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Carbon and nitrogen transfer from a desert stream to riparian predators

Abstract Adult aquatic insects emerging from streams may be a significant source of energy for terrestrial predators inhabiting riparian zones. In this study, we use natural abundance $\delta^{13}C$ and $\delta^{15}N$ values and an isotopic ^{15}N tracer addition to quantify the flow of carbon and nitrogen from aquatic to terrestrial food webs via emerging aquatic insects. We continuously dripped labeled ^{15}N-NH_4 for 6 weeks into Sycamore Creek, a Sonoran desert stream in the Tonto National Forest (central Arizona) and traced the flow of tracer ^{15}N from the stream into spiders living in the riparian zone. After correcting for natural abundance $\delta^{15}N$, we used isotopic mixing models to calculate the proportion of ^{15}N from emerging aquatic insects incorporated into spider biomass. Natural abundance $\delta^{13}C$ values indicate that orb-web weaving spiders inhabiting riparian vegetation along the stream channel obtain almost 100% of their carbon from instream sources, whereas ground-dwelling hunting spiders obtain on average 68% of their carbon from instream sources. During the 6-week period of the ^{15}N tracer addition, orb-web weaving spiders obtained on average 39% of their nitrogen from emerging aquatic insects, whereas spider species hunting on the ground obtained on average 25% of their nitrogen from emerging aquatic insects. To determine if stream subsidies might be influencing the spatial distribution of terrestrial predators, we measured the biomass, abundance and diversity of spiders along a gradient from the active stream channel to a distance of 50 m into the upland using pitfall traps and timed sweep net samples. Spider abundance, biomass and richness were highest within the active stream channel but decreased more than three-fold 25 m from the wetted stream margin. Changes in structural complexity of vegetation, ground cover or terrestrial prey abundance could not account for patterns in spider distributions, however nutrient and energy subsidies from the stream could explain elevated spider numbers and richness within the active stream channel and riparian zone of Sycamore Creek.

Keywords Adult aquatic insects · Aquatic subsidies · Araneae · $\delta^{13}C$ · $\delta^{15}N$ · Spiders

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Introduction

Movement of energy, nutrients and organisms from aquatic to terrestrial habitats is not a new concept for ecologists (Summerhayes and Elton 1923; Leopold 1941; Likens and Bormann 1974), yet relatively few studies have quantified the export of materials from aquatic to terrestrial ecosystems or their effect on recipient populations. Adult aquatic insects emerging from streams, for instance, may be a significant source of nutrients and energy for terrestrial predators living in riparian and upland habitats (Jackson and Fisher 1986; Gray 1989).

The few studies that have looked at the importance of emerging aquatic insects to terrestrial predators have found that aquatic insects provide an additional source of nutrients and energy for riparian predators (Gray 1993; Power and Rainey 2000; Nakano and Murakami 2001; Sabo and Power 2002). In fact, behavioral studies have shown that some spider and bird species choose sites and relocate webs or breeding sites depending on the timing and location of aquatic emergence production (Gillespie 1987; Orians and Wittenberger 1991). But just how important are stream subsidies to the spatial distribution of predators in the surrounding watershed?

Many studies have documented that riparian forests contain a more diverse and abundant assemblage of terrestrial consumers than adjacent upland habitats (Greenwood et al. 1995), although explanations for these differences are poorly understood (Nakano and Murakami 2001). This is especially true in deserts of the southwestern United States, where riparian corridors not only support higher densities and a greater diversity of species than drier upland habitats, but also allow some organisms to remain active in the colder months of autumn and winter (Stamp 1978; Stamp and Ohmart 1979). Jackson (1984) hypothesized that both density and diversity of predators in desert riparian zones respond to the higher prey productivity of desert streams. In Sycamore Creek, a Sonoran desert stream, net emergence of aquatic insects (23.1 g AFDM m^{-2} $year^{-1}$) may exceed that of terrestrial arthropod productivity (Stamp and Ohmart 1979; Jackson and Fisher 1986), further suggesting that aquatic insects are an important energy source controlling the spatial distribution of terrestrial predators in desert watersheds.

Natural abundance of stable isotopes have been used to document trophic interactions and food web relationships in both aquatic (Peterson and Fry 1987; Cabana and Rasmussen 1994; Finlay et al.1999) and terrestrial habitats (Herrera 1998; Ponsard and Arditi 2000; Kelly 2000). Likewise ^{15}N tracer additions have been used in aquatic and terrestrial systems to investigate cycling, uptake (Jordon et al. 1997; Hall et al. 1998; Koba et al.1999; Williams et al. 1999; Mulholland et al. 2000a; Tank et al. 2000) and transfers of N between food web compartments (Winning et al.1999; Mulholland et al. 2000b). Here we use natural abundance ^{13}C and ^{15}N values and a ^{15}N tracer addition to document the flux of organisms and nutrients from streams to terrestrial spider assemblages via emerging aquatic insects. First, we use natural abundance ^{13}C and ^{15}N values to determine the most probable food sources (aquatic vs terrestrial) for spiders with different feeding strategies. We then use a ^{15}N–NH_4 addition to trace the flow of nitrogen from the ^{15}N enriched stream habitat, into the recipient terrestrial habitat. Because the aquatic habitat is 'spiked' with ^{15}N and the terrestrial habitat remains at natural abundance levels, transfer of the labeled ^{15}N can be traced from its aquatic source into the adjacent terrestrial community. By determining the amount of tracer ^{15}N incorporated into spider biomass and comparing it to the ^{15}N tracer found in

aquatic insects, we estimate the proportion of N that spiders obtain from emerging adult aquatic insects compared to that which comes from terrestrially-derived sources. In addition, we determine how the biomass, abundance and diversity of spiders vary along a gradient from stream edge to upland (a distance of 50 m) by pitfall trapping and sweep net sampling. Lastly, we explore the possibility that other factors such as structural complexity of vegetation, or terrestrial prey abundance might be important factors influencing the spatial distribution of spiders in this Sonoran Desert watershed.

Materials and methods

Study site

This study was conducted May–July 1997 along a 300 m reach of Sycamore Creek, an intermittent Sonoran desert stream located 32 km northeast of Phoenix, Arizona. Sycamore Creek is located in a dry and mountainous 505 km^2 watershed (see detailed description in Grimm1987). Characteristic of this region, summer air temperatures were high (mean =28.7°C) and rainfall was minimal (0.05 cm). Riparian vegetation along the stream bank was restricted to high flood areas and was predominately deciduous, including: willow (*Salix exigua* and *S. goodingii*), ash (*Fraxinus pennsylvanica velutina*), sycamore (*Platanus wrighti*), cottonwood (*Populus fremontii*), walnut (*Juglans major*) and mesquite (*Prosopis glandulosa*). Two shrub species also occurred along the stream-riparian edge and within the active channel (as surface flow was significantly reduced): seepwillow (*Baccharis salicifolia*) and burro bush (*Hymenoclea monogyra*). The upland was dominated by drought-tolerant species such as saguaro (*Cereus giganteus*) and prickly pear cactus (*Opuntia spp.*). Ground cover within the riparian zone was predominately sand with occasional patches of grass, leaf litter, bedrock outcrops or woody debris piles.

At the beginning of the study, average stream discharge was 70 l s^{-1}, falling to 15 l s^{-1} by the end of the experiment (Table 1). Similarly, stream width and depth, which averaged 4.8 m and 4.2 cm respectively, decreased significantly during the solute addition and the stream eventually disappeared underground into subsurface flow shortly after our sampling period ended. Stream substrata along the experimental reach consisted mainly of coarse sand (90%) with some gravel/ cobble (10%). This stream has relatively low N and P concentrations and is very productive and autotrophic (Grimm 1987; Table 1).

Aquatic insect sampling

We continuously dripped 10% ^{15}N–labeled NH_4Cl into Sycamore Creek from 1 May to 12 June 1997 to achieve a 500‰ ^{15}N enrichment of streamwater NH_4, while maintaining background concentrations of NH_4. The ^{15}N

Table 1 Physical, chemical and biological characteristics of Sycamore Creek, a Sonoran Desert stream in Arizona. All values are from the beginning of the ^{15}N tracer addition. Metabolism data were collected using the two-station diel oxygen method (Mulholland et al.2001)

Physical	
Stream order	1
Discharge (l/s)	70
Mean width (m)	5.8
Mean depth (cm)	4.2
Average slope (%)	0.3
Temperature (°C)	19.5
Chemical	
NH_4 (µg N/l)	1.9
NO_3 (µg N/l)	16.8
SRP (µg P/l)	13
Metabolism	
GPP ($gO_2m^{-2}day^{-1}$)	15
R ($gO_2m^{-2}day^{-1}$)	8.3
P:R ratio	1.8

addition rate was calculated to raise the background concentration of NH_4 in the stream by less than 1%; hence the $^{15}NH_4$ addition was truly a tracer addition. The solute was released from a 20 l Nalgene carboy connected to a peristaltic pump powered by a solar panel charged battery. The total amount of ^{15}N-NH_4 added to the stream over the 6 week period of the release (1,604.8 mg ^{15}N as $^{15}NH_4Cl$) was estimated based on stream discharge and background ammonium concentrations (Table 1). In-stream insect sampling locations were determined by calculating the ammonium uptake length (96 m) measured previous to the ^{15}N addition using a short-term solute addition (Webster and Ehrman 1996). Two weeks prior to the beginning of the ^{15}N tracer addition, we measured biomass and C:N ratios of all in-stream insect larvae. Biomass estimates of in-stream insect larvae were obtained using an 80 cm^2 Hess sampler at randomly chosen sites along the study reach. Once the addition started, larval insects were sampled from seven stations below the ^{15}N dripper (20, 40, 60, 110, 180 and 280 m), and one site upstream from the addition site (minus 10 m), once a week over the 6 week addition period using Hess samplers and hand collecting.

Quantitative estimates of emergence were made using 0.25 m^2 emergence traps (n=9) (Sanzone 2001). Three traps were placed 20 m upstream from the ^{15}N tracer addition site and six traps were placed downstream (between 15 and 35 m from the release site). Emergence traps were sampled using an aspirator and forceps on five separate dates after collecting emerging insects for 48 h intervals (n=45). Adult aquatic insects flying in the area were sampled using black lights on day 38 and day 42 after the start of the release. Light traps were constructed from white plastic buckets (area =450 cm^2) with battery-operated black lights placed just inside the top of the bucket. One light trap was placed 20 m upstream from the release site and two traps were placed below the release site (at 15 and 35 m downstream) within the center of the

stream channel. Light traps were operated from dusk until dawn (approximately 2000 hours until 0800 hours the following morning). Natural abundance ^{13}C and ^{15}N of dominant aquatic insects were determined from samples taken upstream from the release point. Tracer $\delta^{15}N$ values of immature and adult aquatic insects were determined using insects collected downstream from the release site. All tracer $\delta^{15}N$ values are background corrected (natural abundance $\delta^{15}N$ values subtracted from $\delta^{15}N$ values of labeled taxa) and so represent only the amount of ^{15}N that organisms incorporated from the ^{15}N addition.

Terrestrial invertebrate sampling

To determine stable isotope content and changes in biomass, abundance and assemblage structure of spiders and terrestrial prey, five 50 m stream-to-upland transects were established, running perpendicular to the stream bank. These stream-to-upland transects were located 60, 70, 80, 90 and 100 m downstream from the ^{15}N release site. Spiders and potential prey were sampled along each of the transects as follows: within the active stream channel along the water's edge (0 m), in the riparian zone directly adjacent to the stream-riparian edge (10 m from the water's edge), and in upland areas, 25 and 50 m away from the stream edge. Additional stream bank samples for ^{15}N analysis were taken along the stream edge at eight sites: 20, 50 and 100 m upstream from the release site and at 10 m intervals from 10 to 50 m downstream from the release. Spiders and arthropod prey (from terrestrial and aquatic habitats) were collected from riparian vegetation using timed (5 min) sweep net samples (Coddington et al. 1996) on day 42 of the release along the five stream-to-upland transects and at eight additional sites along the stream channel.

Arthropods inhabiting lower herbaceous vegetation and litter were sampled using 48-h pitfall traps (Sanzone 2001) along the five stream-to-upland transects and at the eight additional sites along the active stream channel. Cups were filled with 70% ethanol and left open for 48-h periods on five sampling dates, over a 3-week period (n=25 traps). Natural abundance ^{13}C and ^{15}N values of spiders and terrestrial prey were determined using samples collected 100 m upstream from the ^{15}N release site. Tracer ^{15}N values were determined using spiders and terrestrial prey collected downstream from the release site.

Sample processing and analysis

Immature and adult insects and spiders were taken back to the lab, sorted and placed in 70% ethanol until adult spiders and aquatic insects could be identified to genus and morphospecies, immature spiders identified to family, and terrestrial prey identified to order. Spiders, once identified were placed into functional feeding guilds

based on current knowledge of natural history and feeding preferences (Kaston 1978; Wise 1993; Nyffeler et al. 1994; Foelix 1996). The five feeding guilds we analyzed were wandering spiders (WND), spiders that use a sit-and-wait strategy on the ground (SWG), orb-web weaving spiders (ORB), sheet-web weaving spiders (SHT) and spiders that use a sit-and-wait strategy on vegetation (SWV). Once identifications were complete, all samples were dried at 60°C for at least 48 h, weighed to estimate biomass (mg DM m^2), ground, and a composite sample of several individuals of the same genus from the same location were analyzed for ^{13}C and ^{15}N (1–2 mg DM).

Natural abundance of stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) and tracer $\delta^{15}N$ values for riparian spiders, terrestrial prey, and immature and emerged adult aquatic insects were calculated as:

$$\delta^{15}N \text{ or } \delta^{13}C = [(R_{sample}/R_{standard}) - 1] \times 1,000 \qquad (1)$$

where, $R_{sample} = ^{13}C:^{12}C$ or $^{15}N:^{14}N$ ratio in the sample and $R_{standard} = ^{13}C/^{12}C$ ratio in Pee Dee Belemnite for $\delta^{13}C$ and $^{15}N/^{14}N$ ratio in the atmosphere for $\delta^{15}N$ (Peterson and Fry 1987). All samples were analyzed by high-temperature direct combustion and continuous flow analysis.

Estimating food sources (C) for riparian predators

To determine which food resources were consumed by spiders living in the active channel and along the riparian edge, we used the following equation to estimate the relative importance of carbon derived from aquatic prey versus carbon derived from terrestrial prey for spiders living in the Sycamore Creek watershed (modified from Doucett et al.1996):

$$P_{aqua} = (\delta^{13}C_{pred} - \delta^{13}C_{terr} - ba)/(\delta^{13}C_{aqua} - \delta^{13}C_{terr})$$

$$(2)$$

where, P_{aqua} = proportion of spider C derived from adult aquatic insects; $\delta^{13}C_{pred}$ = natural abundance $\delta^{13}C$ of spiders collected in pitfall and sweep net samples; $\delta^{13}C_{terr}$ and $\delta^{13}C_{aqua}$ = natural abundance $\delta^{13}C$ of terrestrial and emerging aquatic insects respectively. b is the average trophic enrichment of ^{13}C between predator and prey (approximately 1‰: DeNiro and Epstein 1978), and a is the number of trophic transfers between prey and predator (estimated for each functional feeding guild from actual $\delta^{15}N$ values).

Transfer of tracer ^{15}N from aquatic to terrestrial foodwebs

The proportion of nitrogen that riparian predators obtain from aquatic prey versus that which comes from terrestrial prey was estimated based on $\delta^{15}N$ values from samples collected during the addition along the ^{15}N enriched study reach. Natural abundance values indicate that background $\delta^{15}N$ and C:N ratios are similar among prey species inhabiting similar trophic positions (C:N

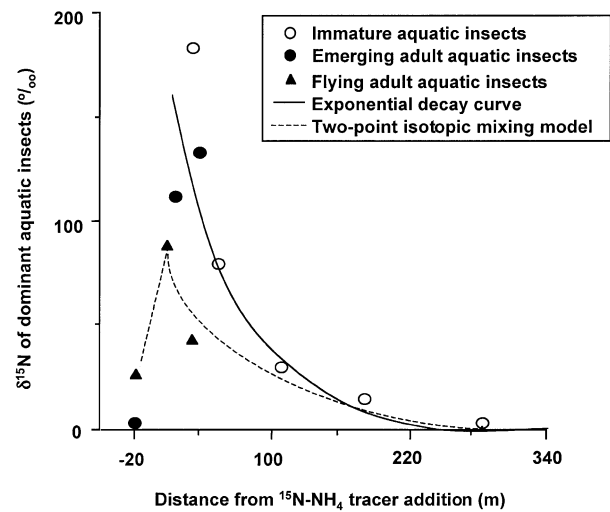**Fig. 1** Exponential decay curve (*solid line*) derived from both in-stream aquatic nymph/ larvae data (averages presented as *open circles*) and emerging aquatic adults (averages presented as *filled circles*) to predict aquatic insect enrichment ($\delta^{15}N_{d,E}$) d meters downstream from the release point: $\delta^{15}N_{d,E} = \delta^{15}N_{0,E} e^{-kd}$ where, $\delta^{15}N_{0,E}$ is the $\delta^{15}N$ signal of emerged aquatic insects just below the source and k is the exponential decay constant (r^2=0.874, P=0.0001, $\delta^{15}N_{0,E}$=202, k=0.01557). The end-point mixing model (*dashed line*) is derived from $\delta^{15}N$ values from aquatic insects captured in light traps at 15 and 35 m (*filled triangles*) on day 42 of the tracer release. The equation used is described in the text. The $\delta^{15}N$ of flying aquatic insects captured in light traps 20 m upstream from the ^{15}N release (*filled triangles*) agrees with model predictions

ratio ranges from 4.1 to 4.6); hence unlabeled terrestrial taxa should have an isotopic signal considerably lower than enriched stream insects. After calculating biomass-weighted average $\delta^{15}N$ values of emerging insects, the proportion of N coming from unlabeled sources (terrestrial prey) and that coming from labeled sources (local populations of emerging aquatic insects) can be calculated using an isotopic mixing model.

Spiders were collected at more sites than were emerging insects; hence we fit an exponential decay curve to predict average $\delta^{15}N$ values for labeled aquatic prey emerging at all points where we collected spiders. We first determined that $\delta^{15}N$ values for in-stream immature insects were not different than the $\delta^{15}N$ values of adult aquatic insects emerging from the same location (n=7, P=0.7915). We then used a combination of immature and emerging adult aquatic insect $\delta^{15}N$ values to derive an exponential decay curve that predicted $\delta^{15}N$ values of emerging adult aquatic insects ($\delta^{15}N_{d, E}$) d meters downstream from the release point (Fig. 1):

$$\delta^{15}N_{d,E} = \delta^{15}N_{0,E}e^{-kd} \qquad (3)$$

where $\delta^{15}N_{0, E}$ is the predicted average $\delta^{15}N$ signal of emerged aquatic insects at the source and k is the exponential decay constant, determined to be 0.01557 (Fig. 1).

A two-point mixing model was then used to estimate the $\delta^{15}N$ signals of adult aquatic insects flying in the air at

point d (modified from Hershey et al. 1993). We chose an upstream flight model because field observations and literature (Jackson and Fisher 1986) indicated predominantly upstream flight and the model provided the best fit to the data:

$$\delta^{15}N_{d,F} = (s)(\delta^{15}N_{0,E}e^{-kd}) + (1-s)(\delta^{15}N_{0,E}e^{-k(d+x)})$$

(4)

where $\delta^{15}N_{d,F} = \delta^{15}N$ of adult aquatic insects flying at point d; s = the proportion of adults emerging at point d; $1-s$ = the proportion of adults emerging downstream at $d+x$ and flying to d; d = distance downstream from the ^{15}N source; x = flight distance of emerged adult aquatic insects; and $\delta^{15}N_{0,E}$ = is the predicted average $\delta^{15}N$ of emerged aquatic insects at the source (from Eq. 3). $\delta^{15}N$ values from aquatic insects captured in light traps at 15 and 35 m were used to estimate the flight distance (x) and the partition coefficient of two subpopulations (s and $1-s$). Using the above equations, and an exponential decay constant (k) of 0.01557, Gauss-Newton Maximum Likelihood Estimation (SAS1996) determined an average upstream flight distance (x) of 109 m and the proportion of labeled insects emerging at point d (s =0.38) (r^2=0.692). To examine the validity of this model, we compared the average $\delta^{15}N$ value of aquatic insects caught 20 m upstream from the ^{15}N tracer release to model predictions for that distance. The model predicted a $\delta^{15}N$ value of 31.41, whereas measured $\delta^{15}N$ was 26.75 (Fig. 1), a reasonable estimate.

Spider N derived from ^{15}N enriched aquatic insects was then calculated using the following equation (Junger and Planas 1994):

$$\delta^{15}N_{pred*} = (P_{aqua})(\delta^{15}N_{aqua*}) + (1-P_{aqua})(\delta^{15}N_{terr*})$$

(5)

where, $\delta^{15}N_{pred*} = \delta^{15}N$ of spiders; P_{aqua} = proportion of spider N derived from aquatic insects; $\delta^{15}N_{aqua*} = \delta^{15}N$ of aquatic insects (calculated using Eq. 4) and $\delta^{15}N_{terr*} = \delta^{15}N$ of terrestrial prey. The superscript * indicates numbers are background corrected and represent only tracer ^{15}N.

Characterization of structural complexity of riparian vegetation

In addition to food resources, we also considered the structural complexity of live and decomposing vegetation as a factor that might be influencing the spatial distribution of spiders along the stream-to-upland transect. To compare the changes in structural complexity of terrestrial vegetation with changes in spider abundance, biomass and richness, we sampled vegetation in 1 m^2 plots (n=20). Specifically, we measured plant species richness, number of plants per m^2, number of stalks per m^2, number of vertical points transected ('touches'), and structural complexity of ground cover. Structural complexity of ground cover was determined by placing decomposing plant material into microhabitat classes (Southwood et al. 1979).

Statistical analyses

We used the Shapiro-Wilk procedure to test for normality (Shapiro and Wilk 1965), then compared differences between spider genera, functional feeding guilds, age classes (immature vs adult) and sex. To determine differences in percent N obtained from aquatic insects between spider genera, functional feeding guilds, age classes and sex we performed t-tests for each pair with significance set at 0.05 (JMP 1995). We used an arcsine-square root transformation for all results reported as percentages (Sokal and Rohlf 1995). Differences in adult spider biomass, abundance and richness from riparian to upland habitats (0, 10, 25 and 50 m from the wetted stream channel) were analyzed using a repeated measures ANOVA with time as the repeated measure (t=5) and distance from the river as the blocking factor (b=4); after normalizing the data using a ln (x+1) transformation (JMP 1995).

Linear regression analysis and one-way analysis of variance (ANOVA) procedures were used to compare spider abundance, biomass and richness with measures of structural complexity in the vegetation (plant species richness and average number of vertical touches), and on the ground (microhabitat classes). Linear regression analysis was also used to compare mean spider abundance and biomass with aquatic and terrestrial prey abundance and biomass (JMP, SAS 1995).

Results

Export of aquatic insects

Average (±SE) biomass of aquatic insects emerging during the duration of the ^{15}N tracer addition was 0.221±0.081 g DM m^{-2} day^{-1} or 2% of the instream biomass (n=45). Most of the insects emerging from Sycamore Creek during the ^{15}N release were from three families, Chironomidae (43%), Baetidae (*Fallceon quilleri* Dodds, *Acentrella insignificans* McDunnough, *Callibaetis* sp., *Centroptilum* sp.) (11%) and Stratiomyiidae (7%). Jackson and Fisher (1986) also found the largest proportion of emerging insects from Sycamore Creek on a yearly basis were from the families Chironomidae and Baetidae which accounted for 79% of emergence. The second largest group of aquatic insects emerging during the ^{15}N release came from the order Trichoptera (11%), which was dominated by three families: Helicopsychidae (*Helicopsyche* sp.), Limnephilidae (*Limnephilus* sp.) and Philopotamidae (*Chimarra* sp.). By day 42 of the ^{15}N tracer addition, all dominant aquatic insects emerging from the experimental reach were labeled with tracer ^{15}N and had reached isotopic equilibrium (i.e. a plateau in $\delta^{15}N$ values) (Fig. 2).
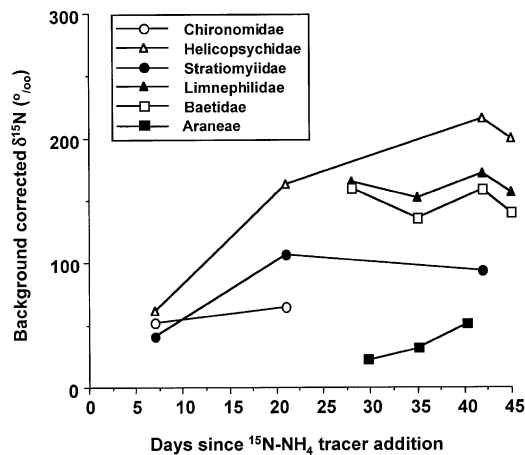
Fig. 2 $\delta^{15}N$ signals over time (40m downstream from the ^{15}N tracer addition for dominant aquatic insects (Chironomidae, Helicopshychidae, Limnephilidae, Stratiomyiidae, and Baetidae) and spiders (Araneae) collected in Sycamore Creek during the ^{15}N tracer release. Data points represent composite samples of 5 or more individuals (accuracy is ±0.5 ‰). All aquatic insects have reached isotopic equilibrium by the end of the experiment, however spiders have not

Carbon sources for spiders

Natural abundance $\delta^{13}C$ and $\delta^{15}N$ values of spiders and their potential prey show that spiders living within the stream channel and riparian zone rely, at least in part, on emerging aquatic insects (Fig. 3). Using an isotopic mixing model (Eq. 2), we determined that wandering spiders that capture prey by freely hunting on the ground (WND) (Lycosidae and some Gnaphosidae) obtained on average 68% of their carbon from aquatic resources. In contrast, natural abundance values from spiders that capture prey using a sit-and-wait strategy on the ground (SWG) (Agelenidae and some Gnaphosidae) are most likely feeding on terrestrial prey (63% terrestrial). Results from the mixing model also show that spiders that capture prey by building horizontal or vertical orb webs (ORB) (Araneidae and Tetragnathidae) on vegetation along the wetted stream channel obtain almost 100% of their carbon from aquatic prey. Spiders that build sheet-webs (SHT) (Linyphiidae), or use a sit-and-wait strategy to capture prey in and among vegetation (Salticidae and Thomisidae) also feed predominantly on emerging aquatic insects (69 and 73% respectively). Natural abundance data show that spiders feed mainly on: Chironomidae (Diptera), Stratiomyiidae (Diptera), and Baetidae (Ephemeroptera), all three of which feed on algae and organic matter and have relatively short life cycles (Gray 1981; Grimm 1987) (Fig. 3). During the sampling period, these three families comprised 61% of the total emergence biomass from Sycamore Creek and had similar natural abundance ^{13}C values to spiders from four of the five functional feeding guilds.
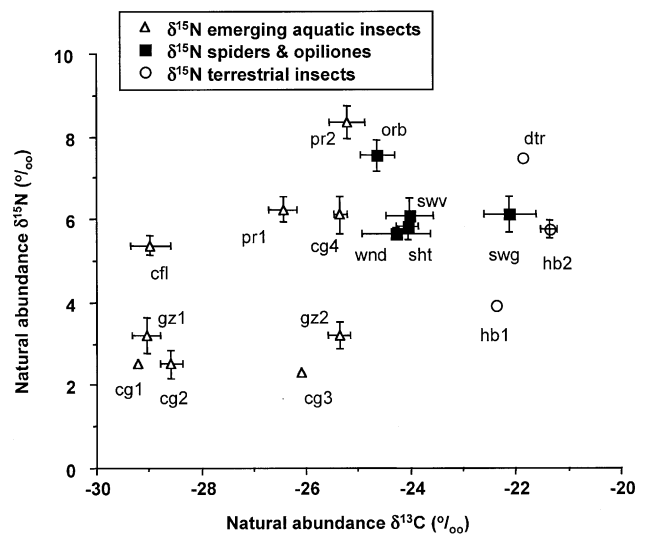

Fig. 3 Natural $\delta^{13}C$ and $\delta^{15}N$ values (mean ± SE) of spiders (*filled squares*), and aquatic (*open triangles*) and terrestrial insects (*open circles*) collected from the Sycamore Creek watershed. Individual numbers represent composite samples (3–6 individuals) of different species that were placed into functional feeding guilds. Letter codes indicate different 'feeding guilds'. Spiders (*solid squares*) that capture prey by wandering on the ground (*wnd*) (Lycosidae), or sitting and waiting for prey on vegetation (*swv*) (Salticidae and Thomisidae), or that build aerial orb webs (*orb*) (Araneidae and Tetragnathidae) or sheet-webs (*sht*) (Linyphiidae) are feeding mainly on aquatic insects emerging from Sycamore Creek. Spiders that capture prey using a sit-and-wait strategy on the ground (*swg*) (Agelenidae and Gnaphosidae) are most likely feeding on terrestrial prey. Abbreviations for potential terrestrial insect prey are: herbivores, mainly lepidopterans and homopterans (*hb1*), and coleopterans (*hb2*); and detritivores, mainly coleopterans (*dtr*). Abbreviations for potential aquatic prey are: collector-filterers from the genera *Cheumatopsyche*, *Hydropsyche*, *Chimarra* and *Polycentropus* (Trichoptera) (*cfl*); collector-gatherers from the genera *Limnephilus* (Limnephilidae, Trichoptera) (*cg1*), *Caenis*, *Tricorythodes* (Ephemeroptera) (*cg2*), Stratiomyiidae (Diptera) (*cg3*) and Chironomidae (Diptera) (*cg4*); grazers from the genera *Helicopsyche* (Helicopsychidae, Trichoptera) (*gz1*) and *Fallceon* (Baetidae, Ephemeroptera) (*gz2*); and aquatic predators from the suborders Zygoptera (*pr1*) and Anisoptera (Odonata) (*pr2*)

N transfer from aquatic foodwebs to terrestrial consumers

The average % N riparian spiders obtain from emerging aquatic insects was highest for ground-dwelling spiders that actively hunt for prey, and for those that build orb-webs adjacent to the stream channel (Table 2). Results from the mixing model indicate that orb-web weavers rely more heavily on aquatic resources, than sheet-web weavers or spiders that use a sit-and-wait strategy to capture prey on vegetation (n=35, P=0.0243, n=35, P=0.0347, respectively) (Fig. 4). Similarly, wandering spiders rely more heavily on emerging adult aquatic insects than spiders that use a sit-and-wait strategy on the ground (n=8, P=0.0446, n=8, P=0.0556, respectively) (Fig. 4).

For spiders inhabiting riparian vegetation, % N coming from aquatic insects was higher for females than for males (64% vs 7%, n=8, P=0.0001); however differences

Table 2 Average (±SE) and range of percent N in spiders (by feeding guild/ hunting strategy and family) obtained from flying adult aquatic insects (all values are background corrected and calculated using Eq. 5). Spiders inhabiting riparian vegetation were collected using timed sweep net samples, and ground-dwelling spiders were collected in pitfall traps within the active channel (0 m) and along the stream-riparian edge (10 m) from the wetted stream channel. Composite samples consist of 6–10 individuals. *NC* Standard error not calculated because *n*=1

| Spider families	No. of composite samples analyzed	Average (±SE)	%N range
Vegetation-inhabiting spiders			
Orb-web weaving spiders (ORB)	11	38.3 (8.8)	5–68%
Tetragnathidae (horizontal orb-web weavers)	10	35.3 (9.5)	5–68%
Araneidae (vertical orb-web weavers)	1	59.3 (NC)	NC
Sheet-web spiders (SHT)	4	10.6 (3.4)	7–14%
Linyphiidae (Linyphiinae) (sheet-web spiders)	4	10.6 (3.4)	7–14%
Sit-and-wait spiders (SWV)	8	15.3 (3.4)	7–24%
Thomisidae (crab spiders)	3	15.0 (7.6)	7–23%
Salticidae (jumping spiders)	5	15.6 (4.5)	8–24%
Ground-dwelling spiders			
Wandering/hunting spiders (WND)	95	26.9 (2.8)	4–96%
Lycosidae (wolf spiders)	94	26.4 (2.9)	4–96%
Gnaphosidae (*Cesonia*)	1	56.6 (NC)	NC
Sit-and-wait spiders (SWG)	8	5.62 (1.1)	3–10%
Agelenidae (funnel-web weavers)	4	4.3 (0.8)	3–5%
Gnaphosidae (*Drassyllus* and *Zelotes*)	4	7.6 (1.9)	6–10%
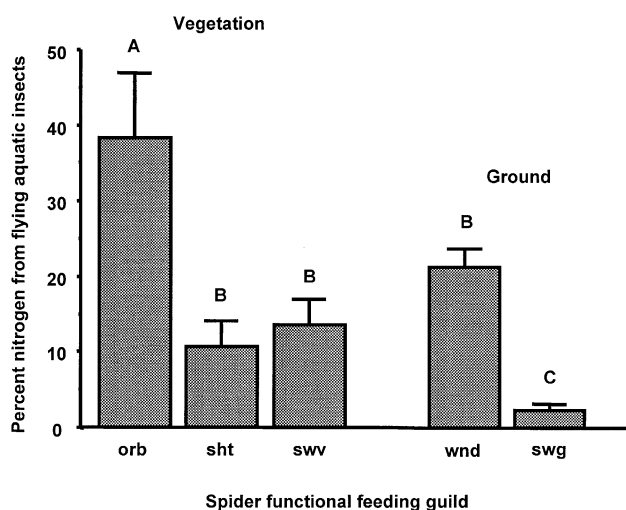
Fig. 4 Percent of riparian spider N (by functional feeding guild) obtained from aquatic insects. Spiders collected on vegetation using timed beat nets were divided into three groups: aerial orb-web weavers (*orb*) (Araneidae and Tetragnathidae), sheet-web spiders (*sht*) (Linyphiidae) and sit-and-wait strategists (*swv*) (Salticidae and Thomisidae). Ground-dwelling spiders collected in pitfall traps were divided into two groups: hunting spiders that find prey by wandering (*wnd*) (Lycosidae) on the ground, and those that use a sit-and-wait strategy (*swg*) (Agelenidae and Gnaphosidae). Different letters above each functional feeding guild show statistical differences (*P*<0.05)

between male and female spiders hunting on the ground were not significant (18% vs 23%, *n*=25, *P*=0.58). When looking at differences in age class, adult female spiders inhabiting vegetation derived more N from aquatic insects than immatures (64% vs. 27%, *n*=8, *P*=0.001), whereas adult males did not (7% vs 27%, *n*=8, *P*=0.21). Adult and immature ground-dwelling spiders were not significantly different from one another (18% and 23% vs 25% for immatures, *n*=25, *P*=0.60).

In general, spiders collected within the active stream channel obtained a greater percentage of their total nitrogen from aquatic sources, as compared to those collected in riparian (10 m) or upland areas (25–50 m) (*n*=5, *P*=0.01) (Table 3). Wandering spiders living along the active stream channel, in particular, obtained a much higher percentage of their total N from aquatic insects, compared to those captured 10 m or more from the active channel (*P*=0.0006). Spiders that use a sit-and-wait strategy on the ground were less labeled with tracer ^{15}N and obtained a smaller percentage of total N from aquatic insects, than wandering spiders (Fig. 4). Although some sit-and-wait ground strategists captured along the stream bank and in riparian areas were feeding on aquatic prey, we found no δ^{15}N labeling beyond 25 m (Table 3). Orb-web weaving spiders collected adjacent to the active stream channel had significantly higher δ^{15}N values than those collected in riparian areas (*P*=0.001).

Stream subsidies and the spatial distribution of spiders

Abundance (number of individuals per pitfall trap), biomass and richness of ground-dwelling spiders were highest along the active stream channel (Fig. 5a–c). More than four times as many spiders were collected adjacent to the active stream channel than were collected within the riparian zone (only 10 m away from the active channel); stream-side numbers were seven times higher than those collected 25 m or more from the channel (*df*=3, *P*=0.0001) (Fig. 5a). Wolf spiders (family Lycosidae) were the most abundant taxa collected adjacent to the stream edge (88% of all individuals). These spiders were

Table 3 Percent of spider N (by functional feeding guild) obtained from flying adult aquatic insects with distance from the active stream channel (all values are background corrected and calculated using Eq. <equationcite>5</equationcite>). Wandering spiders (*WND*) collected along the active stream channel were significantly more labeled than spiders collected in the riparian zone or upland ($n=12$, $p=0.0006$). Likewise orb-web weavers collected on vegetation along the active channel were more labeled than those collected in the vegetation only 10 m from the active channel ($n=5$, $p=0.0112$). *NP* None collected in timed sweep nets, *NC* standard error not calculated because $n=$ one individual, *NA* not analyzed for $\delta^{15}N$, *NL* not considered labeled if $\delta^{15}N$ value is less than 2

Distance from active channel	Ground			Vegetation		
	WND	SWG		ORB	SWV	SHT
Stream channel (0 m)	20.04 (3.24) **	5.25 (0.971)		40.84 (8.39) **	12.48 (4.05)	14.04 (NC)
Riparian edge (10 m)	5.24 (1.72)	3.64 (2.04)		2.23 (0.80)	10.26 (2.10)	6.67 (NC)
Upland area (25 m)	3.09 (2.24)	NL		NP	4.58 (NC)	NA
Upland area (50 m)	NL	NL		NP	NA	NA

** Statistically significantly different from other distances

collected more often within the drying stream channel than at any other place along the transects, with 64% collected within the banks of the stream channel, 25% collected within the riparian zone, and the remaining 11% collected in the upland (25–50 m pitfall traps).

Spider biomass was also significantly higher along the stream edge than anywhere else along the transect (*df*=3, *P*=0.0002) (Fig. 5b). Because of their large size and greater abundance relative to other families, wolf spiders also accounted for the greatest differences in biomass along the transects. Spider species richness (mean per trap) was also highest adjacent to the active stream channel (*df*=3, *P*=0.0001) (Fig. 5c). Complete spider species turnover occurred 25 m from the stream bank, suggesting there are two different spider assemblages in this watershed, one that contains "riparian species" and another that contains "upland species". Among the ground-dwelling spiders, those that actively hunt for prey by wandering were collected most often within the active channel, whereas sit-and-wait ground spiders were collected more frequently away from the stream edge (Fig. 6a). Data from timed beat-net samples indicate that orb web weavers (especially tetragnathids) occur almost entirely within the active channel and riparian zone (0–10 m from the bank), whereas sit-and-wait spiders are found more often away from the stream (Fig. 6b.)

We compared changes in spider abundance, biomass and diversity along the stream to upland transects with changes in the structural complexity of the live and decomposing vegetation and changes in aquatic and terrestrial prey availability. Ground-dwelling riparian spider biomass was positively related to emergence biomass at Sycamore Creek (Fig. 7; *n*=9, r^2=0.74, *P*=0.003). Ground-dwelling spider abundance or richness were not correlated with structural complexity of litter (*n*=25, r^2=0.31, *P*=0.44 and *n*=25, r^2=0.21, *P*=0.54 respectively), nor was species richness of vegetation-dwelling spiders correlated with plant species richness (*n*=5, r^2=0.55, *P*=0.26), or average number of vertical touches (*n*=5, r^2=0.34, *P*=0.42). Terrestrial prey abundance and biomass, although correlated with spider abundance (*n*=20, r^2=0.14, *P*=0.003) and biomass (*n*=20, r^2=0.19, *P*=0.02), explained little of the variation in spider distributions along the transect.
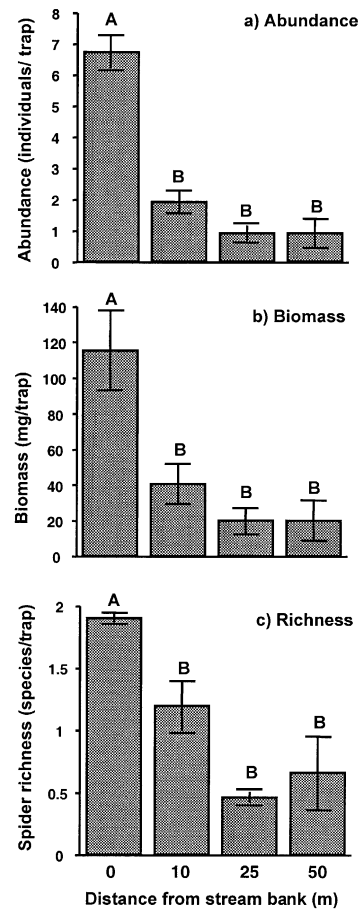

Fig. 5a–c Mean ground-dwelling spider **a** abundance, **b** biomass, and **c** diversity collected in 48 h pitfall traps from five transects (0–50 m). Traps 0 m from the stream are within the active (dry) channel along the wetted stream edge, traps 10 m from the wetted stream are along the stream-riparian edge, and 25 and 50 m traps are in the upland. Different letters indicate mean values are significantly different from one another (repeated measures ANOVA, *t*=5, *b*=4, *P*=0.05)
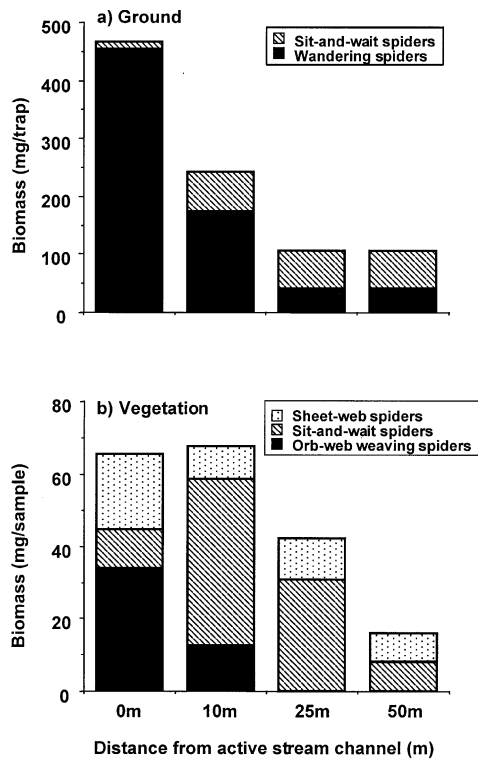
Fig. 6a, b Spider biomass from each functional feeding guild collected **a** on the ground in pitfall traps and **b** in vegetation using timed beat net samples
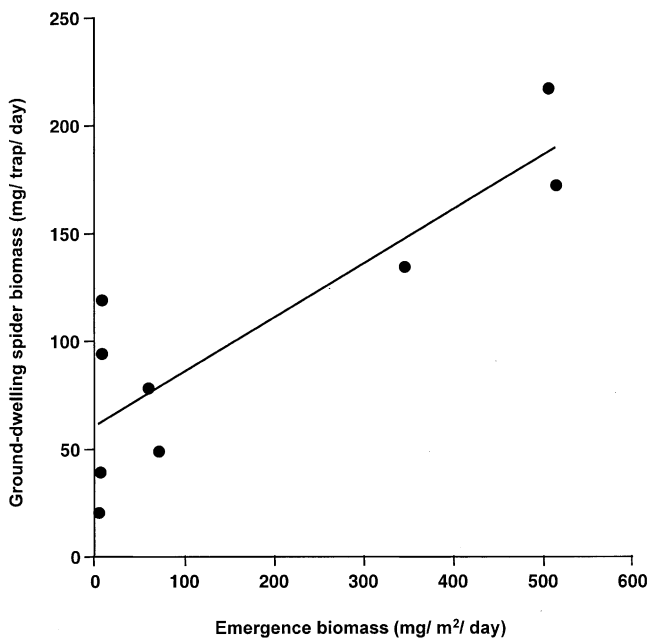

Fig. 7 Results of linear regression analysis showing that ground-dwelling spider biomass was positively correlated with emergence biomass during the ^{15}N tracer release ($n=9$, $r^2=0.74$, $P=0.003$)

Discussion

Movement of aquatic prey into recipient habitats

Discrete communities living in disparate habits are often tightly linked by energy and nutrient fluxes from one system to the next. Studies conducted in Sycamore Creek have shown that aquatic insect production is greater than in most temperate streams (Fisher and Gray 1983), and that net export of aquatic insects into the terrestrial watershed is much greater than the return of those insects back to the stream (Jackson 1984); hence, we expected the export of aquatic insects to be important to terrestrial food webs in this system. In Sycamore Creek, high temperatures, adequate food supply and short development times for insects (5–20 generations per year) contribute to this high yearly insect production (estimates range from 120 g m^{-2} year^{-1}, Jackson and Fisher 1986 to 135 g m^{-2} year^{-1}, Fisher and Gray 1983). This relatively high aquatic insect production coupled with high export of aquatic insects (16.6% to 20% of total insect production; Busch and Fisher 1981, Jackson and Fisher 1986), may explain why spider abundance and biomass is higher in riparian areas than upland areas in the Sycamore Creek watershed. It has been hypothesized that aquatic prey productivity fuels this enhanced riparian predator community (Jackson and Fisher 1986); here we provide conclusive documentation that riparian predators do in fact incorporate a significant proportion of energy from insects exported from river ecosystems.

Aquatic- terrestrial trophic relationships

The strength of the natural abundance stable isotope approach is that it incorporates δ^{13}C and δ^{15}N values of food resources over time with respect to the organism of study. In this ecosystem, the δ^{13}C of the two sources of prey available for spider consumption were isotopically distinct; hence we could distinguish between potential food resources for spiders. In four out of the five spider feeding guilds studied, spiders were relying mainly on aquatic resources for their carbon supply (Fig. 3). Specifically, δ^{13}C values show that these spiders are feeding mainly on aquatic insects from the families Chironomidae (Diptera), Baetidae (Ephemeroptera) and Stratiomyiidae (Diptera). Since Chironomidae and Baetidae account for more than 93% of total yearly insect production and the greatest amount of emergence (79%) in Sycamore Creek, it makes sense that spiders would consume these species, which are one of the main energy sources in this system. Williams et al. (1995) also found that two species of orb-web weaving spiders fed predominantly on Chironomidae (Diptera) and Baetidae (Ephemeroptera) which were the most common aquatic taxa emerging during their study period. In contrast, spiders that sit-and-wait in decomposing litter or under woody debris piles were feeding primarily on terrestrial insects.

Transfer of ^{15}N tracer from streams to terrestrial predators

We were able to quantify the export of nitrogen via emerging aquatic insects from Sycamore Creek and its uptake by terrestrial consumers living in the surrounding watershed using a ^{15}N tracer addition. Because of the large separation between terrestrial and aquatic δ^{15}N values, we could determine the proportion of N spiders obtained from aquatic versus terrestrial insects using two-source mixing models. For instance, we found that orb-web weaving spiders obtain a large portion of their N from aquatic insects (Table 2). Many of these orb-web weavers found along the banks of Sycamore Creek build sticky horizontal (Tetragnathidae–long-jawed orb weavers) or vertical webs (Araneidae) over the stream channel, and relocate their web in reaction to emergence production (Gillespie 1987) or migrating prey (Heiling 1999). This type of web facilitates capture of swarming insects that emerge in pulses. In contrast, spiders that build small flat non-sticky sheet-webs (Linyphiidae) in vegetation were less labeled with tracer ^{15}N (Fig. 4). These smaller webs are probably more effective at capturing single individuals, as linyphiids usually hang underneath their webs waiting for prey which they pull through the sheet after it becomes tangled (Wise 1993). Similarly, spiders that wait in flowers, leaves or on tree trunks to ambush their prey (Thomisidae, crab spiders), or spiders that capture prey visually with a stalk and pounce strategy (Salticidae, jumping spiders) were also less labeled with tracer ^{15}N (Table 2). Because these spiders sit and wait for prey rather than actively pursue them, it makes sense that they would take longer to reach isotopic equilibrium with respect to the ^{15}N tracer addition.

Wandering spiders such as those from the family Lycosidae (wolf spiders) are probably best adapted to disturbed environments and spatially patchy resources (Anderson 1974). Our data show that wolf spiders relied heavily on emerging adult aquatic insects. We observed these wandering spiders feeding on aquatic insects from drying algal mats along the edges of the wetted stream channel, as has been observed elsewhere (Power et al. 2002). Spiders that build funnel webs in litter or woody debris piles (Agelenidae) or that sit and wait for prey in litter (some Gnaphosidae) were the least labeled spiders (Fig. 4). At Sycamore Creek most of these spiders were collected in or near woody debris piles created by previous flooding events; most of which were located far into the riparian zone.

Patterns of dependence on aquatic resources based on tracer ^{15}N agree with those found for the natural abundance of carbon. Yet estimates from the ^{15}N tracer enrichment are lower than those predicted by the natural abundance of ^{13}C. Tracer δ^{15}N estimates are most likely lower than those predicted by ^{13}C because all spiders have not reached isotopic equilibrium with respect to their ^{15}N labeled food source over the course of the 6 week experiment (Fig. 2). Also, natural abundance values integrate δ^{13}C and δ^{15}N values over time with respect to food resources (you are what you eat) and so provide an overall indication of the importance of aquatic subsidies, whereas δ^{15}N values based on isotope additions provide a more detailed picture of N transfers to the riparian zone at any one point in time. Since there is considerable variability in the spatial distribution and timing of emergence in the Sycamore Creek watershed (due to flash flooding in spring and drying of the stream channel in summer), dependence of terrestrial predators on emerging aquatic insects may vary seasonally. This seasonal variability would not be detected using natural abundance values alone. This is especially important in watersheds with high seasonal fluctuations in emergence like Sycamore Creek, or where natural abundance values of stream and terrestrial organisms are similar (Sanzone 2001).

In general, spiders collected within the active stream channel obtained a greater percentage of their total nitrogen from aquatic sources, as compared to those collected in riparian (10 m) or upland areas (25–50 m) (Table 3). Wandering and orb-web weaving spiders living within the active stream channel, in particular, obtained a much higher percentage of their total N from aquatic insects, compared to those captured 10 m or more from the active channel. The reliance of these groups on emerging aquatic insects explains, at least in part, why these species (wandering and orb-web weaving spiders) were collected almost exclusively within the first 10 m of the active stream channel. This result is consistent with the hypothesis that invertebrate insectivores (such as spiders and odonates) are facilitating the transfer of energy from aquatic to terrestrial habitats by consuming emerging aquatic prey along the stream edge, which, in turn increases the density and diversity of vertebrate predators in riparian zones (Jackson and Fisher 1986). These larger riparian predators often move from lowland foraging sites along river corridors, further upslope to forest ridge habitats where they relocate stream-derived nutrients (Rainey et al. 1992).

Stream subsidies and their effect on spider assemblages

We found a more abundant and diverse spider assemblage adjacent to the active stream channel than anywhere else along the transect in the Sycamore Creek watershed. Several researchers have hypothesized that edge habitats contain greater numbers of individuals (Polis and Hurd 1996; Fagan et al. 1999) and larger-bodied organisms (Ferguson 2000) than interior habitats. Recent studies concerned with a wide variety of taxonomic groups in a variety of different habitats have found increasing numbers of terrestrial predators inhabiting edge habitats (Kareiva 1987; Greenwood et al. 1995; Malt 1995; Ferguson 2000; Henschel et al. 1996, 2002; Sanzone 2001). Our results enhance earlier findings by demonstrating that spiders are not only concentrated at the land-water margin but are also feeding directly on aquatic insects.

We have quantified a direct trophic link between streams and the surrounding watershed using natural abundance stable isotopes and a ^{15}N tracer addition. However other biological factors that we examined could not explain the increases in spider numbers or richness along the stream channel. Although structural complexity of vegetation or ground cover is often cited as one of the main factors influencing the diversity and abundance of spiders (Greenstone 1984; Sanzone and Draney 1996), we found that spider abundance, biomass or richness were not related to increased structural complexity or diversity of vegetation or to increased structural complexity of ground cover. Similarly, another study found that several structural measures of vegetation were unrelated to bird diversity along Sycamore Creek (Stamp 1978). We also found no evidence that spiders were responding to terrestrial prey availability. Differences in abiotic factors (such as moisture and temperature) have also been found to be important variables influencing the spatial distribution of terrestrial invertebrates in riparian zone habitats (Bastow et al. 2002). Stream corridors in arid environments are most likely providing these types of subsidies as well.

Although aquatic insect emergence constitutes a small portion of the total energy budget in desert streams (Busch and Fisher 1981), and represents a minor loss in terms of the nitrogen balance (Grimm 1988), the importance of this additional temporal and spatial subsidy to terrestrial communities appears to be great. Based on the total biomass and energy requirements of spiders collected within the riparian zone at Sycamore Creek one can determine if the spider biomass we found could be supported by terrestrial sources alone. To determine if emerging stream insects could be subsidizing the spider community, an energy budget for riparian spiders was calculated based on the energy requirements (μl VO_2 mg^{-1} h^{-1}) of spiders and the potential energy supplied by terrestrial and aquatic insects (kJ) in the riparian zone. Calculations suggest that terrestrial prey alone could not support the spider biomass found in the riparian zone at Sycamore Creek, however the additional energy supplied by emerging aquatic insects could support the observed spider biomass (Sanzone 2001).

Many studies over the last few decades have clearly shown that materials and organisms cross spatial boundaries (Hansson 1994; Cadenasso and Pickett 2000); however, the effect that these subsidies have on communities and ecosystem processes in adjacent habitats remains unclear. The riparian zone, because it is an obvious transitional zone between aquatic and upland habitats, is an ideal place to study the effects of spatial subsidies on adjacent habitats. Although much is known about the movement of energy, carbon, nutrients and materials from terrestrial to aquatic habits (Nakano et al. 1999), little is known about the relocation of materials and organisms in the other direction, from aquatic to terrestrial habitats. Unlike more mesic streams where the main direction and flow of nutrients and energy is from upland to riparian zone to stream channel, the predom-inant flow pathway in Sycamore Creek (with its high autochthonous production) is in the opposite direction, from the stream into the riparian zone (Marti et al. 2000). For example, leaves contribute less than 1% of the total organic inputs (g AFDM m^{-2} year^{-1}) to Sycamore Creek (Busch and Fisher 1981; Schade and Fisher 1997), yet more than 19% of instream secondary production emerges on a yearly basis (Jackson and Fisher 1986). This additional source of energy and nutrients from the stream appears to be subsidizing spider communities living in this arid watershed.

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