively reduced grasshopper density, probably because its hunting activity (1700–2200) coincided with the use of the lower canopy and ground

story by grasshoppers. Grasshoppers thermoregulate by moving to the lower canopy to avoid cooler temperatures in the upper canopy later in the day and during the night (Schmitz et al. 1997, Pitt 1999). However, the habitat switch exposes them to greater predation risk by *Hogna*. Actively hunting *Phidippus* also caused significant reductions in grasshopper density, again because foraging by grasshoppers in the canopy throughout the day (1000–1600 [Schmitz et al. 1997]) coincided with the period of greatest hunting effort by *Phidippus*.

Clearly, the direct effects of spiders on grasshopper diet selection and mortality manifested themselves in very different ways in the experimental food webs (Table 4). These data illustrate the variety of cascading effects that can emerge as a result of the interplay between trait-mediated and density-mediated effects of different predator species. The sit-and-wait *Pisaurina* had no direct effects on grasshopper density, yet it had a significant positive indirect effect on grass and a significant negative effect on herbs (Table 4). These results are consistent with the grasshopper foraging shifts—reduction in grass consumption and increase in herb consumption—in response to this predator species that we observed in the grasshopper foraging experiments. Thus, this indirect effect was strictly trait mediated in the manner hypothesized by Schmitz (1998).

The sit-and-pursue *Hogna* had a positive indirect effect on both grass and herbs, despite causing a significant shift in grasshopper diet from grass to herbs, implying that the density-mediated positive indirect effect obscured the trait-mediated effect (Table 4). Finally, the actively hunting *Phidippus* had a positive indirect effect on grass, even though grasshoppers in the presence of this species did not alter their diets, due entirely to a reduction in grasshopper density (Table 4). There was, however, no net effect of *Phidippus* on herb biomass. However, removing one outlier of this treatment (biomass = 8.6 g dry mass/cage) caused *Phidippus* to have a marginally significant ($P \leq 0.10$) positive effect on herb biomass. This result is consistent with expectations for a density-mediated cascading effect (Schmitz 1998).

The concept of a cascading trophic effect provides

a powerful framework for understanding the importance of indirect effects in food webs (Hairston et al. 1960, Paine 1980, Carpenter et al. 1985). Experimental tests of this have shown that reasonable characterizations of community dynamics must begin with an understanding of interactions among at least three species each belonging to different trophic positions in a food web. Current theory assumes that these indirect effects emerge either from direct density reductions of herbivores due to predation (Rosenzweig 1973, Oksanen et al. 1981, Carpenter et al. 1985, Menge and Sutherland 1987, Leibold 1989, Schmitz 1992) or from reductions in feeding activity by herbivores to increase vigilance (Abrams 1992, 1995). In both cases, predators are expected to have positive indirect effects on plants by reducing the ability of herbivores to damage plants. These predictions result from aggregating species into one of three distinct trophic levels.

Our data demonstrate that because of the differential effects of spider species on plant groups one must be careful not only about aggregating predator species within the same guild but also aggregating plants into single groups when modeling cascading trophic interactions. This is especially important in cases where consumers have choices among resources and thus undergo diet or habitat shifts (see also Power et al. 1985, Turner and Mittelbach 1990, Beckerman et al. 1997, Schmitz et al. 1997, Turner et al. 1999). Consequently, current theory on trophic interactions in food webs is insufficient to explain the range of direct and indirect effects observed in our study system. We therefore suggest that studies on cascading effects in communities should probably move away from a classical "community-cascade" viewpoint, in which species within the same level in a food web are assigned to single group, and alternatively examine "species cascades" (sensu Polis 1999). Species cascades may be a better conceptualization because they allow the freedom to explore the rich range of behavior species exhibit as a consequence of the ability to choose among resources and habitats.

We demonstrate that in this old-field system the effects of predators on grasshopper behavior, density, or both may dominate depending on species of top predator. This study further illustrates that we need to integrate the nature of interactions among species within functional groups and the interplay between predator effects on prey behavior and density into a new theoretical conceptualizations of food-web dynamics.

ACKNOWLEDGMENTS

We wish to thank A. Beckerman for assistance in the field. A. Beckerman, P. Hambäck, J. Kiesecker, B. Luttbeg, M. McPeck, J. Moll, B. Peckarsky, K. Rothley, and D. Skelly provided very helpful comments. This research was funded by NSF grant DEB-9508604 to O. J. Schmitz, the Yale School of Forestry and Environmental Studies, and the generous support of Mrs. E. Storm-Dwyer.

LITERATURE CITED

- Abrams, P. A. 1992. Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptations. *American Naturalist* **140**:573–600.
- Abrams, P. A. 1995. Implications of dynamically-variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. *American Naturalist* **146**:112–134.
- Abrams, P. A., B. A. Menge, G. G. Mittelbach, D. Spiller, and P. Yodzis. 1996. The role of indirect effects in food webs. Pages 371–395 in G. Polis and K. Winemiller, editors. *Food webs: integration of patterns and dynamics*. Chapman & Hall, New York, New York, USA.
- Abrams, P. A., and O. J. Schmitz. 1999. The effect of risk of mortality on the foraging behavior of animals faced with time and gut-capacity constraints. *Evolutionary Ecology Research* **1**:285–301.
- Beckerman, A. P., M. Uriarte, and O. J. Schmitz. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proceedings of the National Academy of Science (USA)* **94**:10735–10738.
- Belovsky, G. E., and J. B. Slade. 1993. The role of vertebrate and invertebrate predators in a grasshopper community. *Oikos* **68**:193–201.
- Belovsky, G. E., and J. B. Slade. 1995. Dynamics of some Montana grasshopper populations: relationships among weather, food abundance and intraspecific competition. *Oecologia* **101**:383–396.
- Belovsky, G. E., J. B. Slade, and B. Stockhoff. 1990. Susceptibility to predation of different grasshoppers: an experimental approach. *Ecology* **71**:624–634.
- Bouskila, A., and D. T. Blumstein. 1992. Rules of thumb for predation hazard assessment: predictions from a dynamic model. *American Naturalist* **139**:161–176.
- Bristowe, W. S. 1971. *The world of spiders*. Collins, London, UK.
- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* **35**:634–639.
- Cherill, A. J., and M. Begon. 1989. Predation on grasshoppers by spiders in sand dune grasslands. *Entomologia Experimentalis et Applicata* **50**:225–231.
- Ford, M. J. 1977. Metabolic costs of the predation strategy of the spider *Pardosa amentata* (Clerk) (Lycosidae). *Oecologia* **28**:333–340.
- Ford, M. J. 1978. Locomotory activity and the predation strategy of the wolf spider *Pardosa amentata* (Clerk) (Lycosidae). *Animal Behavior* **26**:31–35.
- Forster, L. M. 1977. A qualitative analysis of hunting behavior in jumping spiders (Araneae: Salticidae). *New Zealand Journal of Zoology* **4**:51–62.
- Forster, L. M. 1982. Vision and prey capture strategies in jumping spiders. *American Scientist* **70**:165–175.
- Gardner, B. T. 1964. Hunger and the sequential response in the hunting behavior of salticid spiders. *Journal of Comparative and Physiological Psychology* **58**:167–173.
- Givens, R. P. 1978. Dimorphic foraging strategies of a salticid spider (*Phidippus audax*). *Ecology* **59**:309–321.
- Hairston, N. E., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* **94**:421–425.
- Houston, A. I., J. M. McNamara, and J. M. C. Hutchinson. 1993. General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society of London Series B* **341**:375–397.
- Huang, C., and A. Sih. 1991. Experimental studies on direct and indirect interactions in a three trophic-level system. *Oecologia* **85**:530–536.
- Janssen, A., A. Palini, M. Venzon, and M. Sabelis. 1998.

- Behavioral and indirect interactions in food webs of plant-inhabiting arthropods. *Experimental and Applied Acarology* **22**:497–521.
- Johnson, S. R. 1996. Use of coleopteran prey by *Phidippus audax* (Araneae, Salticidae) in tallgrass prairie wetlands. *The Journal of Arachnology* **24**:39–42.
- Kajak, A., L. Andrzejewska, and Z. Wojcik. 1968. The role of spiders in the decrease of damages caused by *Acridoidea* on meadows-experimental investigations. *Ekologia Polska (A)* **26**:755–746.
- Lavigne, R. J., and R. E. Pfadt. 1966. Parasites and predators of Wyoming rangeland grasshoppers. University of Wyoming Agriculture Experiment Station Science Monograph **3**.
- Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *American Naturalist* **134**:922–949.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation. *Canadian Journal of Zoology* **68**:619–640.
- Mangel, M., and C. W. Clark. 1986. Toward a unified foraging theory. *Ecology* **67**:1127–1138.
- McIntosh, A. R., and B. L. Peckarsky. 1999. Criteria determining behavioral responses to multiple predators by a stream mayfly. *Oikos* **85**:554–564.
- McIntosh, A. R., and C. R. Townsend. 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: Trophic cascade mediated by fish-induced changes to grazer behavior? *Oecologia* **108**:174–181.
- McPeck, M. A. 1998. The consequence of changing the top predator in a food web: a comparative experimental approach. *Ecological Monographs* **68**:1–23.
- Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to gradients of environmental stress and recruitment. *American Naturalist* **130**:730–757.
- Messina, F. J. 1981. Plant protection as a consequence of an ant-membracid mutualism: interactions on goldenrod (*Solidago* sp.). *Ecology* **62**:1433–1440.
- Moran, M. D., T. P. Rooney, and L. E. Hurd. 1996. Top-down cascade from a bitrophic predator in an old-field community. *Ecology* **77**:2219–2227.
- Oedokoven, M. A., and A. Joern. 2000. Plant quality and spider predation affects grasshoppers: food-quality-dependent compensatory mortality. *Ecology* **81**:66–77.
- Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemelä. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* **118**:240–262.
- Paine, R. T. 1980. Food webs: linkage, interaction strength, and community infrastructure. *Journal of Animal Ecology* **49**:667–685.
- Peacor, S., and E. E. Werner. 1997. Trait-mediated indirect interactions in a simple aquatic food web. *Ecology* **78**:1146–1156.
- Persson, L. 1999. Trophic cascades: abiding heterogeneity and the trophic level concept at the end of the road. *Oikos* **85**:385–397.
- Pitt, W. C. 1999. Effects of multiple vertebrate predators on grasshopper habitat selection: trade-offs due to predation risk, foraging and thermoregulation. *Evolutionary Ecology* **13**:499–515.
- Polis, G. A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos* **86**:3–15.
- Polis, G. A., and D. R. Strong. 1996. Food-web complexity and community dynamics. *American Naturalist* **147**:813–846.
- Power, M. E., W. J. Matthews, and A. J. Stewart. 1985. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. *Ecology* **66**:1448–1456.
- Rosenzweig, M. L. 1973. Exploitation in three trophic levels. *American Naturalist* **107**:275–294.
- Rothley, K. D., O. J. Schmitz, and J. L. Cohon. 1997. Foraging to balance conflicting demands: novel insights from grasshoppers under predation risk. *Behavioral Ecology* **8**:551–559.
- Schmitz, O. J. 1992. Exploitation in model food webs with mechanistic consumer-resource dynamics. *Theoretical Population Biology* **41**:161–183.
- Schmitz, O. J. 1993. Trophic exploitation in grassland food webs: simple models and a field experiment. *Oecologia* **93**:327–335.
- Schmitz, O. J. 1997. Press perturbation experiments and the predictability of ecological interactions in a food web. *Ecology* **78**:55–69.
- Schmitz, O. J. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. *American Naturalist* **151**:327–342.
- Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. Behaviorally mediated trophic cascades: the effects of predation risk on food web interactions. *Ecology* **78**:1388–1399.
- Schoener, T. W. 1969. Models of optimal size for solitary predators. *American Naturalist* **103**:277–313.
- Siegel, S. 1956. *Nonparametric statistics for the behavioral sciences*. McGraw-Hill, New York, New York, USA.
- Sih, A. 1980. Optimal behavior: Can foragers balance two conflicting demands? *Science* **210**:1041–1043.
- Sih, A. 1992. Prey uncertainty and the balancing of anti-predator feeding needs. *American Naturalist* **139**:1052–1069.
- Turner, A. M., S. A. Fetterolf, and R. J. Bernot. 1999. Predator identity and consumer behavior: differential effects of fish and crayfish on habitat use of a freshwater snail. *Oecologia* **118**:242–247.
- Turner, A. M., and G. G. Mittelbach. 1990. Predator avoidance and community structure: interactions among piscivores, planktivores, and plankton. *Ecology* **71**:2241–2254.
- Uetz, G. W. 1979. The influence of variation in litter habitats in spider communities. *Oecologia* **40**:29–42.
- Uriarte, M., and O. J. Schmitz. 1998. Trophic control across a natural productivity gradient. *Oikos* **82**:552–568.
- Wagner, J. D., and D. H. Wise. 1997. Influence of prey availability and conspecifics on patch quality for a cannibalistic forager: laboratory experiments with the wolf spider *Schizocosa*. *Oecologia* **109**:474–482.
- Watt, K. E. F. 1968. *Ecology and resource management*. McGraw-Hill, New York, New York, USA.
- Werner, E. E., and B. R. Anholt. 1996. Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae. *Ecology* **77**:157–169.
- Wise, D. H. 1993. *Spiders in ecological webs*. Cambridge University Press, Cambridge, UK.
- Yodzis, P. 1996. Food webs and perturbation experiments: theory and practice. Pages 192–200 in G. Polis and K. Winemiller, editors. *Food webs: integration of patterns and dynamics*. Chapman & Hall, New York, New York, USA.