Oecologia (1997) 109:108–113

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Establishing pathways of energy flow for insect predators using stable isotope ratios: field and laboratory evidence

Received: 17 November 1995 / Accepted: 20 June 1996

Abstract Quantifying pathways of energy transfer between plants, pests, and beneficial insects is a necessary step toward maintaining pest stable agroecosystems in the absence of chemical subsidies. A diet switching experiment utilizing a predatory ladybird beetle, *Hippodamia variegata* (Goeze), evaluated the use of naturally occurring stable C and N isotopes as an economically feasible and safe method for quantifying pathways of energy flow within agroecosystems. Stable isotope values of the ladybird beetle *Coleomegilla maculata lengi* (Timberlake) collected from an agroecosystem were used to estimate the relative amount of C and N derived from agricultural plants and incorporated by ladybird beetles based on mass balance equations. At the beginning of the diet-switching experiment $\delta^{13}C$ and $\delta^{15}N$ values of *H. variegata* (–12.0‰ and 6.3‰, respectively) differed by –0.2‰ and 2.9‰ from the aphids that were provided exclusively as their diet. These data are consistent with previous estimates of trophic level isotope effects. After switching the diet of *H. variegata* to an alternative food, isotope values of *H. variegata* gradually shifted toward expected values for individuals fed this diet (–22.9‰ and 8.8‰ for $\delta^{13}C$ and $\delta^{15}N$ values, respectively). Isotope values of another ladybird beetle, *C. maculata*, collected from the field indicated that in May, alfalfa and maize (pollen) obtained in the previous year contributed 32% and 68% of the C or N to the diets of these individuals and in August, 52%, 6%, and 42% of the C or N assimilated by these insects was derived from alfalfa, wheat, and maize, respectively. These data are consistent with expectations based on the relative abundance of *C. maculata* in various crops during the season. The field and laboratory data are a clear indication that isotope values are sensitive to dietary changes on a relatively short time scale (days) and provide a strong basis for the use stable C and N isotope to trace energy flow patterns of these beneficial organisms within agroecosystems.

Key words Stable isotopes · Agroecosystems · Energy flow · Food webs · Lady beetles

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Introduction

Ladybird beetles are an important component of the complex of beneficial insects which feed on pests such as aphids within agroecosystems. These highly mobile insects traverse the landscape in search of their prey. Individual species will select specific habitats depending on food availability and habitat characteristics (Maredia et al. 1992a). Consequently, to enhance the role of ladybird beetles in reducing pest populations in agroecosystems, knowledge of the distribution of adults with respect to habitat type is necessary. An important step toward developing this knowledge will be to identify the habitat in which feeding predominates by delineating pathways of energy flow or material transfer.

Radioactive isotopes have been introduced to biotic systems to directly track material flow but the obvious disadvantage of this method is the hazardous nature of the material (Warembourg and Paul 1977). Mark-recapture methods are difficult because a large number of individuals must be marked to provide accurate estimates of abundance. The analysis of naturally occurring stable isotope ratios of plants, pests and predators, provides a less direct but safer approach for delineating pathways of material transfer from a specific plant to a pest and, subsequently, to a predator. However, the stable isotope approach requires that isotopic values of food sources are distinct and that these values are passed on to consumers in a predictable manner. Several studies have documented that the stable C or N isotopic composition ($\delta^{13}C$ or $\delta^{15}N$, respectively) of an organism is similar to or deviates by a consistent amount

from its food source (Teeri and Schoeller 1979; Boutton et al. 1983; Wada et al. 1987; Harrigan et al. 1989; Ostrom and Fry 1993). Whereas the $\delta^{13}C$ of a consumer differs by ± 0.5–1‰ from its diet, the $\delta^{15}N$ value of an organism is approximately 3‰ greater than its food source (DeNiro and Epstein 1978, 1981; Macko et al. 1982; Wada et al. 1987; Harrigan et al. 1989; Ostrom and Fry 1993; Michener and Schell 1994). A 3‰ increase in $\delta^{15}N$ occurs with each trophic level in a food web (Wada et al. 1987; Harrigan et al. 1990; Michener and Schell 1994). Thus, the magnitude of the $\delta^{15}N$ value of a consumer relative to that of plants that supply N to the base of the food chain is a function of trophic level (Wada et al. 1987; Harrigan et al. 1989). A secondary consumer, for example, is expected to have a $\delta^{15}N$ value that is about 6‰ greater than the plants from which it ultimately derives its nitrogen. If trophic level isotope effects are accounted for, the $\delta^{13}C$ and $\delta^{15}N$ of a consumer can be used to estimate the average isotopic composition of the plants that serve as the base of the food web (Harrigan et al. 1989). Stable isotope analysis is an ideal method to track and model energy flow patterns in agroecosystems.

In this study we have developed methods and have used stable C and N isotope ratios to evaluate pathways of energy flow within the food web of the predatory ladybird beetle, *Coleomegilla maculata lengi* (Timberlake). Specifically, isotopic mass balance equations were used to quantify the relative importance of different plants (alfalfa, wheat, and maize) to the food web base of ladybird beetles obtained from an agroecosystem. Given that there is a paucity of data characterizing trophic level isotope effects on $\delta^{13}C$ or $\delta^{15}N$ values or turn-over time (time required to completely exchange the C or N of an organism) in insect food webs, the results of a laboratory-based diet switching experiment, in addition to measurements of trophic shifts from an agroecosystem, are presented.

Materials and methods

Diet switching experiment

A diet switching experiment was performed to estimate the time required to turn over C and N in the ladybird beetle *Hippodamia variegata* (Goeze). The experiment was conducted in cooperation with the USDA/APHIS Biological Control Laboratory in Niles, Michigan. The evaluation of turn-over time required an isotopically homogenous group of ladybird beetles and two food sources that were distinct in both their $\delta^{13}C$ and $\delta^{15}N$ composition and capable of maintaining healthy viable populations of ladybird beetles. Two dietary sources fed to ladybird beetles in the standard protocols at the USDA laboratory were determined to be isotopically distinct and, thus, were used in the diet switching experiment. One food source was aphids raised on monospecific stands of sorghum (*Sorghum bicolor*) and the other was pork liver mixture (a paste composed primarily of ground pork liver to which small amounts of glycerin, olive oil, sucrose, wheat, bee pollen and streptomycin sulfate were added).

To obtain an isotopically homogeneous group of ladybeetles, *H. variegata* were reared from existing egg cultures. Larvae were fed exclusively on aphids. Adults were fed aphids for the first 4 days after emergence from pupation. The 5th day after emergence marked the beginning of the diet switching experiment. At this time aphids were discontinued as a food source and adult *H. variegata* were switched to a pork liver diet for an additional 25 days. A sucrose water supplement provided to the *H. variegata* was a second source of dietary C. The amount of C that was assimilated by the insects from sucrose could not be determined because accurate estimates of water intake could not be obtained. The C and N isotopic composition of the adults were monitored by analyzing a subset of four individuals taken on the 5th day after emergence and every other day thereafter for a total of 28 days. Each feeding cohort of *H. variegata* was maintained at 0°C prior to isotopic analysis.

Collection of aphids and alfalfa for estimates of trophic level isotope effects

Isotopic shifts between plants and aphids were determined by analyzing the $\delta^{13}C$ and $\delta^{15}N$ of individuals collected from a monospecific field of alfalfa in the summer of 1992. Aphids were collected from plants with tweezers, placed in glass vials, and frozen prior to isotopic analysis. Large samples (more than 10 g dry weight) of alfalfa were collected, cleaned of aphids, and freeze-dried.

Estimates of *C. maculata* abundance and collection of insects and plants

Estimates of *C. maculata* abundance were obtained from an agroecosystem at the Kellogg Biological Station (KBS; Hickory Corners, Mich.) during 1992 to assess the spatial and temporal distribution of this species. The agroecosystem consisted of adjacent unfertilized fields of maize (33 × 200 m), wheat (33 × 200 m) and rye (33 × 200 m) that were separated by a dirt road (10 × 200 m) from an alfalfa field (100 × 200 m). The alfalfa was 4 years old, winter wheat was planted in fall 1991 and maize seed was sown in spring 1992.

Yellow sticky panels (Pherocon, Salinas, Calif.) were used to trap dispersing adults. These traps consisted of a double sided yellow panel (22.5 × 14.0 cm, unbaited and coated with tanglefoot) attached to a dowel 1 m above the vegetation as described by Maredia et al. (1992b). Six insect traps were placed in each crop. Trapped insects were enumerated weekly ten times throughout the season. All *C. maculata* adults were removed from the traps, placed in glass vials and stored at 0°C prior to isotopic analysis. Large samples (more than 10 g dry weight) of wheat, pollen from maize, and alfalfa were also collected for isotopic analysis during the growing season of 1992.

Isotopic analyses

In preparation for isotopic analysis samples of *H. variegata*, *C. maculata*, aphids, pork liver, and plants were freeze-dried and ground to a fine powder. The $\delta^{13}C$ and $\delta^{15}N$ values for *H. variegata* and *C. maculata* represented a single insect. Data for aphids and plants were determined from an aliquot of the homogenate (5 mg and 20 mg for aphids and plants, respectively). Isotopic analyses were performed by a modified Dumas combustion (Macko et al. 1987). Purified gases were obtained by cryogenic gas separation and isotopic determinations were performed using a PRISM stable isotope ratio mass spectrometer (VG Isogas Ltd.).

Stable C and N isotope ratios are expressed as:

$$\delta^{13}C \text{ or } \delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$ for $\delta^{13}C$ or $\delta^{15}N$, respectively. The standard for C is the Chicago Peedee Belemnite (PDB) and for N the standard is atmospheric N_2. Reproducibility of these measurements is 0.1‰ (Macko et al. 1987).

Contribution of C or N from alfalfa, wheat or maize to *C. maculata*

The relative contribution of C or N from maize, wheat, or alfalfa to the food web of *C. maculata* was determined using the following mass balance equations:

$$\delta^{13}C_p = f_a\delta^{13}C_a + f_w\delta^{13}C_w + f_c\delta^{13}C_c \quad \text{or} \quad \delta^{13}C_p = \delta^{13}C_{cmac} - X$$

$$\delta^{15}N_p = f_a\delta^{15}N_a + f_w\delta^{15}N_w + f_c\delta^{15}N_c \quad \text{or} \quad \delta^{15}N_p = \delta^{15}N_{cmac} - Y$$

$$f_a + f_w + f_c = 1$$

Where

f_a = fractional contribution of C or N from alfalfa to the diet of *C. maculata*

f_w = fractional contribution of C or N from wheat to the diet of *C.maculata*

f_c = fractional contribution of C or N from maize to the diet of *C. maculata*

$\delta^{13}C_a$ = δ^{13}C of alfalfa

$\delta^{13}C_w$ = δ^{13}C of wheat

$\delta^{13}C_c$ = δ^{13}C of maize

$\delta^{13}C_p$ = the average δ^{13}C value of the mixture of plants that provide C to the base of the food web of *C. maculata* weighted by the fractional contribution of each plant

$\delta^{15}N_p$ = the average δ^{15}N value of the mixture of plants that provide N to the base of the food web of *C. maculata* weighted by the fractional contribution of each plant

$\delta^{13}C_{cmac}$ = the δ^{13}C value of *C. maculata*

$\delta^{15}N_{cmac}$ = the δ^{15}N value of *C. maculata*

X = estimate of the C isotopic effect between *C. maculata* and $\delta^{13}C_p$

Y = estimate of the N isotopic effect between *C. maculata* and $\delta^{15}N_p$

Table 1 The δ^{13}C and δ^{15}N values and estimates of trophic level isotope effects for *Hippodamia variegata*, aphids raised on sorghum, sorghum, and pork liver from a laboratory study and for aphids and alfalfa obtained from the field. Trophic level isotope effects on δ^{15}N and δ^{13}C are designated by $\Delta\delta^{15}$N and $\Delta\delta^{13}$C, respectively

	n	δ^{13}C±SE	δ^{15}N±SE	$\Delta\delta^{13}$C	$\Delta\delta^{15}$N
Laboratory samples					
H. variegata	3	−12.2±0.1	6.3±0.3		
Aphids	H[a]	−12.0[b]	3.4[b]		
Sorghum	H[a]	−10.9[b]	3.4[b]		
Pork liver	3	−22.7±0.1	5.9±0.1		
H. variegata-aphids				−0.2	2.9
Aphids-sorghum				−1.1	0.0
H. variegata-sorghum				−1.3	2.9
Field organisms					
Aphids	H[a]	−26.5[b]	−0.5[b]		
Alfalfa	H[a]	−26.4[b]	−1.2[b]		
Aphids-alfalfa				−0.1	0.7
Average trophic level Isotope effect					
Aphids-plants[c]				−0.6	0.4
H. variegata-plants[d]				−0.8	3.3

[a] H refers to an aliquot of a homogenous mixture of a large sample of aphids (more than 10 mg)

[b] The reproducibility of the measurement (0.1‰ for both δ^{15}N and δ^{13}C; Macko et al. 1987) is a good estimate of the error associated with a homogenate

[c] Aphids-plants is the average of trophic level isotope effect for aphids-sorghum and aphids-alfalfa

[d] *H. variegata*-plant is the sum of aphids-plants and *H. variegata*-sorghum

Results and discussion

This study is the first to demonstrate that the δ^{15}N and δ^{13}C values of ladybird beetles provide a record of material that has been assimilated, are sensitive to changes in food source, and, through the implementation of mass balance equations, can be used to quantify the relative contribution of C or N from different plants at the base of the food web. The mass balance equations require estimates of the magnitude of the change in δ^{13}C or δ^{15}N values between trophic levels and verification that isotope ratios of consumers are sensitive to changes in food source. We obtained estimates of trophic level effects on δ^{13}C and δ^{15}N through the analysis of individuals from the laboratory and the field (Table 1). A comparison of aphids and plants shows that the δ^{13}C value of laboratory aphids (−12.0‰) is 1.1‰ less than that of their sorghum diet (−10.9‰) and that aphids obtained from the field have a δ^{13}C value (−26.5‰) that is 0.1‰ lower than that of the alfalfa (−26.4‰) from which they were obtained. Progressing up the food chain, laboratory results indicated that *H. variegata* differ in δ^{13}C from aphids supplied to them as a food source by −0.2‰. These estimates of C isotopic shifts between aphids and plants (average = −0.6‰) and between *H. variegata* and aphids (−0.2‰), are consistent with previous studies that have documented differences of approximately ± 0.5–1‰ between the δ^{13}C of consumers and their diets (DeNiro and Epstein 1978; Wada et al. 1987; Ostrom and Fry 1993; Michener and Schell 1994).

No difference was observed between the δ^{15}N values of laboratory aphids and their sorghum diet (δ^{15}N for aphids and sorghum = 3.4‰). The difference in δ^{15}N between aphids collected in the field (δ^{15}N = −0.5) and the alfalfa plants (δ^{15}N = −1.2) from which they were obtained is 0.7‰. The difference in δ^{15}N between laboratory raised *H. variegata* (δ^{15}N = 6.3) and aphids supplied to them as a dietary source (δ^{15}N = 3.4‰) is 2.9‰. Unlike the estimated shift in δ^{15}N between *H. variegata* and aphids, the average difference in δ^{15}N between aphids and plants based on laboratory and field data, 0.4‰, is unusually low when compared to previous estimates of the shift in δ^{15}N between trophic levels (typically 3.0–3.5‰; DeNiro and Epstein 1981; Wada et al. 1987; Ostrom and Fry 1993). Taking into account isotopic shifts between plants and aphids and between aphids and *H. variegata*, the increase in δ^{15}N between *H. variegata* and plants is 3.3‰.

The increase in the δ^{15}N of an organism relative to its food source is a function of the degree to which isotopic discrimination (preferential incorporation of one isotope into the product of a single reaction) during uptake, metabolism, and excretion is expressed and the size of the N pool. In the case where a metabolic reaction goes to

completion, i.e. all of the substrate is converted to product, the isotopic composition of the product will be similar to that of the initial substrate (Mariotti et al. 1981). Consequently, the small difference in $\delta^{15}N$ between aphids and plants could be explained if the majority of the N consumed by aphids from sorghum is assimilated. Alternatively, the small trophic level effect on $\delta^{15}N$ values arising between aphids and plants may indicate a unique metabolism whose net isotope effect is minimal. The possibility that the similarity in the $\delta^{15}N$ of the aphid and its host plant is a function of the degree of N assimilated is important because it implies a very efficient transfer of energy.

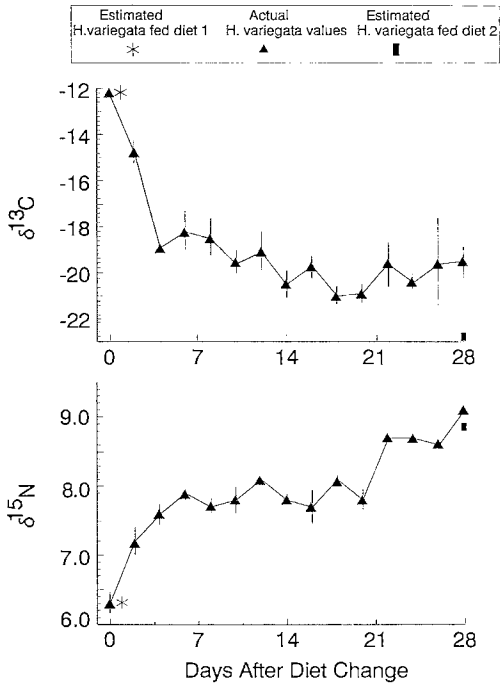

Fig. 1 The $\delta^{13}C$ and $\delta^{15}N$ values of *Hippodamia variegata* (Goeze) adults throughout a diet switching experiment. The experiment commenced on the 4th day after emergence of adults (defined as day 0) when the diet was changed from one that consisted entirely of aphids raised on sorghum (diet 1) to one consisting solely of pork liver (diet 2). *Vertical bars* associated with each data point represent the standard error of the estimate

To verify that isotope ratios are sensitive to changes in food source the $\delta^{15}N$ and $\delta^{13}C$ of laboratory raised *H. variegata* were monitored after they were switched from the aphid diet to pork liver (Table 1, Fig. 1). These food sources differ by 10.7‰ and 2.5‰ in $\delta^{13}C$ and $\delta^{15}N$, respectively. At the beginning of the experiment (day 0), adult *H. variegata* have the lowest $\delta^{15}N$ value (6.3 ± 0.3‰) and highest $\delta^{13}C$ value (–12.2‰ ± 0.1‰) of all individuals analyzed in this study (Fig. 1). As the experiment progressed, we hypothesized that the isotope values of *H. variegata* would shift towards those predicted values for individuals fed a diet of pork liver. Prediction of values for *H. variegata* utilizing a pork liver diet required estimates of the magnitude of the isotopic shift between a ladybird beetle and its diet. The best estimate of the isotope effect for this laboratory experiment is the difference between the isotope values of *H. variegata* and those of aphids used as a food source (–0.2‰ and 2.9‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively; Table 1). Utilizing this estimate the $\delta^{13}C$ and $\delta^{15}N$ values for *H. variegata* fed a pork liver diet are –22.9‰ and 8.8‰, respectively. In the experiment, we observed that as time progressed, isotope values of *H. variegata* shifted toward the predicted values (Fig. 1).

During the course of the experiment, 75% or more of the shift in the $\delta^{13}C$ and $\delta^{15}N$ was observed within the first 6 and 21 days, respectively. The 3‰ difference in $\delta^{13}C$ between the average value for *H. variegata* at the

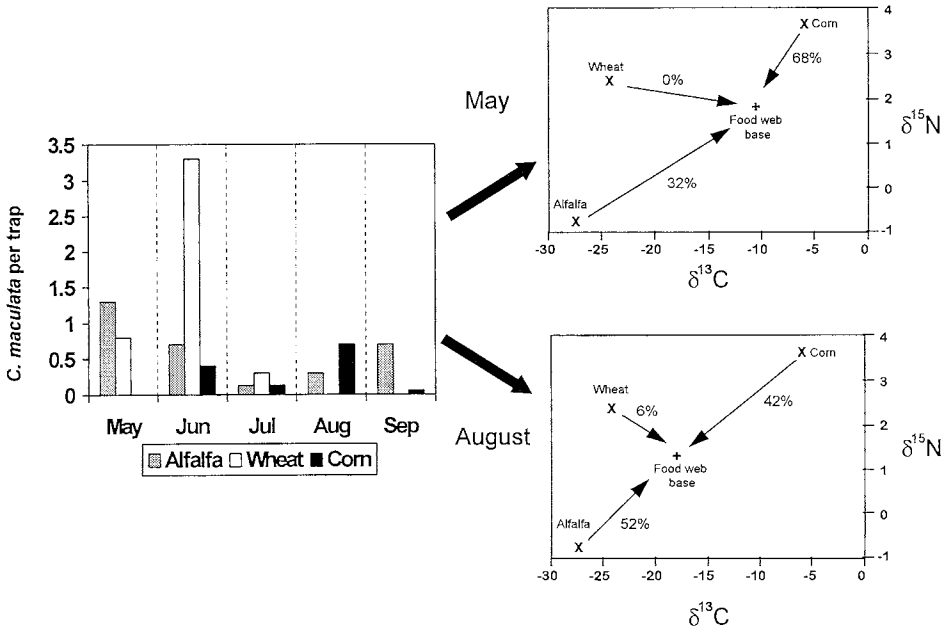

Fig. 2 Comparison of the relative abundance of *Coleomegilla maculata lengi* (Timberlake) to C and N flow in an agroecosystem. Estimates are presented for the temporal abundance of *C. maculata* in different agricultural plants, the isotopic composition of agricultural plants and the mixture of plants at the base of the food web, and the percent contributions of C or N from different plants to the base of the food web of *C. maculata*. Percent contributions are derived from mass balance equations and are indicated at the end of arrows

end of the experiment and the expected value for an individual utilizing a pork liver diet likely reflects the influence of C from sucrose in water supplied to the ladybeetles. We could not accounted for the contribution of C from sucrose when estimating the expected value of *H. variegata* because water intake could not be quantified. Despite this discrepancy, the $\delta^{13}C$ and $\delta^{15}N$ data strongly suggest that isotope values of ladybird beetles are sensitive to dietary changes on relatively short time scales (days) and provide a basis for establishing pathways of energy flow or material transfer for insects in natural ecosystems.

Quantitative estimates of material transfer between *C. maculata* and plants from an agroecosystem were determined using isotopic mass balance equations (Fig. 2). These equations require estimates of C and N isotope values for individual plants, *C. maculata* and the plant mixture comprising the base of the food web. Plants in this system included alfalfa ($\delta^{15}N$ = –0.8‰ and $\delta^{13}C$ = –27.0‰), wheat ($\delta^{15}N$ = 2.4‰ and $\delta^{13}C$ = –24.0‰), and maize ($\delta^{15}N$ = 3.7‰ and $\delta^{13}C$ = –6.7‰; Fig 2). The $\delta^{13}C$ and $\delta^{15}N$ values of *C. maculata* obtained in May are –11.9‰ ± 1.1 and 5.1‰ ± 0.3, respectively. During August the isotope values of *C. maculata* are –19.0‰ and 4.6‰ ± 0.9 for $\delta^{13}C$ and $\delta^{15}N$, respectively. The average $\delta^{13}C$ or $\delta^{15}N$ of the mixture of plants at the base of the food web of *C. maculata* (previously defined as $\delta^{13}C_p$ and $\delta^{15}N_p$, respectively in equations delineated in the Methods) can be determined if the isotopic values of *C. maculata* are corrected for trophic level isotope effects. An estimate of the change in $\delta^{13}C$ and $\delta^{15}N$ values between *C. maculata* and vegetation at the base of the food web is the difference in $\delta^{15}N$ and $\delta^{13}C$ between *H. variegata* and plants obtained in the laboratory and field studies (Table 1). These values were –0.8‰ and 3.3‰, for the change in $\delta^{13}C$ and $\delta^{15}N$ respectively and represent the sum of the average difference in C or N isotopic composition between aphids and plants (average = –0.6‰, and 0.4‰, respectively) and between *H. variegata* and aphids (–0.2 and 2.9, respectively; Table 1). Mass balance equations which incorporate isotope values of *C. maculata* corrected for trophic level effects indicate that $\delta^{13}C$ and $\delta^{15}N$ values of the base of the food web during May were –11.1 and 1.8, respectively and during August were –18.2 and 1.2, respectively.

The isotopic composition of the base of the food web in May indicates that 32% and 68% of the C or N of *C. maculata* was obtained from alfalfa and maize pollen, respectively (Fig. 2). The *C. maculata* did not obtain C or N from wheat at this time. The influence of alfalfa-derived C is consistent with data on *C. maculata* abundance (Fig. 2). *C. maculata* predominated in alfalfa during the early spring (Fig. 2). The large percentage of C or N derived from maize was likely assimilated by *C. maculata* during the previous growing season since this species overwinters as an adult.

During August, the highest abundance of *C. maculata* was found in maize. At this time, the isotope values of *C. maculata* (–19.0‰ and 4.6‰ ± 0.9 for $\delta^{13}C$ and $\delta^{15}N$, respectively) suggest that 52%, 6%, and 42% of their C or N was derived from alfalfa, wheat, and maize, respectively. This likely reflects C and N assimilated from wheat prior to mid-July when *C. maculata* abundance was declining and more recent assimilation of C and N from corn and alfalfa during July when the abundance of *C. maculata* in these plants increased.

The results from May and August suggest that ladybird beetles such as *C. maculata* are able to exploit different habitats during the growing season. In addition, isotope and abundance data on *C. maculata* within an agroecosystem are complementary, and this suggests the success of the isotope technique for delineating material transfers in the field and signifies the potential of this approach for addressing the complex issue of feeding dynamics and local dispersal of insects.

In conclusion, this study represents the first important steps in establishing the use of stable isotopes to quantify material transfer between plants, pests, and beneficial insect predators. The diet switching experiment demonstrated that isotope values of adult ladybird beetles provide a record of isotopically distinct food sources and that the shift in $\delta^{13}C$ or $\delta^{15}N$ of the beetle that occurs in response to a change in diet can take place within 21 days. Field results confirm the observation that a history of the diet is reflected in $\delta^{13}C$ and $\delta^{15}N$ values. Through an experimental design that incorporates the use of plants with unique $\delta^{13}C$ and/or $\delta^{15}N$ values, the isotope technique can assist in delineating the complex patterns of dispersal among ladybird beetles in local habitats and, as a result, should enhance the success of manipulating populations of this insect. In this regard, information on overwintering behavior obtained from the isotopic values of insects obtained in the early spring would be an extremely important contribution.

Acknowledgements We thank the USDA/APHIS Biological Laboratory in Niles, MI for their assistance in rearing ladybird beetles. We thank S. Clouthier for technical assistance. This work was supported by funds from the General Electric Foundation (PHO) and by NSF DEB 922130 (PHO and SHG) and BIR9120006 to the Center for Microbial Ecology at Michigan State University.

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