DIANE MARY SANZONE
Linking Communities Across Ecosystem Boundaries: The Influence of Aquatic Subsidies on Terrestrial Predators
(Under the direction of JUDITH L. MEYER)

Movement of nutrients and organisms between aquatic and terrestrial habitats may have a greater impact on assemblage structure and community dynamics than within-habitat inputs. In this study, I document the effect of aquatic prey subsidies on surrounding terrestrial predators in eight riparian zones using a stable isotopic ^{15}N tracer experiment to quantify the flow of nitrogen from aquatic to terrestrial food webs via emerging aquatic insects. I continuously dripped ^{15}N-NH_4Cl for six weeks into four temperate forested streams (North Carolina, Tennessee, New Hampshire and Oregon), one tropical forest stream (Puerto Rico), a desert stream (Arizona), a grassland stream (Kansas), and one arctic stream (Iceland), and traced the flow of ^{15}N from the streams into spiders living in the riparian zone. After correcting for background ^{15}N values, I used mixing models to calculate the proportion of ^{15}N tracer from emerging aquatic insects incorporated into spider biomass. In addition, I documented spider abundance, biomass and diversity along a transitional gradient at various distances from the stream bank (0-50m).

Although sites were located in different biogeographic regions, varied greatly in temperature and precipitation, and were sampled in different seasons, consistent patterns in the spatial distribution of spiders among the eight sites were found. Lower canopy and ground-dwelling spiders were significantly more abundant in riparian zones than in upland habitats in at least four of the eight sites, whereas upland habitats never contained more spiders. Ground-dwelling and lower canopy spider richness was also higher along the stream edge in seven of the eight sites.

Evidence from the eight different biogeographic regions suggests that aquatic insect emergence and microhabitat availability are important predictors of spider biomass, abundance and diversity. Stream-derived ^{15}N tracer was incorporated into spider tissue in eight riparian zones located in eight different biogeographic regions. Stream-derived N was highest in riparian spiders in desert, arctic and tall-grass prairie, tropical and northern conifer forest sites and lowest in temperate deciduous forest sites. ^{15}N labeling in spiders tracked that of emerging aquatic insects, indicating spiders are relying, at least in part, on aquatic resources. There was a direct positive relationship between incorporation of stream-derived N by spiders and biomass of emerging aquatic insects.

INDEX WORDS: Aquatic Insects, Aquatic Subsidies, Araneae, Arctic Stream, Coleoptera, $\delta^{13}C$, $\delta^{15}N$, Desert Stream, Eastern Deciduous Forest Stream, Emergence, ^{15}N Tracer Addition, Iceland, Northern Conifer Forest Stream, Opiliones, Predators, Riparian Zone, Spiders, Stable Isotopes, Streams, Tall-Grass Prairie Stream, Tropical Forest Stream.

LINKING COMMUNITIES ACROSS ECOSYSTEM BOUNDARIES: THE INFLUENCE OF AQUATIC SUBSIDIES ON TERRESTRIAL PREDATORS

by

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DEDICATION

This dissertation is dedicated to my sister, Patricia Kathleen Sanzone,
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CHAPTER 1

GENERAL INTRODUCTION AND LITERATURE REVIEW

Spatial subsidies occur when energy, carbon, nutrients or organisms cross spatial boundaries, thereby influencing populations, communities or ecosystem function in the recipient habitat. Prey subsidies from one habitat migrating into an adjacent habitat, for instance, may enhance predator populations beyond what even local resources can support (Polis et al. 1995). Increases in predator populations could, in turn, affect local community dynamics, foodweb interactions and ecosystem processes (Polis et al. in press). Similarly, nutrient and energy fluxes across spatial boundaries can have a multitude of effects on neighboring ecosystem processes and community dynamics (Polis et al. 1997). Boundaries (or ecotones) may serve, not only as recipients of these spatial subsidies, but also as areas of transformation or regulation of these cross-habitat subsidies (Osborne and Kovacic 1993, Pickett and Cadenasso 1995, Wiens 1995, Correll et al. 1992, Carpenter et al. 1998).

Riparian habitats are one of the most common and obvious examples of spatial boundaries in nature (Forman and Godron 1986). They are multidimensional zones of interaction controlled by both internal and external processes, that both receive and transform cross-habitat subsidies. Because of their position in the landscape, riparian zones are strongly influenced by adjacent upland and aquatic ecosystems (Gregory et al. 1991). Riparian zones also connect the larger terrestrial landscape to stream networks by transferring energy, carbon and nutrients between aquatic and upland habitats (Likens and Bormann 1974).

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. To better understand the importance of aquatic subsidies to terrestrial communities the following questions need to be addressed: 1) How common and widespread are aquatic subsidies? 2) What effect do aquatic subsidies have on the spatial distribution of communities in the adjacent terrestrial habitat? 3) How far into the upland do aquatic subsidies influence terrestrial communities? 4) What attributes of terrestrial and aquatic ecosystems influence the importance of aquatic subsidies to terrestrial communities (e.g., structural complexity of terrestrial vegetation or amount of terrestrial or aquatic insect productivity)? The research presented in this dissertation addresses these questions through field surveys of spider communities in riparian and upland habitats, and ^{15}N tracer additions into eight streams located in different biogeographic regions.

Spatial subsidies across ecosystem boundaries: an historical perspective

Historically, community and ecosystem ecologists studied natural communities and ecosystems as relatively closed (autonomous) units, where populations are in balance with local resources and conditions (Golley 1993). During the last several decades, however, ecologists have recognized that ecosystem processes and community dynamics are often influenced by fluxes of material and energy from adjacent ecosystems (Pulliam and Johnson 2001). In the 1970's, ecosystem ecologists began to study the influences of allochthonous inputs of energy, carbon and nutrients on local ecosystem processes and community dynamics (Likens et al. 1970, Likens and Bormann 1974, Meyer and Likens 1979). As population and community ecologists became more aware of ecosystem theory, they too began to focus on the importance of fluxes of organisms and materials across ecosystem boundaries (Pulliam and Johnson 2001). For example, the conceptualization of island biogeography theory and metapopulation dynamics which subdivided communities into spatially separated subunits linked by immigration and emigration brought the importance of cross-habitat fluxes to the forefront of ecology (Morin 1999).

Not soon after, “landscape ecology”, a new subdiscipline which viewed the natural world as a complex network of spatially heterogeneous landscape units, was recognized in the United States (Zonneveld 1995). One of the main goals of this new subdiscipline was to begin to understand how neighboring elements affect one another in the landscape (Zonneveld and Forman 1990, Pickett et al. 1992). This ‘landscape perspective’ enabled ecologists to incorporate larger landscape level fluxes (such as spatial subsidies) into a broader perspective that took into account the influence of both local resources and larger landscape-scale processes (such as disturbance and past land use) (Pulliam and Johnson 2001). The merging of these disciplines in the last few years has resulted in a more complete picture of the factors that influence the abundance, distribution and diversity of organisms in the landscape. The research that follows is an attempt to gain a broader landscape-level perspective on the transfers of carbon, nitrogen and organisms from aquatic to terrestrial ecosystems and their effect on recipient terrestrial communities.

The land-water interface: an ideal place to study spatial subsidies

Ecosystem processes and community composition within riparian zones are affected by lateral inputs from stream and upland ecosystems, and vertical inputs from the atmosphere and sub-surface zones, as well as internal ecosystem processes and community interactions (Gregory et al. 1991, Naiman and Decamps 1997, Martí et al. 2000). Because of the inherent complexity created at this land-water-air interface, riparian zones often harbor a unique, abundant and diverse community of organisms. In fact, riparian zones often contain a more abundant and diverse community of organisms than their upland counterparts (Henschel et al. 1996).

Most studies of the abundance and diversity of terrestrial consumers in riparian zones have found that small mammals (Herman et al. 1990), birds (Stauffer and Best 1980, Gray 1993), bats (Rainey et al. 1992) and terrestrial invertebrate predators (Gillespie 1987, Williams et al. 1995, Deharveng and Lek 1995, Henschel et al. 1996) are concentrated at the land-water margin. Several explanations have been proposed to explain increases in the diversity and abundance of these consumers. For instance, such factors as: changes in microhabitat (Uetz 1976, Naiman and Rodgers 1997, Ellis et al. 2001) or microclimate (Wenninger and Fagan 2000); changes in predator- prey interactions or shifts in foodweb structure (Caraco and Gillespie 1986, Reichert and Hall 2000); increases in structural complexity or productivity of terrestrial vegetation (Williams et al. 1995, Aiken and Coyle 2000); or changes in nutrient availability (Vargas 2000) all have been proposed. However, none of these explanations have provided definitive evidence to explain this pattern in a wide variety of riparian zone habitats.

Another possible explanation for the higher densities and diversity of terrestrial predators found along the land-water margin is the availability of aquatic insect subsidies (Jackson and Fisher 1986). Behavioral studies have shown that spiders feed directly on aquatic prey (Greenstone 1979, Gillespie 1987, Williams et al. 1995) and are often a significant source of mortality for aquatic prey (Gribbin and Thompson 1990, Rehfeldt 1990, 1992). Spiders, then, make useful organisms to model the flux of organisms from aquatic to terrestrial systems and their effect on the recipient terrestrial community.

Aquatic subsidies to terrestrial riparian predators

Riparian zones, in addition to harboring a unique community of organisms and internally cycling nutrients and energy, are areas of active exchange of organisms and nutrients between aquatic and terrestrial ecosystems. Traditionally, landscape-level stream research has focused on the unidirectional flow of energy and organisms from terrestrial to aquatic systems, and their effect on ecosystem processes and foodweb interactions in streams (Meyer and Likens 1979, Wallace et al. 1997, Nakano et al. 1999). Few papers, however, have tried to quantify the movement of nutrients or organisms in the other direction, from streams to adjacent terrestrial habitats (Polis and Hurd 1996, Martí et al. 2000).

Emergence production may be an important factor regulating terrestrial predator densities. This may be especially true in streams where emergence production most likely exceeds terrestrial insect production by several orders of magnitude (Jackson and Fisher 1986). In spite of the potential importance of aquatic insects to riparian and upland habitats, few data have been collected on the export of aquatic insects from streams, and the importance of those insects to terrestrial predators (Orians and Wittenberger 1991, Gray 1993, Nakano and Murakami 2001, Henschel et al. in press, Power et al. in press). It is possible that even in watersheds where out-of stream export of insects is low, compared to the within-stream energy budget, aquatic insects may be a critical food source for many terrestrial predators inhabiting the riparian zone.

Part of the difficulty in determining the importance of aquatic subsidies to terrestrial predators has been our inability to directly quantify the proportion of nutrients and energy that terrestrial predators obtain from aquatic sources versus that which comes from terrestrially-derived sources. Natural abundance of stable isotopes have been used with great success in recent years to document flows of organisms and nutrients across ecosystem boundaries (Wipfli 1997, Anderson and Polis 1998, Hilderbrand et al. 1999, Stapp et al. 1999). This technique is limited, however, to watersheds where natural isotopic signatures are distinct between aquatic and terrestrial systems, which is not the case for most forested watersheds. Because natural isotopic signatures are often not distinct enough to distinguish between aquatic and terrestrial food resources, employing ^{15}N tracer additions may be a useful technique to distinguish between aquatic and terrestrial food sources available to terrestrial predators.

The ^{15}N tracer approach has been used successfully to study nitrogen flows and identify food web linkages in both aquatic and terrestrial systems (Fry et al. 1995; Peterson and Fry 1987) and so could be used to trace trophic transfer of ^{15}N between ecosystems. This approach involves adding enough ^{15}N labeled ammonium to the stream to increase the ^{15}N: ^{14}N ratios by at least 50%, while at the same time not increasing (or only in trace amounts) overall N concentrations in that habitat. Because organisms living in the aquatic habitat are labeled with ^{15}N, and terrestrial organisms are not, transfer of the labeled N can be traced from its aquatic source into the adjacent terrestrial habitat. This approach is used in the dissertation.

The influence of increased structural complexity or productivity on terrestrial arthropod predators at the land-water margin

Throughout the history of ecological studies, there are many examples of increased structural diversity or architectual complexity influencing faunal richness or abundance (Elton and Miller 1954, MacArthur and MacArthur 1961, MacArthur et al. 1966, Cody 1968, Karr 1971, Karr and Roth 1971, Terborgh 1977, Strong and Levin 1979, Southwood 1979). Many studies have correlated increased spider richness or abundance with increased structural complexity (Hatley and MacMahon 1980, Rypstra 1986, and Gunnarsson 1988). Web-building spiders, in particular, rely heavily on the presence of physical structures to support and anchor their webs (Wise 1993); thus it is no surprise that structural attributes of the vegetation have a positive impact on the composition of spider communities (Greenstone 1984, Gillespie 1987). It is possible that increases in structural complexity of vegetation along the land-water margin might influence canopy spider abundance, biomass or diversity.

In addition to the structural importance of live vegetation, dead and decaying plant material has also been the focus of many studies concerned with measuring the impact of structure on ground-dwelling spider communities (Uetz 1991). Increased ground cover, for instance, could provide more sites for web building or increased hiding places from larger predators. Numerous authors have found that ground-dwelling spider abundance or richness is impacted by type, presence or diversity of litter on the forest floor (Jocque 1973, Uetz and Denterlein 1979, Uetz 1979, Bultman and Uetz 1984). Therefore, one might expect that differences in litter between riparian and upland habitats might influence spider abundance or richness.

Differences in standing stock biomass or productivity of terrestrial vegetation along the stream edge could also be an important factor in influencing the abundance and diversity of spiders. It is possible that increased plant productivity along the stream edge could provide increased cover for spiders from extreme temperatures or predation, thereby increasing spider abundance or biomass along the stream edge.

Other factors that might be important in determining terrestrial invertebrate predator distributions along the stream-to-upland gradient

It is possible that changes in terrestrial prey availability at the land-water margin could influence spider abundance or biomass in the riparian zone. Since orb-web weaving spiders will relocate their webs to areas where more prey is available (Gillespie 1987, Kensuke and Ushimaru 1999), if terrestrial prey availability increases in the riparian zone, one would expect to find a correlation between terrestrial prey and orb-web weaving spiders. Similarly, ground-dwelling spider abundance or biomass could be influenced by terrestrial prey availability in the riparian zone. Johnson (1995), for example, found that spider numbers were correlated with abundance of the most common insects in canopies of *Spartina pectinata* (Poaceae) wetlands. Since some species of hunting spiders increase their foraging activity when prey is limited (Walker et al. 1999), a negative correlation between hunting spiders and terrestrial prey might also be expected.

Predation pressure is another factor that might influence the distribution of spiders along the stream-to-upland gradient. Previous studies have found that web-weaving spiders occupying narrow stretches of riparian habitat where prey is abundant, display behavioral characteristics that are less aggressive toward prey and more fearful of bird predation than their upland counterparts (Riechert and Hall 2000).

It is also possible that differences in physical factors along the stream bank are influencing the distribution of spiders. Abiotic factors such as temperature, rainfall, light, soil moisture or nutrient availability could also be controlling the distribution of spiders along stream-to-upland gradients. Henschel et al. (1996) found no differences in microclimate between upland and edge habitats in his study of macroarthropod distributions along the banks of the Main River in Germany. A controlled enclosure experiment also found no significant relationship between invertebrate predators and changes in temperature or moisture with distance to artificial edge (Ferguson 2000).

The mechanistic function of edges themselves, which cause active foragers to move linearly along corridors in search of food, could also be an important determinant of spider densities at the aquatic-terrestrial margin (Oehler and Litvaitis 1996, Fagan et al. 1999). This seems less likely because most spiders can cross small headwater streams using drag lines or walking.

Objectives of the Research

The objectives of the research that follows is threefold. First, I examine the spatial distribution of spiders (Araneae) along a gradient from stream to upland habitats in eight watersheds located in different biogeographic regions which differ greatly in attributes likely to influence the spatial distribution of spiders (Figure 1.1). I hypothesize that where aquatic insect emergence is high and riparian vegetation differs greatly in structure from upland vegetation (e.g., desert, tall-grass prairie and arctic sites) spiders will be concentrated along the stream bank (Figure 1.2). In forested watersheds, where only a small proportion of the instream insect biomass emerges and no distinct riparian zone exists, spiders will be evenly distributed along the stream to upland gradient. In Chapters 2 and 3, I examine site specific trends in the distribution of terrestrial invertebrate predators along the stream-to-upland gradient. In Chapter 2, I examine how spider (Araneae), harvestmen (Opiliones) and predatory beetle (Coleoptera) abundance and biomass change along a gradient from stream edge to upland habitats in an arctic watershed, and in Chapter 3, I determine the differences in spider biomass, abundance and diversity along a gradient from stream to upland in a desert watershed. In Chapter 4, I compare differences in ground-dwelling and canopy spider abundance, biomass and richness between riparian and upland habitats in eight sites located in different biogeographic regions.

The second objective of this research was to determine what factors might be important in influencing the spatial distribution of spiders along the stream-to-upland gradient. In Chapter 2, I determine if patterns in arctic spider distributions might be related to aquatic or terrestrial prey distributions or to patterns in vegetation along the stream-to-upland transect. In Chapter 4, I relate patterns in spider biomass, abundance and richness to differences in environmental variables such as terrestrial and aquatic insect biomass, structural complexity of vegetation and temperature and rainfall between the eight sites. I calculate an energy budget for ground-dwelling spiders to determine if emerging aquatic insects could be subsidizing spider communities in any of the eight riparian zones studied.

The third objective was to determine whether spiders are feeding directly on aquatic insects based on studies of natural abundance of ^{13}C and ^{15}N isotopes and eight ^{15}N tracer additions. Natural abundance values of ^{13}C and ^{15}N were used to determine the most probable food sources for spiders in arctic and desert sites. Because natural δ^{15}N values of aquatic prey emerging from forested headwater streams could not be distinguished from terrestrial prey in these watersheds, ^{15}N tracer additions were used to determine if terrestrial predators are feeding directly on aquatic insects at those sites. By increasing the ^{15}N label of prey in the aquatic habitat, while maintaining background ^{15}N concentrations of terrestrial prey, I was able to quantify the flow of nitrogen from aquatic to terrestrial food webs via emerging aquatic insects. Mixing models were used to quantify the proportion of nitrogen incorporated into spider biomass from aquatic insects in the eight different biogeographic regions. I hypothesize that the proportion of N that riparian spiders obtain from emerging insects will vary across biogeographic regions, depending on emergence biomass and level of structural complexity in the riparian zone. Chapters 2 and 3 report specific results from the arctic and desert sites and Chapter 5 compares the ^{15}N tracer results from the eight watersheds.

The fourth objective of this dissertation was to determine the distance aquatic subsidies travel into the upland. In order to accomplish this, I calculated % N that spiders obtain from aquatic insect subsidies along the 50 m stream-to-upland transects. Chapter 3 contains a detailed analysis of % N from aquatic subsidies incorporated into spider biomass in riparian versus upland habitats in the desert. Chapter 5 contains a cross-site comparison of %N found in riparian versus upland spiders along the 50 m stream-to-upland transects.

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Figure 1.1 Map showing location of eight sites where sampling was conducted.

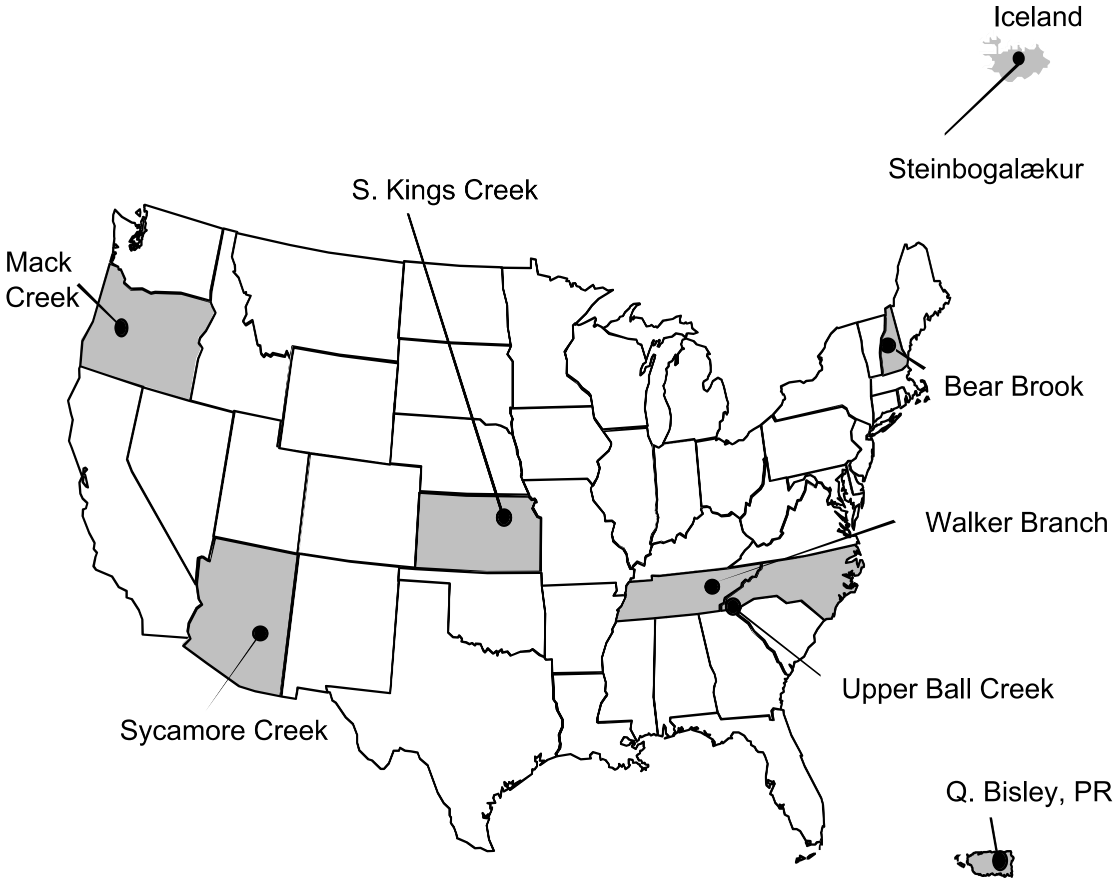
Iceland
Steinbogalækur
S. Kings Creek
Mack
Creek
Bear Brook
Walker Branch
Upper Ball Creek
Sycamore Creek
Q. Bisley, PR

Figure 1.2 Conceptual classification of the eight riparian zones.

Structural Complexity of Terrestrial Vegetation

Aquatic Emergence Biomass	Higher in the riparian zone	Similar in riparian and upland habitats
High	Highest Spider Biomass *Sycamore Creek, AZ* *Steinbogalaekur River, IS*	Intermediate Spider Biomass *Mack Creek, OR* *Walker Branch, TN*
Low	Intermediate Spider Biomass *South Kings Creek, KS* *Upper Ball Creek, NC*	Lowest Spider Biomass *Bear Brook, NH* *Q. Bisley, PR*

CHAPTER 2

LINKING COMMUNITIES ACROSS ECOSYSTEM BOUNDARIES: THE INFLUENCE OF AQUATIC SUBSIDIES ON TERRESTRIAL PREDATORS IN THE ARCTIC[1]

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[1] Sanzone, D. M., J. L. Tank, J. L. Meyer, H. Óskarsson and Á. Einarsson. To be submitted to *Oikos*.

Abstract. In this study, we document the transfer of nutrients and organisms from aquatic to terrestrial habitats and the effect of this transfer on recipient terrestrial predator assemblages. We determine how the biomass, abundance and diversity of arthropod predators, prey and vegetation change along a 75m gradient perpendicular to the stream bank, using timed sweep net samples and vegetation transects. Using both natural abundance ^{13}C and ^{15}N values and a ^{15}N tracer addition, we document the flow of nitrogen from aquatic to terrestrial food webs via emerging aquatic insects in an arctic watershed in Northern Iceland. Stable isotopic ^{13}C and ^{15}N data are used to determine feeding relationships among different trophic levels. A ^{15}N tracer addition experiment enabled us to trace the flow of ^{15}N from the stream into terrestrial plants, insects, spiders and harvestmen. To accomplish this, we added ^{15}N labeled NH_4Cl into Steinbogalækur, a first order arctic stream, for 25 days. An isotopic mixing model was used to calculate proportion of ^{15}N from emerging aquatic insects incorporated into terrestrial predator biomass. Spiders, the most abundant and diverse predator, were concentrated at the stream bank on days when average temperatures exceeded 14°C. Spider diversity was also higher at the stream bank with 12 species found exclusively along the stream edge. *Mitopus morio* (Opiliones) and predatory beetles (Carabidae and Staphylinidae) were also found in greater abundance at the stream edge. Natural ^{13}C and ^{15}N isotope values and the ^{15}N tracer experiment demonstrated that terrestrial predators are feeding on both aquatic and terrestrial resources, and that emerging aquatic insects are providing a nitrogen subsidy (4-28%) to terrestrial invertebrate predators.

Key words: aquatic insects, Araneae, Arctic heathland, Chironomidae, Coleoptera, Diptera, emergence, Iceland, Lake Myvatn, Opiliones, predators, riparian zone, Simuliidae, spiders, streams.

INTRODUCTION

The movement of nutrients, energy and individuals across spatially heterogeneous landscapes and their effect on recipient populations is one of the most common, yet poorly understood phenomena in ecological systems. Effects of these across-habitat influences can often exceed internal factors. For example, prey or energy subsidies from one system may enhance predator abundance in an adjacent system, beyond what even local resources can support (Polis and Hurd 1996, Polis et al. 1997). Many studies have documented the energetic link between aquatic and terrestrial systems; however most studies have focused on the unidirectional flow of energy, nutrients and organisms from terrestrial watersheds to adjacent aquatic habitats (Goulding 1980, Wallace et al. 1997). For instance, the contribution of terrestrial invertebrates to aquatic foodwebs has been well documented (Cloe and Garman 1996, Edwards and Hurn 1996, Wipfli 1997, Nakano et al. 1999).

Only recently ecologists have begun to quantify the translocation of organisms, nutrients and energy in the opposite direction, from aquatic systems to surrounding terrestrial habitats (Hilderbrand et al. 1999, Stapp et al. 1999, Anderson and Polis 1999). For instance, adult aquatic insect emergence from streams may be an important factor regulating terrestrial predator densities. This may be especially true in watersheds where aquatic emergence production exceeds terrestrial insect production by several orders of magnitude (Jackson and Fisher 1986). In spite of the potential importance of aquatic insects to terrestrial foodwebs, few data have been collected on the export and movement of aquatic insects emerging from stream habitats (Jackson and Fisher 1986), and the importance of those insects to terrestrial predators (Gillespie 1987, Orians and Wittenberger 1991, Rainey et al. 1992, Gray 1993, Anderson and Polis 1998). It has been hypothesized that this type of ‘trophic subsidy’ from adjacent habitats may constitute a significant portion of the terrestrial energy budget, which would support higher densities of terrestrial predators (Polis et al. 1995, Polis and Hurd 1996).

This counter-flow has, in part, been neglected because of the difficulty in quantifying not only the movement of nutrients and organisms from aquatic to terrestrial systems (Hershey et al. 1993), but also its effect on the recipient terrestrial foodweb (Polis and Hurd 1996, Stapp et al. 1999). Natural abundance stable isotope studies (Peterson and Fry 1987, Junger and Planas 1994, Fry et al. 1995, Doucett et al. 1996) and stable isotopic tracer experiments developed over the last decade (Peterson et al. 1993, 1997, Hall 1998) have been used to determine trophic relationships and identify food web linkages within either aquatic or terrestrial systems, and so could be used to trace trophic transfer between these two systems.

The ^{15}N tracer addition approach involves adding enough ^{15}N (NH_4 or NO_3) to one ecosystem to increase the ^{15}N: ^{14}N ratio, while at the same time not increasing overall N concentrations. This is important since an increase in overall N would impact nitrogen dynamics, and primary and secondary production, hence affecting trophic dynamics and foodweb relationships. The flow of this isotopically enriched energy can then be traced from its source into the recipient habitat. Because the aquatic habitat is ‘spiked’ with ^{15}N and the terrestrial habitat remains at background levels, transfer of the labeled N can be traced from its aquatic source into the adjacent terrestrial foodweb.

In this study, we document the effects of in-stream insect subsidies on the spatial distribution and foodweb dynamics of terrestrial predators in the arctic. First, we determine how the biomass, abundance and diversity of arthropod predators (aerial-web and wandering spiders, opiliones and predatory beetles) change along a gradient from stream edge to a distance of 75m by pitfall trapping and sweep net sampling. In addition, we measure changes in temperature, terrestrial prey abundance and biomass, structural complexity and diversity of the vegetation, and habitat heterogeneity to determine if there are any indirect effects of stream subsidies on the terrestrial community. This gradient study enabled us to determine if stream subsidies are influencing the spatial distribution of arthropod predators in the landscape.

Using both natural abundance stable isotope values and an experimental ^{15}N tracer addition, we document the flow of nitrogen from aquatic to terrestrial foodwebs via emerging aquatic insects. We determine the proportion of nitrogen that invertebrate predators obtain from emerging insects in an arctic watershed in Northern Iceland. The natural isotope abundance approach has been used to determine the importance of marine subsidies to island communities in the Gulf of California (Polis and Hurd 1996, Anderson and Polis 1998), and the ^{15}N tracer approach has been used successfully to quantify out of stream export and flight distance of emerging aquatic insects in the Kuparuk River (Hershey et al. 1993), but no one has yet documented the impact of this aquatic subsidy on terrestrial foodwebs using a tracer approach. By determining the tracer ^{15}N found in terrestrial predators and comparing that to the ^{15}N found in aquatic insect populations emerging nearby, we estimate the proportion of N that invertebrate predators (aerial-web and wandering spiders, opiliones and predatory beetles) obtain from emerging adult aquatic insects, compared to that which comes from terrestrially derived sources.

METHODS

Study site

This experiment was conducted just after snowmelt in June- July 1999 along a 500 meter reach of Steinbogalækur, an arctic stream located in the Lake Myvatn Region of Northern Iceland ($65^{o}35'N$, $17^{o}00'W$). Steinbogalækur is a spring-fed headwater stream that originates approximately 1.7 km upstream from our study site and drains into the larger River Laxá 400m downstream (Figure 2.1). Laxá, which also drains the spring fed Lake Myvatn and River Kráká just upstream from the confluence with Steinbogalækur, runs 58 km north to the Arctic Ocean (watershed area= 2150 km^{2}). Average air temperatures in this region range from 10-$14^{o}C$ in summer (June- August) and 0-$5^{o}C$ in winter (September– May).

Average stream discharge in Steinbogalækur during the experiment was 156 L/s (Table 2.1). The stream bottom in the experimental reach consisted mainly of bedrock, gravel/cobble and sand, with 88% riffle habitat and 12% pool habitat. This stream has relatively low N and P concentrations and is predominantly autotrophic (Table 2.1).

Terrestrial vegetation in our experimental area was predominantly arctic heathland, including an upper canopy layer of shrubs: dwarf birch (*Betula nana*) and several species of willows (*Salix lanata, S. phylicifolia and S. callicarpaea*), which averaged 15 cm in height. A second layer of vegetation was dominated by bog bilberry (*Vaccinium uliginosum*) and crowberry (*Empetrum nigrum*). The herb layer was diverse, including at least 25 species of herbaceous vegetation, 9 species of grasses, rushes and sedges and 3 species of *Equisetum* (Table 2.2). The ground layer consisted of dead herbaceous material, and several species of moss and lichens.

Terrestrial predator and prey sampling

To determine changes in biomass, abundance and assemblage structure of terrestrial invertebrate predators and prey, five 75m transects were established, running perpendicular to the stream bank. Spiders, harvestmen, predatory beetles and terrestrial prey were sampled along each of the five transects directly adjacent to the stream bank (at 0m), and at 10, 25, 50 and 75m away from the stream edge (n=25). Spiders and arthropod prey (terrestrial and aquatic) were collected from riparian vegetation and the air using timed (5 min) sweep net samples (Coddington et al. 1991).

Arthropods inhabiting the lower herbaceous vegetation and litter layer were sampled using 48-hour pitfall traps. Pitfall traps consisted of a small inner plastic sampling cup and funnel, enclosed by an outer cup (9.5 cm diameter) which was dug into the ground. The top of the cup was flush with the soil/litter surface. Cups were filled with 70% ethanol and left open for 48 hour periods on five different sampling dates over approximately five weeks (n=25). Insects, spiders and harvestmen were returned to the lab, sorted and placed in 70% ethanol until adult spiders and harvestmen could be identified to species, immature spiders and predatory beetles identified to family, and terrestrial prey identified to order. Once identified, all samples were dried at 60^oC for approximately 48 hours and weighed for biomass.

Differences between mean abundance of spiders, harvestmen, predatory beetles and terrestrial prey along the transect were analyzed using one-way analysis of variance (ANOVA) (JMP, SAS 1999). Predator and prey biomass along the transect were analyzed using a one-way analysis of covariance (ANCOVA), with temperature as the covariate to account for extreme fluctuations in temperatures from one day to the next. We applied a ln(x+1) transformation (Sokal and Rohlf 1981) when data were not normally distributed (Shapiro and Wilk 1965).

Spider diversity is reported as species richness and as Fisher's log series α which has good discriminant ability and is robust to sample size (Fisher et al. 1943, Magurran 1988). To compare similarity of species composition between transects along the gradient, we calculated a coefficient of community similarity for all possible pairwise combinations (Sorenson 1948). We then performed a cluster analysis using these proportions with arithmetic averaging to determine similarities among points along the transect.

Abiotic and biotic factors affecting terrestrial arthropods

We measured terrestrial vegetation using 1 m^2 plots along the transects from the stream bank to 75m (n=15). In each 1 m^2 plot we measured plant species richness, average height of terrestrial vegetation (AVH), number of vertical points transected ('touches'), total foliage volume (TFV), and foliage height diversity (FHD). Number of 'touches' and FHD were calculated using a 1 m rod in each of the m^2 plots. To calculate vertical points transected (touches) we counted the number of times vegetation touched the 1 m high vertical rod in each of the transects (n=6). FHD was determined by calculating the total cm of rod intercepted by vegetation within three horizontal sublayers: canopy layer (15-50 cm), shrub layer (8-15 cm), and herb, grass, rush and sedge layer (0-8cm) (MacArthur and Horn 1969, Dobkin et al. 1998). TFV was calculated by summing the total foliage volume in those three horizontal layers. Total foliage volume of each layer (TFV_{layer}) was estimated by quantifying the proportion of each layer occupied by leaves, twigs, stems or branches, which was then multiplied by the height of that layer (Estades 1997). Percent ground cover (PGC) was measured by placing ground cover collected from m^2 plots into micro-habitat classes, then calculating structural complexity of ground cover (Southwood et al. 1979).

Linear regression analysis and a one-way analysis of variance (ANOVA) were used to compare spider species richness with measures of structural complexity (average number of vertical touches, FHD, TFV and GCD), and to compare spider abundance and biomass with surrogate measures of terrestrial productivity (AVH and TFV). In order to determine habitat heterogeneity along the transect, linear regression analysis was used to compare the coefficient of variation of FHD, TFV, AVH and TFV to spider abundance, biomass and diversity. We applied an arcsin transformation to % ground cover data to normalize it for parametric analysis (Sokal and Rohlf 1981).

Minimum/ maximum temperature gauges that were set up at the stream edge and at 75 meters from the bank were checked every 48 hours in conjunction with pitfall collections. Onset Hobo temperature gauges were also placed along the stream bank to monitor daily fluctuations in temperature at more frequent intervals (every 5 minutes). We determined if temperature varied from stream edge to upland by performing paired t-tests (JMP,SAS 1999).

Aquatic insect sampling

Quantitative estimates of aquatic insect emergence were made using 0.25 m^2 emergence traps (n=9). Traps were constructed from PVC pipes and covered with window screening (0.3 mm mesh). The base of the traps were anchored into the stream substrate to prevent insect drift from entering the traps. The top of the traps contained an inverted funnel and glass jar. This design, while preventing drift, allowed water to flow through the traps at a velocity similar to that of the surrounding water. Two traps were placed upstream from the experimental ^{15}N release, at minus 20m and minus 40m, and seven traps were placed downstream at 20, 40, 69, 85, 99, 118, 145 m. Emergence traps were sampled using an aspirator and forceps on 5 days after traps were allowed to collect emerging insects for 48 hours. All insects were taken to the lab, identified to family (Diptera) or genus (Trichoptera and Plecoptera), dried at 60^o for 48 hours, and weighed to estimate biomass (mg m^{-2} d^{-1}).

Adult aquatic insects flying in the area were sampled using window traps (Jónsson et al. 1986) and sweep nets of the vegetation and air, on Day 23 and Day 25 after the start of the ^{15}N tracer release. Window traps were placed along the stream edge 20 meters upstream from the tracer addition site and at 15 and 35 meters below the release site. Timed sweep net samples (5 min) were collected along the bank at 20, 50 and 100 m upstream from the ^{15}N release site and 20, 40, 60, 80, 100, 200 and 300 m downstream from the release site. Sweep net samples were also collected along the five transects out to 75m (n=20), in order to determine changes in abundance and biomass of aquatic insects from stream bank to upland habitats.

Biomass estimates (DM/ m^2) of all aquatic insect larvae from Steinbogalækur were determined using a small 400cm^2 Surber sampler at randomly chosen sites along the experimental reach. Immature insects were returned to the lab, identified to subfamily or genus, dried at 60^{o}C for 48 hours, and weighed to estimate biomass. We estimated total % of instream insects emerging by dividing total biomass of emerged insects (mgDM/m^2) by instream insect biomass (mgDM/m^2).

Stable isotope analysis

We calculated natural abundance stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) and tracer $\delta^{15}N$ values for riparian spiders, opiliones, predatory beetles, terrestrial prey, immature and emerged adult aquatic insects, and terrestrial and aquatic primary producers. All $\delta^{15}N$ and $\delta^{13}C$ values were calculated as:

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

where, R_{sample}= ^{15}N:^{14}N or ^{13}C:^{12}C ratio in the sample and $R_{standard}$ = $^{15}N/^{14}N$ ratio in the atmosphere (0.003663) for $\delta^{15}N$, or $^{13}C/^{12}C$ ratio in Pee Dee Belemnite for $\delta^{13}C$ (Peterson and Fry 1987). Values are expressed as parts per thousand ($^{o}/_{oo}$). All samples were analyzed for ^{15}N by high temperature direct combustion and continuous flow analysis using a Finnigan Delta C Stable Isotope Ratio Mass Spectrometer at the Institute of Ecology Analytical Chemistry Laboratory, University of Georgia (Athens, GA), or using an automated sample combustion isotope ratio mass spectrometer at the Environmental Isotope Lab, University of Waterloo (Waterloo, Ontario).

Food web characterization using natural abundance stable isotope

We collected filamentous green algae, epilithon, bryophytes, fine benthic organic matter (FBOM) and larval aquatic insects 10m upstream from the experimental ^{15}N release in Steinbogalækur to obtain natural abundance ^{13}C and ^{15}N values. Epilithon was scraped from the surfaces of 3-4 randomly chosen rocks using a stiff brush; the slurry was then washed into a small volume of water. Filamentous green algae and bryophytes were removed from rocks by hand from 3-4 locations. Surface FBOM was collected from areas of sediment accumulation using a suction device and metal corer. Larval aquatic insects were sampled using a kick net or by hand collecting organisms from rocks. Green algae, epilithon, fine benthic organic matter (FBOM) and aquatic insects were also collected from Laxá in a similar manner, just downstream from where Steinbogalækur joins it, to determine natural abundance ^{13}C and ^{15}N values.

Large vertebrate predators such as fish were absent from Steinbogalækur, except for occasional waterfowl seen near the stream. In July 2000, we sampled the breast muscles of one species of top predator, *Bucephala islandica* (Barrow's goldeneye) that commonly feeds in Laxá (and occasionally Steinbogalækur) to determine natural abundance ^{13}C and ^{15}N values.

Spiders, harvestmen, predatory beetles and terrestrial prey were sampled 20, 50 and 100 meters upstream from the release point using pitfall traps and timed beat net samples to estimate natural abundance $\delta^{13}C$ and $\delta^{15}N$ values. Spiders and arthropod prey were collected from the ground using pitfall traps and from riparian vegetation using sweep nets. Two woody species, *Betula nana* (dwarf birch) and *Salix phylicifolia* (tea-leaved willow), two herb species, *Bistorta vivipara* (alpine bistort) and *Alchemilla vulgaris* (common lady's mantle), one grass species, *Alopecurus aequalis*, orange foxtail, and common terrestrial moss and liverworts found commonly along the stream bank were analyzed for naturally occurring ^{13}C and ^{15}N. All samples from Steinbogalækur, Laxá and the surrounding watershed were dried at $60^{o}C$ for 48 hours, then ground for natural abundance stable isotope analysis.

We calculated the % of adult aquatic insects coming from each of the two sources: Steinbogalækur and Laxá using the following natural abundance ^{13}C isotopic mixing model:

$$[(P_{LX})(\delta^{13}C_{LX}) + (1-P_{LX})(\delta^{13}C_{ST})] * 100 = \delta^{13}C_{FL} \qquad (2)$$

where, P_{LX} = proportion of flying adult aquatic insect C derived from Laxá; $\delta^{13}C_{FL}$= pooled $\delta^{13}C$ signal of flying adult aquatic insects; $\delta^{13}C_{ST}$ and $\delta^{13}C_{LX}$ = $\delta^{13}C$ of larval aquatic insects from Steinbogalækur and Laxá respectively. To determine the % of flying adult aquatic insects derived from the two sources we solved the above equation for simuliids and chironomids using average $\delta^{13}C$ values from immature and adult insects. We report % of adult aquatic insects coming from each of the two sources for both simuliids and chironomids.

Tracer ^{15}N release and sampling

We continuously dripped 10% enriched ^{15}N-NH_4Cl into Steinbogalækur from June 5- 30 1999 to raise the ^{15}N-NH_4Cl pool to a del value of 500 $^{o}/_{oo}$, while maintaining background concentrations of NH_4 . The solute was released from a 20L Nalgene carboy connected to a peristaltic pump which was run by a deep cycle marine battery. The total amount of ^{15}N added to the stream over the 25 day period of the release (3.166g^{15}N- NH_4Cl) was based on stream discharge and background ammonium concentrations (Table 2.1). For more detail of methods see Mulholland et al. 2000a, Tank et al. 2000.

For tracer ^{15}N analysis, larval aquatic insects were sampled from 7 stations below the ^{15}N dripper (25, 50, 75, 110, 160, 233 and 337m) and one site upstream from the addition site (minus 10m) using kick nets and hand collecting. Dominant aquatic insects collected on Day 25 of the experiment from 4-5 locations at each sampling station were analyzed for ^{15}N:^{14}N ratios. Emerging aquatic insects were sampled from Steinbogalækur 20 and 40m upstream, and at 20, 40, 69, 85, 99, 118, 145 m downstream from the release point. Adult aquatic insects flying in the area were sampled using window traps (Jónsson et al. 1986) and sweep nets of the vegetation and air on Day 23 and Day 25 after the start of the release. Because window traps were ineffective in capturing many groups of insects, we used sweep net samples to analyze ^{15}N in emerged aquatic insects. Sweep net samples were collected along the bank at 20, 50 and 100 m upstream from the dripper and 20, 40, 60, 80, 100, 200 and 300 m downstream from the dripper.

Spiders, harvestmen, predatory beetles and terrestrial prey were sampled along each of the five transects directly adjacent to the stream bank (at 0m), and at 10, 25, 50 and 75m from the stream edge (n=25). Additional samples for ^{15}N analysis were taken along the stream bank at 20, 50 and 100 meters upstream from the release point, at 20 meter intervals from 10 to 100 meters downstream, and at 50 meter intervals from 100 to 300 m downstream from the dripper. Spiders and arthropod prey used for ^{15}N analysis were collected from riparian vegetation using sweep net samples at 20, 50 and 100 m upstream from the dripper and 20, 40, 60, 80, 100, 200 and 300 m downstream from the dripper. Flying insects (aquatic and terrestrial) were captured on the fly using timed aerial sweep net samples. We analyzed four species of wolf spiders *(Arctosa alpigena, Pardosa hyperborea, P. palustris and P. sphagnicola*), a composite sample of several species from the family Linyphiidae which because of their small size had to be combined, one common species of harvestmen *Mitopus morio* (Phalangiidae, Opiliones), and two families of predatory beetles (Carabidae and Staphylinidae).

Two terrestrial plant species, *Betula nana* (dwarf birch) and *Salix phylicifolia* (tea-leaved willow), two herb species, *Bistorta vivipara* (alpine bistort) and *Alchemilla vulgaris* (common lady's mantle), and one grass species, *Alopecurus aequalis*, orange foxtail, found commonly along the stream bank were analyzed for ^{15}N enrichment. One terrestrial moss and one lichen were also analyzed for ^{15}N incorporation. Once identified, all enriched samples were dried, ground for ^{15}N analysis, and a composite sample of several individuals of the same species from the same location were analyzed for ^{15}N (1-2 mg DM).

Isotopic mixing model for ^{15}N tracer addition

Background-corrected δ^{15}N values were used to determine proportion of nitrogen that riparian predators obtain from aquatic prey versus that which comes from terrestrial prey. Since spiders are polyphagous generalist predators that move according to prey availability (Gillespie 1987, Wise 1993), we can assume that proportion of prey assimilated into tissue is a function of microhabitat choice rather than selective feeding. Because spiders are feeding on both unlabeled terrestrial prey and labeled aquatic prey, we can determine the relative proportion of spider N obtained from emerged adult aquatic insects if we measure the δ^{15}N of spiders and their two sources of prey. Preliminary data indicated that background ^{15}N levels and C:N ratios were similar among all prey species inhabiting similar trophic positions; hence terrestrial prey should have an isotopic signal considerably lower than enriched stream insects. After calculating biomass-weighted average δ^{15}N values for 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 a two-source isotopic mixing model. The simplest version of this model assumes two discrete populations, labeled aquatic insects and unlabeled terrestrial insects at point *x*, but considers no upstream or downstream movement of unlabeled aquatic insects. This first model therefore may provide an underestimate of stream-derived N in spiders because aquatic insects fed upon by spiders could have come from outside the experimental reach, where the ^{15}N label is weaker.

We calculated spider N derived from ^{15}N enriched aquatic insects using the following equation (modified from Junger and Planas 1994 and Doucett et al. 1996):

$$(P_{aqua})\,(\delta^{15}N_{aqua}{}^{*})+(1-P_{aqua})\,(\delta^{15}N_{terr}{}^{*})=\delta^{15}{}_{Npred}{}^{*} \tag{3}$$

where, P_{aqua} = proportion of spider N derived from aquatic insects; $\delta^{15}N_{pred}{}^{*}$ = δ^{15}N of spiders; $\delta^{15}N_{terr}{}^{*}$ and $\delta^{15}N_{aqua}{}^{*}$ = δ^{15}N of terrestrial and emerging aquatic insects respectively. The superscript * indicates numbers are background corrected.

Equation (3) can be solved for P_{aqua} to determine the proportion of labeled adult aquatic insects incorporated into spider biomass.

To determine the % of spider N derived from labeled aquatic insects we used an average biomass- weighted, background-corrected δ^{15}N value for all labeled aquatic prey emerging at point *x*. Percent of spider δ^{15}N derived from emerging aquatic insects was calculated from spider δ^{15}N values for individuals collected at point x and composited as described in the previous section. We report mean and standard error for each species.

To account for dilution of $\delta^{15}N$ signals from unlabeled aquatic insects flying into the reach, we used the same isotopic mixing model with values for emerged aquatic insects ($\delta^{15}N_{aqua}*$) that were captured at each sampling station using sweep nets. The prey captured in sweep nets were split into two groups, aquatic and terrestrial. We then sorted the aquatic sub-sample and separated out midges, blackflies, stoneflies, caddisflies and miscellaneous aquatic Diptera to be analyzed for $\delta^{15}N$. The terrestrial subsample was sorted to order and consisted mainly of individuals from the following orders: Homoptera, Diptera, Lepidoptera, Hymenoptera, Coleoptera and Acari (Trombidiidae, Prostigmata). Because these samples are composite samples of several individuals, the $\delta^{15}N$ values reported represent average $\delta^{15}N$ values of each group at each sampling station. We then calculated biomass-weighted $\delta^{15}N$ values for all aquatic insects combined and all terrestrial insects combined using arithmetic averaging. These values assume that the proportion of insects in the air and on the vegetation is the same as that available to an individual predator at a given location along the stream reach. Again we report average $\delta^{15}N$ values and standard error for each species of predator. To estimate the total N subsidy to the riparian predator assemblage we multiplied the relative biomass of each species by their average $\delta^{15}N$ value and then summed those numbers.

RESULTS

Concentration of predators at the land- water margin

Spiders were the most abundant and diverse invertebrate predator. Ground-dwelling spider abundance was highest at the stream edge on warm sunny days, when average temperatures were greater than 14^{o}C (n=10, p< 0.0001) and decreased by more than half 10 to 75m from the stream bank (Figure 2.2a). While a similar pattern was observed on cold, wet days (average temperatures < 8^{o}C), the trend was not significant (n=15, p=0.174). Spider biomass was also highest on warm days at the stream bank and decreased only 10m from the stream edge (n=25, p=0.048) (Table 2.3). Ground-dwelling spiders from the family Lycosidae (wolf spiders) were the most abundant group along the stream bank, followed by members of the family Linyphiidae (Erigoninae). In fact, on warm days *P. palustris and P. hyperborea* were captured 4 times more and *P. sphagnicola* was captured 24 times more frequently at the stream bank than at any other place along the transect (n=10, p=0.0014, p=0.0002 and p=0.0004 respectively). Because of their large size and greater abundance relative to other families, wolf spiders accounted for the greatest differences in biomass (88% of total biomass) along the transect. Differences in temperature extremes between the stream bank and upland habitat could not explain differences in spider abundance and biomass because although air temperatures varied a great deal from day to day (range = -4-30^{o}C), we found no difference in minimum or maximum temperatures between stream bank and upland habitats (n=5, p= 0.9662).

Another common arthropod predator in this system, *Mitopus morio* (Fabricius, 1779) (Phalangiidae, Opiliones) was also relatively more abundant at the stream edge than in upland areas (n=25, p=0.0003) (Figure 2.2b). *Mitopus morio* biomass was also higher at the stream edge (n=25, p=0.03), then dropped off within 10m of the stream bank (Table 2.3). Common predatory beetles in this region of Northern Iceland (Carabidae and Staphylinidae), had higher biomass ($n=25$, $p=0.0002$) (Table 2.3), and were more abundant at the stream edge than away from the stream (Figure 2.2c), although this trend was not significant on warm days (average temperatures > 14^{o}C).

We found a total of 36 spider species from 7 families at the study site (Table 2.4). Linyphiidae were the most diverse family with 25 species, followed by Lycosidae (4 species) and Gnaphosidae (3 species). Spider richness and diversity (Fisher's log series α) was highest at the stream edge with almost twice as many species found along the stream (Table 2.5). The distribution of spider species along the gradient from stream edge to upland suggests that many rare spider species are concentrated near the stream edge (Table 2.4). In fact, twelve species were found exclusively at the stream edge, and four species were collected only within 25m of the stream bank. The dendrogram (Figure 2.3) shows a major break in similarity (56% difference) between spider species composition at the stream edge (0m), versus 'transitional' (10-25m) and upland (50- 75m) areas.

Factors influencing abundance, biomass and diversity of terrestrial predators

At the beginning of this experiment, we hypothesized that the influence of stream subsidies on the spatial distribution of terrestrial predators would most likely be related to three factors: aquatic secondary production (Jackson and Fisher 1986), structural complexity of riparian vegetation (MacArthur 1964), and an increased diversity of microsites along the stream edge (Gregory et al. 1991). In this study, we found that spider biomass, abundance and diversity was correlated with the timing of aquatic emergence and two surrogate measures of riparian plant productivity. However, no relationship was found between spiders and structural complexity or habitat heterogeneity of riparian vegetation.

Average height of terrestrial vegetation (AHV) and total foliage volume (TFV), which were highest along the stream bank, were correlated with spider species richness, abundance and biomass (Figure 2.4 a-c). Percent ground cover (grasses, lichens, mosses and plant and animal detritus) which was significantly higher at the stream bank than away from the stream ($n=3$, $p<0.001$) was also correlated with spider species richness ($n=5$, $r^2=0.833$, $p=0.031$). Spider species richness, however, was not correlated with average number of vertical touches ($n=5$, $r2=0.763$, $p=0.063$) or foliage height diversity ($n=5$, $r=0.372$, $p=0.274$), two measures of structural complexity. Plant species richness was also not correlated with spider species richness ($n=5$, $r^2=0.067$, $p=0.674$). Our coefficient of variation calculations for FHD, TFV and AVH when compared to spider species richness, did not produce significant regressions ($n=5$, $r2=0.048$,0.001, 0.116 respectively) indicating that structural heterogeneity of vegetation was not as important as total biomass.

A second factor which was important in determining differences in the distribution of terrestrial predators along the gradient was aquatic prey availability. Aquatic prey were always more abundant (96%) than terrestrial prey (4%) in sweep net samples ($n=25$, $p=0.0009$) and the number of aquatic insects emerging from Steinbogalækur was almost twice as high (1.97 times higher) on warm days than cold ones (n=15, p= 0.024). Aquatic insects, although less common in pitfall traps (8%) compared to sweep net samples, were also captured more frequently on warm days than cold ones (n=15, p= 0.04). Spider biomass which was also higher along the stream bank on warm days was correlated with aquatic insect emergence (n=25, p<0.0001).

Terrestrial prey were more numerous in pitfall traps on warm days than cold ones (n=5, p= 0.001); however, terrestrial prey abundance was not significantly higher at the stream edge than in the upland areas on warm (n=10, 0.5412) or cold days (n=15, p= 0.058). Terrestrial prey abundance was evenly distributed along the transect from stream bank to upland in sweep net samples (n=5, p= 0.063). Looking more closely at predator-prey interactions, spider abundance was positively correlated with terrestrial prey abundance along the stream bank (Figure 2.5), but not in the upland areas (n=25, r^2= 0.085, p= 0.211), indicating that spiders living near the stream bank may be switching between terrestrial and aquatic prey depending on availability.

Foodweb characterization using ^{15}N and ^{13}C natural abundance

Species diversity and number of trophic levels in the aquatic foodweb in Steinbogalækur is much reduced (compared to temperate zone streams) due to both its latitude and Iceland's location in the middle of the North Atlantic Ocean. During our sampling period, we estimated that 30% of the instream aquatic insect biomass from Steinbogalækur emerged from the stream (209 mg/m^2); the most abundant groups being from the dipteran families Chironomidae (90% of total biomass) and Simuliidae (2% of total biomass). Dominant species of chironomids were from two subfamilies Diamesinae (*Diamesa zernyi* being the most common) and Orthocladiinae (mainly *Orthocladius frigidus* and *O. consobrinus*, *Eukiefferiella minor,* and *Thienemanniella* sp.). One species of Tanytarsini, *Microspectra atrofasciata,* was also found in this stream. Rare chironomid species were not identified to genus due to time constraints. Simuliidae in Steinbogalækur were from two genera *Prosimulium* and *Neosimulium*. Much less abundant was one species of Trichoptera (*Limnephilus* sp., Limnephilidae) and one species of Plecoptera (*Capnia vidua*) which when combined represented 6% of total biomass captured in emergence traps.

The dominant group collected along the stream bank in sweep net samples were blackflies, *Neosimulium* and *Prosimulium* spp. (48% of biomass) and midges from the genera *Diamesa, Orthocladius, Eukiefferiella, Microspectra, Tanytarsus and Thienemanniella* (44% of biomass). Trichopterans and plecopterans accounted for 8% of the aquatic insect biomass collected in sweep net samples.

Natural δ^{13}C and δ^{15}N values of all dominant prey, predators and primary producers were measured from Steinbogalækur, its surrounding riparian zone and the river Laxá (Figure 2.6). Aquatic insect δ^{15}N values from Steinbogalækur were higher than those from the River Laxá (confluence 400 meters downstream). δ^{13}C values of aquatic insects and their in-stream food resources, however, were much lower in Steinbogalækur than in Laxá (and it's source, Lake Myvatn); hence flying individuals from the two sources could be separated

(Figure 2.6). Mixing model results indicate that dominant aquatic insects (blackflies and midges) captured in sweep nets in the Steinbogalækur watershed came from two sources, Steinbogalækur and Laxá. Of the chironomids captured in sweep nets, on average 72% emerged from Laxá (and it's source, Lake Myvatn), with the remaining 28% coming from Steinbogalækur. Of the simuliids captured in sweep nets, on average 60% appear to be coming from Laxá (and Lake Myvatn) and 40% from Steinbogalækur.

Based on natural abundance ^{13}C and ^{15}N values, it appears that wolf spiders, the top invertebrate predators in this watershed, are feeding on both aquatic and terrestrial insects. In fact, because aquatic insects were much more abundant than terrestrial insects (only 4% of total biomass) these large wolf spiders (*Pardosa* and *Arctosa* spp.) may be feeding predominantly on aquatic insects from both Laxá and Steinbogalækur (Figure 2.6). This is in contrast to the top vertebrate predator in this system, Barrow's Goldeneye, which appears to be feeding predominantly on aquatic insects emerging from the River Laxá (Figure 2.6).

^{15}N tracer addition

Because tracer $\delta^{15}N$ values allow us to separate the two pools (aquatic and terrestrial prey) by a larger margin than natural abundance values, they can be used to determine the relative contribution of aquatic subsidies with greater precision. During the 25 day release all primary ^{15}N uptake compartments (green algae, epilithon, bryophytes and FBOM) were labeled above background levels, with labeling of autochthonous food resources peaking between 20 and 50 meters downstream from the release, then decreasing in a downstream direction. Dominant in-stream insects (blackflies and chironomids) were highly labeled by Day 25 and appeared to reach isotopic equilibrium during the release (Tank and Sanzone, unpublished data). Emerged adult aquatic insects captured in emergence traps and larvae/ nymphs from the same location in the stream (+/- 5m) had similar ^{15}N values (n= 14, p= 0.952).

Spiders inhabiting the area along the stream edge were also labeled above background levels, and their labeling tracked that of emerging insects from Steinbogalækur (Figure 2.7). Composite samples of *Mitopus* sp., *Pardosa* spp. and Linyphiidae suggest that these three groups are feeding, at least partially, on labeled Chironomids from Steinbogalækur (Figures 2.7 a-c, note different scales). In contrast, *Arctosa* sp., the largest wolf spiders at this site, appear to be feeding on blackflies emerging from Steinbogalækur (Figure 2.7d, note different scales), as well as insects emerging from the River Laxá, as suggested by natural abundance ^{13}C values (Figure 2.6).

The relative proportion of nitrogen in a spider's diet coming from emerging aquatic insects was determined using the two-source isotopic mixing model (Equation 3). The first model (% emerging) assumes all aquatic insects flying in the air are coming directly from the adjacent stream reach (Table 2.6). Since some emerged aquatic insects will be coming from areas unlabeled with tracer ^{15}N, this assumption results in an underestimate of stream-derived N. The second model (% flying) is a more accurate measure of spider N coming from aquatic resources because it incorporates aquatic insects flying into the experimental reach from further downstream or upstream (Table 2.6). Analyzing the data using this model, the relative contribution of aquatic insect N to spiders increases 4-12 fold.

Harvestmen *(Mitopus morio)* and spiders from the smaller- bodied family Linyphiidae are significantly more labeled than the larger-bodied wolf spiders ($n=15$, $p= 0.0001$). This difference is likely due to the fact that the larger-bodied species (which are 1-2 trophic levels higher) did not reach isotopic equilibrium over the course of the experiment. After calculating biomass- weighted $\delta^{15}N$ averages for the dominant groups (93% of the total predatory biomass), we determined the %N coming from aquatic insects to the entire predator assemblage was approximately 7%. Because insects from the River Laxá (400m downstream from the release) were not enriched with ^{15}N, we have surely underestimated the contribution of aquatic insects to the terrestrial foodweb.

The ^{15}N tracer release began immediately following snowmelt when plants were beginning to leaf out, so we were also able to determine if terrestrial plants directly adjacent to the stream were using stream derived N, thereby incorporating tracer ^{15}N into leaves (Figure 2.8). The two larger shrub species *Betula nana* (dwarf birch), which was found along the entire gradient, and *Salix phylicifolia* (tea-leaved willow) which was restricted to wetter soils along the stream bank were not labeled above background levels. Of the two herb species, *Bistorta vivipara* (alpine bistort) and *Alchemilla vulgaris* (common lady's mantle) that incorporated ^{15}N tracer into leaf tissue, *A. vulgaris* (found only along the stream bank) was more highly labeled than *B.* vivipara which was found throughout the transect. The semi-aquatic riparian grass species, *Alopecurus aequalis* (orange foxtail), and an unidentified moss and liverwort species found commonly along the stream bank were highly labeled with ^{15}N from our tracer experiment (Figure 2.8). Although terrestrial plants were labeled, terrestrial prey (including herbivores) collected along the stream edge were not enriched above background levels with ^{15}N.

DISCUSSION

The distribution of terrestrial arthropod predators along a gradient from stream edge to upland habitats

Because of the inherent complexity created at the land-water interface, riparian zones are thought to contain high densities and numbers of species (Naiman and Decamps 1997). Although there was no obvious transitional gradient in vegetation (i.e., distinct riparian zone) surrounding Steinbogalækur, we found a more diverse and abundant community of terrestrial arthropod predators along the edge of this first order stream. This result is similar to what researchers found along the shores of the Main River (Henschel et al. in press), the River Trent (Greenwood et al. 1995), and the River Ilm (Malt 1995) in Europe, where abundance and diversity of terrestrial arthropod predators were higher along the stream edge than away from the bank.

These more recent studies contrast with what earlier North American studies found (Barnes 1953, Uetz 1976). For example, floodplain areas closer to the stream bank along the Sangamon River in Illinois had fewer individuals and a less diverse assemblage of wandering spiders than upland areas; this reduction in spider abundance and diversity was attributed to factors related to the flooding regime (e.g., compaction, siltation or removal of litter from the forest floor) of these ‘bottomland’ forests (Uetz 1976). This study failed to include the most diverse spider family in North America north of Mexico, the Linyphiidae. In Iceland, the higher spider species richness along the stream bank was due mostly to the presence of rare species from the family Linyphiidae, the richest family in arctic habitats. Draney (1997) also found a higher percentage of rare linyphiids in forested riparian habitats than in five upland forests of the Southeastern coastal plain.

In addition to increased diversity, we also found greater abundance and biomass of spiders, harvestmen and predatory beetles at the land-water interface. This was especially true with larger-bodied wolf spiders from the family Lycosidae which were collected 4-24 times more frequently at the stream edge than at any other place along the transect. Several researchers have hypothesized that edge habitats, in general, contain greater numbers of individuals (Polis and Hurd 1996, Fagan et al. 1999) and larger-bodied organisms (Ferguson 1999). Recent studies concerned with a wide variety of taxonomic groups, in a variety of different habitats have found increasing numbers of individuals inhabiting edge habitats (Kareiva 1987, Ferguson 1999). Our results support earlier findings by demonstrating that all groups of terrestrial arthropod predators inhabiting this arctic watershed were concentrated at the land-water interface, a common feature in a wide array of landscapes. Seven other studies recently conducted along riparian corridors in prairie, desert, tropical, northern deciduous and old-growth conifer forests show similar trends, indicating this pattern is more wide spread than originally thought (Sanzone, unpublished data).

Factors influencing the distribution of terrestrial predators in the landscape

There are three possible pathways by which Steinbogalækur might be influencing terrestrial predators in this arctic watershed. The first, which is a direct trophic subsidy, occurs when terrestrial predators feed directly on aquatic insects (Jackson and Fisher 1986). In this study, we were able to quantify this direct trophic link via emerging aquatic insects using both natural abundance ^{13}C and ^{15}N values and the ^{15}N tracer addition. The second, which is an indirect trophic link, occurs when aquatic subsidies in the form of nutrients or water from root uptake, condensation of evaporated stream water, or in-stream detrital sources increases terrestrial primary productivity or structural complexity of the vegetation near the stream edge, thereby increasing terrestrial prey densities and/ or predator densities. Our results also provide evidence for this indirect trophic link. The third possibility, which is much harder to quantify, has to do with physical forces created along edge habitats. For instance, differences in abiotic factors (such as microclimate variability) along stream edges or increased boundary effects (like the creation of linear corridors or increases in three-dimensional space) may be important determinants of predator behavior at the aquatic-terrestrial margin (Oehler and Litvaitis 1996, Fagan et al. 1999). In this study, we found that a combination of factors occurring along the stream edge were most likely controlling the increased abundance, biomass and diversity of terrestrial arthropod predators in this arctic heathland watershed.

Differences in amount of vegetation along the gradient from stream bank to upland seems to be an important factor in determining abundance and diversity of spiders in this system. Both measures of terrestrial plant productivity (average vertical height and total foliage volume), and structural complexity of the vegetation (foliage height diversity and number of vertical ‘touches’) were significantly higher at the stream edge than away from the stream. In addition, vertical height and total volume of terrestrial vegetation were highly correlated with increases in spider abundance, biomass and richness, which were highest at the stream bank. It is possible that increased plant productivity along the stream edge provides increased cover for terrestrial predators during extreme temperature fluctuations, a greater number of microsites for foraging activites, or additional cover from bird predation. A reciprocal transplant experiment of *Agelenopsis aperta* (Gertsch) conducted in riparian and dry woodland habitats showed that individuals occupying narrow stretches of riparian habitat displayed behavioral characteristics that were less aggressive toward prey and more fearful of bird predation than their ‘dryland’ counterparts (Riechert and Hall 2000).

We found that increased ground cover, which was also characteristic of the stream edge habitat, was correlated with ground-dwelling spider species richness. Linyphiids (Erigoninae) which accounted for most of the differences in diversity, are small ground-dwelling spiders that build small webs (mm-cm in diameter) in litter. Additional ground cover could provide more sites for web building or increased hiding places from larger spiders or other predators. Increased habitat heterogeneity, however, did not seem to be an important factor in determining increases in predator numbers, biomass or diversity, as habitat heterogeneity was not higher along the stream bank than in upland areas (e.g., coefficient of variation vs. spider biomass, $r^2= 0.001$, $p=0.68$). Increased ground cover then is most likely an important factor to these species as they spend most of their time in this habitat.

Prey availability may also play a role in determining the spatial distribution of terrestrial arthropod predators along the gradient. Emergence production was almost twice as high on warm days as cold ones, which corresponds to the greater number of spiders captured on warm days along the stream bank; however we did not find a greater abundance of terrestrial prey on warm or cold days along the stream edge. Johnson (1995) also found spider numbers were correlated with abundance of the most common insects in canopies of *Spartina pectinata* (Poaceae) wetlands.

We found that spider abundance was positively correlated with terrestrial prey abundance along the stream bank, but not in the upland habitat (75m from the bank). Since two sources of prey exist along the land-water margin (aquatic insects emerging from the stream and terrestrial insects), some predation pressure may be removed from terrestrial prey. This hypothesis is in agreement with other studies which found that predation by spiders on emerged aquatic insects is often a significant source of prey mortality (Gribbin and Thompson 1990, Rehfeldt 1990 and 1992), and that predation of aquatic insects causes an increase in numbers of terrestrial prey along river margins (Henschel et al. in press). In this study, Henschel and colleagues found that terrestrial predators directly foraged on aquatic prey, and experimental removal of predators along the stream bank caused an increase in terrestrial prey; in contrast experimental removal of invertebrate predators did not affect terrestrial prey densities 30m from the stream. It is possible then that increased prey availability (aquatic + terrestrial) at the land-water margin is removing some of the predation pressure from terrestrial prey. Although predation pressure on terrestrial prey may be lower at edges, another possibility is that plants are providing refugia (e.g., additional hiding spaces) for terrestrial prey along the bank; hence spiders are having less of an impact on terrestrial prey.

In general, we found no evidence that physical factors are controlling the distribution of terrestrial predators in this watershed. Like Henschel et al. (1996) we found no differences in microclimate between upland and edge habitats although our min./max. temperature gauges were not sensitive to minor fluctuations in temperature or moisture regimes. But our results are consistent with a controlled enclosure experiment that found no significant relationship between invertebrate predators and changes in temperature or moisture with distance to artificial edge (Ferguson 2000).

The mechanistic function of edges themselves at the land-water margin, which cause active foragers such as ground-dwelling predators to move linearly along corridors in search of food (Oehler and Litvaitis 1996) was also not evident in this arctic watershed. If this were the case, we would have found predators concentrated at the stream edge on all days when individuals were actively foraging, and found predation pressure to be negatively impacting terrestrial predators at the stream edge, but this was not the case.

Direct impact of stream subsidies on terrestrial predators in the arctic

In this study, we have been able to document a direct trophic link between stream subsidies and terrestrial predators in the arctic using a combination of stable isotope approaches. δ^{13}C values of aquatic insects and their in-stream food resources were much lower in Steinbogalækur than in Laxá; hence flying individuals from the two sources could be readily separated. Natural abundance δ^{13}C and δ^{15}N values show that flying aquatic insects (blackflies and midges) collected along the banks of Steinbogalækur were from two sources, Steinbogalækur (33%) and the larger river Laxá (67%), 400 meters downstream. Natural abundance values also indicate that terrestrial invertebrate predators consume both aquatic and terrestrial prey (Figure 2.8). These data show that the larger wolf spiders (family Lycosidae), litter spiders (family Linyphiidae), harvestmen (Opiliones) and predatory beetles are feeding on aquatic prey from both Steinbogalækur and Laxá, in addition to feeding on terrestrial prey (Figure 2.8). The strength of the natural abundance approach is that it integrates assimilation of N over time and so predators are likely to be at equilibrium with respect to their food resources (Mulholland et al. 2000b). The weakness is that calculations of relative proportions of terrestrial versus aquatic prey incorporated into predator biomass is confounded by the fact that both composite samples of flying adult aquatic insects and terrestrial insects (although from three distinct sources) have similar average $\delta^{13}C$ and $\delta^{15}N$ values.

Although many studies have used natural abundance stable isotope values to trace marine sources into terrestrial producers or consumers (Polis and Hurd 1996, Anderson and Polis 1999, Hilderbrand et al. 1999, Stapp et al. 1999), no one has used a ^{15}N tracer addition to trace the flow of nitrogen from the aquatic food web into terrestrial consumers. In addition to comparing natural abundance ^{13}C and ^{15}N values from the three sources, the ^{15}N tracer experiment enabled us to quantify the proportion of nitrogen in a terrestrial predator's diet that comes from aquatic sources. Although terrestrial herbs, grasses, mosses and liverworts along the stream bank were labeled above background levels with tracer ^{15}N, we found no indication that terrestrial prey were labeled above background levels indicating that predators did not become labeled by foraging on terrestrial prey that was labeled during the course of the experiment.

Although spiders and Opiliones are polyphagous predators that generally eat most insects, certain groups of spiders become more specialized through feeding strategies and/ or web design and relocation (Shear 1986, Nakata and Ushimaru 1999). Orb-weaving tetragnathids from the genus *Tetragnatha* and araneids from the genus *Larinioides* in particular, are considered obligate riparian species that feed mainly on aquatic insects and relocate their web in relation to availability of emerging aquatic insects (Luczak 1970, Gillespie 1987); their maximum prey capture coincides with maximum aquatic insect emergence (Williams et al. 1995). But to what extent is this aquatic subsidy a common feature among the various ‘functional’ groups of terrestrial predators? In this study, we show that, at least in this arctic system, wandering spiders (Lycosidae, Gnaphosidae, Thomisidae), litter-dwelling spiders (Linyphidiidae) and harvestmen (Opiliones) are also feeding directly on aquatic insects.

Combining the data from the two stable isotope approaches we get a clearer picture of trophic relationships in this watershed. Our ^{15}N tracer addition demonstrated that the larger lycosids were not as highly labeled as smaller-bodied predators. Utilizing natural abundance values and biomass estimates, we can conclude that Lycosids are feeding predominantly on insects emerging from the River Laxá and only a small proportion of insects emerging from Steinbogalækur. This could be due to the fact that they prefer larger prey (blackflies) which were more abundant in Laxá. Blackflies that were present in Steinbogalækur (2% of total emergence biomass) emerged early in the experimental release, just after snowmelt, and as such were not as highly labeled as chironomids. Blackflies that were emerging upstream from the release point (as snow pack gradually declined) were also unlabeled. If we had begun the ^{15}N tracer release before snowmelt we may have been able to label the blackflies before they emerged from our experimental reach.

In contrast to the larger lycosids, smaller-bodied litter spiders (Linyphiidae) and harvestmen (Opiliones) were most likely more enriched with tracer ^{15}N than wolf spiders because they were feeding predominantly on highly labeled smaller-bodied chironomids emerging from Steinbogalækur. Our calculations show that at least 7% of the total tracer ^{15}N taken up by terrestrial invertebrate predators (over the 25 days of the release) is from stream derived sources. Still this may be an underestimate of stream-derived N sources, as some terrestrial invertebrate predators may have not reached isotopic equilibrium during the release. This may explain why the smaller-bodied taxa (linyphiids and Opiliones) are more highly labeled than larger taxa (lycosids. The Myvatn-Laxá ecosystem is exceptionally fertile despite its latitude of 65^{o} N (Jónasson 1979). This may contribute to the strong coupling of aquatic and terrestrial foodwebs in this region.

Ecological significance of aquatic subsidies

Transfers of energy and nutrients from marine to terrestrial systems has recently been studied in great detail. For instance, using natural abundance stable isotopes, Stapp et al. (1999) found that seabird-derived nutrients from the ocean play a crucial role in plant productivity and terrestrial consumer densities on islands where seabirds occur in the Gulf of California, and Hilderbrand et al. (1999) found that salmon-derived nutrients from the ocean are exported to terrestrial plant communities via brown bears (*Ursus arctos*) along river corridors in Alaska.

How common is the river to watershed trophic exchange? If this phenomenon is wide-spread, what impact might it have on terrestrial food webs and tranfers of nutrients and organic matter? It has been hypothesized that this type of trophic exchange across habitats is common and may constitute a significant portion of the energy budget within habitats (Polis and Hurd 1996). Although the flows of nutrients, energy and organisms from rivers to adjacent watersheds is probably widespread, few data have been collected on the export and movement of river-derived resources to the surrounding terrestrial community. This study confirms the export of aquatic subsidies and its importance to terrestrial consumers. Using a ^{15}N tracer addition we were able to quantify the flow of nitrogen from aquatic to terrestrial foodwebs and show that emergence production is an additional source of nutrients and energy for terrestrial predators.

Nitrogen is vital for sustaining biological production and as such, is an important element in the biosphere. In recent decades, human activities have altered the N-cycle on both local and global scales through increased use of fertilizers, poor grazing practices, and increased atmospheric N deposition (Vitousek et al. 1997). In addition to affecting water quality, increased N inputs may alter biodiversity and food web dynamics along the riparian corridor as N is transferred from primary to secondary consumers within the stream, and then to adjacent terrestrial communities. This may be especially true in increasingly fragmented landscapes where in-stream secondary production in isolated riparian corridors provides one of the only food sources for terrestrial predators. In order to predict the effects of human-induced increases of nitrogen, we must develop an understanding of both the direct effects of increased nitrogen in aquatic and terrestrial systems (N-cycling, food web dynamics), and the indirect effects of increased N in these systems, such as transfers of N across ecosystem boundaries into recipient populations. Using ^{15}N tracer experiments to follow the flow of nitrogen from one habitat to another may be a useful tool that enables ecologists not only to model the flow of N across habitats, but also to model the flow and biomagnification of persistent contaminants from one habitat to the next (Cabana and Rasmussen 1994, Kiriluk et al. 1995).

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Table 2.1 Physical, chemical and biological characteristics of Steinbogalækur, a spring-fed stream in the Lake Myvatn region of Northern Iceland. All values are averaged over the period during the ^{15}N tracer addition (June 5- 30 1999), except nutrient concentrations which represent the range of values observed during this period.

Stream order	1
Discharge (L/s)	156
Mean width (m)	1.75
Mean depth (cm)	15
Average slope (%)	12.5
Water temperature (^{o}C)	6.9
NH4-N (μg/L)	4-6
NO3-N (μg/L)	8-30
SRP (μg/L)	5-15
Chlorophyll a (mg/m^{2})	11.07

Table 2.2 Plant species collected from m^2 plots (n= 15) in the immediate area adjacent to Steinbogalækur (0- 75 meters from the bank) in the Myvatn watershed.

Woody species

Betula nana	dwarf birch
Salix lanata	wooly willow
Salix phylicifolia	tea-leaved willow
Salix callicarpaea	blueish willow

Herb species

Ranunculus acris	meadow (common) buttercup
Tofieldia pusilla	Scottish asphodel
Armeria maritima	thrift
Cerastium fontanum	common mouse-ear
Loiseleuria procumbens	trailing azalea
Silene acaulis	moss campion
Dryas octopetala	mountain avens
Taraxacum spp.	common dandelion
Bistorta vivipara	alpine bistort
Alchemilla vulgaris	common lady's-mantle
Pinguicula vulgaris	common butterwort
Platanthera hyperborea	northern green orchid
Coeloglossum viride	Frog orchid
Trifolium repens	white clover
Viola palustris	alpine marsh violet
Thymus praecox ssp. arcticus	wild thyme
Empetrum nigrum	crowberry
Vaccinium myrtillus	common bilberry
Vaccinium uliginosum	bog bilberry (blueberry)
Thalictrum alpinum	alpine meadow rue
Bartsia alpina	alpine bartsia
Equisetum pratense	shady horsetail
Equisetum arvense	field horsetail
Equisetum variegatum	variegated horsetail

Grasses/ rushes/ sedges

Kobresia myosuroides	Bellard's kobresia
Anthoxanthum odoratum	sweet vernal grass
Luzula multiflora	heath wood rush
Deschampsia caespitosa	tufted hair grass
Alopecurus aequalis	orange foxtail
Carex bigelowii	stiff sedge
Juncus trifidus	three leaved rush
Juncus arcticus	Iceland rush
Carex rariflora	mountain bog sedge

Table 2.3 Average biomass (mg/ trap) and standard error (in parentheses) of spiders, predatory beetles and harvestmen on warm days (average temperatures above 14°C) and cold days (average temperatures below 8° C). Groups where average biomass is significantly higher at the stream edge than away from the edge have an asterisk above that column.

	Relative biomass (mg per trap)					
Meters from stream bank	**Araneae**		**Coleoptera**		**Opiliones**	
	warm	**cold**	**warm**	**cold**	**warm**	**cold**
	*****			*****	*****	*****
0	**156.1 (22.2)**	**9.1 (2.59)**	**13.8 (4.13)**	**6.2 (1.60)**	**6.6 (1.95)**	**0.9 (0.24)**
10	**56.3 (9.01)**	**10.3 (3.46)**	**5.5 (2.64)**	**1.1 (0.84)**	**2.1 (0.65)**	**0.4 (0.12)**
25	**76.1 (15.6)**	**8.9 (1.76)**	**9.6 (4.08)**	**0.2 (0.23)**	**2.7 (1.03)**	**0.3 (0.10)**
50	**72.3 (14.9)**	**6.7 (1.57)**	**3.8 (2.06)**	**0.1 (0.12)**	**2.3 (0.70)**	**0.4 (.21)**
75	**48.6 (9.22)**	**10.9 (2.64)**	**1.5 (1.16)**	**4.6 (3.13)**	**4.0 (1.69)**	**0.3 (.12)**

Table 2.4 Spider species found in the Steinbogalækur watershed which is located in the Lake Myvatn region of Northern Iceland, from June- July 1999. Ground-dwelling (GRND) indicates the species was collected in pitfall traps and vegetation-dwelling (VEGN) indicates the species was collected on the vegetation using sweep nets. The letter A indicates the species was found exclusively along the stream edge, the letter B indicates it was found within the first 25m of the bank, the letter C denotes the species was found along the entire transect, and the letter D indicates the species was found only in the upland area (50-75 m from the stream).

Araneidae	*Larinioides*	*cornutus*	(Clerck 1757)	GRND	VEGN	C
Dictynidae	*Dictyna*	*arundinacea*	(Linnaeus 1758)	GRND	VEGN	C
Gnaphosidae						
	Haplodrassus	*signifer*	(C.L. Koch 1839)	GRND		D
	Micaria	*pulicaria*	(Sundevall 1832)	GRND		A
	Gnaphosa	*lapponum*	(L. Koch 1866)	GRND		C
Linyphiidae	*Agyneta*	*decora*	(O. P. Cambridge 1870)	GRND		A
		similis	(Kulczynski 1926)	GRND		C
	Bathyphantes	*gracilis*	(Blackwall 1841)	GRND		A
	Bolyphantes	*index*	(Thorell 1856)	GRND	VEGN	C
	Cnephalocotes	*obscurus*	(Blackwall 1834)	GRND		C
	Dimodicus	*bifrons*	(Blackwall 1841)	GRND		C
	Erigone	*arctica*	(White 1852)	GRND		A
		atra	(Blackwall 1833)	GRND		A
		tirolensis	(L. Koch 1872)	GRND	VEGN	B
	Gonatium	*rubens*	(Blackwall 1833)	GRND		D
	Hilaira	*frigida*	(Thorell 1872)	GRND		C
	Latithorax	*faustus*	(O. P. Cambridge 1900)	GRND		A
	Leptothrix	*hardyi*	(Blackwall 1850)	GRND		B
	Leptrohoptrum	*robustum*	(Westring 1851)	GRND		A
	Lepthyphantes	*complicatus*	(Emerton 1882)	GRND		C
		leprosus	(Ohlert 1867)	GRND		D
		mengei	(Kulczynski 1887)	GRND		A
		zimmermanni	(Bertkau 1890)	GRND		B
	Savignya	*frontata*	(Blackwall 1833)	GRND		A
	Scotinotylus	*evansi*	(O. P. Cambridge 1894)	GRND		D
	Tiso	*aestivus*	(L. Koch 1872)	GRND		C
	Walckenaeria	*clavicornis*	(Emerton 1882)	GRND		C
		cuspidata	(Blackwall 1833)	GRND		A
		nodosa	(O. P. Cambridge 1873)	GRND		D
		nudipalpis	(Westring 1851)	GRND		A
Lycosidae	*Arctosa*	*alpigena*	(Doleschall 1852)	GRND		C
	Pardosa	*hyperborea*	(Thorell 1872)	GRND		C
		palustris	(Linnaeus 1758)	GRND		C
		sphagnicola	(Dahl 1908)	GRND		B
Tetragnathidae	*Tetragnatha*	*extenesa*	(Linnaeus 1758)	GRND	VEGN	A
Thomisidae	*Xysticus*	*cristatus*	(Clerck 1757)	GRND	VEGN	C

Table 2.5 Total number of adults, species richness and Fisher's log series α of spiders captured in 25 pitfall traps over 5 days along transects running perpendicular to the stream bank. Fisher's α was chosen because of its discriminant ability and sensitivity to sample size (Magurran 1988).

Meters from stream bank	**Number of adults**	**Species Richness**	**Fisher's log series α**
0	**448**	**27**	**6.31**
10	**169**	**14**	**3.63**
25	**221**	**16**	**3.96**
50	**189**	**14**	**3.49**
75	**150**	**13**	**3.42**

Table 2.6 Estimates of the relative importance of N from aquatic insects to spiders and harvestmen living within 10m of Steinbogalækur during the experimental ^{15}N release. Percent nitrogen from aquatic insects was estimated using the two-source isotopic mixing model described in the text. Aquatic insect values for the first model (% emerging) were obtained using biomass-weighted average δ^{15}N values from insects collected in emergence traps. Values for the second model (% flying) were obtained using biomass-weighted average δ^{15}N values from aquatic insects captured in sweep nets. Values reported are % of spider N (standard error) derived from aquatic sources.

Araneae			**# of samples analyzed**	**% using emerging aquatic insects**	**% using flying aquatic insects**
	Lycosidae (wolf spiders)				
	Pardosa	*hyperborea*	15	1.1 (0.4)	8.8 (1.9)
	Pardosa	*palustris*	15	1.0 (0.1)	5.3 (1.0)
	Pardosa	*sphagnicola*	15	1.0 (0.1)	4.2 (0.6)
	Arctosa	*alpigena*	6	1.0 (0.2)	8.4 (1.5)
	Linyphiidae (litter spiders)				
	Various species		18	2.8 (0.3)	21.7 (5.8)
Opiliones					
	Phalangiidae (harvestmen)				
	Mitopus	*morio*	16	2.3 (0.3)	27.5 (6.7)

Figure 2.1 This experiment was conducted just after snowmelt in June- July 1999 along a 500 meter reach of Steinbogalækur, an arctic stream located in the Lake Myvatn Region of Northern Iceland (65°35'N, 17°00'W). Inset is a map of Iceland showing the location of the Lake Myvatn Region.

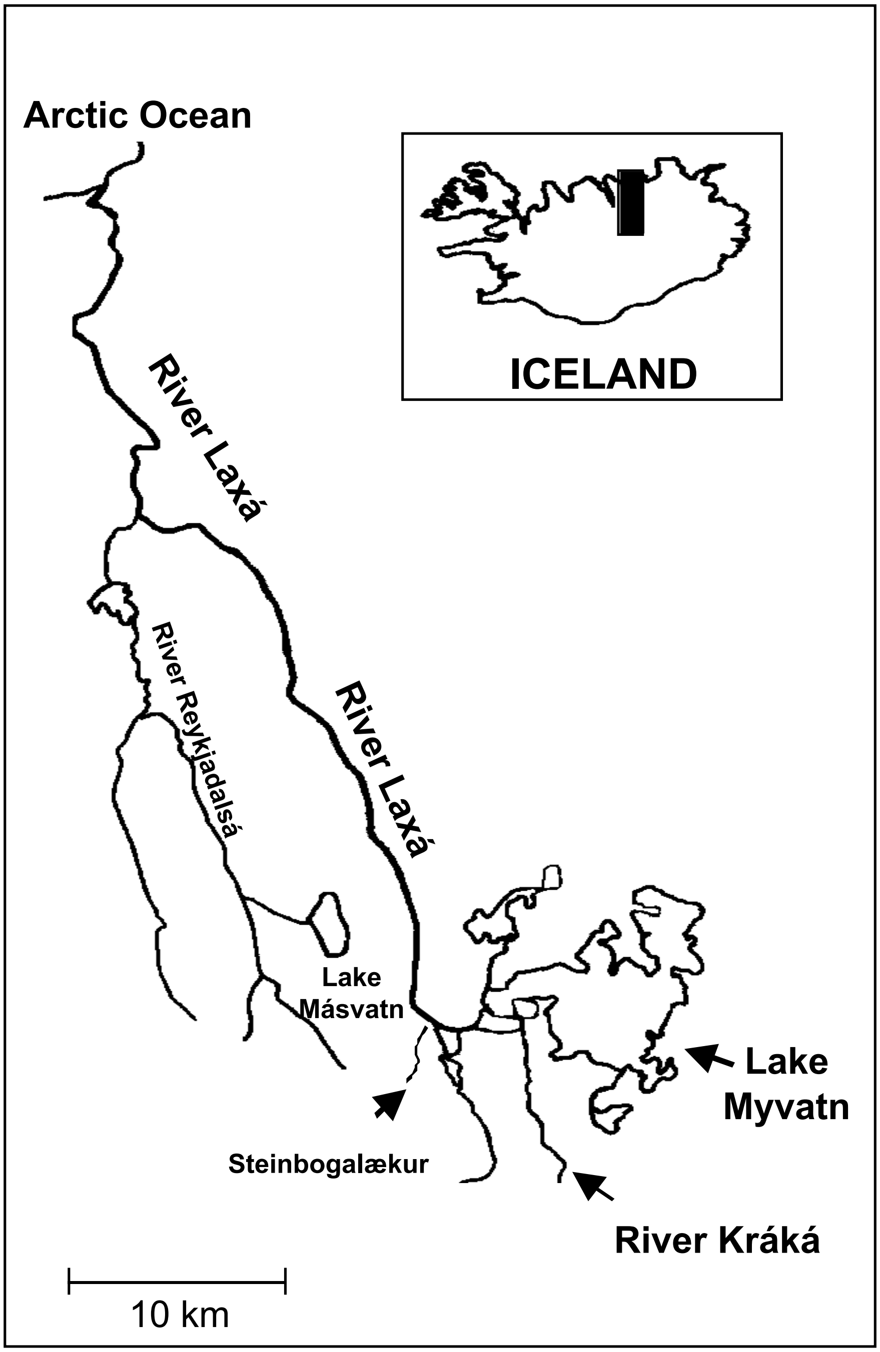
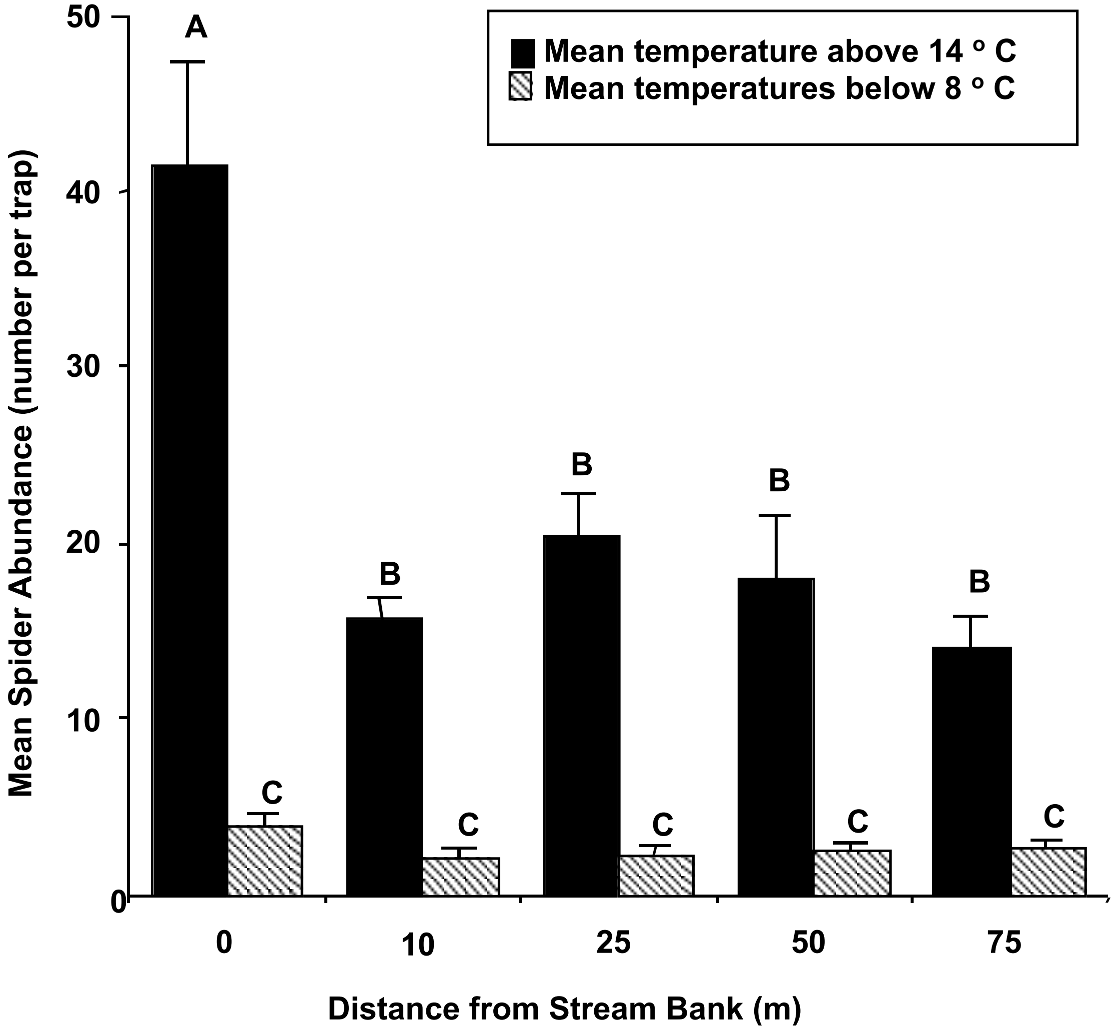
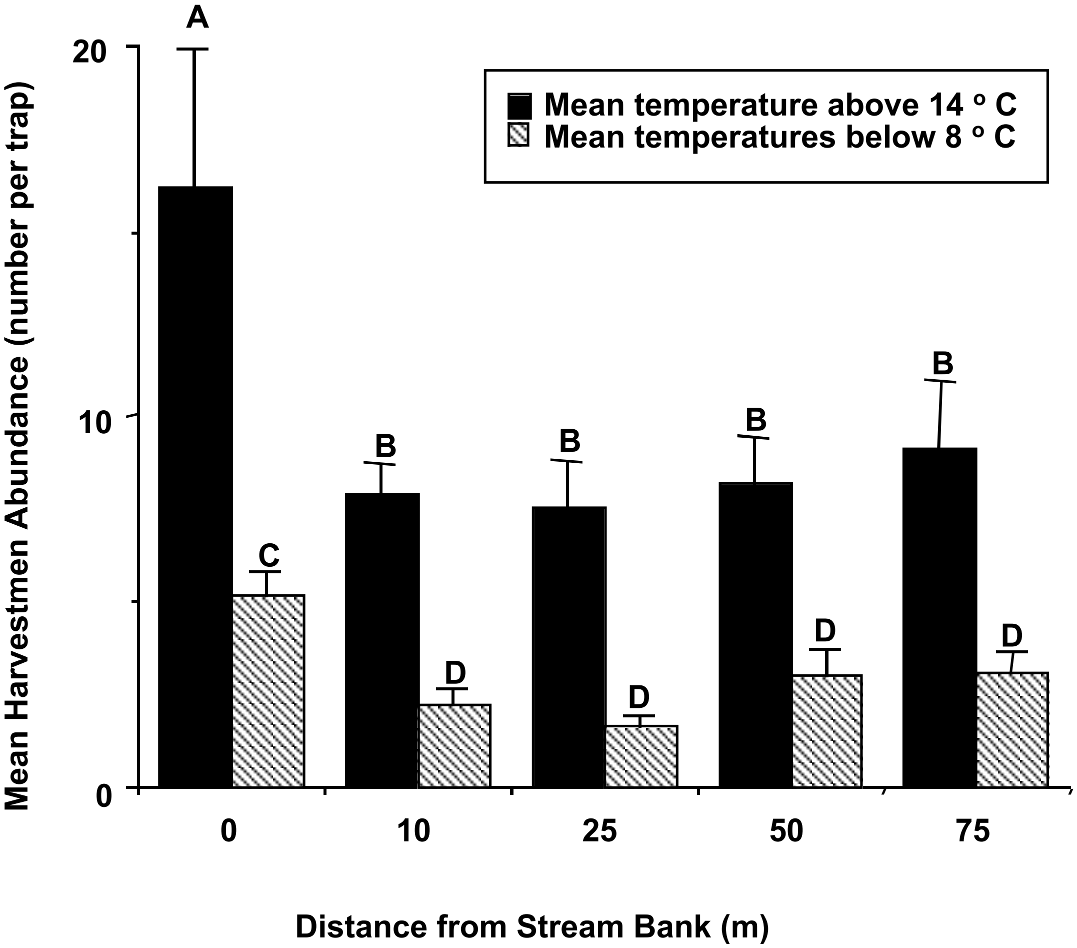

Arctic Ocean
ICELAND
River Laxá
River Laxá
River Reykjadalsá
Lake Másvatn
Lake Myvatn
Steinbogalækur
River Kráká
10 km

Figure 2.2 (a) Mean spider (b) harvestmen and (c) predatory beetle (Carabidae and Staphylinidae) abundance (number of individuals per trap) collected on warm (average temperatures above 14^{o}C) and cold (average temperatures below 8^{o}C) days in 48 hour pitfall traps. Different letters indicate mean values are significantly different from one another. Mean spider abundance was significantly higher at the stream bank on warm sunny days ($p<0.0001$); mean harvestmen abundance was significantly higher at the stream bank on all days ($p=0.0003$); and mean predatory beetle abundance was significantly higher at the stream bank on cold days ($p<0.0001$).

(a)


Mean Spider Abundance (number per trap)
50
40
30
20
10
0
A
B
B
B
B
C
C
C
C
C
■ Mean temperature above 14 ° C
▨ Mean temperatures below 8 ° C
0
10
25
50
75
Distance from Stream Bank (m)

(b)


A
20
10
0
■ Mean temperature above 14 ° C
▨ Mean temperatures below 8 ° C
Mean Harvestmen Abundance (number per trap)
C
B
D
B
D
B
D
B
D
0
10
25
50
75
Distance from Stream Bank (m)

(c)

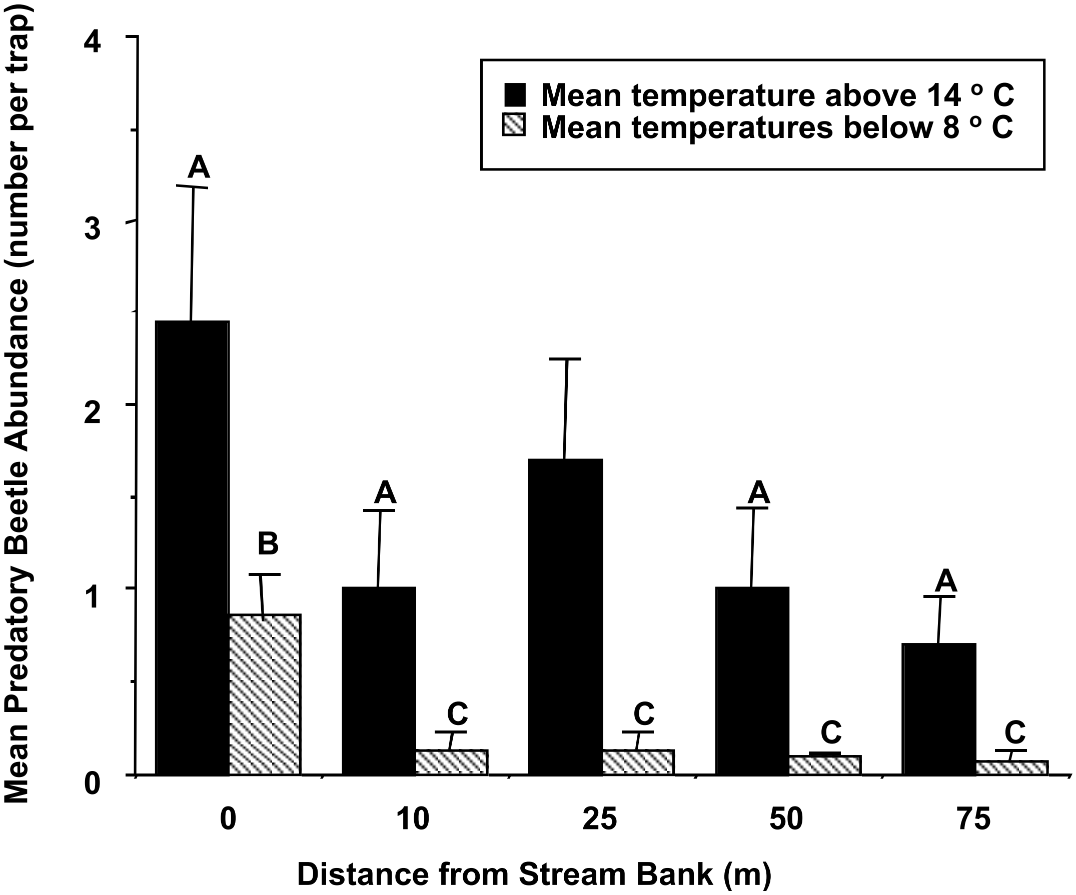

Mean Predatory Beetle Abundance (number per trap)
4
3
2
1
0
■ Mean temperature above 14 ° C
▨ Mean temperatures below 8 ° C
A
B
A
C
C
A
C
A
C
0
10
25
50
75
Distance from Stream Bank (m)

Figure 2.3 Dendrogram showing the similarity of spider assemblages along a gradient from stream edge (0m) to upland (75m) in the Steinbogalækur watershed. To compare similarity of spider species between transects we calculated a coefficient of community similarity for all possible pairwise combinations (Sorenson 1948), and then performed a cluster analysis by using these proportions with arithmetic averaging to determine similarities among points along the transect.

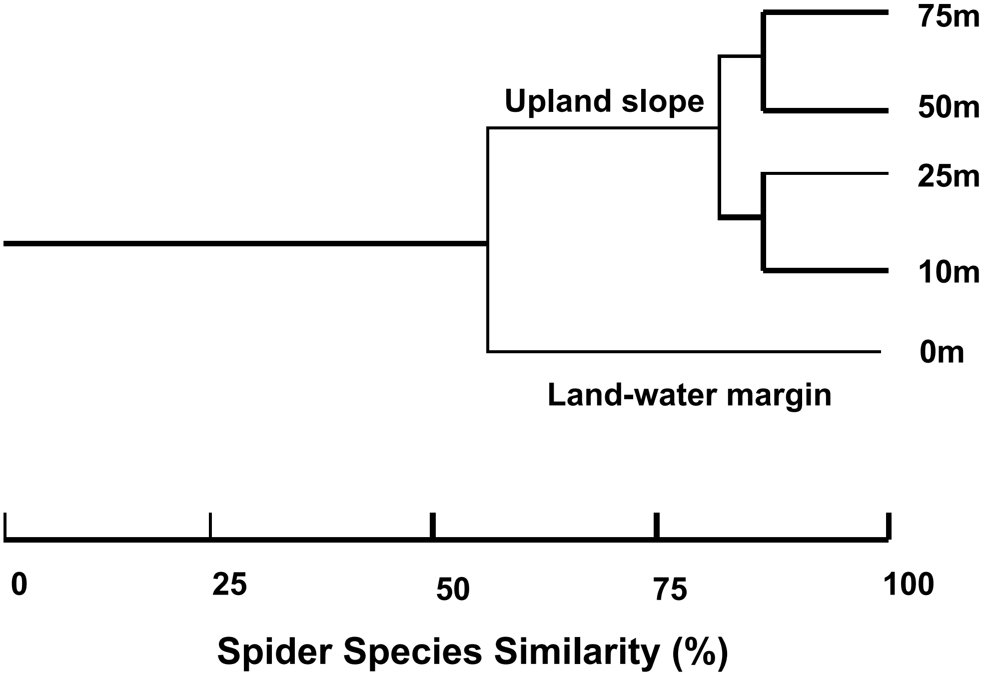

75m
50m
25m
10m
0m
Upland slope
Land-water margin
0
25
50
75
100
Spider Species Similarity (%)

Figure 2.4 Total foliage volume (TFV) (cm^3/ m^2) along the terrestrial gradient (0-75 m) versus (a) total spider biomass (n= 5, y= -0.0113 + 0.0524x, r^2=0.981, p< 0.001), (b) spider abundance (number of individuals) (n= 5, y= -47.466 + 14.907x, r^2= 0.967, p= 0.003) and (c) spider species richness (n=5, y=3.292 + 0.712x, r^2= 0.969, p= 0.002). Average vegetation height (not shown) versus total spider biomass (n= 5, y= 0.341+ 0.043x, r^2= 0.970, p= 0.002), spider abundance (number of individuals) (n=5, y= 49.594 + 12.323x, r^2= 0.987, p= 0.0006), and spider species richness (n=5, y=7.912 + 0.589x, r^2= 0.993, p= 0.0003) were also significant.

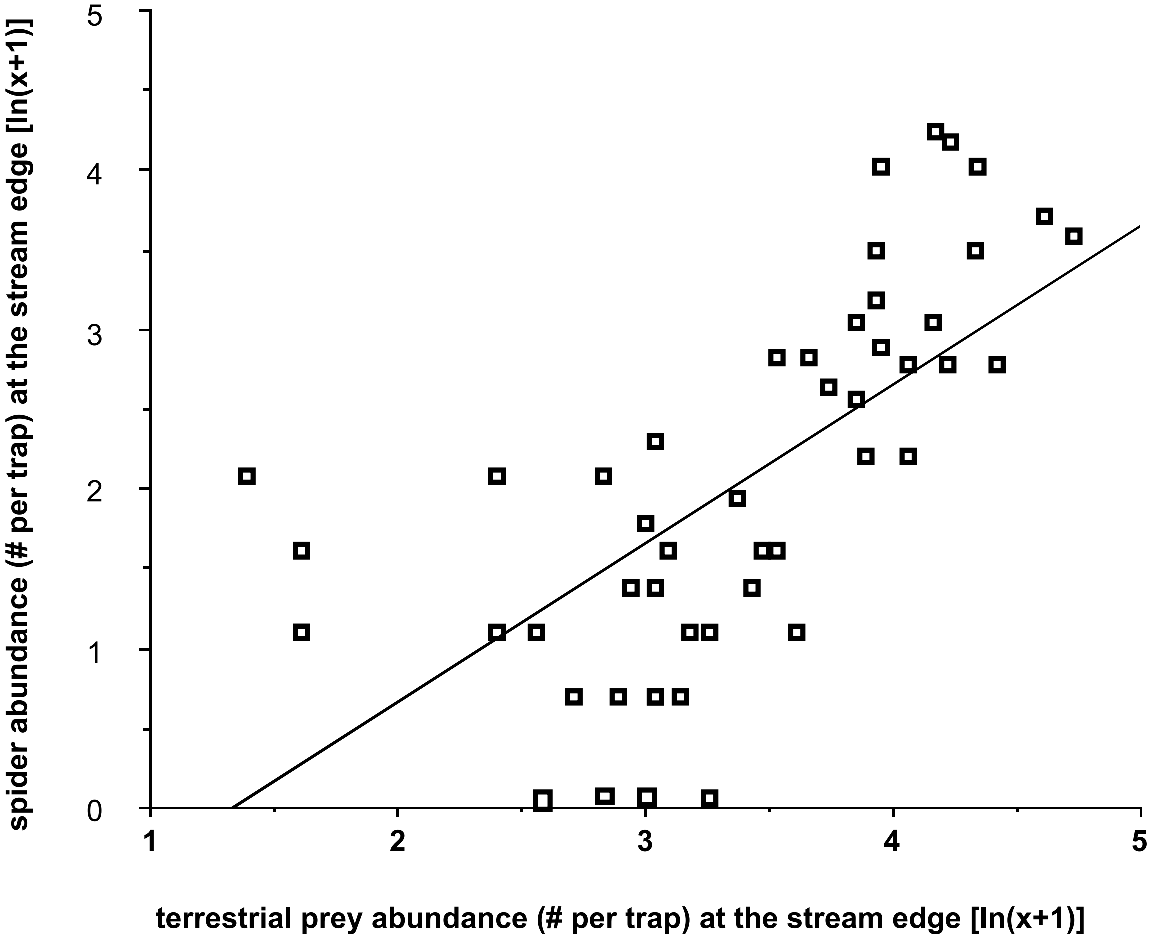
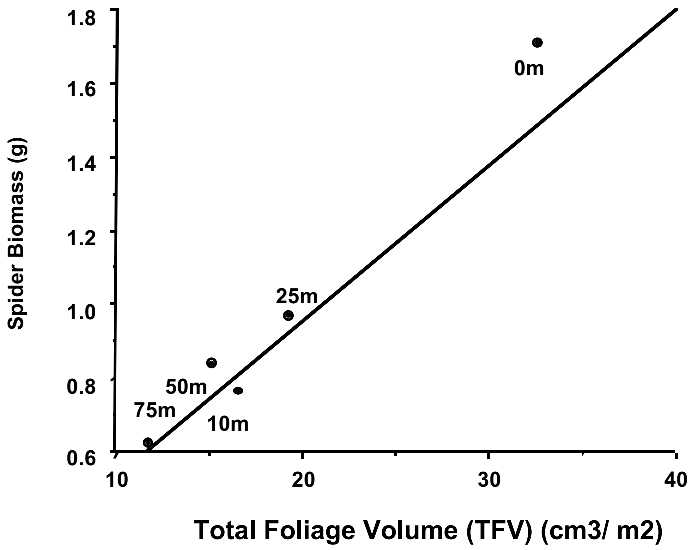
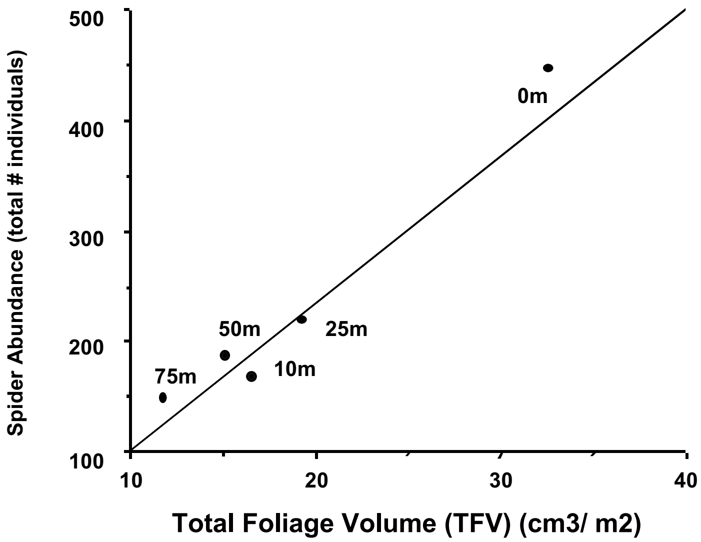

5
4
3
2
1
0
1
2
3
4
5
spider abundance (# per trap) at the stream edge [ln(x+1)]
terrestrial prey abundance (# per trap) at the stream edge [ln(x+1)]

Figure 2.5 Mean spider abundance versus terrestrial prey abundance along the stream bank (0-10m). Data were log transformed ln(x+1) prior to regression analysis (y= -1.3179 + 0.99330x, n=50, r^2=0.448, p<0.001).

(a)


Spider Biomass (g)
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0m
25m
50m
75m
10m
10
20
30
40
Total Foliage Volume (TFV) (cm3/ m2)

(b)


Spider Abundance (total # individuals)
500
400
300
200
100
0m
50m
25m
75m
10m
10
20
30
40
Total Foliage Volume (TFV) (cm3/ m2)

(c)

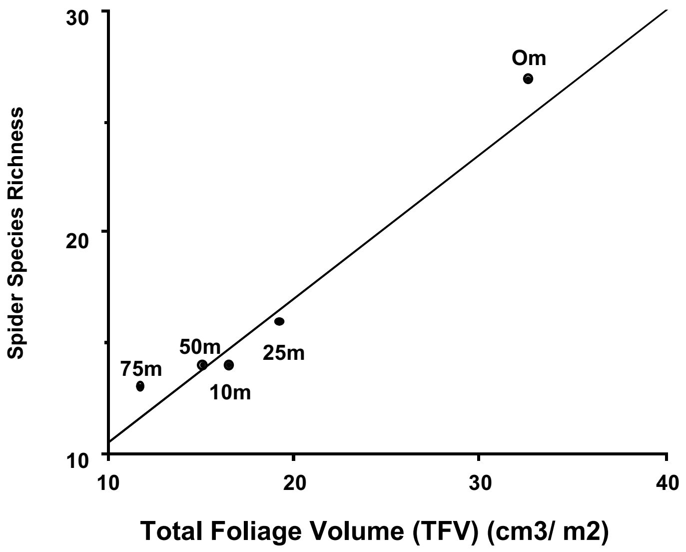

Spider Species Richness
30
20
10
Om
50m
75m
25m
10m
10
20
30
40
Total Foliage Volume (TFV) (cm3/ m2)

Figure 2.6 Natural δ^{13}C and δ^{15}N values (mean +/- s.e.) of three foodwebs in the Steinbogalækur watershed: Rivers Laxá (open circles) and Steinbogalækur (filled circles) and the terrestrial foodweb (filled squares) from the surrounding watershed. Terrestrial predators (open squares) and flying aquatic insects (open triangles) lie outside the three foodwebs. The top invertebrate predators in this system, large wolf spiders from the genera *Pardosa* (PR2) and *Arctosa* (PR3) are most likely feeding on resources from both aquatic and terrestrial habitats, whereas spiders from the family Linyphiidae, Opiliones and predatory beetles (PR1) are most likely feeding on terrestrial prey. Other abbreviations include: foodweb compartments from Steinbogalækur [filamentous algae (*fa*), epilithon (*ep*), the bryophyte *Fontinalis antipyretica* (*br*), fine benthic organic matter (*fb*), chironomids (*ch*), simuliids (*bf*), plecopterans (*pl*) and trichopterans (*tr*)]; Laxá [filamentous algae (fa), fine benthic organic matter (fb), simulids (bf), chironomids (ch) and breast muscles of adult Barrow's goldeneye, *Bucephala islandica* (wf)]; the surrounding terrestrial watershed [woody vegetation, *Betula nana* and *Salix phylicifolia* (wv), herbaceous vegetation, *Bistorta vivipara* and *Alchemilla vulgaris* (hv), mosses and liverworts (ms), terrestrial herbivores (tp); and flying aquatic insects from both rivers [chironomids (CH) and simuliids (BF)].

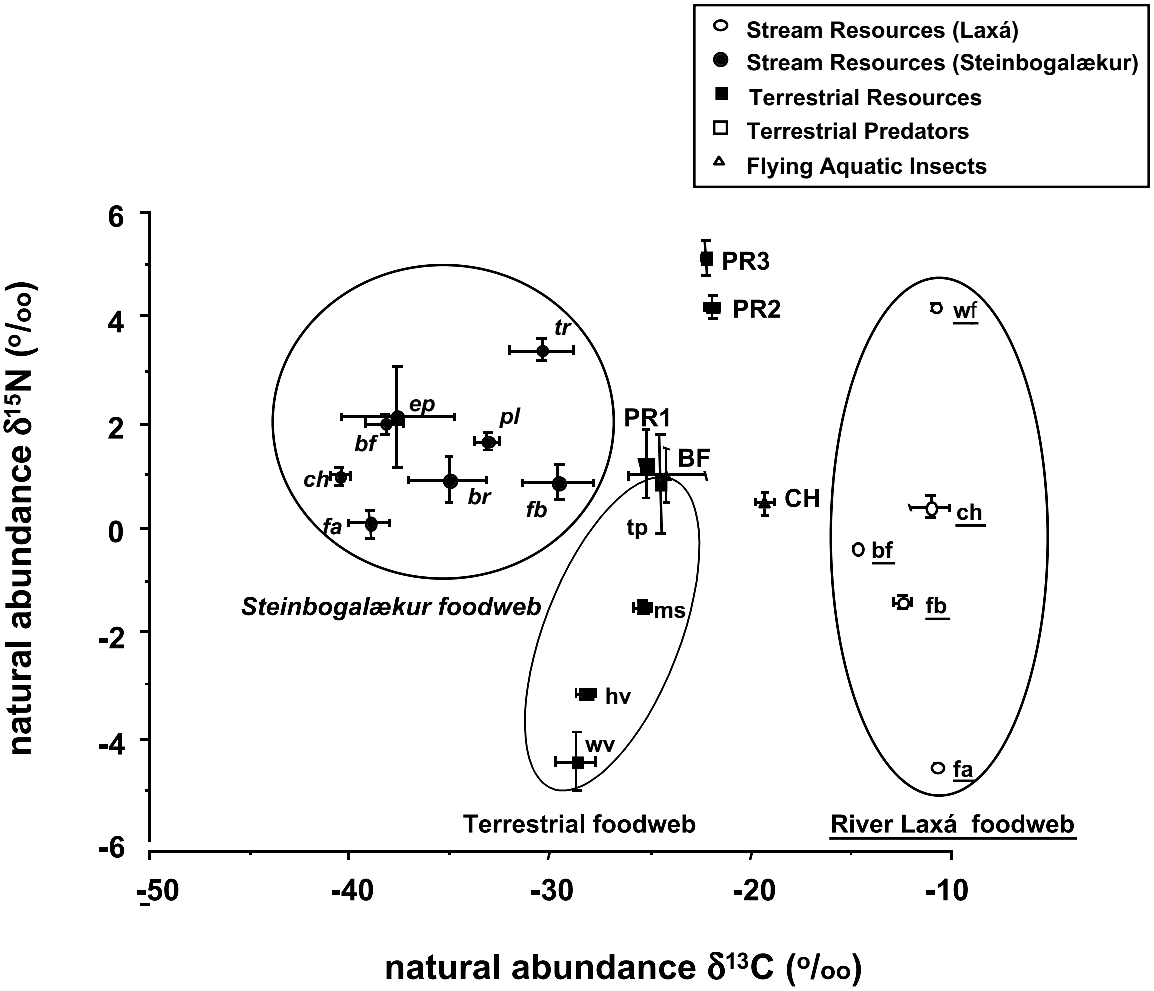
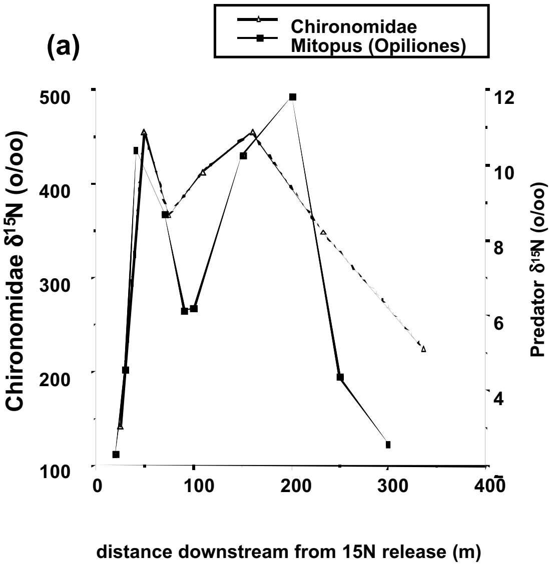
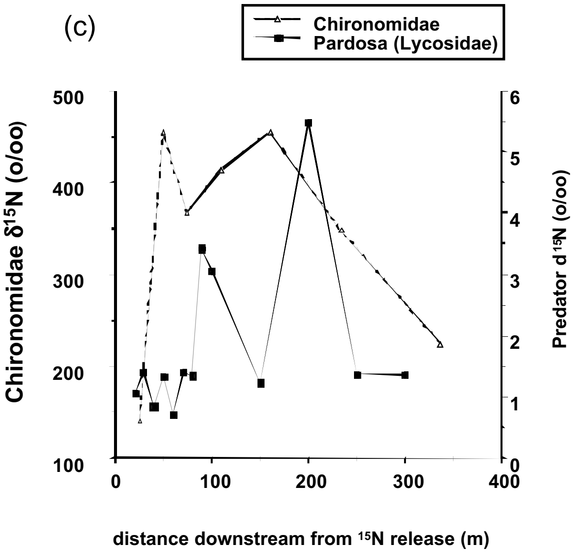

○ Stream Resources (Laxá)
● Stream Resources (Steinbogalækur)
■ Terrestrial Resources
□ Terrestrial Predators
△ Flying Aquatic Insects
natural abundance δ15N (o/oo)
natural abundance δ13C (o/oo)
6
4
2
0
-2
-4
-6
-50
-40
-30
-20
-10
tr
ep
pl
bf
ch
br
fb
fa
Steinbogalækur foodweb
PR3
PR2
PR1
BF
CH
tp
ms
hv
wv
Terrestrial foodweb
wf
ch
bf
fb
fa
River Laxá foodweb

Figure 2.7 Average enriched $\delta^{15}N$ values (background corrected) of (a) *Mitopus* (Opiliones), (b) Linyphiidae (various genera), (c) *Pardosa* (Lycosidae) plotted with mean chironomid $\delta^{15}N$ from Steinbogalækur in a downstream direction from the ^{15}N release point. Average enriched $\delta^{15}N$ values (background corrected) of (d) Arctosa (Lycosidae) is plotted with mean simulid $\delta^{15}N$ in a downstream direction from the release.

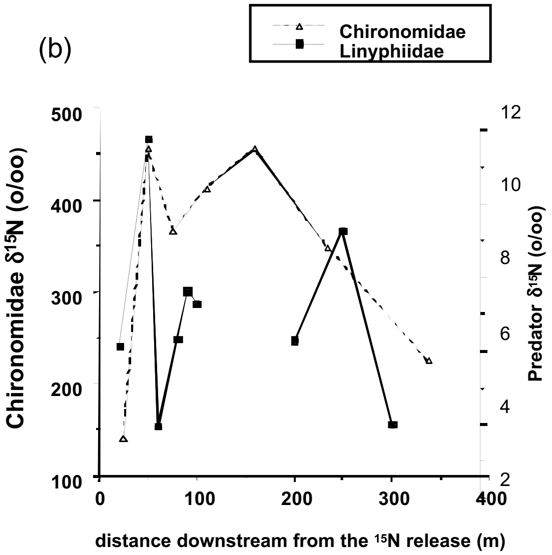
(a)


Chironomidae
Mitopus (Opiliones)
Chironomidae δ15N (o/oo)
500
400
300
200
100
Predator δ15N (o/oo)
12
10
8
6
4
0
100
200
300
400
distance downstream from 15N release (m)

(c)


Chironomidae
Pardosa (Lycosidae)
Chironomidae δ15N (o/oo)
500
400
300
200
100
Predator d15N (o/oo)
6
5
4
3
2
1
0
0
100
200
300
400
distance downstream from 15N release (m)

(b)


Chironomidae
Linyphiidae
Chironomidae δ15N (o/oo)
500
400
300
200
100
Predator δ15N (o/oo)
12
10
8
6
4
2
0
100
200
300
400
distance downstream from the 15N release (m)

(d)

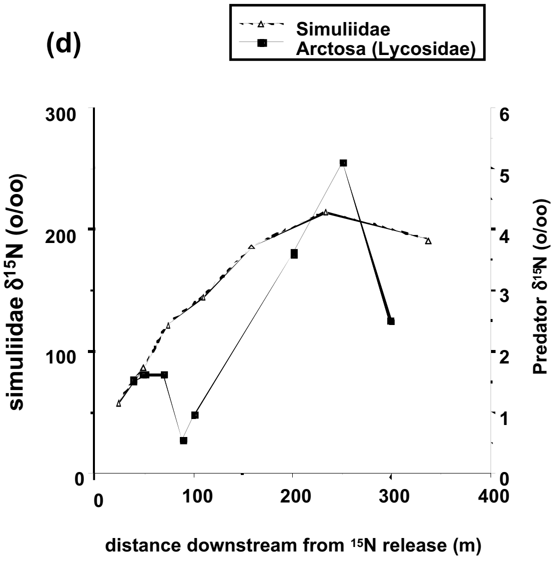
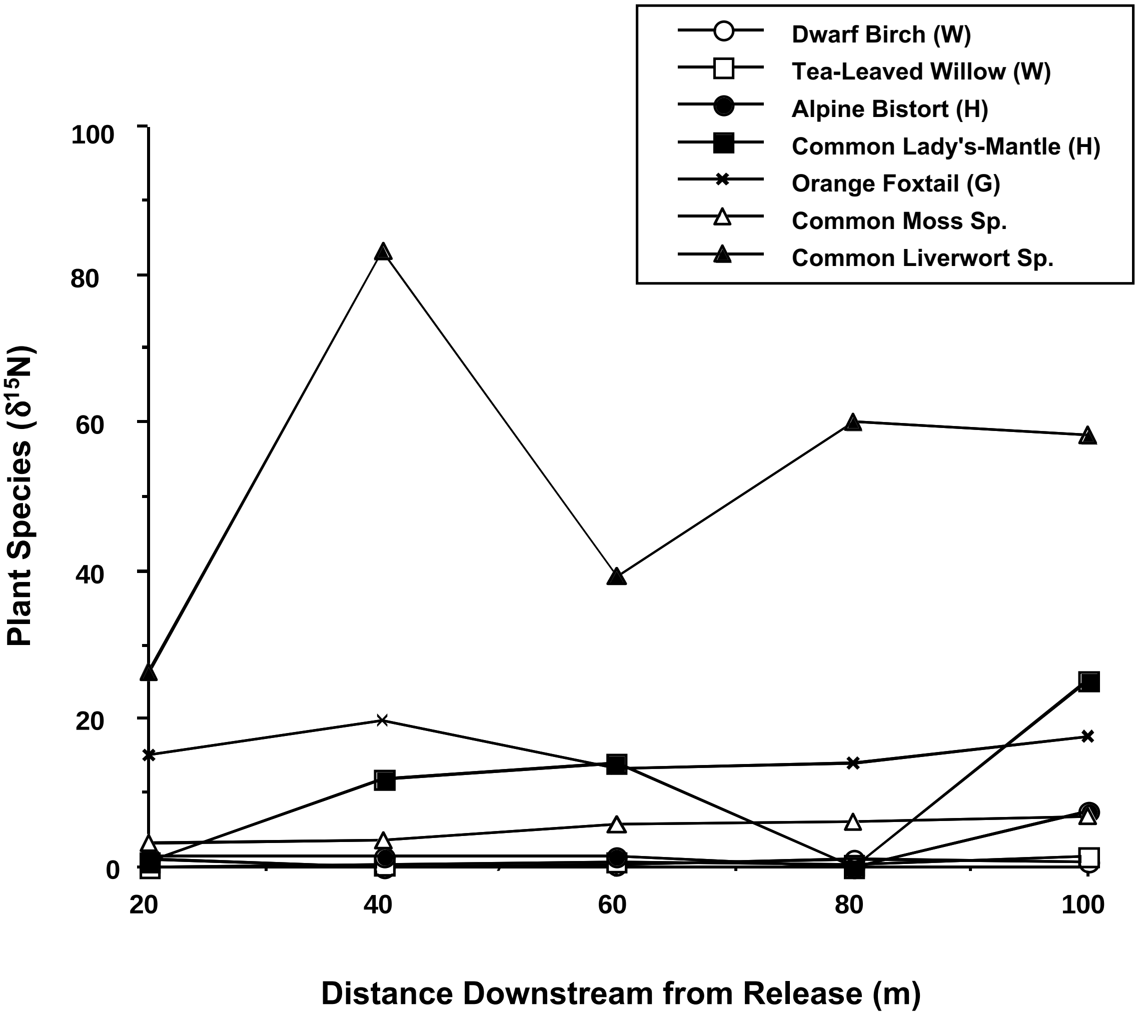

Simuliidae
Arctosa (Lycosidae)
simuliidae δ15N (o/oo)
300
200
100
0
Predator δ15N (o/oo)
6
5
4
3
2
1
0
0
100
200
300
400
distance downstream from 15N release (m)

Figure 2.8 Tracer $\delta^{15}N$ (background corrected) of composite samples of two commonly found woody species, *Betula nana* (dwarf birch) and *Salix phylicifolia* (tea-leaved willow); two herb species, *Bistorta vivipara* (alpine bistort) and *Alchemilla vulgaris* (common lady's mantle); one grass species, *Alopecurus aequalis* (orange foxtail) and one unidentified riparian moss and one lichen plotted with distance downstream from the ^{15}N release point. X-axis begins at 20m because that is the first meter mark at which we sampled terrestrial vegetation.


Dwarf Birch (W)
Tea-Leaved Willow (W)
Alpine Bistort (H)
Common Lady's-Mantle (H)
Orange Foxtail (G)
Common Moss Sp.
Common Liverwort Sp.
Plant Species ($\delta^{15}N$)
100
80
60
40
20
0
20
40
60
80
100
Distance Downstream from Release (m)

CHAPTER 3

CARBON AND NITROGEN TRANSFER FROM A DESERT STREAM TO RIPARIAN PREDATORS[1]

[1] Sanzone, D.M., E. Martí, J. L. Meyer, E. P. Gardiner, J. L. Tank, and N. B. Grimm. To be submitted to *Ecology*.

Abstract. Current ecological theory suggests that inter-habitat interactions can have a greater influence on community dynamics than intra-habitat interactions. Anecdotal evidence suggests this is true in riparian environments, where adult aquatic insects emerging from streams may be a significant source of energy for terrestrial predators inhabiting the riparian zone. Ecologists have been limited in their ability to quantify such across-habitat trophic links partly because of the difficulty in measuring complex flow pathways between adjacent habitats. 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 $^{15}N\text{-}NH_4$ 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 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. Some individuals obtained as much as 96% of their nitrogen from emerging aquatic insects.

Female orb-web weaving spiders obtained a larger proportion of their N from instream sources than males or immatures of the same species. 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, timed sweep net samples and vegetation transects. Spider abundance and biomass were highest within the active stream channel but decreased more than seven-fold 25m from the bank. Spider species richness was also highest within the active channel with complete species turnover occurring 25 meters from the stream edge. Changes in structural diversity 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 diversity within the active stream channel and riparian zone of Sycamore Creek.

Key words: adult aquatic insects, aquatic subsidies, Araneae, $\delta^{13}C$, $\delta^{15}N$, emergence, ^{15}N tracer addition, Sonoran Desert, spiders, stable isotopes.

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 stream habitats, for instance, may be a significant source of nutrients and energy for terrestrial predators living in the riparian zone (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. For example, in gallery forests along Kings Creek in the Konza Prairie Natural Area (Long Term Ecological Research Site: Manhattan, Kansas), Gray (1993) found that insectivorous bird densities were correlated with aquatic insect emergence both spatially and temporally. Aquatic prey also provided a significant seasonal subsidy (50-90% of the monthly energy budget) to forest birds during defoliation periods along the Horonai Stream in Hokkaido, Japan (Nakano and Murakami 2001). Evidence from the shores of the Main River in southern Germany (Henschel et al. in press), and the Eel River in California (Power and Rainey 2000, Power et al. in press) also suggest that bats, spiders and lizards may be deriving a large portion of their total energy budget from aquatic resources. 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 how important are stream subsidies to the spatial distribution and community composition 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). In addition, many of these desert riparian communities support species that are phenotypically different from their upland counterparts. For instance, a reciprocal transplant experiment of the spider *Agelenopsis aperta* (Gertsch) conducted in riparian and dry woodland habitats showed that individuals occupying narrow stretches of riparian habitat displayed behavioral characteristics that were less aggressive toward prey and more fearful of bird predation than their ‘dryland’ counterparts (Reichert and Hall 2000).

Current food web theory suggests that inter-habitat interactions can have a greater influence on community dynamics than intra-habitat interactions and that movement of prey across spatially heterogeneous landscape units can often enhance predator abundance beyond what local resources can support (Polis et al. 1995, Polis and Hurd 1996). Jackson (1984) hypothesized that both density and diversity of vertebrate predators in desert riparian zones respond to the higher prey productivity of desert streams. Invertebrate insectivores (such as spiders and odonates) may facilitate this transfer of energy from aquatic to terrestrial habitats by consuming emerging aquatic prey (Jackson and Fisher 1986); yet this transfer of energy has never been quantified. In Sycamore Creek, net emergence of aquatic insects (23.1g AFDM m^{-2} yr^{-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 this watershed.

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 flow 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 varies 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 Grimm 1987). Characteristic of this region, summer air temperatures were high (mean = 28.7 ^{o}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 occured 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 3.1). 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 sub-surface 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 3.1).

Natural abundance of stable isotopes and labeling of aquatic insects using a^{15}N tracer addition

We continuously dripped 10% ^{15}N-labeled NH_4Cl into Sycamore Creek from May 1 to June 12, 1997 to achieve a 500 $^{o}/_{oo}$ ^{15}N enrichment of streamwater NH_4, while maintaining background concentrations of NH_4. 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 (1604.8 mg ^{15}N as $^{15}NH_4Cl$) was estimated based on stream discharge and background ammonium concentrations (Table 3.1). 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). Larval insects were sampled from 7 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).

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 a 80 cm^2 Hess sampler at randomly chosen sites along the study reach. Larvae were identified to genus, and biomass estimates (dry mass per unit area) were determined for each genus. Once the addition started, larval insects were collected once a week over a 6 week period using Hess samplers and hand collecting. Natural abundance ^{13}C and ^{15}N of dominant aquatic insects were determined from samples taken upstream from the dripper (minus 10 m), and at sampling stations below the release point before the start of the ^{15}N tracer addition.

Quantitative estimates of emergence were made using 0.25 m^2 emergence traps (n=9). Traps were constructed from PVC pipes and covered with window screening (0.3 mm mesh). The base of the traps were anchored into the stream substrate to prevent insect drift from entering the traps. The top of the traps contained an inverted funnel and glass jar. This design, while preventing drift, allowed water to flow through the traps at a velocity similar to that of the surrounding water. Three traps were placed 20 meters upstream from the ^{15}N tracer addition site and 6 traps were placed downstream (between 15 and 35m from the release site). Emergence traps were sampled using an aspirator and forceps on 5 separate dates after collecting emerging insects for 48 hour intervals (n=45). All insects were taken back to the lab, sorted and preserved in alcohol until they were identified to genus. Once identified, samples were dried, weighed to estimate biomass (mg DM m^{-2}), ground for ^{15}N analysis, and a composite sample of several individuals of the same genus from the same location were analyzed for tracer ^{15}N (1-2 mg DM).

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 2 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 8pm until 8am the following morning). Samples were sorted, identified and processed as described above.

Stable isotopes and 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 on day 42 of the release along the five stream-to-upland transects and at eight additional sites along the wetted stream channel (following methods described in Coddington et al. 1996).

Arthropods inhabiting lower herbaceous vegetation and litter were sampled using 48-hour pitfall traps (Sanzone et al. in review) 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-hour periods on 5 sampling dates, over a three-week period (n=25 traps). Adult insects and spiders were taken back to the lab, sorted and placed in 70% ethanol until adult spiders 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 1972, Wise 1993, Nyffeler et al. 1994, Foelix 1996). The five feeding/hunting 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 hours, weighed for biomass, and ground. A composite sample of several individuals from the same genus, collected at the same location were analyzed for ^{13}C and ^{15}N isotopic signatures. Natural abundance ^{13}C and ^{15}N values were determined using samples collected upstream from the ^{15}N release site. Tracer ^{15}N values were determined using spiders and terrestrial prey collected downstream from the release site. All tracer $\delta^{15}N$ values are background corrected and so represent the amount of ^{15}N that organisms incorporated from the ^{15}N addition.

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 one-way analysis of variance (ANOVA) design after normalizing the data using a ln (x+1) transformation (JMP, SAS 1995). Using the General Linear Model Procedure (GLM), we tested to see whether there were differences in mean abundance, biomass, and richness (number per trap) of spiders between riparian and upland habitats.

Stable isotope analysis

We calculated 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. All $\delta^{15}N$ and $\delta^{13}C$ values were calculated as:

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

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 (0.003663) for $\delta^{15}N$ (Peterson and Fry 1987). Values are expressed as parts per thousand ($^{o}/_{oo}$). All samples were analyzed for ^{13}C and ^{15}N by high-temperature, direct combustion and continuous flow analysis using a Finnigan Delta C Stable Isotope Ratio Mass Spectrometer at the Institute of Ecology Analytical Chemistry Laboratory, University of Georgia (Athens, GA) or using a Europa Model 20/20 Isotope Ratio Mass Spectrometer located at the Ecosystem Center, Marine Biological Laboratory (Woods Hole, MA).

Estimating carbon sources to riparian predators

To estimate which food resources spiders living in the active channel and along the stream-riparian edge were consuming, we used natural abundance $\delta^{13}C$ and $\delta^{15}N$ values (mean +/- s.e.) of spiders and terrestrial insects collected in pitfall traps and sweep net samples, and adult aquatic insects collected in emergence traps. Individual numbers represent composite samples (6-10 individuals) of different species that were placed into 'functional feeding guilds', then averaged.

We used the following equation to determine 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):

$$\delta^{13}C_{pred} = (P_{aqua})\,(\delta^{13}C_{aqua} + ba\,) + (1-P_{aqua})\,(\delta^{13}C_{terr} + ba) \qquad (2)$$

where, P_{aqua} = proportion of spider C derived from aquatic insects; $\delta^{13}C_{pred} = \delta^{13}C$ of spiders; $\delta^{13}C_{terr}$ and $\delta^{13}C_{aqua} = \delta^{13}C$ of terrestrial and emerging aquatic insects respectively. *b* is the average trophic enrichment of ^{13}C between predator and prey (approximately 1 $^{o}/_{oo}$: DeNiro and Epstein 1978), and *a* which is based on $\delta^{15}N$ values is the number of trophic transfers between prey and predator. Different values of *a* for each functional feeding guild were determined using average natural abundance ^{15}N values for predators in that feeding guild to infer trophic position. Equation (2) can then be solved to determine the percentage of C derived from adult aquatic insects that was incorporated into spider biomass (P_{aqua} * 100), compared to that which comes from terrestrial sources.

Trophic transfer of tracer ^{15}N across ecosystem boundaries

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 (spiders and aquatic and terrestrial insects) collected during the addition along the ^{15}N enriched study reach. Since spiders are polyphagous generalist predators, we can assume that proportion of prey assimilated into tissue is a function of microhabitat choice and feeding strategy rather than prey species preference (Wise 1993, Nyffeler et al. 1994). Natural abundance values indicate that background $\delta^{15}N$ and C:N ratios are similar among prey species inhabiting similar trophic positions; 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. The simplest version of this model is a two-source mixing model that assumes two discrete populations exist, labeled aquatic insects and unlabeled terrestrial insects. This model however considers no upstream movement of unlabeled aquatic insects from locations further downstream from the study site. Field observations indicate that aquatic insects fly upstream in the Sycamore Creek watershed. This model therefore is an underestimate of stream-derived N in spiders because it overestimates ^{15}N label of aquatic insects (i.e., assumes all aquatic insects flying at a given point, emerged at that point).

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

$$\delta^{15}N_{pred}* = (P_{aqua})\ (\delta^{15}N_{aqua}*\ ) + (1-P_{aqua})\ (\delta^{15}N_{terr}*\ ) \qquad (3)$$

where, P_{aqua} = proportion of spider N derived from aquatic insects; $\delta^{15}N_{pred}*$ = δ^{15}N of spiders; $\delta^{15}N_{terr}*$ and $\delta^{15}N_{aqua}*$ = δ^{15}N of terrestrial and emerging aquatic insects, respectively. The superscript * indicates numbers are background corrected and represent only tracer ^{15}N. Equation (3) can be solved for P_{aqua} to determine the proportion of labeled adult aquatic insects incorporated into spiders.

Spiders were collected at more sites than were emerging insects; hence we fit an exponential decay curve to predict average δ^{15}N values for labeled aquatic prey emerging at all points where we collected spiders. We first determined that δ^{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 (Figure 3.1):

$$\delta^{15}N_{d,E} = \delta^{15}N_{0,E}\, e^{-kd} \qquad (4)$$

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 (Figure 3.1).

Percentage of spider $\delta^{15}N$ derived from emerging aquatic insects (% N) was calculated using equation 3 from spider $\delta^{15}N$ values (6-10 individuals per ^{15}N analysis) collected at point d. We averaged the $\delta^{15}N$ values of several individuals from each genus collected at each point along the stream and upland transects (total number of samples analyzed for $\delta^{15}N$= 95). To determine differences in % N between spider functional feeding guilds, we performed paired t-tests. To determine differences in % N of spiders along the stream-to-upland gradient we used one way ANOVA procedures (JMP; SAS 1995). We used an arcsine-square root transformation for all results reported as percentages (Sokal and Rohlf 1995).

Accounting for flight of adult aquatic insects

We modified the two-point upstream flight model first proposed by Hershey et al. (1993), to account for N coming from unlabeled aquatic insects that emerged downstream of the experimental reach, flew upstream and were captured by spiders. We chose an upstream flight model because field observations indicated predominantly upstream flight, the model met maximum likelihood convergence criteria, and provided the best fit to the data.

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

$$\delta^{15}N_{d,F} = (s)(\delta^{15}N_{0,E}\, e^{-kd}) + (1-s)\,(\delta^{15}N_{0,E}\, e^{-k(d+x)}) \qquad (5)$$

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 equation 4). $\delta^{15}N$ 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 derived from equation 4, Gauss-Newton Maximum Likelihood Estimation (SAS,1996) determined an average upstream flight distance (x) of 109 m and the proportion of 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 (Figure 3.1), a reasonable estimate.

To determine the percentage of spider N derived from labeled (i.e., those that emerged at the experimental reach) and unlabeled aquatic insects flying in the air (i.e., those that came from sites located downstream from the experimental release), we used $\delta^{15}N_{d,F}$ from equation 5 for $\delta^{15}N_{aquatic}*$ in equation 3 to estimate the average $\delta^{15}N$ signal of emerged aquatic insects flying in the air at point d. Percent of spider $\delta^{15}N$ derived from flying aquatic insects was then recalculated from spider $\delta^{15}N$ values (3-6 individuals per sample) collected at point d. The $\delta^{15}N$ values were averaged for each spider genus, family and functional feeding guild. We used the Shapiro-Wilk procedure to test for normality (Shapiro and Wilk 1965), then compared differences between spider genera, families, functional feeding guilds, age classes (immature vs. adult) and sex by performing one-way ANOVA procedures (JMP; SAS 1995). We used an arcsine- square root transformation for all results reported as percentages (Sokal and Rohlf 1995). We compared results of the two-point mixing model (which incorporates percentage of spider N derived from aquatic insects flying upstream) to the results of the simpler model (Equation 3) which assumes no upstream flight of aquatic insects.

Factors influencing the spatial distribution of spiders

In addition to food resources as a factor influencing the spatial distribution of spiders, we also considered the structural complexity of live and decomposing vegetation. To examine the effects of structural complexity, we measured plant species richness, number of stalks m^{-2} (a surrogate measure of horizontal complexity), number of vertical points transected (‘touches’), and structural diversity of ground cover (measured by placing ground cover into micro-habitat classes) (Southwood et al. 1979), along the same five stream-to-upland transects (n=20). Vertical points transected (‘touches’) was determined by averaging the number of times vegetation touched a 3 m high vertical rod in each of the transects (n=6). 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 terrestrial prey abundance and biomass (JMP, SAS 1995). We applied a ln (x+1) transformation (Sokal and Rohlf 1995) when data were not normally distributed (Shapiro and Wilk 1965).

RESULTS

Export of aquatic insects

Based on analysis from emergence traps (n= 36), average (+/- s.e.) biomass of aquatic insects per day emerging during the duration of the ^{15}N tracer addition was 0.221 (+/- 0.081) g DM m^{-2} d^{-1}. Most (54%) of insects emerging from Sycamore Creek during the ^{15}N release were from two families, Chironomidae (43%) and Baetidae (11%). Jackson and Fisher (1986) also found the largest proportion (77%) of emerging insects from Sycamore Creek were from these two families. The other 17 aquatic insect families collected during this period (46% of emerging biomass) were from three orders, Ephemeroptera, Trichoptera and Diptera (Table 3.2).

Food sources for spiders

Natural abundance δ^{13}C and δ^{15}N values of spiders and their potential prey show that spiders living within the active stream channel and riparian zone rely, at least in part, on emerging aquatic insects (Figure 3.2). Using the isotopic mixing model which is based on natural abundance of ^{13}C and ^{15}N (Equation 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 showed that spiders that capture prey by building horizontal or vertical orb webs (orb) (Araneidae and Tetragnathidae) on vegetation along the wetted stream channel obtained 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).

From natural abundance data it appears that spiders feed mainly on aquatic insects which are classified as collector-gatherers in Sycamore Creek: Chironomidae (Diptera) (cg4), Stratiomyiidae (Diptera) (cg3) and Baetidae (Ephemeroptera) (gz2), all three of which feed mostly on algae and organic matter and have relatively short life cycles (Gray 1981, Grimm 1987) (Figure 3.2). During the sampling period, these three families comprised 61% of total emergence biomass from Sycamore Creek and had similar natural abundance ^{13}C values to spiders from four of the five functional feeding guilds we studied (Figure 3.2).

N-dynamics across spatially explicit landscape boundaries

By Day 42 of the ^{15}N tracer addition, all aquatic insects in the experimental reach were labeled with tracer ^{15}N and most had reached isotopic equilibrium (i.e., a plateau in δ^{15}N values) (Figure 3.3a). Tracer δ^{15}N values show similar ^{15}N enrichment patterns for dominant aquatic insects, with little or no tracer found in insects 280 m downstream from the ^{15}N release site (Figure 3.3b).

Using the simplest version of the two-source mixing model (Equation 3), the average % N spiders obtain from emerging aquatic insects was highest for ground-dwelling spiders that actively hunt for prey (wnd), and for those that build orb-webs in and around vegetation adjacent to the stream channel (orb) (Figure 3.4a). Spiders that use a sit-and-wait strategy on the ground (swg) (Agelenidae and Gnaphosidae), or in and around vegetation (swv) (Salticidae and Thomisidae), or those that build sheet-webs (shw) (Linyphiidae) obtain a lower percentage of their N from emerging aquatic insects (Figure 3.4a). Because the simplest version of this two-source mixing model assumes only two possible ^{15}N sources, labeled aquatic insects and unlabeled terrestrial insects, but considers no upstream or downstream movement of unlabeled aquatic insects, these results are an underestimate of stream-derived N in spiders.

The more complex version of this two-source mixing model (Equation 5) incorporates δ^{15}N values from unlabeled aquatic insects that may be flying upstream into the area (Table 3.3). Because this version of the model includes the average δ^{15}N signal of unlabeled aquatic insects from downstream as well as insects emerging immediately adjacent to spider traps, it provides a more accurate estimate of N coming from aquatic insects. This model also indicates that orb-web weavers (orb) rely more heavily on aquatic resources than do sheet-web weavers (sht) or spiders that use a sit-and-wait strategy (swv) to capture prey on vegetation (Figure 3.4b). Similarly, wandering spiders (wnd) relied more heavily on emerging adult aquatic insects than spiders that use a sit-and-wait strategy (swg) on the ground (Figure 3.4b).

Because of the high variability in labeling between functional guilds, we found no statistically significant differences in %N coming from aquatic resources between families living on either the ground (p=0.47) or in vegetation (p=0.41) (Table 3.3). For spiders inhabiting both riparian vegetation and hunting on the ground, %N coming from aquatic insects was higher for females than for males (64% vs. 7%, n=8, p=0.0001); however differences between ground-dwelling male and female spiders were not significant (18% vs. 23%, n=25, p=0.58). When looking at differences in age class, adult female spiders inhabiting the vegetation derived more N from aquatic insects than immatures from the same species (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).

Lateral movement of carbon and nitrogen into the watershed

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 3.4). 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 10m or more from the active channel ($p=0.0006$). In fact, we did not find any tracer $\delta^{15}N$ in wandering spiders beyond 25 meters. Spiders that use a sit-and-wait strategy on the ground were less labeled overall with tracer ^{15}N and obtained a smaller percent of total N from aquatic insects, than wandering spiders (Figure 3.4). Although some sit-and-wait ground strategists captured along the stream bank and in riparian areas were feeding on aquatic prey, we found no $\delta^{15}N$ labeling beyond 25m (Table 3.4). Orb-web weaving spiders were collected almost exclusively within the first 10m adjacent to the active stream channel. It is not surprising then, that percentage nitrogen from aquatic resources was significantly higher in individuals collected along the stream channel than anywhere else along the transect ($n=5$, $p=0.01$) (Table 3.4).

By calculating biomass-weighted average %N coming from aquatic sources for dominant spider functional feeding groups collected at given distances from the active stream channel, we estimated the average % N coming from emerging aquatic insects to ground-dwelling and vegetation-inhabiting spider assemblages. Average %N coming from emerging aquatic insects to spiders collected on terrestrial vegetation was 28% along the active stream channel (0m), 10% in the riparian zone (10m), and less than 3% in the upland (25- 50m from the stream). The ground-dwelling spider community living along the stream edge obtained on average 20% of their N from aquatic insects, whereas spiders collected in the riparian zone and upland habitats obtained 5% and 1% of their N from instream sources, respectively.

The influence of stream subsidies on the spatial distribution of spiders

Abundance (number of individuals per pitfall trap), biomass and richness of ground-dwelling spiders was highest along the active stream channel (Figures 3.5a-c). More than four times as many spiders were collected adjacent to the active stream channel than were collected within the riparian zone (only 10m away from the active channel); stream-side numbers were seven times higher than those collected 25m or more from the channel (n=25, p=0.0001) (Figure 3.5a). Spider biomass was also significantly higher along the stream edge (within the bank) than anywhere else along the transect (n=25, p= 0.012) (Figure 3.5b). Wolf spiders (family Lycosidae) were the most abundant taxa of ground spiders collected adjacent to the stream edge (88% of all individuals). These spiders were 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). 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 (n=25, p=0.005) (Figure 3.5c). Complete spider species turnover occurred 25 meters 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, where they represented 97% of the total spider biomass and in the riparian zone where they represented 71% of the total spider biomass. Sit-and-wait ground spiders were collected more frequently away from the stream edge near woody debris piles (29% of total spider biomass in the riparian zone and 64% in the upland) (Figure 3.6a). Data from timed beat-net samples indicate that orb web weavers (especially tetragnathids) occur almost entirely within the active channel and riparian zone (0-10m from the bank), whereas sit-and-wait spiders are found more often away from the stream (Figure 3.6b). At least half of the spider species collected on vegetation (25 to 50m from the bank) were spiders that use a sit-and-wait strategy (Figure 3.6b). Along the active stream channel, 51% of total spider biomass collected from vegetation were orb-web weavers, whereas no orb-web weavers were collected in the upland. Sheet-web spiders did not seem to prefer any one habitat along the transect (Figure 3.6b).

Other factors influencing spiders along the edge

Spider abundance, biomass and diversity were higher along the active stream channel, in part because spiders were feeding directly on aquatic insects. Other factors such as changes in structural diversity of the vegetation or ground cover, or increases in terrestrial prey availability along the stream-to-upland transects were not correlated with spider abundance, biomass or diversity.

Ground-dwelling spider abundance and diversity, for instance, 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 in the vegetation (n=5, r^2=0.34, p=0.42).

Availability of terrestrial prey was also unrelated to spider distribution. Terrestrial prey abundance was evenly distributed along the transect from stream bank to upland in pitfall traps (n=25, p=0.78) and timed sweep net samples (n=5, p=0.36). 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 distribution along the transect.

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. We found strong evidence for this linkage in the Sycamore Creek watershed. By using a combination of descriptive (natural abundance ^{13}C and ^{15}N values and analysis of assemblage structure) and experimental (^{15}N-NH_4 tracer addition) approaches, we were able to document flux of nutrients and movement of organisms from aquatic to terrestrial systems and their importance to recipient terrestrial populations.

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 aquatic-terrestrial link to be very strong 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} yr^{-1}, Jackson and Fisher 1986 to 135 g m^{-2} yr^{-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 stream channel and riparian spider abundance are so high relative to 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 have provided conclusive documentation of this transfer of nutrients and organisms and its importance to terrestrial consumers.

Aquatic- terrestrial trophic relationships

The strength of the natural abundance stable isotope approach is that it incorporates $\delta^{13}C$ and $\delta^{15}N$ values of food resources over time with respect to the organism of study. In this ecosystem, the $\delta^{13}C$ of the two sources of prey available for spider consumption were isotopically distinct; hence we could distinguish between potential food resources for spiders. Since many of the larger spiders (both on the ground and in the vegetation) are long-lived (1-2 years or more) and travel fair distances (several to many meters), spiders are most likely at or near equilibrium with respect to their food resources. In four out of the five spider feeding guilds studied, spiders were relying mainly on aquatic resources for their carbon supply (Figure 3.2). In contrast, spiders that sit-and-wait (Gnaphosidae) or build funnel-webs (Agelenidae) in decomposing litter or under woody debris piles were feeding primarily on terrestrial insects.

Because long-term behavioral studies or gut content analyses are not always possible (e.g., for spiders or very small organisms), stable isotope studies can provide new insight into trophic relationships. In this study, $\delta^{13}C$ values show that spiders that build orb-webs or sheet webs or use a sit-and-wait strategy in the vegetation, or spiders that hunt by wandering on the ground looking for prey 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 his study period.

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 $\delta^{15}N$ values, we could determine the proportion of N that 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 3.3). 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 relation 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 (Figures 3.4a and b). These smaller webs are probably more effective at capturing single individuals, as linyphiids usually hang underneath their webs waiting for prey which they usually pull through the sheet after it has become 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 3.3). 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, which has also been observed along the Eel River in Northern California (Power et al. in press). 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 (Figures 3.4a and b). 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 $\delta^{15}N$ 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. Also, natural abundance estimates integrate $\delta^{13}C$ 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 $\delta^{15}N$ 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 et al. in review).

Lateral movement of carbon and nitrogen into the watershed

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 (10m) or upland areas (25- 50m) (Table 3.4). 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, Sanzone et al. in review). 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 we found no evidence that other biological or physical factors explain the increases in spider numbers or diversity along the stream channel. Patterns of spider abundance, biomass and diversity were not related to increased structural complexity or diversity of vegetation, increased ground cover or increased terrestrial prey abundance.

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); however we found this not to be the case at Sycamore Creek. Similarly, 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. In this watershed, the stream did not act as a barrier causing active foragers such as ground-dwelling predators to move linearly along corridors in search of food (Oehler and Litvaitis 1996), as many of the larger spider species we sampled can cross the river, either by crawling across overhanging vegetation, ballooning or walking on water. Results from this study indicate that streams provide a direct trophic subsidy via emerging aquatic insects to spiders living in the surrounding watershed.

Inputs versus outputs: fluxes across habitats, but in which direction?

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. A combination of descriptive (natural abundance isotope data) and experimental (^{15}N tracer addition) stable isotope approaches have shown the importance of stream subsidies to terrestrial consumers.

In Sycamore Creek, leaves contribute less than 1% of the total organic inputs (g AFDM m^{-2} yr^{-1}) to the stream (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). Unlike more mesic stream where the main direction and flow of nutrients and energy is from upland to riparian zone to stream channel, the predominant flow pathway in Sycamore Creek (with its high autochthonous production) is in the opposite direction, from the stream into the riparian zone (Martí et al. 2000). This additional source of energy and nutrients from the stream appears to be subsidizing spider communities living in this arid watershed. Recent studies have shown that this type of stream subsidy may be more common in mesic watersheds, as well (Nakano and Murakami 2001, Sanzone et al. in review).

The drastic fluctuations in flow regime (seasonal flooding and drying) and the temporal and spatial variation in productivity and nutrients in desert streams may serve as models for streams that have been drastically altered due to dams or water diversions in temperate zones. Man-made structures such as dams or diversions that cause drastic alterations in flow or cause periodic and unnatural flooding events have a great impact on surrounding riparian fauna and flora, as the riparian habitat is severed from the stream channel and its subsidies (Iversen et al. 1993). The importance of landscape scale influences on stream habitats and biota have been well documented over the last decade (Roth et al. 1996, Richards et al. 1996); however, the impact of stream degradation on surrounding terrestrial communities is poorly understood. Wenninger and Fagan (2000), studied areas along the Salt River, near Phoenix, Arizona just before the river is diverted into a complex series of urban canals. They found spiders were more abundant and diverse upstream than in similar habitat further downstream where the flow regime had been drastically altered. In this study, spiders (which are good models for other terrestrial predators) were highly dependent on carbon and nitrogen subsidies from Sycamore Creek. As humans continue to alter streams and their surrounding riparian zones, terrestrial predators will also be affected.

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Table 3.1 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. in review).

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 ($gO_2m^{-2}d^{-1}$)	15
R ($gO_2m^{-2}d^{-1}$)	8.3
P:R ratio	1.8

Table 3.2 Adult aquatic insect genera collected in the Sycamore Creek watershed in emergence traps and light traps in June- July of 1997.

Order	Family	Genus	"morphospecies"
Ephemeroptera			
	Baetidae	*Fallceon*	*quilleri* Dodds
		Acentrella	*insignificans* McDunnough
		Callibaetis	sp.
		Centroptilum	sp.
	Caenidae	*Caenis*	sp.
	Tricorythidae	*Tricorythodes*	sp.
		Leptohyphes	sp.
Trichoptera			
	Glossosomatidae	*Culoptila*	sp.
	Helicopsychidae	*Helicopsyche*	sp.
	Hydropsychidae	*Hydropsyche*	sp. "A"
		Hydropsyche	sp. "B"
		Cheumatopsyche	sp.
	Hydroptilidae	*Ochrotrichia*	sp.
	Limnephilidae	*Limnephilus*	sp.
	Odontoceridae	*Marilia*	sp.
	Philopotamidae	*Chimarra*	sp.
	Polycentropidae	*Polycentropus*	sp.
	Sericostomatidae	*Gumaga*	sp.
Diptera			
	Chironomidae		spp.
	Dolichopodidae		spp.
	Simulidae	*Simulium*	sp.
	Stratiomyiidae		spp.
	Tabanidae	*Tabanus*	sp.
	Tipulidae	*Cryptolabis*	sp.

Table 3.3 Average (+/- s.e.) 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 equation 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.

Spider families	# of composite samples analyzed	average %N (+/- s.e.)	%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 & Zelotes*)	4	7.6 (1.9)	6-10%

NC= Standard error not calculated because n=1

Table 3.4 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 equation 5). 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 10m from the active channel (n=5, p=0.0112).

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

** Statistically significantly different from other distances
NP= None collected in timed sweep nets
NC= Standard error not calculated because n= one individual
NA = Not analyzed for δ^{15}N
NL= Not considered labeled if δ^{15}N value is less than 2

Figure 3.1 Exponential decay curve (solid line) is derived from both in-stream aquatic nymph/ larvae data (averages presented as open circles) and emerging aquatic adults (averages presented as closed 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. $\delta^{15}N_{0,E}$ was determined to be 202 and the decay constant was –0.01557 (r^2=0.874, p= 0.0001). The end-point mixing model (dashed line) is derived from $\delta^{15}N$ values from aquatic insects captured in light traps at 15 and 35m (closed 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 20m upstream from the ^{15}N release (closed triangles) agrees with model predictions.

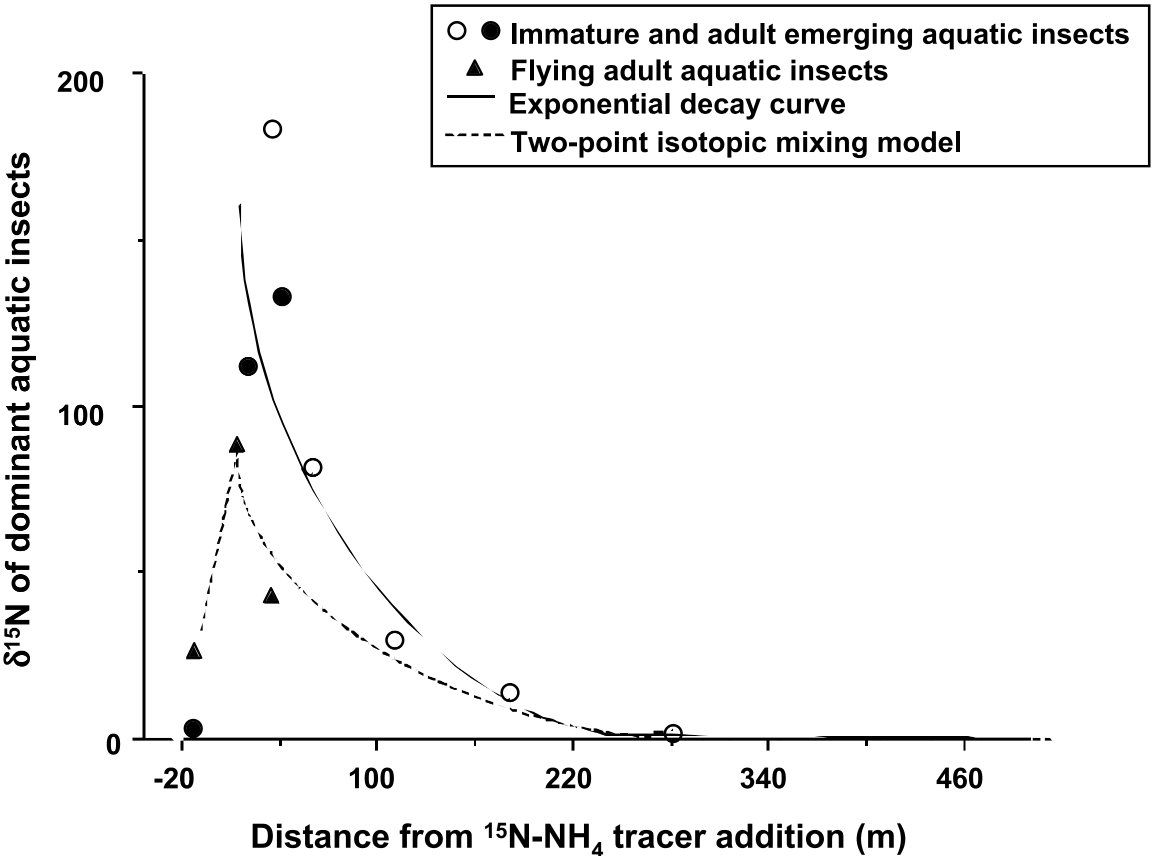

○ ● Immature and adult emerging aquatic insects
▲ Flying adult aquatic insects
Exponential decay curve
Two-point isotopic mixing model
$\delta^{15}N$ of dominant aquatic insects
200
100
0
-20
100
220
340
460
Distance from ^{15}N-NH_4 tracer addition (m)

Figure 3.2 Natural δ^{13}C and δ^{15}N values (mean +/- s.e.) 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 (shw) (Linyphiidae) are feeding mainly on aquatic insects emerging from Sycamore Creek (large open ellipse), whereas spiders that capture prey using a sit-and-wait strategy on the ground (swg) (Agelenidae and Gnaphosidae) are most likely feeding on terrestrial prey (outside ellipse). 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* (Trichoptera) (cg1), *Caenis, Tricorythodes* (Ephemeroptera) (cg2), Stratiomyiidae (Diptera) (cg3) and Chironomidae (Diptera) (cg4); grazers from the genera *Helicopsyche* (Trichoptera) (gz1) and *Fallceon* (Ephemeroptera) (gz2); and aquatic predators from the suborders Zygoptera (pr1) and Anisoptera (Odonata) (pr2).

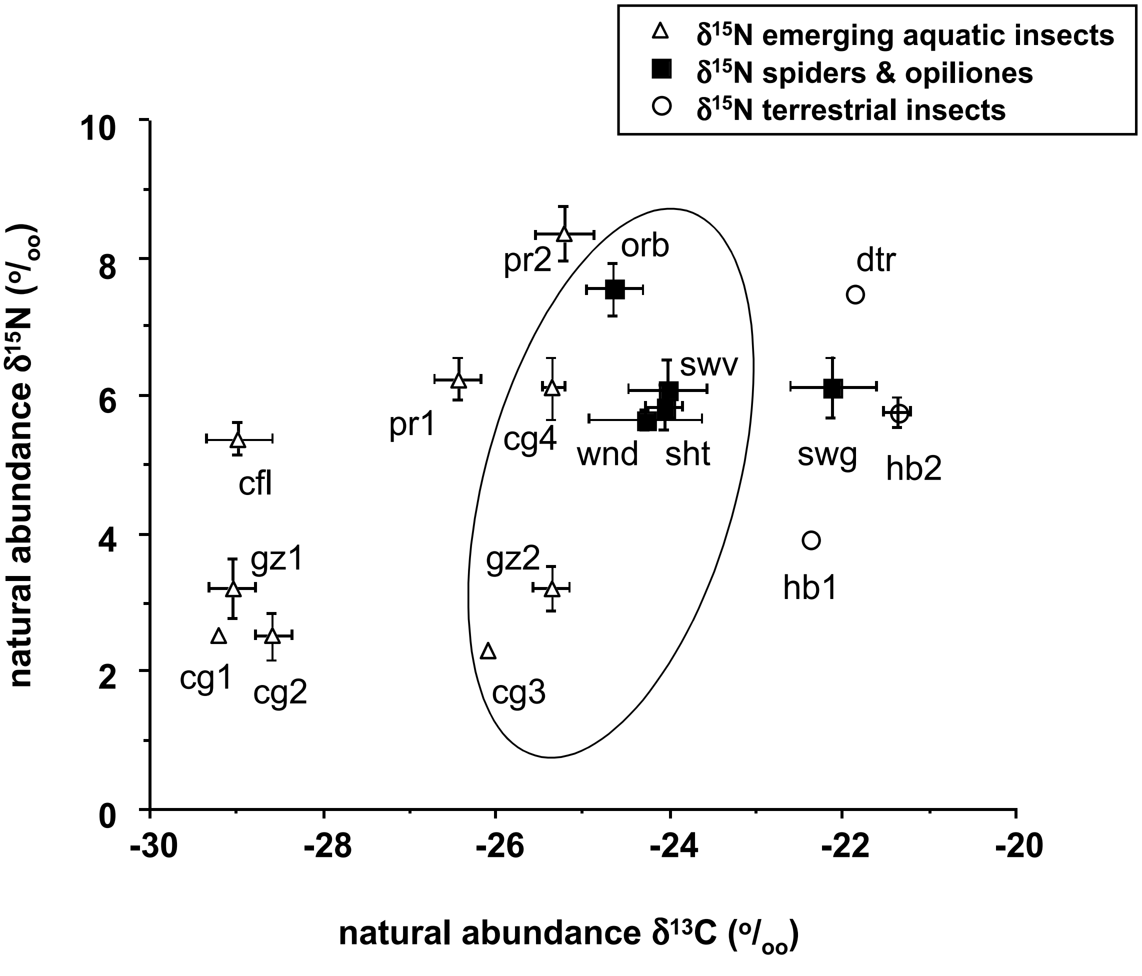
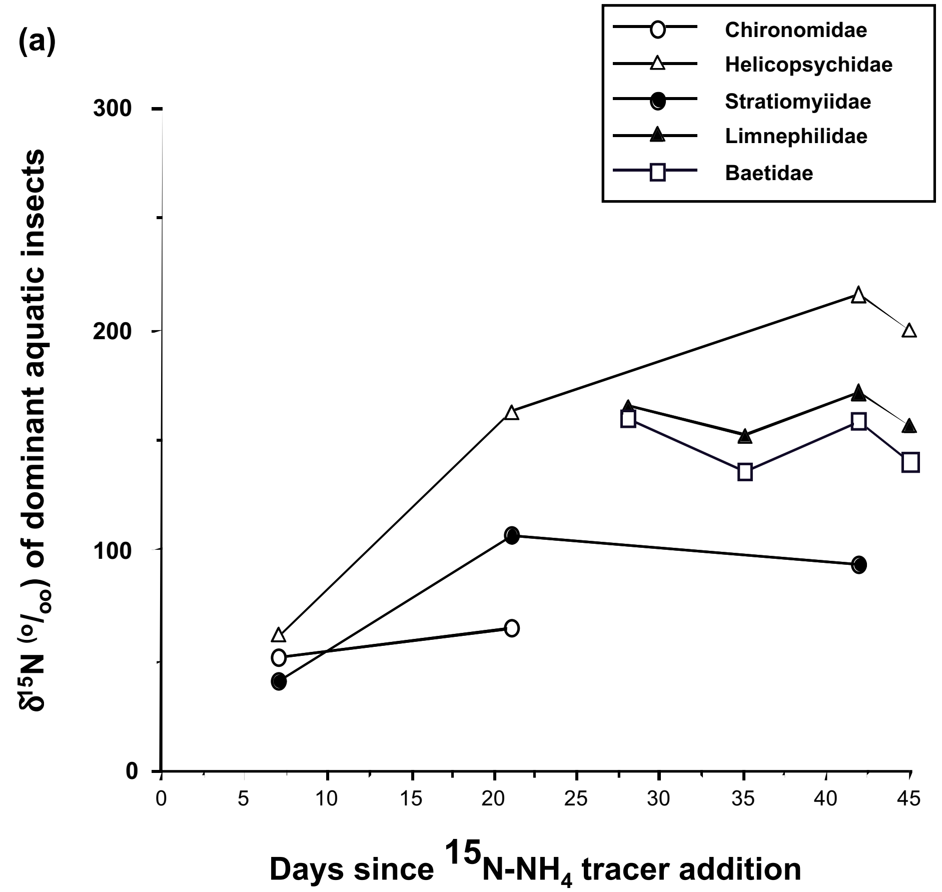

△ δ15N emerging aquatic insects
■ δ15N spiders & opiliones
○ δ15N terrestrial insects
natural abundance δ15N (o/oo)
natural abundance δ13C (o/oo)
10
8
6
4
2
0
-30
-28
-26
-24
-22
-20
pr2
orb
dtr
swv
pr1
cg4
wnd
sht
swg
hb2
cfl
gz1
gz2
hb1
cg1
cg2
cg3

Figure 3.3 (a) $\delta^{15}N$ signals over time (40m downstream from the ^{15}N tracer addition) and (b) distance downstream (20-280 m) on Day 42 of the release, for dominant aquatic insects (Chironomidae, Helicopsychidae, Limnephilidae, Stratiomyiidae, and Baetidae) collected in Sycamore Creek during the ^{15}N tracer release. Data points represent composite samples of 5 or more individuals (accuracy is +/- 0.5 $^{o}/_{oo}$). All aquatic insects have reached isotopic equilibrium by the end of the experiment (a) and tracer $\delta^{15}N$ values show similar downstream patterns for most dominant species (b).

(a)


Chironomidae
Helicopsychidae
Stratiomyiidae
Limnephilidae
Baetidae
300
200
100
0
0
5
10
15
20
25
30
35
40
45
$\delta^{15}N$ (°/$_{oo}$) of dominant aquatic insects
Days since $^{15}N-NH_4$ tracer addition

(b)

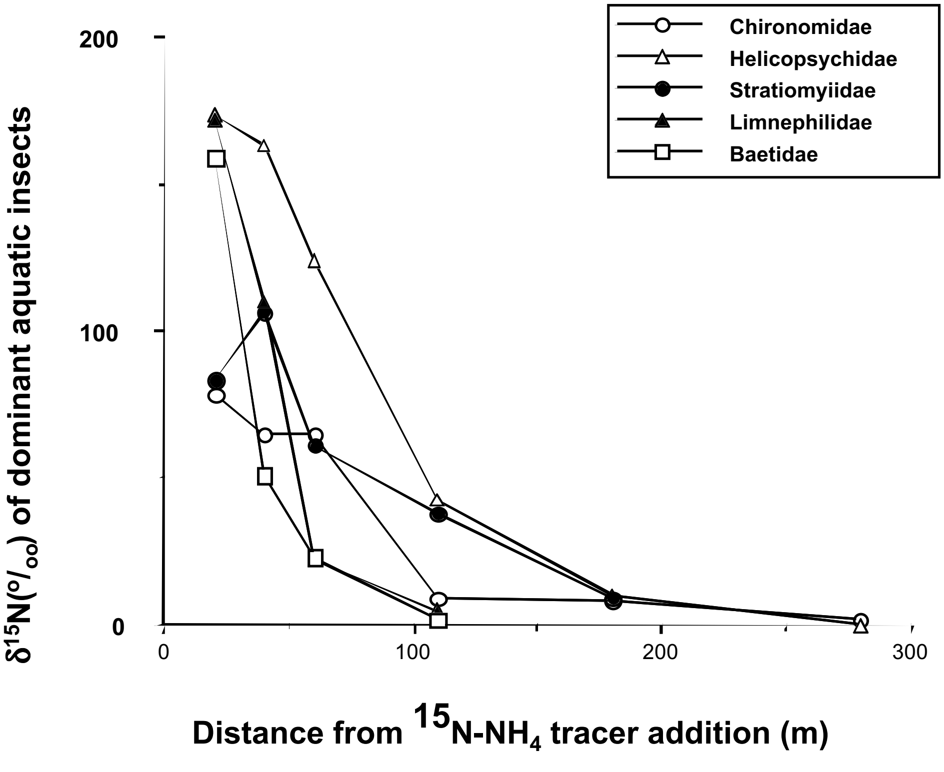
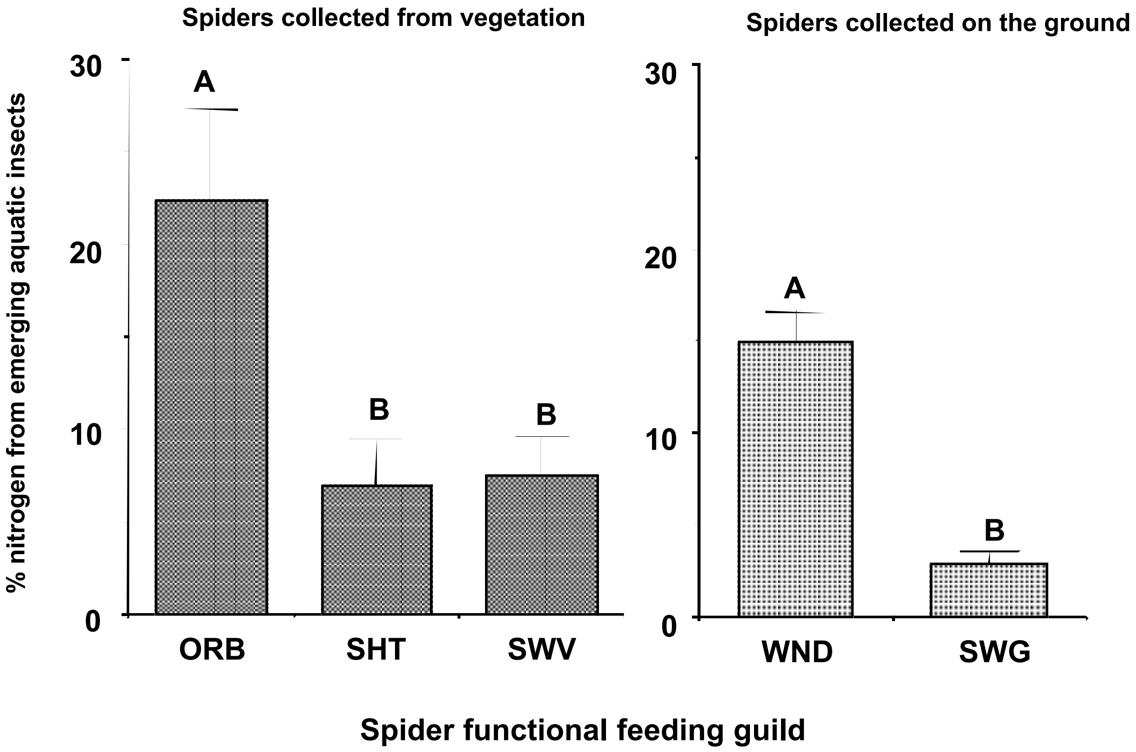

Chironomidae
Helicopsychidae
Stratiomyiidae
Limnephilidae
Baetidae
200
100
0
0
100
200
300
$\delta^{15}N$(°/$_{oo}$) of dominant aquatic insects
Distance from $^{15}N-NH_4$ tracer addition (m)

Figure 3.4 Percent of spider N (by functional feeding guild) obtained from emerging (a) and flying (b) aquatic insects. 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). Spiders collected on vegetation using timed beat nets were divided into three groups: sit-and-wait strategists (swv) (Salticidae and Thomisidae), aerial orb-web weavers (orb) (Araneidae and Tetragnathidae), and sheet-web spiders (shw) (Linyphiidae). We calculated spider N derived from ^{15}N enriched aquatic insects using a two-source isotopic mixing model (a) that underestimates the fraction of N coming from aquatic sources (see text). Spider N derived from aquatic insects is more accurately determined with a more complex two-point mixing model (b) that takes into account unlabeled aquatic insects flying upstream. Both the two-source and end-point mixing models indicate that orb-web weavers (orb) relied more heavily on aquatic resources, than sheet-web weavers (sht) or spiders that use a sit-and-wait strategy (swv) to capture prey on vegetation (n=35, p=0.0243, n=35, p=0.0347, respectively). Similarly, wandering spiders (wnd) relied more heavily on emerging adult aquatic insects than spiders that use a sit-and-wait strategy (swg) on the ground (n=8, p=0.0446, n=8, p=0.0556, respectively).

(a)


Spiders collected from vegetation
Spiders collected on the ground
% nitrogen from emerging aquatic insects
30
20
10
0
A
B
B
ORB
SHT
SWV
30
20
10
0
A
B
WND
SWG
Spider functional feeding guild

(b)

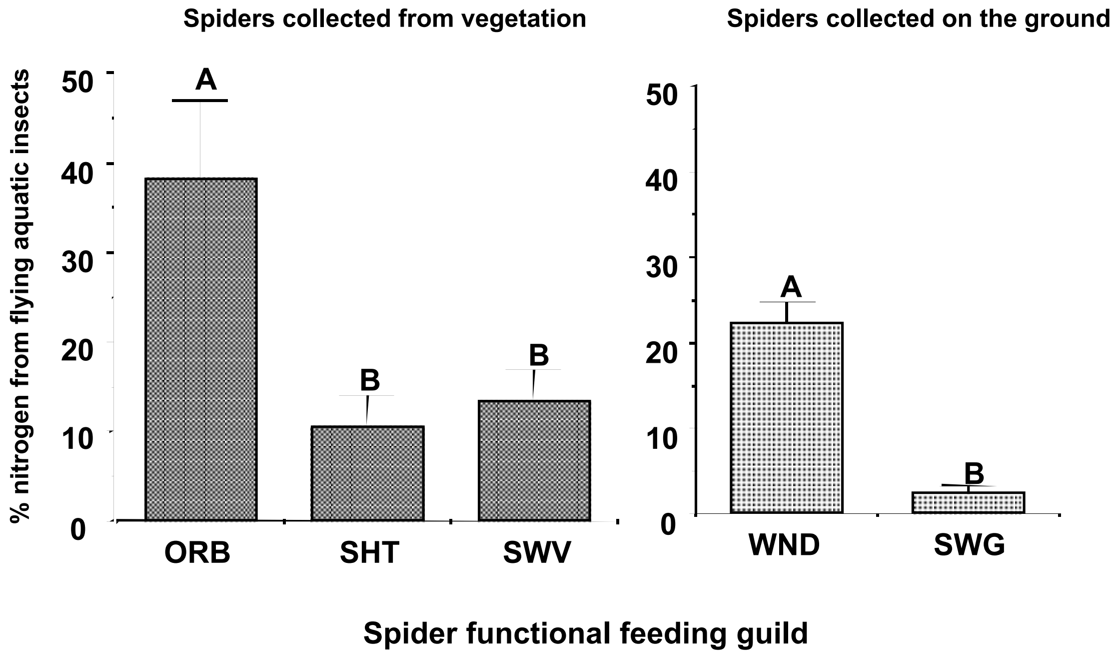

Spiders collected from vegetation
Spiders collected on the ground
% nitrogen from flying aquatic insects
50
40
30
20
10
0
A
B
B
ORB
SHT
SWV
50
40
30
20
10
0
A
B
WND
SWG
Spider functional feeding guild

Figure 3.5 Mean spider abundance (number of individuals per trap) (a), biomass (b) and diversity (c) collected in 48 hour pitfall traps from 5 transects (0-50m). Traps 0 meters from the stream are within the active (dry) channel along the wetted stream edge, traps 10m 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 (ANOVA, p= 0.05).

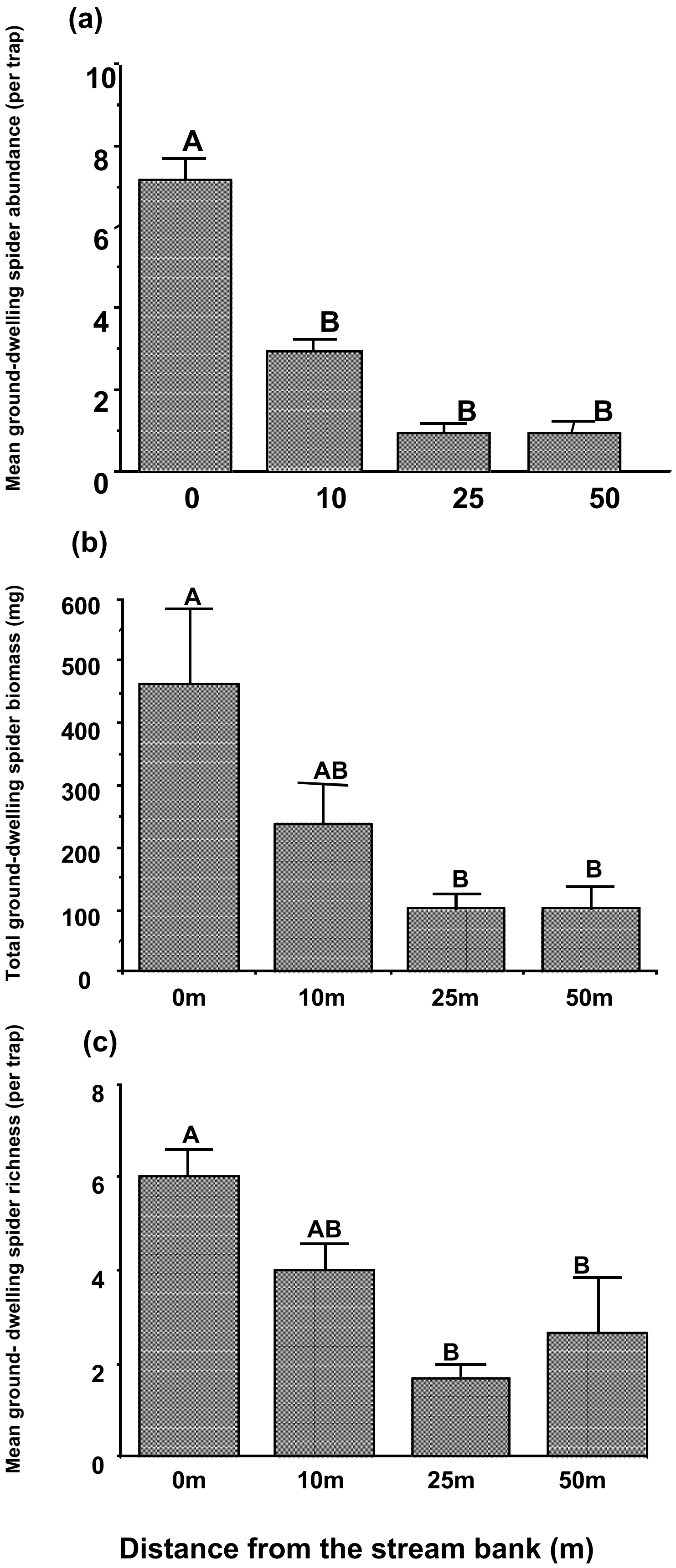
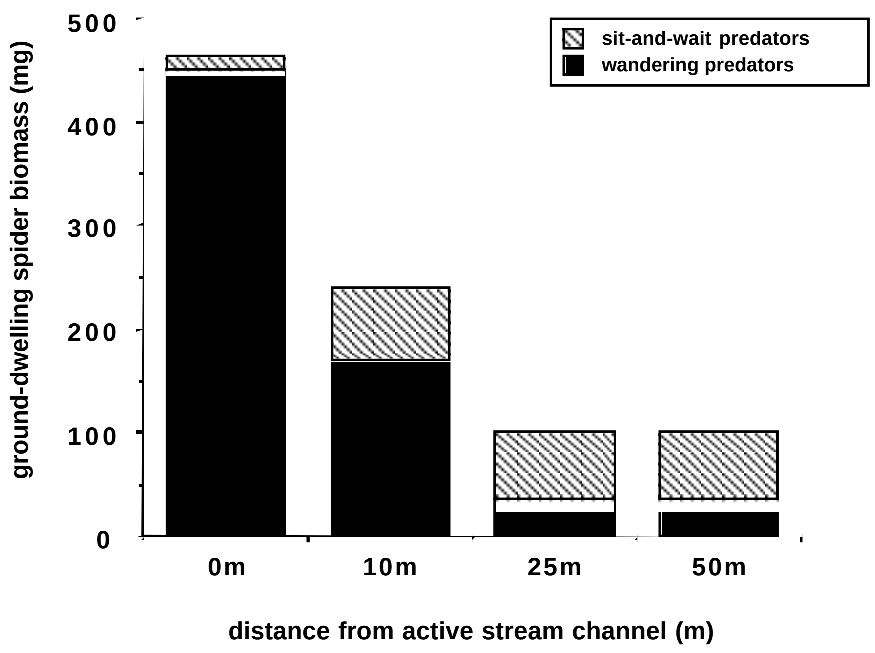
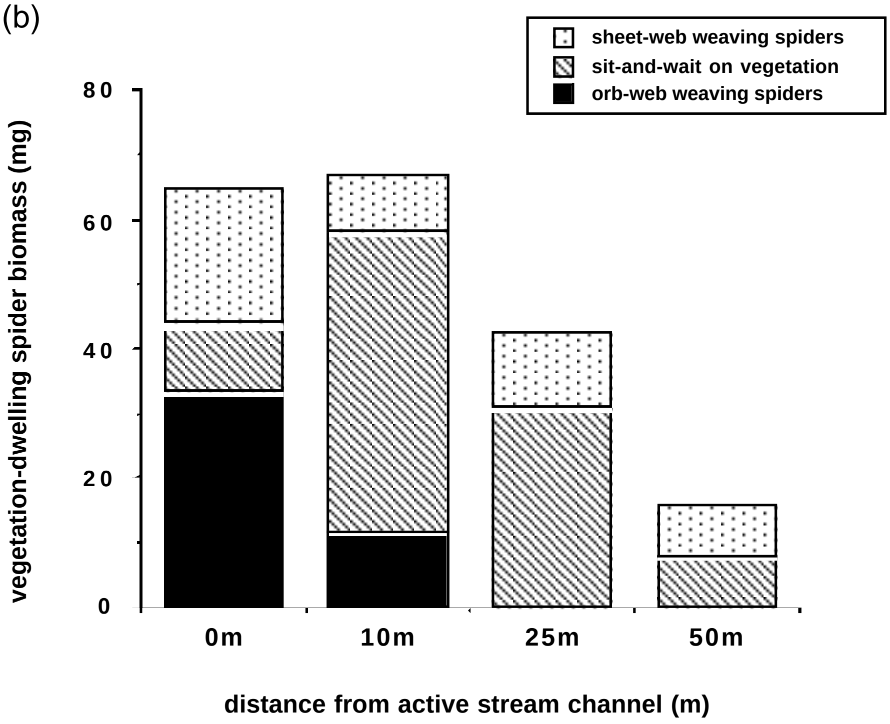

(a)
Mean ground-dwelling spider abundance (per trap)
10
8
6
4
2
0
A
B
B
B
0
10
25
50
(b)
Total ground-dwelling spider biomass (mg)
600
500
400
300
200
100
0
A
AB
B
B
0m
10m
25m
50m
(c)
Mean ground- dwelling spider richness (per trap)
8
6
4
2
0
A
AB
B
B
0m
10m
25m
50m
Distance from the stream bank (m)

Figure 3.6. Percent of total spider biomass from each functional feeding guild collected on the ground in pitfall traps (a) and in vegetation using timed beat net samples (b).

(a)


sit-and-wait predators
wandering predators
500
400
300
200
100
0
ground-dwelling spider biomass (mg)
0m
10m
25m
50m
distance from active stream channel (m)

(b)


sheet-web weaving spiders
sit-and-wait on vegetation
orb-web weaving spiders
80
60
40
20
0
vegetation-dwelling spider biomass (mg)
0m
10m
25m
50m
distance from active stream channel (m)

CHAPTER 4

THE INFLUENCE OF STREAM SUBSIDIES ON SPIDER COMMUNITIES IN EIGHT RIPARIAN FORESTS

[1] Sanzone, D. M. To be submitted to *Environmental Entomology*

Abstract. The riparian zones and adjacent upland habitats of eight streams located in different biogeographic regions were examined to determine patterns of spider biomass, abundance and diversity. Riparian spider biomass, abundance and diversity was compared to physical and biological parameters to determine which factors might be important in predicting the spatial distribution of spiders between riparian and upland habitats. Pitfall traps and timed beat net samples were used to collect ground-dwelling and lower canopy spiders along a gradient from stream edge to upland habitats in each of the eight watersheds. In addition, emerging aquatic insects and terrestrial prey were collected, temperature and rainfall were measured, and differences in the structural complexity of live and decomposing vegetation were determined. Although sites were located in different biogeographic regions, varied greatly in temperature and precipitation, and were sampled in different seasons, consistent patterns in the spatial distribution of spiders among the eight sites were found. Lower canopy and ground-dwelling spiders were significantly more abundant in riparian zones than in upland habitats in at least four of the eight sites, whereas upland habitats never contained more spiders. Ground-dwelling and lower canopy spider richness was also higher along the stream edge in seven of the eight sites. Lower canopy and ground-dwelling spider biomass and abundance were related to emergence biomass, which varied greatly between the sites. Spider abundance and biomass in the lower canopy were also influenced by structural complexity of vegetation and temperature. Richness of ground-dwelling spiders was related to litter depth, whereas richness of lower canopy spiders was related to emergence biomass. Evidence from the eight different biogeographic regions suggests that aquatic insect emergence and microhabitat availability are important predictors of spider biomass, abundance and diversity. Terrestrial insects alone could not support the spider biomass found in the riparian zones of five of the eight sites; however, the additional energy supplied by aquatic insects could support the elevated spider biomass in all five of those riparian habitats.

Key words: aquatic insects, Araneae, emergence, predators, riparian zone, spiders.

INTRODUCTION

Riparian zones contain high densities and numbers of predators (Gray 1993, Knopf and Samson 1994, Naiman and Decamps 1997); however, reasons for this high concentration of species and individuals are poorly understood. Studies that have focused on the distribution of consumers in riparian zones have considered such influences as: changes in microhabitat (Uetz 1976, Naiman and Rogers 1997, Ellis et al. 2001) or microclimate (Wenninger and Fagan 2000); changes in predator- prey interactions or shifts in foodweb structure (Caraco and Gillespie 1986, Reichert and Hall 2000); increased structural complexity or productivity of terrestrial vegetation (Williams et al. 1995, Aiken and Coyle 2000); or changes in nutrient availability (Vargas 2000). Although some of these factors may be important at a local or regional scale, they are not sufficient to explain patterns in the distribution of terrestrial predators in riparian habitats across biomes.

Many stream studies have emphasized the linkages between riparian and aquatic ecosystems (Gregory et al. 1991, Wallace et al. 1997), and the importance of terrestrial insect subsidies to stream predators (Edwards and Huryn 1996, Cloe and Garman 1996, Nakano et al. 1999); however, the importance of aquatic subsidies to terrestrial predators remains poorly understood (Nakano and Murakami 2001, Polis et al. in press). Recent studies indicate that spiders, bats and birds inhabiting some forested riparian zones are relying on emerging aquatic insects for a substantial portion of their energy needs (Gillespie 1987, Power and Rainey 2000, Henschel et al. in press, Sanzone et al. in review-a); however, aquatic subsidies may be site specific and seasonally variable (Nakano and Murakami 2001). For instance, in desert or arctic streams where aquatic insect emergence most likely exceeds terrestrial insect productivity (Jackson and Fisher 1986), aquatic subsidies may be one of the most important factors regulating terrestrial predator densities (Sanzone et al. in review-b). In forested headwater streams or large rivers with extensive floodplains, where emergence production is seasonal and dependent on a multitude of factors, the importance of aquatic subsidies to terrestrial communities may vary both spatially and temporally.

In spite of the potential importance of emerging aquatic insects to riparian predators, few data been collected on the export of aquatic insects from streams to riparian zones, and their importance to terrestrial invertebrate predators (Power et al. 1998, Nakano and Murakami 2001, Henschel et al. in press). In this study, biomass, abundance and diversity of spiders is documented along a gradient from stream edge to upland habitats (to a distance of 50 m) in eight sites located in different biogeographic regions**.** To determine patterns of spider abundance and species composition between riparian and upland habitats, spiders were collected at each of the eight sites using pitfall traps and timed beat net samples. Data were analyzed from the spider community as a whole (both ground-dwelling and lower canopy spiders). In addition, a more detailed analysis of the two most common spider ‘feeding guilds’, wandering and web-weaving spiders, were analyzed for differences in abundance and biomass between upland and riparian habitats.

The distribution of terrestrial predators from riparian to upland habitats was hypothesized to be related to two factors: aquatic insect emergence (Power and Rainey 2000, Sanzone et al. in review-a), and structural complexity of live and decomposing vegetation (MacArthur 1964, Uetz 1976). Therefore sites with the greatest aquatic insect emergence during the sampling period and with riparian zone vegetation that differed greatly in structure from that of the upland (e.g., desert and arctic sites) were predicted to contain the highest concentration of spiders in riparian zones relative to upland (Figure 4.1). Sites with little aquatic emergence during the sampling period and no structural differences in vegetation or litter between riparian and upland habitats (e.g., eastern deciduous forested sites) were predicted to show little or no differences in spider abundance, biomass or diversity with respect to the different habitats (Figure 4.1). In order to determine the importance of emerging aquatic insects and structural complexity of vegetation, along with other factors such as temperature, rainfall and terrestrial prey availability, data were collected from eight sites located in different biogeographic regions. This study enhances our understanding of the factors which are most important in influencing the spatial distribution of spiders in riparian habitats.

METHODS

Study sites

Spiders were collected from riparian zones of eight streams located in different biogeographic regions of North America and Iceland (Figure 4.2). The riparian zones were located in watersheds dominated by tall-grass prairie, desert, arctic and forest habitats; all were relatively undisturbed by human activities (Table 4.1). Dominant riparian vegetation at the desert site (Sycamore Creek watershed, Arizona, SCAZ) was very different from upland areas and consisted of: willow (*Salix exigua* and *S. goodingii*), ash (*Fraxinus pennsylvanica velutina*), sycamore (*Platanus wrighti*), cottonwood (*Populus fremontii*), walnut (*Juglans major*), mesquite (*Prosopis gladulosa*), seepwillow (*Baccharis salicifolia*) and burro bush (*Hymenoclea monogyra*). The upland areas of the desert site were dominated by drought tolerant species such as: saguaro (*Cereus giganteus*) and prickly pear cactus *(Opuntia spp.*). Dominant riparian vegetation at the tall grass prairie site (South Kings Creek watershed, Kansas, KCKS) also differed drastically from upland areas and was dominated by the following tree species: American elm (*Ulmus americana*), common cottonwood (*Populus deltoides*), roughleaf dogwood (*Cornus drummondi*) and fragrant sumac (*Rhus aromatica*). Prairie grasses (*Andropogon gerardii, A. scoparius* and *Sorghastrum nutans*) dominated the upland areas at KCKS.

The remaining six sites were forested throughout their watersheds. The tropical forest site (Quebrada Bisley watershed, Puerto Rico, QBPR) was located in a subtropical wet forest (Ewel and Whitmore 1973) and contained three dominant woody species: *Dacryodes excelsa*, *Sloanea berteriana* and *Prestoea montana* which accounted for over 60% of the above ground biomass (Chinea et al. 1993). The two southern deciduous forest sites (Upper Ball Creek watershed, North Carolina, UBNC and Walker Branch watershed, Tennessee, WBTN) contained similar tree species. WBTN was dominated by several species of oak

(*Quercus* spp.), yellow poplar (*Liriodendron tulipifera*) and red maple (*Acer rubrum*), and UBNC was dominated by oak (*Quercus* spp.), hickory (*Carya* spp.), and yellow poplar (*Liriodendron tulipifera*). The main difference between the two was that UBNC contained a thick understory of rhododendron (*Rhododendron maximum*) which formed a closed canopy over the stream throughout the year, whereas WBTN did not. The northern conifer forest site (Mack Creek watershed, Oregon, MCOR) was dominated by Douglas-fir (*Pseudotsuga menziessii*), western red cedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*). The northern deciduous forest site (Bear Brook watershed, New Hampshire, BBNH) was dominated by American beech (*Fagus grandifolia*), yellow birch (*Betula lutea*) and sugar maple (*Acer saccharum*). The arctic watershed (Steinbogalækur, Iceland, STIC) was dominated by smaller species of woody shrubs including: dwarf birch (*Betula nana*), several species of willow (*Salix lanata, S. phylicifolia and S. callicarpaea*), bog bilberry (*Vaccinium uliginosum*) and crowberry (*Empetrum nigrum)*. Although plant species were similar throughout the watershed, standing stock biomass was concentrated along the stream edge at the arctic site (Sanzone et al. in review-b)

Data collection and analysis

To determine changes in biomass, abundance and diversity of spiders, five 50m transects were established, running perpendicular to the stream bank (transects were approximately 10 m apart, hence we sampled a 50 x 50 m area adjacent to the stream reach). Spiders and potential prey were sampled along each of the five transects directly adjacent to the stream bank (at 0 m), and at 10, 25 and 50 m away from the stream edge. Sampling areas located along the active stream channel and 10 m from the stream edge were considered to be riparian habitat, whereas sampling areas located 25 and 50 m from the stream edge were considered upland habitat. Arthropods inhabiting lower herbaceous vegetation and the litter layer were sampled using 48-hour pitfall traps (Sanzone et al. in review-b). Pitfall traps were left open for 48 hour periods on five different sampling dates over approximately a three week sampling period (n=100 at each site: 5 dates * 5 transects * 4 distances). Spiders and arthropod prey (terrestrial and aquatic) were collected from riparian vegetation less than 3 m in height using timed (5 min) sweep net samples (n=20 at each site: 5 transects * 4 distances) (Coddington et al. 1996). Spiders collected in the lower canopy using timed beat nets are referred to as ‘canopy spiders’ throughout this paper. All insects and spiders were returned to the lab, sorted and placed in 70% ethanol until adult spiders could be identified to genus and morphospecies, immature spiders identified to family, aquatic prey identified to genus or family (Diptera) and terrestrial prey identified to family when possible, order when not. Once identified, each taxonomic groups in each sample was dried at 60^{o}C for approximately 48 hours and weighed for biomass. Total biomass of terrestrial prey (TRBM) collected in riparian habitats at each of the sites was calculated by summing the weights of all insects collected in pitfall traps within a grid (10 m wide by 50 m long- along the stream edge) over the 10 day period (5 sampling dates *48 hour sampling periods).

Two-way ANOVA (n=160, 10 traps per habitat x 8 sites x 2 habitats) procedures were used to compare differences between riparian and upland spiders among the eight sites (JMP, SAS 1995). The analysis was done for both ground-dwelling and canopy spiders separately. The two-way ANOVA (site x habitat) results showed significant disorderly interaction effects for abundance and biomass of both ground-dwelling and canopy spiders, hence main effects could not be tested using this procedure. Differences in mean abundance of ground-dwelling and canopy spiders between riparian (0 and 10m transects) and upland habitats (25 and 50 m transects) at each site were analyzed separately using one-way analysis of variance procedures (ANOVA) instead (JMP, SAS 1995). A ln (x+1) transformation (Sokal and Rohlf 1981) was applied when data were not normally distributed (Shapiro and Wilk 1965). Spider biomass is reported as total biomass, which was calculated by summing the weights of all individuals collected on all dates. Spider richness is reported as total number of genera found in each of the habitats (riparian vs. upland). Differences in mean abundance and biomass of web-spinning spiders (collected using beat nets) and wandering (hunting) spiders (collected in pitfall traps) in riparian and upland habitats were also analyzed separately, using ANOVA procedures (JMP, SAS 1995).

Quantitative estimates of aquatic insect emergence were made using 0.25 m^2 emergence traps (n=9 at each site). Traps were constructed from PVC pipes and covered with window screening (0.3 mm mesh). The base of the traps were anchored into the stream substrate to prevent insect drift from entering the traps.

The top of the traps contained an inverted funnel and glass jar. This design, while preventing drift, allowed water to flow through the traps at a velocity similar to that of the surrounding water. Emergence traps were sampled using an aspirator and forceps on 5 separate dates after traps were allowed to collect emerging insects for 48 hours (45 samples at each site). All aquatic insects were taken to the lab, identified to genus or family, dried at 60^o for 48 hours, and weighed to estimate emergence biomass in each taxonomic group. Total biomass of aquatic insects (AQBM) emerging from each of the stream reaches over the 10 sampling days was estimated by summing the weights of all insects emerging on all dates. To compare the relative biomass of emerging aquatic insects to terrestrial insects, biomass of emerging aquatic insects (g m^{-2}) was multiplied by reach area (50 m long x average stream reach width) and compared to TRBM as described previously. AQBM* is biomass of emerging aquatic insects (g m^{-2}) * 10 d * reach area.

Terrestrial vegetation was measured using 1 m^2 plots along the transects from the stream bank to 50 m (n=20). In each m^2 plot, plant species richness (PLTSPP), total number of vegetative stalks (NMSTLK), number of vertical points transected (VRTPNT), litter depth (LTDPTH) and structural diversity of ground cover (SDGCVR) was documented. Number of ‘vertical points’ was calculated by counting the number of times vegetation intercepted a 3 m high rod in each of the m^2 plots (MacArthur and Horn 1969, Dobkin et al. 1998). Structural diversity of ground cover was measured by placing ground cover collected from m^2 plots into micro-habitat classes, then calculating structural complexity of ground cover

(Southwood et al. 1979). Temperature (MNTEMP) and rainfall (TOTRNF) data were collected by US Forest Service or NOAA personnel (WBTN) as part of long-term data collection efforts. Temperature measurements in Iceland (STIC) were made using Onset Hobo temperature gauges and rainfall data was collected by Myvatn Research Station personnel as part of a long-term data collection effort.

Multiple regressions were used to identify empirical relationships between physical and biological parameters and spider biomass, abundance and richness found in the eight riparian zones. In addition, I used multiple regressions to determine the relationship between independent parameters and differences between riparian and upland spider biomass and abundance among the eight sites. All independent parameters (AQBM, TRBM, PLTSPP, NMSTLK, VRTPNT, LTDPTH, SDGCVR, MNTEMP, TOTRNF) were tested for autocorrelation before being entered into stepwise regressions. Only variables significant at the 0.05 level were added to the standard least squares multiple linear regression model (Sokal and Rohlf 1981).

RESULTS

Prey available for spider consumption

Aquatic insect emergence varied from 0.09 (UBNC) to 206.9 (STIC) mg $m^{-2}d^{-1}$ during the sampling periods. Total biomass of aquatic insects (AQBM) emerging over the 10 day period from each of the 50 m stream reaches ranged from 0.01 g in North Carolina (less than 1% of total instream biomass) to 18.6 g in Iceland (30% of total instream biomass) (Appendix 4.1). Total biomass of terrestrial insects collected directly adjacent to the stream edge (500 m^2), over the same 10 day period, varied from 0.47 g in Iceland (STIC) to 11.76 g in Tennessee (WBTN) (Appendix 4.1). The arctic (STIC), desert (SCAZ), tropical montane (QBPR) and conifer (MCOR) forest sites had a greater biomass of emerging aquatic insects than terrestrial insects. The tall-grass prairie (KCKS) and three eastern deciduous sites (WBTN, BBNH and UBNC) had a greater biomass of terrestrial insects.

Spiders in riparian versus upland habitats

Ground-dwelling spiders were 2-6 times more abundant in riparian zones than upland habitats in the desert, tall-grass prairie and arctic sites during the sampling periods (Table 4.2). Of the forested watersheds, Walker Branch (WBTN), one of the eastern deciduous sites, contained 50% more ground-dwelling spiders in riparian zone than upland habitats. The tropical (QBPR) and northern conifer forest (MCOR) sites had a greater number of spiders in riparian zone habitats, although differences were not significant (Table 4.2). Ground-dwelling spider biomass and richness was higher in riparian zones than in upland habitats in seven of the eight sites; the greatest differences were in desert, tall-grass prairie and arctic sites (Tables 4.3 and 4.4).

The only environmental parameter that had a significant positive relationship with ground-dwelling spider abundance and biomass in riparian zone habitats across all biomes was aquatic emergence (AQBM) (Table 4.5). Despite the large variability among the sites with respect to temperature, rainfall and structural complexity of vegetation (Table 4.1 and Appendix 4.1), I found no relationship between any of those variables and ground-dwelling spider biomass or abundance. The differences in ground-dwelling spider biomass between riparian and upland habitats was calculated for each site. There was a positive relationship between emergence biomass and difference between upland and riparian spider biomass ($n=8$, $r^2=0.52$, $p<0.04$). In addition, ground-dwelling spider generic richness was positively related to litter depth (LTDPTH) across sites ($n=8$, $r^2=0.61$, $p<0.02$).

Spiders collected on vegetation were significantly more abundant in the riparian zone than in upland habitats in five of the eight sites (Table 4.2). Of the remaining three sites, two showed a trend towards higher canopy spider abundance in riparian zone habitats, though not significant. Canopy spider biomass and richness was higher in riparian habitats than in upland habitats in seven of the eight sites, further supporting the hypothesis that canopy spiders are concentrated at the land-water margin (Tables 4.3 and 4.4).

Environmental variables of importance to canopy spiders were: AQBM, VRTPNT and MNTMP for abundance (Table 4.5); AQBM and VRTPNT for biomass (Table 4.5); and AQBM for richness ($n=8$, $r^2= 0.823$, $p=0.012$). Other factors such as TPBM, NMSTLK and TORNFL were not correlated with ground or canopy-dwelling spider biomass or abundance (Table 4.5). Sites with both high emergence biomass and a more complex structure along the bank (VRTPNT) were also the sites that had the greatest differences between riparian and upland spider biomass ($n=8$, $r^2=0.974$, $p<0.0001$).

Wandering spiders in riparian and upland habitats

Wandering spiders collected on the ground were from the families Clubionidae, Gnaphosidae, Hahniidae, Lycosidae, Salticidae, Sparassidae, Thomisidae and some Agelenidae (*Coras, Wadotes*). Abundance of wandering spiders was higher in riparian habitats than upland habitats in the desert (n=50, p=0.014), arctic (n=50, p=0.009) and tall grass prairie sites (n=50, p=0.020). Because of the large body size and greater abundance of wolf spiders (family Lycosidae) relative to other groups, wandering spiders also accounted for the greatest differences in biomass between riparian and upland habitats at these sites (n=50, p=0.065, 0.002, 0.054, respectively). In fact, more than 92% of the ground-dwelling spider biomass in these riparian zones was from the family Lycosidae. Wolf spiders also dominated the upland areas of these sites, indicating that lycosid distributions were driving the patterns of biomass and abundance observed for wandering spiders. The litter layers in riparian and upland areas in the northern conifer (MCOR) and two eastern deciduous sites (UBNC and BBNH) were dominated by wandering spiders from the family Agelenidae, whereas riparian zone habitats in the eastern deciduous forest site (WBTN) were dominated by spiders from the family Gnaphosidae, with similar numbers of Lycosidae and Gnaphosidae in the upland. The tropical forest site (QBPR) had very few wandering spiders (18 individuals total), but of the wandering spiders collected, almost equal numbers of individuals from the families Lycosidae, Gnaphosidae, Salticidae and Clubionidae were found in both riparian and upland habitats.

Biomass and abundance of wandering spiders was positively related to emergence biomass (Table 4.5), but none of the other environmental variables showed a significant relationship with wandering spiders. Differences between biomass and abundance of wandering spiders in riparian versus upland habitats was positively related to litter depth (r^2=0.679, p=0.012 and r^2=0.0.651, p=0.016, respectively). In general, sites with a higher proportion of aquatic prey relative to terrestrial prey had a greater biomass of wandering spiders in riparian zone habitats (n=8, r^2=0.71, p<0.008).

Web-spinning spiders in riparian and upland habitats

Web-spinning spiders collected from the lower canopy were from the families Araneidae, Linyphiidae, Dictynidae, Pholcidae, Tetragnathidae, Theridiidae, Theridiosomatidae, Uloboridae and select Agelenidae (*Agelenopsis*). Abundance of web-spinning spiders was higher in riparian habitats in the arctic, desert, and tall-grass prairie sites (n=10, p<0.0001, 0.017 and 0.0001, respectively). Biomass of web spinners was also was also higher in the riparian zones of the arctic, desert and tall-grass prairie sites, along with the two southern deciduous forest sites (n=10, p<0.0006, 0.036 and 0.0001, 0.0007and 0.015 respectively). In desert and arctic sites, riparian zones were dominated by web-spinning spiders from the families Tetragnathidae and Araneidae (52% in the desert and 70% in the arctic), whereas upland areas were dominated by individuals from the family Linyphiidae (91 and 97% of the total). Riparian areas in the tall grass prairie site were dominated by all three families (83% combined), whereas grasses in the upland were dominated by spiders from the family Linyphiidae.

None of the five forested watersheds studied, had significantly higher numbers of web-spinning spiders in riparian zone than upland habitats, although the tropical, northern conifer and two southern deciduous forest sites showed a trend towards higher numbers of spiders in the riparian zone ($n=10$, $p< 0.26$, 0.25, 0.12, 0.07, respectively). All four riparian zones located in forested sites in the continental US were dominated by the families Araneidae, Tetragnathidae, and Linyphiidae, whereas upland areas had very few tetragnathids. The riparian zone of the tropical forest site was dominated by individuals from the families Araneidae, Pholcidae and Theridiidae, whereas upland areas were dominated by individuals from the families Araneidae, Pholcidae and Uloboridae. In general, differences in spider abundance and biomass between riparian and upland habitats in the arctic, tall-grass prairie, desert and two southeastern deciduous forest sites can be attributed to differences in total abundance and biomass of orb web weavers from the families Araneidae and Tetragnathidae. Sheet-web spiders (mainly Linyphiidae and Theridiidae) were more evenly distributed throughout the five watersheds.

Total biomass of web-spinning spiders was related to aquatic insect emergence (AQBM) and number of stalks (NMSTLK), and abundance was related to number of stalks (NMSTLK)(Table 4.5). Differences in web-spinning spider abundance between riparian and upland habitats was related to the number of vertical points transected (VRTPNT) ($n=8$, $r^2=0.639$, $p< 0.017$), and differences in biomass was related to both aquatic biomass (AQBM) and the number of vertical points transected (VRTPNT) ($n=8$, $r^2= 0.962$, $p<0.0003$).

DISCUSSION

The distribution of spiders in riparian and upland habitats

Ecologists have hypothesized that edge habitats contain greater numbers of individuals (Polis and Hurd 1996, Fagan et al. 1999) and larger-bodied organisms (Ferguson 2000). Recent studies concerned with a wide variety of taxonomic groups in many habitats have found increasing numbers of individuals inhabiting edge habitats (Kareiva 1987, Ferguson 2000); however reasons for these increases are poorly understood.

Riparian corridors, one of the most abundant edge habitats in nature, often contain more organisms than adjacent upland habitats (Nilsson et al. 1989, Spackman and Hughes 1995). A greater abundance, biomass and diversity of ground-dwelling and canopy spiders was found in riparian habitats in desert, arctic and tall-grass prairie sites than in upland habitats. In the desert site, mean ground-dwelling spider abundance was almost seven times higher, and diversity was almost twice as high in riparian habitats than in upland habitats. In the tall-grass prairie and arctic sites, ground-dwelling spider richness and abundance was 60-70% higher in riparian zones than in upland habitats. Recent studies have also found that spiders are more abundant and diverse in riparian zone habitats than adjacent upland areas (Greenwood et al. 1995, Henschel et al. 1996), with some species found almost exclusively in riparian areas (Greenstone 1979, Gillespie 1987, Aiken and Coyle 2000). Spiders, with their ability to withstand long periods of starvation, are prime candidates to utilize temporally and spatially patchy subsidies (Anderson 1974) such as those found in riparian zones (Gregory et al. 1991).

Desert, arctic and tall grass prairie sites also had the largest proportion of wolf spiders (family Lycosidae) relative to other families in riparian habitats. Wolf spiders represented 94% of the ground species collected in the desert, 86% of those collected in the tall-grass prairie and 94% of those collected in the arctic. This high proportion of wolf spiders may be because wolf spiders are especially adapted to disturbed environments, as they can carry their egg sacs with them and keep them safe from the flooding that often occurs in riparian zones (Anderson 1974).

Canopy spider abundance was 3-10 times higher within riparian corridors than in upland habitats in the desert, arctic and tall-grass prairie sites. The northern conifer forest site had 25% more spiders, and the tropical forest site had 12% more spiders in riparian zone than upland habitats. The most abundant group of canopy spiders, web-spinners, were more abundant in riparian zones of the desert, arctic and tall grass prairie sites than in upland areas. Most of the differences in web-spinning spider biomass and abundance between upland and riparian habitats can be attributed to the greater number of spiders from the families Tetragnathidae and Araneidae, many of which prefer vegetation overhanging streams rather than vegetation in less productive upland areas (Gillespie 1987, Williams et al. 1995). The third most common web-spinning spider family at the study sites, Linyphiidae, were more evenly distributed along the riparian to upland transects. This result is similar to what Power et al. (in press) finds along the Eel River in Northern California, where species of Linyphiidae are evenly distributed along the river to ridge gradient, whereas Tetragnathidae are concentrated along the river margin.

Factors influencing the distribution of terrestrial predators

Spatial subsidies occur when material and energy flow from one habitat, affecting the spatial or temporal distribution of at least one trophic level in the adjacent habitat (Polis et al. 1997). Although many studies have examined the behavioral responses of terrestrial predators to aquatic subsidies (Orians and Wittenberger 1991, Williams 1992, Williams et al. 1995, Gillespie 1987), far fewer have tried to quantify the effect of aquatic subsidies on the spatial distribution of terrestrial predators (Gray 1993, Anderson and Polis 1998). In this study, ground-dwelling and canopy spider abundance and biomass was highly correlated with emergence biomass, suggesting that emerging aquatic insects are providing a direct trophic subsidy to spiders feeding adjacent to the stream bank. This result is similar to what many have hypothesized (Likens and Bormann 1974, Jackson and Fisher 1986), and recent studies have found (Nakano and Murakami 2001, Henschel et al. in press).

Vertical complexity (number of vertical touches) also helped to explain differences in canopy spider biomass, abundance and diversity among the eight sites (Table 4.5). A large proportion of the spiders that were collected in the lower canopy were web builders, many of which depend on structural complexity of vegetation and a minimum number of attachment sites to secure webs for prey capture (Uetz et al. 1978, McNett and Rypstra 2000). Ground-dwelling spider richness was highly correlated with litter depth, and the riparian zones with the greatest litter height also contained the greatest number of hunting (wandering) species. Others have found litter depth or amount of vegetative debris to be an important factor determining the distribution of wandering spiders (Uetz 1979, Marshall and Rypstra 1999). Increased structure may also be providing more refugia (e.g., additional hiding spaces) for spiders living along stream banks, as riparian spiders may be more fearful of bird predation than their upland counterparts (Reichert and Hall 2000).

In this study, terrestrial insect biomass was unrelated to spider biomass or abundance (Table 4.5). When prey was limited in a desert upland, spiders attempted to capture 99% of prey encountered, verses 59% in riparian zone habitats where they encountered three times as much prey and fed more selectively (Riechert and Harp 1987). This change in spider feeding behavior with increased prey availability may reduce some of the spider predation pressure on terrestrial insects. Although some studies have found that predation by spiders directly on aquatic insects causes an increase in the number of terrestrial prey along river margins (Henschel et al. in press), no relationship was found between terrestrial insect biomass and spider biomass or abundance in this study (Table 4.5). Although it is possible that increased prey availability (aquatic + terrestrial) at the land-water margin could remove some of the terrestrial predation pressure, I found no evidence for this in any of the biomes.

Temperature or precipitation could not explain any of the differences in spider biomass or abundance between the sites despite wide ranges in these variables across biomes. These results are consistent with both a field experiment (Henschel et al. 1996), and a more controlled enclosure experiment (Ferguson 2000) that found no significant relationship between invertebrate predators and changes in temperature or moisture with distance to edge.

Stream subsidies and ground-dwelling riparian spiders

To determine if emerging aquatic insects could be subsidizing spider communities in any of the riparian zones, an energy budget for ground-dwelling riparian spiders was calculated (see example in Table 4.6) based on the energy requirements (kJ) of spiders and the potential energy supplied by terrestrial and aquatic insects in all eight riparian zones. First, the total amount of energy from aquatic and terrestrial insects available to spiders in each of the riparian zones over a 10 day period was calculated (Table 4.6a). Because spiders feed on insect taxa in proportion to what is emerging in the greatest number (Williams 1992, Williams et al. 1995), dry mass of insects was calculated based on total mass of emerging insects in a 50 m reach minus mass of those species that are frequently rejected by spiders (Nentwig 1983, Riechert and Harp 1987). Since 1g dry mass of insect is approximately equal to 24.8 kJ of energy (Cummins and Wuycheck 1971, Gray 1993), a 50 m stream reach supplied between 0.3 kJ (UBNC) and 1,187 kJ (SCAZ) of energy in the form of aquatic insects; in contrast, the adjacent 50 x 10 meters of riparian zone habitat provided between 7 kJ (UBNC) and 143 kJ of energy (WBTN) in the form of terrestrial prey to riparian predators.

Since spiders are clearly not eating all of the insect prey available, predation rates by spiders were estimated to be between 0.2% (Williams et al. 1995) and 1.8 % (Rehfeldt 1992, Gribbin and Thompson 1990) of emergence (Table 4.6b). Of the prey that spiders come in contact with, assimilation efficiency or feeding efficiency (net energy intake of prey) is not 100%. For spiders, this variation in feeding efficiency is a function of prey density and handling time (i.e., the proportion of prey eaten decreases as prey density increases; Sih 1980, Samu 1993), rather than the ability of a predator to assimilate prey. Feeding efficiency was approximated as 0.50 (Table 4.6c), which is the average of published data on the proportion of prey eaten with different prey density scenarios (calculated from Sih 1980).

To estimate the energy needed to maintain observed spider biomass, an average metabolic rate for spiders (V_{O2} / mass) was determined (Table 4.6d), based on reported literature values for standard metabolic rate (μL V_{O2} mg^{-1} hr^{-1}, determined under conditions designed to obtain the lowest rate compatible with life when organisms are at minimum level of activity) (Anderson 1970, Greenstone and Bennett 1980, and Anderson and Prestwich 1982). An average V_{O2} for the whole community was used, since there are no significant differences in resting rates of energy utilization that are reflective of different modes of prey capture or foraging strategy in spiders (Greenstone and Bennett 1980). This estimate is a conservative one because the two extremes, high and low metabolic rates experienced by spiders, both during prey location and capture, and during periods of severe food limitation and starvation are not included in this estimate (Anderson 1974).

Since temperatures varied between the sites, Q_{10} was used to calculate adjusted metabolic rates for spiders. Metabolic rate was calculated for spiders at different temperatures using the following equation: $Q_{10} = 1.27295 + 0.03897$ (t ^{o}C), r^2=0.844 p<0.0005), which was calculated from data in Anderson 1970. Average metabolic rate for one mg of spider per 10 day period at each site was calculated by multiplying temperature adjusted V_{O2} (µL mg^{-1} h^{-1}) * 24 hr * 10 d (Table 4.6d). The total energy needed (Kj) to support 1 mg of spider biomass (at each site) over the 10 day period was calculated by multiplying temperature adjusted L V_{02} mg^{-1} 10 d^{-1} * 20.1 kJ, which is the average amount of energy (kJ) needed for each liter of oxygen used in metabolism (a constant irrespective of whether fat, carbohydrate or protein is oxidized) (Schmidt-Nielsen 1997).

Total spider biomass (g) that could theoretically be supported by the energy supplied by aquatic and terrestrial insects at each site over the 10 day period was calculated as energy needed to support 1 mg of spider biomass (kJ) divided by total energy supplied by both terrestrial and aquatic insects (Table 4.6e). From these calculations it was possible to estimate how many grams of spider biomass could be supported from aquatic and terrestrial prey (Table 4.7). Those numbers were then compared to actual spider biomass collected in the riparian zones of the eight streams. The calculations suggest that terrestrial insects alone could not support the spider biomass found in the riparian zone habitats of the desert, arctic, tall-grass prairie, northern conifer and tropical forest sites (Table 4.7), however terrestrial insects could support the spider biomass found in riparian zones of all three eastern deciduous forest sites (WBTN, UBNC and BBNH). The additional energy (kJ) supplied by aquatic insects to the desert, arctic, tall-grass prairie, northern conifer and tropical forest sites could support the existing spider biomass at all five sites (Table 4.7).

The importance of aquatic subsidies to terrestrial predators

This study is the first to examine the importance of stream-derived subsidies to terrestrial predators, and possible effects on the spatial distribution of terrestrial predators across biomes. Spider biomass, abundance and richness was positively correlated with aquatic insect emergence; sites with the greatest aquatic insect emergence also had the greatest concentration of spiders at the land-water margin.

The data presented here support the initial hypothesis, that sites where insect emergence was greatest and where structural complexity of the vegetation varied the most from riparian-to-upland habitats (SCAZ and STIC) would have the greatest concentration of spiders directly adjacent to the stream channel (Figure 4.1). In general, spider abundance, biomass and richness were related to emergence biomass and secondarily to measures of structural complexity. Sites with relatively high emergence biomass, yet little or no differences in vegetation from riparian-to-upland habitats (WBTN and MCOR), also had a high biomass and abundance of spiders in riparian habitats relative to upland areas; this observation is consistent with the overriding impact of emergence biomass on riparian spider communities. It is important to note, however, that because aquatic subsidies vary spatially and temporally, sites that had relatively low aquatic insect emergence during the sampling period might have a much higher biomass of aquatic insects emerge at other times of year. Our data predict that an increase in emergence biomass at those sites would positively impact the abundance, biomass and richness of spiders concentrated along the stream edge. Alternatively, if human alteration of the stream were to decrease emergence biomass, we would predict decreases in riparian spider abundance, biomass and richness.

The importance of river-derived subsidies to adjacent terrestrial communities is probably widespread (Hilderbrand et al. 1999, Vander Zanden and Sanzone in press, Power et al. in press). This may be especially true in riparian zones of headwater streams, where the interdependence between terrestrial and aquatic foodwebs are great (Nakano and Murakami 2001), and in increasingly fragmented landscapes where in-stream secondary production in isolated riparian corridors provides one of the only food resources for terrestrial predators (Prenda and Lorencio 1996). Recent studies have shown that some species of bats and birds are also dependant on aquatic subsidies (Rainey et al. 1992, Nakano and Murakami 2001). Additional results from the desert (SCAZ) and arctic (STIC) sites suggest that predatory beetles (Coleoptera) and harvestmen (Opiliones) are also concentrated at the land-water margin and may be utilizing aquatic subsidies (Sanzone et al. in review-a, Sanzone et al. in review-b). These findings make clear the need to apply techniques for quantifying the flow of nutrients and energy from aquatic to terrestrial ecosystems in a wide range of biomes, because aquatic subsidies may be more important to terrestrial consumers than ecologists have previously thought.

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Table 4.1 Mean air temperature and total rainfall at each of the sites during the sampling period.

Stream	Location	ID	Location	Sampling Period	Air Temp. °C (min-max)	Total Rainfall (cm)
Quebrada Bisley	Puerto Rico	QBPR	18°N, 66°W	15 Jan. - 5 Mar. 1998	23.7 (20.5 - 27.0)	52.3 cm
Sycamore Creek	Arizona	SCAZ	33°N, 112°W	1 May - 12 June 1997	28.7 (19.6 - 37.8)	0.05 cm
Upper Ball Creek	North Carolina	UBNC	35°N, 83°W	4 Nov. - 16 Dec. 1996	6.2 (-0.6 - 12.3)	1.7 cm
Walker Branch	Tennessee	WBTN	36°N, 84°W	1 Apr. - 13 May 1997	13.4 (5.9 - 20.8)	28.2 cm
South Kings Creek	Kansas	KCKS	39°N, 94°W	7 Apr. - 12 May 1998	16.6 (9.7 - 23.6)	7.1 cm
Mack Creek	Oregon	MCOR	44°N, 122°W	21 July - 1 Sept. 1998	16.2 (12.8 - 22.2)	1.2 cm
Bear Brook	New Hampshire	BBNH	44°N, 72°W	17 June - 29 July 1997	16.5 (13.3 - 20.1)	25.1 cm
Steinbogalækur	Northern Iceland	STIC	65°N, 17°W	5 - 30 June 1999	11.1 (2.3 - 20.8)	5.1 cm

Table 4.2 Mean spider abundance (+/- s. e.) in riparian and upland pitfall traps (number per trap) and timed beat nets (number per 5 min beat sample). Asterisks indicate mean ground-dwelling or canopy spider abundance is significantly different between riparian and upland habitats.

Stream	Location	Mean spider abundance (+/- se)			
		Ground-dwelling spiders		Lower canopy spiders	
		Riparian	Upland	Riparian	Upland
Quebrada Bisley	Puerto Rico	0.76 (0.12)	0.50 (0.10)	*17.4 (1.17)	15.5 (0.97)
Sycamore Creek	Arizona	***7.15 (0.56)	1.27 (0.18)	**7.8 (2.67)	1.0 (0.61)
Upper Ball Creek	North Carolina	0.37 (0.13)	0.43 (0.11)	17.1 (2.12)	13.6 (2.54)
Walker Branch	Tennessee	**4.2 (0.43)	2.7 (0.44)	7.9 (1.18)	7.3 (1.54)
South Kings Creek	Kansas	**2.8 (0.29)	1.6 (0.20)	***9.6 (1.26)	0.8 (0.24)
Mack Creek	Oregon	1.3 (0.18)	1.0 (0.15)	*35.9 (2.26)	29.0 (1.64)
Bear Brook	New Hampshire	1.2 (0.21)	1.2 (0.17)	15.8 (1.77)	18.7 (2.68)
Steinbogalækur	Northern Iceland	**13.3 (1.47)	9.12 (1.13)	*36.87 (4.32)	13.8 (2.95)

* $p<0.05$
** $p<0.01$
*** $p<0.0001$

Table 4.3 Total biomass (mg) of ground-dwelling and canopy spiders collected in riparian and upland pitfall traps (total biomass from 50 traps) and sweep net samples (total biomass from 10 traps). Here we report total biomass, rather than biomass per trap because total biomass is what was used in multiple regression analysis.

Stream	Location	Total Spider Biomass			
		Ground-dwelling spiders		Lower canopy spiders	
		Riparian	Upland	Riparian	Upland
Quebrada Bisley	Puerto Rico	106.8	42.7	509.2	198.1
Sycamore Creek	Arizona	3573.7	1007.2	781.7	103.9
Upper Ball Creek	North Carolina	57	156.5	62.3	34.4
Walker Branch	Tennessee	492.7	528.6	104.7	27.7
South Kings Creek	Kansas	682.4	376.6	72.4	0.0007
Mack Creek	Oregon	621.6	420.4	759.2	252.1
Bear Brook	New Hampshire	77.9	70.1	138.3	98.2
Steinbogalækur	Northern Iceland	2478.5	1813.2	1173.8	133.0

Table 4.4 Total richness (# genera) of ground-dwelling and canopy spiders collected in riparian and upland pitfall traps (total richness from 50 traps) and sweep net samples (total richness from 10 traps).

Stream	Location	Spider diversity			
		Ground-dwelling spiders		Lower canopy spiders	
		Riparian	Upland	Riparian	Upland
Quebrada Bisley	Puerto Rico	14	12	20	16
Sycamore Creek	Arizona	23	15	15	7
Upper Ball Creek	North Carolina	10	7	9	9
Walker Branch	Tennessee	17	14	11	7
South Kings Creek	Kansas	21	14	9	1
Mack Creek	Oregon	9	5	9	7
Bear Brook	New Hampshire	13	10	10	7
Steinbogalækur	Northern Iceland	21	15	16	9

Table 4.5 Results of stepwise multiple regression analysis. Dependent variables tested were: ground-dwelling spider biomass (GDSB), and abundance (GDSA); a subset of that group, wandering spider biomass (WNDB) and abundance (WNDA); lower canopy spider biomass (LCSB) and abundance (LCSA); and a subset of that group, web-weaving spider biomass (WEBB) and abundance (WEBA). Environmental variables are listed according to decreasing importance. AQBM is total biomass of emerging aquatic insects, LTDPTH is litter depth (cm), SDGCVR is structural complexity of ground cover, VRTPNT is number of vertical points transected, MNSTLK is mean number of stalks per m^2 plot, MNTEMP is mean temperature (^{o}C) during the study, TOTRNF is total rainfall (cm) during the study and TRBM is total biomass of terrestrial insects. Negative correlations are marked by (-); ns is non-significant.

Variable	**GDSB**	**GDSA**	**WNDB**	**WNDA**
AQBM	***	***	***	**
LTDPTH	ns	ns	ns	ns
SDGCVR	ns	ns	ns	ns
MNTEMP	ns	ns	ns	ns
TOTRNF	ns	ns	ns	ns
TRBM	ns	ns	ns	ns
Regression *F* -value	35.58	38.87	42.22	11.79
Variance explained (r^2)	0.852	0.866	0.876	0.663
Significance	***	***	***	**

	LCSB	**LCSA**	**WEBB**	**WEBA**
AQBM	***	*	***	ns
VRTPNT	**	**	ns	ns
NMSTLK	ns	ns	*	**
MNTEMP	ns	*** (-)**	ns	ns
TOTRNF	ns	ns	ns	ns
TRBM	ns	ns	ns	ns
Regression *F* -value	60.63	6.82	43.32	12.87
Variance explained (r^2)	0.960	0.836	0.945	0.682
Significance	***	*	***	**

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

Table 4.6 Calculations used to estimate potential energy available from aquatic and terrestrial sources. Example calculation is based on data from a 50 m stream reach and a 10 x 50 m terrestrial area along the stream bank in the Quebrada Bisley watershed in Puerto Rico.

(A) Available energyfrom aquatic and terrestrial sources (kJ)	**Values**
Total energy supplied by aquatic prey during study period (kJ/ 50 m reach)	17.92
Total energy supplied by terrestrial prey during study period [kJ/ (10 X 50 m area)]	10.5
(B) Predicted spider biomass assuming spiders capture 0.2 - 1.8 % of available prey (mg)	
Additional spider biomass predicted from aquatic prey (mg)	35.8-322.6
Predicted spider biomass from terrestrial prey (mg)	21.0-188.9
Predicted spider biomass from all sources (mg)	**56.8-511.5**
(C) Energy available after including spiders ability to assimilate food resources (kJ)	
Spider Assimilation/ Feeding Efficiency (from Sih 1980)	0.50
Aquatic prey available to spiders (kJ/ 50 m reach * 0.5)	17.9-161.3
Terrestrial prey available to spiders (kJ/ 10 x 50 m area * 0.5)	10.5-94.5
Total prey available to spiders (aquatic + terrestrial * 0.5)	28.4-255.8
(D) Energy needed for spider metabolism (V_{O2})	
Average spider metabolic rate/ mg spider @ 20° C (µL V_{O2}/ mg/ h)	0.27071
Adjusted spider metabolic rate / mg spider (µL V_{O2}/ mg/ h at 23.7 °C)	0.37730
Daily metabolic rate/ mg spider (µL V_{O2}/ mg/ h * 24 h= µL V_{O2}/ mg/ d)	9.05500
Average spider metabolic rate/ mg spider (L V_{O2}/ mg/ d * 10 d = L V_{02}/ mg/ 10 d)	**0.00009**
Energy needed to maintain resting metabolism (L V_{02}/ mg/ 10 d * 20.1 =kJ/ mg/10d)	0.00182
(E) Total biomass of spiders that could be supported from available energy (g)	
Total biomass of spiders that could be supported from aquatic prey	9.8-88.6
Total biomass of spiders that could be supported from terrestrial prey	5.8-51.9
Total biomass of spiders that could be supported from all sources	**15.6-140.5**

Table 4.7 The range of spider biomass (g) that could be supported by aquatic and terrestrial prey on the ground within the 10 x 50 m area adjacent to the streams. Range is calculated based on the assumption that spiders consume between 0.2 and 1.8% of available prey items (Williams et al. 1995, Rehfeldt 1992, Gribbin and Thompson 1990) as described in text and Table 4.6. Single asterisk indicates spider biomass could be supported by terrestrial insects alone, double asterisk indicates spider biomass could be supported only with the additional aquatic insect subsidy.

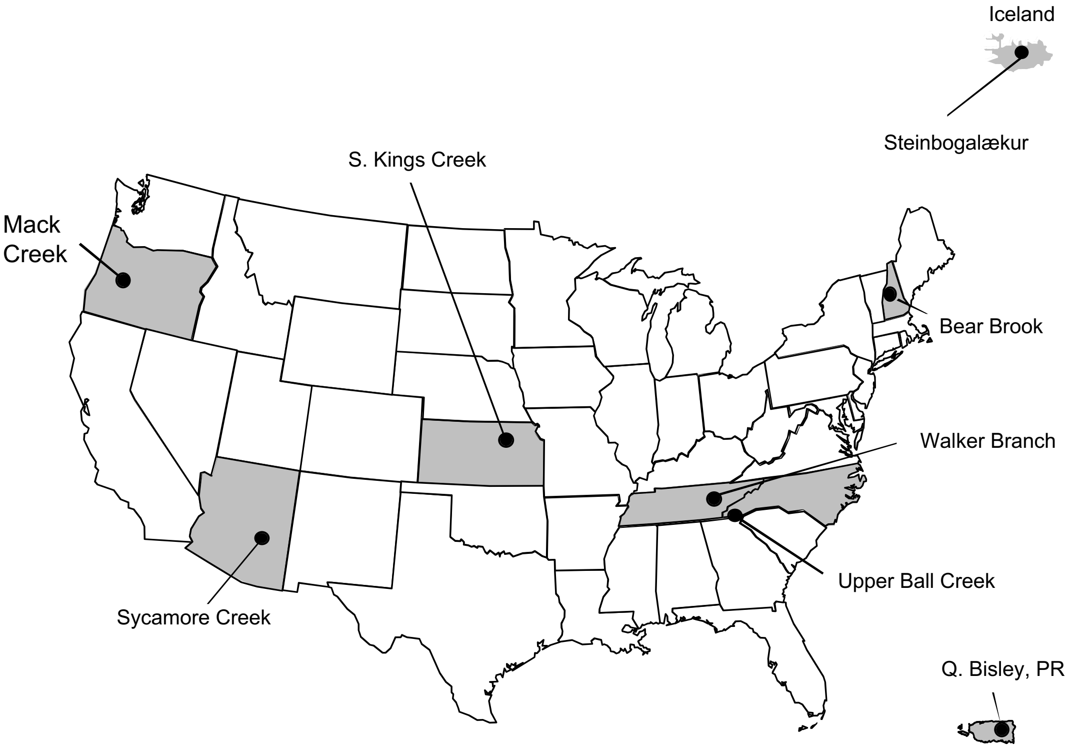
Site	Spider biomass (g) that could be supported by terrestrial prey	Spider biomass (g) that could be supported by aquatic prey	Spider biomass (g) that could be supported by all sources	Observed spider biomass (g)
QBPR	5.8 - 51.9	9.9 - 88.6	15.6 - 140.5	106.8**
SCAZ	26.8 - 241.4	416.6 - 3749.1	443.4 - 3990.4	3573.7**
UBNC	17.5 - 157.7	1.0 - 7.4	18.3 - 165.1	57.0*
WBTN	197.8 - 1780.5	98.6 - 887.2	296.4 - 2667.7	492.7*
KCKS	71.7 - 644.9	7.8 - 70.0	79.4 - 992.9	682.4**
MCOR	15.4 - 138.5	220.8 - 1987.9	236.2 - 2125.4	621.6**
BBNH	25.1 - 226.3	12.2 - 109.7	37.3 - 336.1	77.9*
STIC	19.8 - 177.9	786.1 - 7074.5	805.8 - 7252.3	2478.5**

Figure 4.1 Conceptual classification of riparian zones.

Structural Complexity of Terrestrial Vegetation

Aquatic Emergence Biomass		Higher in the riparian zone	Similar in riparian and upland habitats
	High	Highest Spider Biomass *Sycamore Creek, AZ* *Steinbogalaekur River, IS*	Intermediate Spider Biomass *Mack Creek, OR* *Walker Branch, TN*
	Low	Intermediate Spider Biomass *South Kings Creek, KS* *Upper Ball Creek, NC*	Lowest Spider Biomass *Bear Brook, NH* *Q. Bisley, PR*

Figure 4.2 Map showing location of eight sites where sampling was conducted.


Iceland
Steinbogalækur
S. Kings Creek
Mack Creek
Bear Brook
Walker Branch
Upper Ball Creek
Sycamore Creek
Q. Bisley, PR

Appendix 4.1 Terrestrial prey biomass (TRBM) is calculated by summing the total biomass of all potential terrestrial prey items collected in pitfall traps within the first 10m of the stream bank over a 10 day period (n=50, 5 collection dates * 10 traps). Aquatic prey biomass (AQBM) is calculated by summing the total biomass of all aquatic insects collected in emergence traps over a 10 day period (n=45, 5 collection dates * 9 traps). Number in parentheses in this column is biomass of aquatic insects (g m^{-2}) multiplied by reach area (50 m long x average stream reach width). Average plant species richness (PLTSPP), total number of vegetative stalks (NMSTLK: # m^{-2}), number of vertical points transected (VRTPNT: # m^{-2}), average litter depth (LTDPTH) and structural diversity of ground cover (SDGCVR: average # of ground cover types m^{-2}) (+/-se) was collected from m^2 plots located within the first 10 m of the stream bank (n=10 at each site).

Stream	Location	AQBM (mg)*†	TRBM (mg)*†	PLTSPP	NMSTLK†	VRTPNT†	LTDPTH (cm)*	STGCVR*[c]
Quebrada Bisley	Puerto Rico	138.4 (722.8)	997.1	5.9 (0.63)	20.7 (5.68)	5.1 (0.38)	1.9 (0.27)	5.8 (0.35)
Sycamore Creek	Arizona	7430.0 (47882.2)	3082.7	1.8 (0.31)	2.0 (0.32)	1.8 (0.22)	0.05 (0.03)	2.7 (0.36)
Upper Ball Creek	North Carolina	4.2 (12.5)	832.8	1.3 (0.41)	4.3 (1.84)	1.4 (0.18)	3.9 (0.32)	9.2 (0.74)
Walker Branch	Tennessee	833.5 (2870.9)	11763.8	4.8 (0.83)	22.7 (4.61)	1.7 (0.29)	3.6 (0.39)	4.67 (0.50)
South Kings Creek	Kansas	113.2 (301.9)	9471.1	6.5 (0.75)	54.8 (10.66)	2.9 (0.18)	2.0 (0.28)	5.1 (0.57)
Mack Creek	Oregon	1458.8 (8266.5)	6499.9	4.9 (0.46)	55.1 (14.23)	4.9 (0.46)	3.5 (0.70)	7.53 (0.42)
Bear Brook	New Hampshire	201.4 (469.9)	1966.0	5.2 (0.34)	77.6 (17.64)	3.1 (0.40)	3.2 (0.59)	5.0 (0.54)
Steinbogalækur	Northern Iceland	9312.0 (18624)	468.3	11.1 (1.20)	134.5 (15.22)	2.7 (0.20)	0.45 (0.02)	6.8 (0.24)

*indicates variable was used in ground-dwelling spider multiple regression analysis

† indicates variable was used in lower canopy spider multiple regression analysis

[c] ground cover types as in Southwood (1979)

CHAPTER 5

STABLE ISOTOPES PROVIDE EVIDENCE THAT STREAM SUBSIDIES INFLUENCE THE SPATIAL DISTRIBUTION OF TERRESTRIAL PREDATORS IN EIGHT BIOMES[1]

[1] Sanzone, D. M., J. L. Meyer, J. L. Tank, E. P. Gardiner, B. J. Peterson, P. J. Mulholland, S. Gregory, N. Grimm, W. H. McDowell, W. B. Bowden, W. K. Dodds, and J. R. Webster. To be submitted to Ecology.

Abstract. Stable isotopic tracers are useful for determining complex flow pathways across ecosystem boundaries. Although natural abundance of stable isotopes have been used widely to understand these flow pathways, this technique is limited to systems where natural isotopic signatures are distinct between the two ecosystems. This study is the first to use a ^{15}N addition to trace the flow of nitrogen (N) from aquatic to terrestrial foodwebs. This cross-biome study of N export from stream foodwebs (via emerging aquatic insects) and subsequent uptake by riparian predators demonstrates that nitrogen flux from aquatic to terrestrial foodwebs is more significant and widespread than thought. Stream-derived ^{15}N tracer was incorporated into spider tissue in eight riparian zones located in eight different biogeographic regions. Stream-derived N was highest in riparian spiders in desert, arctic and tall-grass prairie, tropical and northern conifer forest sites and lowest in temperate deciduous forest sites. ^{15}N labeling in spiders tracked that of emerging aquatic insects, indicating spiders are relying, at least in part, on aquatic resources. The greatest uptake of stream-derived N by spiders occurred in riparian zones where emerging aquatic insect biomass was highest. Ground-dwelling and lower canopy spider biomass in the riparian zone was also related to emerging aquatic insect biomass; indicating that stream subsidies are influencing spiders in the riparian zone. Percentage of nitrogen coming from aquatic sources was highest in spiders collected directly adjacent to the active stream channel and decreased exponentially with distance from the stream bank (out to 50 m) in five of the eight watersheds.

INTRODUCTION

Nitrogen (N) loading to aquatic ecosystems from surface runoff and groundwater infiltration (Jordan and Weller 1996, Kortelainen et al. 1997), and its impact on nutrient cycling and foodweb interactions in streams has been widely studied over the last few decades (Nienhuis 1998, Davis and Minshall 1999, Townsend and Riley 1999). Recent studies have found that headwater streams are more effective in N retention and processing than larger streams (Alexander et al. 2000), and that during seasons of high biological activity headwater streams typically export less than half of the dissolved inorganic N input entering the watershed (Peterson et al. 2001). In addition to the multiple cycles of uptake, storage, regeneration and removal of N from these streams due to denitrification, organisms may remove a substantial portion of N from headwater streams, returning it to the terrestrial landscape (Hilderbrand et al. 1999) where it can have substantial impacts on surrounding terrestrial communities (Polis et al. 1997, Anderson and Polis 1999). In fact, terrestrial foodwebs may be tightly linked to instream foodwebs through this counter flow of nutrients and organisms (Likens and Bormann 1974, Jackson and Fisher 1986). This cross-biome study documents the transfer of N from eight headwater streams into surrounding terrestrial foodwebs, and the impact of this aquatic subsidy on the spatial distribution of terrestrial predators.

Natural abundance of stable isotopes have been used to document trophic interactions and food web dynamics across ecosystem boundaries (Wipfli 1997, Anderson and Polis 1998, Hilderbrand et al. 1999, Stapp et al. 1999). This technique is limited, however, to watersheds where natural isotopic signatures are distinct between aquatic and terrestrial systems, as is the case in watersheds where anthropogenic or marine-derived inputs of N are common (such as in agricultural or urban watersheds) or where stream production is mainly autochthonous. In forested headwater streams, natural isotopic signatures are often not distinct enough to distinguish between aquatic and terrestrial food resources. The ^{15}N tracer approach is useful in distinguishing between aquatic and terrestrial food resources available to terrestrial predators in these watersheds.

The ^{15}N tracer addition approach involves adding sufficient ^{15}N (NH_4 or NO_3) to one ecosystem to increase the ^{15}N: ^{14}N ratio, while at the same time not increasing overall N concentrations in that ecosystem. The flow of this isotopically enriched N can then be traced from its source into the recipient habitat (Hershey et al. 1993). 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.

In this study, we used a ^{15}N tracer addition to quantify the flow of nitrogen from aquatic to terrestrial food webs. We added ^{15}N- NH_4Cl to four temperate forest streams (North Carolina, Tennessee, New Hampshire and Oregon), a tropical forest stream (Puerto Rico), a desert stream (Arizona), a grassland stream (Kansas), and an arctic stream (Iceland), and traced the flow of nitrogen from the ^{15}N enriched stream foodwebs, via emerging aquatic insects, into recipient terrestrial foodwebs. By determining the amount of tracer ^{15}N incorporated into predator (spider) biomass and comparing it to the ^{15}N tracer found in aquatic insects, we estimated the proportion of N that spiders obtain from emerging adult aquatic insects compared to that which comes from terrestrially-derived sources.

METHODS

Study sites

Spiders and insects were collected from headwater streams and riparian zones of eight sites, located in different biogeographic regions of North America and Iceland (Figure 5.1). The riparian zones were located in watersheds dominated by tall-grass prairie, desert, arctic, northern conifer, eastern deciduous and tropical forest habitats (Table 5.1); all were relatively undisturbed by human activities. Physical, chemical and biological attributes of both stream and riparian zones varied greatly between the eight sites (Appendix 5.1). In all but one stream, detrital standing stocks were greater than autochthonous standing stocks (Appendix 5.1). Riparian vegetation in the desert (Sycamore Creek watershed, Arizona, SCAZ), tall-grass prairie (South Kings Creek watershed, Kansas, KCKS), arctic (Steinbogalækur, Iceland, STIC), and Southern Appalachian Mountain (Upper Ball Creek watershed, North Carolina, UBNC) sites contained distinct riparian vegetation, whereas the remaining four forested sites contained similar plant assemblages throughout the watershed (Appendix 5.2).

Field sampling and sample processing

We continuously dripped 10% ^{15}N-labeled NH_4Cl into the eight streams to achieve a 500$^{o}/_{oo}$ ^{15}N enrichment of streamwater, while maintaining background concentrations of NH_4. The total amount of ^{15}N-NH_4 added to the streams was estimated based on stream discharge and background ammonium concentrations (Appendix 5.1). NH_4Cl was dripped into the desert (SCAZ), eastern deciduous (UBNC, WBTN and BBNH), northern conifer (MCOR) and tropical forest (QBPR) sites for 42 days, the tall-grass prairie stream (KCKS) for 35 days, and the arctic stream for 25 days.

Biomass estimates of in-stream insect larvae were obtained using a 400cm^2 Surber or 80 cm^2 Hess sampler (SCAZ) at randomly chosen sites along the study reach. Larvae were identified to genus, and biomass estimates (mg DM m^{-2}) were determined. Larval insects were collected once a week using D-nets and hand collecting from 7 stations below the ^{15}N tracer release and one station above (10 m upstream). The upstream sampling station was used to determine background (natural abundance) ^{15}N values of instream insects.

Quantitative estimates of emergence were made using 0.25 m^2 emergence traps (n=9). Traps were constructed from PVC pipes and covered with window screening (0.3 mm mesh). The base of the traps were anchored into the stream substrate to prevent insect drift from entering the traps. The top of the traps contained an inverted funnel and glass jar. This design, while preventing drift, allowed water to flow through the traps at a velocity similar to that of the surrounding water. Three traps were placed 20 m upstream from the

^{15}N tracer addition sites and 6 traps were placed downstream of the release sites. Emergence traps were sampled using an aspirator and forceps on 5 separate dates after traps were left to collect emerging insects for 48 hour periods (n=45). All insects were taken back to the lab, then sorted and preserved in alcohol until they were identified to genus (or family for dipterans). Once identified, samples were dried, weighed to estimate biomass (mg DM m^{-2}), ground for ^{15}N analysis, and a composite sample of several congeneric individuals from the same location were analyzed for tracer ^{15}N (1-2 mg DM).

Adult aquatic insects flying in the area were sampled using black lights on Day 38 and Day 42 (Day 33 and 35 at KCKS) 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 2 traps were placed below the release site (15 and 35 m downstream) in the center of the stream channel. Light traps were operated from dusk until dawn (approximately 8pm until 8am the following morning). Because there was never complete darkness at the arctic site, adult aquatic insects flying along the stream channel at STIC could not be sampled using light traps. Instead we sampled flying adult aquatic insects using timed sweep net samples (5 min) on Day 23 and Day 25 after the start of the ^{15}N release. Sweep net samples were collected along the bank at 20, 50 and 100 m upstream from the ^{15}N release site and 20, 40, 60, 80, 100, 200 and 300 m downstream from the release site. All light trap and sweep net samples were sorted, identified and processed as described above.

Spiders and terrestrial prey were sampled along the stream bank at 10 m intervals from 10-100 m downstream from the ^{15}N tracer release and 20, 50 and 100 m upstream from the release. Natural abundance ^{15}N values of spiders and terrestrial prey were determined from samples taken 50 and 100 m upstream from the release site, and ^{15}N tracer values were determined using spiders and terrestrial prey collected downstream from the release site. All tracer $\delta^{15}N$ values were background corrected and so represent only ^{15}N that organisms incorporate due to the ^{15}N tracer addition during the course of the release.

Arthropods inhabiting lower herbaceous vegetation and litter were sampled using 48-hour pitfall traps along the active stream channel. Cups were filled with 70% ethanol and left open for 48-hour periods on 5 sampling dates (n=25 traps). Spiders and terrestrial prey were collected from the lower canopy using timed (5 min) sweep net samples on the last day of the ^{15}N tracer release (n=10). Adult insects and spiders were taken back to the lab, sorted and placed in 70% ethanol until adult spiders could be identified to genus and morphospecies, immature spiders identified to family, and terrestrial prey identified to order. Once identifications were complete, all samples were dried at 60^{o}C for 48 hours, weighed for biomass, and ground. A composite sample of several individuals from the same genus or family, collected at the same location were analyzed for ^{15}N.

To determine ^{15}N content of spiders and terrestrial prey collected away from the stream bank (as far as 50 m into the upland), five stream-to-upland transects were established, running perpendicular to the stream bank. These stream-to-upland transects were located between 10 and 100m downstream from the ^{15}N release sites. Spiders and potential prey were sampled along each of the transects as follows: along the water's edge (0 m), in the riparian zone (10 m from the water's edge), and in upland areas, 25 and 50 m away from the stream edge. Spiders and arthropod prey (terrestrial and aquatic) were collected along the five stream-to-upland transects using timed (5 min) sweep net samples on the last day of the release, and from the ground using 48-hour pitfall traps on 5 sampling dates. Spiders and terrestrial prey were processed as described above.

Isotope analysis and mixing-model calculations

We calculated natural abundance and tracer δ^{15}N values for riparian spiders, terrestrial prey, and immature and emerged adult aquatic insects. All δ^{15}N values were calculated as:

$$\delta^{15}N = [(R_{sample}/R_{standard}) - 1] * 1000 \qquad (1)$$

where, R_{sample}= ^{15}N:^{14}N ratio in the sample and $R_{standard}$ = ^{15}N/^{14}N ratio in the atmosphere (Peterson and Fry 1987). Values are expressed as parts per thousand ($^{o}/_{oo}$). All samples were analyzed for ^{15}N by high-temperature, direct combustion and continuous flow analysis using a Finnigan Stable Isotope Ratio Mass Spectrometer at the Institute of Ecology Analytical Chemistry Laboratory, University of Georgia (Athens, GA) or using a Europa Model 20/20 Isotope Ratio Mass Spectrometer located at the Ecosystem Center, Marine Biological Laboratory (Woods Hole, MA).

Mixing-model calculations

Proportion of nitrogen that riparian spiders obtain from aquatic prey versus that which comes from terrestrial prey at each of the eight sites was estimated using isotopic mixing models. The proportion of N incorporated into spider biomass from aquatic versus terrestrial sources was calculated using enriched $\delta^{15}N$ values of spiders and potential prey.

Spiders were collected at more sampling stations 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 used a combination of immature and emerging adult aquatic insect $\delta^{15}N$ values to derive exponential decay curves that predicted $\delta^{15}N$ values of emerging adult aquatic insects ($\delta^{15}N_{d,E}$) d meters downstream from the release point at each of the sites (Appendix 5.3):

$$\delta^{15}N_{d,E} = \delta^{15}N_{0,E}\, e^{-kd} \qquad (2)$$

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. We used a combination of $\delta^{15}N$ values of both immature and adult aquatic insects emerging from the same location because $\delta^{15}N$ values of immature aquatic insects were not different than the $\delta^{15}N$ values of adults (see results from Chapter 2).

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. We chose an upstream flight model because field observations and literature (Jackson and Fisher 1986, Hershey et al. 1993) indicate adult aquatic insects fly predominantly upstream:

$$\delta^{15}N_{d,F} = (s)(\delta^{15}N_{0,E}\, e^{-kd}) + (1\text{-}s)\,(\delta^{15}N_{0,E}\, e^{-k(d+x)}) \qquad (3)$$

where $\delta^{15}N_{d,F}$ = δ^{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; $\delta^{15}N_{0,E}$ = is the predicted average δ^{15}N of emerged aquatic insects at the source (from equation 2), d= distance downstream from the ^{15}N source and x= flight distance of emerged adult aquatic insects. δ^{15}N values from aquatic insects captured in light traps (or sweep net samples at STIC) were used to estimate the flight distance (x) and the partition coefficient of two subpopulations (s and 1-s). Using the above equation, and exponential decay constant (k) derived from equation 2, Gauss-Newton Maximum Likelihood Estimation (SAS,1996) predicted the average upstream flight distance (x) of emerging aquatic insects from each of the streams, and the proportion of insects emerging from that point d+x (1-s) (Appendix 5.3). To examine the validity of this model, we compared the average δ^{15}N value of aquatic insects caught 20 m upstream from the ^{15}N tracer release to model predictions for that distance (see results from Chapter 2).

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

$$\delta^{15}N_{pred}^{*} = (P_{aqua})\,(\delta^{15}N_{aqua}^{*}) + (1\text{-}P_{aqua})\,(\delta^{15}N_{terr}^{*}) \qquad (4)$$

where, $\delta^{15}N_{pred}^{*}$ = δ^{15}N of spiders; P_{aqua} = proportion of spider N derived from aquatic insects; $\delta^{15}N_{terr}^{*}$ = δ^{15}N of terrestrial prey and $\delta^{15}N_{aqua}^{*}$ = δ^{15}N of aquatic insects as calcuated using equation 3. The superscript * indicates numbers are background corrected and represent only tracer ^{15}N.

Data analysis

Total biomass of aquatic insects (AQBM) emerging from each of the stream reaches over the 10 sampling days was estimated by summing the weights of all insects emerging on all dates (9 traps * 5 collection dates). Biomass of emerging aquatic insects was multiplied by reach area (50 m long x average stream reach width) in order to determine emerging aquatic insect biomass over the 50 m stream reach (g m^{-2} * reach area over 10 days). Percentage of instream insects emerging per day from the eight streams during our sampling period (mg DM m^{-2} d^{-1}) was determined by comparing instream biomass estimates (mg DM m^{-2}) with estimates of emergence biomass (mg DM m^{-2} d^{-1}). Linear regression analysis was used to compare emergence biomass with total ground-dwelling and canopy spider biomass between the eight sites (JMP, SAS 1995). Analysis was done on all sites combined and then on the five forested sites separately.

Mixing models were used to determine % N that riparian spiders obtain from aquatic prey versus that which comes from terrestrial prey. Average % N for each spider 'feeding guild' (wandering spiders, sit-and-wait spiders, and orb and sheet web-weaving spiders) at each of the sites was calculated by averaging % N found in composite samples of each genera from each feeding group. Linear regression analysis was used to compare emergence biomass (g 50 m^{-1} reach 10 d^{-1}) with average % N spiders obtained from emerging aquatic insects. We used an arcsine- square root transformation for all results reported as percentages (Sokal and Rohlf 1995).

To determine if spiders collected within the active stream channel and riparian area (0-10 m from the bank) obtained a greater percentage of their total nitrogen from aquatic sources compared to those collected in upland areas (25-50 m), we determined the average % N of all spiders collected at 0, 10, 25 and 50 m transects. We then fit a negative exponential decay curve to data from each of the sites (JMP, SAS 1995). Sites that showed a significant ($p< 0.05$) negative relationship with distance from the stream bank were included in a larger cross-stream comparison.

RESULTS

Instream insect biomass ranged from 17 (QBPR) to 9000 (SCAZ) mg DM m^{-2} during the ^{15}N tracer releases (Table 5.2). The site with the greatest aquatic insect emergence relative to instream biomass (during the course of the tracer releases) was the arctic site (STIC), where almost 30% of instream insect biomass emerged during the course of that ^{15}N tracer addition. The tropical (QBPR), northern conifer (MCOR) and desert (SCAZ) sites also had a relatively high proportion of instream insects emerge during those ^{15}N tracer releases (Table 5.2). Composition of emerging aquatic insects varied greatly between the eight streams, with QBPR and WBTN dominated by species from the order Ephemeroptera, UBNC and MCOR dominated by Plecoptera, and SCAZ, KCKS BBNH and STIC dominated by Diptera (Table 5.3).

Ground-dwelling spider biomass was positively related to emergence biomass (Figure 5.2a, n=8, r^2=0.85, p=0.001) in the eight riparian zones. When analyzing the five forested watersheds alone, the relationship between emergence biomass and ground-dwelling spider biomass was even stronger (Figure 5.2b, n=5, r^2=0.95, p=0.005). Canopy spider biomass was also related to emergence biomass across all sites (Figure 5.3a, n=8, r^2=0.71, p=0.009). A similar trend was observed when analyzing emerging aquatic insects and canopy spiders from the five forested watersheds (Figure 5.3b), however the relationship was not significant (n=5, r2= 0.39, p=0.26).

Mixing model results show that adult aquatic insects fly on average between 67 (QBPR) and 2,340 m (STIC) upstream (Appendix 5.3), and that between 31 and 94 % of insects available to spiders come from downstream reaches. Once the average upstream flight distance (x), proportion of adults flying upstream (1-s) and δ^{15}N values of all adult aquatic insects flying at point d ($\delta^{15}N_{d,F}$ from equation 3) were determined, we calculated the proportion of spider N derived from enriched aquatic sources (those emerging and those emerging and flying upstream) versus those that come from terrestrial sources (Equation 4). After correcting for natural abundance of ^{15}N, some spiders at all eight sites showed enrichment with stream-derived tracer ^{15}N; however, the proportion of spider N derived from aquatic sources varied greatly between sites and among spider ‘feeding groups’.

Spiders living in desert (SCAZ), arctic (STIC), tropical (QBPR) and northern conifer forest (MCOR) sites obtained the greatest proportion of nitrogen from aquatic sources, whereas spiders collected in two of the eastern deciduous forest sites (UBNC and BBNH) obtained little nitrogen from aquatic sources during the course of the ^{15}N tracer releases (Table 5.4). In general, orb-web weaving and wandering spiders obtained the greatest proportion of N from aquatic insects, whereas spiders that use a sit-and-wait strategy (either on the ground or in the vegetation) are much less labeled with stream-derived ^{15}N (Table 5.4).

When comparing across sites, the percentage of total nitrogen that ground-dwelling spiders obtained from enriched aquatic insects was positively related to emerging aquatic insect biomass (r^2=0.754, p= 0.005) (Figure 5.4a). In other words, sites with relatively high aquatic insect emergence biomass during the ^{15}N tracer releases also contained spiders that incorporated more stream-derived ^{15}N into tissue than sites with little emergence during the course of the ^{15}N tracer releases. Similarly, % N from aquatic sources in canopy spiders was directly related to emerging aquatic insect biomass at each of the sites (r^2=0.740, p= 0.006) (Figure 5.4b).

The % N spiders obtained from aquatic sources was highest in individuals collected directly adjacent to the active stream channel and decreased exponentially with distance from the stream bank in the desert, arctic, tall-grass prairie, northern conifer and tropical forest sites (Figure 5.5a). Riparian and upland spiders in the three eastern deciduous forest sites showed little or no labeling with tracer ^{15}N over the course of the ^{15}N additions (Figure 5.5 b). Since five of the sites showed a similar trend ($p<0.05$) with respect to %N incorporation along the stream-to-upland transect, we fit a negative exponential decay curve to the data (Figure 5.6). The % N in spiders from aquatic insects decreased exponentially laterally away from the stream bank (n=20, r^2=0.677, p< 0.0001) in five of the eight sites.

DISCUSSION

The movement of nutrients, energy and individuals from aquatic to terrestrial ecosystems and their effect on recipient terrestrial populations is one of the most common, yet poorly understood phenomena in ecological systems (Polis in press). In this cross-biome study, we directly quantified the transfer of stream-derived N from eight headwater streams via emerging aquatic insects to recipient terrestrial populations. The flux of prey from aquatic to terrestrial ecosystems can be large (Jackson and Fisher 1986) and can exceed that of terrestrial insect productivity (Gray 1989). In tall-grass prairie streams, for instance, emerging aquatic insect production exceeds terrestrial insect productivity by at least an order of magnitude (Gray 1993). This aquatic subsidy may be crucial for the survival of terrestrial consumers living in adjacent habitats (Polis et al. 1997). For instance, terrestrial consumers may be relying on aquatic insect subsidies to supplement dietary needs in a diversity of biomes (Greenstone 1979, Duffy 1991, Grey 1993, Polis et al. 1997, Stapp et al. 1999, Nakano and Murakami 2001); but just how common and widespread is this phenomenon across biomes and among species?

This study is the first to document a large scale pattern in the transfer of nitrogen from aquatic to terrestrial foodwebs. Nitrogen was removed from eight headwater streams via emerging aquatic insects, and entered the terrestrial foodweb through direct consumption by terrestrial invertebrate predators.

Although the eight study sites were located in different biomes and varied greatly with respect to physical, chemical and biological parameters (e.g., aquatic and terrestrial insect productivity), riparian spiders in at least six of the eight sites were obtaining a significant proportion of their nitrogen from aquatic sources over the course of the ^{15}N tracer additions. Since spiders probably did not reach isotopic equilibrium with respect to their food resources over the course of the tracer releases, the reported percentages are an underestimate of stream-derived N.

Riparian spiders in the desert, arctic, northern conifer, and tropical forest sites obtained a significantly greater percentage of their total nitrogen from aquatic insects, than spiders in the tall-grass prairie or eastern deciduous forest sites. This may be due to the fact that the desert, arctic, northern conifer and tropical forest sites had a greater % of instream biomass emerge during the course of the release, as compared to the total biomass emerging from the tall-grass prairie or eastern deciduous forest streams during the ^{15}N releases at those sites. Although the arctic site had the greatest instream biomass during the course of the ^{15}N tracer release and the tropical site had the lowest, % of insects emerging from those streams was relatively high. Hence % N from aquatic insects incorporated into spiders biomass was not related to standing stock biomass of immature insects collected during the ^{15}N tracer releases (r^2=0.36 p=0.11). It was directly related to emergence biomass. In the tropical forest site, for instance, where instream insect biomass was very low (17 mg DM m^{-2}), yet % of aquatic insects emerging was relatively high compared to other sites, % N from aquatic insects incorporated into riparian spiders was also relatively high (Tables 5.2 and 5.3).

Interactions at the aquatic-terrestrial interface of headwater streams are dynamic in space and time. Instream and emerging insect biomass from arctic, temperate and tropical forest streams can vary greatly with season (Wallace 1990). Similarly, the relationship between aquatic subsidies and terrestrial consumers living in recipient habitats can vary with season (Nakano and Murakami 2001). At the arctic site (STIC) for instance, where aquatic emergence, terrestrial production and spider activity is limited to summer months the aquatic-terrestrial linkage is strongest that time of year. Likewise in the desert (SCAZ) and tropical forest sites, in-stream insect and emergence biomass will vary depending on the seasonality of wet-dry cycles. In mid-summer, for example, Sycamore Creek (SCAZ) eventually disappears underground into sub-surface flow. In temperate forest headwater streams, the dependence of terrestrial consumers on aquatic subsidies has also been shown to vary temporally and spatially. In the Southern Appalachian Mountains of North Carolina, for instance, only 24% of aquatic insect emergence occurs in fall (Webster 1975) and 4-5% occurs in winter (Webster 1975, Houston 1993). Because the ^{15}N release at Upper Ball Creek (UBNC) was carried out from Nov. 4- Dec. 16th when aquatic insect emergence was at its lowest, it makes sense that terrestrial consumers were not concentrated at the land-water margin during that ^{15}N release. This study predicts, however, that if UBNC had been sampled during peak emergence, spider biomass would have been higher along the stream edge.

Terrestrial consumers (insects, arachnids, amphibians, reptiles, birds and mammals) are often concentrated at the land-water margin (Polis and Hurd 1995, Greenwood et al. 1995, Malt 1995, Polis and Hurd 1996, Henschel et al. 1996, Rose and Polis 1998, Sanzone et al. in review). Although many reasons for this have been proposed (see citations in Chapter 4), few studies have tried to directly quantify the linkage between aquatic and terrestrial ecosystems and its effect on the spatial distribution, feeding behavior or reproductive success of terrestrial predators (Gillespie 1987, Orians and Wittenberger 1991, Williams et al. 1995, Anderson and Polis 1998, Riechert and Hall 2000). In this study, we found that ground-dwelling and canopy spider abundance and biomass was positively related to emergence biomass. In addition, we found that the % of N that spiders obtain from aquatic sources is directly related to emergence biomass. Previous chapters have shown that aquatic insects are important to the spatial distribution of spiders in a variety of habitats (Chapters 2-4). The results of this study indicate that emerging aquatic insects are an important (and possibly essential) food resource for spiders living in riparian zone habitats in many different biomes.

Although spiders living along the land-water margin are utilizing stream subsidies, we found an exponential decline in reliance of spiders on aquatic resources with distance from the stream edge. Many of the studies that have looked at flows of energy and nutrients from water to land have divided the landscape into marine- (or freshwater-) influenced versus terrestrially-influenced habitats that are separated by more than 1 km (Anderson and Polis 1998, Anderson and Polis 1999). Far fewer studies have quantified the actual distance aquatic subsidies travel into upland habitats (Hershey et al. 1993). Power and her colleagues (2000) working in the Eel River watershed in Northern California have shown an exponential decline in aquatic insect abundance with distance from the river, typically so steep within the first 10m of the stream bank that this flux is less than half of its value at the rivers' edge. In this study, we were able to directly quantify not only the distance that subsidies travel into upland habitats, but also how far into the upland these subsidies were consumed by terrestrial predators. In small relatively undisturbed headwater streams where total dissolved inorganic nitrogen is low and the interdependence between terrestrial and aquatic ecosystem processes and foodweb dynamics are great (Nakano and Murakami 2001), the direct uptake of stream-derived N by spiders was significantly reduced in spiders collected more than 10 m from the stream bank. Although this relationship varied between sites and among organisms, evidence from this and previous chapters show both an exponential decline in uptake of stream subsidies and a turnover in species composition with distance from stream edge (Chapters 2-4).

The distance that biologically-mediated aquatic subsidies travel into upland habitats probably depends on several factors, including such things as: type and densities of insects emerging, rates of dispersal of emerging insects, availability of habitat structures that retain or disperse aquatic insects, interception by different types of terrestrial predators and densities of those predators, and physical factors such as temperature and wind (Power et al. 2000). These mediating factors are, in turn, influenced by such things as nutrient availability and primary productivity both within the stream and in surrounding riparian zones. In disturbed watersheds that contain streams with no riparian buffer, lateral prey dispersal and movement of nutrients into the upland areas may be greatly reduced. Preservation and restoration efforts should be a high priority for these streams and surrounding riparian corridors because although these landscape units are relatively small in area compared to surrounding upland habitats, they may be critical transition zones that have far greater implications for the overall functioning of surrounding ecosystems than originally thought (Ewel et al. 2001).

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Table 5.1 Sampling periods and location of the eight ^{15}N- NH_4 tracer additions and mean air temperature and total rainfall at each of the sites during the sampling period.

Stream	Location	ID	Location	Sampling Period	Air Temp. °C (min-max)	Total Rainfall (cm)
Quebrada Bisley	Puerto Rico	QBPR	18°N, 66°W	15 Jan. - 5 Mar. 1998	23.7 (20.5 - 27.0)	52.3 cm
Sycamore Creek	Arizona	SCAZ	33°N, 112°W	1 May - 12 June 1997	28.7 (19.6 - 37.8)	0.05 cm
Upper Ball Creek	North Carolina	UBNC	35°N, 83°W	4 Nov. - 16 Dec. 1996	6.2 (-0.6 - 12.3)	1.7 cm
Walker Branch	Tennessee	WBTN	36°N, 84°W	1 Apr. - 13 May 1997	13.4 (5.9 - 20.8)	28.2 cm
South Kings Creek	Kansas	KCKS	39°N, 94°W	7 Apr. - 12 May 1998	16.6 (9.7 - 23.6)	7.1 cm
Mack Creek	Oregon	MCOR	44°N, 122°W	21 July - 1 Sept. 1998	16.2 (12.8 - 22.2)	1.2 cm
Bear Brook	New Hampshire	BBNH	44°N, 72°W	17 June - 29 July 1997	16.5 (13.3 - 20.1)	25.1 cm
Steinbogalækur	Northern Iceland	STIC	65°N, 17°W	5 - 30 June 1999	11.1 (2.3 - 20.8)	5.1 cm

Table 5.2 Instream and emergence biomass estimated during the ^{15}N tracer release at each of the study sites. Percentage of instream biomass emerging per day was estimated by dividing emergence biomass (mg DM m^{-2} d^{-1}) by instream biomass (mg DM m^{-2}) and multiplying by 100. *Emergence biomass was estimated to be less than 0.1% of instream biomass for Upper Ball Creek (Wallace, personal communication).

Site	Instream Biomass (mg DM m^{-2})	Emergence Biomass (mg DM m^{-2} d^{-1})	% Emerging
QBPR	17	3.1	17.9
SCAZ	9000	165.1	1.8
UBNC	932	*0.9	0.1
WBTN	4463	18.5	0.4
KCKS	866	2.5	0.3
MCOR	234	32.4	13.9
BBNH	350	4.5	1.3
STIC	698	206.9	29.6

Table 5.3 Percentage of emerging aquatic insect biomass from each aquatic insect order collected during the ^{15}N tracer release at each of the study sites. Percentage of emerging insect biomass from each order was estimated by dividing emergence biomass from each order (mg DM m^{-2} d^{-1}) by total emergence biomass (mg DM m^{-2} d^{-1}) and multiplying by 100. * Data for Upper Ball Creek (UBNC) was estimated based on life history strategies and instream biomass collected during the period April 1991- March 1992 (Houston 1995). Other† includes Odonata, Megaloptera and aquatic Lepidoptera, Hemiptera, Neuroptera and Coleoptera. NC= not collected.

SITE	Ephemeroptera	Plecoptera	Trichoptera	Diptera	Other†
QBPR	69	NC	3	23	5
SCAZ	13	NC	38	46	3
UBNC*	NC	58	9	33	1
WBTN	75	13	3	8	1
KCKS	2	39	1	54	4
MCOR	2	61	29	6	2
BBNH	15	14	10	60	1
STIC	NC	1	6	92	1

Table 5.4 Percentage of spider N (+/- s.e.) obtained from ^{15}N enriched aquatic insects at each of the sites was calculated using mixing models (see text for details). The most common spiders collected on vegetation using timed beat nets were divided into three groups: sit-and-wait strategists (SWV), aerial orb-web weaving (ORB) and sheet-web weaving spiders (SHT). Ground-dwelling spiders collected in pitfall traps were divided into two groups: hunting spiders that find prey by wandering on the ground (WND) and those that use a sit-and-wait strategy (SWG).

SITE	CANOPY-DWELLING SPIDERS			GROUND-DWELLING SPIDERS	
	ORB	SHT	SWV	WND	SWG
QBPR	19.9 (4.7)	33.9 (16.9)	1.3 (1.1)	12.3 (8.9)	3.9 (0.05)
SCAZ	38.3 (8.8)	10.6 (3.4)	15.3 (3.4)	26.9 (2.8)	5.6 (1.1)
UBNC*	1.3 (0.6)	< 1.0	< 1.0	1.5 (0.8)	2.1 (0.7)
WBTN	7.5 (3.2)	4.6 (2.4)	9.9 (4.2)	9.6 (4.7)	8.1 (1.7)
KCKS	7.8 (3.2)	4.5 (2.1)	3.3 (0.6)	3.5 (0.7)	9.1 (1.9)
MCOR	19.0 (5.8)	< 1.0	< 1.0	15.1 (6.7)	< 1.0
BBNH	2.2 (0.8)	3.9 (0.9)	< 1.0	3.7 (0.8)	1.6 (0.8)
STIC	29.7 (2.5)	21.7 (5.8)	NA	10.8 (2.3)	NA

NA = feeding guild was absent or not present in high enough numbers to obtain a sample for ^{15}N analysis

Figure 5.1 Map showing location of eight sites where sampling was conducted.

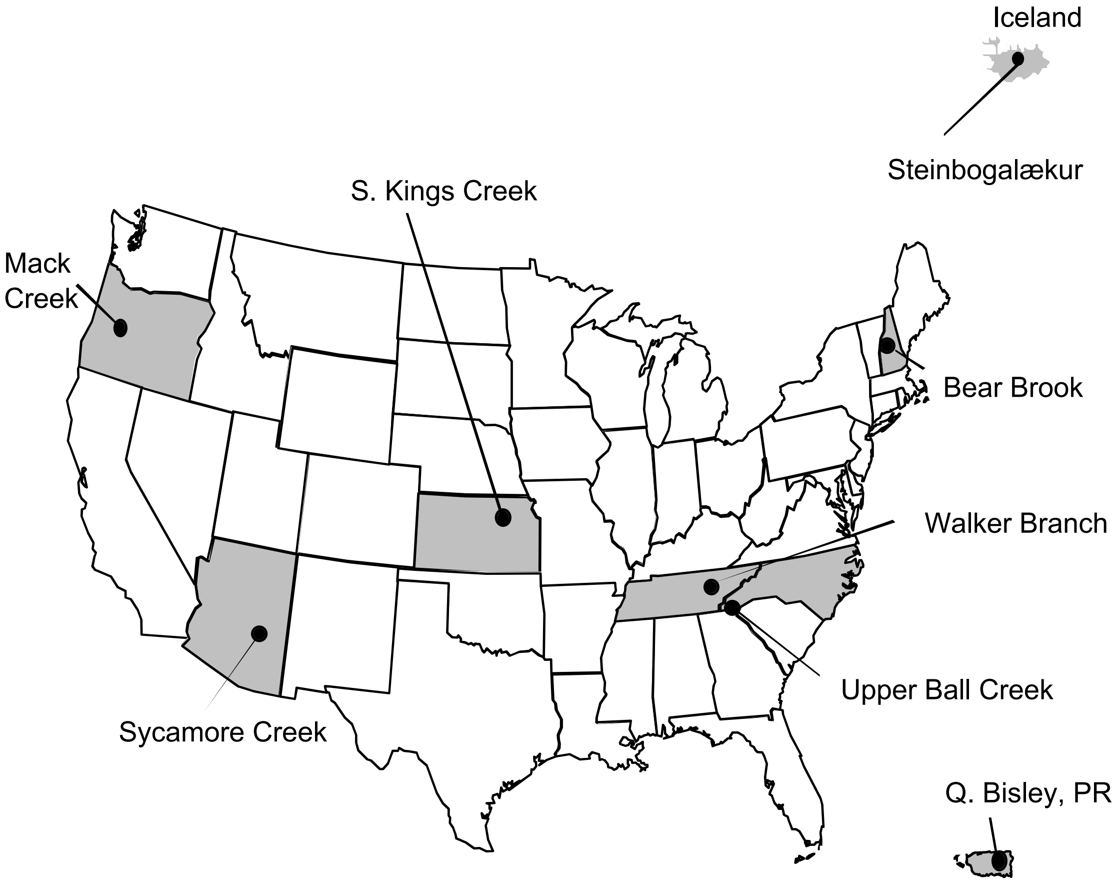
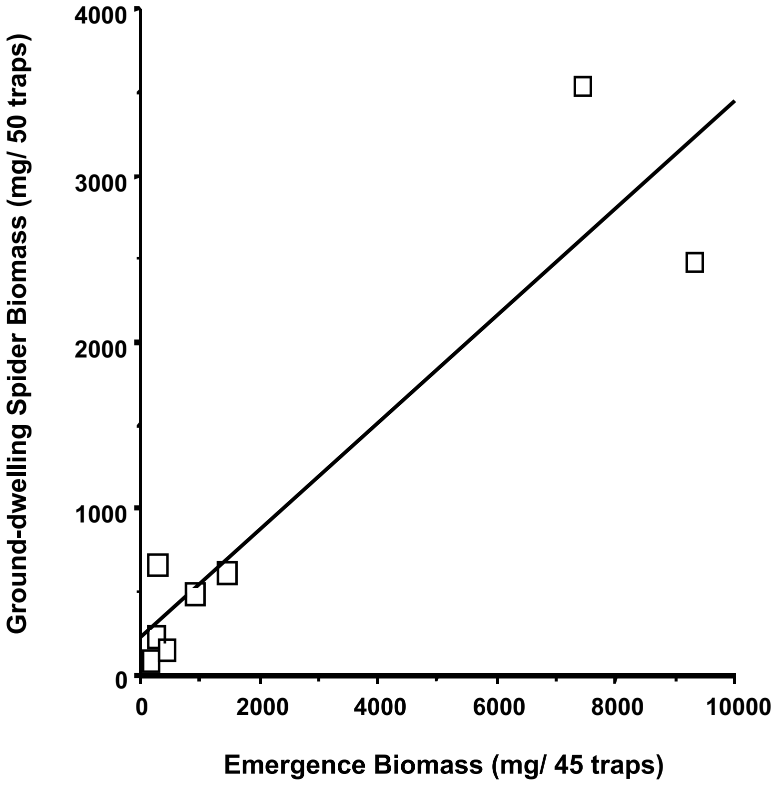

Iceland
Steinbogalækur
S. Kings Creek
Mack
Creek
Bear Brook
Walker Branch
Upper Ball Creek
Sycamore Creek
Q. Bisley, PR

Figure 5.2 Results of linear regression analysis showing that ground-dwelling spider biomass is positively related to emergence biomass during the ^{15}N tracer releases. The relationship is significant when comparing across all eight sites (a), and when looking at forested sites alone (b).

(a)


Ground-dwelling Spider Biomass (mg/ 50 traps)
4000
3000
2000
1000
0
0
2000
4000
6000
8000
10000
Emergence Biomass (mg/ 45 traps)

(b)

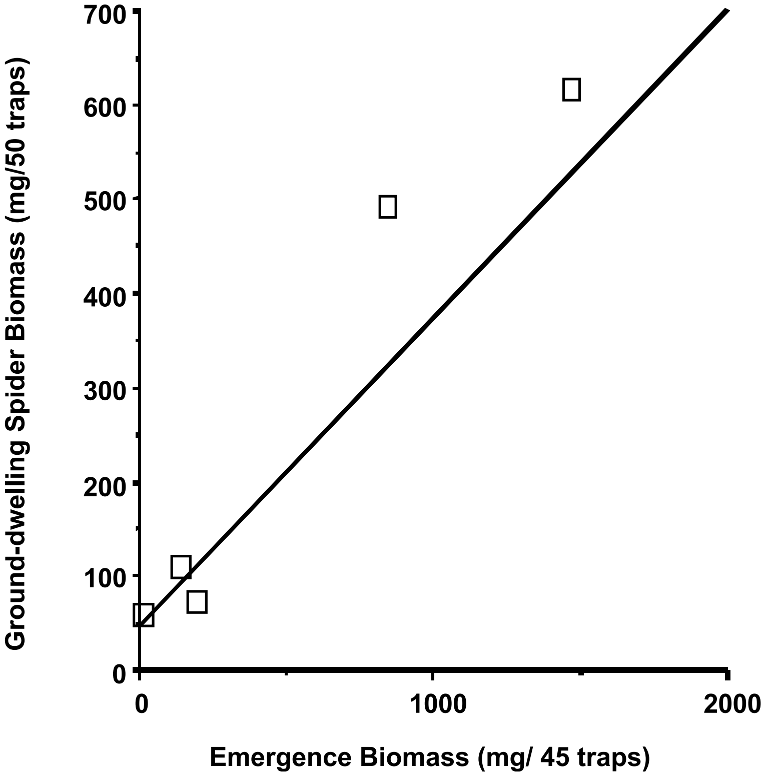
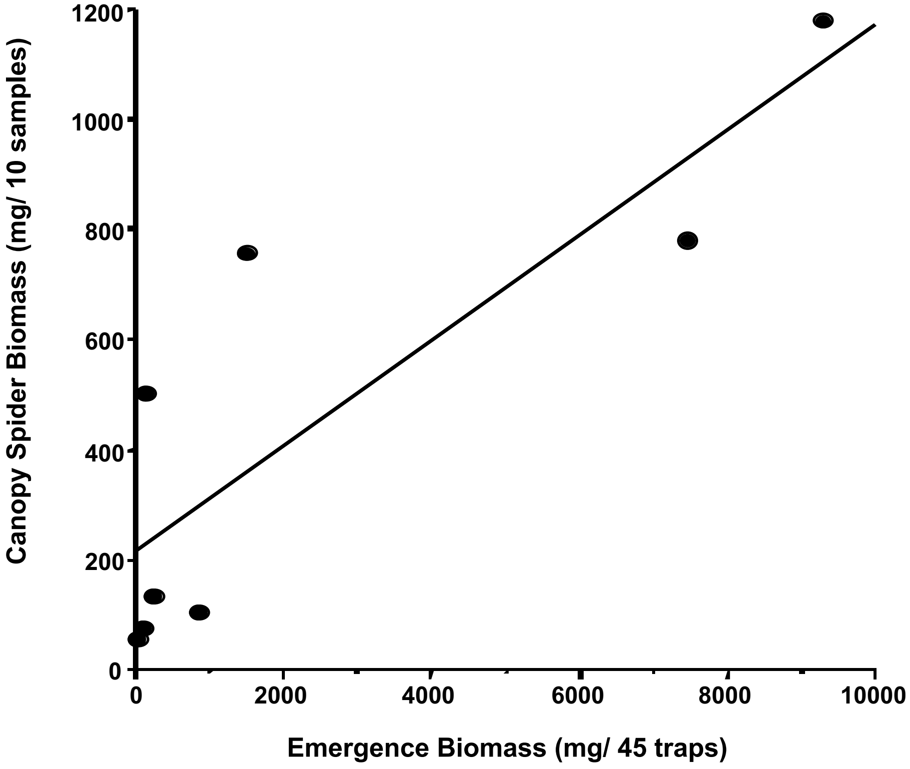

Ground-dwelling Spider Biomass (mg/50 traps)
700
600
500
400
300
200
100
0
0
1000
2000
Emergence Biomass (mg/ 45 traps)

Figure 5.3 Results of linear regression analysis showing that lower canopy spider biomass is positively related to emergence biomass during the ^{15}N tracer releases (a). Although a similar trend is observed when analyzing forested sites only, the relationship is not significant (b).

(a)


Canopy Spider Biomass (mg/ 10 samples)
1200
1000
800
600
400
200
0
0
2000
4000
6000
8000
10000
Emergence Biomass (mg/ 45 traps)

(b)

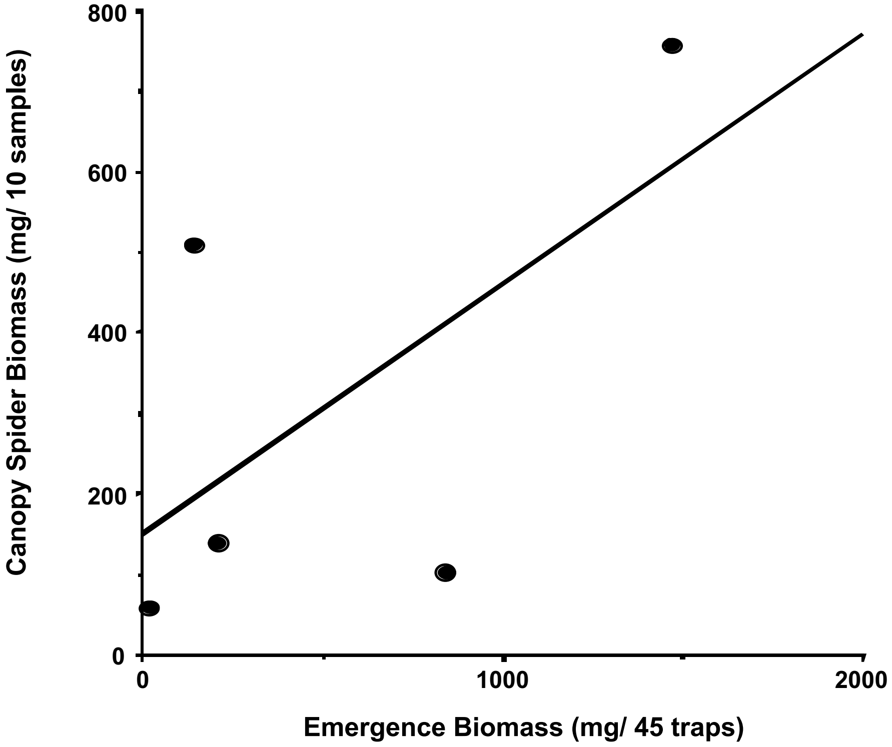
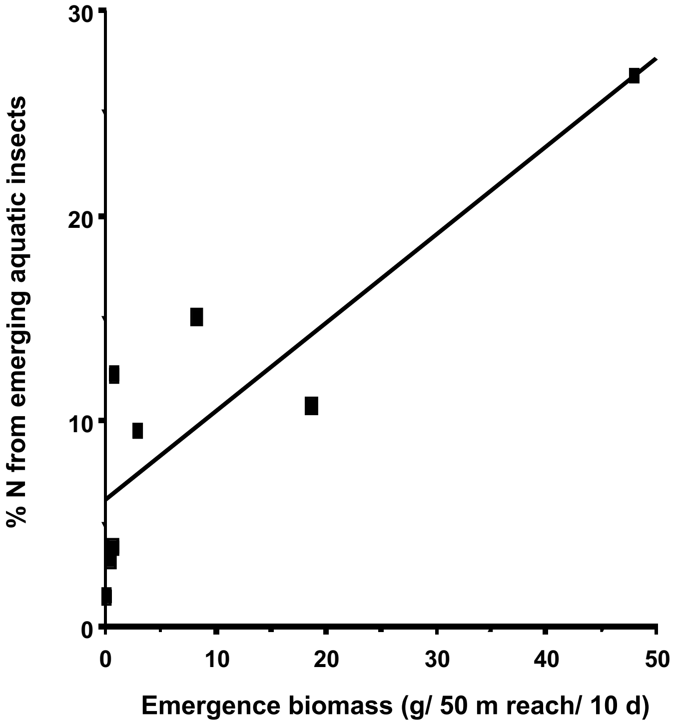

Canopy Spider Biomass (mg/ 10 samples)
800
600
400
200
0
0
1000
2000
Emergence Biomass (mg/ 45 traps)

Figure 5.4 Percentage of N that ground-dwelling (a) and lower canopy (b) spiders obtain from ^{15}N enriched aquatic insects at each of the sites was positively related to total biomass of aquatic insects emerging during the ^{15}N tracer additions [g (50 m reach)$^{-1}$ 10d^{-1}].

(a)


% N from emerging aquatic insects
0
10
20
30
0
10
20
30
40
50
Emergence biomass (g/ 50 m reach/ 10 d)

(b)

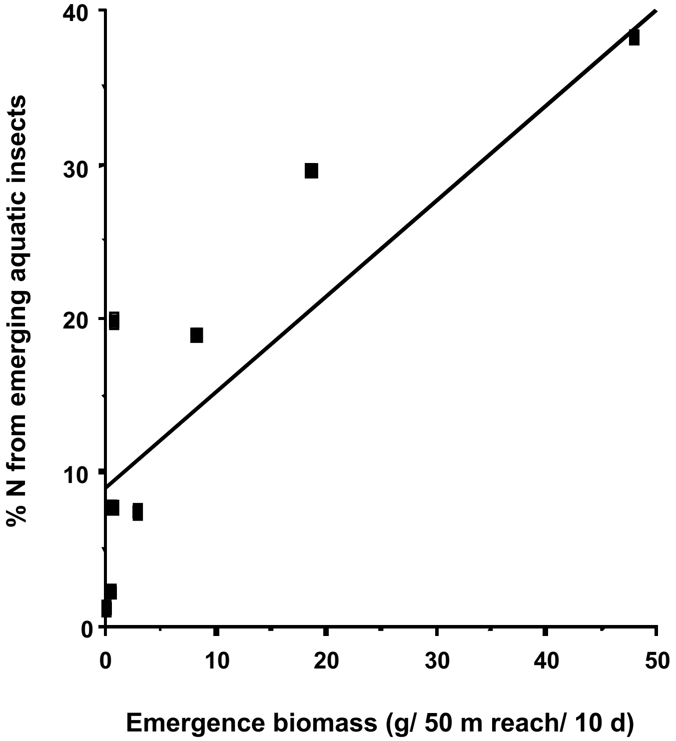
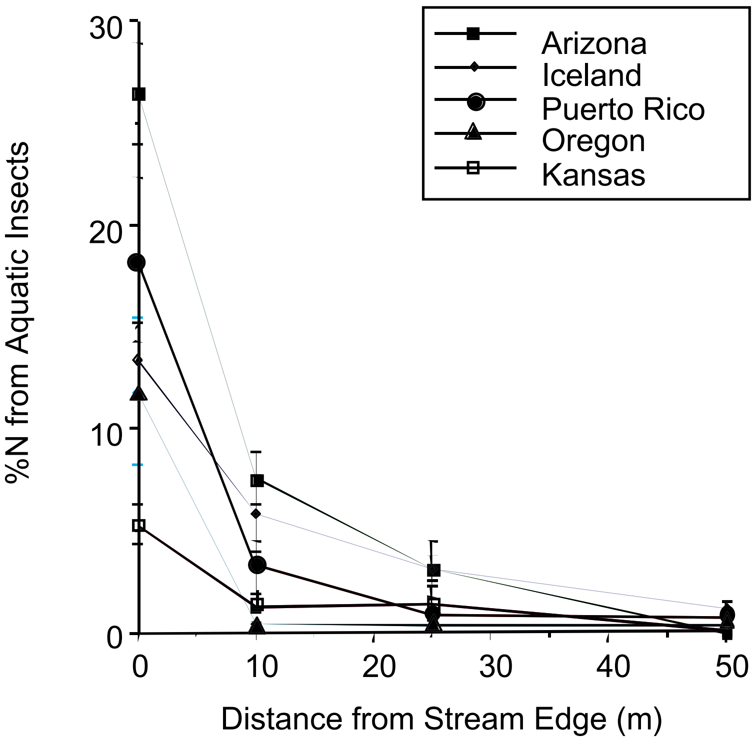

% N from emerging aquatic insects
0
10
20
30
40
0
10
20
30
40
50
Emergence biomass (g/ 50 m reach/ 10 d)

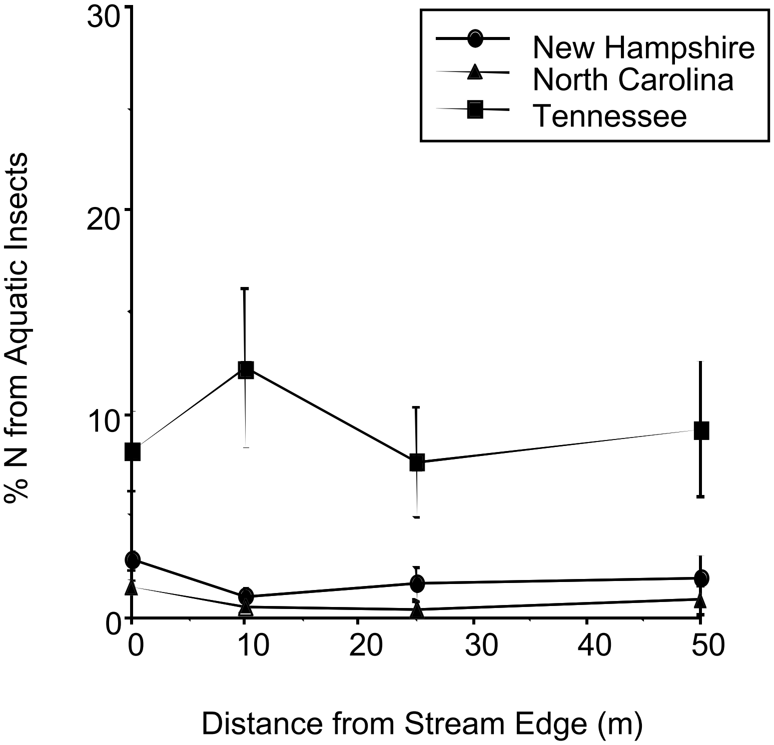
Figure 5.5 Percentage of spider N obtained from adult aquatic insects along the stream-to-upland transects in the desert, arctic, tall-grass prairie, northern conifer and tropical forest sites (a), and in the three eastern deciduous forest sites (b) over the 6 week period of the tracer releases.

(a)



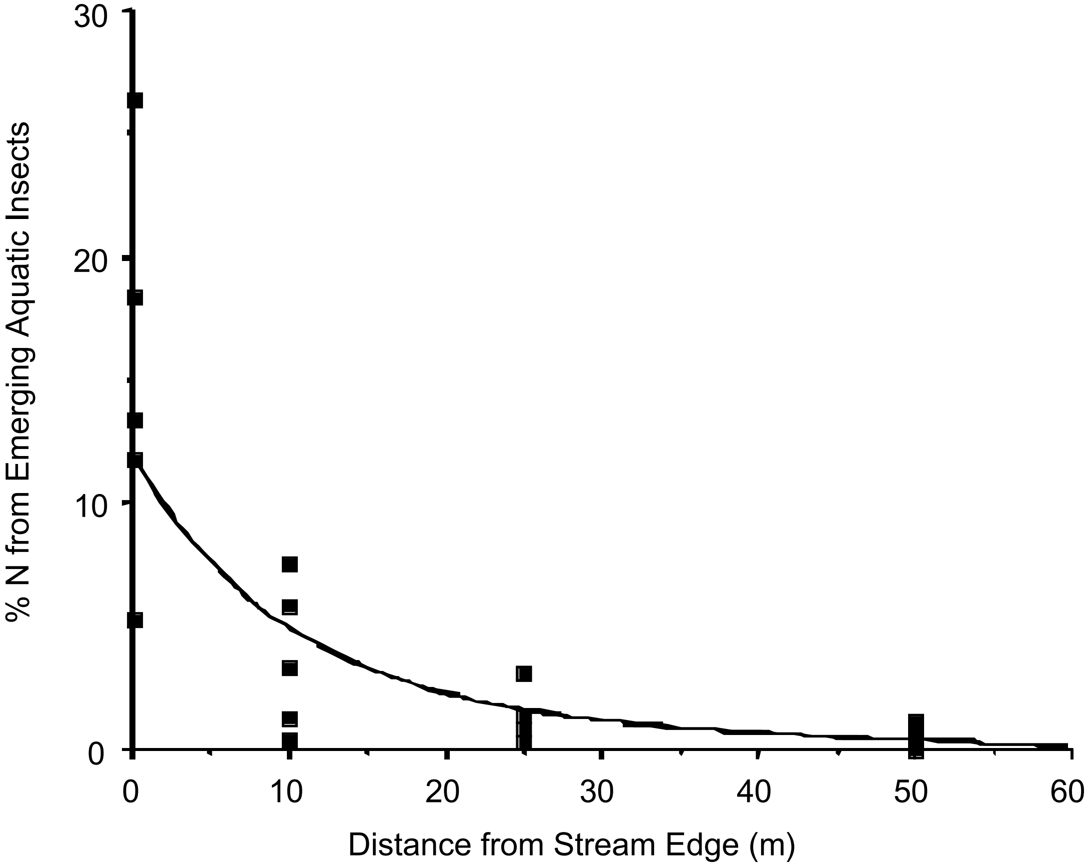
Arizona
Iceland
Puerto Rico
Oregon
Kansas
%N from Aquatic Insects
30
20
10
0
0
10
20
30
40
50
Distance from Stream Edge (m)

(b)



New Hampshire
North Carolina
Tennessee
% N from Aquatic Insects
30
20
10
0
0
10
20
30
40
50
Distance from Stream Edge (m)

Figure 5.6 Percentage of spider N obtained from emerging aquatic insects was directly related to distance from stream edge in the desert, arctic, tall-grass prairie, northern conifer and tropical forest sites. Plotting the data from these five sites we determined an exponential decline ($n=20$, $r^2=0.677$, $p< 0.0001$) in percent N of spiders from aquatic sources with distance from stream edge (m).


30
20
10
0
0
10
20
30
40
50
60
% N from Emerging Aquatic Insects
Distance from Stream Edge (m)

Appendix 5.1 Mean physical, chemical and biological characteristics from the first day of the ^{15}N tracer additions at each of the eight streams. Streams are listed from lowest to highest in latitude.

Stream	Riparian canopy	Wetted width (m)	Mean depth (cm)	Discharge (L s^{-1})	Mean Temp. (°C)	DIN (µg/ L)	SRP µg/ L) (µg/ L)	Ratio of autotrophic to detrital biomass
QBPR	closed	4.7	12	17	21.9	132	14	0.03
SCAZ	open	5.8	4	31	23	15	14	8.90
UBNC	closed	2.7	18	51.4	7.2	3	2	0.001
WBTN	closed	3.1	4	7.8	11.9	23	3	0.11
KCKS	open	2.4	10	10.4	12.1	5	3	0.05
MCOR	closed	5.1	11	60	13.8	61	13	0.16
BBNH	closed	2.1	13	2.3	14.5	59	4	0.21
STIC	open	1.8	15	156	6.9	24	10	0.45

Appendix 5.2 Dominant vegetation types in riparian and upland habitats. *Dominant riparian vegetation differed from upland vegetation in the desert (SCAZ), arctic (STIC), tall-grass prairie (KCKS) and one of the eastern deciduous forest sites (UBNC).

SITE	DOMINANT VEGETATION	
	Riparian	Upland
QBPR	*Dacryodes excelsa* *Sloanea berteriana* *Prestoea montana*	*Dacryodes excelsa* *Sloanea berteriana* *Prestoea montana*
SCAZ*	*Salix exigua* *S. goodingii* *Fraxinus pennsylvanica* *Platanus wrighti* *Populus fremontii* *Juglans major* *Prosopis gladulosa*	*Cereus giganteus* *Opuntia spp.*
UBNC*	*Quercus spp.* *Carya spp.* *Liriodendron tulipifera* *Rhododendron maximum* *Kalmia latifolia*	*Quercus spp.* *Carya spp.* *Liriodendron tulipifera*
WBTN	*Quercus spp.* *Liriodendron tulipifera* *Acer rubrum*	*Quercus spp.* *Liriodendron tulipifera* *Acer rubrum*
KCKS*	*Ulmus americana* *Populus deltoides* *Cornus drummondi* *Rhus aromatica*	*Andropogon gerardii* *A. scoparius* *Sorghastrum nutans*
MCOR	*Pseudotsuga menziessii* *Thuja plicata* *Tsuga heterophylla*	*Pseudotsuga menziessii* *Thuja plicata* *Tsuga heterophylla*
BBNH	*Fagus grandifolia* *Betula lutea* *Acer saccharum*	*Fagus grandifolia* *Betula lutea* *Acer saccharum*
STIC*	*Betula nana* *Salix lanata* *S. phylicifolia* *S. callicarpaea* *Vaccinium uliginosum* *Empetrum nigrum*	*Betula nana* *Salix lanata* *Vaccinium uliginosum* *Empetrum nigrum*

Appendix 5.3 ^{15}N mixing model results for each of the eight sites. Exponential decay constants (*k*) were derived using both in-stream aquatic nymph/ larvae data and emerging aquatic insect data (when available) to predict aquatic insect enrichment ($\delta^{15}N_{d,E}$) d meters downstream from the release point using the following equation: $\delta\,^{15}N_{d,E} = \delta^{15}N_{0,E}\ e^{-kd}$. The parameters *s* (proportion of adults emerging at point d) and *x* (average upstream flight distance of emerged adult aquatic insects) was calculated using the following equation: $\delta\,^{15}N_{d,F} =$ $(s)(\ \delta^{15}N_{0,E}\ e^{-kd}) + (1\text{-}s)\ (\delta^{15}N_{0,E}\ e^{-k(d+x)})$. δ^{15}N values from aquatic insects captured in light traps or sweep net samples (STIC) on the last day of each of the releases was used to estimate the flight distance (*x*) and the partition coefficient of two subpopulations (*s* and *1*-*s*).

SITE	*k*	$\delta^{15}N_{d,E}$	s	x
QBPR	0.01894	550.19	0.68	67 m
SCAZ	0.01557	202.53	0.38	109 m
UBNC	0.00767	36.73	0.54	201 m
WBTN	0.01331	45.3	0.28	218 m
KCKS	0.01201	203.70	0.69	352 m
MCOR	0.01597	387.24	0.66	261 m
BBNH	0.00588	102.69	0.76	471 m
STIC	0.00058	303.09	0.06	2,340 m

CHAPTER 6

GENERAL CONCLUSIONS

Nutrients, energy, materials and organisms cross spatial boundaries, often with a multitude of effects on neighboring ecosystem processes and community dynamics. The research presented in this dissertation has revealed that stream-derived nutrients and organisms are important to terrestrial invertebrate predators in many different biomes. Field surveys of spider communities in riparian and upland habitats, and ^{15}N tracer additions into eight streams reveal the following:

1. *Aquatic subsidies are common and widespread.*

This study provides evidence that aquatic subsides are being utililized by terrestrial invertebrate predators in many different biomes. Using ^{15}N tracer additions, I determined that spiders in desert, arctic, tall-grass-prairie, northern conifer, tropical and eastern deciduous forest sites were directly consuming aquatic insects (Chapters 2, 3 and 5), and that % of nitrogen from aquatic sources incorporated into spider biomass was directly related to the amount of aquatic insects emerging during ^{15}N tracer releases (Chapter 5).

2. *Although spiders living along the land-water margin are utilizing stream subsidies, reliance of spiders on aquatic resources declined exponentially with distance from the stream edge.*

The detailed analysis of spiders in the Sonoran desert watershed in Chapter 3 provides evidence that spiders collected within the active stream channel obtained a greater percentage of their total nitrogen from aquatic sources, as compared to those collected in upland areas. 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. In fact, spiders in five of the eight sites showed an exponential decline in reliance of spiders on aquatic insects with distance from edge (Chapter 5). This trend was unrelated to the types of insects emerging during the ^{15}N releases.

3. Ground-dwelling and canopy spider abundance and biomass was highly correlated with emergence biomass, suggesting that emerging aquatic insects are providing a direct trophic subsidy to spiders.

Despite the large variability among the sites with respect to temperature, rainfall and structural complexity of vegetation, aquatic insect emergence was the environmental parameter most correlated with ground-dwelling and lower canopy spider abundance and biomass in riparian zone habitats across all biomes (Chapters 4 and 5). Structural complexity of vegetation on the ground and in the canopy also helped to explain differences in spider biomass, abundance and diversity among the eight sites (Chapters 2 and 4).

4. Aquatic subsidies impact the spatial distribution of spiders in adjacent terrestrial habitats.

In all but two of the sites (UBNC and BBNH), spiders were concentrated at the land-water margin. The reliance of orb-web weaving and wandering spiders on emerging aquatic insects explains, at least in part, why these groups are concentrated along stream channels (Chapters 3 and 4). By calculating an energy budget for spiders living in each of the eight riparian zones, I determined that terrestrial insects alone could not support the spider biomass found in the riparian zone habitats of the desert, arctic, tall-grass prairie, northern conifer and tropical forest sites (Chapter 4). The additional energy (kJ) supplied by aquatic insects could, however, support the existing spider biomass at all five sites.

Spatial subsidies vary in both space and time. The results of this study suggest that when aquatic insect emergence is high relative to terrestrial insect biomass, aquatic subsidies may be an important factor influencing the spatial distribution of terrestrial consumers. In this study, differences between biomes in reliance of spiders on aquatic resources represents a sample taken at one point in time. Because spider biomass is directly related to emergence biomass this study predicts that when emergence biomass is high (irrespective of where samples are taken) terrestrial consumers will be more abundant and diverse along the stream bank than in upland habitats. To better understand the relationship between aquatic subsidies and terrestrial consumers, temporal variation in fluxes between aquatic and terrestrial ecosystems should also be considered.

Implications for Future Research and Management Practices

Riparian zones are critical, not only for the maintenance of species and ecosystem processes unique to them, but because they are active areas that transform and regulate fluxes between streams and surrounding upland habitats. Many studies conducted at the land-water margin have shown that riparian zones are important in regulating the fluxes of energy, nutrients and organisms from terrestrial to aquatic ecosystems. The research presented in this dissertation shows that nutrients and organisms from stream habitats can greatly impact the distribution of consumers living in adjacent terrestrial habitats.

Because food webs are extremely complex and vary with even minor variation in nutrient inputs, transfer of nutrients across ecosystem boundaries may be even more important than the flux of organisms across such boundaries (Polis and Strong 1996). Using ^{15}N tracer additions, the transfer of nitrogen from aquatic to terrestrial ecosystems was directly measured in watersheds of eight relatively undisturbed headwater streams. It is possible that stable isotopes could be used to trace the flux of N between aquatic and terrestrial ecosystems in human-impacted watersheds, where streams are often decoupled from surrounding terrestrial landscapes.

Human activities have altered the N-cycle on both global and local scales through increased use of fertilizer, poor grazing practices, and increasing atmospheric N deposition (Vitousek et al. 1997). In addition to affecting water quality, increased N inputs may alter biodiversity and food web dynamics along the riparian corridor as N is transferred from primary to secondary consumers within the stream, and then to adjacent terrestrial communities. This may be especially true in increasingly fragmented landscapes where in-stream secondary production in isolated riparian corridors provides one of the only food sources for terrestrial insectivores. In order to predict the effects of human-induced increases of nitrogen to streams and surrounding riparian zones, we must develop not only an understanding of instream nitrogen cycling and fluxes of N from upstream habitats, but also develop an understanding of the transfers of N between streams and surrounding terrestrial habitats.

Results of this and other studies suggest that the preservation and restoration of stream ecosystems must include not only protection of instream processes and function, but also must consider the protection of surrounding riparian corridors. As Doppelt (1993) so eloquently points out, “Most people think of rivers simply as water flowing through a channel. This narrow view fails to capture the actual complexity and diversity of riverine systems, and is one of the reasons for failed policies.” If we are to succeed in preservation, conservation or restoration efforts at the watershed scale, we must develop an understanding of the fluxes that occur across critical ecosystem boudaries and apply that understanding to such efforts.

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