

Forest structure and stream salamander diets: Implications for terrestrial-aquatic connectivity

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Introduction

The concept of the ecological boundary is emerging as a useful tool for investigating and understanding ecological processes in heterogeneous landscapes (CADENASSO et al. 2003). Ecosystem ecologists have provided valuable perspectives on the behavior of ecological boundaries, elucidating the regulation of boundary permeability and its implications for energy and nutrient cycles within contiguous patches of different habitat types (BORMANN & LIKENS 1979, HEDIN et al. 1998). These boundary-mediated fluxes and direct effects of ecological boundaries on the distribution and dispersal of organisms (e.g., HADDAD 1999) can strongly influence emergent properties of natural systems, including resource dynamics (JEFFERIES 2000), secondary productivity (POLIS & HURD 1996), and food web composition and stability (HUXEL & MCCANN 1998).

The ecological boundary between aquatic and terrestrial habitats exerts fundamental control on headwater stream systems, where both ecosystem processes and food webs of terrestrial and stream habitats are widely viewed as coupled (ROSS 1963, WALLACE et al. 1997). The structure and composition of terrestrial vegetation influence the transfer of dissolved substances to the stream (e.g., LIKENS & BORMANN 1995) and regulate in-stream processing of these substances by affecting light, temperature, and hydrologic regimes (HILL et al. 2001, VALETT et al. 2002). Species inhabiting headwater systems rely on the flow of resources from terrestrial to stream habitats (WALLACE et al. 1997, NAKANO et al. 1999b), stream to terrestrial habitats (HELFIELD & NAIMAN 2001, SABO & POWER 2002), and reciprocal flows between these two habitats (NAKANO & MURAKAMI 2001). Research is limited on how terrestrial-aquatic connectivity in headwater food webs responds to natural variation in terrestrial vegetation conditions, and the research that has been done focuses on stream fish (WIPFLI 1997, ALLAN et al. 2003). Broader understanding in this area will create valuable opportunities to bridge ecosystem- and community-oriented

research in stream systems, and to elucidate more fully the implications of well-established patterns of forest succession (e.g., YODA et al. 1963, SCHWARZ et al. 2001). This understanding of how riparian forest vegetation affects terrestrial-aquatic links may also be important for forest management that aims to preserve natural ecosystem processes.

Salamanders are common in first-order, headwater streams of eastern and western North America (PETRANKA 1998). While the larvae of stream salamanders are strictly aquatic, adults exhibit different degrees of association with the stream itself and are often found in streamside forests (GROVER & WILBUR 2002). Consequently, adult salamanders may influence across-boundary connectivity in headwater food webs by selecting aquatic versus terrestrial prey. The salamander *Gyrinophilus porphyriticus* (Plethodontidae) occurs in headwater systems of the eastern United States and southern Quebec (PETRANKA 1998, LOWE & BOLGER 2002). Adults can reach 21 cm in total length and are highly aquatic, but can forage along the stream bank at night (DEGRAAF & RUDIS 1990). In the northeastern United States, this species feeds primarily on aquatic and terrestrial invertebrates (BURTON 1976). The contributions of these two prey pools to adult *G. porphyriticus* diets is likely to be influenced by the availability and accessibility of constituent species. Prey availability and accessibility may respond to direct effects of riparian forest conditions on prey density (e.g., WALLACE et al. 1997, HALL et al. 2001) or effects of these conditions on attributes of the stream and riparian environments that influence the foraging behavior of adult salamanders (e.g., temperature, moisture, cover, predators: BRODIE et al. 1979, GROVER & WILBUR 2002).

We hypothesized that riparian forest conditions in headwater drainages, including (1) forest structure (i.e., the density and size of trees), (2) forest composition (i.e., the relative abundance of deciduous versus coniferous trees), and (3) canopy cover over the stream, influence the relative contributions of terrestrial and aquatic prey to adult *G. porphyriticus* diets.

In the focal drainages, forest structure is likely regulated by successional dynamics following natural disturbances (e.g., wind, fire, drought; YODA et al. 1963, SCHWARZ et al. 2001) and may influence physical conditions and prey availability in the stream and riparian zone through associated variation in canopy architecture, litter quantity and quality, or ground cover (BORMANN & LIKENS 1979, SCHEU & SCHULZ 1996, GUO et al. 2002). The relative abundance of deciduous and coniferous trees also affects the quality and quantity of litter delivered to the stream and forest floor. This litter serves as a food resource for aquatic and terrestrial invertebrates (e.g., SCHEU & SCHULZ 1996, WALLACE et al. 1997, RICHARDSON et al. 2004), and may affect microhabitat conditions on the forest floor such as moisture and acidity (e.g., NEIRYNCK et al. 2000). Canopy cover can regulate the amount of sunlight that reaches the stream, controlling in-stream primary productivity and production of aquatic prey that rely on periphyton as a food resource (e.g., FEMINELLA et al. 1989). These aquatic prey may be used by the salamanders, but may also benefit stream fish that prey on salamanders (e.g., RESETARITS 1991).

To explore directly the mechanism(s) underlying relationships between forest variables and salamander diet composition, we tested two additional hypotheses. We hypothesized that forest conditions affect the availability of aquatic invertebrates that *G. porphyriticus* adults prey on (WALLACE et al. 1997, HALL et al. 2001), and we expected the relative contribution of terrestrial prey to salamander diets to be negatively correlated with aquatic prey availability in the stream. Source availability has been shown to influence the diets of stream fishes, both in experiments (NISLOW et al. 1998) and under natural conditions (CADA et al. 1987), and may influence stream salamander diets as well. Alternatively, we hypothesized that forest conditions affect the abundance of brook trout (*Salvelinus fontinalis*), the only fish species we have found to occur in first-order streams in New Hampshire (LOWE & BOLGER 2002, NISLOW & LOWE 2003), one we have shown to respond to forest management (NISLOW & LOWE 2003), and one known to compete with and prey on *G. porphyriticus* (RESETARITS 1991). We expected the relative contribution of terrestrial prey to adult salamander diets to be positively correlated with trout abundance because salamanders in high-trout streams would be less likely to forage in the stream, where they would experience competition and predation from trout.

Key words: streams; riparian zone; food webs; amphibians; foraging; invertebrates

Methods

Study sites and data collection

This research was conducted in 10 first-order stream drainages in New Hampshire, USA. To examine the effects of natural variation in forest conditions on salamander diet composition, we selected drainages that had not been exposed to human disturbance (i.e., logging or road building) in the last 50 years using land-use data collected for a previous study (LOWE & BOLGER 2002). These streams had moderate slopes (2–4%) and small drainage areas (< 1 km²). In the temperate forests of these sites, dominant deciduous tree species were *Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia*, and *B. papyrifera*. Dominant coniferous tree species were *Picea rubens*, *Abies balsamea*, and *Tsuga canadensis*. We established 100-m study sections along each stream, starting 25 m upstream of the confluence of the first-order study stream with a larger stream.

To assess riparian forest structure and composition, we set six, 50 m-long by 1 m-wide belt transects perpendicular to the stream channel at random locations along each study section. The maximum distance from the stream that *G. porphyriticus* individuals move during terrestrial foraging bouts is unknown. Based on our own experience and discussions with other researchers (J.S. ANDREWS, H.M. WILBUR, pers. comm.), we assumed that this distance is less than 50 m and selected the transect length based on this assumption. Three transects were placed on each side of the stream. We then counted and measured the diameter at breast height (DBH, cm) of all trees within the transects with DBH \geq 3 cm. These data were used to calculate mean tree density (individuals / 500 m² transect) and mean tree DBH (calculated using mean DBH values from each of the six transects). We also identified trees as either deciduous or coniferous to estimate the proportion of deciduous trees in the riparian forest (1 – proportion coniferous trees), pooling individuals across all transects. Standing in the middle of the channel with a spherical densiometer, we measured proportion canopy coverage over the stream at six locations randomly selected along the length of the 100-m long study section and used these data to calculate mean proportion canopy coverage.

We conducted three salamander surveys in these study sections at approximately three-week intervals beginning in mid-June and ending in mid-August of 2001 using a cover-controlled active-search sampling method (HEYER et al. 1994). Moving upstream, one rock between 64 and 256 mm in diameter was turned per meter of stream length. Rocks were selected from the channel and edge of the stream. An aquarium dipnet was used to capture salamanders, including those

flushed by the current. Gut contents of *G. porphyriticus* adults were collected by stomach flushing and immediately placed in 70% ETOH for preservation. All *G. porphyriticus* were individually marked by subcutaneous injection of a fluorescent elastomer (Northwest Marine Technologies, Shaw Island, Washington, USA), allowing us to avoid re-sampling the same animal in subsequent surveys. Other salamander species were encountered infrequently in these surveys, and included *Desmognathus fuscus* and *Eurycea bislineata* (both Plethodontidae).

Our survey methodology was based on the assumption that salamanders found in and along the stream during the day were a random subset of the entire population, including both those animals that remain in the stream at night to forage and those that leave the stream at night to forage in the riparian zone. Because *G. porphyriticus* adults need to keep their skin moist to respire (RAY 1958), and because we have only observed them away from streams at night, we think it unlikely that they stay away from streams during summer days.

Individual prey items were identified to order. Based on taxonomic information and direct examination of morphological traits, prey were characterized as originating in either the aquatic or terrestrial habitat. The length and width of prey items (mm) were measured with an ocular micrometer and these measurements were used to calculate volume, assuming each item to be a cylinder (HYNES & COLEMAN 1968). This method allowed us to include items that were not intact animals in calculations of prey biovolume. We calculated total gut content biovolume for each salamander and the proportion of total biovolume derived from terrestrial and aquatic prey. Mean proportion terrestrial biovolume in salamander guts was then calculated for each stream, combining individuals across sampling dates.

To assess aquatic prey availability, we collected benthic invertebrates from all ten streams the last week of June 2001, the middle of the salamander survey period. Invertebrates were sampled at three stations located randomly within the upper, middle, and lower reaches of the study sections. At each station, six randomly-placed Surber samples were collected (sample area 0.33 m², net mesh size = 600 µm) and then composited into a single sample, resulting in three replicates per site. Invertebrates were preserved in 95% ETOH and transported to the laboratory, where all individuals in each sample were identified to order, and individuals in those orders found in *G. porphyriticus* gut contents were pooled to estimate aquatic prey density (mean no. individuals / m² of stream bottom).

To estimate brook trout abundance, we conducted electrofishing censuses of the study sections during a

one-week period in late August of 2001. These censuses involved multiple-pass removal using a Smith-Root BP-12 backpack electroshocker set to 500V DC. Fish captured in each pass were anesthetized using MS-222. They were then counted, weighed, measured and returned to the stream. A modified Zippin maximum likelihood method was used to estimate brook trout abundance (no. individuals / 100 m study section: CARLE & STRUB 1978).

Statistical analysis

Under the *a priori* assumption that mean tree density and mean DBH would be highly correlated (YODA et al. 1963), we used principal components analysis to collapse these two variables into a single independent variable representing forest structure. Mean tree density and mean DBH were square root-transformed for principal component analysis. We used Pearson product-moment analyses to evaluate multicollinearity among the three forest-related independent variables: structure, proportion deciduous trees, and canopy cover.

We used regression analyses to assess relationships between each forest-related independent variable and the three dependent variables: (1) mean proportion terrestrial prey (measured as proportion of total biovolume) in salamander guts, (2) mean aquatic prey density, and (3) brook trout abundance. Regression analysis of mean proportion terrestrial biovolume in salamander guts was weighted by the number of gut content samples obtained from each stream. We then tested for correlation between mean proportion terrestrial prey in salamander diets and the remaining dependent variables. All statistical tests were conducted using SAS (SAS INSTITUTE 1990).

Results

Forest structure

Mean tree density (± 1 S.E.) in the study drainages ranged from 11 ± 1.91 to 28.5 ± 4.4 individuals / 500 m² transect, mean tree DBH ranged from 6.36 ± 0.53 to 18.99 ± 2.13 cm, proportion deciduous trees ranged from 0.33 to 0.9, and proportion canopy coverage ranged from 0.84 ± 0.11 to 0.95 ± 0.33 . Mean tree density and mean tree DBH were negatively correlated ($r = -0.83$, $n = 10$, $P < 0.01$). The first principal component (structure PC-1) accounted for 92% of the variability in these two measures (eigenvalue = 1.83) and was negatively correlated with mean tree density and positively correlated with mean tree DBH (Table 1). In pairwise analyses, there was no significant au-

Table 1. Factor loading for forest structure variables produced by principal component analysis of data from 10 focal headwater drainages in New Hampshire, USA. Mean tree density (individuals / 500 m² transect) and mean tree diameter at breast height (DBH, cm) were square root-transformed for principal component analysis.

Variable	PC-1	PC-2
Mean tree density	-0.96	0.29
Mean tree DBH	0.96	0.29

tocorrelation among structure PC-1, proportion deciduous trees, and canopy cover. Structure PC-1 and proportion deciduous trees were uncorrelated ($r = 0.21$, $n = 10$, $P = 0.56$), and canopy cover and proportion deciduous trees were uncorrelated ($r = -0.29$, $n = 10$, $P = 0.42$). Canopy cover tended to increase with decreasing tree density and increasing tree DBH (i.e., increasing structure PC-1 values), but this relationship was not statistically significant ($r = 0.57$, $n = 10$, $P = 0.09$).

Factors influencing salamander diet

Stomach samples from a total of 76 *G. porphyriticus* adults were collected across the ten study streams. Variation among streams in the number of gut content samples collected resulted from variation in the abundance of *G. por-*

phyriticus adults (LOWE & BOLGER 2002, LOWE et al. 2004). Adult *G. porphyriticus* gut samples contained both aquatic- and terrestrial-derived prey in all but three sites, with mean relative proportion of terrestrial-derived prey varying substantially across sites (0 to 74%, Fig. 1). Orders of aquatic invertebrate prey identified in salamander gut contents (% of total aquatic prey biovolume, pooled across all individuals) were Coleoptera (47%), Trichoptera (22%), Hemiptera (9%), Diptera (8%), and Plecoptera (7%). Aquatic larvae of another stream salamander, *E. bislineata*, were also found in adult *G. porphyriticus* gut contents (7%). Orders of terrestrial invertebrate prey (% of total terrestrial prey biovolume) were Oligochaeta (32%), Gastropoda (32%), Arachnida (18%), Myriapoda (14%), and Lepidoptera (4%). Mean aquatic prey density (± 1 S.E.) ranged from 16 ± 3.51 to 88.67 ± 4.49 individuals / m². All orders of aquatic prey found in *G. porphyriticus* gut contents were also represented in benthic samples. Estimated trout abundances ranged from 0 to 47 individuals / 100 m study section. A second round of electrofishing in August 2002 obtained similar results, indicating that differences among sites were consistent across years.

Forest structure was a significant predictor of the proportion of terrestrial-derived prey in salamander diets (Table 2, Fig. 1). Salamanders

Table 2. Results of regression analyses of the relationships between three riparian forest-related variables and mean proportion terrestrial biovolume in salamander guts, aquatic prey density (mean no. individuals / m²), and brook trout abundance (no. individuals / 100 m study section, square root-transformed). Data are from 10 focal headwater drainages in New Hampshire, USA.

Variable	b^a	R^2	P
Proportion terrestrial biovolume in salamander guts			
Structure PC-1	-	0.94	<0.0001
Proportion deciduous trees	-	0.03	0.61
Canopy cover	-	0.30	0.10
Aquatic prey density			
Structure PC-1	-	0.12	0.33
Proportion deciduous trees	-	0.02	0.67
Canopy cover	+	0.001	0.92
Brook trout abundance			
Structure PC-1	-	0.13	0.30
Proportion deciduous trees	-	0.10	0.37
Canopy cover	-	0.05	0.52

^a Indicates whether regression coefficient was positive or negative

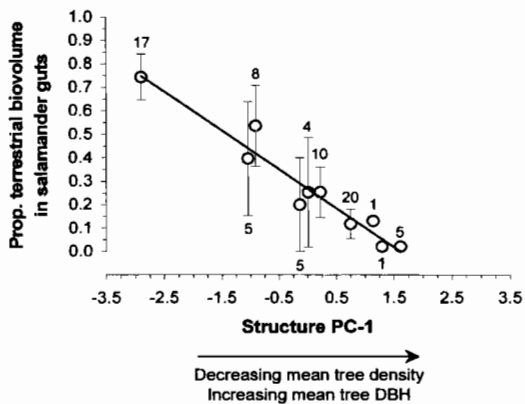


Fig. 1. Relationship between the first forest structure principal component (structure PC-1) and proportion terrestrial biovolume in the guts of adult *Gyrinophilus porphyriticus* individuals (1 – proportion aquatic biovolume; mean \pm 1 S.E.) in 10 headwater drainages. Structure PC-1 accounted for 92% of the negative covariation in mean tree density and mean tree diameter at breast height (DBH) in riparian forests (Table 1). Sample sizes for gut content analyses are adjacent to error bars. The linear regression line is plotted.

in streams draining stands with high mean tree densities and low mean tree DBH within paired 50-m wide riparian corridors (i.e., low structure PC-1 scores) had a high proportion of terrestrial prey in their diets. Structure PC-1 scores accounted for 94% of the total variation in mean proportion terrestrial prey in salamander diets. The other forest variables (proportion deciduous trees, canopy cover) were not related to proportion terrestrial prey in salamander guts. Neither aquatic prey density nor brook trout abundance were related to any of the three independent forest variables (Table 2), and neither were correlated with proportion terrestrial prey in salamander guts ($|r| < 0.27$, $n = 10$, $P > 0.27$).

Removing the two streams where a single individual was sampled (Fig. 1) had no effect on results of the terrestrial prey \times structure PC-1 regression ($R^2 = 0.96$, $n = 8$, $P < 0.0001$). Pooling individuals across all sites, there was no effect of sampling date on proportion terrestrial prey in salamander guts (ANOVA: $F_{2,73} = 1.18$, $P = 0.31$), indicating that results of gut content

analyses were not sensitive to the timing of sample collection or associated variation in climatic conditions. In the two streams where a single gut content sample was collected, one sample was collected in July and the other was collected in August. Gut content samples were collected on all three sampling dates in the remaining streams. There was no significant correlation between adult *G. porphyriticus* abundance (mean no. individuals / 100 m study section) and proportion terrestrial-derived prey in salamander diets ($r = -0.53$, $n = 10$, $P = 0.12$).

Discussion

In forested headwaters, ecosystem processes linking terrestrial and aquatic habitats are influenced by forest conditions (e.g., LIKENS & BORMANN 1995, VALETT et al. 2002). Pathways between these two habitats are also common in headwater food webs (e.g., WALLACE et al. 1997, NAKANO & MURAKAMI 2001). Our results link these findings, documenting a relationship between forest structure and terrestrial-aquatic connectivity in headwater food webs. We found that a large portion of stream salamander diets consists of terrestrial-derived prey. The magnitude of this terrestrial contribution was significantly influenced by forest structure characteristics (mean tree density and mean tree size) that define a major gradient in forest recovery from disturbance (BORMANN & LIKENS 1979, SCHWARZ et al. 2001).

Contrary to our predictions, aquatic prey density and brook trout abundance were not related to riparian forest conditions along the 10 study streams, and were not correlated with the proportion of terrestrial prey in the diets of *G. porphyriticus* adults. These results suggest that the relationship between forest structure and salamander diet was not a function of effects of forest structure on the availability of aquatic prey or on the abundance of aquatic predators – two aspects of the stream environment reported to influence salamander foraging behavior (ANTHONY et al. 1992, SIH & WOOSTER 1994). Other mechanisms acting within the stream may link salamander diet to forest structure, including the availability and size distribution of in-stream cover (SHANNON 2000), and physical or chemical conditions affecting salamander per-

formance (e.g., water flow, water temperature, dissolved oxygen: SHEAFOR et al. 2000, MARVIN 2003). However, given (1) the strength of the relationship between diet composition and forest structure, and (2) the lack of empirical links to the two aquatic conditions with the most obvious implications for salamander foraging activity, we believe that a terrestrial mechanism is more probable.

Increased use of terrestrial prey is likely associated with forest conditions that increase the profitability of foraging in the riparian zone. Two general mechanisms may underlie enhanced terrestrial foraging opportunity in high-density, low-mean DBH stands. First, in forests of the northeastern USA, the production of leaf litter tends to be highest during intermediate successional stages (BORMANN & LIKENS 1979, COVINGTON & ABER 1980), which probably correspond to those with a structure PC-1 value of ≤ 0 in our study (BORMANN & LIKENS 1979). By increasing the size of a resource pool critical to many terrestrial invertebrates, high litter production may lead to high availability of terrestrial prey, especially of those forest floor species found in the highest proportions in gut contents of *G. porphyriticus* adults (SCHEU & SCHULZ 1996). Second, salamander activity and the density and behavior of terrestrial prey and predators are likely influenced by abiotic conditions at the riparian forest floor that are linked to forest structure and underlying successional dynamics. These conditions include soil moisture and soil temperature, both of which are sensitive to the structure of the boundary layer created by terrestrial vegetation (GUO et al. 2002). Due to the threat of desiccation (RAY 1958), use of terrestrial habitats by stream salamanders may be particularly sensitive to these factors. Forest structure and correlated successional changes may also influence the availability of different types of vegetative cover (living and dead / downed) used by adult salamanders during terrestrial foraging bouts (JOHNSTON & FRID 2002).

The ability of *G. porphyriticus* adults to exploit both terrestrial and aquatic invertebrate prey is likely to add resiliency to salamander populations exposed to disturbance and increase net *G. porphyriticus* productivity (POLIS

& HURD 1996). These effects may be particularly important for headwater stream populations, as many exist as small semi-isolated subpopulations that are vulnerable to local extirpation (LOWE & BOLGER 2002). This plasticity in the foraging behavior of adult *G. porphyriticus* and resulting partitioning of top-down effects across both aquatic and terrestrial invertebrate communities may also have implications for the stability of headwater food webs. Brook trout, the other top predator in first-order streams of the northeastern USA (LOWE & BOLGER 2002, NISLOW & LOWE 2003), are limited to feeding on aquatic prey and terrestrial prey that accidentally fall into the stream. As a result, the top-down effects of trout are concentrated on aquatic invertebrate populations (NAKANO et al. 1999a, NAKANO et al. 1999b). Contingent on the structure of the riparian forest (Fig. 1), increased likelihood of strong top-down effects may reduce the stability of aquatic food webs in trout-dominated headwater streams relative to those where *G. porphyriticus* is the dominant top predator (MCCANN et al. 1998).

BORMANN & LIKENS (1979) described the dynamic pattern of variability in ecosystem processes among forest patches of the northeastern United States as a "shifting mosaic". The research presented here suggests that the organization of headwater food webs also displays a shifting-mosaic pattern in this region: representation of terrestrial and aquatic prey in salamander diets was shown to track spatial variation in riparian forest structure among headwater drainages, but is also likely to track temporal changes in forest structure resulting from successional dynamics within drainages. Although further work is needed to identify specific mechanisms underlying the use of terrestrial versus aquatic prey by *G. porphyriticus* adults, our results indicate that maintaining forested buffers that allow these natural successional dynamics to occur may be necessary to preserve the full range of variability in the food-web structure of small, often disregarded headwater streams (MEYER & WALLACE 2001). These results also highlight the role of stream amphibians as inter-habitat links in headwater ecosystems and provide initial evidence that forest structure and underlying successional

dynamics are important in regulating the scope and intensity of species interactions that cross the terrestrial-aquatic boundary.

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