

# Identification of critical prey items to Appalachian brook trout (*Salvelinus fontinalis*) with emphasis on terrestrial organisms

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**Abstract** Brook trout (*Salvelinus fontinalis*) in Appalachia experience prolonged periods of poor feeding conditions, particularly during summer and fall. To determine which prey organisms are important in sustaining brook trout populations, we monitored the feeding patterns of a population of brook trout over the course of 2 years with an emphasis on seasonal change. We employed a bioenergetics model to estimate whether or not each fish had obtained enough energy to meet daily metabolic demand. As a result, qualitative comparisons between fish feeding above maintenance ration (successfully feeding fish) and fish feeding below maintenance ration (unsuccessfully feeding fish) were possible. With the exception of winter, brook trout derived significantly more energy from terrestrial organisms than aquatic organisms. During each season, successfully feeding brook trout fed on greater proportions of specific prey types.

Terrestrial Coleoptera and Lepidoptera consistently proved to be important prey during warmer seasons, while large organisms such as vertebrates and crayfish appeared to be important during winter. Our findings suggest that terrestrial organisms are more important than aquatic organisms in sustaining brook trout populations. Further, certain large and abundant terrestrial taxa are critical in providing energy to brook trout.

**Keywords** Brook trout · Feeding ecology · Terrestrial input · Prey

## Introduction

Lotic salmonids often inhabit environments of low productivity, such as headwater streams. Consequently, the quality and quantity of food intake plays an important role in shaping salmonid growth, recruitment, and mortality. The most frequently cited source of energy for salmonids in such ecosystems is the aquatic macroinvertebrate community (Neveu, 1999), which derives most energy from allochthonous sources in the surrounding watershed (Vannote et al., 1980). Such sources of energy often result in stream communities low in productivity and thus offer limited resources to higher trophic levels (stream fish). However, recent surveys in Japanese streams have indicated that terrestrial invertebrates may

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play a dominant role over aquatic sources in providing energy to resident salmonids (Nakano et al., 1999; Kawaguchi & Nakano, 2001). This idea is not new to stream fish ecology, as Allan (1951) noted that fish biomass existed above the energetic capacity provided by the aquatic prey community. Edwards & Huryn (1995) suggested that terrestrial prey consumption acted as one possible explanation for this phenomenon. Nevertheless, studies which examine the specific importance of individual prey taxa (either terrestrial or aquatic) to lotic salmonids during episodes of low prey availability are rare.

Brook trout (*Salvelinus fontinalis*) in Appalachia occupy environments of low productivity, with consequences for growth and management. The growth of individuals and populations may be shaped by feeding dynamics in this region (Cada et al., 1987; Ensign et al., 1990). Particularly, feeding rates drop from spring to summer and brook trout may be subjected to prolonged periods of feeding at or below maintenance ration (Ensign et al., 1990; Sweka, 2003; Utz, 2005). Studies of stream salmonids have concluded that drops in feeding rates during stressful times are caused by decreasing rates of drift, as insect activity decreases during such periods (Ensign et al., 1990; de Crespín de Billy, 2002). Low food availability in the summer may be compounded by the effects of periodic drought in the region (Hakala & Hartman, 2004). Because prey may be limited during typical years and critically low during stressful events, determining items of specific importance in the diverse group of prey items exploited by brook trout could help in understanding the ecology of this species.

We observed the feeding trends of a brook trout population over the course of 2 years in order to identify temporal changes in energetically important prey. Particular prey organisms may be important in supporting fish during periods of low productivity or driving growth rates during periods of abundant food resources. Although considerable literature has examined trout diet patterns, many studies considered only select seasons and most categorized all terrestrial prey taxa into one group (Cada et al., 1987; Thonney & Gibson, 1989; Forrester et al., 1994; Bridcut & Giller, 1995; Mookerji et al., 2004). However,

when the taxonomic detail of terrestrial organisms is considered, studies have found that some taxa may be of particular importance while others are relatively negligible as energetic input to aquatic ecosystems (Wipfli & Gregovich, 2002) or fish diet (Wipfli, 1997; Webster & Hartman, 2005).

Our study sought to quantify which prey items, aquatic or terrestrial, help constitute successful feeding by brook trout across a central Appalachian watershed. Of particular interest was identifying the relative importance of terrestrial and aquatic resources, as well as the key prey taxa that allowed brook trout to feed in excess of maintenance ration. Estimates of prey availability would have allowed considerable inference. However, due to the nature of brook trout prey a measurement of prey abundance would have proven extremely difficult. Brook trout feed on drifting and non-drifting aquatic prey organisms as well as terrestrial organisms (Sweka, 2003), rendering drift an inappropriate measure of prey availability. The findings from this study are not meant to imply which prey types brook trout select over others or highlight differences in prey abundance by taxa, rather, the current study highlights temporal variation in which prey items allow a brook trout to feed above daily energetic requirements.

### Study area

The study was conducted within the Middle Fork watershed, a north flowing tributary of the Tygart River in the central Appalachian Mountains of Randolph County, West Virginia. The majority of land cover within the watershed is secondary growth hardwood deciduous forest. All sites in the study were located in the southernmost extent of the watershed and were of low order and high gradient; they are therefore typical of brook trout streams in the region. Nine-200 m sites were selected based on a number of criteria: each site contained a resident brook trout population, consistently supported age-0 brook trout (suggesting physiochemical conditions were adequate for spawning), and was devoid of fish barriers between other sites. Site sizes varied in order to

encompass the typical range for Appalachian brook trout (Table 1). Brook trout density in Appalachia decreases with stream size, most likely due to a lack of movement from natal stream reaches by a majority of fish (Petty et al., 2005). In the Middle Fork watershed this pattern held true, as adult brook trout density decreased exponentially with basin area but remained temporally stable within a site (Utz, 2005). Therefore, though smaller streams were more represented than large streams in the current study, more fish were found in these reaches. First-order and small second-order streams contained a disproportionate number of brook trout, and accordingly, the current study sampled a greater number of these reaches. Temperature regimens in reaches were suitable for trout; temperatures rarely exceeded 20°C throughout the duration of the study. The West Virginia Division of Natural Resources and the West Virginia Department of Environmental Protection have actively added limestone sand to riparian areas of streams within the watershed to remediate the effects of acid precipitation and acid mine drainage in the Middle Fork since the 1990's (WVDNR, 2001). This process is commonly used in the region and successfully increases pH, restores fish communities, and increases invertebrate abundance (Clayton et al., 1998). Some sites selected in this study were not actively treated with limestone. However, each site without a limestone treatment retained the ability to support brook trout spawning and carry fish populations.

**Table 1** Stream name, liming status, and size variables for each of the sites sampled in the study

Stream	Limed (Y/N)	Basin area (km <sup>2</sup> )	Mean wetted width (m)
Brush Run	N	0.83	1.46
Kittle Creek	Y	15.38	4.77
Kittle Creek	Y	5.26	2.44
Kittle Creek	Y	2.05	2.19
Light Run	N	5.24	3.13
Mitchell Lick Fork	Y	1.78	2.08
Rocky Run	Y	9.94	4.36
Rocky Run	Y	6.44	3.76
Sugar Drain	N	1.64	2.42

Some streams contained multiple sites at locations at least 1 km apart

The diversity of fishes differed across sites but was typical of Appalachian headwater systems. The number of fish species encountered increased with stream size; however, in nearly all sites fish fauna was dominated by brook trout and mottled sculpin (*Cottus bairdi*). Other fish sampled include blacknose dace (*Rhynchithys obtusis*), longnose dace (*R. cataractae*), creek chub (*Semotilus atromaculatus*), white sucker (*Catostomus commersoni*), northern hogsucker (*Hypentelium nigricans*), and fantail darter (*Etheostoma flabellare*)

## Materials and methods

### Fish collection

Fish sampling occurred eleven times over the course of 2 years (Table 2). All sampling events were divided into four seasons based on similarities in mean consumption estimates (taken from Utz, 2005) and temperature for statistical analyses (Table 2). Sampling was conducted between 0800 and 1600-h and the order of sites to sample were randomly chosen during each day. A three-pass electrofishing procedure (Platts & Nelson, 1988) was used to estimate fish populations within the 200 m section. Before sampling, block nets were placed at the top and bottom of each section to restrict fish movement in or out of sections. Sampling teams used a backpack electrofishing unit (Smith-Root, DC, 60 hz, 500–750 V, Vancouver, WA) and dip nets to capture fish.

Following collection, fish were processed at a streamside station. All fish were immobilized with a clove oil and 95% ethanol solution. Brook trout were weighed to the nearest 0.5 g, and total length was taken to the nearest mm. A subset of 10 brook trout per site per month was chosen for stomach content removal. Only fish > 110 mm fork length were considered eligible for stomach content removal due to gear restrictions; the tube used in flushing water into the foregut was usually larger than the gape of fish below this size (7 mm diameter). However, fish that were stomach pumped generally represented age 1-and older fish. An attempt was made to collect an equal range of fish sizes to analyze for dietary

**Table 2** Designated seasons, sampling dates, corresponding mean temperatures and consumption estimates

Season	Sampling periods	Sampling dates	Mean temperature (°C)	Mean consumption (J g <sup>-1</sup> d <sup>-1</sup> )	# Fish above maint.	# Fish below maint.
Spring	May 2004	5/10–5/12	11.0	57.1	67	20
	June 2004	6/13–6/16	15.9	49.7	67	18
	May 2005	5/9–5/11	12.5	59.7	87	3
Summer	June 2005	6/9–6/11	15.4	38.6	62	28
	July 2004	7/16–7/19	16.2	16.9	28	60
	August 2004	8/16–8/18	18.0	18.6	24	59
Fall	July 2005	7/12–7/13	16.9	22.9	33	57
	September 2004	9/24–9/26	14.4	21.0	37	47
	Winter	March 2004	3/13–3/20	5.3	7.0	14
Winter	December 2004	12/2–12/5	5.2	11.5	33	44
	March 2005	3/12–3/18	2.6	7.9	22	67

The number of fish feeding above and below maintenance ration during each season is provided. Consumption estimates were obtained from Utz (2005)

composition at each site. Stomach contents were removed by directing a constant flow of stream water into the foregut until all items were removed (Twomey & Giller, 1990). Gut items were filtered with a 250 µm sieve and transferred to 95% ethanol. A sample of 10 trout was randomly selected from sites, frozen, and kept for dry weight analysis during select sampling periods. Dry weight estimates were needed in order to calculate an estimate of fish energy density (described below).

#### Laboratory procedures

All prey items were identified to the Family level or the lowest taxonomic classification possible (Merritt & Cummins, 1996; Borror et al., 1989) in order to quantify prey exploitation by frequency and energy. Extremely small organisms (< 0.5 mm length) or organisms partially destroyed beyond identification to Family were classified to Order. The lengths of prey items were measured via an ocular micrometer to the nearest 0.1 mm; when lengths were unavailable head capsules widths were measured to the nearest 0.1 mm. Crayfish (*Cambarus bartonii*) carapace lengths were measured rather than head capsule width or body length. The dry mass of each organism was estimated using published length- or head width-dry mass equations, with the exception of crayfish in which a carapace length-dry mass equation was used (Sample et al., 1993; Benke et al., 1999; Johnston & Cunjak,

1999; Sabo et al., 2002). Using lengths and head widths to estimate weights allowed for approximation of weight when prey items were partially destroyed. Vertebrate food items, such as frogs, salamanders, and fish were dried at a temperature of 60°C for 48-h to calculate dry weight. Each prey item was further classified as either aquatic or terrestrial, with aquatic organisms possessing a life stage with an obligate aquatic phase. Therefore, adult aquatic insects, such as Ephemeroptera, were classified as aquatic. Each prey item was converted to energy using dry weight–energy equations (Cummins & Wuycheck, 1971), and the total energy in the stomach was summarized for each fish.

#### Estimates of consumption and daily ration

We calculated maintenance rations for each fish in order to classify whether or not a particular fish had achieved enough energy to maintain body weight at the time of sampling. Maintenance rations (in Joules per gram of fish wet weight per day) were calculated based on a bioenergetics model for brook trout (Hartman & Sweka, 2001). To calculate brook trout energy density, frozen brook trout were thawed, weighed to the nearest 0.1 g, and dried at 60°C for 72-h to obtain dry weight. Energy densities were then calculated from observed mean energy density in collected fish using a dry weight–energy equation for Salmonidae (Hartman & Brandt, 1995). For sampling events when no fish were collected, energy

density was estimated by linearly interpolating between known dry weight estimates taken when fish were collected. Mean fish energy density was assumed to be equal across sites during a given month. Site temperatures, fish and prey energy densities, and fish sizes were applied to the brook trout bioenergetics model and maintenance ration was calculated by determining the energy required to maintain zero growth over the course of one day.

Daily ration values were calculated using summarized prey energy per fish and the gastric evacuation rate. The total energy intake was multiplied by the brook trout gastric evacuation rates (based on temperature, Sweka et al., 2004) and divided by fish weight to calculate an observed consumption value ( $\text{J g}^{-1} \text{ fish h}^{-1}$ ) as suggested by Eggers (1977). This estimate was multiplied by 24 to convert it to a daily ration. The mean daily consumption estimates in this study were based on stomach contents obtained during the daylight hours only. Though daily consumption typically requires estimates of feeding activity across a diel cycle (Bowen, 1996), multiple studies of indigenous brook trout feeding trends revealed no significant diel pattern in multiple diet variables (Forrester et al., 1994; Sweka, 2003; Mookerji et al., 2004). Further, the evacuation rate of brook trout has proven to be low relative to other salmonids (Sweka et al., 2004). Thus the study made the assumption that a measurement of diet during daylight hours provided sufficient data to calculate typical feeding conditions for the corresponding season.

### Statistical analyses

Consumption estimates by origin (aquatic or terrestrial) were calculated separately in order to determine if fish were deriving a majority of energy from either source. Mean consumption values were calculated for both prey categories. A *t*-test was run on the means between aquatic and terrestrial consumption for each month to determine if one category was significantly higher than the other.

In order to determine if specific feeding patterns affected whether or not a fish was eating above or below maintenance ration, all fish with

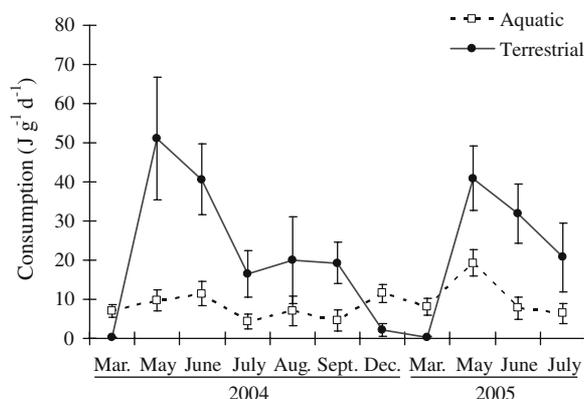
stomach contents present were classified as either above or below maintenance ration for use in several analyses. Fish were placed into the successfully feeding fish category if the observed consumption exceeded their maintenance ration. Differences in consumption of specific prey items were tested between fish eating above and below maintenance ration. For this analysis, prey categories were classified first by origin (aquatic or terrestrial) and then by taxonomic Order. Because of the high diversity of prey exploited by brook trout, further categorization of prey items was necessary for analysis. Within each season, the highest four orders by count and the highest four by energy were selected for analysis. If a prey category fell into both the top four by count and energy, it was only represented once and the next in rank was considered. All remaining prey items that did not fall into the first eight prey categories were placed into a broad aquatic or terrestrial 'other' category. As a result, each prey item consumed by brook trout fell into one of ten categories defined by taxonomic Order and ecosystem origin (aquatic or terrestrial). An analysis of variance (ANOVA) was run on the mean energy contents of each of the ten prey categories followed by Duncan's repeated measures test post-hoc in order to identify significant differences in mean energy per prey category. While differences likely existed in the exploitation of different prey organisms between sites (Thorne, 2004; Utz, 2005), this study was concerned with the general nature of successfully feeding fish throughout the watershed. Therefore, differences in food composition between sites were not considered.

Statistical analyses were performed on proportional prey values as suggested by Somerton (1991) and Chipps and Garvey (in press). The approach we used, originally described by Somerton (1991), was specifically designed to test for qualitative differences in prey composition between groups of fish consuming a highly diverse prey assemblage. The proportional energy derived from each of the ten prey categories was calculated for each fish within a season. These proportions were square-root then arcsine transformed to approximate normality. A multivariate analysis of variance (MANOVA) was performed on the transformed proportions to test for differences in proportional

prey exploitation between fish eating above and below maintenance ration. Because two groups were being compared, Hotelling's  $T^2$  statistic was used to determine if a statistical difference in exploitation rates existed between fish eating above and below maintenance ration. If an overall significant difference existed, differences in exploitation rates of specific prey were tested. An empirical probability distribution was computed by randomly sorting all transformed proportions of a given prey item into equal sized samples as the original data and computing a  $t$ -statistic with 5000 repetitions. Following the randomization procedure, a  $t$ -test was performed on the transformed proportions of fish above and below maintenance ration. The  $t$ -statistic was then compared to the empirical probability distribution to determine significance. Because these tests were performed *a posteriori*, the  $\alpha$ -level was adjusted using the Bonferroni correction. Ten prey categories per season were tested, consequentially, differences were considered significant at  $\alpha = 0.005$ . All statistical and analytical procedures were completed with SAS<sup>®</sup> 9.1 software.

## Results

Consumption estimates by origin of prey varied significantly among seasons. Terrestrial prey consumption of brook trout significantly exceeded aquatic prey consumption during all months except those during winter (Fig. 1). Terrestrial prey con-



**Fig. 1** Mean consumption by prey source (aquatic or terrestrial) for each sampled month. Error bars represent 95% confidence intervals

sumption peaked in May and declined with the arrival of summer. During the winter months (March and December), terrestrial prey consumption fell to near zero and aquatic prey significantly exceeded terrestrial energy input. Over the course of the study, terrestrial prey consumption was more variable than aquatic prey consumption.

Significant differences were observed in mean energy of prey categories and the occurrence rate of specific prey between fish feeding above and below maintenance ration. The results of a MANOVA test on proportional prey by energy showed that during each season whether or not a fish was feeding above or below maintenance ration was significantly related to exploitation of particular prey taxa (Table 3). Further, prey categories significantly differed in the amount of energy provided to the fish (Table 4). Differences between fish feeding above and below maintenance ration of particular prey exploitation rates varied with seasonal change (Table 5). Throughout spring, fish feeding above maintenance ration fed on a significantly higher proportion of terrestrial Coleoptera and significantly less terrestrial Hemiptera/Homoptera and aquatic Trichoptera. Fish feeding above maintenance ration through the summer fed on a significantly higher proportion of terrestrial Coleoptera and Lepidoptera. During fall, fish feeding above maintenance ration consumed terrestrial Lepidoptera at a significantly higher proportion.

**Table 3** Results of MANOVA tests of differences in prey proportions (by energy) between fish eating above and below maintenance ration

Season	Categorical df	Den df	Hotelling's $T$	$P$ -value
Spring	10	340	0.410	<0.0001
Summer	10	223	0.248	<0.0001
Fall	10	70	0.360	0.0117
Winter	10	222	0.141	0.0009

**Table 4** Results of ANOVA on the differences in mean energy content between prey types within each season

Season	Df	$F$	$P$
Spring	9	78.80	<0.0001
Summer	9	21.64	<0.0001
Fall	9	48.03	<0.0001
Winter	9	69.65	<0.0001

**Table 5** Mean energetic content, number encountered, and differences in exploitation rates of each prey type within each season

Season	Order	Origin (A/T)	<i>n</i>	Mean Energy per Item (J)	Above MR		Below MR		df	T	<i>P</i>
					Mean	SE	Mean	SE			
Spring	Other	A	174	649.1 <sup>A</sup>	0.0573	0.0098	0.1093	0.0268	349	-1.79	0.0178
	Coleoptera	T	1821	536.3 <sup>B</sup>	0.4327	0.0197	0.1816	0.0335	349	6.53	<0.0001*
	Other	T	441	491.9 <sup>B</sup>	0.1238	0.0141	0.0678	0.0217	349	2.38	0.0188
	Plecoptera	A	401	200.0 <sup>C</sup>	0.0594	0.0083	0.0913	0.0202	349	-1.58	0.1108
	Hymenoptera	T	566	155.2 <sup>C,D</sup>	0.0523	0.0072	0.0617	0.0194	349	0.16	0.8660
	Diptera	T	1176	120.1 <sup>C,D,E</sup>	0.0970	0.0088	0.1306	0.0283	349	-0.12	0.8968
	Ephemeroptera	A	383	77.7 <sup>D,E</sup>	0.0327	0.0048	0.0543	0.0129	349	-1.44	0.1452
	Trichoptera	A	429	52.1 <sup>D,E</sup>	0.0192	0.0023	0.1249	0.0287	349	-6.07	<0.0001*
	Diptera	A	3113	41.4 <sup>E</sup>	0.1197	0.0112	0.1392	0.0247	349	-0.30	0.7580
	Hemiptera/Homoptera	T	492	17.1 <sup>E</sup>	0.0059	0.0007	0.0393	0.0133	349	-3.98	<0.0001*
Summer	Vertebrata	A	14	2748.5 <sup>A</sup>	0.0436	0.0193	0.0358	0.0140	232	0.44	0.6538
	Decapoda	A	32	1540.9 <sup>B</sup>	0.1069	0.0300	0.0554	0.0160	232	1.70	0.0888
	Lepidoptera	T	155	851.0 <sup>C</sup>	0.1923	0.0332	0.1033	0.0200	232	3.24	0.0020*
	Coleoptera	T	186	332.5 <sup>D</sup>	0.2122	0.0332	0.1039	0.0186	232	3.45	0.0006*
	Other	T	226	234.8 <sup>D</sup>	0.1151	0.0256	0.1499	0.0218	232	-0.84	0.4032
	Hymenoptera	T	219	157.5 <sup>D</sup>	0.0802	0.0202	0.0709	0.0165	232	0.87	0.3944
	Other	A	188	140.9 <sup>D</sup>	0.0635	0.0156	0.1581	0.0240	232	-2.26	0.0224
	Diptera	T	290	136.2 <sup>D</sup>	0.1246	0.0255	0.1718	0.0241	232	-1.10	0.2668
	Trichoptera	A	79	62.4 <sup>D</sup>	0.0100	0.0041	0.0548	0.0143	232	-2.16	0.0266
	Diptera	A	793	19.3 <sup>D</sup>	0.0517	0.0158	0.0963	0.0174	232	-2.08	0.0382
Fall	Vertebrata	A	5	3426.3 <sup>A</sup>	0.0448	0.0319	0.0326	0.0237	79	0.17	0.8623
	Decapoda	A	3	3419.2 <sup>A</sup>	0.0506	0.0339	0.0000	0.0000	79	-	-
	Orthoptera	T	9	1416.7 <sup>B</sup>	0.0514	0.0245	0.0432	0.0276	79	0.50	0.6260
	Lepidoptera	T	164	770.7 <sup>C</sup>	0.5496	0.0580	0.2833	0.0509	79	3.55	0.0006*
	Coleoptera	T	28	196.6 <sup>D</sup>	0.0560	0.0279	0.0396	0.0205	79	0.74	0.4602
	Other	T	69	193.6 <sup>D</sup>	0.0747	0.0308	0.1470	0.0352	79	-1.75	0.0852
	Other	A	83	87.0 <sup>D</sup>	0.0409	0.0148	0.1065	0.0367	79	-1.33	0.1916
	Diptera	A	148	29.9 <sup>D</sup>	0.0186	0.0068	0.0290	0.0076	79	-0.81	0.4196
	Hymenoptera	T	303	24.4 <sup>D</sup>	0.0474	0.0170	0.1490	0.0347	79	-2.51	0.0122
	Hemiptera/Homoptera	T	395	22.5 <sup>D</sup>	0.0662	0.0280	0.1697	0.0360	79	-2.51	0.0136
Winter	Vertebrata	A	12	3388.2 <sup>A</sup>	0.0544	0.0239	0.0064	0.0049	231	2.95	0.0032*
	Decapoda	A	11	556.1 <sup>B</sup>	0.0099	0.0077	0.0101	0.0051	231	0.09	0.9352
	Coleoptera	A	40	422.8 <sup>B,C</sup>	0.0517	0.0160	0.0276	0.0094	231	1.94	0.0476
	Other	A	15	299.3 <sup>C,D</sup>	0.0194	0.0133	0.0081	0.0055	231	1.35	0.1687
	Plecoptera	A	276	189.8 <sup>C,D</sup>	0.1581	0.0354	0.0982	0.0162	231	1.68	0.0962
	Non-insect Arthropoda	T	34	177.9 <sup>C,D</sup>	0.0108	0.0072	0.0111	0.0056	231	0.46	0.6238
	Diptera	A	175	129.2 <sup>D</sup>	0.0570	0.0142	0.0547	0.0129	231	0.85	0.3718
	Ephemeroptera	A	289	117.1 <sup>D</sup>	0.0931	0.0216	0.1373	0.0189	231	-1.05	0.2906
	Trichoptera	A	1713	107.4 <sup>D</sup>	0.5300	0.0400	0.6335	0.0270	231	-1.84	0.0678
	Other	T	86	44.0 <sup>D</sup>	0.0156	0.0073	0.0130	0.0037	231	0.85	0.8614

Means with different letters are significantly different from each other based on ANOVA and Duncan's multiple range test post-hoc. The mean proportions of prey exploitation rates by fish feeding above and below maintenance ration (MR) are provided, followed by *t*-test values between the proportions. Significantly different proportional exploitation rates are denoted with an asterisk, proportions were considered significantly different at the  $\alpha = 0.005$  level

All fish that fed on crayfish were calculated as feeding above maintenance ration during the fall, preventing a statistical comparison of crayfish proportions between groups of fish. Vertebrate taxa (fish and salamanders) during the winter were consumed at a significantly higher proportion by fish eating above maintenance ration.

Some prey organisms were of obvious importance but were not exploited more by fish feeding above maintenance ration. For instance, Trichoptera dominated winter consumption, contributing > 50% of energetic input for both groups of fish, however, no significant difference in Trichoptera occurrence existed between groups of fish. To

**Table 6** The percentage of energy and total count captured by the top eight prey categories for each season

Season	Percentage of total consumption per season	
	By count	By energy
Spring	92.7	82.8
Summer	81.0	82.5
Fall	87.4	90.4
Winter	96.2	97.8

The remaining prey organisms were placed into either 'Other-aquatic' or 'Other-terrestrial' categories

make sure the eight taxonomic selected categories represented a majority of what the trout consumed, the proportion of total energy and total number of prey consumed represented by the eight taxonomic categories was calculated (Table 6). The eight categories represented a minimum of 81.0% and a maximum of 97.8% of the total consumption for either variable.

## Discussion

Terrestrial prey is more heavily consumed by Middle Fork River brook trout than aquatic prey throughout a majority of the year. Several dietary studies have found terrestrial food items to be important (Allan, 1981; Forrester, 1994; Bridcut & Giller, 1995), but studies showing terrestrial insects may significantly exceed aquatic prey sources in importance have been limited to Japanese streams (Kawaguchi & Nakano, 2001; Kawaguchi et al., 2003), Alaskan streams (Wipfli, 1997), and one in central Appalachia (Sweka & Hartman (in press)). Findings in the current study show that terrestrial energy input consistently exceeds aquatic input during all but the winter months. Contrary to Japanese streams where terrestrial consumption peaked in summer (Kawaguchi et al., 2003), brook trout in the Middle Fork River consumed the largest amount of terrestrial energy during the spring and terrestrial insect consumption decreased as summer progressed yet remained greater than aquatic energy input. Such findings concur with Sweka & Hartman (in press), who found terrestrial organisms to be critical in allowing brook trout growth in the Middle Fork watershed.

Extreme variations from mean annual precipitation and temperature may affect trout habitat and feeding in this region (Hakala & Hartman, 2004); however, such conditions were not experienced over the course of the current study. Therefore, we feel that the feeding trends observed here represent those of a typical year for Middle Fork River brook trout.

Specific taxa, usually terrestrial organisms, were critical in maintaining energy input for brook trout. During spring, summer, and fall, terrestrial organisms (terrestrial Coleoptera during spring and summer and terrestrial Lepidoptera during summer and fall) were consumed more by successfully feeding fish than by fish foraging below maintenance ration. However, most other terrestrial organisms were not significantly different between fish feeding above and below maintenance ration and one terrestrial prey class (Hemiptera/Homoptera during the spring) were consumed more by fish feeding below maintenance ration. Therefore, while terrestrial organisms exceed aquatic prey in energetic input for brook trout, particular terrestrial organisms play a dominant role in sustaining fish populations, while others offer comparatively little energetic benefit. This suggests that classifying all terrestrial insects into one group as in other salmonid taxonomic diet studies (Forrester et al., 1994; Bridcut & Giller, 1995; Mookerji et al., 2004) may distort the true values of prey importance. One study that did consider terrestrial taxonomic detail (Webster & Hartman, 2005), found that certain terrestrial organisms may score higher in the index of relative importance (IRI) than others. Another study with terrestrial taxonomic detail (Allan, 1981) found that non-native brook trout may specifically target Coleoptera in Colorado. Terrestrial Coleoptera were also considered the largest contributor of energy among terrestrial organisms to Alaskan streams (Wipfli & Gregovich, 2002). The findings of the current study demonstrate that particular terrestrial organisms, such as Coleoptera and Lepidoptera, may be of disproportionate importance relative to all other prey items during certain seasons.

Critically important prey taxa consistently ranked high, but not highest, in energy per item and frequency of occurrence. With the exception

of winter, all prey organisms that were calculated as exploited by fish above maintenance ration were near the higher end of the energy per item scale, but were not ranked highest in energy content. Such prey items were not consumed at the greatest frequency, yet were consumed at greater rates than a number of other prey categories. Therefore, the important prey items consistently contained relatively high energy content and were encountered more frequently than some other organisms, but did not occupy the topmost rank of either variable. These qualifications for items of particular importance held true when food was abundant (during the spring) and when food was very limited (summer and fall, Utz, 2005). Thus both size and abundance become important variables in determining the importance of prey taxa for Appalachian brook trout. Once winter arrived, however, large, rare food items in brook trout diet proved significantly important over others.

While brook trout consuming very large organisms (fish, salamanders, and crayfish) were usually calculated as feeding above maintenance ration, these prey organisms were detected as significantly important only during the fall (all fish consuming crayfish were feeding above maintenance ration) and winter (Vertebrata). This likely occurred due to the low number of these organisms in the diet content. Therefore, while these organisms offer substantial energy to brook trout capable of capturing them, such captures occur rarely, rendering the statistical method employed in our study not capable of detecting them as consumed more significantly by fish feeding above maintenance ration during spring and summer. Such a finding may suggest that large organisms play a limited role in sustaining the overall population. These results contrast those of Thorne (2004), which found that vertebrate and crayfish prey dominated brook trout diet by weight. Differences between Thorne (2004) and the current study could have been attributed to a number of factors: energetic prey values were calculated differently between the studies, the current study sampled a larger number of fish, and Thorne (2004) included two larger (30 and 41.7 km<sup>2</sup> basin area) mainstem reaches of a stream where brook trout consumed a disproportionate number of fish

relative to smaller reaches. Nevertheless, in the current study crayfish and vertebrate prey were detected at higher proportions in fish eating above maintenance ration during fall and winter. Therefore, these large prey organisms may become increasingly important as terrestrial organisms grow scarce during colder seasons.

Despite taxonomic prey differences between fish eating above and below maintenance ration, other prey taxa (those not collected in significantly different numbers between groups of fish) did appear to be important prey to the Middle Fork brook trout population. For example, during the winter months, Trichoptera were found in very high numbers in a majority of the fish. High Trichoptera consumption during the winter are common in lotic salmonids (Cunjak & Power, 1987; Lehane et al., 2001; Sweka & Hartman, 2001). While differences in Trichoptera consumption were not significant between groups of fish, the high energetic contribution by Trichoptera implies that this particular taxa constitutes an important part of the diet during winter. Therefore, prey items that were not found in at significantly different numbers between groups of fish should not be discarded as unimportant. Rather, items found in significantly higher numbers in fish feeding above maintenance ration should be considered a component of successful feeding along with the exploitation of other organisms.

Over the course of the study, aquatic insects never emerged as contributing a greater amount of energy in fish feeding above maintenance ration. During spring, specialization on aquatic taxa seemed correlated with daily ration estimates below maintenance, as fish feeding above maintenance ration had ingested significantly less Trichoptera. While aquatic insects provided a majority of energy during the winter, brook trout grow little and experience low rates of mortality once acclimated to cold water temperatures (Cunjak & Power, 1987; Utz, 2005). Therefore aquatic insects seem to play a minor role relative to terrestrial insects in shaping and sustaining brook trout populations in this Appalachian watershed. Most dietary studies of lotic salmonids focus taxonomic detail on aquatic insects and group all terrestrials into one broad category (Cada et al., 1987; Forrester et al., 1994; Bridcut

& Giller, 1995; Mookerji et al., 2004). Findings in this study and others (Kawaguchi & Nakano, 2001; Sweka, 2003) imply that future diet studies of headwater stream salmonids should focus more attention on terrestrial organisms.

The importance of terrestrial organisms apparent in the current study suggests that vegetative manipulation or long-term changes in the riparian zone could result in changes to salmonid diets. Multiple studies have shown that differences in riparian vegetation may influence the taxonomy of terrestrial input of invertebrates to streams (Allan et al., 2003) and salmonid diet (Wipfli, 1997; Kawaguchi & Nakano, 2001). Such changes in land cover may occur through active manipulation through timber harvest or development. Long-term changes in forests in the region, such as the potential reduction of eastern hemlock (*Tsuga canadensis*) due to introduced pests could also change riparian structure (Ellison et al., 2005) and brook trout diet.

While which organisms are important in providing energy to brook trout has been highlighted, we caution against certain inferences that may be taken from this study. We did not attempt to calculate prey abundance due to the difficulty in assessing terrestrial and non-drifting prey abundance. Previous work has shown that brook trout show some foraging selectivity in drifting organisms (Sweka and Hartman, 2001), however, our lack of prey availability means that findings in this study do not translate to selectivity. The seasonal variation in prey importance that we detected could be due to variation in abundance of certain organisms, as brook trout are consistently feeding below maintenance ration (Cada et al., 1987; Ensign et al., 1990; Utz, 2005) and therefore likely accept most prey that is readily available. This assertion is backed by the fact that once terrestrial organisms became available due to seasonal change (winter versus non-winter months), they dominated the dietary composition. However, other factors may play a role in what dominates trout diet, such as inter- and intraspecific competition or habitat variability. The current study offers a bridge to answering such questions. The items of disproportional importance in providing energy throughout the year have been highlighted; future work could determine how these

findings relate to selectivity, habitat selection, and growth.

## Conclusions

This study highlights multiple traits of central Appalachian brook trout prey. Terrestrial insects provided the most energy for brook trout during every season except for winter. Select organisms during the warmer months, such as terrestrial Coleoptera and Lepidoptera, were found in greater numbers by fish meeting their daily metabolic demands. Aquatic organisms rarely appeared as substantially important with the exception of winter when terrestrial arthropod activity diminished. During winter, large vertebrate organisms, such as fish and salamanders, appeared to be of particular importance. Our findings suggest that active manipulation or long term change of the riparian zone will likely affect brook trout diet by changing the riparian vegetation and the associated arthropod community.

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