CONTRASTING TROPHIC CASCADES GENERATED BY A COMMUNITY OF GENERALIST PREDATORS

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Abstract. We examined whether intraguild predation (IGP) weakens the ability of two taxa of generalist predators, carabid beetles and lycosid spiders, to control herbivore densities in gardens of cucumber and squash. We also measured fruit production to determine whether IGP weakens the ability of the predators to impact plants indirectly through trophic cascades. These predators did impact herbivore densities, but their impact on different herbivores varied dramatically. As the herbivore community changed through the season, so too did the predators’ indirect effect on fruit production.

In spring cucumber gardens, lycosids caused fruit production to increase by reducing densities of striped cucumber beetles, which are important early-season herbivores. Carabids also weakly reduced cucumber beetle densities, and the entire carabid–lycosid guild enhanced cucumber yield. However, the carabid–lycosid guild’s impact changed dramatically later in the season. In summer squash gardens, carabids increased fruit production by reducing densities of the squash bug, the major late-season herbivore. In marked contrast, lycosid spiders strongly reduced squash yield, possibly by IGP on important hemipteran predators of the squash bug. The late-season effects of carabids and lycosids counteracted one another, so that the complete carabid beetle–lycosid spider guild had no impact on squash fruit production. Thus, the complex trophic connections between generalist predators and the rest of the community made the predators’ impact relatively fluid, changing even within a single season. Results of pairing predators with herbivores or other predators in laboratory microcosms supported hypothesized trophic interactions in both spring and summer food webs.

Key words: biological control; carabid beetle; generalist predator; indirect effects; intraguild predation; trophic cascade; trophic-level omnivory; wolf spider.

INTRODUCTION

Intraguild predation (IGP) complicates the impact of generalist predators on herbivore populations. Generalists can directly reduce herbivore densities by preying on them, but can also indirectly increase herbivore numbers by preying on other natural enemies. Thus, IGP can limit the ability of generalist predators to control herbivore densities (Polis et al. 1989, Polis and Holt 1992, Rosenheim et al. 1993, 1995, Rosenheim 1998). Terrestrial communities often contain many species of generalist predators (e.g., Polis 1991, Rosenheim et al. 1999), with species impacting herbivores through complex webs of direct predation and indirect release from predation due to IGP. The combination of some species reducing herbivores, while other predators prey mainly upon one another, could render species-diverse predator guilds unable to initiate strong top-down control of herbivores, which in turn could dilute the predator guild’s ability to reduce herbivore damage to plants via a three-trophic level cascade (Polis 1991, Strong 1992, Polis and Strong 1996).

Intraguild predation appears to be common in both agricultural (Rosenheim et al. 1995, Rosenheim 1998) and less-disturbed (Polis et al. 1989, Polis and Holt 1992) terrestrial communities. Despite the apparent commonness of IGP, which should weaken the cascading impact of generalist predators (Strong 1992, Polis and Strong 1996), several experimental studies in terrestrial communities have uncovered impacts of generalist predators that propagate across multiple trophic levels (e.g., Schmitz 1994, Spiller and Schoener 1994, Moran et al. 1996, Schmitz et al. 1997, Chase 1998). Agricultural systems, which frequently are dominated by one or a few plant species, may harbor relatively simple species assemblages compared to some less-disturbed communities. Low species diversity in agro-ecosystems may lead to simpler trophic connections, and thus make strong predator impacts more likely (Strong 1992). Riechert and Bishop (1990), Helenius (1990), and Carter and Rypstra (1995), for example, found that the presence of spiders and other generalist predators was associated with reduced herbivore damage to crop plants. Unfortunately, none of the studies in agricultural systems examined effects of the manipulated predators on other predators, so it is unclear what role, if any, IGP played in moderating the observed predator effects.

Wolf spiders and carabid beetles are ubiquitous
members of temperate terrestrial ecosystems and together comprise a large component of the guild of ground-dwelling generalist predators. Typical of generalist predators, both taxa are reported to interfere with other predators (Sunderland 1975, Chiverton 1986, Hayes and Lockley 1990, Wise 1993, Nyffeler et al. 1994, Fagan et al. 1998), which could dampen their community-wide impact and limit their effectiveness as biocontrol agents. Still, there is evidence that wolf spiders (Wise 1993, Nyffeler et al. 1994) and carabid beetles (Chiverton 1986, Clark et al. 1994) can reduce herbivore numbers and increased squash productivity (Snyder and Wise 1999). Because both predators were manipulated simultaneously, we could not determine to what extent each taxon was responsible for decreasing herbivore densities and increasing fruit production, nor to what degree negative interactions between lycosids and carabids reduced their combined impact on herbivores. We address these issues here with two field experiments in which we separately manipulated immigration of carabid beetles and lycosid spiders into spring gardens of cucumber, and continued the manipulations through a summer crop of squash.

**Materials and Methods**

**Overview**

We manipulated carabid and lycosid immigration into vegetable gardens, using the methods of Snyder and Wise (1999), to achieve the following treatments: (1) Neither carabid nor lycosid immigration allowed (O), (2) carabid immigration only (C), (3) lycosid immigration only (L), and (4) both carabid and lycosid immigration (C+L). Our design also included open reference plots (OPEN), where carabid and lycosid immigration was not manipulated; these plots allowed us to measure the accuracy of our artificial immigration procedure in replicating natural densities of carabids and lycosids. We then periodically measured densities of the manipulated predators, other arthropods, and fruit yields. We repeated the experiment in a second year.

**Study organisms**

Cucurbit plantings at our study site are rapidly colonized by a diverse group of arthropods (Snyder 1999, Snyder and Wise 1999). The generalist predators primarily immigrate from adjacent refuge habitats (Wissinger 1997, Snyder and Wise 1999), while the more specialized cucurbit herbivores may travel longer distances (Grant and Seevers 1989, Lawrence and Bach 1989).

**Manipulated predator guild.**—Carabid beetles include species that are primarily predators, primarily granivores, or primarily scavengers; many species combine these feeding strategies (Lovei and Sunderland 1996). Three carabid taxa are numerically dominant at our field site, together making up 60–88% of the carabid community (Barney and Pass 1986a, Snyder and Wise 1999): *Scuritis* spp., *Cyclocephalas sodalis*, and *Harpalus pennsylvanicus*. At least three *Scuritis* species are present at our site; all are relatively large (adult body length 10–20 mm), predatory carabids that are largely fossorial (Barney and Pass 1986b). *Cyclocephalas sodalis* is of similar size (adult body length ~15–17 mm) and is also predatory (Barney and Pass 1986b). *C. sodalis* hunts mostly on the ground surface, but will also sometimes climb into plant foliage (Barney and Pass 1986b). *Harpalus pennsylvanicus* is also a fairly large carabid (adult body length 14–16 mm), but is more omnivorous than the other two, including seeds as a large fraction of its diet (Barney and Pass 1986b). At least 10 other less common carabid species, covering a range in adult size from 5 to 20 mm, and including a wide range of feeding habits, also occur (see Barney and Pass 1986a). We manipulated adults of all carabid species we captured.

Most carabid larvae live in subterranean burrows, and their biology is poorly known (Thiele 1977). Barney and Pass (1986c), working at our study site, ran 64 pitfall traps through three field seasons. These traps captured over 12,000 adult carabids but only 300 carabid larvae. This limited surface activity of larvae probably means that they do not immigrate into agricultural fields in large numbers (Barney and Pass 1986c), although the long duration of our experiments could have allowed carabids to reproduce within the plots. Thus, while we did not directly manipulate carabid larvae, or measure their densities, immature stages could have contributed to the effects we recorded.

Although laboratory studies indicate that lycosids will feed on dead prey (Knoost and Rovner 1975), lycosid spiders are probably largely predatory in nature (Wise 1993). The lycosid spider community at our site is dominated by members of two genera: *Pardosa* and *Hogna*, which together make up ~60–75% of the lycosid community (Culin and Yeargan 1983, Snyder and Wise 1999). The most common *Pardosa* species are *P. milvina* and *P. saxatilis* (Culin and Yeargan 1983). Both are relatively small wolf spiders (adult body length ~5 mm). *Hogna helluo* is the most common *Hogna* species (Culin and Yeargan 1983, Snyder and Wise 1999); *Hogna* are relatively large spiders (adult body length 15–20 mm). Wolf spiders are difficult to identify to species in the field, so we identified individuals only to genus. Both adult and juvenile wolf spiders were collected and released into the plots.

**Foliage-dwelling predators.**—Cucurbit plantings at our research site attract a diverse group of generalist predators. Two groups dominate numerically: hemipteran predators, mostly nabid (*Nabis* spp.) and minute pirate (*Orius* spp.) bugs; and a diverse assemblage of
spiders, mostly Liniphyiidae, Tetragnathidae, Araneidae, Thomisidae, and Salticidae (Snyder and Wise 1999, Tuntibunpakul 1999). In a previous experiment, Hemiptera and Araneae comprised 61% of the total foliage-dwelling predator community (Snyder and Wise 1999). Nabids eat both insect eggs and smaller soft-bodied stages (Lattin 1989), and among the hemipterans and non-lycosid spiders are probably the only predators large enough to prey regularly upon the most common cucurbit herbivores (Snyder 1999, Tuntibunpakul 1999). The feeding biology of these predators, their relative abundance, and the results of a previous field experiment (Snyder and Wise 1999), suggest that nabid bugs are probably the most important predators, other than carabid beetles and wolf spiders, of the herbivores in our system.

**Herbivores.—** Two cucurbit herbivores dominate at our site: striped cucumber beetles, Acalymma viptata, and squash bugs, Anasa tristis. Spotted cucumber beetles, Diabrotica undecimpunctata howardi, also occurred in our plots, but were relatively rare during the growing season, representing ~6% of the herbivorous beetle catch in D-vac samples (Rincon-Vitova Insectaries, Ventura, California). Melon aphids, Aphis gossypii, were also found but never became abundant. Due to their relative rarity, we chose not to include spotted cucumber beetles and melon aphids in our study.

Striped cucumber beetles feed on cucurbit roots as larvae, pupate in the soil, and then emerge as foliage-feeding adults (Elsey 1988, Godfrey et al. 1988). Striped cucumber beetles continue to spend time on the soil surface as adults, often taking refuge in ground cover when disturbed (W. Snyder, personal observation). Squash bugs overwinter as adults, then emerge and begin laying eggs in May–June. Both nymphs and adults are phloem feeders, feeding externally on cucurbit stems and leaves (Godfrey et al. 1998). Squash bugs often take refuge in ground cover (Cartwright et al. 1990), and females deposit eggs primarily on lower leaves or on ground debris (Palumbo et al. 1991). Thus, both striped cucumber beetles and squash bugs spend time on the ground, where they might encounter carabids and lycosids. There is evidence that both carabids and lycosids can impact cucumber beetle populations (Brust 1991, Snyder and Wise 1999, 2000); impacts of these predators on squash bugs in the field have not been previously reported.

**Field site and planting methods**

Our field site was a 5.6-ha field on the University of Kentucky Spindletop Research Farm in Fayette County, Kentucky. In both experiments 8 × 8-m plots, each separated by 20 m of open field, were plowed in late May. In 1997, 20 plots were assigned to the five treatments in a randomized block design. In 1998, 25 new plots were plowed, and treatments were assigned in a completely randomized design, because there were no block effects the previous year for any response variables. Thus, separate experiments with the same basic design were conducted in each of the two years.

Immediately after plowing, 36-cm metal fences were installed around 16 plots in 1997, and 20 plots in 1998, in order to block immigration by lycosids and carabids. Against the outside of the fence we placed 1 m long trench pitfall traps, separated by 3 m, with 8 traps per plot (Fig. 1). Traps were checked daily, and arthropods other than carabids or lycosids were added to the plots immediately, whereas carabids and lycosids were collected, haphazardly mixed, and then added as required to treatment plots at the mean immigration rate. Details of this technique for regulating natural immigration rates have been presented elsewhere (Snyder and Wise 1999). Snyder and Wise (1999) found that this artificial immigration procedure successfully established carabid and lycosid densities in fenced plots that were similar to those in open reference plots. The low fence barrier allowed us to control immigration by ground-active arthropods, but did not prevent colonization of the plots by winged insect pests or winged natural enemies.

Carabid activity at our site fluctuates dramatically through the season as different species become active (Barney and Pass 1986a, Snyder and Wise 1999). Mean carabid capture rates in the trench traps lining the outside of the plots ranged from 0.8 to 6.7 beetles per trap per day, with a mean (±1 se) immigration rate of 2.2 ± 0.2 beetles per trap per day. To help avoid inflated carabid densities within fenced plots, we limited releases of any one carabid species to 1 individual/m² of plot area (64 individuals/plot) within any 2-wk release period (see Snyder and Wise 1999). Lycosid capture rates in the outer trench traps were between 0.0 and 0.34 spiders per trap per day, with a mean (±1 se) im-
migration rate of 0.14 ± 0.01 spiders per trap per d. Due to the generally low rate of lycosid immigration we did not limit the number released (see Snyder and Wise 1999).

On 4 June in 1997, and on 26 May in 1998, we transplanted cucumber plants (Cucumis sativus, variety ‘Spacemaster’), which were started in the greenhouse 4 wk before planting, into the field plots. Plots contained seven rows of plants, nine plants per row. In 1997 cucumbers were harvested on 16 July, and in 1998 they were harvested first on 13 July and then again on 28 July. A second crop of squash (Cucumis pepo, variety ‘Yellow Crookneck’) was planted from seed on 28 July in 1997 and on 29 July in 1998. Squash were planted in mounds of five seeds per mound, with seven mounds per row in each of seven rows. Squash fruit were harvested on 15 September in 1997 and on 8 September in 1998. Planting techniques for each crop followed University of Kentucky extension recommendations (Strang et al. 1994). No pesticides or fertilizers were applied to the plots, and plots were never irrigated. All gardens were covered with 10 cm of straw mulch immediately after the first crop was planted, with that depth maintained by periodic additions of fresh straw.

**Sampling**

After 10 consecutive daily releases of immigrating predators, trenched traps were closed, and ground predator activity densities within the plots (including the open reference plots) were estimated by running six live cup-pitfall traps and two interior trenched traps per plot for 3 d (Fig. 1). Interior traps were then closed, external trench traps were reopened, and manipulation of immigration was resumed. This cycle of trapping and monitoring was followed from June (immediately after first cucumber planting) until early September (just before squash harvest).

The impact of carabid and lycosid immigration on foliage arthropods was measured by taking D-vac suction samples from one randomly selected plant or mound per row (seven subsamples per plot) on 3 July, 22 July, and 13 September in 1997, and on 9 July, 24 July, 20 August, and 9 September in 1998. Thus samples corresponded with mid- and late cucumber growth and late squash growth in both years, respectively; the additional sample in 1998 corresponded with early squash growth. For each sample the D-vac was placed over the entire plant or mound for three passes of 10 s each (30 s/plant). Arthropods were frozen for later sorting.

To obtain an additional measure of squash bug density early in squash growth, when feeding by squash bugs has the greatest impact (Woodson and Fargo 1992), we counted the number of squash bugs on one randomly chosen plant per row, in each of seven rows per plot. We attempted to minimize disturbance to the nymphs during this count, and no nymphs were collected. The count was made on 26 August in 1997 and 18 August in 1998, in both cases 1 mo after squash were planted.

We measured cucumber yield by collecting all fruit from two randomly selected plants per row (14 plants/plot) on 20 July in 1997; all fruit were collected from each plot in 1998. We collected all squash fruit from each plot in the summer gardens in both years. Squash were harvested on 15 September in 1997 and on 8 September in 1998. Fruit production was expressed as kg of cucumber or squash per plot.

**Statistical analyses**

In preliminary data analyses, we separately tested each year’s data from D-vac and pitfall trap samples for statistically significant treatment × time interactions in repeated measures MANOVA. Treatment × time interactions were never statistically significant (Wilks’ lambda, $P > 0.05$); neither was the block effect ($P > 0.30$) that was part of the experimental design in 1997. Because we were primarily interested in whether predator impacts were consistent between years, we analyzed and present here seasonal mean responses from the two field experiments together, in a $2 \times 2 \times 2$ factorial ANOVA, with year, carabid addition, and lycosid addition as the factors with blocking, which was part of the design only in the first year, dropped from the analysis.

Since our system was open to immigration and in situ reproduction, we tested an additive model of interaction (i.e., we did not systematically log transform data before statistical analyses; Sih et al. 1998). Independence of treatments between years was achieved by using new plots in 1998. For all analyses, data were log transformed when necessary to meet assumptions of ANOVA.

**Laboratory feeding trials**

We have published the results of feeding trials that were simple pairings of predator and prey in small arenas containing only the two arthropods and a thin layer of soil (Snyder and Wise 1999). However, in many instances the interaction web derived from these initial pairings seemed unable to explain the results of the field experiments we report here. For example, in the simple arenas, wolf spiders readily preyed upon squash bug nymphs. In contrast, in the field experiments squash bug densities were higher in the presence of lycosids. We suspected that the lack of spatial complexity was inflating the likelihood of some interactions. Thus, we repeated the laboratory trials of selected species pairings in larger microcosms that more accurately reproduced field conditions.

All arthropods used in the feeding trials were collected from the University of Kentucky’s Spindletop Research Farm. Carabids and lycosids were collected in pitfall traps. Herbivores and predatory hemipterans were collected by aspirator or by hand by gently knock-
squash bug nymphs; Ð, pairing was not attempted.

run as part of that study, but were not reported); StCB, striped cucumber beetle; SQB-egg, squash bug eggs; SQB-nymph, occur with this pairing in a previous study with structurally simple microcosms (Snyder and Wise 1999; nabid pairings were killed/number of replicates for nabids. Abbreviations and symbols are: na, pairing not attempted because predation did not

data are presented as mean number killed, with number of replicates in parentheses, for herbivores and as total number killed/number of replicates for nabids. Abbreviations and symbols are: na, pairing not attempted because predation did not occur with this pairing in a previous study with structurally simple microcosms (Snyder and Wise 1999; nabid pairings were run as part of that study, but were not reported); StCB, striped cucumber beetle; SQB-egg, squash bug eggs; SQB-nymph, squash bug nymphs; —, pairing was not attempted.

ing them off vegetation and into collecting jars. Herbivores and nabids were collected from gardens of squash (Cucurbita pepo, var. “Yellow Crookneck”) that were planted for this purpose. Squash bug eggs were collected from the same squash plantings. All arthropods used in feeding trials had been collected within the previous 24 h.

Our microcosms consisted of 37 45-L (10-gallon) aquaria, covered with a screen lid, and housed in a greenhouse with temperatures that fluctuated between 22°C at night and 30°C in the day and a photoperiod of 14:10 (L:D) h. Each microcosm contained two 10-d old squash plants in 5 cm of moist potting soil covered with a 1–2-cm layer of straw mulch. Aquaria were misted daily with distilled water to provide drinking water for the arthropods.

Herbivores were released into the aquaria first; predators were released 24 h later. Squash bug eggs were placed as intact clutches of four eggs at the base of squash plants. It is typical for squash bugs to deposit their eggs low on squash foliage (Palumbo et al. 1991), and in fact all the eggs used in these trials were field collected from the base of squash plant stems within 3 cm of the ground surface. Squash bug egg masses were left on a short section (2 cm) of the stem of the plant from which they had been field collected; the stem was planted upright in the soil. After 7 d the aquaria were carefully searched for surviving arthropods. Aquaria were then re-covered and searched again 24 h later. Few arthropods were recovered in the second search, so the aquaria were not searched a third time. Each pairing was replicated four to six times (Table 1). We also established an equal number of concurrent controls, which contained the focal herbivore but no predator. Predators were only paired with herbivores that they had consumed in the microcosm feeding trials reported previously (Snyder and Wise 1999).

Interaction strengths were calculated as the mean proportion of prey eaten in each predator treatment, corrected for mortality in the control microcosms. These corrected mortality rates were used to construct an interaction web. We then constructed a similar interaction web based on the results of the field experiments reported here. For the field-based web, we drew interaction arrows when carabid or lycosid manipulation significantly altered the density of another arthropod. The arrows were then scaled according to the percent change in arthropod density.

Our artificial immigration procedure effectively altered both carabid and lycosid densities, leading to a three-fold difference in activity densities of both predators between plots in which their immigration was allowed vs. plots where immigration was blocked ($F = 75.50, df = 1, 28, P < 0.001; F = 63.00, df = 1, 28, P < 0.001$ for carabid main effect and lycosid main effect, respectively; Figs. 2 and 3).

Overall, there is little evidence that carabids had negative effects on lycosids or that lycosids negatively affected carabids. Lycosids did not reduce the activity densities of carabids. If anything, carabid activity densities were slightly increased in the presence of lycosids (Fig. 2), although this effect is not significant ($F = 2.03, df = 1, 28, P = 0.17$). A significant carabid × lycosid interaction effect on carabid densities ($F = 5.71, df = 1, 28, P = 0.02$) is difficult to interpret without additional information. Carabids did not significantly reduce lycosid activity densities ($F = 0.07, P = 0.79$, Fig. 3), and the interaction term is not significant ($F = 3.41, df = 1, 28, P = 0.08$).

Carabid and lycosid activity densities did not significantly differ between years, and the predator treatment × year interactions were never significant ($P > 0.10$ for all effects). Generally, carabid densities increased through cucumber growth, plateaued, and then dropped at the last sample date (Fig. 2B and C). Lycosid densities remained relatively constant through each season (Fig. 3B and C).

**Plant survivorship and fruit production**

In 1998, the only year when plant mortality was recorded, cucumber survivorship declined steadily through the season. Predator treatments did not lead to altered seasonal mortality of cucumber plants ($F = 0.25, df = 1, 16, P = 0.56; F = 0.53, df = 1, 16, P

### Table 1. Mean mortality for each pairing of predator and prey.

<table>
<thead>
<tr>
<th>Prey</th>
<th>Carabids</th>
<th>Lycosids</th>
<th>Nabis</th>
<th>Control</th>
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<tr>
<td></td>
<td>C. sodalis</td>
<td>H. pennsylvanicus</td>
<td>P. milvina</td>
<td>H. helluo</td>
</tr>
<tr>
<td>StCB</td>
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<td>na</td>
<td>4.3 (5)</td>
<td>na</td>
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<td>4.0 (4)</td>
<td>na</td>
<td>na</td>
</tr>
<tr>
<td>SQB-nymph</td>
<td>1.6 (5)</td>
<td>na</td>
<td>2.2 (5)</td>
<td>1.8 (5)</td>
</tr>
<tr>
<td><em>Nabis</em></td>
<td>na</td>
<td>4/6 (5)</td>
<td>6/6 (5)</td>
<td>6/6</td>
</tr>
</tbody>
</table>

Notes: A single predator was paired with five herbivores, four squash bug eggs, or a single nabid within each microcosm. Data are presented as mean number killed, with number of replicates in parentheses, for herbivores and as total number killed/number of replicates for nabids. Abbreviations and symbols are: na, pairing not attempted because predation did not occur with this pairing in a previous study with structurally simple microcosms (Snyder and Wise 1999; nabid pairings were run as part of that study, but were not reported); StCB, striped cucumber beetle; SQB-egg, squash bug eggs; SQB-nymph, squash bug nymphs; —, pairing was not attempted.
Fig. 2. Carabid activity densities based on pitfall trap catches per plot, expressed as (A) means of all sample dates for each year of the field experiment, (B) means by sample date for 1997, and (C) means by sample date for 1998. Error bars, in this and subsequent figures, are ±1 se. Treatment codes in this and subsequent figures: O, neither carabid nor lycosid immigration allowed; C, carabid immigration only; L, lycosid immigration only; C+L, both carabid and lycosid immigration; OPEN, unfenced reference plots (carabid and lycosid immigration not manipulated).

Fig. 3. Lycosid activity densities based on pitfall trap catches per plot, expressed as (A) means of all sample dates for each year of the field experiment, (B) means by sample date for 1997, and (C) means by sample date for 1998.

Squash mortality was initially high, but after mid-growth no additional mortality occurred (Fig. 4B). Lycosid immigration significantly reduced mean survivorship of squash plants ($F = 6.75, df = 1, 16, P = 0.02$), but the carabid main effect and the interaction between the two predators were not significant ($F = 0.50, df = 1, 16, P = 0.49$; $F = 0.23, df = 0.48$ for carabid and lycosid main effects, respectively; Fig. 4A).
Figu. 4. Plant survivorship per plot through each cropping cycle in 1998 for (A) cucumber plants, which were the spring crop, and (B) squash plants, which followed in the summer. Squash were planted as groups of five seeds per mound; mounds with ≥1 living plant were scored as viable. Plant survivorship was not recorded in 1997.

Fig. 5. Fruit production for each year of the field experiment, for (A) cucumber and (B) squash.

1, 16, P = 0.64 for the carabid and interaction effects, respectively). Lycosids increased cucumber fruit production in the spring gardens (F = 8.60, df = 1, 28, P = 0.007; Fig. 5A). Carabids did not significantly affect yield in the spring (F = 2.24, df = 1, 28, P = 0.15), although in both years there was a trend for productivity to be higher in the presence of carabids. Carabids did not alter the impact of lycosids (F = 0.08, df = 1, 28, P = 0.78; carabid × lycosid interaction). Overall, cucumber yield was significantly higher in 1997 (F = 8.92, df = 1, 28, P = 0.005), but treatment effects did not significantly differ between years (P > 0.27 for all year × treatment interactions).

The impacts of the two predators on fruit production changed dramatically in squash, the second crop. Carabids increased, but lycosids decreased, squash production (carabid main effect: F = 13.40, df = 1, 28, P = 0.001; lycosid main effect: F = 9.26, df = 1, 28, P = 0.005, Fig. 5B). When years are pooled, the effect of the two predators was additive (carabid × lycosid interaction: F = 0.01, df = 1, 28, P = 0.92). Carabids only slightly increased fruit production but counteracted the negative effects of lycosids in 1997, while in 1998 carabids strongly increased squash production, but this effect was counteracted by the negative effect of lycosids [year × (carabid × lycosid) interaction; F = 6.90, df = 1, 28, P = 0.014]. Despite these complexities, in both years fruit production was increased by carabids and decreased by lycosids, with production in plots containing both predators not significantly different from the treatment in which carabid and lycosid immigration had been blocked. Squash yield was significantly higher in 1998 (F = 5.00, df = 1, 28, P = 0.03), but the predator × year interactions were not significant (P > 0.30 in each case).

Foliar arthropods

Lycosids reduced densities of the striped cucumber beetle, the most abundant herbivore early in the season (F = 9.19, df = 1, 28, P = 0.005; Fig. 6). Carabids did not significantly impact striped cucumber beetle densities (F = 0.94, df = 1, 28, P = 0.34), although...
in both years striped cucumber beetle densities were lower in the presence of carabids. Carabids reduced the effectiveness of spider predation on this herbivore where immigration of both predators was allowed (carabid × lycosid interaction; F = 12.30, df = 1, 28, P = 0.002). Striped cucumber beetle densities were significantly higher in 1997 (F = 11.71, df = 1, 28, P = 0.002, Fig. 6A), but the year × treatment interactions were not significant (P > 0.14 in each case). Striped cucumber beetle densities were intermediate on the first sample date, increased near cucumber harvest, and then declined through squash harvest (Fig. 6B and C).

Carabids significantly decreased squash bug densities in D-vac samples (F = 5.20, df = 1, 28, P = 0.03, Fig. 7). Lycosids did not significantly affect seasonal mean abundance of squash bugs (F = 0.10, df = 1, 28, P = 0.76); the interaction between the two predators was marginally significant (F = 3.83, df = 1, 28, P = 0.06), suggesting that the presence of lycosids...
Fig. 8. Squash bug densities per plant recorded during a visual count taken early in squash growth.

Fig. 9. Numbers of nabid bugs in D-vac samples, expressed as (A) means of all sample dates for each year of the field experiment, (B) means by sample date for 1997, and (C) means by sample date for 1998.

reduced the ability of carabids to limit squash bug numbers. Mean seasonal squash bug densities were similar in both years \( (F = 0.19, \text{df} = 1, 28, P = 0.67, \text{Fig. 7A}) \); year × predator effects were not significant \( (P > 0.50 \text{ in all cases}) \). Squash bugs were either absent (1997, Fig. 7B), or rare (1998, Fig. 7C) in the first D-vac samples, near the mid-point of cucumber growth. Squash bugs hatched near the end of cucumber growth, leading to a peak in abundance at the end of July (Fig. 7B and C). Squash bug densities then declined through squash growth.

A visual count of squash bugs (Fig. 8) early in squash growth confirmed that allowing carabid immigration led to lower squash bug densities, and revealed an important additional effect: lycosid immigration led to significantly higher squash bug densities on squash seedlings, when herbivory has the greatest effect on plant growth (Woodson and Fargo 1992). Carabids reduced densities of squash bug nymphs \( (F = 5.02, \text{df} = 1, 28, P = 0.03) \), but allowing lycosid immigration led to increased densities of squash bug nymphs \( (F = 20.22, \text{df} = 1, 28, P < 0.001) \). The effects of the two predators were additive \( [F \text{ (carabid} \times \text{lycosid}) = 0.43, \text{df} = 1, 28, P = 0.52] \). At the time of the visual sample, squash bugs were significantly more abundant in 1997 than in 1998 \( (F = 15.27, \text{df} = 1, 28, P < 0.001) \). Both the reduction of squash bugs by carabids and the increase in squash bugs by lycosids occurred both years (all year × predator treatment interactions \( P > 0.30) \).

Nabid bugs, the most abundant foliage-dwelling predators on cucurbit crops at our site (representing >30% of the predator community in D-vac samples [Snyder and Wise 1999]), and probably the only abundant predators large enough to prey upon squash bug nymphs (Snyder 1999, Snyder and Wise 1999, Tuntibunpakul 1999), were significantly less abundant where lycosid immigration was allowed \( (F = 7.78, \text{df} = 1, 28, P = 0.009, \text{Fig. 9A}) \); carabids did not have a significant impact on these predators \( (F = 1.95, \text{df} = 1, 28, P = 0.17) \), although nabid densities tended to be lower in carabid-immigration plots. The carabid × lycosid interaction term was marginally significant \( (F = 4.00, \text{df} = 1, 28, P = 0.055) \) suggesting that effects of carabids and lycosids were nonadditive, which could be interpreted as a result of carabids weakly reducing *Nabis* numbers, with lycosids having a stronger effect. Nabids were more abundant in 1998 than in 1997 \( (F = 5.15, \text{df} = 1, 28, P = 0.03, \text{Fig. 9A}) \); the predator treatment × year interactions were not significant \( (P > 0.20) \). Nabid densities both years were low in the
first sample, increased near cucumber harvest, then
were somewhat lower at squash harvest (Fig. 9B and
C).

Evaluation of possible fence effects
We evaluated possible effects of fencing by com-
paring reference plots (OPEN) to C+L plots for all
response variables. Carabid activity densities in C+L
plots were significantly higher than in the OPEN plots
\((P = 0.02, \text{t test})\). Average lycosid activity densities
in the C+L plots were significantly lower than in open
reference plots \((P = 0.03)\). However, in both cases
values for the fenced treatments were within the range
of variation recorded in individual open reference plots
in these and previous (Snyder and Wise 1999) exper-
iments.

In general, values of response variables in our fenced
control treatments closely resembled those in unman-
ipulated open reference gardens. Densities of non-
manipulated arthropods (seasonal means of squash
bugs, striped cucumber beetles, and hemipteran pred-
ators) and cucumber yield did not differ signifi-
cantly between C+L and OPEN plots \((P > 0.10, \text{all com-
parisons})\). However, squash production was lower in
the OPEN than in C+L plots \((P = 0.001)\) due to the
absence of squash production in the open plots in 1997.

Interaction webs based on laboratory feeding trials
and the field experiments
In the laboratory microcosms, only the large wolf
spider \(H. \) helluo successfully captured striped cucum-
ber beetles (Table 1; Fig. 10A). Neither carabids nor
nabids preyed upon striped cucumber beetles. Similarly-
ly, in the field experiments, striped cucumber beetle
densities were significantly reduced in the presence of
lycosids (Figs. 6, 10B); carabids did not cause a sta-
tistically significant change in striped cucumber beetle
densities.

In the laboratory, squash bug eggs were heavily
preyed upon by both carabid species examined (Table
1, Fig. 10A). Lycosids and nabids never preyed upon
squash bug eggs. Squash bug nymphs were most
strongly preyed upon by nabids (Table 1, Fig. 10A)
although \(C. \) sodalis and both lycosids sometimes cap-
tured squash bug nymphs also. Nabids were consumed
by all of the predators that we tested (Table 1; Fig.
10A). The interactions recorded in the laboratory are
qualitatively similar to those recorded in the field ex-
periments. In the field, carabids reduced squash bug
densities, consistent with the strong direct predation of
squash bug eggs by these predators in the laboratory
(Figs. 8, 10B). In the field, lycosid immigration in-
creased squash bug densities (Figs. 8, 10B), as we
would expect if they impact squash bugs indirectly
through predation on nabids.

DISCUSSION
We found little evidence for predation between ca-
rabids and lycosids, although intraguild predation be-
tween the two taxa has been found to occur in simple
arenas in the laboratory (Snyder and Wise 1999). Ca-
rabids had no impact on lycosid activity densities. Ly-
cosids appeared to affect carabid activity densities, but
increased rather than decreased activity densities of the
beetles. It is possible that predation within each family,
probably including both cannibalism and intraguild
predation, is more important in determining their den-
sities than is predation between the two taxa. Also,
carabids and lycosids might be separated spatially with
respect to microhabitat use, or the two may actively
avoid one another. Moran and Hurd (1994) found that
lycosid spiders left areas containing predatory mantids,
apparently to avoid being preyed upon by the mantids.

Carabids and lycosids had very different impacts on
the two most abundant herbivores. Lycosid spiders re-
duced striped cucumber beetle densities. Carabids also
appeared to reduce striped cucumber beetle densities,
although the effect was weaker and not statistically
significant. Thus, in the spring, when striped cucumber
beetles were the dominant herbivore, carabids and lycosids acted in concert to increase cucumber fruit production.

Carabids and lycosids had complicated effects on squash bugs, which became the dominant herbivores later in the season. Carabids directly reduced squash bug densities. On the other hand, lycosids reduced predatory hemipterans, apparently sufficiently to release squash bugs from control by these predators. Thus, later in the year carabids acted to increase squash yield while lycosids decreased squash yield. Because of these counteracting effects, squash bug densities and squash yield were similar in gardens with and without the complete carabid–lycosid predator guild. Species pairings in the laboratory yielded interaction webs that are consistent with our interpretation of how dominant interactions in the cucurbit food web changed through the season (Fig. 10).

Arthropod densities and fruit production within fenced plots containing the complete predator guild were generally statistically indistinguishable from unfenced reference areas. The single exception to this pattern was squash fruit production, which was lower in open plots primarily due to the failure of squash to produce fruit in open reference plots in 1997. It is possible that vertebrate seed predators or herbivores (e.g., mice, birds, rabbits) destroyed squash plants in the open gardens in that first year; fencing would have retarded the entry of many vertebrates into the experimental plots. However, it is also possible that the failure of squash plots in the OPEN plots was due to heightened predation of squash bug natural enemies by lycosids. Lycosid activity densities were higher in the OPEN plots than the fenced plots in 1997, and squash bug densities were higher overall. Thus, in the first year the negative impact of lycosids on enemies of squash bugs may have been strong enough to indirectly elevate squash bug densities to levels that prevented fruit production.

The results of a previous field experiment in gardens of cucumber and squash also reveal fluidity of the multi-trophic level impact of carabids and lycosids (Snyder and Wise 1999). In this previous study cucumbers were planted with three other vegetables in the spring, followed by a summer planting of squash. The carabid–lycosid guild reduced densities on cucurbits of the spotted cucumber beetle, Diabrotica undecimpunctata howardi, a generalist herbivore that can become abundant in diverse plantings like those used in the study (Bach 1980, 1988a, b). In this previous study spotted cucumber beetles continued their dominance into the summer crop (Snyder and Wise 1999), so that the carabid–lycosid guild increased the productivity of squash plants relative to plots lacking these predators. Thus, the carabid–lycosid–cucumber beetle interaction web appeared to dominate into the later planting.

The results presented here and by Snyder and Wise (1999) demonstrate that a guild of generalist predators can have dramatically different impacts on primary production. In our study system, these changes in the predators’ impact on the first trophic level were mediated by changes in the dominant herbivore and a shift in the importance of interactions with other generalist predators (e.g., nabids). Difficulty anticipating the variable effects of generalist predators hinders our ability to predict the indirect effects of IGP in many, if not most, ecological communities. Rates of intraguild predation, for example, can increase when other prey are scarce (e.g., Lucas et al. 1998) or are relatively well defended (Lucas et al. 1998, Snyder and Ives 2001), and can change in response to changing relative size differences between predators and intraguild prey (Snyder and Hurd 1995, Wissinger et al. 1996, Cisneros and Rosenheim 1997). As the relative intensity of direct predation and indirect effects due to intraguild predation fluctuate, so too will the net impact of predators on herbivore densities (Snyder and Ives 2001). The dynamical nature of intraguild predation may be widely important in mediating the impact of generalist predators in terrestrial communities.

Implications for top-down control theories and biological control

Hairston, Smith, and Slobodkin (1960) argued for the ubiquity in terrestrial food webs of three-level trophic cascades in which predators enhance primary production. This view was initially controversial (Murdoch 1966, Ehrlich and Birch 1967) and has been refined and expanded by the original authors and others (e.g., Slobodkin et al. 1967, Oksanen 1983, Fretwell 1987, Hairston and Hairston 1993, 1997). In contrast, other authors (e.g., Sih et al. 1985, Polis 1991, 1994, Strong 1992, Polis and Strong 1996) have argued that the diffusive effects of extensive IGP and trophic-level omnivory in terrestrial systems will dampen trophic cascades. However, even opponents of the green world hypothesis of Hairston et al. (1960) allow that strong trophic cascades might occur in relatively species-poor communities, such as those characteristic of islands or extreme climates (Strong 1992). Agroecosystems, which often demonstrate reduced species diversity, would seem to be likely places to look for strong cascading effects of generalist predators. We found clear evidence of strong trophic cascades in our vegetable-crop system, but impacts on plants varied dramatically due to complicating, counteractive effects of intraguild predation. These interactions caused the primary cascading effects of the entire assemblage of ground predators (carabids and lycosids combined) to switch seasonally, from an increase in fruit production induced by a three-level chain in the spring, to a complex mix of effects of three- and four-level chains later in the season. As a trophic level, carabids and lycosids together had no impact on primary production later in the season because the two groups of predators induced counteractive trophic cascades. Thus, we found support
for both sides of the contentious debate over the role of generalist predators in terrestrial communities. Our results have important consequences for predicting the biocontrol effectiveness of specific generalist predators. Lycosids were effective biocontrol agents in the spring, when they interacted directly with pests, but interfered with biocontrol in the summer, when they impacted pests primarily through an indirect channel by consuming other natural enemies. Carabids had no marked impact on crop yield in the spring, but clearly were beneficial later in the year. Further complicating matters, the benefits of one predator were sometimes outweighed by the negative impact of the other, yet at other times the effects of the two predators were additive. It seems that the role of a given predator taxon can be fluid, changing seasonally from an effective biological control agent to effectively a pest, even within a single season and type of crop. Such fluidity in trophic interactions hinders our ability, in the absence of experimentation, to assign a given generalist predator the role of effective biological control agent.

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