Food web subsidies in intermittent streams: Implications for small isolated populations of native brook trout

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Food web subsidies in intermittent streams: Implications for small isolated populations of native brook trout

Jennifer Courtwright

A thesis submitted to the Graduate Faculty of JAMES MADISON UNIVERSITY In Partial Fulfillment of the Requirements for the degree of Master of Science

Department of Biology

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ABSTRACT

Recent studies in perennial streams have shown that reduction of stream-side vegetation can reduce terrestrial invertebrate inputs to streams and can cause trophic cascades throughout aquatic and terrestrial food webs; however, aquatic-terrestrial food web linkages have not been studied in intermittent streams. Food webs in intermittent streams may be even more dependent on terrestrial invertebrate fluxes because of limited aquatic invertebrate resources; thus intermittent streams may represent unique systems that warrant special attention. The objective of this research was first to quantify the abundance, biomass, and energetic content of available brook trout and insectivorous stream-side predator invertebrate resources in two Appalachian intermittent streams to determine how these resources vary with environmental factors such as stream flow and canopy cover. Secondly, the consequences of experimental reductions in terrestrial invertebrate fluxes on brook trout diet and other invertebrate resources were investigated. Total food resources for brook trout and insectivorous stream-side predators appear to be lower in intermittent Appalachian streams than other systems, and stream flow was the main factor driving resource availability. Terrestrial invertebrate resources only made up 7% of available resources, but made up 50% of brook trout diet. Insectivorous stream-side predators also appeared to be largely dependent on this resource, because, in contrast to studies in perennial streams, 73%-86% of emerging adult aquatic invertebrates fell back into the stream instead of feeding surrounding forest. Experimental reductions in terrestrial invertebrate resources resulted in a 43% decrease in abundance of winged terrestrial invertebrates, which cascaded into a 55% decrease in total brook trout consumption and reduced total caloric intake by 46%. In contrast to studies of other
salmonids in perennial streams, brook trout did not switch to consuming more aquatic invertebrates when terrestrial invertebrates were experimentally reduced potentially due to competition with sculpin, other brook trout, or unavailability of benthic resources. Therefore, no trophic cascades occurred when terrestrial invertebrate fluxes were experimentally reduced, but land use changes that cause reductions in terrestrial invertebrate resources may detrimentally impact already stressed brook trout populations in intermittent streams by reducing caloric intake as fish prepare for fall spawning and by decreasing over-winter survival rates.
INTRODUCTION

Intermittent streams do not flow continuously along the length of their channel and are common worldwide in arid as well as humid climates (Poff and Ward 1989; Poff et al. 2006). In the U.S., the status of intermittent streams under the Clean Water Act has been debated, and intermittent streams have less protection than perennial streams (Downing 2003; Blinn and Kilgore 2004; Wigington et al. 2006; Leibowitz et al. 2008). Intermittent streams are likely to become more common with climate change as drought conditions and human demands for water increase (Milly et al. 2005; Cowell and Urban 2010); however, limited knowledge of these systems is currently hampering efforts to conserve them worldwide (Uys and O’Keefe 1997).

In humid climates, small headwater streams that have fluctuating water tables near the top of a catchment can become intermittent during summer low-water periods (Hansen 2001), especially when storing high sediment loads (May and Lee 2004). Because headwater streams tend to be narrow and have high canopy cover, they are often light limited with very little in-stream primary production; therefore, their food webs are mostly driven by external energy inputs such as leaf litter from riparian forests (Vannote et al. 1980). Consequently, nutrient cycling in headwater streams is tightly coupled to riparian forests. Much research has been done on the importance of riparian leaf litter for headwater stream food webs (e.g., Wallace et al. 1997; England and Rosemond 2004); however, only recently have studies addressed the importance of invertebrate fluxes to and from the riparian forest for perennial stream food webs (Baxter et al. 2005; Wipfli and Baxter 2010), and no studies have assessed aquatic-terrestrial linkages in intermittent streams.
Aquatic-terrestrial linkages

Terrestrial invertebrate fluxes to streams can provide important food resources for fish. Energy from leaf litter that falls into streams is only indirectly available for top consumers such as fish, through aquatic invertebrate production. In contrast, invertebrate fluxes from riparian forests can be directly consumed by predators. Terrestrial invertebrate subsidies may explain how fish populations persist in streams with aquatic invertebrate production below levels necessary to sustain these fish populations (Allen 1951; Waters 1988; Edwards and Huryn 1995). Terrestrial invertebrates falling into headwater streams have been found to contribute up to half the annual energy budget for drift feeding fish such as salmonids (Kawaguchi and Nakano 2001; Sweka and Hartman 2008).

Terrestrial invertebrates are typically more common in stream drift during the middle of the day and at dusk (Rader 1997; Nakano et al. 1999a), while aquatic invertebrates are typically most abundant in the drift at sunset and during the night. Salmonids feed mostly during daylight hours and have been shown to prey selectively on terrestrial invertebrates potentially because of their larger size, greater visibility, and greater availability in the drift during these hours (Nakano et al. 1999a). Terrestrial invertebrate inputs are also seasonal and are typically highest during the spring and summer, and adult aquatic invertebrates emerge from streams during this time lowering aquatic invertebrate resources. During the late summer and fall, terrestrial invertebrate biomass can become greater than aquatic invertebrate biomass, and the contribution of terrestrial invertebrates to salmonid diets can increase throughout the summer months as
the availability of aquatic invertebrates decreases (Romaniszyn et al. 2007; Sweka and Hartman 2008).

Headwater streams can also provide important food sources for many riparian predators such as birds, bats, spiders, and lizards (e.g., Gray 1993; Power and Rainey 2000; Sabo and Power 2002a,b). Fluxes of emerging aquatic invertebrates can contribute 25-100% of the energy or carbon to these species (Baxter et al. 2005). In addition to providing an important food source, fluxes of aquatic invertebrates may alter the distribution and behavior of riparian predators (Nakano and Murakami 2001). In temperate zones, fluxes of aquatic invertebrates to riparian zones tend to be greatest in the early summer and decline sharply in late summer (Sweeny and Vannote 1982). This summer flux may be the most important to most riparian predators, but low level fluxes from autumn to spring when terrestrial invertebrate abundances are low may also be important for riparian predators (Nakano and Murakami 2001). Total annual fluxes of emerging aquatic invertebrates may be up to half of benthic production, and few adults return to the water (Jackson and Fisher 1986).

Because of the seasonal nature of subsidies, forests may feed stream food webs during the summer, but streams may feed forest food webs from autumn to spring (Power 2001). Reciprocal fluxes of invertebrates can also have indirect positive and negative effects on in-situ food resources. Subsidies of resources from donor habitats may elevate densities of consumers in the recipient habitat (Polis et al. 1997). This can in turn lead to more predation of consumers on in-situ prey, or if there is no numerical response of the consumer, the subsidy may alleviate pressure on in-situ prey (Baxter et al. 2005). For
example, terrestrial invertebrate subsidies may release pressure of fish predation on benthic aquatic invertebrates (Nakano et al. 1999c).

**Interruptions in reciprocal subsides**

Land use changes have the potential to interrupt invertebrate fluxes to and from the riparian zone. Deforestation can impact aquatic invertebrates through alterations in flow, increased sedimentation, changes in leaf litter quality, altering of light availability, and temperature changes. Forest removal has been shown to influence the flux of aquatic invertebrates from perennial and intermittent streams to riparian forests (Price et al. 2003; Banks et al. 2007). Banks et al. (2007) found that more insects emerged from clearcut streams regardless of intermittent or perennial status, but functional feeding group was not affected by flow or harvest condition. Price et al. (2003) found that invertebrate communities were affected by clearcutting in both kinds of streams, and that the hydrology of intermittent streams was so greatly altered by clearcutting that they became perennial for at least 4-8 years after clearcutting.

Forestry practices have also been shown to influence the input of terrestrial invertebrates into perennial streams. Streams with an intact forest and high canopy cover generally have greater inputs of terrestrial invertebrates than clearcut forests or grassland streams due to more overhanging vegetation (Kawaguchi and Nakano 2001). Fluxes can also be higher in young growth forests with dense understories than in old growth (Wipfli 1997). In addition, Edwards and Huryn (1996) found a higher biomass of terrestrial invertebrate inputs into streams with riparian zones composed of native reserve forests and intensely grazed native tussock grasses compared to intensely grazed exotic pasture.
Abundance and species richness did not differ with land use, but morphological characteristics (i.e., presence or absence of wings) of the species in the drift did differ with land use. While terrestrial invertebrate inputs are generally higher in streams with closed canopies (Baxter et al. 2005), a few studies have shown higher inputs in open canopies possibly due to increased exposure to rain and wind (Romaniszyn et al. 2007; Hoover et al. 2007). Hoover et al. (2007) compared terrestrial and aquatic invertebrates in the drift in clearcut forests, forests with buffers around streams, and intact forests. Intact forests had more aquatic invertebrates, but fewer terrestrial invertebrates in the drift. Vegetation type and species can also influence fluxes of terrestrial invertebrates. Inputs vary by species but tend to be greater in streams with deciduous canopies compared to streams with coniferous canopies (Mason and McDonald 1982; Wipfli 1997; Allan et al. 2003; Romero et al. 2005).

**Ecological consequences of interruptions in subsidies**

While there have been many studies on how riparian zones and forestry practices influence fluxes of terrestrial invertebrates to streams, the impacts of reducing terrestrial invertebrate flux to streams has been considered only recently and primarily in only one ecosystem (Baxter et al 2005). In Japan, reductions in terrestrial and aquatic invertebrate fluxes have caused trophic cascades within perennial stream communities (Nakano et al. 1999b; Baxter et al. 2004), and have been shown to influence fish abundance and distribution (Kawaguchi et al. 2003). When Nakano et al. (1999b) experimentally reduced terrestrial invertebrate inputs to a stream, salmonids switched their feeding from terrestrial invertebrates to aquatic invertebrates. This caused lower abundances of aquatic
invertebrates and increased algae. Baxter et al. (2004) saw a similar switch from salmonids foraging on drifting terrestrial invertebrates to foraging on bottom dwelling aquatic invertebrates when nonnative fish consumed a large portion of terrestrial insects falling into streams. This caused a reduction in the flux of invertebrates from the stream to riparian predators. The seasonality of terrestrial prey flux from forest to stream, coupled with the switching of fish foraging behavior, may stabilize stream ecosystems and make them less susceptible to land use changes and disturbances that interrupt subsidies (Takimoto et al. 2002).

Intermittent streams may be more susceptible to land use changes and disturbances that interrupt subsides than perennial streams; however, no studies have been conducted under these flow conditions. In intermittent streams with low overall food availability and reduced terrestrial subsidies, fish cannot migrate to areas that have greater terrestrial inputs because fish are confined to isolated pools during summer low flow conditions. In addition, salmonids in isolated pools in intermittent streams may not have the ability to switch from drift feeding on terrestrial invertebrates to benthic feeding on aquatic invertebrates because growing conditions for benthic invertebrates will be limited to isolated pools, and this resource may be quickly depleted during the summer season.

**Intermittent stream food webs**

At the base of the food web, studies comparing invertebrate communities in intermittent and perennial streams have found that communities may range from having considerable overlap of species to having very little overlap. Intermittent streams tend to
have lower total densities, taxa richness, and diversity of aquatic invertebrates than perennial streams due to harsh hydrological conditions (Feminella 1996; Miller and Golladay 1996; Del Rosario and Resh 2000). However, intermittent streams that lack vertebrate predators may have higher densities of aquatic invertebrates than perennial streams due to lower predation rates (Progar and Moldenke 2002).

To avoid desiccation during summer low flow conditions in intermittent streams, invertebrates may burrow into saturated sediments, migrate into pools, have life history adaptations, or have desiccation resistant forms (Williams 1984; Delucchi and Peckarsky 1989). The hyporheic zone is the area beneath and lateral to the streambed where shallow groundwater and surface water mix. This zone may be an importance refuge for invertebrates in intermittent streams (Williams 1984; Datry et al. 2007), and aquatic invertebrates have been observed emerging from intermittent streams even where there was no surface flow (Banks et al. 2007). A study of invertebrates in an Australian intermittent stream found that total abundance of invertebrates peaked in summer when flow started to decrease and peaked again in fall when flow returned. Species richness in riffles peaked right before flow ceased in the summer and peaked in pools shortly after flow stopped, implying emigration from the drying riffles (Boulton and Lake 1992). However, other studies have not found that invertebrates preferentially move towards pools during drying (Deluchi 1989; Del Rosario and Resh 2000), and this increase in invertebrate densities in pools during drying is likely short lived as predators in the pools consume them. Composition of invertebrates in isolated pools may change temporally due to different trophic positions of invertebrates, and predator recolonization after summer dry periods has been found to lag behind detritivores (Closs and Lake 1994).
Fish in intermittent streams also have strategies for surviving low flow conditions, and intermittent streams provide important habitat for many fish (Wigington et al. 2006). Many fish may survive low flow periods by migrating to perennial streams or reaches (Davey and Kelly 2007); however, despite high mortality due to drying, many fish may persist in isolated pools during the summer in intermittent streams (May and Lee 2004).

**Anthropogenic impacts on fish in intermittent streams**

Land use practices can limit fish survival in intermittent streams by impacting processes that create pools via altering stream morphology, increasing sediment loads, and decreasing amount of large wood available in streams (Labbe and Fausch 2000). Increased course sediment loads can lead to decreased pool persistence due to high porosity (May and Lee 2004). Pool abundance may also be decreased by forestry practices that decrease the amount of large wood in streams (e.g. Montgomery et al. 1996). Many studies have looked at the importance of large wood in structuring the stream channel, forming pools, providing refuge for fish and other invertebrates, and providing a food source and substrate (e.g., Keller and Swanson 1979; Andrus et al. 1988; Beechie and Sibley 1997; Sweka 2003; Mossop and Bradford 2004). However, no study has looked at large in-stream wood as a direct pathway for terrestrial invertebrates to enter the stream. A reduction in the amount of large wood in streams may reduce the amount of terrestrial invertebrates entering the stream. Therefore, in addition to reducing available pool habitat, land use changes that reduce terrestrial invertebrate inputs in intermittent streams may also lead to increased fish mortality during already stressful low flow conditions, but no study has investigated this.
Potential impacts of flow reduction and interruptions in subsidies on brook trout

Intermittent streams in the Appalachian Mountains contain small isolated populations of native brook trout (*Salvelinus fontinalis*) that are currently being threatened by acid rain, climate change, and habitat alteration and fragmentation (Hudy et al. 2000; Nislow et al. 2006; Hudy et al. 2008; Nislow et al. 2011). Reductions in terrestrial invertebrate food sources could be detrimental to this iconic species because many studies have shown that brook trout obtain most of their energy from terrestrial invertebrates in perennial Appalachian streams (Webster and Hartman 2005; Utz and Hartman 2006; Utz et al. 2007; Utz and Hartman 2007; Sweka and Hartman 2008). For example, an energetics study of West Virginia brook trout populations in perennial streams by Sweka and Hartman (2008) found that terrestrial invertebrates accounted for 38-47% of the biomass consumed annually and an estimated 51-63% of the energy consumed. In another study, brook trout obtained more energy from terrestrial invertebrates than aquatic invertebrates except in the winter. Coleoptera and Lepidoptera were particularly important in the summer (Utz and Hartman 2007). One terrestrial beetle family, Scarabaeidae, was particularly important and provided 39.6% of the energy consumed by brook trout during May and June (Utz et al. 2007); however, large organisms such as vertebrates and crayfish were important during the winter (Utz and Hartman 2007). Additionally, a study done in perennial streams of Virginia and West Virginia showed that brook trout had little effect on the abundance of the benthic grazer invertebrate community (Cheever and Simon 2009), suggesting that brook trout may have been subsidized by terrestrial invertebrate fluxes.
None of these studies have quantified how brook trout diet compares to available food resources in these streams. Food resources for salmonids can come from local benthic invertebrate production, drifting invertebrate production from upstream (aquatic, adult aquatic, and terrestrial), local adult aquatic invertebrates that fall back into the stream after emerging, and local riparian terrestrial invertebrate production (Wipfli and Baxter 2010). Traditionally fisheries managers have only assessed local benthic invertebrate production when determining available resources for fisheries production, and few studies have quantified all four food sources (Wipfli and Baxter 2010).

Overall resources and trout production in the central Appalachians is considered low compared to productive streams (Wallace et al. 1992; Habera and Strange 1993). This is partially due to low benthic production and low density of invertebrate drift in the central Appalachians (Grubaugh et al. 1997; Romanisyn et al. 2007). Terrestrial invertebrate production may also be low. Romanisyn et al. (2007) found that inputs of rates of terrestrial invertebrates to the drift in Appalachian streams were lower than studies done in New Zealand, Alaska, and Japan but were still important for fish production. No studies have estimated fluxes of emerging adult aquatic invertebrates from Appalachian streams. Adult aquatic invertebrates are often considered a loss of energy from the stream; however, several studies have shown that emerged aquatic adults can be an important potential energy source in the drift (Mason and Macdonald 1982; Bridcut 2000; Romanisyn et al. 2007).

In addition to overall low resources in Appalachian streams, resources may be reduced even further during frequent low flow conditions in headwater streams, and this may have important consequences for brook trout in these streams (Sotiropoulos et al.
Discharge may affect benthic, drifting, and falling adult aquatic and terrestrial sources of invertebrates. Discharge and volume may influence available habitat for benthic invertebrates and determine the probability of invertebrates becoming dislodged from benthos and drifting downstream (Rader 1997). Discharge may also be correlated with rainfall, which may influence the probability of terrestrial and adult aquatic invertebrates falling into the stream (Edwards and Huryn 1995), and discharge may influence the wetted stream surface area that terrestrial and adult aquatic invertebrates can fall into (Edwards and Huryn 1995). Studies assessing drift components of fish food resources in other regions have found a correlation between stream discharge and abundance of aquatic and terrestrial invertebrates in the drift (Edwards and Huryn; 1995; Rader 1997; Wipfli 1997); however, Romanisyn et al. (2007) did not find that discharge influenced terrestrial invertebrate inputs in Appalachian streams.

Reduced food resources and high densities of brook trout during low flows may have negative consequences for brook trout. Hakala and Hartman (2004) found that during a severe drought, in which flows were 96% lower than normal, brook trout populations experienced 60% mortality and attributed this to increased sediment loads and decreased food resources, rather than water temperature or dissolved oxygen concentrations. Another study found that during low flow conditions, brook trout occupied deeper microhabitats that had lower energy costs but also lower food resources and therefore had low growth rates (Sotiropoulos et al. 2006). Growth rates during these conditions of low resource availability have also been shown to be density dependent (Utz and Hartman 2009), and survival during these periods may be size dependent (Xu et al. 2010).
Land use changes that cause reductions in terrestrial invertebrate inputs during periods of low flow may be detrimental to brook trout populations because of limited growth and feeding potential. When the energetic consequences of reductions in terrestrial invertebrate consumption by brook trout has been modeled, Sweka and Hartman (2008) found that to maintain the same growth in the absence of terrestrial invertebrates, brook trout would need to increase yearly consumption of aquatic invertebrates by an average of 130% because the energy density of terrestrial invertebrates is typically greater than that of aquatic invertebrates. Studies that have examined salmonid diet when terrestrial invertebrates were reduced or unavailable due to experimental reductions or low natural abundance or availability, have found that salmonids switched from feeding on drifting terrestrial invertebrates to feeding on benthic invertebrates when food items are scarce in the drift (Nakano et al. 1999b; Baxter et al. 2004; Kawaguchi et al. 2003; Tippets and Moyle 1978; Bechara et al. 1992). Despite this, it is unknown if brook trout in Appalachian streams demonstrate this switching behavior or if it is feasible under intermittent flow conditions. Competition with other fish in Appalachian streams such as sculpin may prevent this switching behavior, and the energy spent actively searching the benthos may reduce energy available for other uses.

**Summary and objectives**

Terrestrial-aquatic food web linkages are still poorly understood and have not been studied in intermittent streams. Benthic invertebrate production in small headwater of the central and southern Appalachians is considered to be low (Wallace et al. 1992),
and intermittent streams in this region with vertebrate predators may have even lower aquatic invertebrate production due to less than ideal hydrologic conditions (Del Rosario and Resh 2000). The importance of emerging aquatic invertebrate subsides in intermittent streams is unknown, but this subsidy may not be as important for insectivorous predators in riparian forests of intermittent streams as it is for predators in riparian forests of perennial streams because of decreased aquatic invertebrate production in isolated pools of intermittent streams. In contrast, terrestrial subsidies may be even more important for intermittent stream food webs than perennial stream food webs. In intermittent streams of the Appalachian Mountains, it is hypothesized that reductions in terrestrial invertebrate fluxes to streams caused by reductions in riparian vegetation or large wood in streams may be detrimental to already stressed populations of brook trout.

The objectives of this study were as follows:

1. Quantify abundance, biomass, and caloric content of fluxes of invertebrates into and out of intermittent streams as flow decreases throughout the summer dry season to determine how food resources for riparian predators and brook trout vary with respect to time, discharge, pool size, distance from headwaters, fish density, canopy cover, and in-stream wood.

2. Determine important prey taxa in the diet of brook trout in intermittent streams.

3. Examine the effect of experimental reductions in terrestrial invertebrate fluxes on food web dynamics to simulate deforestation in intermittent streams.

   a. Determine how brook trout density, abundance and composition of standing stock of invertebrates, and experimental reductions in terrestrial
invertebrate fluxes affect brook trout diet composition and energetic intake.

b. If experimental reductions in terrestrial invertebrate resources affect composition of brook trout diet, determine if this causes cascading effects on aquatic and adult aquatic resources in these streams.
METHODS

Study area and pool selection

The study was conducted from mid-June to late August 2011 in the Dry River watershed in the George Washington National Forest, Virginia (Figure 1). Due to the surrounding Blue Ridge Mountains to the east and Allegheny Mountains to the west, this area in the Ridge and Valley Region of Virginia experiences a double ‘rain shadow effect’ with a mean annual precipitation of 90.4 cm compared to the state-wide average of 108.7 cm per year (Southeast Regional Climate Center, 2011a,b). Additionally, due to the prevalence of debris flows in mountain streams in the Ridge and Valley Region, channels in this portion of the drainage network contain thick, highly porous deposits from past debris flows, which limit persistence of surface stream flow (L. S. Eaton, personal communication 2012). As a result, many headwater streams in this area typically become intermittent during July and August (M. Hudy, personal communication 2012). The majority of the land cover in the headwaters of the Dry River watershed is within the George Washington National Forest and is heavily forested with secondary growth oak-hickory forest. Riparian areas are dominated by red-maple (Acer rubrum), hemlock (Tsuga canadensis), and black birch (Betula lenta). Soils are predominantly sandstone, and many streams have little buffering capacity from acid rain, which has heavily impacted the area (Webb et al. 1989; Herlihy et al. 1993; Hudy et al. 2000). Many of the tributaries of the Dry River are dammed for flood control, and streams below the dams are stocked with non-native and native fish species. Despite these anthropogenic impacts, streams above the dams provide critical habitat for small isolated populations of native brook trout (Hudy et al. 2008). The study was conducted
in these headwater areas, where other fish species are limited to mottled sculpin (*Cottus bairdi*) and blacknose dace (*Rhinichthys atratulus*). The selected study streams only contained brook trout, or contained brook trout and mottled sculpin.

Two first-order tributaries of the Dry River, Union Springs (38.47 N, 79.08 W) and Dry Run (38.55 N, 79.11 W) (Figure 1), were selected for the study to complement a separate investigation in this watershed on the effective population size of brook trout conducted during the summers of 2010 and 2011 (Whiteley et al. 2012). My initial objective was to compare an intermittent and a perennial stream food web. Therefore, stream selection was based largely on flow persistence, and streams were expected to have contrasting flows conditions based on preliminary field data of 2010. Casual observations during summer 2010 showed that Union Springs was the only neighboring stream that had persistent flow throughout the summer; therefore, Union Springs was selected as the perennial stream for this study. Dry Run was selected for this study from a group of five intermittent streams that had preliminary data on effective population size of brook trout. Of these five streams, Dry Run was selected because it was the most similar to Union Springs in terms of basin size, channel slope, morphological reach type, bankfull width, pool area, pool volume, and accessibility (Table 1). Despite expectations of contrasting flow persistence, both streams became intermittent from late July to late August during 2011. This was especially surprising given that the mean summer (May-August) rainfall during 2010 was 14.5 cm, which was well below the 118 year average of 30.5 cm, but mean summer rainfall during 2011 was about average at 30.0 cm (Southeast Regional Climate Center 2011a). It is possible that Union Springs became intermittent during the summer of 2010 after the stream was surveyed.
Figure 1. Study area in the Dry River watershed in the George Washington National Forest indicating the location of sample pools at Dry Run and Union Springs.
Table 1. Stream characteristics (A) and pool and riffle characteristics (B) of Union Springs and Dry Run (data from USDA Forest Service 2003, 2004).

A.

<table>
<thead>
<tr>
<th></th>
<th>Union Springs</th>
<th>Dry Run</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basin Size (km(^2))</td>
<td>18.3</td>
<td>12.2</td>
</tr>
<tr>
<td>Basin Size Above Selected Pools (km(^2))</td>
<td>8.9</td>
<td>8.7</td>
</tr>
<tr>
<td>Morphological Reach Type(^a)</td>
<td>Step Pool</td>
<td>Step Pool</td>
</tr>
<tr>
<td>Mean Channel Gradient (%)</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Mean Riparian Width (m)</td>
<td>9</td>
<td>19</td>
</tr>
<tr>
<td>Mean Bankfull Width (m)</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Pieces of In-Stream Wood (&gt;10 cm diameter) per km</td>
<td>61</td>
<td>122</td>
</tr>
<tr>
<td>Mean Water Temperature (C)</td>
<td>18</td>
<td>18</td>
</tr>
</tbody>
</table>

\(^a\) Montgomery and Buffington 1997

B.

<table>
<thead>
<tr>
<th></th>
<th>Union Springs</th>
<th>Dry Run</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pools</td>
<td>Riffles</td>
</tr>
<tr>
<td>Percent of Total Stream Area</td>
<td>51</td>
<td>49</td>
</tr>
<tr>
<td>Total Area (m(^2))</td>
<td>3082±635</td>
<td>2912±712</td>
</tr>
<tr>
<td>Total Count</td>
<td>53</td>
<td>49</td>
</tr>
<tr>
<td>Number per km</td>
<td>23</td>
<td>21</td>
</tr>
<tr>
<td>Mean Area (m(^2))</td>
<td>56</td>
<td>59</td>
</tr>
<tr>
<td>Mean Maximum Depth (cm)</td>
<td>38</td>
<td>17</td>
</tr>
<tr>
<td>Mean Average Depth (cm)</td>
<td>19</td>
<td>9</td>
</tr>
<tr>
<td>Mean Residual Depth (cm)</td>
<td>12</td>
<td>--</td>
</tr>
</tbody>
</table>
Six pools in each stream were chosen for the study (Figure 2 and 3). These pools were selected based on summer 2010 preliminary field data of persistence, area, volume, fish abundance, and accessibility. Pool selection at Dry Run was largely based on expected pool persistence and fish abundance because only seven pools with fish persisted during preliminary observations in the summer of 2010. Patterns of pool persistence were similar in 2011, with the exception of one pool that did not have enough volume to support fish. Therefore, these pools were used for the study, with the exception of the fishless pool, because pools for this study had to be able support at least three adult brook trout per pool to determine composition of brook trout diet (see fish sampling below).

At Union Springs, six pools were selected for the study from a group of 50 potential pools. Pool selection at Union Springs was not based on persistence because all pools were thought to have persisted at Union Springs during the summer of 2010. Pools were chosen to maximize logistical efficiency, and based on area and volume constraints. All pools at Dry Run had a wetted area of less than 32 m\(^2\), with the exception of one large bedrock pool that was 52 m\(^2\). Therefore, pools at Union Springs were constrained to a wetted area less than 32 m\(^2\), which also facilitated logistics of experimental manipulation of terrestrial invertebrate inputs. Pool volume at Union Springs had to be large enough to support at least three adult fish, and volume was standardized between the two streams.
Figure 2. Topographical map of Union Springs; this map shows the six pools that were used for the study and the position of terrestrial exclusion nets.
Figure 3. Topographical map of Dry Run; this map shows the six pools that were used for the study and the position of terrestrial exclusion nets.
Invertebrate sampling

Abundance, biomass, and caloric content of fluxes of invertebrates into and out of all twelve pools at Dry Run and Union Springs were quantified to determine how food resources for insectivorous riparian predators and brook trout varied with respect to time, discharge, pool size, distance from headwaters, fish density, and canopy cover. Fluxes of four different sources of invertebrates into pools were quantified to determine food resources for brook trout using the following equation:

\[ F = B + D + A + T \]

- \( F \) = total amount of food in fish habitat
- \( B \) = benthic invertebrates
- \( D \) = drifting invertebrates (including aquatic, adult aquatic, and terrestrial)
- \( A \) = falling adult aquatic invertebrates
- \( T \) = falling terrestrial invertebrates (including winged and crawling)

Additionally, fluxes of emerging adult aquatic invertebrates to the surrounding riparian forest were quantified to determine the importance of this resource for insectivorous riparian predators. Invertebrate food resources for insectivorous riparian predators were determined using the following equation:

\[ P = T + E \]

- \( P \) = total amount of food accessible for riparian predators
- \( T \) = terrestrial invertebrates
- \( E \) = emerging adult aquatic invertebrates

Drifting (D), falling adult aquatic (A), falling terrestrial (T), and emerging adult aquatic invertebrates (E), were measured five times biweekly from June 13 – August 27, 2011 (June 13-16, June 29-July 1, July 25-July 27, August 9-11, and August 23-25; see Figure 4 and Table 2). Benthic invertebrates (B) were assessed concurrent with the sampling of drifting, emerging, and falling invertebrates; however, due to time
constraints, no benthic, sample was taken on June 29-July 1, making a total of four benthic samples (Figure 4 and Table 2). For all invertebrate sampling, all pools at a stream were sampled concurrently, but due to gear and time restrictions, pools at one stream were sampled one day and pools at the other stream were sampled the next day.

Table 2. Number of collections made during each sampling period.

<table>
<thead>
<tr>
<th>Source of Sample</th>
<th>Jun 13-16</th>
<th>Jun 29-Jul 1</th>
<th>Jul 25-27&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Aug 9-11</th>
<th>Aug 23-25</th>
<th>Total # of collections</th>
</tr>
</thead>
<tbody>
<tr>
<td>Falling Terrestrial and Adult Aquatic</td>
<td>12</td>
<td>12</td>
<td>18&lt;sup&gt;b&lt;/sup&gt;</td>
<td>18&lt;sup&gt;b&lt;/sup&gt;</td>
<td>18&lt;sup&gt;b&lt;/sup&gt;</td>
<td>78</td>
</tr>
<tr>
<td>Benthic</td>
<td>24&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0&lt;sup&gt;d&lt;/sup&gt;</td>
<td>12&lt;sup&gt;e&lt;/sup&gt;</td>
<td>10&lt;sup&gt;e,f&lt;/sup&gt;</td>
<td>12&lt;sup&gt;e&lt;/sup&gt;</td>
<td>58</td>
</tr>
<tr>
<td>Drift</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>4&lt;sup&gt;g&lt;/sup&gt;</td>
<td>4&lt;sup&gt;g&lt;/sup&gt;</td>
<td>44</td>
</tr>
<tr>
<td>Emerging Aquatic</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>60</td>
</tr>
<tr>
<td>Wood</td>
<td>6</td>
<td>6</td>
<td>5&lt;sup&gt;h&lt;/sup&gt;</td>
<td>6</td>
<td>5&lt;sup&gt;h&lt;/sup&gt;</td>
<td>28</td>
</tr>
</tbody>
</table>

a. Invertebrate sampling did not follow bi-weekly pattern due to time restrictions imposed by experiment set up and fish sampling.
b. An extra sample was added at each exclosure pool to determine terrestrial exclusion net efficiency.
c. One sample was taken at each pool and upstream riffle.
d. Time restrictions prevented benthic sampling during this period.
e. Flow restricted fish foraging to pools; therefore, no riffle samples were taken.
f. Benthic samples were not taken in pool 2 in Dry Run, and pool 4 in Union Springs because they did not contain enough water to sample.
g. Flow was only capturable at pool 6 at Dry Run, and pools 1, 5, and 6 at Union Springs.
h. One trap spilled due to loose bindings; therefore the sample could not be collected.
Figure 4. Timeline of field sampling; boxes indicate each sampling period, and the blue line above indicates average stream discharge for each sampling period. Boxes are color coded based on type of sampling (see legend), and width of boxes corresponds with sampling duration. Faded red (terrestrial exclusion net) and yellow (fences) rectangles indicate duration of terrestrial exclusion experiment and fence placement.
Benthic invertebrates (B) were assessed using a Hess benthic sampler (Wildlife Supply Company, 36 cm diameter, 40 cm height, 500 µm mesh). One sample per pool was taken on a representative area of stream bottom. An additional benthic sample was taken in the riffle upstream of each pool for the first sampling period because fish were still able to forage in these areas. After the first sampling period, reductions in flow made foraging in these areas impossible, and therefore no subsequent benthic samples were taken in riffles.

To capture drifting invertebrates (D), one drift net (Wildlife Supply Company, 31 X 50 cm opening, 82 cm long, 500 µm mesh; or WaterMark®, 45 X 27 cm opening, 93 cm long, 500 µm mesh) was placed at the head of each pool for ~24 hours. Nets were placed where the maximum discharge occurred, and net openings extended above the water surface to capture floating terrestrial invertebrates in the drift sample. Nets were deployed upstream to downstream, and collected in reverse order to prevent disturbance of downstream nets. To estimate the volume of water sampled relative to the total discharge in each riffle, current velocity was measured in the center of the net and across the head of the pool using a flow meter (Flo-Mate 2000; Marsh-McBriney Inc., New York, NY, U.S.A.) at the time of net collection. Once a pool became isolated (i.e., no flow coming into it) drift nets were no longer deployed. Four pools (three at Union Springs and one at Dry Run) maintained an average flow of 0.0049 m$^3$s$^{-1}$ throughout the summer, but all other pools became completely isolated on the fourth sampling date, August 10th and 11th.

To capture falling adult aquatic (A) and terrestrial invertebrates (T), one tethered floating pan trap (53 X 35 cm area, 15 cm depth) was placed for ~24 hours in each pool.
Pan traps were filled with approximately 10 cm of water and a few drops of surfactant to prevent invertebrates from escaping. Tabasco was also added to deter insectivores such as birds from feeding on the collection. Pan contents were sieved through 500 µm mesh. To capture emerging adult aquatic invertebrates (E), one tethered floating PVC pyramidal trap (45 X 45 cm base, 38 cm height) was covered on all sides except the base with 1 mm heavy mosquito netting (230 holes/in², Mosquito Curtains Inc.) and was placed for ~24 hours in each pool. Placement of pan traps and emergence traps was not randomized within a pool; however, most pools were small with little leeway for trap placement, and emergence traps were always placed upstream of pan traps (Figure 5).

![Invertebrate sampling trap placement including wood, emergence, and pan traps.](image)

In addition to quantifying the food resources for brook trout and riparian predators listed above, the flux of falling aquatic and terrestrial invertebrates from in-stream wood was assessed to determine the relative importance of this pathway compared to adult aquatic and terrestrial fluxes into pools from the overhead canopy. To capture this flux of
invertebrates, two pan traps (41 cm X 15 cm area and 15 cm depth) per pool were prepared similarly to floating pan traps and were suspended underneath in-stream wood in the three pools formed by in-stream wood (Figure 5 and 6). Trap placement was not randomized, but traps were suspended so that they were centered and equally spaced on the in-stream wood. These traps were deployed for ~24 hours, and sampling occurred five times throughout the summer concurrent with the sampling of drifting, emerging, and falling canopy invertebrates.

**Invertebrate sample analyses**

To assess each taxon’s importance to the food web, the abundance, biomass, and caloric content of each taxon was determined. All invertebrates were preserved in 95% ethanol in the field until laboratory analysis could be completed. For each pool, aquatic invertebrates and adult aquatic invertebrates were identified to family (with the exception of Oligochaetes and adult Diptera), and terrestrial invertebrates were identified to order (Borror et al. 1989; Merritt and Cummins 1996). Due to the large abundance, family diversity, and variation in life history of Diptera present in samples and due to the difficulty in identifying adult invertebrates in this order to family, only adult Chironomidae and Tipulidae were identified to family. One adult Diptera family, Empididae, was particularly abundant, so this taxon was also separated out and identified to family and assumed to be terrestrial because no Empididae larvae were found in the streams.

Abundance and biomass per unit area (m\(^2\)d\(^{-1}\)) were determined for each taxonomic group in the benthic, drift, emergence, and pan trap samples. Benthic
sampling was area constrained but had no time constraints; therefore, daily benthic abundance m$^{-2}$ and biomass m$^{-2}$ were assumed to be equal to the benthic abundance m$^{-2}$ and biomass m$^{-2}$ taken on a specific sampling date. To obtain a total abundance and biomass of invertebrates per pool for each sample for each source (except the drift), the average length and width of each pool was measured during collection of each sample, and the abundance and biomass per unit area (m$^{-2}$d$^{-1}$) was multiplied by the wetted area of the pool. To estimate abundance and biomass in riffles available to fish during the first benthic sampling, it was assumed that the continuous movement path of fish was limited to one channel width upstream of each pool due to low flow conditions. Therefore, the abundance and biomass per unit area (m$^{-2}$d$^{-1}$) of each riffle sample was multiplied by the wetted width of the riffle and one channel width to obtain total abundance and biomass per riffle. The abundance and biomass in each riffle was then added to the available benthic resources in each pool to calculate the total available benthic resources.

Drift abundance and biomass per unit volume (m$^{3}$d$^{-1}$) were estimated by dividing the total abundance or biomass of invertebrates retained in the net during a ~24 hour period by the discharge that flowed through the drift net during that sampling period. To determine the total daily input of drifting invertebrates per pool, the abundance or biomass (m$^{3}$d$^{-1}$) was multiplied by the daily discharge that flowed through the drift net plus the daily discharge not captured by the net at that pool. Drift abundance and biomass was measured per unit volume, whereas the other sources (B, A, or T) were measured per unit area; therefore, a common unit of measure was needed to compare the quantity of resources each source provided and to determine the total available food.
resources for brook trout. To enable this comparison, drift abundance and biomass by volume (m$^{-3}$d$^{-1}$) was converted to area (m$^{-2}$d$^{-1}$) by dividing the total daily input of drifting invertebrates per pool by the area of the pool.

Biomass of each individual in each taxon was measured as dry mass to the nearest 0.0001 mg after drying at 105°C for 24 hours and storing in a desiccator. If a taxonomic group contained more than 20 individuals, a random source (benthic, drift, terrestrial, or emergence), date, stream, and pool was chosen, and all individuals in that sample were selected for measuring dry mass. Random samples were selected until a subsample of 20 individuals was obtained. Individuals in the subsample were weighed, and the theoretical mean of the best-fit distribution was used as the mass for all individuals in that taxon. Subsampling was used because weighing all individuals individually was impractical because many taxa had hundreds to thousands of individuals.

Thirty taxa out of 81 had more than 20 individuals and were randomly subsampled to estimate mean biomass of individuals in these taxa (Appendix 1). To determine the best-fit distribution for each taxon, distributions were modeled using EasyFit, a distribution fitting software program, with the lower bound fixed at zero to exclude distributions with negative values for mass. The following eight distributions were fitted for each taxon: Exponential, Gamma (2 parameter), Generalized Extreme Value (GEV), Inverse Gaussian, Log-Logistic, Lognormal, Power Function, and Chi-Squared. Kolmogorov–Smirnov ranking was used to determine goodness of fit for each distribution, and the parameters of the top ranked model were used to calculate the theoretical mean for each taxon.
Caloric content of individuals was determined using dry-weight – energy equations based on taxonomy and life stage (Appendix 2) from data presented in Cummins and Wuycheck (1971). For taxonomic groups without caloric data, caloric values for the closest related taxonomic group were used. If a taxon had Cal/g ash-free dry-weight or Cal/g wet weight values but no values for Cal/g dry weight, a proportional relationship between Cal/g ash-free dry weight or Cal/g wet weight values and Cal/g dry weight was determined using a related taxon that had data for all three units. This proportion was then applied to convert to Cal/g dry weight using the procedures described by Johnson et al. (2006).

Factors determining standing stock of invertebrate resources

To determine how brook trout and riparian predator food resources varied with environmental conditions, seven different environmental factors were assessed: discharge, pool volume, distance of pool from the study pool farthest upstream, approximate sculpin density, adult brook trout density, and percent canopy cover and composition. Discharge and pool volume were assessed for each pool during each invertebrate collection as described above. Distance of each study pool from the study pool farthest upstream at Dry Run or Union Springs was assessed because pools closer together may have similar characteristics that may cause pools closer together to have similar invertebrate resources. Distance of pool from the study pool farthest upstream was measured using ArcGIS. Approximate sculpin density, brook trout density, and percent canopy cover and composition were assessed as described below.
Fish sampling

Quantity and quality of invertebrate fluxes may be dependent on fish densities; therefore, fish abundances were assessed after stream flow restricted fish movement. Fish abundances were not assessed during the first two sampling periods because spatially continuous stream flow allowed for fish movement among pools (e.g., brook trout were found trapped in drift nets). Reductions in flow restricted fish movement after this, making it possible to census and manipulate fish populations. On July 21, 22, and 25, three pass depletion surveys were conducted for all fish in each pool using a backpack electrofishing unit (model LR-24; Smith Root Inc., Vancouver, WA, U.S.A.) (Figure 4). Brook trout and mottled sculpin were found in Dry Run; however, pools in Union Springs only contained brook trout. Initial abundances of brook trout and sculpin were recorded, and this abundance was assumed to be the abundance of fish for the first two invertebrate sampling periods for purposes of analyzing variation in invertebrate fluxes; however, fish movement could have occurred during the first two invertebrate sampling periods. Thus, this may not be representative of actual abundances during these two time periods.

Approximately equal fish densities were necessary for brook trout diet composition to be assessed and compared between pools and over time (see brook trout diet section below). Therefore, an attempt was made to equalize brook trout densities. Many pools had no brook trout or only one adult brook trout. For these pools, adult brook trout from nearby pools were moved into each pool to obtain approximately equal fish densities so that all of these pools contained three adult brook trout. Three brook trout were placed in each pool because this was the lowest feasible number for statistical
analysis of diets and the highest number that was practical for the available habitat. Two pools at Dry Run had significantly higher initial brook trout abundances and densities than the rest of the pools. Pool 1 and 3 (Figure 6) had 27 and 16 brook trout and densities of 3.4 and 1 adult brook trout per m$^3$ respectively. Adult brook trout were removed from these pools to subsidize study pools without adult brook trout to obtain similar fish densities. Even after 8 fish removed from pool 1, it still had a higher density than other pools (2.4 compared to a mean of 1.3 adult fish per m$^3$), but more fish were not removed because this was the only viable habitat for this population of brook trout. Sculpin densities were not manipulated. Total length of all individual brook trout caught during both depletion surveys was recorded to the nearest mm, and a fin clip was taken for genetic analysis in a separate ongoing study (Whiteley et al. 2012) and for future studies to track overwinter survival. Fish from each pool had unique fin clips enabling determination of movement between pools in case any dispersal occurred during storm events.

To maintain equal fish densities, compare available food resources with actual brook trout diet, and prevent fish movement in the event of rainstorms, plastic mesh fencing (Aquatic Eco-systems Inc, N1170; 6.35 mm) supported by rocks, fence posts, and rebar was placed at the downstream and upstream end of each pool on July 18 and 19 prior to the three-pass fish surveys. Fencing was cleaned as needed and still allowed for the passage of invertebrates. On August 13, ~6 cm of rainfall caused stream levels to rise ~30 cm at Union Springs. This flood overtopped some fences, and some fish movement occurred between pools at Union Springs; however, stream levels at Dry Run were unaffected, and no movement of fish occurred at this stream. Another three-pass
depletion survey was conducted at the end of the study on August 22 and 23 to determine final fish densities (Figure 4). For purposes of analyzing variation in invertebrate fluxes and brook trout diet, fish densities between July 21 and August 22 were calculated based on pool volume on the date of invertebrate or diet sampling and the assumption that fish abundances between the two three-pass surveys were equal to abundances during the first three-pass survey.

Canopy cover and composition

Quantity and quality of invertebrate fluxes have been found to be correlated with the percent canopy cover and composition; therefore, canopy characteristics of each stream were assessed to determine if these canopy characteristics explained variation in invertebrate fluxes. Percent total canopy cover of each pool was assessed on September 30, 2011 with a convex spherical densiometer. The densiometer was held level and stationary as four measurements in the cardinal directions were taken per pool. To avoid overlap among measurements and to increase accuracy, presence or absence of canopy cover was determined at each grid intersection using only a 90 wedge of the densiometer’s surface (Strickler 1959; Fiala et al. 2006). Canopy cover was calculated as the proportion of the 68 points (17 per direction) that was intersected by cover.

Canopy composition for each pool was determined using a line intercept method (Canfield 1941; O’Brien 1989; Fiala et al. 2006). For each species present, the horizontal distance covered by the live crown along a line-transect length-wise down the center of the stream bed was recorded. A clinometer was used to verify crown interception directly overhead. The percentage of the line-transect covered by the species was
recorded as the species’ percent cover. Canopy species richness and diversity of each pool was also calculated.

**Experimental design of terrestrial exclusion nets**

To examine the effect of experimental reductions in terrestrial invertebrate fluxes on food web dynamics that simulate canopy reduction, three of the six pools at each stream had 1 mm heavy mosquito netting (230 holes/in², Mosquito Curtains Inc.) exclosures placed over them for six weeks from July 18 – August 25 to reduce the abundance of falling terrestrial invertebrates (Figures 2, 3, and 6). The other three pools at each stream served as a control. Logistical problems such as large in-stream wood and pool size made randomization of treatments for pools impossible. At Dry Run, one pool was too large to have an exclusion net placed over it and two pools had in-stream wood; therefore, the remaining pools had terrestrial exclusion nets placed over them. At Union Springs, one pool was also too large to have an exclusion net placed over it, and one pool had in-stream wood. Two of the remaining pools at Union Springs had very similar morphology. Therefore, in attempt to reduce variation between treatments, only one pool in the pair had a terrestrial exclusion net placed over it, and the remaining two pools had exclusion nets. Exclusion nets were supported with ropes to trees on the stream’s banks and were about 1 m off the surface of the water. A 20 cm x 20 cm hole was cut in the center of each enclosure to allow emerging aquatic insects to escape. Exclusion nets covered the entire pool and 3 m upstream of the pool, but they only excluded falling insects and did not prevent crawling or flying insects from entering the pool.
Terrestrial exclusion net efficiency was determined by placing two pan traps, described above, at each pool. One pan trap was placed just outside of the exclosure and was used to quantify baseline flux of falling adult aquatic and terrestrial invertebrates. A second pan trap was placed underneath the exclosure, and the abundance and biomass of falling adult aquatic and terrestrial invertebrates was compared to the pan trap outside of the exclosure. Abundance and biomass of fluxes of aquatic and terrestrial invertebrates and their contribution to the diet of brook trout was compared between the exclosure pools and the control pools.

<table>
<thead>
<tr>
<th>A.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Dry Run</strong></td>
</tr>
<tr>
<td><strong>Pool 6</strong></td>
</tr>
<tr>
<td>(Wood)</td>
</tr>
</tbody>
</table>

| **Union Springs** |
| **Pool 6** | **Pool 5** | **Pool 4** | **Pool 3** | **Pool 2** | **Pool 1** |
| (Wood) |

**Stream Flow**

![Figure 6](image)

Figure 6. A. Schematic diagram of Dry Run and Union Springs showing pools with terrestrial exclusion nets (boxed) and control pools (un-boxed), and the presence of wood formed pools. Photograph illustrating pool with terrestrial exclusion net (B) compared to a control pool (C).
**Brook trout diet sampling**

To determine if the diet of adult brook trout differed between experimental treatments relative to available food resources, adult brook trout diet was assessed every two weeks for a six week period after fish movement was restricted by decreased stream flow. Diet was assessed 5 days after terrestrial exclusion nets were deployed at Union Springs, and 2 to 3 days after nets were deployed at Dry Run. To minimize shocking trauma, diet was assessed during both depletion surveys (July 21, 22 and 25 and August 22 and 23) and once in the middle of the study on August 8th and 9th (Figure 4). The first 10 adult brook trout caught from each pool were immobilized with Tricaine methanesulfonate (MS-222), weighed to the nearest g on a portable balance, photographed to enable tracking of individuals based on spotting patterns, and stomach pumped using gastric lavage. Fish were allowed to recover and were returned back to the pool. During the first sampling period, only the diet of adult brook trout that were not moved to equalize fish densities was assessed so that all fish had been in treatment pools for at least 48 hours before diet was assessed. During the final sampling period, all adult brook trout caught were used for this portion of the study to increase sample size.

Stomach contents of brook trout were removed by directing a constant stream of water into the foregut with a 4 mm diameter tube and syringe (Meehan and Miller 1978; Light et al. 1983). Gut items were filtered through a 500 µm sieve and transferred to 95% ethanol. The 4 mm diameter tube was larger than the gape of fish <100 mm; therefore, only fish with a total length >100 mm were able to be used for this gastric lavage procedure.
Due to the difficulty of identifying partially digested invertebrates, not all stomach contents were identified to family. In some cases the lowest possible taxonomic identification was only aquatic, adult aquatic, or terrestrial. Many studies only count head capsules when determining abundance of prey items in diet samples because this body part is easily identifiable and not digested as easily; however, due to a low number of head capsules in the diet samples, both heads and wings were counted to determine abundance. Only the body part (either wings or heads) that was most abundant for each taxon in each sample was used to determine abundance to avoid counting the same individual twice. If wings were used to determine abundance, the number of wings in the sample was divided by the number of wings an individual in the taxon possesses. To determine the biomass of individuals in the diet samples, the abundance of each taxon was multiplied by the mean mass of that taxa calculated for invertebrates in the standing stock sampling (described above). Caloric content was then calculated from dry-weight energy equations from the literature (also described above).

Statistical analysis

Characterization of standing stock invertebrate resources

The abundance, biomass, caloric content, and composition of each source of invertebrates (B, D, A, T, and E) was compared over time, between streams, and to other systems. The percentage that each taxon made up of the benthic, drifting, falling, emerging and total invertebrates was calculated by adding values for all individuals of a taxon from all dates and pools and dividing by the total number of individuals of all taxa sampled from that source.
Factors determining standing stock invertebrate resources

Because there was particular interest in the effects of canopy cover on terrestrial invertebrate resources, t-tests were used to compare the following variables between streams: terrestrial invertebrate abundance on a per m² basis, percent canopy cover, canopy diversity and richness, and percent cover of each species. Linear regressions were used to determine if any of the above variables were correlated to the mean number of terrestrial invertebrates falling into the streams on a per m² basis. To determine if in-stream wood was a significant pathway for terrestrial invertebrates entering the stream, the abundance of terrestrial invertebrates per m² from in-stream wood was compared to the abundance of terrestrial invertebrates per m² from the canopy using a t-test.

A linear model was developed to determine how total abundance and biomass of invertebrates per pool and per m² varied with respect to seven candidate explanatory variables: approximate sculpin density, adult brook trout density, pool volume, discharge, percent canopy cover, distance of each study pool from the pool farthest upstream at Dry Run and Union Springs, and stream (Table 3). To account for available pool habitat and for the conditions under which the invertebrates were produced, pool volume was included in the analysis in three separate ways: pool volume at each sampling date, change in pool volume from the previous sampling date, and mean pool volume during the study. Because benthic samples were not taken on the second invertebrate sampling date (June 29-July 1) due to time constraints, benthic invertebrate abundance and biomass was interpolated from first and third sampling dates for the second sampling date when calculating total abundance and biomass of invertebrates from all sources. Caloric content was not included as a response variable because trends in biomass and caloric
content were similar. The presence of experimental terrestrial exclusion nets was not included as a covariate because it would have masked effects of canopy cover. To ensure that fluxes could be compared independent of experimental treatment, control traps outside of terrestrial exclusion nets were used to calculate falling terrestrial and adult aquatic abundances used in this model.

Table 3. Fixed explanatory variables included in the mixed-linear modeling of invertebrate abundance and the justification for inclusion of each parameter.

<table>
<thead>
<tr>
<th>Candidate Variables</th>
<th>Justification for Inclusion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Discharge coming into each pool</td>
<td>Discharge may affect the probability of invertebrates becoming dislodged from benthos and drifting downstream. Discharge may be correlated with rainfall, which may influence falling terrestrial and adult aquatic invertebrates, and discharge may influence hydrologic conditions required by benthic invertebrates.</td>
</tr>
<tr>
<td>Adult brook trout density</td>
<td>Brook trout eat invertebrates, and trout density may have an impact on population size of invertebrates.</td>
</tr>
<tr>
<td>Approximate sculpin density</td>
<td>Sculpin compete with brook trout for invertebrates, and sculpin density may have an impact on the population size of invertebrates.</td>
</tr>
<tr>
<td>Pool volume</td>
<td>Pool volume may affect the amount of available habitat for invertebrates and influence wetted stream surface area that terrestrial and adult aquatic invertebrates fall into.</td>
</tr>
<tr>
<td>Percent canopy cover</td>
<td>Percent canopy cover may influence abundance of falling terrestrial invertebrates. Percent canopy cover also influences the availability of light driving photosynthesis and biomass of leaves falling into the stream which provide the base of the food web for invertebrates.</td>
</tr>
<tr>
<td>Distance of each study pool from the study pool farthest upstream at Dry Run or Union Springs</td>
<td>Pools closer together may have similar characteristics that may cause pools closer together to have similar invertebrate resources.</td>
</tr>
<tr>
<td>Stream</td>
<td>Pools at one stream may be more similar to each other than pools between streams because of the different environmental conditions present in each system.</td>
</tr>
</tbody>
</table>

a Removed from final analysis due to strong correlation with adult brook trout density and stream.
b Removed from final analysis due to extremely high ΔAIC for single variable model (ie. low support).

A best fit model was selected using Akaike information criterion (AIC) scores for mixed linear models fit by restricted maximum log-likelihood with nlme package in R version 2.14.0 (R Development Core Team 2011; Pinheiro and Bates 2000). Pool was
specified as a random variable to factor out correlation of repeated observations for each pool, and all other variables were considered fixed. To factor out possible correlations between observations closer together in time, models were run with a first order autocorrelation and a continuous time first order autocorrelation; however, when likelihood ratio tests were run comparing models with and without autocorrelations, there was no significant difference in model fit. Therefore, no autocorrelation parameter was included in models.

To determine which of the seven potential explanatory variables to include in candidate submodels, all single variable models were run along with an intercept-only (null) model and a global model containing all seven variables plus the intercept and potential interactions between stream and adult brook trout density, percent canopy cover, and distance of each study pool from the farthest upstream study pool at each stream. Additionally, Pearson’s correlation values were used to assess multiple collinearity among variables. Only the interaction between stream and adult brook trout density was significant; therefore, this was the only interaction included in subsequent submodels. To compare models, the difference in AIC values between the model and the most strongly supported model (∆AIC) was determined. Distance of each pool from the farthest upstream study pool had an extremely high ∆AIC value (i.e., weakly supported model). Therefore, distance of each pool from the farthest upstream study pool was not included in candidate submodels. Sculpin density was strongly positively correlated with adult brook trout density (df=16, \( R^2=0.605, p<0.001 \)), which had a lower ∆AIC (i.e., more strongly supported model). Single variable models were then run to determine if total fish density was a better predictor of total standing stock invertebrate abundance.
than either sculpin or brook trout density alone; however, the model containing only brook trout density had a lower ΔAIC value than total fish density or sculpin density. Therefore, out of these three variables, only brook trout density was included in the candidate submodels.

Using ΔAIC values for single variable models, a list of four candidate submodels were generated for each response variable (total abundance and total biomass per m$^2$ and per pool). Models with ΔAIC values between 0 and 2 were considered strongly supported (Anderson and Burnham 2002). The most parsimonious strongly supported model was then chosen, and significant factors were determined from type I tests on factor coefficients, which test if a variable is significant after including all other variables. To determine how much variation in the response variable the top model explained, an $R^2$ for mixed linear models was calculated using the following equation:

$$R^2 = 1 - \exp\left(-\frac{2}{n}(\log L_m - \log L_0)\right)$$

where $\log L_m$ is the maximum log-likelihood of the model of interest (that includes fixed and random effects), $\log L_0$ is the maximum log-likelihood of the intercept only model, and $n$ is the number of observations (Kramer 2005; Magee 1990). In addition to modeling factors affecting abundance and biomass of invertebrates in both streams, separate models were run for Dry Run and Union Springs using the above steps to determine factors influencing abundance and biomass of invertebrates within a stream. Response variables for all models were log transformed to meet assumptions of normality and heteroscedasticity.
Experimental reduction of invertebrate fluxes to the streams

Abundance

To determine terrestrial exclusion net efficiency of reducing total flux of invertebrates to the stream from the surrounding forest, the total flux of invertebrates per pool to the stream at terrestrial exclusion pools was compared between control pan traps placed just outside terrestrial exclusion nets and pan traps placed under nets using a paired t-test. The total flux of invertebrates to the stream from the surrounding forest was termed “falling invertebrates” and included adult aquatic, winged terrestrial, and crawling terrestrial invertebrates. The effect of exclusion nets on the abundance per pool of each type of falling invertebrate (adult aquatic, winged terrestrial, and crawling terrestrial) was also assessed, using paired t-tests for adult aquatic and winged terrestrial invertebrates and a related samples Wilcoxon Signed Rank test for crawling invertebrates because the assumptions of homoscedasticity and normality could not be met for this group.

A t-test was then used to determine if invertebrate fluxes into pools differed between terrestrial exclusion pools and control pools. Total abundance of falling invertebrates was log-transformed to meet assumptions of homoscedasticity and normality. These assumptions could not be met for abundance of adult aquatic, crawling, or winged terrestrial invertebrates; therefore, a Mann-Whitney U test was used for these groups.

Biomass

To determine terrestrial exclusion net efficiency of reducing the biomass of falling invertebrates, the total falling mass and crawling terrestrial invertebrate mass per
pool at terrestrial exclusion pools was compared between control pan traps placed just outside terrestrial exclusion nets and pan traps placed under nets using a paired t-test. Total mass of falling invertebrates was log-transformed and mass of crawling terrestrial invertebrates was log \((x+1)\) transformed to meet assumptions of homoscedasticity and normality. The assumptions of homoscedasticity and normality could not be met for adult aquatic and winged terrestrial invertebrates; therefore, a related samples Wilcoxon Signed Rank test was used for these groups.

A t-test was then used to determine if mass of falling invertebrates into pools differed between terrestrial exclusion pools and control pools. Total mass of falling invertebrates and mass of winged terrestrial invertebrates were log \((x+1)\) transformed to meet assumptions of homoscedasticity and normality. These assumptions could not be met for abundance of adult aquatic and crawling invertebrates; therefore, a Mann-Whitney U test was used for these groups.

**Brook trout diet**

Models were generated to determine factors influencing the probability of a brook trout having an empty stomach and to determine factors influencing the abundance and composition of invertebrates in diet samples that contained at least one prey item. A logistic regression was done to determine if sampling date, stream, and terrestrial exclusion nets had an effect on the probability of a fish having an empty stomach. To determine what factors influenced the total number of invertebrates eaten by individual fish across all three diet sampling dates (July 25-27, August 8-9, and August 23-25), a stepwise multiple linear regression was done using AIC values to select the top model
with the MASS package in R version 2.14.0 (R Development Core Team 2011; Venables and Ripley 2002). Models with ΔAIC values between 0 and 2 were considered strongly supported (Anderson and Burnham 2002). The most parsimonious strongly supported model was then chosen, and significant factors were determined. The response variable was total number of invertebrates eaten by an individual fish, and candidate explanatory variables were total standing stock of terrestrial invertebrates per pool, total standing stock of aquatic invertebrates per pool, brook trout density, sculpin density, wet weight of the individual fish, presence of terrestrial exclusion nets, and stream. All significant interactions with stream were also included. Similar to methods for models of invertebrate abundance, sculpin density was excluded from final models because sculpin presence was confounded with stream and because sculpin densities were strongly correlation with brook trout (df=16, R^2=0.605, p<0.001), which had a lower ΔAIC value. Because terrestrial invertebrates were of particular interest in this study, a similar stepwise regression was done with the number of terrestrial invertebrates eaten for each fish as the response variable. Both response variables for the stepwise regressions were log (x+1) transformed to meet assumptions of normality and heteroscedasticity.

In addition to the above modeling, t-tests were done to compare the number of total invertebrates and terrestrial invertebrates eaten between streams and experimental treatments. Additionally a t-test was done to compare total caloric intake of each fish between treatments. All three response variables were log-transformed to meet assumptions of normality and heteroscedasticity. To determine if observed differences in terrestrial invertebrate consumption between streams was due to the availability of terrestrial invertebrates, the number of terrestrial invertebrates in the standing stock was
compared between streams using a Mann-Whiney U test. To assess whether trout ate more aquatic invertebrates to make up for reduced terrestrial abundance, Mann-Whitney U tests were conducted in order to compare total aquatic invertebrates eaten by a fish between streams and experimental treatments. To determine if terrestrial exclusion nets had cascading effects on benthic, drifting, and emerging invertebrate abundance, Mann-Whitney U tests were done to compare benthic, drifting, and emerging invertebrate abundance between pools with terrestrial exclusion nets and control pools. Mann-Whitney U tests were done instead of t-tests because assumptions of normality and heteroscedasticity could not be met. All statistical analyses for the study were performed using R version 2.14.0 (R Development Core Team 2011) with an alpha level of 0.05.

The composition and abundance of invertebrates in diet samples from all three sampling dates were compared between streams and terrestrial exclusion treatments taking into account differences in standing stock abundance and biomass. The total abundance, biomass, or caloric content of a particular taxon was summed across all diet samples or the last three standing stock sampling dates and divided by the total for all taxa to determine percent composition of each taxon in the diet or standing stock. The Strauss selectivity index was then used to determine how diet composition related to composition of standing stock, and to determine key diet items in terms of abundance, biomass, and caloric content. The Strauss index (L) was calculated as:

\[ L = r_i - p_i \]

where \( r_i \) is the relative abundance of prey type \( i \) in the diet (as a proportion of the total number of prey in the diet) and \( p_i \) is the relative abundance of prey type \( i \) in the
environment (Strauss 1979). Possible values range from +1, which indicates perfect selection for a prey type, and -1, which indicates perfect selection against it.
Invertebrate resources

Abundance of brook trout invertebrate resources

Dry Run had more benthic, drifting, falling terrestrial, and falling adult aquatic resources than Union Springs (Figure 7). Benthic invertebrates were the most abundant macroinvertebrate source of food for brook trout at both Dry Run and Union Springs. Benthic invertebrates peaked as flows diminished, potentially indicating emigration from drying riffles, but were quickly depleted once pools became isolated (Figure 7). Drifting invertebrates were the second most abundant but also dramatically declined as flow diminished throughout the summer. Falling terrestrial and adult aquatic invertebrates stayed low and decreased slightly throughout the summer. Trends for abundance, biomass and caloric content were similar on a per m$^2$ and per pool basis (Figures 7, 9, and 10; Appendices 3-5). Results are presented on a per m$^2$ basis to enable comparison to literature values (Table 4 and 5); however, results on a per pool basis are included as well to enable calculations of total available resources for fish in isolated pools and to account for shrinking pool area throughout the summer (Appendices 6 and 7).

When total available resources food brook trout were calculated at both streams using the following equation:

\[ F = B + D + A + T \]

F = total amount of food in fish habitat
B = benthic invertebrates
D = drifting invertebrates (including aquatic, adult aquatic, and terrestrial)
A = falling adult aquatic invertebrates
T = falling terrestrial invertebrates (including winged and crawling)
benthic (B), drifting (D), falling adult aquatic (A), and falling terrestrial (T) invertebrates made up 80, 10, 6, and 4% of all resources respectively at Dry Run and 84, 7, 4, and 5% respectively at Union Springs (Table 4). By type of invertebrate, aquatic invertebrates (B+D), adult aquatic (A+D), and terrestrial invertebrates (T+D) made up 83, 7, and 10% of all resources respectively for both streams (Figure 8). Due to low flows, falling terrestrial and adult aquatic resources were more important than inputs of terrestrial and adult aquatic resources from the drift. In terms of abundance, falling terrestrial invertebrates made up 87% of the total terrestrial invertebrate inputs into streams, compared to 17% coming from the drift. Falling adult aquatic invertebrates also made up the majority of total adult aquatic inputs into streams (85% compared to 15% from drift).

Table 4. Available invertebrate abundance for brook trout as flow decreased throughout summer 2011 from June 13 – July 25 (flow) and August 9 – August 25 (isolated).

<table>
<thead>
<tr>
<th>Stream</th>
<th>Flow status</th>
<th>Total Abundance (F)</th>
<th>Benthic (B)</th>
<th>Drift (D)</th>
<th>Adult Aquatic (A)</th>
<th>Terrestrial (T)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry Run</td>
<td>Flow</td>
<td>1002</td>
<td>851</td>
<td>91</td>
<td>28</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>Isolated</td>
<td>215</td>
<td>179</td>
<td>0</td>
<td>10</td>
<td>25</td>
</tr>
<tr>
<td>Union Springs</td>
<td>Flow</td>
<td>455</td>
<td>393</td>
<td>29</td>
<td>16</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>Isolated</td>
<td>102</td>
<td>83</td>
<td>0</td>
<td>4</td>
<td>15</td>
</tr>
</tbody>
</table>

Mean Abundance (invertebrates/m²/day)

Over half of benthic invertebrates at both streams were from the family Chironomidae (Appendix 8A and B). This taxon was so abundant that it made up ~43% of all standing stock invertebrates at both streams. Leptophlebiidae were also abundant in the benthos at both streams. Leuctridae were the next most abundant taxa but were more important at Union Springs. These two taxa were also so abundant that they also contributed significantly to overall standing stock of invertebrates. Leptophlebiidae made up 15% and 8% of the total standing stock, and Leuctridae made up 5% and 13% of the total standing stock at Dry Run and Union Springs respectively (Appendix 8A and B).
The composition of the drift differed between the two streams. Over half of the drift at Dry Run was made up of Baetidae (Appendix 8A). The next most abundant taxon was Leptophlebiidae. Adult aquatic and terrestrial invertebrates only made up 6% and 9% of the drift at Dry Run respectively (Figure 8). In contrast, adult aquatic invertebrates and terrestrial invertebrates made up 17% and 28% of the drift at Union Springs respectively (Figure 8). The most abundant taxa in the drift at Union Springs were Leuctridae, Simuliidae, and adult Chironomidae.

Approximately, 40% of falling invertebrates were composed of adult aquatic invertebrates for both streams and were predominantly from Leptophlebiidae and Chironomidae families (Figure 8). Falling terrestrial invertebrates were mainly Diptera at both streams. Hymenoptera and Homoptera were the second most abundant families.
Figure 7. Mean number of invertebrates per m$^2$ per day for each source at Dry Run (A) and Union Springs (B). Error bars indicate ± standard error.
Figure 8. Percent composition of aquatic, adult aquatic, and terrestrial invertebrates that makeup the drifting, falling, and total abundance, biomass, and caloric content at Dry Run and Union Springs.

*Biomass and caloric content of brook trout resources*

Trends in biomass and caloric content were very similar (Figure 9 and Figure 10); therefore, only biomass results are discussed. Similar to the invertebrate abundance, biomass of available resources dramatically declined throughout the summer as flow declined, with the exception of a peak in falling terrestrial invertebrates at Union Springs. Benthic invertebrates were also the most important source in terms of biomass (Figure 9), and benthic, drifting, falling adult aquatic, and falling terrestrial made up 82, 11, 2 and 4% of available biomass resources respectively at Dry Run and 83, 5, 1, and 11% respectively at Union Springs (Table 5). While the relative importance of the benthos was not changed when assessed by biomass, different families of aquatic invertebrates were important in terms of biomass. Chironomidae decreased in importance in terms of biomass at both streams and especially at Union Springs. At Dry Run, Leptophlebiidae was still important but Ameletidae was also important in terms of biomass. At Union
Springs, Gomphidae made up 43% of the benthic biomass and 32% of the total biomass.

Limnephilidae also was important in the benthos.

Table 5. Available invertebrate biomass for brook trout as flow decreased throughout summer 2011 from June 13 – July 25 (flow) and August 9 – August 25 (isolated).

<table>
<thead>
<tr>
<th>Stream</th>
<th>Flow status</th>
<th>Total Biomass (F)</th>
<th>Benthic (B)</th>
<th>Drift (D)</th>
<th>Adult Aquatic (A)</th>
<th>Terrestrial (T)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry Run</td>
<td>Flow</td>
<td>215</td>
<td>181</td>
<td>25</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Isolated</td>
<td>61</td>
<td>47</td>
<td>2</td>
<td>1</td>
<td>11</td>
</tr>
<tr>
<td>Union Springs</td>
<td>Flow</td>
<td>288</td>
<td>218</td>
<td>14</td>
<td>2</td>
<td>54</td>
</tr>
<tr>
<td></td>
<td>Isolated</td>
<td>66</td>
<td>53</td>
<td>1</td>
<td>1</td>
<td>11</td>
</tr>
</tbody>
</table>

Drifting invertebrate inputs by biomass were made up of mostly of aquatic invertebrates, and aquatic invertebrates made up 67% of the drift biomass at Dry Run, but only 37% of the drift biomass at Union Springs (Figure 8). The importance of adult aquatic and terrestrial invertebrates in the drift also differed between streams. Adult aquatic invertebrates were more abundant in the drift at Union Springs, but adult aquatic invertebrates in the drift were more important in terms of biomass at Dry Run (Figure 8). Terrestrial invertebrates were more important in the drift in terms of biomass at Union Springs than Dry Run because there were more Coleoptera in the drift (Figure 8).

Most of the falling adult aquatic biomass was largely composed of Leptophlebiidae; however, the majority of falling invertebrate biomass was composed of terrestrial invertebrates at both streams (Figure 8). The biomass of falling terrestrial invertebrates was higher at Union Springs than Dry Run due to a few large Arachnids in the Phalangiidae family and a few Orthoptera. These few large Phalangiidae and Orthoptera made up 84% of the falling biomass at Union Springs. Mean falling terrestrial biomass for Dry Run was 8 mg m$^{-2}$d$^{-1}$ compared to 37 mg m$^{-2}$d$^{-1}$ at Union.
Springs. Without the above mentioned Phalangiidae, Union Springs had a mean terrestrial biomass of
7 mg m\(^{-2}\) d\(^{-1}\).

The relative biomass of total adult aquatic and terrestrial invertebrates (drifting (D) + falling (T or A)) also differed between streams (Figure 8). Total adult aquatic invertebrate inputs made up 5% of the total biomass at Dry Run and only 1% of the total biomass at Union Springs. Total terrestrial invertebrate inputs made up 20% of the total biomass at Union Springs and 11% of the total biomass at Dry Run. Even though drifting adult aquatic and terrestrial invertebrates were not very important in terms of abundance compared to falling invertebrates of these types, drifting adult aquatic and terrestrial invertebrate inputs increased in significance in terms of biomass. Drifting inputs of each type made up 45 and 31% of total adult aquatic and terrestrial invertebrate biomass in the stream respectively.

Despite Union Springs having higher falling terrestrial biomass, overall trends in all other sources over time were similar at Dry Run and Union Springs. While the total number of aquatic invertebrates was higher at Dry Run than Union Springs, total biomass of aquatic invertebrates was similar at both streams likely due to Dry Run having more Ephemeroptera, which were smaller than the Plecoptera that were abundant at Union Springs. The large Odonata and Trichoptera at Union Springs also likely contributed to the large aquatic biomass at Union Springs.
Figure 9. Mean biomass of invertebrates (mg) per m$^2$ per day for each source at Dry Run (A) and Union Springs (B). Error bars indicate ± standard error.
Figure 10. Mean caloric content of invertebrates per m$^2$ per day for each source at Dry Run (A) and Union Springs (B). Error bars indicate ± standard error.
Abundance, biomass, and caloric content of insectivorous riparian predator resources

When resources for insectivorous riparian predators were calculated using the following equation:

\[ P = T + E \]

- \( P = \) total amount of food accessible for riparian predators
- \( T = \) terrestrial invertebrates
- \( E = \) emerging adult aquatic invertebrates

Emerging adult aquatic invertebrate resources made up 29% and 51% of the total available resources for insectivorous riparian predators by abundance at Dry Run and Union Springs respectively (Figure 11 and Table 6; Appendices 9 and 10). On average, 14 adult aquatic invertebrates emerged from each stream per m\(^2\) per day. Because terrestrial invertebrates weighed more, emerging adult aquatic invertebrates only made up 26% and 10% of available biomass at Dry Run and Union Springs respectively (Figure 12 and Table 6; Appendices 10 and 11). Mean emerging adult aquatic biomass was 2.5 and 2.0 mg m\(^{-2}\)d\(^{-1}\) for Dry Run and Union Springs respectively; however, much of this may not be available to insectivorous riparian predators because mean biomass of adult aquatic invertebrates falling back into the stream was 2.1 mg m\(^{-2}\)d\(^{-1}\) and 1.5 mg m\(^{-2}\)d\(^{-1}\) for Dry Run and Union Springs respectively.

The majority of emerging aquatic invertebrates in terms of abundance, biomass, and caloric content were from the family Chironomidae (Table 7). Ephemeroptera, Plecoptera, and Trichoptera, decreased in abundance throughout the summer and Chironomidae increased in abundance as the summer progressed. The peak in overall emerging adult aquatic invertebrates corresponded to the peak in benthic abundance. Caloric content trends were similar to that of biomass.
Figure 11. Abundance of riparian predator resources showing mean number of terrestrial and emerging adult aquatic invertebrates per m$^2$ per day for Dry Run (A) and Union Springs (B).
Figure 12. Biomass of riparian predator resources showing mean biomass of terrestrial and emerging adult aquatic invertebrates per m$^2$ per day for Dry Run (A) and Union Springs (B). The spike in terrestrial biomass on July 26 was due to a few large Arachnids in the Phalangiidae family.
Table 6. Available invertebrate abundance (A) and biomass (B) for insectivorous riparian predators as flow decreased throughout summer 2011 from June 13 – July 25 (flow) and August 9 – August 25 (isolated).

<table>
<thead>
<tr>
<th>Stream</th>
<th>Flow Status</th>
<th>Total Abundance (P)</th>
<th>Terrestrial (T)</th>
<th>Emerging Adult Aquatic (E)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry Run</td>
<td>Flow</td>
<td>44</td>
<td>31</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>Isolated</td>
<td>41</td>
<td>25</td>
<td>16</td>
</tr>
<tr>
<td>Union Springs</td>
<td>Flow</td>
<td>34</td>
<td>18</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>Isolated</td>
<td>25</td>
<td>15</td>
<td>9</td>
</tr>
</tbody>
</table>

Mean Abundance (invertebrates/m²/day)

<table>
<thead>
<tr>
<th>Stream</th>
<th>Flow Status</th>
<th>Total Biomass (P)</th>
<th>Terrestrial (T)</th>
<th>Emerging Adult Aquatic (E)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry Run</td>
<td>Flow</td>
<td>9</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Isolated</td>
<td>13</td>
<td>11</td>
<td>2</td>
</tr>
<tr>
<td>Union Springs</td>
<td>Flow</td>
<td>56</td>
<td>54</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Isolated</td>
<td>12</td>
<td>11</td>
<td>1</td>
</tr>
</tbody>
</table>

Mean Biomass (mg/m²/day)

Table 7. Percent composition of each emerging adult aquatic invertebrate taxa resource for insectivorous riparian predators by abundance, biomass, and caloric content.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Dry Run</th>
<th>Union Springs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number</td>
<td>Mass</td>
<td>Calories</td>
</tr>
<tr>
<td>Ephemeroptera</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Heptageniidae</td>
<td>1.30</td>
<td>3.70</td>
</tr>
<tr>
<td>Leptophlebiidae</td>
<td>10.41</td>
<td>9.60</td>
</tr>
<tr>
<td>Baetidae</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Plecoptera</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leuctridae</td>
<td>6.07</td>
<td>25.46</td>
</tr>
<tr>
<td>Nemouridae</td>
<td>0.67</td>
<td>1.11</td>
</tr>
<tr>
<td>Trichoptera</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Polycentropodida</td>
<td>0.79</td>
<td>2.13</td>
</tr>
<tr>
<td>Diptera</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chironomidae</td>
<td>79.42</td>
<td>55.88</td>
</tr>
<tr>
<td>Neuroptera</td>
<td>1.33</td>
<td>2.12</td>
</tr>
</tbody>
</table>
Factors determining standing stock invertebrate resources

Discharge

Flow peaked on the second invertebrate sampling date after a rainstorm (Figure 13). Four pools (three at Union Springs and one at Dry Run) maintained an average flow of 0.0049 m$^3$s$^{-1}$ throughout the summer, but the rest became completely isolated by the fourth sampling date, August 10$^{th}$ and 11$^{th}$.

![Graph showing mean discharge of Dry Run and Union Springs during the summer of 2011. Error bars indicate ± 1 standard error.](image)

Brook trout and sculpin density

Initial brook trout abundances were very low at Union Springs. While there were 50 pools that provided potential brook trout habitat, only one pool out of the six investigated in this study contained adult brook trout; therefore, three fish were transplanted into each pool (Figure 14A). No pools at Union Springs contained sculpin. Initial abundances of brook trout at Dry Run were higher (Figure 14B) likely due to potential habitat being limited to seven pools for the entire stream compared to Union
Springs where many more pools were potentially available. Still, three pools at Dry Run did not contain any brook trout, and three fish were transplanted into each of these pools. Two pools at Dry Run had extremely high densities of adult brook trout and were the main habitat for this population. Sculpin were present in all pools, and initial abundances ranged from 5 to 71 fish per pool (Figure 14B). Sculpin densities were positively correlated with brook trout densities before transplanting (df=10, $R^2=0.257$, $p=0.053$), and after transplanting brook trout (df=16, $R^2=0.605$, $p<0.001$), and ranged from 3 to 8 sculpin per m$^3$ (Table 8).

Fish densities generally increased as the summer progressed and pool volume shrank (Table 8); however, there was substantial natural mortality at both streams, which may be typical of intermittent streams (May and Lee 2004). At the beginning of the study, there were 18 adult brook trout in the six pools at Union Springs, and 44 adult brook trout in the six pools at Dry Run. At the end of the study, there was 61% mortality at Union Springs and 25% mortality at Dry Run. It is possible that true mortality may have been slightly lower and that missing individuals were either not able to be detected during electroshocking (i.e., hidden under rocks) or moved between pools. However, this is unlikely because individual fish were identified based on spotting patterns and tracked, and pools were small with few hiding places. Movement of two fish occurred at Union Springs due to a flood on August 13th that overtopped fences. Individuals were able to be tracked based on spotting patterns, and no other detectable movement of fish occurred during the study. There were two young of the year brook trout at Union Springs at the beginning of the study; however, only one survived the summer. At Dry Run, there were 8 young of the year at the beginning of the study, but only one survived the summer. The
six study pools at Dry Run provided the only available habitat for adult brook trout; however, 19 young of the year brook trout were found in riffles below the study pools.

At Union Springs, total brook trout populations for the whole stream were unknown.

Table 8. Area, volume, and fish densities of study pools (downstream to upstream) at Union Springs (US) and Dry Run (DR). Mean area was calculated from June 13 through August 25. Pool volume and density of adult brook trout in each pool are given for July 25 after fish were transplanted to achieve similar densities. Pool volume and adult brook trout densities at the end of the study on August 25 is also given along with sculpin densities on July 25.

<table>
<thead>
<tr>
<th>Pool</th>
<th>Mean Area (m²)</th>
<th>Volume on July 25 (m³)</th>
<th>Volume on August 25 (m³)</th>
<th>Transplanted Adult Density on July 25 (fish/m³)</th>
<th>Adult Density on August 25 (fish/m³)</th>
<th>Sculpin Density on July 25 (fish/m³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>US</td>
<td>DR</td>
<td>US</td>
<td>DR</td>
<td>US</td>
<td>DR</td>
<td>US</td>
</tr>
<tr>
<td>1</td>
<td>26.04</td>
<td>23.81</td>
<td>3.97</td>
<td>7.95</td>
<td>5.87</td>
<td>0.76</td>
</tr>
<tr>
<td>2</td>
<td>18.06</td>
<td>10.89</td>
<td>6.62</td>
<td>4.48</td>
<td>0.23</td>
<td>0.45</td>
</tr>
<tr>
<td>3</td>
<td>28.17</td>
<td>46.77</td>
<td>6.50</td>
<td>15.47</td>
<td>6.30</td>
<td>10.08</td>
</tr>
<tr>
<td>4</td>
<td>13.15</td>
<td>7.41</td>
<td>5.06</td>
<td>1.55</td>
<td>1.00</td>
<td>0.70</td>
</tr>
<tr>
<td>5</td>
<td>10.94</td>
<td>16.34</td>
<td>2.57</td>
<td>4.67</td>
<td>2.82</td>
<td>1.08</td>
</tr>
<tr>
<td>6</td>
<td>17.12</td>
<td>9.98</td>
<td>10.92</td>
<td>2.48</td>
<td>3.23</td>
<td>0.88</td>
</tr>
<tr>
<td>mean</td>
<td>18.91</td>
<td>19.20</td>
<td>5.94</td>
<td>5.93</td>
<td>3.95</td>
<td>3.00</td>
</tr>
</tbody>
</table>

Sculpin Density on July 25 (fish/m³)
Figure 14 A. Schematic of the number of brook trout (adult and young of the year (Y.O.Y.)) in each pool throughout the study at Union Springs. No sculpin were present at Union Springs. Numbers on arrows indicate the number of adult brook trout that moved. Purple arrows indicate fish that were transplanted into study pools from other pools upstream and downstream of study pools, and the red arrows indicate unintentional movement of fish due to a flood that overtopped fences on August 13th. This flood did not occur at Dry Run. Pool 4 went completely dry between July 24th and August 8th, so presumably the three transplanted fish in this pool died due to desiccation. Pools with terrestrial exclusion nets are boxed.
Figure 14 B. Schematic of the number of brook trout (adult and young of the year (YOY)) and sculpin (sculp) in each pool throughout the study at Dry Run. nd indicates no data collected. Numbers on arrows indicate the number of adult brook trout that moved. Purple arrows indicate fish that were transplanted, and the red arrows indicate unintentional movement of fish: a. Two brook trout died from electroshocking; b. One brook trout was moved to non-study pool for ethical reasons because pool was nearly dry. The other fish in this pool could not be caught to also be moved; c. One new brook trout appeared from an unknown source. Additionally, three YOYs were transplanted into the second pool on July 21 because other habitat for these individuals was quickly drying riffles between fenced study pools. Pools with terrestrial exclusion nets are boxed.
Canopy cover and composition

Union Springs had higher percent canopy cover and species diversity than Dry Run (Table 9); however, Dry Run had more terrestrial invertebrates falling into the streams per m² than Union Springs (Table 9). Both streams had relatively high percent canopy cover with a range of 72%-94%. Riparian forest species richness did not differ between the two streams (Table 9). Species composition varied considerably between pools, and there were no significant differences in percent cover of species between streams (Appendix 12). Both streams were dominated by red maple, hemlock, and black birch (Figure 15). Union Springs also had a significant amount of red oak (Figure 15). Union Springs had deciduous and evergreen shrubs present, while Dry Run had no shrubs overhanging the stream likely due to having a larger channel size.

Table 9. Total percent canopy cover, species richness, species diversity, and mean number of terrestrial invertebrates per m² with t-tests comparing values between the two streams and linear regressions comparing percent cover of each species per pool and the mean abundance of terrestrial invertebrates for each pool.

<table>
<thead>
<tr>
<th></th>
<th>Union Springs</th>
<th>Dry Run</th>
<th>T-test</th>
<th>Regression</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean ± std error</td>
<td>mean ± std error</td>
<td>p-value</td>
<td>p-value</td>
</tr>
<tr>
<td>Total % canopy cover</td>
<td>89 ±2</td>
<td>81 ±3</td>
<td>0.048</td>
<td>0.571</td>
</tr>
<tr>
<td>Species richness per pool</td>
<td>4 ±0.5</td>
<td>3 ±0.6</td>
<td>0.172</td>
<td>0.958</td>
</tr>
<tr>
<td>Shannon-Wiener species</td>
<td>1.26 ±0.07</td>
<td>0.77 ±0.19</td>
<td>0.034</td>
<td>0.618</td>
</tr>
<tr>
<td>Mean # inverts per m²</td>
<td>16 ±3</td>
<td>28 ±3</td>
<td>0.005</td>
<td>NA</td>
</tr>
</tbody>
</table>

Figure 15. Mean percent cover of each species at Union Springs (US) and Dry Run (DR).
In-stream wood

There was no difference in the abundance per m² per day of terrestrial invertebrates falling into the stream from in-stream wood compared to the canopy (paired t-test, t=1.414, df=14, p=0.179). Therefore, in-stream wood did not appear to be a preferential pathway for terrestrial invertebrates to enter the stream, and because the area of in-stream wood is smaller than the area of pools covered by canopy, in-stream wood is not likely an important source of terrestrial invertebrates for brook trout. Despite this, composition of the invertebrates falling into the stream appeared to differ between these two sources. Homoptera made up 38% of invertebrates falling off of wood, whereas this taxon only made up 1% of invertebrates falling from the canopy.

Linear model assessing factors influencing standing stock invertebrate abundance and biomass

When AIC was used to select the most parsimonious, information rich mixed linear model that explained total abundance of standing stock invertebrates per m², the top model contained discharge, stream, and adult brook trout density as explanatory variables (Table 10). Total abundance per m² was significantly correlated with discharge (p<0.001) and stream (p=0.006). Adult brook trout density was also significantly negatively correlated with abundance but only at Dry Run (p=0.020) and not at Union Springs (p=0.301). For every 0.01 m³ s⁻¹ increase in discharge, invertebrate abundance per m² was 1.39 times higher. Invertebrate abundance per m² was 4.97 times lower at Union Springs compared to Dry Run. For every 1 fish m⁻³ increase in adult brook trout density at Dry Run, total invertebrate abundance per m² was reduced by 1.48 times. These three fixed explanatory variables (discharge, stream, and brook trout density) with pool as a
random variable explained 40.0% of the variation in total abundance of invertebrates per m$^2$. Submodels with other explanatory variables were not strongly supported (Table 10).

Table 10. The submodels and global model generated in the mixed linear modeling of standing stock invertebrate abundance and biomass. / indicates that main and interaction effects were considered. Bdensity and sdensity are adult brook trout and sculpin densities. All covariates were considered fixed except pool, which was random. ΔAIC values for models with pool volume are based on pool volume at each sampling date, but pool volume was not in the top model regardless of whether it was included as pool volume at each sampling date, change in pool volume from the previous sampling date, or mean pool volume throughout the study.

<table>
<thead>
<tr>
<th>model rank</th>
<th>covariates included in each model</th>
<th>abundance per m$^2$</th>
<th>abundance per pool</th>
<th>mass per m$^2$</th>
<th>Δ AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>top model</td>
<td>discharge+stream/bdensity, random=pool</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>submodel 2</td>
<td>discharge+stream/bdensity+volume, random=pool</td>
<td>5.3182</td>
<td>4.9134</td>
<td>4.796</td>
<td></td>
</tr>
<tr>
<td>submodel 3</td>
<td>discharge+stream/bdensity+canopy, random=pool</td>
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<td>5.1781</td>
<td>6.344</td>
<td></td>
</tr>
<tr>
<td>submodel 4</td>
<td>discharge+stream/bdensity+volume+canopy, random=pool</td>
<td>11.9918</td>
<td>10.7142</td>
<td>11.42</td>
<td></td>
</tr>
<tr>
<td>global</td>
<td>discharge+stream/bdensity+stream/canopy+stream/distance +sdensity+volume, random=pool</td>
<td>46.6617</td>
<td>43.1945</td>
<td>44.52</td>
<td></td>
</tr>
</tbody>
</table>

The top model explaining total abundance of standing stock invertebrates per pool also contained discharge, stream, and adult brook trout density. Total abundance per pool was significantly correlated with discharge (p<0.001), stream (p=0.008), and adult brook trout density (p=0.005) at Dry Run (Table 10) and showed similar trends to those for total abundance per m$^2$. For every 0.01 m$^3$s$^{-1}$ increase in discharge the abundance of invertebrates per pool increased by 1.35 times. The abundance of invertebrates per pool was 5.6 times lower at Union Springs compared to Dry Run. For every 1 fish per m$^3$ increase in adult brook trout density at Dry Run, total abundance per pool was reduced by 1.68 times. These three fixed explanatory variables with pool as a random variable explained 38.3% of the variation in total abundance of invertebrates per pool. Submodels with other explanatory variables were not strongly supported (Table 10).
Because models run with abundance per pool and abundance per m² were similar (Table 10), models run for mass and models run separately for each stream were only performed on a per m² basis. Total mass per m² showed the same trends as total abundance per m². The same factors were significant, and the same covariates were in the top model, which explained 25.2% of the variation in total mass per m² (Table 10). When models were run separately for Dry Run and Union Springs with total abundance per m² as the response variable, the same results were found as when streams were analyzed together. The top model at both streams included only the parameters of discharge and brook trout density, even though brook trout density was not significantly correlated with abundance of invertebrates per m² at Union Springs (p=0.138). Although this model was statistically significant it only explained 29.0% and 24.6% of the variation in total abundance per m² at Dry Run and Union Springs respectively. The concordance of results indicates that discharge is an important factor influencing invertebrate abundance between streams and within a stream, and that brook trout density was only an important factor at Dry Run, likely due to the higher densities of brook trout present in this stream. Additionally, while sculpin density was not used as a parameter in the top model, it was positively correlated with brook trout density (df=16, R²=0.605, p<0.001), and could also be an important factor influencing invertebrate availability at Dry Run, where sculpin were present, but not at Union Springs, where they were absent.
Experimental reduction of terrestrial invertebrates

Abundance

Pan traps underneath terrestrial exclusion nets had significantly fewer falling invertebrates (adult aquatic, winged terrestrial, and crawling terrestrial) than pan traps outside terrestrial exclusion nets (paired-t-test, t=2.893, df=17, p=0.010). Terrestrial exclusion nets reduced total falling invertebrate abundance by 53% (an average of 184 invertebrates per pool per day) (Figure 16). Nets reduced the abundance of adult aquatic by 34% (an average of 40 invertebrates per pool per day) (paired t-test, t=2.116, df=17, p=0.049) and winged terrestrial invertebrates by 43% (an average of 72 invertebrates per pool per day) (paired t-test, t=2.016, df=17, p=0.060). Nets had no effect on the abundance of crawling terrestrial invertebrates (Wilcoxon Signed Rank test, Z=0.968, df=17, p=0.333). Due to high variance (CV=189%), total abundance of falling invertebrates did not significantly differ between terrestrial exclusion pools and control pools despite a 62% reduction with a mean difference of 259 falling invertebrates per pool per day (t-test, t=2.247, df=34, p=0.263) (Figure 17). The abundance of adult aquatic, and crawling terrestrial invertebrates did not differ between treatments (Mann-Whitney U test, U=124, Z=1.398, df=34, p=0.239; Mann Whitney U test, U=156, Z=0.223, df=34, p=0.839); however, there was a marginally significant difference in the abundance of winged terrestrial invertebrates per pool per day between treatments, with fewer winged terrestrial invertebrates in pools with terrestrial exclusion nets (Mann-Whitney U test, U=103, Z=1.897, df=34, p=0.059).
Figure 16. Box plot comparing the total number of falling invertebrates (winged terrestrial, adult aquatic, and crawling invertebrates) between pairs of pan traps placed outside and under the experimental terrestrial exclusion net at each exclosure pool at Dry Run and Union Springs.

Figure 17. Box plot comparing the total number of falling invertebrates (winged terrestrial, adult aquatic, and crawling invertebrates) between control pools without terrestrial exclusion nets and pools with terrestrial exclusion nets at Dry Run and Union Springs.
**Biomass**

Despite a reduction in abundance, the total mass of falling invertebrates (adult aquatic, winged terrestrial, and crawling terrestrial) did not significantly differ between pan traps underneath terrestrial exclusion nets and control pan traps placed just outside of nets (paired-t-test, \( t=0.966, \text{df}=17, p=0.348 \)). Adult aquatic, crawling, and winged terrestrial invertebrate biomass did not significantly differ between traps underneath nets and control traps (Wilcoxon Signed Rank test, \( Z=0.594, \text{df}=17, p=0.552 \); paired t-test, \( t=0.512, \text{df}=17, p=0.615 \); Wilcoxon Signed Rank test, \( Z=0.414, \text{df}=17, p=0.679 \)). Contrary to expectations, total falling mass was greater in pools with terrestrial exclusion nets than in control pools (t-test, \( t=2.558, \text{df}=34, p=0.016 \)). Even though adult aquatic, crawling, and winged terrestrial invertebrate biomasses did not significantly differ between treatments (Mann-Whitney U test, \( U=138, Z=0.883, \text{df}=34, p=0.377 \); Mann-Whitney U test, \( U=136, Z=0.891, \text{df}=34, p=0.373 \); t-test, \( t=0.434, \text{df}=34, p=0.667 \)), it appeared that the difference in total biomass between treatments was due to a large biomass of Phalangiidae in pools with terrestrial exclusion nets.

**Brook trout diet**

A total of 101 diet samples were collected and analyzed (Table 11A). Twenty-four percent of brook trout sampled had empty stomachs, which is within the normal range for gastric lavage of salmonids (21.9 – 30.9% empty, as reviewed by Vinson and Angradi 2011). The percentage of trout with empty stomachs increased as the summer progressed (Table 11B). The probability of a fish having an empty stomach was significantly higher on the last date (logistic regression, \( z=2.478, \text{df}=100, p=0.013 \) and
marginally higher on the second sampling date compared to the first sampling date (logistic regression, \( z=1.738, \text{df}=100, p=0.082 \)). The odds of an individual fish having an empty stomach increased by a factor of 14 if diet samples were taken on the last sampling date compared to the first, corresponding with a decrease in available resources. The percentage of trout with empty stomachs was 29% for pools with terrestrial exclosures compared to 19% for pools without exclosures; however, the probability of a fish having an empty stomach did not significantly differ between treatments (logistic regression, \( z=1.108, \text{df}=100, p=0.268 \)). There was no difference in the probability of a fish having an empty stomach between streams (logistic regression, \( z=0.513, \text{df}=100, p=0.608 \)).

Table 11. Sample size of diet samples taken on each date at Dry Run and Union Springs in pools with and without terrestrial exclusion nets (A) and percentage of those fish that did not have at least one prey item in their stomach (B).

<table>
<thead>
<tr>
<th></th>
<th>Dry Run</th>
<th></th>
<th></th>
<th>Union Springs</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>21-Jul</td>
<td>9-Aug</td>
<td>22-Aug</td>
<td>24-Jul</td>
<td>8-Aug</td>
<td>23-Aug</td>
</tr>
<tr>
<td>terrestrial excluded</td>
<td>10</td>
<td>11</td>
<td>16</td>
<td>1</td>
<td>7</td>
<td>4</td>
</tr>
<tr>
<td>terrestrial not excluded</td>
<td>13</td>
<td>14</td>
<td>17</td>
<td>0</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>Total</td>
<td>23</td>
<td>25</td>
<td>33</td>
<td>1</td>
<td>12</td>
<td>7</td>
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</tbody>
</table>

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<th></th>
<th>Union Springs</th>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>21-Jul</td>
<td>9-Aug</td>
<td>22-Aug</td>
<td>24-Jul</td>
<td>8-Aug</td>
<td>23-Aug</td>
</tr>
<tr>
<td>terrestrial excluded</td>
<td>0</td>
<td>27</td>
<td>44</td>
<td>0</td>
<td>29</td>
<td>50</td>
</tr>
<tr>
<td>terrestrial not excluded</td>
<td>8</td>
<td>29</td>
<td>29</td>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>4</td>
<td>28</td>
<td>36</td>
<td>0</td>
<td>17</td>
<td>29</td>
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</tbody>
</table>

When AIC was used in a stepwise regression to select the most parsimonious, information rich model that explained the number of terrestrial invertebrates eaten per fish across all three diet sampling dates, the top model contained whether pools had
terrestrial exclusion nets or not (p=0.011) and stream (p=0.076) (df=74, R^2=0.101) (Table 12). Of the fish that had at least one prey item in their stomach, fish that were in pools with terrestrial exclusion nets had on average 2.57 terrestrial invertebrates in their stomach, whereas fish that were in control pools had on average 4.38 terrestrial invertebrates in their stomach (t-test, df=75, p=0.009) (Figure 18). Fish at Union Springs ate an average of 2.4 terrestrial invertebrates compared to fish at Dry Run, which ate an average of 3.8 terrestrial invertebrates (t-test, t=1.856, df=75, p=0.076). This may have been because the total standing stock of terrestrial invertebrates was greater at Dry Run than Union Springs regardless of experimental treatment (Mann-Whitney U test, U=30, Z=2.425, df=22, p=0.014). Other differences between streams such as sculpin densities may have also contributed to this difference.

Despite a reduction in terrestrial invertebrates consumed, fish did not eat more aquatic invertebrates to make up for this reduction in invertebrate intake. Fish at Union Springs ate more aquatic invertebrates than fish at Dry Run (Mann-Whitney U test, U=309, Z=2.300, df=75, p=0.021), but there was no difference in number of aquatic invertebrates eaten per fish between experimental treatments at either stream (Mann-Whitney U test, U=608, Z=1.169, df=75, p=0.242) (Figure 19). Consequently, benthic, drifting, or emerging invertebrate abundance per pool did not differ between treatments (Mann-Whitney U tests, U=134, Z=0.902, df=34, p=0.372; U=128, Z=1.138, df=34, p=0.293; U=141, Z=0.665, df=34, p=0.521), and there were no cascading effects of reducing terrestrial invertebrate abundance.

Because terrestrial invertebrate consumption was reduced in pools with terrestrial exclusion nets, but aquatic invertebrate consumption was not increased, total invertebrate
consumption was also reduced. There was a significant difference in the total number of invertebrates in the fish’s stomach between pools with terrestrial exclusion nets and without nets (t-test, t=2.648, df=75, p=0.010) (Figure 20). Of the fish that had at least one prey item in their stomach, fish that were in pools with terrestrial exclusion nets had on average 2.9 invertebrates in their stomach, whereas fish that were in control pools had on average 5.3 invertebrates in their stomach. Due to the reduction in total invertebrates and terrestrial invertebrates consumed, fish in control pools had on average 2.19 times as many calories in their stomach as fish in pools with terrestrial exclusion nets (t-test, t=2.624, df=75, p=0.011), with mean total calories of an individual fish’s stomach contents equal to 17,236 and 7,885 calories respectively.

While the presence of terrestrial exclusion nets was significantly correlated with total number of terrestrial invertebrates consumed, this parameter was not in the top model explaining variation in total number of terrestrial invertebrates consumed when stepwise regressions were conducted using AIC to select the most parsimonious, information rich model. The top model explaining total number of invertebrates eaten per fish contained weight of the fish (p=0.017) and brook trout density and its interaction with stream (brook trout density at Dry Run, p=0.002; brook trout density at Union Springs, p=0.002) (df= 73, R²=0.206) (Table 12). Total number of invertebrates eaten per fish was positively correlated with the weight of the fish. For every 10 g increase in a fish’s weight, the total number of invertebrates in the fish’s diet increased by 1.05 times. Brook trout density was negatively correlated with the total number of invertebrates eaten at Dry Run and even more strongly negatively correlated with the total number of invertebrates eaten at Union Springs. For every increase of 1 fish per m³, the total
number of invertebrates in a fishes diet decreased by 1.61 times at Dry Run and by 8.67 times at Union Springs. Additionally, while sculpin density was not used as a parameter in the final analysis, it was positively correlated with brook trout density and could also be an important factor influencing brook trout diet at Dry Run, where sculpin were present, but not at Union Springs, where they were absent.

Table 12. Three stepwise regressions conducted using AIC to choose the most parsimonious, information rich linear model that described brook trout diet across all three diet sampling dates (July 25-27, August 8-9, and August 23-25). Response variables are on top, with all covariates in the global model listed below. * indicates covariates in the top selected model. The R² for the top model is also given.

<table>
<thead>
<tr>
<th>Response variables</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>log number of terrestrial invertebrates in a fish's diet</td>
<td></td>
</tr>
<tr>
<td>presence of exclosure*</td>
<td>0.101</td>
</tr>
<tr>
<td>stream*</td>
<td></td>
</tr>
<tr>
<td>adult brook trout density main and interaction effects with stream</td>
<td></td>
</tr>
<tr>
<td>fish wet weight</td>
<td></td>
</tr>
<tr>
<td>total number of terrestrial invertebrates in pool's standing stock</td>
<td></td>
</tr>
<tr>
<td>total number of aquatic invertebrates in pool's standing stock</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>log total number of invertebrates in a fish's diet</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>adult brook trout density main and interaction effects with stream*</td>
<td>0.206</td>
</tr>
<tr>
<td>fish wet weight*</td>
<td></td>
</tr>
<tr>
<td>total number of aquatic invertebrates in pool's standing stock</td>
<td></td>
</tr>
<tr>
<td>total number of terrestrial invertebrates in pool's standing stock</td>
<td></td>
</tr>
<tr>
<td>presence of exclosure</td>
<td></td>
</tr>
<tr>
<td>stream</td>
<td></td>
</tr>
</tbody>
</table>
Figure 18. Box plot comparing the number of terrestrial invertebrates eaten per fish between pools with terrestrial exclusion nets and pools without exclosures for all three diet sampling dates (July 25-27, August 8-9, and August 23-25) at Union Springs and Dry Run.

Figure 19. Box plot comparing the number of aquatic invertebrates eaten per fish between pools with terrestrial exclusion nets and pools without exclosures for all three diet sampling dates (July 25-27, August 8-9, and August 23-25) at Union Springs and Dry Run.
Despite experimental reduction in terrestrial invertebrate resources from July 19-August 25, brook trout preyed selectively on terrestrial invertebrates across all three diet sampling dates (July 25-27, August 8-9, and August 23-25) (Table 13). Source (benthic vs. drift or falling vs. drift) could not be determined in diet samples, so conclusions were made by type of invertebrate (aquatic, adult aquatic, and terrestrial); however, drift contributions to standing stock during this time were negligible. Even though terrestrial invertebrates only made up 7% of the total standing stock of invertebrates by abundance from July 25-August 25, they made up 50% of brook trout diet by abundance (Figure 21). Similar to stepwise regression results, brook trout at Dry Run preyed more selectively on terrestrial invertebrates across all three diet sampling dates than brook trout at Union Springs despite no difference in the percent composition of the standing stock between
streams (Table 13 and Figure 21). Even though fish at Dry Run in exclosure pools ate fewer terrestrial invertebrates than fish in control pools, experimental reductions in terrestrial invertebrate resources did not appear to affect the percentage of the diet composed of terrestrial invertebrates at Dry Run, suggesting that fish in exclosure pools may have also eaten fewer aquatic invertebrates. At Union Springs, the percentage of a fish’s diet composed of terrestrial invertebrates was lower and the percentage of the diet composed by aquatic invertebrates was higher in exclosure pools compared to control pools because fish in exclosure pools ate fewer terrestrial invertebrates (Figure 21).

Table 13. Strauss selectivity index for brook trout at Dry Run and Union Springs for pools with terrestrial exclusion nets and pools without these nets for July 25 – August 25. Possible values range from +1, which indicates perfect selection for a prey type, and -1, which indicates perfect selection against it. B, D, A, and T refer to benthic, drifting, falling adult aquatic, and falling terrestrial invertebrates respectively.

<table>
<thead>
<tr>
<th>type of invertebrate</th>
<th>Strauss Selectivity Index</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dry Run</td>
</tr>
<tr>
<td></td>
<td>exclosure</td>
</tr>
<tr>
<td>aquatic (B+D)</td>
<td>-0.82</td>
</tr>
<tr>
<td>adult aquatic (A+D)</td>
<td>0.15</td>
</tr>
<tr>
<td>terrestrial (T+D)</td>
<td>0.67</td>
</tr>
</tbody>
</table>
Figure 21. The percent composition by abundance of brook trout diet and standing stock invertebrate resources made up of adult aquatic, aquatic, and terrestrial resources from July 25 to August 25.

Most invertebrates consumed were from the orders Diptera, Coleoptera, Hymenoptera, and Homoptera (Table 14). At Dry Run flies in the family Empididae were by far the most important in terms of abundance, biomass, and caloric content in pools with exclosures (Tables 14 and 15). While this taxon was abundant in pools during the first two invertebrate sampling dates, it was scarce during the later invertebrate sampling dates, which were concurrent with the diet sampling, and fish highly selected for this taxon in pools with exclosures (Strauss Selectivity Index=0.44) (Appendix 13). While fish at Dry Run in exclosure pools did not have a greater percentage of their diet coming from aquatic sources, Chironomidae pupa and larvae made up 12% of the diet of
fish in these pools, but only made up 5% of the diet of fish in control pools (Table 14). Aquatic Hemiptera were also an important taxon in terms of mass eaten for fish in exclosure pools (Table 14). Fish in pools without exclosures consumed mostly Homoptera, Coleoptera, and Hymenoptera at Dry Run (Table 14 and 15). At Union Springs, Chironomidae larvae were abundant in diet samples of fish in exclosure pools, while Hymenoptera were the most abundant in diet samples of fish in control pools; however, Coleoptera were more important in terms of mass and caloric content for both treatments (Table 15).

Although Orthoptera and Arachnids in the Phalangiidae family and were important determinants of overall available terrestrial biomass, they were never observed in diet samples. These few large taxa may not actually be available for brook trout, and therefore, available terrestrial invertebrate biomass may be much lower than reported above. Other significant sources of food in terms of biomass and caloric content were crayfish and sculpin. On July 21st, one brook trout sampled at Dry Run in a pool without a terrestrial exclusion net had eaten a sculpin. Two brook trout on August 8th and three brook trout on August 23rd in exclosure and control pools at Union Springs had crayfish claws in their stomach. Unknown terrestrial invertebrates made up 5% of brook trout diet in exclosure pools and 10% of brook trout diet in control pools at Dry Run. All invertebrates in diet samples at Union Springs were able to be identified at least to order. Curiously, 16 nematodes were found in diet samples at both Dry Run and Union Springs but not found in the standing stock of invertebrates at either stream (Appendix 8). It could be that this was a parasitic worm living in the fish that was flushed out by gastric lavage.
Table 14. The top 10 taxa in brook trout diet for July 25 – August 25 at Dry Run (A) and Union Springs (B) ranked by percent composition by abundance. Green, red, and blue rows indicate terrestrial, adult aquatic, and aquatic taxa respectively.

A.

<table>
<thead>
<tr>
<th>Order</th>
<th>Family</th>
<th>% of diet</th>
<th>Order</th>
<th>Family</th>
<th>% of diet</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diptera</td>
<td>Empididae</td>
<td>44.31</td>
<td>Homoptera</td>
<td>NA</td>
<td>15.71</td>
</tr>
<tr>
<td>Diptera</td>
<td>NA</td>
<td>8.98</td>
<td>Hymenoptera</td>
<td>NA</td>
<td>14.18</td>
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<tr>
<td>Diptera</td>
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<td>8.38</td>
<td>Diptera</td>
<td>NA</td>
<td>11.49</td>
</tr>
<tr>
<td>Diptera</td>
<td>Chironomidae pupa</td>
<td>7.78</td>
<td>Plecoptera</td>
<td>NA</td>
<td>8.05</td>
</tr>
<tr>
<td>Diptera</td>
<td>Chironomidae larvae</td>
<td>4.19</td>
<td>Diptera</td>
<td>Empididae</td>
<td>7.66</td>
</tr>
<tr>
<td>Ephemeroptera</td>
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<td>3.59</td>
<td>Ephemeroptera</td>
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<td>5.36</td>
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<tr>
<td>Nematoda</td>
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<td>2.99</td>
<td>Coleoptera</td>
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<td>4.60</td>
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<td>Plecoptera</td>
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<td>Chironomidae pupa</td>
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B.

<table>
<thead>
<tr>
<th>Order</th>
<th>Family</th>
<th>% of diet</th>
<th>Order</th>
<th>Family</th>
<th>% of diet</th>
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<tr>
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<td>Homoptera</td>
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<td>Empididae</td>
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<tr>
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<td>Diptera</td>
<td>NA</td>
<td>6.15</td>
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<td>Coleoptera</td>
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<td>Nematoda</td>
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<td>Homoptera</td>
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<td>6.25</td>
<td>Plecoptera</td>
<td>NA</td>
<td>3.08</td>
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</table>
Table 15. The top 10 taxa in brook trout diet for July 25 – August 25 at Dry Run (A) and Union Springs (B) ranked by percent composition by mass. Green, red, and blue rows indicate terrestrial, adult aquatic, and aquatic taxa respectively.

A.  

<table>
<thead>
<tr>
<th>Order</th>
<th>Family</th>
<th>Dry Run % of diet</th>
<th>No Exclosure % of diet</th>
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</thead>
<tbody>
<tr>
<td>Diptera</td>
<td>Empididae</td>
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<tr>
<td>Coleoptera</td>
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<td>10.25</td>
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<td>Homoptera</td>
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<td>Chironomidae pupa</td>
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<tr>
<td>Trichoptera</td>
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</table>

B.  

<table>
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<th>Union Springs % of diet</th>
<th>No Exclosure % of diet</th>
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<td>Hymenoptera</td>
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<td>Homoptera</td>
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<td>8.80</td>
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<td>Other</td>
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<td>Trichoptera</td>
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<td>Plecoptera</td>
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<td>2.16</td>
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<tr>
<td>Plecoptera</td>
<td>NA</td>
<td>1.52</td>
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DISCUSSION

Invertebrate resources in Appalachian intermittent streams

Flow at Dry Run and Union Springs dramatically declined throughout the summer leaving most pools completely isolated from August 8-August 25. Abundance, biomass, and caloric content of brook trout invertebrate resources and riparian predator resources declined throughout the summer with declining flow. Stream flow was the predominant factor influencing total abundance and biomass of invertebrate resources, and because of this, it is likely that Dry Run and Union Springs have lower invertebrate resources than neighboring perennial streams. As expected, drifting resources declined with flow and became negligible during the isolation period. Benthic invertebrate resources peaked as pools became isolated potentially indicating emigration from drying riffles; however, these resources were quickly depleted likely due to increased fish predation, emergence of adult aquatic invertebrates, and limited habitat. Fluxes of adult aquatic invertebrates emerging from the stream and falling back into the stream after emerging declined throughout the summer likely due to the seasonal nature of invertebrate life-cycles and due to declining benthic invertebrate resources.

The abundance of falling terrestrial invertebrate resources decreased with time and as flow declined likely due to declining wetted-surface area or the seasonal nature of this subsidy; however, the biomass of falling terrestrial invertebrates appeared to be largely stochastic and dependent on a few large crawling invertebrates in the Phalangiidae family, although these were not found in diet samples and may not be available for brook trout. Other studies have also shown that this subsidy is extremely
variable and may be dependent on weather and local conditions (Mason and MacDonald 1982; Edwards and Huryn 1995).

This was the first study to assess whether in-stream wood was a preferential pathway for terrestrial invertebrates entering streams. It was hypothesized that in-stream wood may provide habitat and be a migration corridor for terrestrial invertebrates; therefore, it may provide an important source of falling terrestrial invertebrates. Despite this prediction, invertebrates falling off of in-stream wood were not more abundant than invertebrates falling from the canopy but did differ in composition, with in-stream wood having a higher abundance of Homoptera.

In contrast to other studies, canopy cover and composition were not correlated with the abundance of falling terrestrial invertebrate resources. This may have been due to the low range of percent canopy cover observed between pools (72%-94%). While other studies have found that streams with higher canopy cover have higher terrestrial invertebrate resources (Cloe and Garman 1996; Nakano et al. 1999b; Kawaguchi and Nakano 2001), Dry Run had higher abundances of falling terrestrial invertebrates but lower canopy cover than Union Springs. This suggests that other differences between the two streams were responsible for differences in terrestrial invertebrate resources.

In addition to flow, stream was a large factor influencing total available resources, with abundance of invertebrates five times lower at Union Springs than Dry Run. This would suggest that other attributes of the streams not quantified in this study may cause Dry Run to be more productive than Union Springs. One difference between streams that was also correlated with abundance of total invertebrates was adult brook trout density. For every 1 fish per m³ increase in adult brook trout density, invertebrate abundance per
pool and per m$^2$ declined by 1.4 times at Dry Run. Alternatively, differences in invertebrate abundance between pools at Dry Run could have been due to sculpin densities, which were positively correlated with brook trout densities. Adult brook trout density did not affect invertebrate abundance at Union Springs likely due to lower densities of brook trout and lower total fish densities, with sculpin being completely absent at this stream. Brook trout densities could have been lower at Union Springs due to the lower invertebrate abundances because even after brook trout were transplanted into pools at Union Springs, densities were still lower throughout the study because of high mortality rates. Flow, stream, and brook trout density together still only explained ~40% of the variation in total invertebrate abundance per m$^2$ after accounting for differences between pools. This highlights the complexity of these systems and the inherent difficulty in deciphering the mechanisms behind stream productivity.

Benthic invertebrates were the largest source of brook trout invertebrate prey resources in the standing stock numerically, gravimetrically, and energetically; however, they decreased in importance throughout the summer as they were depleted. Additionally, many invertebrates in the benthos may not have been available for brook trout consumption. Chironomidae were the predominant component of the benthos, but many species of Chironomidae in the samples were likely burrowing species (i.e., individuals were found in sediment tubes) and therefore may not be readily available for brook trout consumption. This taxon was not abundant in most brook trout diet samples. Yet, when terrestrial invertebrates were scarce (i.e., in pools with terrestrial exclusion nets) and when there were low brook trout and sculpin densities, Chironomidae made up 25% of brook trout diet. This suggests that this taxon may be eaten under duress, at least
when there is no competition with sculpin, but it may be an inferior resource because it was the smallest taxon observed in these streams. Due to its small size and potential burrowing behavior, this taxon may require more time and energy spent by a fish in order to ingest the same total biomass and caloric intake as when a fish consumes larger terrestrial invertebrates. Additionally, many of the other benthic taxa in these streams were small and may have been costly and hard to obtain. This may have been due the nature of invertebrate life-cycles in intermittent streams. Large, long life-cycle taxa, such as Megaloptera or Odonata, that require multiple years to complete their aquatic stages may not be abundant or present in streams that are consistently intermittent because of the annual drying of these streams. Thus, environmental selection pressures in intermittent streams may result in small aquatic invertebrates that are lower in biomass and caloric content. Therefore, benthic invertebrates in these intermittent streams may be more costly to obtain than larger individuals that may be present in perennial streams. Differences in the frequency of stream intermittency may have been a contributing factor to differences in benthic taxa between the streams in this study. Union Springs had larger taxa such as Odonata and Megaloptera, but these taxa were absent from Dry Run, which was much drier than Union Springs during the summer prior to the study.

As benthic resources were depleted throughout the summer, terrestrial invertebrates made up a higher percentage of available of brook trout resources. Terrestrial invertebrate resources also made up a large portion of available resources for insectivorous riparian predators. Emerging adult aquatic invertebrates could be important for riparian predators numerically, but gravimetrically and energetically this was an inferior food resource compared to terrestrial invertebrates. Additionally, the biomass of
adult aquatic invertebrates that fell back into the stream was almost equal to that
emerging from the stream, and therefore, this resource may be largely unavailable for
riparian predators. This indicates that, at least in the summer, terrestrial subsidies are an
important contribution to stream food webs but that aquatic subsidies to forests may not
be as important. Alternatively, adult aquatic invertebrate fluxes in this study and others
may be highly stochastic and composed of large short lived peaks that are hard to capture
with sampling (Judd 1962; Harper 1978; Nakano and Murakami 2001). Studies in
perennial streams have found that emerging adult aquatic fluxes can be much larger and
can be very important for riparian predators (e.g., Gray 1993; Power and Rainey 2000;
Sabo and Power 2002a,b). The main taxon making up the flux of adult aquatic
invertebrates in this study and others was Chironomidae (Jackson and Fisher 1986;
Baxter et al. 2005). The percentage of adult aquatic invertebrates falling back into
streams in this study was 86% at Dry Run and 73% at Union Springs, and this was much
higher than previous studies, which has ranged from <1 to 60% (summarized by Jackson
and Fisher 1986).

Despite its apparent importance for brook trout and riparian predators, the
biomass of falling terrestrial invertebrates in this study ranked lower than forested
streams in other systems (Baxter et al. 2005) (Figure 22). Terrestrial biomass at Dry Run
was more similar to streams with grassland vegetation than other forested streams. Union
Springs had higher biomass, but this was due to a few large spiders, which were not
found in brook trout diet samples, and without these spiders mean falling terrestrial
biomass was lower than Dry Run. Romanisyn et al. (2007) also found that the biomass of
drifting terrestrial invertebrates in Appalachian streams was lower than other systems and
speculated that this may have been due to the riparian vegetation being dominated by rhododendron, which has leathery leaves that protect it from insect herbivory. While this taxon was not present at Dry Run and Union Springs, mountain laurel was a riparian shrub that was present at all pools at Union Springs and has similar herbivory deterrents. This could have contributed to low terrestrial abundance at this stream; however, terrestrial biomass at this stream was higher than Dry Run, which did not have this shrub, and other canopy characteristics were not correlated with terrestrial invertebrate inputs. Alternatively, intermittent streams may have fewer falling terrestrial invertebrates than perennial streams in other systems due to drier microclimate conditions. Interestingly, a new study has suggested that the composition and percent cover of herbaceous riparian vegetation of intermittent streams may differ from perennial streams (Katz et al. 2012). Future studies should determine if herbaceous riparian vegetation has a greater impact on terrestrial invertebrate inputs than canopy vegetation, particularly because the largest component of terrestrial biomass in this study was from crawling invertebrates that may have entered the stream directly from the banks rather than the canopy.
Figure 22. Comparison of biomass of terrestrial invertebrates falling into streams throughout the world during the summer (Baxter et al. 2005). * indicates values are combined adult aquatic and terrestrial invertebrate biomass. ** indicates terrestrial invertebrate biomass at Union Springs excluding a few large Arachnids in the Phalangiidae family, which were not found in diet samples.

Trends in invertebrate biomass over time were similar to trends in invertebrate caloric content over time because the caloric values used for this study were limited to available literature, which was very generalized. Caloric values in the literature are very incomplete for taxa (e.g., Plecoptera is completely missing), and most diet studies use Cummins and Wuycheck (1971) values, which are compiled from a variety of sources and methods and have not been updated (James et al. 2012). This data is likely not an adequate assessment of taxonomic, seasonal, or regional variation in caloric values.
(James et al. 2012). Caloric values are used in many ecological studies, but more detailed estimations are sparse in the literature due to the time and expense in assessing caloric content (James et al. 2012). Traditionally, caloric values are assessed using bomb calorimetry, which requires the taxa to be combusted and the amount of energy released is measured (Cummins and Wuycheck 1971). Caloric values of invertebrates are difficult and time consuming to assess because such a large mass of invertebrates is needed to combust in order to get an accurate measure of the amount of energy released.

Preliminary bomb calorimetry values for aquatic invertebrate samples in this study were assessed to try to determine the caloric content of aquatic invertebrates in these streams at a finer scale. Caloric values of aquatic invertebrate taxa were low compared to the literature values (Appendix 14); however, these values were not used for this study because caloric values for terrestrial taxa were not determined and using data from multiple sources may skew results. Values may have been lower in these streams because these streams are highly oligotrophic. Additionally, some studies have suggested that acidification of streams could lower the biomass and caloric content of invertebrates by lowering the quality of available food resources for invertebrates (Groom and Hildrew 1989; Engstrom 1996). Low caloric content of invertebrates could add to the additional stress of low quantity of available resources when flows are reduced. Future studies should confirm this low caloric content of aquatic invertebrates, determine mechanisms behind the low caloric content, and determine caloric content of terrestrial invertebrates. In addition, a recent study has suggested a novel and simplified method of determining invertebrate caloric content (James et al. 2012). Instead of using bomb calorimetry, the wet and dry mass of invertebrates are measured, and because the
proportion of dry mass to wet mass is correlated to lipid content, this proportion can be used in a linear model to determine caloric content (James et al. 2012).

**Effects of flow reduction on brook trout**

Brook trout in this study had approximately the same frequency of empty stomachs on average as other salmonid studies (Vinson and Angradi 2011), but as the summer progressed empty stomachs were more common. This was likely due to reduction in flow, a decrease in available resources, and increased competition. During this time, brook trout populations in these streams were extremely stressed, and percent mortality from July 21 through August 25, 2011 was 43% for both streams combined, indicating the potentially strong bottleneck caused by dry conditions during the summer. This is similar to other estimates of natural mortality during periods of drought and in intermittent streams in other regions (Hakala and Hartman 2004; May and Lee 2004). In 2010, the total population size at Dry Run was estimated to be 88 adults and 117 young of the year, with an effective population size of 5 individuals, but at the beginning of this study in July 2011 only 44 adults and 23 young of the year remained, with an effective population size of less than 5 individuals (M. Hudy unpublished data). Mortality and genetic structure in other intermittent streams in this watershed was similar during this time period, although other streams had larger overall and effective population sizes (Whiteley et al. 2012). Total population estimates were not available for Union Springs. Mortality in study pools in this stream was even higher than Dry Run, although this could have been due to a greater effect of transplanting fish in this stream.
The summer of 2010 was exceptionally dry, with mean summer rainfall 52% below the 118 year average (Southeast Regional Climate Center 2011a), and streams in the study area were intermittent from July through November, which likely contributed to such a high mortality rate. Although May and August were exceptionally wet (61% and 51% greater than the monthly average) and July was exceptionally dry (40% below the monthly average), total summer rainfall during the summer of 2011 was approximately equal to the 118 year average (Southeast Regional Climate Center 2011a). Despite this, these streams still became intermittent from late July to the end of August, with Hurricane Irene ending the intermittent period on August 27. This suggests that these streams frequently become intermittent even during years of average rainfall conditions. If weather patterns become more erratic with climate change, fish populations may have difficulty to adapting to these drastic changes in flow, and intermittent streams may become more common. Additionally, increased human use of water may decrease stream flows and increase the frequency of intermittent streams, which may negatively impact fish populations though decreasing available food resources, increasing risk of desiccation, and increasing competition.

**Effects of experimental reductions in terrestrial invertebrate abundance on brook trout diet and energetic gain**

Reductions in forest cover could detrimentally impact stressed and isolated populations of brook trout by further reducing the available terrestrial food resources and reducing caloric intake. Natural terrestrial invertebrate fluxes in these two streams were already lower than other studies in other systems (reviewed by Baxter et al. 2005), and terrestrial fluxes were a small component of available resources in this study regardless
of experimental reductions of terrestrial fluxes. Even though terrestrial invertebrate resources only made up 7% of the total standing stock of invertebrates by abundance, they made up 50% of brook trout diet. Similarly, terrestrial invertebrates have made up more than a third of the diet of fish in other systems where terrestrial invertebrates have only made up 10-15% of the drift (Hubert and Rhodes 1989; Young et al. 1997).

Many other studies in streams in the Appalachian Mountains have found that brook trout selectively prey on terrestrial taxa (Webster and Hartman 2005; Utz and Hartman 2006; Utz et al. 2007; Utz and Hartman 2007; Sweka and Hartman 2008). In this study, Diptera, Hymenoptera, Homoptera, and Coleoptera were of particular importance. Diptera, Hymenoptera, and Coleoptera were also found to be important in other diet studies done in Appalachian streams (Utz et al. 2007; Utz and Hartman 2007); however, Homoptera was more important in this study. This is particularly interesting given that in-stream wood was a major pathway for this taxon to enter the stream, and future studies should determine if there is a correlation between in-stream wood and composition of brook trout diet.

It is possible that diet samples overestimated the importance of terrestrial invertebrates because they typically have harder exoskeletons making them harder to digest. Therefore, they may have a longer retention time in brook trout stomachs than softer, more easily digestible aquatic invertebrates such as Chironomidae. Despite this, it is unlikely that diet samples were biased because Chironomidae made up substantial part of brook trout diet (approximately 25%) at Union Springs in pools with experimentally reduced terrestrial invertebrates, indicating that softer invertebrates were still able to be detected in brook trout diet.
Previous studies have modeled what will happen to caloric intake if terrestrial invertebrates were reduced (Sweka and Hartman 2008), but this is the first study to measure how experimental reductions in terrestrial invertebrates affect trout’s caloric intake. Experimental reductions in terrestrial invertebrate resources resulted in a 43% decrease in abundance of winged terrestrial invertebrates, which cascaded into a 55% decrease in total brook trout consumption and reduced total caloric intake by 46%. While other studies have demonstrated that salmonids switch from feeding on the terrestrial invertebrates to feeding on the benthos when the availability of terrestrial invertebrates is reduced (Nakano et al. 1999b; Baxter et al. 2004; Kawaguchi et al. 2003; Tippets and Moyle 1978; Bechara et al. 1992), brook trout in this study did not consume more aquatic invertebrates to make up for lack of terrestrial invertebrates. Therefore, there were no cascading effects of terrestrial invertebrate reductions on benthic, drifting, or emerging invertebrate resources, and the total number of invertebrates eaten by an individual was reduced in pools with terrestrial exclusion nets at both streams.

In this study, it is possible that brook trout cannot switch to consuming invertebrates in the benthos when there are limited resources during low flow conditions because of competition with sculpin or other brook trout. Additionally, benthic taxa in intermittent streams may be less susceptible to predation than taxa in perennial streams due to their smaller size and hiding potential. Substrate characteristics were not quantified in this study, but benthic taxa in these streams may be less susceptible to predation due to substrate that allows for better concealment. While they did not eat more total aquatic invertebrates, brook trout in exclosure pools at both Dry Run and Union Springs ate more Chironomidae. Brook trout in exclosure pools at Dry Run also
ate more aquatic Hemiptera, which were easily seen on the surface of the water and not a likely source of prey for sculpin. This supports the hypothesis that benthic taxa were not available due to concealment or competition with sculpin.

In addition to the observed effects of terrestrial exclosures on brook trout diet, analysis of factors influencing brook trout diet showed that brook trout density was a significant factor affecting brook trout diet at Dry Run, and an even more important factor effecting brook trout diet at Union Springs even though brook trout densities were lower in this stream. As brook trout density increased, the total number of invertebrates consumed decreased. Sculpin density may have also been an important factor influencing brook trout diet. Competition with sculpin may have prevented brook trout from eating aquatic invertebrates when terrestrial invertebrates were reduced at Dry Run; however, brook trout at Union Springs did not switch to eating more aquatic invertebrates either when terrestrial invertebrates were reduced, and sculpin were not present at this stream. It is hard to distinguish between ecological relationships because sculpin density was highly positively correlated to brook trout density and stream, which was a significant factor affecting the number of terrestrial invertebrates consumed. To try to determine how densities of both species affected standing stock invertebrate resources, analyses were run with either sculpin density, brook trout density, or total fish density. Results showed that brook trout density was more strongly negatively correlated to total standing stock abundance than either sculpin or total fish density. Additionally, the diet of five sculpin was attempted to be assessed using gastric lavage at Dry Run, but this proved to be ineffective because the flushing tube was larger than the throat of the sculpin. Future studies should determine what role sculpin may play in these systems,
and why sculpin were not present at Union Springs. In a study of how brook trout and sculpin influence trophic cascades on benthic invertebrates, Cheever and Simon (2008) found that brook trout and sculpin did not compete for food resources but may have facilitated each other. This may change when flows are reduced and brook trout can no longer feed on the drift. Other studies in Appalachian streams have shown that brook trout density can be an important factor limiting growth when resources are scarce (Utz and Hartman 2009), and these intermittent streams frequently have high trout densities in isolated pools.

Future studies should also do bioenergetic modeling to see how reductions in terrestrial subsidies had a significant impact on if brook trout were feeding at a level required to maintain zero growth and how their condition at the end of the summer affects spawning success and overwinter survival. Brook trout surviving summer low flows after droughts have been found to have low fat reserves, which are crucial to overwinter survival and fall spawning (Hakala and Hartman 2004). Studies in perennial Appalachian streams have found that brook trout only exceed maintenance energy rations consistently and substantially during May and June (Utz and Hartman 2007). Brook trout populations in intermittent streams in this study persisted despite low food resources due to low flow conditions, and other studies have shown that they are also impacted by low genetic variability, acid rain, climate change, and habitat fragmentation (Hudy et al. 2000; Nislow et al. 2006; Hudy et al. 2008; Nislow et al. 2011). The mechanisms behind survival in these unfavorable conditions are poorly understood, but terrestrial invertebrate resources appear to be a major energetic resource supporting this population, and
reduction of this food resource through land use changes may be detrimental to this population.

**Conclusions and management implications**

Food resources for brook trout and insectivorous riparian predators appear to be lower in intermittent Appalachian streams than other systems, and subsidies appear to be limited to one direction (i.e., forest to the stream). This, combined with the inability of brook trout to switch from feeding on terrestrial subsidies to the benthos, may mean that these streams are more susceptible to being destabilized by factors that interrupt subsidies such as land use changes in the riparian zone or introduction of non-native fish (Nakano et al 1999b; Takimoto et al. 2002; Baxter et al. 2004). Reductions in stream flow may also disrupt fluxes of subsidies between forests and streams because reductions in stream flow may reduce the available terrestrial subsidies in the drift and the surface area intercepting terrestrial subsidies. Stream flow was the main factor driving resource availability in this study, and climate change along with increased human demand for water may make these systems more common (Milly et al. 2005; Cowell and Urban 2010). In many places, basic knowledge of frequency and location of intermittent streams is lacking. For example, in this study, Union Springs was thought to be a perennial stream but during the summer of 2011 it had similar flow conditions as Dry Run, becoming intermittent during July and August despite the fact that summer rainfall was approximately equal to the 118 year average. Therefore, it is imperative that more research be done on these still poorly understood systems, so that best management practices such as water conservation, maintenance of riparian buffers, and prevention/
removal of invasive species can be determined and implemented to conserve these threatened ecosystems, which provide critical habitat for isolated populations of native brook trout.
APPENDICES

Appendix 1. Mean biomass for individuals of thirty taxa from standing stock invertebrate resources that had more than 20 individuals and were randomly subsampled to obtain biomass of each taxon. The best fit model of the distribution of each taxon, the best fit model parameters that were used to calculate the theoretical mean mass of each taxon, the Kolmogorov–Smirnov goodness of fit p-value, and the calculated theoretical mean mass of each taxon are given below.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Mean Mass (mg)</th>
<th>Model</th>
<th>Model Parameters</th>
<th>P-value</th>
</tr>
</thead>
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<tr>
<td><strong>Aquatic</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Heptageniidae</td>
<td>0.8042</td>
<td>Exponential</td>
<td>1.2435</td>
<td>0.613</td>
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<td>Leptophlebiidae</td>
<td>0.2166</td>
<td>Lognormal</td>
<td>0.71444; -1.785</td>
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<td>Ameletidae</td>
<td>0.7828</td>
<td>Generalized Extreme Value</td>
<td>-0.32545; 0.31289; 0.68087</td>
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</tr>
<tr>
<td>Baetidae</td>
<td>0.1103</td>
<td>Gamma</td>
<td>2.0042; 0.05503</td>
<td>0.941</td>
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<td>EphemereIIidae</td>
<td>0.8800</td>
<td>Generalized Extreme Value</td>
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<td>Lognormal</td>
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<td>Perlodidae</td>
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<td>Generalized Extreme Value</td>
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Appendix 2. Caloric values based on the literature for each taxon summarized by Cummins and Wuycheck (1971). The notes column specifies where values were taken from if values for a specific taxon were not in the literature or if values had to be calculated from literature values for ash-free dry mass values (AFDM).

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Appendix 2 (continued). Caloric values based on the literature for each taxon.

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Appendix 3. Mean number of invertebrates per pool per day for each source at Dry Run (A) and Union Springs (B). Error bars indicate ± standard error.
Appendix 4. Mean biomass of invertebrates (mg) per pool per day for each source at Dry Run (A) and Union Springs (B). Error bars indicate ± standard error.
Appendix 5. Mean caloric content of invertebrates per pool per day for each source at Dry Run (A) and Union Springs (B). Error bars indicate ± standard error.
Appendix 6. Available invertebrate abundance for brook trout as flow decreased throughout summer 2011 from June 13 – July 25 (flow) and August 9 – August 25 (isolated).

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Mean Abundance (invertebrates/pool/day)

Appendix 7. Available invertebrate biomass for brook trout as flow decreased throughout summer 2011 from June 13 – July 25 (flow) and August 9 – August 25 (isolated).

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Mean Biomass (mg/pool/day)
Appendix 8A. Percent composition of each taxon in the benthic, drifting, falling, and total standing stock by abundance, biomass, and caloric content at Dry Run.

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Appendix 8A (continued). Percent composition of each taxon in the benthic, drifting, falling, and total standing stock by abundance, biomass, and caloric content at Dry Run.

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Dry Run
Appendix 8A (continued). Percent composition of each taxon in the benthic, drifting, falling, and total standing stock by abundance, biomass, and caloric content at Dry Run.

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### Appendix 8B. Percent composition of each taxon in the benthic, drifting, falling, and total standing stock by abundance, biomass, and caloric content at Union Springs.

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Appendix 8B (continued). Percent composition of each taxon in the benthic, drifting, falling, and total standing stock by abundance, biomass, and caloric content at Union Springs.

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Union Springs
Benthic Drifting Falling Total

110
Appendix 8B (continued). Percent composition of each taxon in the benthic, drifting, falling, and total standing stock by abundance, biomass, and caloric content at Union Springs.

<table>
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<th>Taxa</th>
<th>Benthic</th>
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<th>Falling</th>
<th>Total</th>
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<td>Mass</td>
<td>Cal</td>
<td>Number</td>
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<td></td>
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<td>0.00</td>
<td>1.32</td>
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<td>Diptera</td>
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<td></td>
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<td>4.32</td>
<td>4.71</td>
<td>16.84</td>
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<td>0.00</td>
<td>0.00</td>
<td>0.33</td>
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<td>Mecoptera</td>
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<td>0.05</td>
<td>0.05</td>
<td>0.33</td>
</tr>
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<td>0.05</td>
<td>0.05</td>
<td>0.00</td>
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</table>
| Total Terrestrial | NA | NA | NA | 27.65 | 56.90 | 55.58 | 57.26 | 94.72 | 94.80 | 10.66 | 20.44 | 22.99
Appendix 9. Abundance of riparian predator resources showing mean number of terrestrial and emerging adult aquatic invertebrates per pool per day for Dry Run (A) and Union Springs (B).
Appendix 10. Available invertebrate abundance (A) and biomass (B) for insectivorous riparian predators as flow decreased throughout summer 2011 from June 13 – July 25 (flow) and August 9 – August 25 (isolated).

### A. Mean Abundance (invertebrates/pool/day)

<table>
<thead>
<tr>
<th>Stream</th>
<th>Flow Status</th>
<th>Total Abundance (P)</th>
<th>Terrestrial (T)</th>
<th>Emerging Adult Aquatic (E)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry Run Flow</td>
<td>1064</td>
<td>776</td>
<td>288</td>
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<tr>
<td>Isolated Flow</td>
<td>637</td>
<td>415</td>
<td>222</td>
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<tr>
<td>Union Springs Flow</td>
<td>732</td>
<td>335</td>
<td>396</td>
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<tr>
<td>Isolated Flow</td>
<td>362</td>
<td>203</td>
<td>159</td>
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</table>

### B. Mean Biomass (mg/pool/day)

<table>
<thead>
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<th>Stream</th>
<th>Flow Status</th>
<th>Total Biomass (P)</th>
<th>Terrestrial (T)</th>
<th>Emerging Adult Aquatic (E)</th>
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<td>3105</td>
<td>3081</td>
<td>25</td>
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<tr>
<td>Isolated Flow</td>
<td>659</td>
<td>595</td>
<td>64</td>
<td></td>
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<tr>
<td>Union Springs Flow</td>
<td>4071</td>
<td>4039</td>
<td>32</td>
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<tr>
<td>Isolated Flow</td>
<td>880</td>
<td>836</td>
<td>44</td>
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</table>
Appendix 11. Biomass of riparian predator resources showing mean biomass of terrestrial and emerging adult aquatic invertebrates per pool per day for Dry Run (A) and Union Springs (B). The spike in terrestrial biomass on July 26 was due to a few large Arachnids in the Phalangiidae family.
Appendix 12. Mean percent cover of each species at Union Springs and Dry Run with t-tests comparing values between the two streams and linear regressions comparing percent cover of each species per pool and the mean abundance of terrestrial invertebrates for each pool

<table>
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<th>T-test</th>
<th>Regression</th>
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<td></td>
<td>mean ± std error</td>
<td>mean ± std error</td>
<td>p-value</td>
<td>p-value</td>
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<tr>
<td>Acer rubrum</td>
<td>40 ±19</td>
<td>47 ±20</td>
<td>0.809</td>
<td>0.496</td>
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<tr>
<td>Betula lenta</td>
<td>29 ±16</td>
<td>25 ±14</td>
<td>0.868</td>
<td>0.296</td>
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<tr>
<td>Hamamelis virginiana</td>
<td>10 ±5</td>
<td>0</td>
<td>0.105</td>
<td>0.353</td>
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<tr>
<td>Ilex verticillata</td>
<td>8 ±6</td>
<td>0</td>
<td>0.171</td>
<td>0.352</td>
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<tr>
<td>Kalmia latifolia</td>
<td>4 ±4</td>
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<td>0.341</td>
<td>0.505</td>
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<tr>
<td>Lirodendron tulipifera</td>
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<td>0.258</td>
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<tr>
<td>Magnolia acuminata</td>
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<td>10 ±10</td>
<td>0.341</td>
<td>0.86</td>
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<tr>
<td>Pinus strobinus</td>
<td>13 ±9</td>
<td>11 ±7</td>
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<tr>
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<td>3 ±3</td>
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<td>Quercus prinus</td>
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<td>Tilia americana</td>
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<td>Tsuga canadensis</td>
<td>37 ±14</td>
<td>21 ±11</td>
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Appendix 13A. Percent composition of each taxon in brook trout diet compared to standing stock and selectivity index for each taxon in pools with and without terrestrial exclusion nets at Dry Run.

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<td>% composition of Diet by abundance</td>
<td>% composition of standing stock by abundance</td>
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<td>exclosed</td>
<td>not exclosed</td>
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Appendix 13B. Percent composition of each taxon in brook trout diet compared to standing stock and selectivity index for each taxon in pools with and without terrestrial exclusion nets at Union Springs.

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<td>% composition of standing stock by abundance</td>
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Appendix 14. Caloric literature values compared to preliminary caloric data for select aquatic taxa in the standing stock at Dry Run and Union Springs that had enough biomass to combust using a bomb calorimeter to determine caloric content.

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LITERATURE CITED


Southeast Regional Climate Center, University of North Carolina Chapel Hill. 2011a. Dale Enterprise, VA (442208) Period of record monthly climate summary, period


