

USING STABLE ISOTOPES TO REVEAL SHIFTS IN PREY CONSUMPTION BY GENERALIST PREDATORS

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Abstract. The effectiveness of generalist predators in biological control may be diminished if increased availability of alternative prey causes individual predators to decrease their consumption of crop pests. Farming practices that enhance densities of microbi-detritivores in the detrital food web can lead to increased densities of generalist predators that feed on pest species. The ability to predict the net biocontrol impact of increased predator densities depends upon knowing the extent to which individual predators may shift to detrital prey and feed less on crop pests when prey of the detritus-based food web are more abundant. We addressed this question by comparing ratios of stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in generalist ground predators and two types of prey (crop pests and microbi-detritivores) in replicated 8×8 m cucurbit gardens subjected to one of two treatments: a detrital subsidy or no addition of detritus (control).

Small sheet-web spiders (Linyphiidae) and small wolf spiders (Lycosidae) had $\delta^{13}\text{C}$ values similar to those of Collembola in both the detrital and control treatments, indicating that small spiders belong primarily to the detrital food web. In control plots the larger generalist predators had $\delta^{13}\text{C}$ values similar to those of the major insect pests, consistent with their known effectiveness as biocontrol agents. Adding detritus may have caused $\delta^{13}\text{C}$ of one species of large wolf spider to shift toward that of the microbi-detritivores, although evidence is equivocal. In contrast, another large wolf spider displayed no shift in $\delta^{13}\text{C}$ in the detrital treatment. Thus, stable isotopes revealed which generalist predators will likely continue to feed on pest species in the presence of greater densities of alternative prey.

Key words: biological control; carabid beetles; Collembola; cucurbits; $\delta^{13}\text{C}$; $\delta^{15}\text{N}$; detrital subsidy; Diptera; food webs; spiders; stable-isotope ratios; trophic structure.

INTRODUCTION

Although generalist predators lack many attributes of the classical biological control agent (for example, they do not specialize on crop pests but instead consume a wide spectrum of prey), they can be effective in reducing pest densities (Riechert 1999, Sunderland and Samu 2000, Symondson et al. 2002, Nyffeler and Sunderland 2003). Their catholic diet actually can be used to advantage, since engineering the environment in order to boost densities of alternative, non-pest prey can lead to increased densities of generalist predators. Microbi-detritivores of detritus-based food webs are important alternative prey since many generalist ground predators belong to both the grazing food web (i.e., the network of trophic interactions based upon living net primary production with herbivores as the primary consumers) and the detrital food web, in which the microbi-detritivores (i.e., organisms that are both microbivore

and detritivore, consuming detritus and associated fungi and bacteria) play a roughly analogous role (Wise et al. 1999).

Species in the detrital web may promote biological control by maintaining high populations of generalist ground predators early in the crop cycle, leading to control later in the season of hopper pests in rice (Settle et al. 1996) and aphid pests of wheat (Edwards et al. 1979, Chiverton 1986). Since many pests are not high-quality prey, higher numbers of alternative prey may not necessarily lead to increased pest control. For example, the wheat aphid *Rhopalosiphum padi* is more toxic than many non-pest species, so increased numbers of generalist predators in response to increased non-pest prey is no guarantee of increased pest control (Toft 1995). However, even if generalist predators do not prefer pests as prey and the higher numbers of alternative prey lead to lowered per capita rates of feeding on the pest species, the net effect on pest control may be positive if the overall pest mortality caused by the higher density of generalist predators is higher. Such may be the case for the net effect of detrital prey on total mortality of wheat aphids caused by carabid beetles and spiders. It is unknown whether or not such a positive biocontrol impact of increased alternative prey is to be expected in general. Although a shift in diet need not necessarily

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eliminate control of pests by generalist predators, it could weaken their biocontrol effectiveness. Too few studies of how feeding preferences of generalist predators may change under field conditions have been conducted in order to be able to predict the net effect on pest control of higher predator numbers resulting from enhanced densities of alternative prey. The complex of generalist arthropod ground predators in cucurbit crops is one system in which such information is germane to predicting the impact of detrital subsidies on biological control.

In field experiments with cucurbit gardens, carabid beetles (Coleoptera: Carabidae) and wolf spiders (Araneae: Lycosidae) that immigrated into the gardens substantially enhanced crop production (Snyder and Wise 1999, 2001). In spring cucumber gardens wolf spiders exerted the major effect by preying upon striped cucumber beetles, and carabid predators doubled squash production in summer gardens by depressing densities of squash bugs. Interactions were complicated and the entire complex of generalist ground predators did not always control pests (Snyder and Wise 2001). A detrital subsidy increased numbers of generalist predators in this cucurbit system (Halaj and Wise 2002). Adding a shredded, composted mixture of straw from horse stables produced a 3–4 times increase in densities of Collembola, a major microbi-detritivore; an initial five-fold increase in carabids; and a 2–3 times increase in wolf spider densities (Halaj and Wise 2002).

In the study reported here, we inferred possible changes in the feeding preferences of large generalist ground predators—the stages and species that most likely feed on cucurbit pests (Snyder and Wise 1999)—by determining whether or not a detrital subsidy changed the ratio of stable isotopes of carbon (symbolized as $\delta^{13}\text{C}$ for the ratio of ^{13}C to ^{12}C compared to a standard; see *Methods: Field experiment: Stable-isotope ratios*, below) and nitrogen ($\delta^{15}\text{N}$ [$^{15}\text{N}/^{14}\text{N}$]) in the tissues of the predators. Any such changes were interpreted in the context of the overall trophic connections in the control and detritus-addition gardens as revealed by patterns of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in microbi-detritivores, crop pests, and a spectrum of stages and sizes of generalist predators.

Patterns of stable isotopes of C and N have been used for several years to infer trophic connections in aquatic and marine communities (Peterson and Fry 1987, Anderson and Polis 1998, Vander Zanden and Rasmussen 1999, Stapp and Polis 2003), and have been applied increasingly to terrestrial systems, including agroecosystems (McNabb et al. 2001) and detritus-based food webs (Ponsard and Arditi 2000, Ponsard et al. 2000, Scheu and Falca 2000, Halaj et al. 2005). The approach is proving valuable in assigning relative membership of generalist predators to different food webs (Collier et al. 2002, Sanzone et al. 2003). Although several reviews have revealed some general patterns in the magnitudes of carbon and nitrogen fractionation, it is clear that the

substantial variation between systems dictates the need to increase the power of inferences from field data with data from measured trophic transfers in the laboratory (Gannes et al. 1997, Vanderklift and Ponsard 2003). Therefore, we strengthened inferences about trophic connections in the field by examining patterns of change in isotopic ratios in known trophic transfers (isotope fractionation) in a series of model laboratory food chains designed to mimic patterns of predation, cannibalism, and intraguild predation among the lower trophic levels of the detrital food web found in both the control and detritus-addition treatments.

The research reported here focused on ground predators in cucurbit crops because previous field experiments established strong effects of these generalist predators on crop production, and because they responded to a detrital subsidy. The results, however, have implications well beyond cucurbits for several reasons: (1) carabids and/or wolf spiders have been directly and indirectly implicated as major agents of biological control in other agroecosystems (Oraz and Grigarick 1989, Kromp 1999, Lang et al. 1999, Lang 2003, Nyffeler and Sunderland 2003), (2) direct enhancement of the detrital food web has increased spider densities in non-crop systems (Chen and Wise 1999), and (3) indirect enhancement of the fungus-based detrital food web by no-till farming practices may also contribute to elevated densities of these generalist ground predators (Robertson et al. 1994). Thus understanding the extent to which prey selection of carabids and spiders changes in the presence of enhanced densities of detrital prey is of general significance to several IPM (integrated pest management) practices that seek to conserve and enhance densities of generalist predators.

METHODS

Study system

A field experiment was conducted in replicated cucurbit gardens in a 5.6-ha field on the University of Kentucky's Spindletop Research Farm in Fayette County, Kentucky, USA. These gardens and the surrounding field also were the source of animals used in the laboratory experiment. The major insect pests in this system are two coleopterans, the striped (*Acalymma vittata*) and spotted (*Diabrotica undecimpunctata howardi*) cucumber beetles, and two species of squash bugs (*Anasa tristis* and *A. armigera*). Major microbi-detritivores are Collembola, mites (Acari), fungus gnats (Mycetophilidae and Sciaridae), and fruit flies (Drosophilidae). The two most abundant largely predaceous carabid beetles are *Cyclotrachelus sodalis* and *Scarites* species; *Harpalus pennsylvanicus*, an omnivore, is also abundant. The two most abundant spider families of the ground layer are the Linyphiidae and Lycosidae. Linyphiids, although abundant, are too small to feed upon the major cucurbit pests. Adults and the larger juvenile instars of several wolf spiders (*Hogna helluo*, *Rabidosa* spp., and *Schizocosa avida*) attack cucurbit

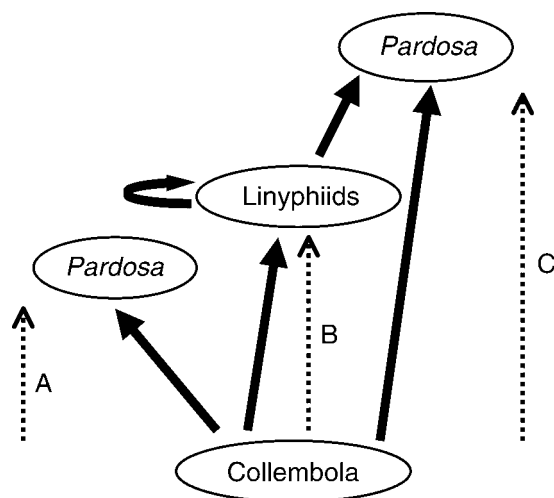


FIG. 1. Design of the laboratory experiment. Different combinations of predators and prey were established in order to determine changes in stable-isotope ratios for energy transfers over different numbers of trophic levels (indicated by dotted lines): (A) one trophic level (Collembola + *Pardosa*), (B) one trophic level + additional transfer due to cannibalism (Collembola + linyphiids), and (C) multiple trophic levels due to cannibalism and intraguild predation (IGP) (Collembola + linyphiids + *Pardosa*). Solid arrows refer to particular predator-prey interactions (including cannibalism).

pests. Smaller species, primarily *Pardosa milvina*, are the most abundant wolf spiders in the system, but they probably rarely attack cucurbit pests. Thus, we hypothesized that the smaller ground spiders, the linyphiids and *Pardosa* spp., belong primarily to the detrital food web; and that the larger generalist predators, the primarily predacious carabids and the large wolf spiders, belong to both grazing and detrital food webs—to the former because they prey upon cucurbit pests, and to the latter because they will attack microbi-detritivores and smaller predators in the detrital web. The large wolf spiders in particular likely prey extensively upon smaller spiders in the detrital web (Snyder and Wise 1999). Identification of the major species in the two food webs, and the hypothesized trophic relationships, are based upon published experiments and literature reviews (McNabb et al. 2001, Snyder and Wise 2001, Halaj and Wise 2002).

Laboratory experiment

Numerous studies have established that the fractionation of stable isotopes of carbon with each trophic transfer is relatively small ($\Delta\delta^{13}\text{C} \sim 0.4\text{‰}$); thus, the $\delta^{13}\text{C}$ values of predators reflect the $\delta^{13}\text{C}$ value at the base of the food web. If basal prey in the web differ substantially in $\delta^{13}\text{C}$, the values of $\delta^{13}\text{C}$ in the predators can be used to estimate the extent to which the predator is feeding on species linked to each of the basal resources (Phillips and Gregg 2001, 2003). The number of trophic transfers (a measure of “trophic level”) can be estimated from $\delta^{15}\text{N}$ of the predator and basal species, because the

fractionation for a trophic transfer of $\delta^{15}\text{N}$ is almost an order-of-magnitude larger than that of $\delta^{13}\text{C}$ (Peterson and Fry 1987). However, fractionation values vary between systems, or between trophic levels in the same food web, particularly for $\delta^{15}\text{N}$ (Vanderklift and Ponsard 2003). Thus, laboratory-obtained estimates of fractionation values for major feeding interactions lead to more accurate inferences about feeding relationships in nature (Gannes et al. 1997). We measured such changes for the Collembola pathway of the lower levels of the detrital web, because we hypothesized that cannibalism and intraguild predation among spiders would be widespread, and that adding detritus might alter the intensity of these interactions.

Three sets of feeding interactions were established (Fig. 1): (A) a one-trophic-level transfer (*Pardosa* fed Collembola), (B) a one-trophic-level transfer + cannibalism (linyphiids cannibalizing other linyphiids and also feeding upon Collembola), and (C) trophic-level omnivory (*Pardosa* feeding upon both linyphiids and Collembola). Collembola (*Entomobrya* spp.) were reared in six, 35-L glass terraria on potato peelings and brewer's yeast placed on soil and covered with straw; the substrate was kept moist to promote fungal growth. Adult linyphiids (predominantly *Eperigone* spp., *Grammonota* sp., and *Eridantes* spp.) were collected from the field and placed together to mate in 28-cm-diameter plastic containers with water and Collembola. Egg sacs were then collected and put into individual 11-cm-diameter plastic containers. Attempts to separate hatched spiderlings and rear them individually on Collembola were unsuccessful; therefore, siblings were reared together in the same containers in order to permit cannibalism. Each group of sibling linyphiids received 20–40 Collembola twice a week until the penultimate or adult stage was reached. Adult field-collected *Pardosa* females and males were allowed to mate and females with sacs were isolated individually. Spiderlings were removed from their mother's abdomen 4–6 days after hatching and were placed in separate 11-cm-diameter plastic containers with water. One group (one-trophic-level transfer) was provided 20–40 Collembola twice a week until the penultimate or adult stage was reached. Another group of *Pardosa* (trophic-level omnivory) was fed 20–40 Collembola twice a week for approximately three weeks and was then switched from Collembola to diets of 5–10 laboratory-reared linyphiids per week for approximately nine weeks until the penultimate or adult stage.

For stable-isotope analysis enough individuals were combined (details in next section) to yield five replicate samples of Collembola and also of each of the three combinations of *Pardosa*, linyphiids, and Collembola (Fig. 1). The laboratory experiment was conducted from 15 May through 28 October 2000.

Field experiment

Planting crops.—Ten 8 × 8 m plots were plowed twice between 19 and 24 April 2000 before cucumbers were

planted, and were raked on 20 July in preparation for squash planting. All plots were planted with cucumbers (*Cucumis sativa* L., variety "Spacemaster") on 8 May, followed by squash (*Cucumis pepo* (L.), variety "Yellow Crook Neck") on 4 August. Three seeds were placed in holes separated by 50 cm (cucumbers) or 1 m (squash) in each of seven rows. Emerged seedlings were thinned to one plant per group. Plots were fertilized with 9 kg N/ha and 6 kg K/ha on 25 April and 20 July. On 19 May a 15-cm layer of wheat straw was added to all 10 plots in order to retard weed growth and to improve the microclimate for generalist predators. Additional straw was added as required. Moisture was maintained with a drip-irrigation system.

Detrital enhancement.—Two treatments, detrital subsidy (detrital plots, $n = 5$) and control (ambient plots, $n = 5$), were established in a completely randomized design. Before the wheat straw was added, the detrital plots received a 5-cm layer of shredded muck mulch (Creech Services, Lexington, Kentucky, USA), a composted mixture of shredded wheat straw (95%) and horse manure (5%) used in commercial mushroom production. These plots were the same "open (unfenced)" plots of an experiment conducted the previous year, and the same assignment of treatments was maintained (Halaj and Wise 2002).

Arthropod densities.—Densities of microbi-detritivores (Collembola and adult Diptera) were estimated by using Berlese funnels to extract them from one 0.05-m² sample of mulch per plot on 3 July (cucumbers) and 29 August (squash). Densities of ground predators were estimated by searching the mulch and examining the soil surface in six 0.25-m² quadrats in each garden plot, on 22 June for cucumbers, and on 21 August for squash. Densities of cucumber herbivores were estimated by D-vac suction samples (Rincon-Vitova Insectaries, Ventura, California, USA) from seven randomly selected plants per plot (one plant per row) on 26 June; densities of squash herbivores were estimated by examining, by hand, 21 randomly selected squash mounds per plot (three mounds per row) on 15 August and then converting to number of herbivores per plant in each plot using the average number of seedlings per mound.

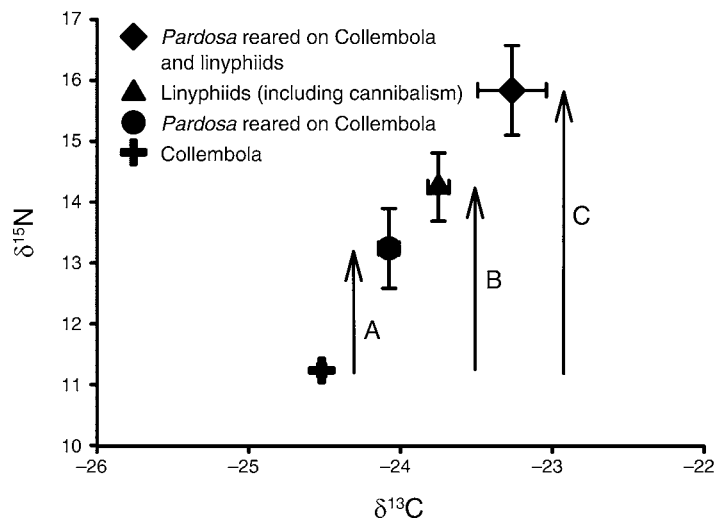
Vegetable production.—Plant nitrogen content was estimated from a composite sample of seven plant petioles per plot for both cucumbers and squash. Two measurements of nitrogen concentration were taken from each composite sample with Cardy ion meters (Spectrum Technologies, Plainfield, Illinois, USA). Plant yield was determined by weighing the total harvest of cucumber and squash fruit from three and four randomly selected rows of plants in each plot, respectively. Cucumbers were harvested twice, 30 June and 20 July, squash yield was estimated from a single harvest on 27 September.

Stable-isotope ratios.—Arthropods were collected from cucumber gardens between 16 May and 28 June, and from squash gardens between 11 August and 8

September, by pitfall trapping, sifting the straw litter, and D-vac sampling of the vegetation. Some species were collected from both cucumbers and squash, others from only one crop. The striped cucumber beetle (*Acalymma vittatum* F.) was the only herbivorous insect pest collected from both crops for stable-isotope analysis; two additional cucurbit pests, spotted cucumber beetles (*Diabrotica undecimpunctata howardi* Barber) and squash bug nymphs (*Anasa tristis* DeGeer), were collected from squash. Microbi-detritivores—Collembola (mostly *Entomobrya* spp.), fungus gnats (Mycetophilidae), and fruit flies (Drosophilidae)—were collected from both cucumber and squash gardens. Spiders collected from cucumber plots for stable-isotope analysis were from the families Linyphiidae (predominantly *Eperigone* spp., *Grammonota* sp., and *Eridantes* spp.) and Lycosidae (*Schizocosa avida* (Walckenaer) adults, two size classes [<10 mg (I) and >100 mg (III)] of *Hogna helluo* Hentz, and three size classes [<3 mg (I), 3–10 mg (II), and >10 mg (III)] of *Pardosa* spp. [*Pardosa milvina* Hentz and *Pardosa saxatilis* (Hentz) were combined because juveniles could not be identified to species]). Spiders collected from squash included all the species collected in cucumbers as well as adult *Alloccosa* sp. and *Rabidosia rabida* Walckenaer (both Lycosidae). Adults of the large predaceous carabid beetles *Scarites* spp. were collected from both cucumber and squash gardens.

Animals were kept alive in the laboratory in separate vials for 2–3 days to allow their digestive tracts to clear in order to reduce contamination of the stable-isotope sample. Specimens were stored at -30°C for approximately three months and then transferred to -80°C for an additional three months before being processed. Two or more individuals of each species were combined for one sample for stable-isotope analysis. Medium-sized individuals, such as Linyphiidae, small carabid beetles, and Staphylinidae, required at least 50 individuals per sample, and small-bodied species required more individuals (e.g., at least 500 individuals per sample for Collembola) in order to provide an adequate amount of tissue for analysis. Specimens were oven-dried at 60°C for three days and then finely ground in a ball mill between 20 s and 6 min, depending on their size and hardness. Between 1 and 2 mg of the finely ground powder were placed in 8×5 mm tin capsules and sent to the University of Georgia Stable Isotope Laboratory (Athens, Georgia, USA) for analysis with an isotope-ratio mass spectrometer. One sample of each taxonomic category (species, genus, family, or order, depending upon the taxon) was prepared for each treatment replicate (i.e., for each 8×8 m garden) for cucumbers and again for squash. One complete set of replicates (both cucumbers and squash) was destroyed in transit to the analysis laboratory, and the mass spectrometer failed when reading $\delta^{15}\text{N}$ for another set of replicates. Therefore, mean values of $\delta^{13}\text{C}$ are based upon four replicates and means of $\delta^{15}\text{N}$ upon three replicates.

FIG. 2. Comparing the fractionation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the top predator (either *Pardosa* or linyphiids) with respect to Collembola in each of the three predator-prey combinations in the laboratory experiment reveals changes in stable-isotope ratios involving transfers over different numbers of trophic levels: (A) one trophic level, (B) one trophic level + additional transfer due to cannibalism, (C) multiple trophic levels due to cannibalism and IGP. Refer to Fig. 1 for details. Arrow lengths reflect the extent of nitrogen fractionation. In this figure and others the data are means \pm SE; all means have associated standard errors, but small standard errors are obscured by the symbol for the mean.



The ratio of two stable isotopes of element X is expressed as a difference in ratios, in parts per thousand, from a standard:

$$\delta X = [(R_{\text{sam}}/R_{\text{std}}) - 1] \times 1000$$

where R_{sam} is the absolute isotopic ratio of the heavy to light isotopes of the sample and R_{std} is the respective ratio of the standard (Peterson and Fry 1987, Ehleringer and Rundel 1988, Hobson et al. 1994). Thus, $\delta^{13}\text{C} = {}^{13}\text{C}/{}^{12}\text{C}$ and $\delta^{15}\text{N} = {}^{15}\text{N}/{}^{14}\text{N}$, each ratio corrected for a standard (for $\delta^{13}\text{C}$, the Chicago PDB Marine Carbonate Standard, obtained from a Cretaceous marine fossil, *Belemnite americana*, from the PeeDee formation in South Carolina, USA; for $\delta^{15}\text{N}$, atmospheric air).

Estimation of trophic position.—The trophic position of predators was estimated using the $\delta^{15}\text{N}$ values of primary consumers (prim), either herbivores or microbiodetritivores, as the baseline because the isotopic signals of primary consumers tend to vary less than those of primary producers, detritus, and primary decomposers (Vander Zanden and Rasmussen 1999). Thus, the equation for predator (pred) trophic position was $[(\delta^{15}\text{N}_{\text{pred}} - \delta^{15}\text{N}_{\text{prim}}) / (\text{N fractionation per transfer})] + 2$. The value used for “N fractionation per transfer” was that revealed in the laboratory feeding experiment with spiders and Collembola. This value is undoubtedly not accurate for other feeding relationships, i.e., those involving all categories of predators feeding on herbivores and microbiodetritivores other than Collembola. Nevertheless, this inaccuracy presents no problem of interpretation within the context of the study, because the primary goal of the research was to compare the influence of a detrital subsidy upon (1) the relative membership of generalist predators in either the detrital or grazing food web, and (2) the predators’ trophic positions. Thus, the study was designed to detect shifts in web membership and relative trophic position, not absolute trophic level.

Statistical Analysis.—Results in the text and figures are presented as means \pm SE. All calculations and statistical analyses were performed on plot means. Arthropod densities were analyzed by 2×2 (crop type \times detritus treatment) ANOVA; t tests were used to determine if $\delta^{13}\text{C}$ signatures differed between consumers, if predators differed in prey base and trophic position, and if adding detritus affected feeding patterns. When necessary, data were log-transformed to make variances homogeneous, and the Mann-Whitney U test was performed whenever variances remained heterogeneous.

RESULTS

Laboratory experiment

The fractionation in $\delta^{13}\text{C}$ from Collembola to *Pardosa* when the wolf spider fed only on Collembola (a single-trophic-level transfer) was $0.5\text{‰} \pm 0.1\text{‰}$ (mean \pm SE) (Fig. 2A). Linyphiids that cannibalized and fed upon Collembola differed from Collembola in $\delta^{13}\text{C}$ by $0.8\text{‰} \pm 0.1\text{‰}$ (Fig. 2B), a degree of fractionation significantly greater than that of the single trophic-level transfer involving *Pardosa* ($t_8 = 41.6$, $P < 0.001$). The value of $\delta^{13}\text{C}$ for *Pardosa* that had fed upon Collembola and linyphiids (trophic-level omnivory) was significantly greater than that of *Pardosa* that had fed solely on Collembola (Fig. 2C; $Z = 2.31$, $P = 0.021$); the degree of fractionation of $\delta^{13}\text{C}$ was $1.3\text{‰} \pm 0.3\text{‰}$ from the Collembola baseline (Fig. 2C).

$\delta^{15}\text{N}$ of *Pardosa* fed only Collembola was $1.8\text{‰} \pm 0.6\text{‰}$ higher than that of Collembola (Fig. 2A). The value of $\delta^{15}\text{N}$ for linyphiids that had fed on conspecifics and Collembola was $2.8\text{‰} \pm 0.6\text{‰}$ greater than that of Collembola (Fig. 2B), although this degree of fractionation from the Collembola baseline was not significantly higher than the increase for the one-trophic-level transfer ($t_8 = 1.17$, $P = 0.29$). The fractionation of $\delta^{15}\text{N}$ for trophic-level omnivory (*Pardosa* that had preyed

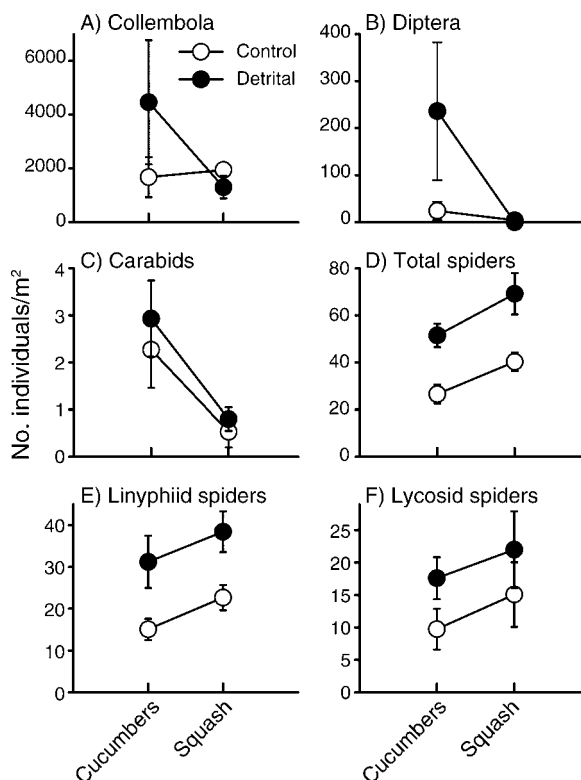


FIG. 3. Densities of arthropods in the cucumber and squash gardens, in both control and detrital treatments. Carabid beetles (C) include *Scarites* sp. (predaceous) and smaller omnivorous species.

upon Collembola and linyphiids) was $4.4\text{‰} \pm 1.2\text{‰}$ (Fig. 2C), which was marginally greater than that of a one-trophic-level transfer ($t_8 = 2.52$, $P = 0.053$).

Field experiment

Arthropod densities.—Densities of microbi-detritivores appeared to be higher in the detrital treatment in the cucumber gardens, but later in the season in the squash gardens Collembola densities did not differ between treatments, and Diptera had practically disappeared by the end of August (Fig. 3A, B). In the spring the effect of the detrital subsidy appeared to be greater for Diptera than for Collembola, although high variances for both groups in the detrital treatment make such a conclusion tentative. The overall treatment effect for adding detritus was not statistically significant for either group, but interactions between crop type and detrital treatment were marginally significant [$P(F_{1,16}) = 0.75$, 0.15 (detrital treatment) and 0.10 , 0.08 (crop \times detritus interaction) for Collembola and Diptera, respectively]. Carabid numbers did not increase in response to the detrital subsidy [Fig. 3C; $P(F_{1,16}) = 0.27$], but densities of spiders were almost two times higher in the detrital plots in both crops [Fig. 3D; $P(F_{1,16}) < 0.001$]. The pattern was similar for linyphiids and lycosids [Fig. 3E, F; $P(F_{1,16}) = 0.003$ and 0.09 ,

respectively]. In cucumber gardens the numbers of striped and spotted cucumber beetles were low, averaging 0.23 ± 0.13 and 0.06 ± 0.03 individuals/plant, respectively, in the control plots; and 0.06 ± 0.06 and 0.08 ± 0.03 individuals/plant, respectively, in detrital plots. Adding detritus had no effect on the densities of either striped or spotted cucumber beetles [$P(F_{1,8}) = 0.26$ and 0.58 , respectively]. Squash bugs did not occur in cucumber gardens, and were rare in squash gardens, averaging 0.020 – 0.026 individuals/plant. Most ($>98\%$) of the cucumber beetles on squash were the striped species, with average densities of 0.67 ± 0.17 and 0.58 ± 0.12 individuals/plant in control and detrital plots, respectively. The detrital subsidy had no effect on either cucumber beetles or squash bugs in squash gardens [$P(F_{1,8}) = 0.69$ and 0.91 , respectively].

Vegetable production.—Although nitrogen levels of both cucumbers and squash were marginally higher in the detrital plots [$P(F_{1,8}) = 0.09$ and 0.03 , respectively], yields (kilograms of fruit per row) did not respond to the detrital subsidy for either cucumbers or squash [$P(F_{1,8}) = 0.36$ and 0.83 , respectively]. Respective yields for control and detrital plots were 23.4 ± 0.9 and 21.9 ± 1.3 kg fruit/row (cucumbers) and 9.4 ± 0.4 and 9.7 ± 0.9 kg fruit/row (squash).

$\delta^{13}\text{C}$ values, cucumber gardens (Fig. 4).—In control plots Collembola, the most abundant microbi-detritivore, and the striped cucumber beetle, the only herbivore from spring gardens that was analyzed for stable-isotope signatures, differed significantly in $\delta^{13}\text{C}$ [$P(t_6) < 0.001$]; the difference was also pronounced in detrital gardens [$P(t_6) < 0.01$]. The $\delta^{13}\text{C}$ value for the spotted cucumber beetle (based on beetles from the summer squash gardens) exhibited higher standard errors, overlapping broadly with both Collembola and spotted cucumber beetles in control plots, but less so in the detrital treatment. In detrital plots the $\delta^{13}\text{C}$ values of the fungus gnats and fruit flies overlapped extensively with those of the striped cucumber beetle, and, to a lesser extent, with those of the spotted cucumber beetle. In control plots there were two distinct clusters of predators. One consisted of the smaller predators (*Pardosa* [all size classes], *Hogna* size class I, and linyphiids) that had $\delta^{13}\text{C}$ values close to those of the Collembola [$P(t_6) > 0.54$]. (For size-class explanation, see *Methods: Field experiment: Stable-isotope ratios*, above.) The second cluster, comprised of the larger predators, had $\delta^{13}\text{C}$ values similar to those of the striped and spotted cucumber beetles. Carbon-ratio values of *Schizocosa* and *Scarites* were similar to those of the striped cucumber beetle [$P(t_6) > 0.67$], whereas values for large *Hogna* (size class III) were larger by $\sim 0.5\text{‰}$ [$P(t_6) = 0.038$]. In contrast to the control plots, in the detrital treatment $\delta^{13}\text{C}$ values were similar for the two size categories of predators, due largely to the shifting of the $\delta^{13}\text{C}$ signatures of *Schizocosa* III and *Scarites* toward those of Collembola and the smaller predators. *Hogna* III, in contrast, displayed no such shift, and

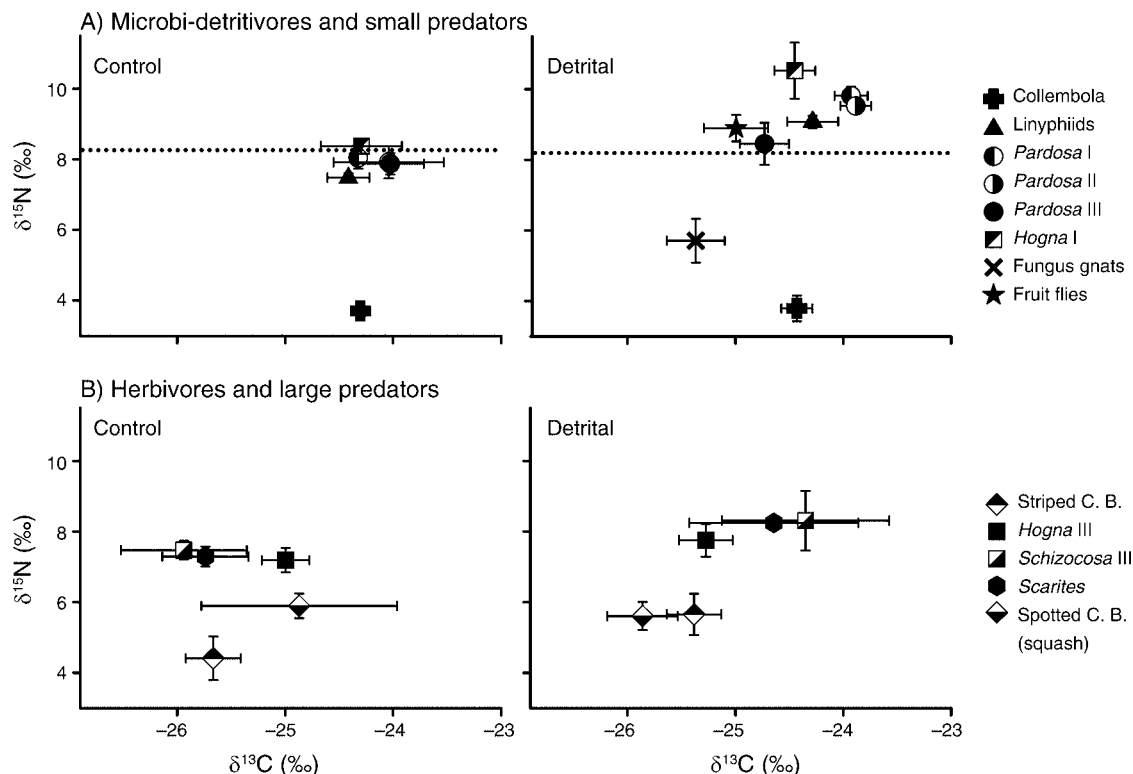


FIG. 4. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of prey and predators collected from control and detrital-treatment cucumber gardens. Data are separated into two groups: (A) Microbi-detritivores and small predators (linyphiid spiders, all stages of the wolf spider *Pardosa*, and the smallest stage of the wolf spider *Hogna*). The dotted lines represent the predicted value for $\delta^{15}\text{N}$ if the predators had exhibited the $\Delta\delta^{15}\text{N}$ from Collembola to *Pardosa* observed in the laboratory feeding experiment with Collembola, linyphiids, and *Pardosa* (Fig. 2). (B) Herbivore prey (striped and spotted cucumber beetles) and the large predators (the largest stage of the wolf spiders *Hogna* and *Schizocosa*, and the carabid *Scarites*). The values for spotted cucumber beetles ("C. B.") from summer squash gardens have been included because, although the spotted cucumber beetle was not collected from spring cucumber plots for isotope analysis, its abundance in cucumber gardens was $\sim 50\%$ that of the striped cucumber beetle.

remained closer to the value of the striped cucumber beetle than that of Collembola. Values of $\delta^{13}\text{C}$ for all predators overlapped with either those of Collembola or those of the other microbi-detritivores, the fungus gnats and fruit flies, which were abundant in the detrital treatment but were rare in the control plots.

$\delta^{13}\text{C}$ values, squash gardens (Fig. 5).—In control plots the carbon signatures of Collembola differed significantly from the most abundant herbivore in squash gardens, the striped cucumber beetle [$P(t_6) < 0.001$]. Differences in $\delta^{13}\text{C}$ between Collembola and the rare herbivores in the summer gardens, spotted cucumber beetles and squash bugs, were in the same direction, but less pronounced [$P(t_6) = 0.046$ and 0.067 , respectively]. In detrital gardens the differences in carbon signatures between Collembola and all three herbivores were highly significant [$P(t_6) < 0.001$]. As in the cucumber gardens, in control plots $\delta^{13}\text{C}$ signatures of the smaller predators *Pardosa* (all size classes), *Hogna* size class I, and the linyphiids were close to those of Collembola [$P(t_6) > 0.21$]. The exception to this pattern was a species not found in the cucumber gardens, the wolf spider *Allocosa*,

whose $\delta^{13}\text{C}$ signatures were lower than the other small predators. None of the larger predators in the control gardens differed in $\delta^{13}\text{C}$ from either the spotted cucumber beetle or the squash bug [$P(t_6) > 0.46$]. In control gardens the signature of *Schizocosa* was similar to that of the striped cucumber beetle [$P(t_6) = 0.68$], but the $\delta^{13}\text{C}$ signatures of *Hogna* III, *Rabidosa*, and *Scarites* were marginally different [$P(t_6) = 0.033$, 0.023 , and 0.064 , respectively]. However, the signatures of the spiders were more similar to those of the herbivores than to that of Collembola. In squash detrital plots, in contrast to the pattern in cucumbers, the two size classes of predators differed markedly in $\delta^{13}\text{C}$, and the values tended to cluster with either the microbi-detritivores (small predators) or the herbivores (large predators). The only exception was *Allocosa*, whose $\delta^{13}\text{C}$ values were intermediate. None of the large predators differed significantly from either the striped or spotted cucumber beetles [$P(t_6) > 0.14$ and 0.35 , respectively]. Squash bug signatures were not different from those of *Rabidosa* or *Schizocosa* [$P(t_6) > 0.10$], but were marginally different from those of *Scarites* and *Hogna* III [$P(t_6) = 0.080$ and

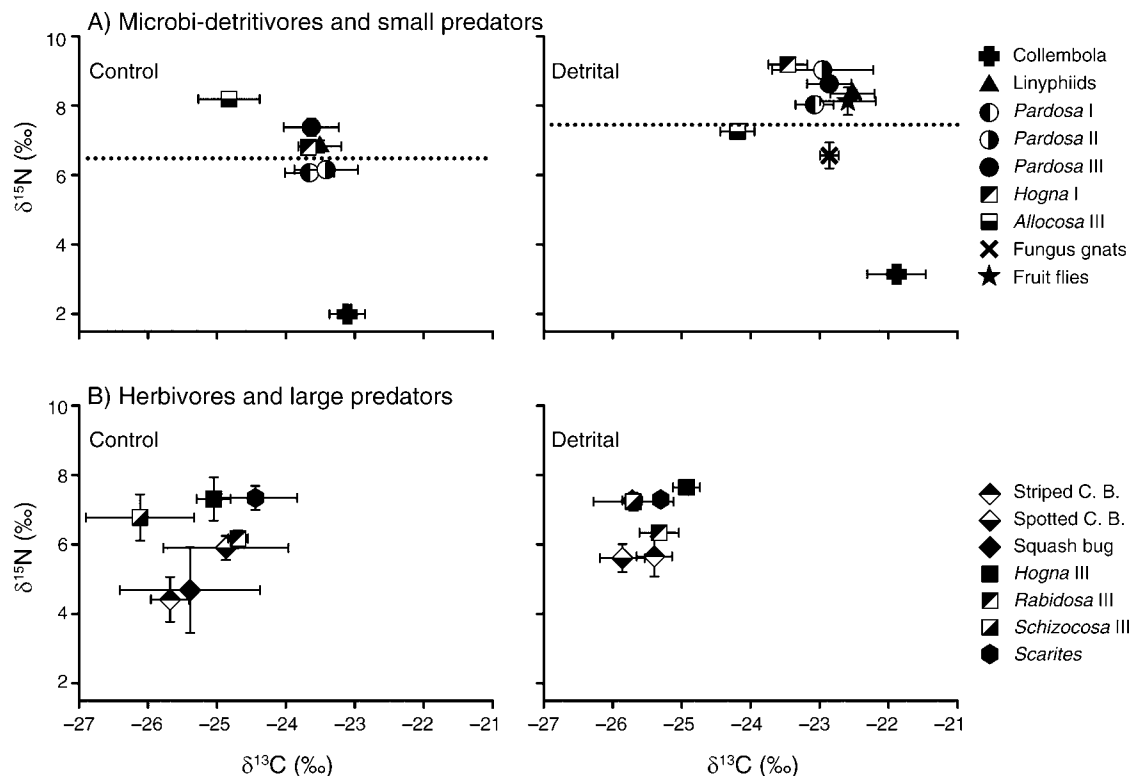


FIG. 5. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of prey and predators collected from control- and detrital-treatment squash gardens. Data are separated into two groups: (A) Microbi-detritivores and small predators (linyphiid spiders, all stages of the wolf spider *Pardosa*, the smallest stage of the wolf spider *Hogna*, and the largest stage of the wolf spider *Allocosa*). The dotted lines represent the predicted value for $\delta^{15}\text{N}$ if the predators had exhibited the $\Delta\delta^{15}\text{N}$ from Collembola to *Pardosa* observed in the laboratory feeding experiment (Fig. 2). The difference in elevation between control and detrital plots reflects the different values of $\delta^{15}\text{N}$ for Collembola in the two treatments, a larger difference than in cucumber gardens (Fig. 4). (B) Herbivore prey (striped and spotted cucumber beetles ["C. B."], and the squash bug) and the large predators (the largest stage of the wolf spiders *Hogna*, *Rabidosa*, and *Schizocosa*, and the carabid *Scarites*).

0.036, respectively]. The clustering of the smaller spiders was less clearly related to the $\delta^{13}\text{C}$ values of potential Collembola prey than in the controls. Carbon signatures of linyphiids and the intermediate-sized *Pardosa* did not differ from those of Collembola [$P(t_6) > 0.18$], but those of *Pardosa* I, III, and *Hogna* I were marginally lower [$P(t_6) = 0.051, 0.067$, and 0.057 , respectively]. In the detrital treatment the $\delta^{13}\text{C}$ of the smaller predators tended to be more similar to that of the other abundant microbi-detritivores, the fungus gnats and fruit flies.

$\delta^{15}\text{N}$ values and trophic levels of small predators in cucumber gardens (Figs. 4, 6A).—Fractionation of $\delta^{15}\text{N}$ was used to calculate trophic position of the small predators (spiders) based upon Collembola. In control plots small sheet-web spiders (linyphiids) and small lycosids (*Pardosa* I, II, III and *Hogna* I) were between 2.1 and 2.6 trophic levels above Collembola; values were higher in detrital plots, between 2.9 and 3.6 trophic levels above Collembola (Fig. 6A). A statistical comparison (Fig. 6A) of these patterns reveals that linyphiids and the two small size classes of *Pardosa* clearly were more elevated above Collembola in the detrital than

control treatments; only adult *Pardosa* (size class III) did not differ between treatments in trophic position calculated with respect to Collembola. The $\delta^{15}\text{N}$ of the small predators in the control plots was very close to that predicted by the fractionation for intraguild predation observed for *Pardosa* in the laboratory, but was clearly elevated above this predicted value in the detrital treatment (dotted lines in Fig. 4A). Higher predator values in the detrital treatment are correlated with the high $\delta^{15}\text{N}$ values of the two Diptera groups, which were greater than those of Collembola.

$\delta^{15}\text{N}$ and trophic levels of small predators in squash gardens (Figs. 5, 6B).—Trophic level was calculated using the same procedure used in cucumber gardens. Linyphiids, all stages of *Pardosa*, and the small *Hogna* (I) were between 2.2 and 2.9 trophic levels above Collembola in control plots, but trophic levels of the small predators were higher in detrital plots, between 2.7 and 3.3 trophic levels above Collembola (Fig. 6B). As in cucumber gardens, the only difference that clearly was not statistically significant was that of *Pardosa* III (Fig. 6B). The lycosid *Allocosa* showed an opposite trend,

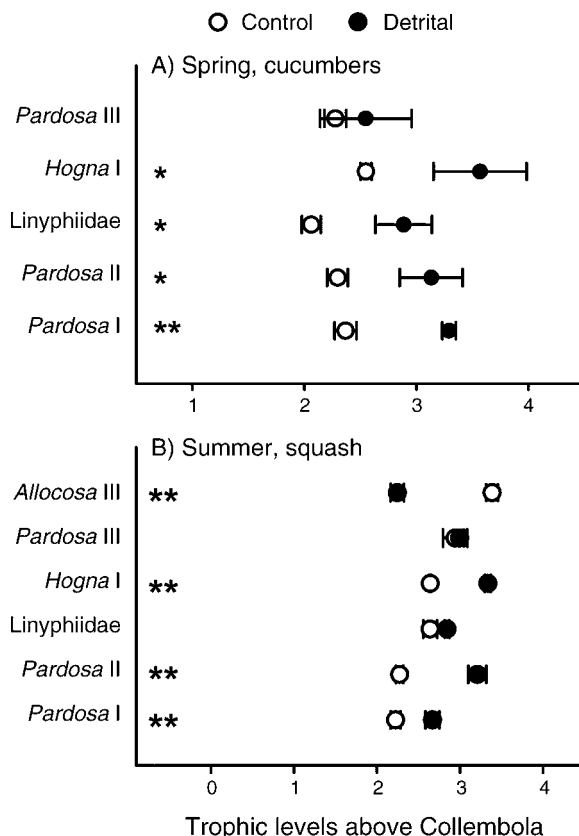


FIG. 6. Trophic positions of small generalist predators (spiders), based upon a fractionation value of $\Delta(\delta^{15}\text{N}) = 1.8\text{‰}$ observed for spiders in the laboratory experiment (Fig. 2), in (A) spring cucumber gardens and (B) summer squash gardens. Probability levels refer to results of simple t tests comparing trophic positions in control and detrital gardens (* $P < 0.05$; ** $P < 0.01$).

having a significantly lower trophic position in detrital plots (Fig. 6B). As in cucumber gardens, the $\delta^{15}\text{N}$ of small predators in the control plots was very close to that predicted by the fractionation for intraguild predation observed for *Pardosa* in the laboratory, but was clearly elevated above this predicted value in the detrital treatment (Fig. 5A). In squash detrital plots the $\delta^{15}\text{N}$ values of fungus gnats and fruit flies also were markedly higher than Collembola.

$\delta^{15}\text{N}$ and trophic levels of large predators.—Fractionation of $\delta^{15}\text{N}$ was used to calculate trophic position of the large predators based upon the cucurbit pests present in each garden. Trophic positions of all large lycosid spiders and the carabid *Scarites* did not differ between control and detrital plots when calculated with respect to both species of cucumber beetles ($P > 0.05$). The only possible differences were some marginally lower trophic positions in the detrital treatment when trophic position was calculated on the basis of the squash bug; however, this cucurbit pest was rare in squash gardens and was absent earlier in the season, so

the meaning of these few statistically marginal differences is unclear.

DISCUSSION

Two major conclusions emerge from this study. First, quantification in the laboratory of isotope fractionation for isolated components of the natural food web aids in interpreting stable-isotope patterns in the field. Second, patterns of fractionation of stable isotopes can reveal which generalist ground predators will likely continue to select pests as prey even in the presence of greater densities of alternative prey. Both findings increase the usefulness of stable isotopes as a tool for unraveling trophic connections in complex food webs in general. In addition, the second finding will strengthen integrated pest management (IPM) programs by increasing our ability to predict the consequences for biological control of enhancing predator numbers through farming practices that affect the detrital food web.

Laboratory quantification of isotope fractionation

A recent review (Vanderklift and Ponsard 2003) reveals a broader range of values for nitrogen fractionation than the earlier figure of 3.4‰, with the overall mean being almost 1‰ less ($2.54\text{‰} \pm 0.11\text{‰}$) (mean \pm SE). The lowest values among predators were exhibited by the lycosid *Pardosa lugubris* (Oelbermann and Scheu 2002), with fractionation on high-quality prey the largest ($\Delta = 2.16\text{‰}$ and 2.5‰ for a fruit fly and collembolan, respectively). In our study $\Delta\delta^{15}\text{N} = 1.8\text{‰} \pm 0.6\text{‰}$ for *Pardosa milvina* reared on an entomobryid collembolan. Thus our results confirm that wolf spiders exhibit a lower nitrogen fractionation than many other predators. Whether or not this pattern is true of spiders in general will require studies with other families. Our findings further highlight the need to base calculations of trophic position upon known, not hypothesized, fractionation values (Gannes et al. 1997, McCutchan et al. 2003, Vanderklift and Ponsard 2003).

The laboratory-derived value of $\Delta\delta^{15}\text{N} = 4.4\text{‰}$ for spiders that fed on Collembola and other spiders yielded a predicted $\delta^{15}\text{N}$ remarkably similar to that observed for small predators in the control plots, particularly in the spring gardens of cucumber. The predicted value was based upon the $\delta^{15}\text{N}$ of field-collected, not laboratory-reared, Collembola, because the two differed substantially. The fact that laboratory and field-collected Collembola differed in $\delta^{15}\text{N}$ is consistent with reported variation among Collembola and other microbi-detritivores (Scheu and Falca 2000). The difference likely reflected differences in microbial food between field and laboratory, and probably did not reflect major differences in the quality of these Collembola as prey for spiders. However, this possibility cannot be ruled out completely, since Oelbermann and Scheu (2002) found that spiders fed low-quality prey exhibited low—even negative—values of $\Delta\delta^{15}\text{N}$. Nevertheless, such a difference in food quality cannot explain the clearly elevated

$\delta^{15}\text{N}$ signature of the small predators over the predicted value in the detrital treatment, particularly in the cucumber gardens. At first glance this shift is perplexing, because an increased abundance of Collembola should decrease rates of cannibalism and intraguild predation, which would yield lower, not elevated, $\delta^{15}\text{N}$ signatures. The apparent paradox disappears after taking into account the $\delta^{15}\text{N}$ signatures of other microbi-detritivores that increased in response to the detrital subsidy. The elevated $\delta^{15}\text{N}$ values of the smaller predators did not reflect a higher trophic position, but rather an altered mixture of prey in their diet. The distribution of carbon signatures of the smaller spiders in the detrital treatment agrees with this interpretation. In squash gardens in particular, the $\delta^{13}\text{C}$ signature of the smaller spiders was markedly lower than that of Collembola, rather than being elevated by $\sim 0.5\text{--}1.3\text{‰}$, which is what one would have expected if Collembola and other spiders were their primary prey (range of $\delta^{13}\text{C}$ fractionation in the laboratory experiment, Fig. 2). The carbon signatures of both families of Diptera were lower than those of Collembola, and the differences were larger, and more consistent, in squash than in cucumber gardens. Thus, laboratory values of both $\Delta\delta^{15}\text{N}$ and $\Delta\delta^{13}\text{C}$ aided in interpreting the shifts in predator isotope ratios observed in the field experiment.

Consumption of insect pests by large generalist predators in the presence of increased densities of detrital prey

At least one large generalist predator, the wolf spider *Hogna*, did not shift to alternative prey when they were more abundant, but instead continued to feed on cucurbit pests in the detrital-subsidy treatment. The stable-isotope patterns for the other large generalist predators was less clear, suggesting a possible partial shift to the detritus-based food web when microbi-detritivores were more abundant. These patterns in isotope fractionation should be evaluated in the context of how the detrital subsidy affected densities of detrital prey, generalist predators, and crop yield. We discuss these latter results before interpreting the isotope data for the large generalist predators.

Effect of the detrital subsidy on population densities and crop yield.—Addition of Creech mulch (see *Methods: Field experiment: Detrital enhancement*, above) caused a doubling of the Collembola standing crop and a larger increase in densities of Diptera (fungus gnats and fruit flies) in the spring cucumber gardens. These effects had disappeared by the end of August. Increased densities of microbi-detritivores were accompanied by a doubling of densities of both linyphiid and lycosid spiders, effects that persisted through the summer gardens. Carabids showed no response to the detrital subsidy. Addition of Creech mulch to the same plots in a previous experiment (Halaj and Wise 2002) produced a 3–4-fold increase in Collembola, an effect that was largest in early August; a several-fold increase in linyphiid numbers; and a doubling of lycosid densities. In the earlier study

carabids were more abundant (5 times) in the detrital addition plots, but only in the spring. These differences suggest that the nutrient quality of the added mulch may have differed between studies.

In the current study the fact that densities of adult *Scarites* (Carabidae) did not increase in response to the subsidy suggests that they may not have been preying heavily on those microbi-detritivores that were more abundant in the detrital treatment. Thus, the stable-isotope pattern for *Scarites* is problematic and cannot easily be interpreted. The spiders, however, clearly responded to the detrital subsidy, a response that persisted despite the weakening with time of the effect of the subsidy on densities of microbi-detritivores. The strong spider response is not inconsistent with a decline in Collembola and Diptera by the end of the experiment because: (1) The rate of production of Collembola and Diptera may have been higher in detrital than control plots through August, but higher predation rates by the elevated spider populations may have lowered standing crops of microbi-detritivores to control levels. (2) Linyphiid spiders maintained their webs in the detrital plots for several weeks after densities of Collembola and Diptera had declined to control values, a delayed response to changes in food supply that has been observed in other Linyphiidae (Janetos 1982). (3) The large lycosids that prey on cucurbit pests are connected to the detrital food web through predation by their younger stages on microbi-detritivores in the spring, and through predation by adult and penultimate stages on linyphiids and small wolf spiders of the detritus-based web in spring and summer. Hence, stable-isotope signatures of the large spiders likely were affected throughout the experiment by increased availability of alternative prey in the detrital web, i.e., both the microbi-detritivores and the small predators that feed heavily upon them.

Adding Creech mulch did not improve cucurbit production. Nitrogen levels of cucumbers and squash were marginally higher in the detrital treatment, which contrasts with the reduced plant nitrogen levels in the same detrital plots, compared to the same control plots, the previous year (1999) (Halaj and Wise 2002). Succession in the soil microflora over two years of detrital supplementation may have changed the complex relationships between N in added organic material, N sequestered in the microflora, and N available to plants—or perhaps the C/N ratio in the detritus of this experiment differed from that of the previous year. The higher abundance of wolf spiders in the detrital treatment also did not enhance crop production. This result contrasts with experiments of earlier years (1997, 1998) on this research site, in which retarding the immigration of spiders into gardens with no detrital supplement clearly reduced cucumber production (Snyder and Wise 2001). In our experiment the densities of the striped cucumber beetle were several times lower than in the earlier experiments. Therefore elevated spider numbers

in our experiment likely failed to improve crop yield because the major pest preyed upon by wolf spiders was not abundant enough to have significantly affected cucumber yield. Nevertheless, despite the relatively low abundance of striped cucumber beetles, the stable-isotope signatures of the large wolf spiders suggest that they were preying upon this cucurbit pest in the control gardens.

Consumption of detrital prey and insect pests by the large spiders.—In cucumber gardens *Schizocosa* III may have shifted toward a diet based on the detrital food web, judging from its higher $\delta^{13}\text{C}$ values in the detrital treatment (Fig. 4B). The high standard errors, however, limit the ability to conclude whether or not a shift occurred. *Schizocosa* III showed no evidence of a diet shift in squash gardens, nor did *Rabidosa* III, although high standard errors in the control plots again limit the ability to make firm conclusions. However, it is relevant that $\delta^{15}\text{N}$ of these large wolf spiders did not increase in response to the detrital subsidy, in contrast to the clear increase in $\delta^{15}\text{N}$ of the small spiders in response to more detrital prey.

In contrast, the pattern exhibited by the large lycosid *Hogna* is clear, at least partly due to the smaller standard errors for $\delta^{13}\text{C}$ —a difference that suggests *Hogna* has a less varied diet than the other wolf spiders. Patterns of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ suggest that *Hogna* continued to feed on insect pests when alternative prey in the detrital web were more abundant. In both control and detrital treatments, the $\delta^{13}\text{C}$ signatures of the smaller instars (size class I) of *Hogna* were practically identical to the $\delta^{13}\text{C}$ signatures of Collembola, yet the signatures of the largest *Hogna* (stage III) in both control and detrital gardens were not significantly different from those of the striped or spotted cucumber beetles, and were closer to that of cucumber beetles than Collembola. As *Hogna* matured, its $\delta^{13}\text{C}$ shifted to resemble that of cucumber beetles more than that of Collembola or the smaller predators (linyphiids and the smaller wolf spider *Pardosa*) that belong to the detrital food web. This shift in *Hogna* $\delta^{13}\text{C}$, and the absence of any effect of detrital prey on the shift in $\delta^{13}\text{C}$ toward that of pests, was particularly evident in the squash gardens. The absence of a shift by *Hogna* may be particularly relevant to the use of detrital subsidies to enhance the biocontrol effectiveness of generalist ground predators in cucurbits, since *Hogna* is the most abundant large wolf spider in this system (Snyder and Wise 1999, 2001, Halaj and Wise 2002), and has been directly implicated in two years of field experiments as a major predator of striped cucumber beetles (Snyder and Wise 2001).

In summary, the use of stable isotopes revealed differences between generalist predators in how their consumption of herbivores in the grazing food web was, or was not, influenced by increased alternative prey in the detritus-based web. This technique promises to reveal valuable insights into how generalist predators are linked to food webs with different resource bases.

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