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Diet of the Black Mountain Salamander (*Desmognathus welteri*) in Southeastern Kentucky

Salamanders play an important role in aquatic and terrestrial ecosystems in eastern North America. Semi-aquatic salamanders are known to account for the majority of the vertebrate biomass in certain low-order stream ecosystems (Hairston 1987; Petranka and Murray 2001) where they efficiently assimilate energy and nutrients into biomass, converting 60% of the food they consume into growth and reproduction (Hairston 1987). Furthermore, stream salamanders often feed in both aquatic and terrestrial habitats, essentially linking aquatic and terrestrial food webs. Because of their substantial biomass and foraging breadth, stream salamanders can regulate both freshwater and terrestrial macroinvertebrate communities through top-down effects in food webs, which in turn influence ecosystem functions such as detritus processing and nutrient cycling (Keitzer and Goforth 2013).

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To better understand the influence of semi-aquatic stream salamanders on ecosystem functions, assessments of their diets are needed (Davic 1991; Vanni 2002; Davic and Welsh 2004). Dietary studies provide information on species foraging habits and the role of habitat-specific subsidies, which can then be used to assist species-specific conservation practices. However, information is lacking on the adult diets of 57% (24 out of 42) of eastern North American semi-aquatic plethodontid species (but see Carr 1940; Weichert 1945; Barbour and Lancaster 1946; Hairston 1949; Chaney 1958; Anderson and Martino 1966; Huheey and Brandon 1973; Peck 1974; Burton 1976; Sites 1978; Tilley et al. 1978; Krzysik 1979; McMillan and Semlitsch 1980; Camp and Lovell 1989; Davic 1991; Petranka 1998; Juterbock and Felix 2005). Additionally, few dietary studies have identified prey beyond the level of order. Although order-level information can be useful, a higher resolution is more appropriate to assess the importance values of aquatic and terrestrial prey subsidies in the overall diet since natural histories can vary widely within the same order or family. Importance values and percent occurrences provide greater informative power and can allow for thorough and statistical comparisons of diet between species, seasons, or age classes (Holomuzki 1980; Davic 1991). Importance values mainly consider the volume of the prey, but frequency of prey incidence is also included, giving an estimate of the prey items that potentially provide the greatest amount of resources to the predator. However, this index can overestimate the importance of large prey (i.e., a large prey item consumed by a single individual) or underestimate the importance of small prey items (i.e., many small prey items consumed by most of the individuals). Occurrence percentages can elucidate overall importance based on the frequency of consumption and percent of individuals consuming that prey item. Therefore, the use of both measures (e.g., diet importance values and occurrence percentages) ultimately provides a comprehensive analysis of the volumetrically and numerically important dietary items.

The Black Mountain Salamander, *Desmognathus welteri*, is a large, semi-aquatic lungless salamander with a biphasic life history. This species occurs in the central Appalachian Mountains ranging across northeast Tennessee, western Virginia, southern West Virginia, and southeastern Kentucky (Redmond 1980; Juterbock 1984; Petranka 1998; Felix and Pauley 2006). Within the central Appalachian Mountains, *D. welteri* is considered one of the more aquatic members of this genus. Individuals are typically found underneath large partially submerged rocks within streams but have also been observed on stream banks (Petranka 1998; Felix 2001). The diet of larval *D. welteri* is unknown across its range, and adult diet is only known from West Virginia (Felix and Pauley 2006). Therefore, descriptions of *D. welteri* diet from Tennessee, Virginia, and Kentucky are lacking (Juterbock and Felix 2005; Felix and Pauley 2006).

We examined the prey compositions of larval and adult *D. welteri* in southeastern Kentucky. Our objectives were to 1) non-lethally stomach flush salamanders and identify stomach contents to the highest possible taxonomic resolution, 2) report the first description of larval *D. welteri* diet, 3) determine the importance of aquatic and terrestrial subsidies in the larval and adult diet of this stream-associated salamander, and 4) compare our findings to *D. welteri* from West Virginia and to other species of *Desmognathus*.

Methods

Field-Site Description.—We analyzed stomach contents of adult *D. welteri* collected in a single stream, Island Branch (37.08685°N, 82.98363°W; WGS 84) within the forest of Eastern Kentucky University's Lilley Cornett Woods Appalachian Ecological Research Station (LCW) in the Cumberland Plateau in Letcher County, Kentucky. Island Branch is a first-order, 2–3 m wide stream, located in mature second growth, mixed mesophytic forest at 380 m elevation. See Martin and Shepherd (1973) and Martin (1975) for a list of vegetation at LCW. We also analyzed the stomach contents of larval *D. welteri* collected at Island Branch and at a second locality, Bucklick stream (37.46458°N, 83.13268°W; WGS 84) in Breathitt County, Kentucky. Bucklick lies approximately 40 km NNE of Island Branch and is also a first-order, 2–3 m wide stream, located in mature second growth, mixed mesophytic forest at 278 m elevation. The vegetation at Bucklick is functionally similar to that at Island Branch.

Amphibian Sampling.—We located salamanders by overturning partially submerged rocks in the stream channel and rocks, logs, and leaf litter along the stream margin. Upon capture, salamanders were placed in plastic containers with a small amount of stream water. We anesthetized all salamanders in the field in a solution of 1g Maximum Strength Orajel®/1 liter of aged tap water (Cecala et al. 2007). Snout–vent length (SVL: from the tip of the snout to the posterior portion of the vent) was measured to the nearest 0.01 mm with a digital caliper. We used a non-lethal gastric lavage technique (Fraser 1976; Hantak et al. 2016) with Nipro® 3 mL syringes with 22 gauge needles and 1.3 mm OD PTFE tubing (Zeus Inc., catalog number AWG24) and flushed stomachs with stream water. Salamanders were then placed in a recovery container of aged tap water until they could right themselves and respond to tapping. No mortality occurred during the gastric lavage. Salamanders were returned to their approximate location of capture within 1.5 h. All sampling was conducted during the early evening (1700–1900 h) from April–June in 2016 and 2017. Unpublished capture, mark, recapture data from JMH suggests there are no negative effects of recapture and stomach flushing on the foraging or prey consumption of plethodontid stream salamanders.

Analysis.—Stomach contents were identified to family and genus, if possible, using a dissecting microscope along with appropriate keys and guides (Peckarsky 1990; Merritt and Cummins 1996; Fisher and Cover 2007; Bradley 2012; Evans 2014). Additionally, presumed habitat of origin (aquatic or terrestrial) and invertebrate life stage (larval or adult) were reported, if applicable. Individual prey items were then grouped into larger sections, referred from here as prey groups, based on order/class, life stage, and presumed origin. Samples were placed into individually labeled vials containing 70% ethanol. Vials are stored in the Branson Museum collection at Eastern Kentucky University, Richmond, Kentucky.

We measured length and width of each prey item to the nearest 0.01 mm using a digital caliper and estimated prey volumes as a prolate spheroid using the equation (Dunham 1983):

$$\text{Prey Volume } (v_x) = (4\pi/3)\ (\text{length}/2)\ (\text{width}/2)^2$$

Dietary niche breadth, representing the variety of prey types that *D. welteri* consumed, was estimated by calculating a Shannon diversity index. Importance values, ranging from 0 to 1, were calculated and used to compare the overall importance of a particular prey group/type to the overall diet of *D. welteri* (Powell et al. 1990; Anderson and Mathis 1999). To calculate importance values (I_x) for the prey groups/types, we used the equation:

$$I_x = [(n_x/N) + (v_x/V) + (f_x/F)]\ /3$$

Where n_x, v_x, and f_x represent the number of a prey type, the volume of the prey type, and frequency or the number of stomachs containing that prey typwe, respectively, and N, V, and F represent their sums across all prey types (Hantak et al. 2016).

We additionally calculated the frequency of occurrence (FO), or the percentage of salamanders that ate a particular prey type, which was calculated as:

$$\text{FO} = (\text{S}*100)/\text{N}$$

where S is the number of stomachs with that prey type and N is the total number of stomachs sampled. The relative occurrence (RO), or the percentage of each prey type's occurrence relative to all of the prey items, was then calculated as:

$$\text{RO} = (\text{P}*100)/\text{T}$$

where P is total number of occurrences for that prey type and T is the total number of prey items recovered (Loveridge and Macdonald 2003). Empty stomachs were not included in the importance and percent occurrence analyses.

Results

We stomach flushed 66 adult *D. welteri* (mean ± SD SVL = 59.97 ± 17.07 mm; range = 30.21–85.10 mm). Overall, 63 of

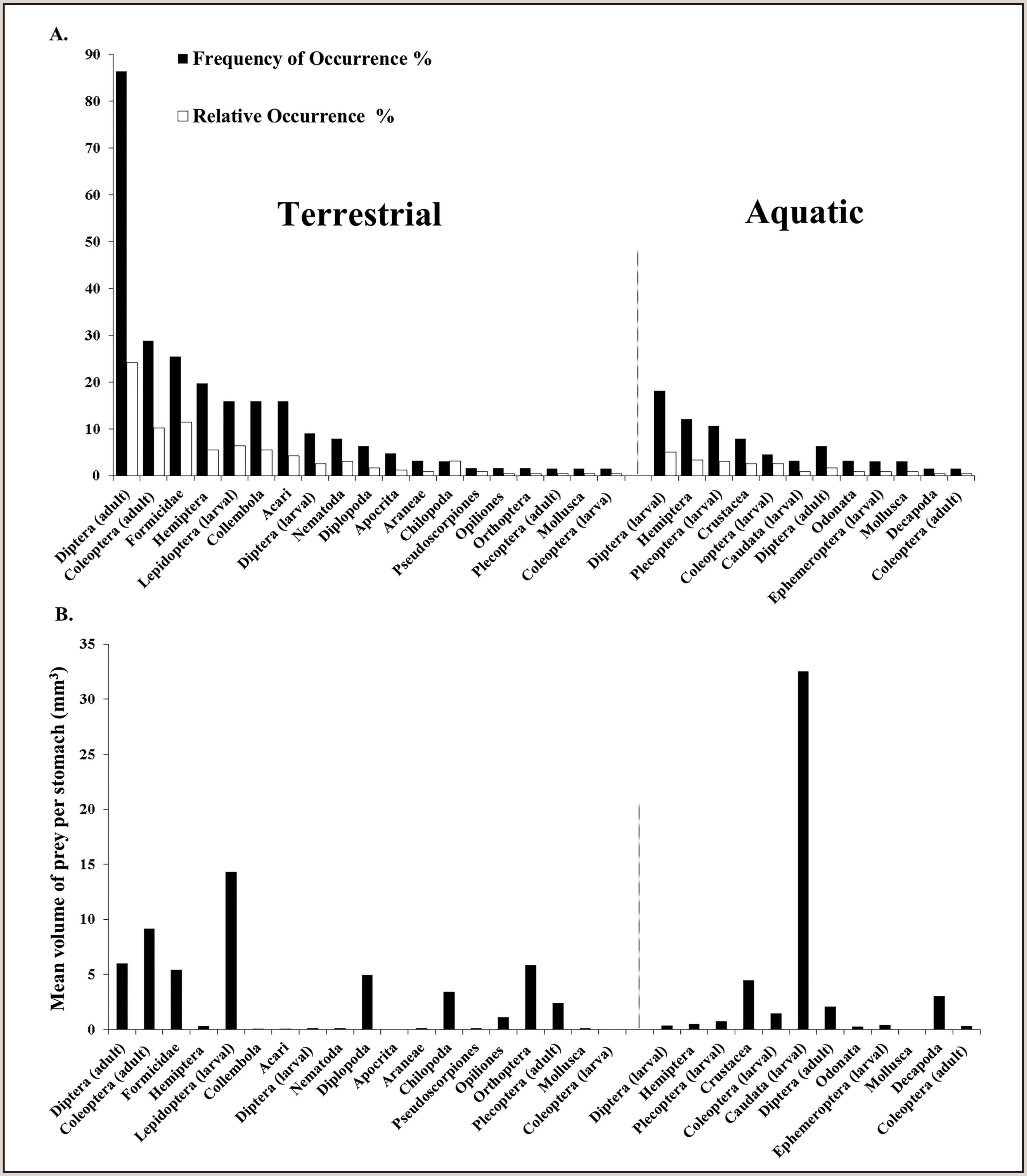

Fig. 1. Prey groups found in adult *Desmognathus welteri* (N = 66) in southeastern Kentucky. Percent occurrences (A) and mean volume (B) of each prey type. The prey groups are split into terrestrial and aquatic based on their presumed origin as designated by the presence of the dashed line (modified from Felix and Pauley 2006).

the 66 sampled individuals contained at least one prey item in their stomachs. We recovered a total of 239 prey items, and on average, individuals contained 3.6 ± 2.5 prey items in their stomachs. Overall, we found 109 distinct prey types from 31 invertebrate prey groups (Table 1, Fig. 1A), and 73 prey types were identified to the level of family or genus (Table 2). The five most numerically important prey, which made up 56% of the total diet, were adult dipterans (flies), adult coleopterans (beetles), larval lepidopterans (moths and butterflies), formicids (ants), and collembolans (springtails; Table 1). The five most

Table 1. Importance values (I_x), frequency of occurrence (FO), and relative occurrence (RO) for 31 terrestrial and aquatic prey groups from adult *Desmognathus welteri* in southeastern Kentucky. Values are listed in decreasing order of I_x, FO, and then RO for terrestrial and aquatic prey.

Prey Group	I_x	FO	RO	Level
Terrestrial				
Diptera (adult)	0.295	80.01	22.36	Order
Coleoptera (adult)	0.279	28.79	10.07	Order
Lepidoptera (larval)	0.123	15.87	6.26	Order
Formicidae	0.107	25.40	11.34	Family
Collembola	0.072	15.87	5.41	Subclass
Hemiptera	0.067	19.70	5.41	Order
Acari	0.067	15.87	4.14	Subclass
Diplopoda	0.044	6.35	1.59	Class
Nematoda	0.037	7.94	2.87	Phylum
Diptera (larval)	0.036	9.09	2.44	-
Orthoptera	0.027	1.59	0.32	Order
Chilopoda	0.025	3.03	3.07	Class
Apocrita	0.020	4.76	1.17	Family
Plecoptera (adult)	0.015	1.52	0.32	Order
Araneae	0.014	3.17	0.75	Order
Opiliones	0.011	1.59	0.32	Order
Pseudoscorpiones	0.008	1.59	0.75	Order
Mollusca	0.007	1.52	0.32	Phylum
Coleoptera (larval)	0.007	1.52	0.32	-
Aquatic				
Caudata (larval)	0.125	3.17	0.75	Order
Diptera (larval)	0.076	18.18	4.98	-
Hemiptera	0.050	12.12	3.29	-
Crustacea	0.050	7.94	2.44	Subphylum
Plecoptera (larval)	0.044	10.61	2.87	-
Coleoptera (larval)	0.040	4.55	2.44	-
Diptera (adult)	0.034	6.35	1.70	
Decapoda	0.017	1.52	0.32	Order
Ephemeroptera (larval)	0.015	3.03	0.75	-
Odonata (larval)	0.014	3.17	0.75	Order
Mollusca	0.014	3.03	0.75	-
Coleoptera (adult)	0.008	1.52	0.42	-

volumetrically important prey, which made up 33% of total diet, were larval caudates (salamanders), larval lepidopterans, adult coleopterans, adult dipterans, and formicids (Fig. 1B). The average volume of prey items per salamander was 75.46 ± 143.58 mm^3. Overall, approximately 19% of the prey items were aquatic in origin, and 81% were terrestrial. For niche breadth, we estimated a mean diversity (H') of 4.33.

Beetles represented the greatest prey diversity; specimens were identified to nine families and 13 genera (Table 2). Beetles from the family Staphylinidae (rove beetles) belonged to five genera and made up 20% of all terrestrial adult beetles. Dipterans were second to the coleopterans, with individuals from 10 families. Ants were identified to seven genera and hemipterans (true bugs) to five families.

Only four (two from Island Branch and two from Bucklick) larval *D. welteri* (mean ± SD SVL = 23.31 ± 1.20 mm; range = 22.21–25.01 mm) were captured and stomach flushed. Thirteen prey items were recovered and identified to nine prey types from five prey groups (listed in order of importance): larval dipterans (Chironomidae, midge flies; 0.886), larval ephemeropterans (Ameletidae, combmouthed minnow mayflies; 0.264), adult dipterans (Cecidomyiidae, gull midges; 0.234), formicids (*Lasius* sp.; 0.160), and terrestrial hemipterans (Aphididae; 0.123). Larval chironomids were found in all of the salamanders and made up 65% of all prey items. Gull midges were found in half the larval salamanders and made up 15% of the prey. Overall, aquatic prey made up 69% of the larval diet.

Discussion

This is the first study to: 1) describe the diet of larval and adult *D. welteri* in Kentucky; 2) identify *D. welteri* diet to family and genus; and 3) calculate individual importance values. Our results demonstrate that the adult diet of *D. welteri* in Kentucky is mostly composed of terrestrial invertebrates, with adult dipterans and coleopterans being both the most volumetrically important and frequently consumed prey. In this study, we reported the importance values for 31 prey groups to adult *D. welteri* from a population in Kentucky to the taxonomic level of family and genus, which were previously lacking in the literature. Overall, *D. welteri* is a generalist feeder, although terrestrial prey accounted for the majority of items consumed. We reported a breadth niche diversity (H') of 4.33. To our knowledge, this is the first reported dietary niche breadth for a semi-aquatic plethodontid salamander. However, mean Shannon diversities ranging from 1.40 to 2.54, have been reported for *Plethodon cinereus* (Eastern Red-backed Salamander), which may be reflective of foraging exclusively within terrestrial environments (Anthony et al. 2008; Hantak et al. 2016).

In the adult *D. welteri* in this study, dipterans were the most important prey group and we identified dipterans to 10 different families, seven of which are considered aquatic. Yet, terrestrial dipterans (adults and larvae) were three times more important and occurred 3.5 times more often than aquatic dipterans within *D. welteri* stomachs. Dipterans have also been previously reported as important prey groups for other large adult semi-aquatic *Desmognathus* (Minton 1972; Krzysik 1979; Mills 1996; Felix and Pauley 2006). Of the studies that identified dipterans to family in several *Desmognathus* species, adult and larval Tipulidae (crane flies), adult and larval chironomids, larval Tabanidae (horse flies), and adult Mycetophilidae (fungus gnats) have been reported (Carr 1940; Barbour and Lancaster 1946; Chaney 1958; Davic 1991; Camp and Tilley 2005). In our study, two adult tipulids were detected, whereas larval tipulids were absent from stomach contents of *D. welteri*. Tipulids comprise the largest family of Diptera, with some 1,500 species recorded in North America (Stone 1965). Bourne (2015) only detected 15 individual tipulids over four sampling periods in a stream within the old-growth forest at LCW (Big Everidge), which is adjacent (2000 m) to Island Branch. Therefore, the lower tipulid availability/stomach presence observed in the *D. welteri* from this study is likely related to regional availability or microhabitat differences.

Coleopterans have also been reported as one of the most important prey groups in other large adult semi-aquatic *Desmognathus* (Minton 1972; Krzysik 1979; Mills 1996; Felix and Pauley 2006). Of the studies that identified coleopterans to family in several *Desmognathus* species, adult Buprestidae (wood-boring beetles), adult Hydrophilidae (water scavenger beetles),

Table 2. Importance values (I_x), frequency of occurrence (FO), and relative occurrence (RO) for the family/genera level taxa from 31 prey groups for adult *Desmognathus welteri* in southeastern Kentucky. Values are listed in decreasing order of I_x, FO, and then RO for each prey type or family/order. Aquatic prey are denoted with an (a).

Prey Type	I_x	FO	RO
Diptera (Adult)			
Mycetophilidae	0.145	28.57	11.86
Sciaridae	0.075	17.46	4.66
Cecidomyiidae	0.060	12.69	4.66
Tipulidae (a)	0.026	4.76	1.27
Unidentified	0.015	3.18	1.27
Dolichopodidae (a)	0.008	1.59	0.42
Diptera (Larval)			
Dolichopodidae (a)	0.028	6.35	1.69
Chironomidae (a)	0.022	4.76	1.69
Cecidomyiidae	0.022	4.76	1.69
Dixidae (a)	0.014	3.18	0.85
Tabanidae	0.007	1.59	0.42
Mycetophilidae	0.007	1.59	0.42
Thaumaleidae (a)	0.007	1.59	0.42
Ceratopogonidae (a)	0.007	1.59	0.42
Coleoptera (Adult)			
Staphylinidae			
Sepedophilus sp.	0.014	3.18	0.85
Quedius sp.	0.016	3.18	0.85
Unidentified	0.010	1.59	0.42
Palaminus sp.	0.007	1.59	0.42
Erichsonius sp.	0.007	1.59	0.42
Hoplandria sp.	0.007	1.59	0.42
Elateridae			
Conoderus sp.	0.017	3.18	0.85
Anchastus sp.	0.008	1.59	0.42
Unidentified	0.008	1.59	0.42
Curculionidae			
Stethobaris sp.	0.008	1.59	0.42
Bagous sp.	0.007	1.59	0.42
Hexarthum ulkei	0.007	1.59	0.42
Carabidae			
Pterostichus sp.	0.022	1.59	0.42
Dryopidae			
Helichus sp. (a)	0.008	1.59	0.42
Nitulidae	0.008	1.59	0.42
Cerambycidae	0.008	1.59	0.42
Tenebrionidae	0.007	1.59	0.42
Unidentified	0.007	1.59	0.42
Coleoptera (Larval)			
Hydrophilidae(a)	0.020	4.76	2.27
Psephenidae			
Ectopria sp. (a)	0.020	3.18	2.27
Carabidae	0.007	1.59	0.42
Caudata (Larval)			
Plethodontidae			
Desmognathus welteri (a)	0.125	3.18	0.85
Lepidoptera (Larval)			
Geometridae	0.089	12.69	4.24
Hesperiidae	0.035	3.18	2.12
Hemiptera			
Aphididae	0.060	12.69	5.09
Hebridae (a)	0.036	7.94	2.54
Saldidae (a)	0.007	1.59	0.42
Cicadellidae	0.007	1.59	0.42
Veliidae (a)	0.007	1.59	0.42
Formicidae			
Aphaenogaster sp.	0.035	7.94	2.12
Pheidole sp.	0.026	4.76	2.97
Lasius sp.	0.024	4.76	2.12
Formica sp.	0.022	1.59	2.54
Camponotus sp.	0.019	3.18	0.85
Crematogaster sp.	0.008	1.59	0.42
Cryptopone gilva	0.007	1.59	0.42
Collembola			
Isotomidae	0.051	11.11	4.24
Symphypleona	0.014	3.18	1.85
Entomobryidae	0.007	1.59	0.42
Acari			
Mesostigmata			
Parasitadae	0.034	7.94	2.12
Oribatida			
Nothrus sp.	0.013	3.18	0.85
Unidentified	0.010	3.18	0.85
Galumnoidea	0.007	1.56	0.42
Plecoptera (Adult)			
Perlidae (a)	0.015	1.59	0.42
Plecoptera (Larval)			
Leuctridae (a)	0.029	6.35	1.69
Unidentified (a)	0.015	3.18	1.27
Crustacea			
Isopoda			
Ligidium eldrodii (a)	0.050	7.94	3.54
Diplopoda			
Spirostreptida			
Cambala sp.	0.017	3.18	0.85
Chordeumatida	0.016	1.59	0.42
Polydesmida			
Polydesmus sp.	0.012	1.59	0.42
Orthoptera			
Acrididae	0.027	1.59	0.42
Chilopoda			
Scolopendromorpha			
Scolopocryptops sexspinosus	0.016	1.59	0.42
Geophilomorpha	0.009	1.59	0.42
Mollusca			
Hydrobiidae (a)	0.014	3.18	0.85
Gastropoda	0.007	1.59	0.42
Apocrita			
Sphecidae	0.014	3.18	0.85
Ichneumonidae	0.007	1.59	0.42
Decapoda			
Cambaridae			
Cambarus sp. (a)	0.017	1.59	0.42
Odonata (Larval)			
Aeshnidae	0.014	3.18	0.85
Araneae			
Araneidae	0.014	3.18	0.85
Ephemeroptera (Larval)			
Ephemeroptera (a)	0.008	1.59	0.42
Ameletidae (a)	0.007	1.59	0.42

adult Scarabaeidae (scarab beetles), and adult Staphylinidae (rove beetles) have been reported (Barbour and Lancaster 1946; Chaney 1958; Sites 1978). In *D. welteri* from our study, buprestids and scarabs were not found in stomach contents, whereas, larval hydrophilids were the most frequently detected aquatic coleopteran. Similarly to Sites (1978), we found staphylinids to be the most abundant coleopteran in the diet of *D. welteri*. The staphylinids represent the largest coleopteran family in North America with 4,400 species (Evans 2014). Many genera are known to occur preferentially along the banks of streams or among the nearby vegetation (Evans 2014).

In addition to dipterans and coleopterans, we found larval lepidopterans, formicids, and collembolans to make up a large portion of the adult *D. welteri* diet. Brown et al. (2003) found Hesperiidae (skippers) lepidopteran larva in *D. monticola*. In our study, hesperiid larvae were nearly three times less important and two times less frequent than Geometridae (loopers, inchworms, and spanworms) larvae. Geometrids are reported to have the greatest abundance and biomass in eastern North America (Wagner 2005), so a microhabitat or seasonal influence may explain the Brown et al. (2003) observation. Barbour and Lancaster (1946) identified ants from the genus *Formica*, to comprise a large portion of the Kentucky diet of *D. fuscus*. Whereas, in Kentucky *D. welteri*, individuals from the genus *Aphaenogaster* were the most important and frequently consumed. Similarly to our *D. welteri*, Sites (1978) found aphids to be the most abundant hemipteran in *D. fuscus*. However, it is uncertain if predation occurred on land or if the aphids fell into the stream from vegetation above (but see McEntire 2016). Adult water bugs (hemipterans) were found in highly aquatic *D. folkersti* from Georgia (Camp and Tilley 2005). In our study, terrestrial hemipterans were 1.3 times more important than aquatic hemipterans, though a slightly greater diversity of aquatic hemipteran families was found. Because of the highly terrestrial ecologies and importance of ants, terrestrial hemipterans, and larval lepidopterans, *D. welteri* foraging likely occurs primarily along the riparian and vegetated bank areas in Island Branch, though it is possible that these subsidies fell into the stream channel from vegetation above.

In this study, we also provide the first description of larval *D. welteri* diet. Larval *Desmognathus* diet studies are scarce (but see Wilder 1913; Martof and Scott 1957; Burton 1976, Davic 1991; Mills 1996). Previous research on *Desmognathus* larvae report that larval dipterans, especially chironomids, were common in the diets across all the study areas (Martof and Scott 1957; Burton 1976; Mills 1996). Larval Plecoptera (stoneflies) and Trichoptera (caddisflies) have also been found in larval *Desmognathus*, and each made up approximately one-sixth of the diets (Martof and Scott 1957; Mills 1996). Larval ephemeropterans comprised more than half of the diet in *D. marmoratus* (Martof and Scott 1957), whereas, they only comprised 7% in *D. welteri* from our study. Davic (1991) reported terrestrial prey items made up 18% of the larval diet of *D. quadramaculatus* from North Carolina. In *D. welteri* from our study area, 30% of the prey importance and occurrence were terrestrial, suggesting the importance of terrestrial prey to the larvae of this species likely through the input of terrestrial prey falling along the shallow banks, as they are unlikely to leave the stream to forage.

The diet composition of adult *D. welteri* in Kentucky appears to be somewhat similar to samples collected in West Virginia (Felix and Pauley 2006) from April to October 2010. However, statistical comparisons are difficult because West Virginia prey items were only identified to order/class and individual aquatic and terrestrial designations were not listed. The most frequently consumed prey in West Virginia populations were adult coleopterans, adult dipterans, hymenopterans (winged, i.e. bees and wasps), larval lepidopterans, and formicids, respectively. Felix and Pauley (2006) found winged hymenopterans (Apocrita) and adult coleopterans approximately seven and two times more frequently than in our individuals, respectively. Whereas, we found adult dipterans nearly two times more often than findings from West Virginia. Furthermore caudates, Chilopoda (centipedes), Diplopoda (millipedes), Mollusca (snails), Opiliones (harvestmen), Odonata (dragonflies and damselflies), pseudoscorpions, and nematodes were found in the stomachs of individuals from Kentucky, but were absent in West Virginia individuals. Larval dipterans and plecopterans were found nearly two times more frequently in salamanders from West Virginia than Kentucky (Felix and Pauley 2006). Additionally, larval Mecoptera, Neuroptera (net-winged insects), and trichopterans were found in salamanders from West Virginia but were absent in Kentucky individuals. Felix and Pauley (2006) reported 4.7 prey per stomach and noted 70% of the West Virginia *D. welteri* diet was assumed to have a terrestrial origin. In our study, salamanders had an average of 3.6 prey per stomach, and 81% of the prey were assumed to have a terrestrial origin. Overall, our general foraging results are comparable to those reported by Felix and Pauley (2006), though differences may be due to their extended sampling from July through October. It is therefore likely that adult foraging in both Kentucky and West Virginia occurs primarily in riparian areas or along stream banks.

Terrestrial prey are known to be important for many *Desmognathus*: Felix and Pauley (2006) found 84% of the prey in *D. monticola* diet to be terrestrial, Sites (1978) reported 85% were terrestrial in *D. fuscus*, Davic (1991) reported 65% of the highly aquatic *D. quadramaculatus* diet was terrestrial, and Shipman et al. (1999) noted terrestrial prey to makeup the majority of the diet of *D. brimleyorum*. Previous studies have reported higher levels of terrestrial prey subsidies than in our study (Felix and Pauley 2006, Sites 1978, and Shipman et al. 1999). However, errors from batch-grouping associated with order-level identification and a lack of aquatic/terrestrial designations (i.e., the high diversity of dipterans, coleopterans, and hemipterans) may have produced higher terrestrial prey counts than actually present in the stomach contents. However, due to the prominence of terrestrial prey in the diet of *D. welteri* and their potential role in nutrient transfer between the terrestrial and aquatic environment, riparian buffers around headwater streams that provide foraging habitat, with an abundant and diverse invertebrate community, appear necessary to sustain *Desmognathus* populations.

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Literature Cited

Anderson, J. D., and P. J. Martino. 1966. The life history of *Eurycea l. longicauda* associated with ponds. Am. Midl. Nat. 75:257–279.

Anderson, M. T., and A. M. Mathis.1999. Diets of two sympatric neotropical salamanders, *Bolitoglossa mexicana* and *B. rufescens*, with notes on reproduction for *B. rufescens*. J. Herpetol. 33:601–607.

Anthony, C. D., M. D. Venesky, and C. A. M. Hickerson. 2008. Ecological separation in a polymorphic terrestrial salamander. J. Anim. Ecol. 77:646–653.

Barbour, R. W., and L. Y. Lancaster.1946. Food habits of *Desmognathus fuscus* in Kentucky. Copeia 1946:48–49.

Bourne, J. C. 2015. Variation in salamander and aquatic insect communities as it relates to stream condition in natural areas of southeastern Kentucky. Master's Thesis. Eastern Kentucky University, Richmond, Kentucky. 79 pp.

Bradley, R. A. 2012. Common Spiders of North America. University of California Press, Berkeley, California. 271 pp.

Brown, W. D., C. T. Georgel, and J. C. Mitchell. 2003. Natural history notes: *Desmognathus monticola* (seal salamander): diet/prey size. Herpetol. Rev. 34:226.

Burton, T. M. 1976. An analysis of the feeding ecology of the salamanders (Amphibia: Urodela) of the Hubbard Brook Experimental Forest, New Hampshire. J. Herpetol. 10:187–204.

Camp, C. D., and D. G. Lovell.1989. Fishing for "spring lizards": a technique for collecting blackbelly salamanders. Herpetol. Rev. 20:47.

———, and S. G. Tilley. 2005. *Desmognathus folkertsi*, dwarf blackbellied salamander. *In* M. J. Lannoo (ed.), Amphibian Declines: The Conservation Status of United States Species, pp. 706–708. University of California Press, Berkeley, California.

Carr, A. F. Jr. 1940. A Contribution to the Herpetology of Florida. University of Florida Biological Publications Science Series, Volume 3, Number 1. University of Florida Press, Gainesville, Florida.

Cecala, K. K., S. J. Price, and M. E. Dorcas. 2007. Diet of larval red salamanders (*Pseudotriton ruber*) examined using a nonlethal technique. J. Herpetol. 41:741–745.

Chaney, A. H. 1958. A comparison of populations of Louisiana and Arkansas populations of *Desmognathus fuscus*. Ph.D. Dissertation. Tulane University, New Orleans, Louisiana. 157 pp.

Davic, R. D. 1991. Ontogenetic shift in diet of *Desmognathus quadramaculatus*. J. Herpetol. 25:108–111.

———, and H. H. Welsh. 2004. On the ecological roles of salamanders. Annu. Rev. Ecol. Evol. Syst. 35:405–434.

Dunham, A. E. 1983. Realized niche overlap: Resource abundance and intensity of interspecific competition. *In* R. B. Huey, E. R. Pianka, and T. Schoener (eds.), Lizard Ecology: Studies of a Model Organism, pp. 261–280. Harvard University Press, Cambridge, Massachusetts.

Evans, A. V. 2014. Beetles of Eastern North America. Princeton University Press, Princeton, New Jersey. 560 pp.

Felix, Z. I. 2001. A natural history study of *Desmognathus welteri* in West Virginia. Master's Thesis. Marshall University, Huntington, West Virginia. 131 pp.

———, and T. K. Pauley. 2006. Diets of sympatric Black Mountain and seal salamanders. Northeast. Nat. 13:469–476.

Fisher, B. L., and S. P. Cover. 2007. Ants of North America: a Guide to the Genera. University of California Press, Berkeley, California. 194 pp.

Fraser, D. F. 1976. Coexistence of salamanders in the genus *Plethodon*: a variation of the Santa Rosalia theme. Ecology 57:238–251.

Hairston, N. G. 1949. The local distribution and ecology of the plethodontid salamanders of the southern Appalachians. Ecol. Monogr. 19:47–73.

———. 1987. Community Ecology and Salamander Guilds. Cambridge University Press, New York, New York. 244 pp.

Hantak, M. M., D. J. Paluh, and C. A. M. Hickerson. 2016. Comparison of the diets of sympatric erythristic and striped morphs of *Plethodon cinereus* (eastern red-backed salamander). Northeast. Nat. 23:219–228.

Holomuzki, J. R. 1980. Synchronous foraging and dietary overlap of three species of plethodontid salamanders. Herpetologica 1980:109–115.

Huheey, J. E., and R. A. Brandon. 1973. Rockface populations of the mountain salamander, *Desmognathus ochrophaeus*, in North Carolina. Ecol. Monogr. 43:59–77.

Juterbock, J. E. 1984. Evidence for the recognition of specific status for *Desmognathus welteri*. J. Herpetol. 18:240–255.

———, and Z. I. Felix. 2005. Black mountain salamander *Desmognathus welteri* (Barbour, 1950). *In* M. J. Lannoo (ed.), Amphibian Declines: The Conservation Status of United States Species, pp. 728–730. University of California Press, Berkeley, California.

Keitzer, S. C., and R. R. Goforth. 2013. Salamander diversity alters stream macroinvertebrate community structure. Freshwater Biol. 58:2114–2125.

Krzysik, A. J. 1979. Resource allocation, coexistence, and the niche structure of a streambank salamander community. Ecol. Monogr. 49:173–194.

Loveridge, A. J., and D. W. MacDonald. 2003. Niche separation in sympatric jackals (*Canis mesomelas* and *Canis adustus*). J. Zool. 259:143–153.

Martin, W. H. 1975. The Lilley Cornett Woods: a stable mixed mesophytic forest in Kentucky. Bot. Gaz. 136:171–183.

———, and C. Shepard. 1973. Trees and shrubs of Lilley Cornett Woods, Letcher County, Kentucky. Castanea 1973:327–335.

Martof, B. S., and D. C. Scott. 1957. The food of the salamander *Leurognathus*. Ecology 38:494–501.

McEntire, K. D. 2016. Arboreal ecology of Plethodontidae: a review. Copeia 2016:124–131.

McMillan, J. E., and R. D. Semlitsch. 1980. Prey of the dwarf salamander, *Eurycea quadridigitata*, in South Carolina. J. Herpetol. 14:424–426.

Merritt, R. W., and K. W. Cummins (eds.). 1996. An Introduction to the Aquatic Insects of North America. 3rd edition Kendall Hunt Publishing, Dubuque, Iowa. 1158 pp.

Mills, G. R. 1996. A study on the life history and seasonal foraging habits of the salamander *Desmognathus quadramaculatus* Holbrook, in WV. Master's Thesis. Marshall University, Huntington, West Virginia. 122 pp.

Minton, S. A., Jr. 1972. Amphibians and Reptiles of Indiana. Monograph Number 3, Indiana Academy of Science, Indianapolis, Indiana. 346 pp.

Peck, S. B. 1974. The food of the salamanders *Eurycea lucifuga* and *Plethodon glutinosus* in caves. Natl. Speleol. Soc. Bull. 36:7–10.

Peckarsky, B. L. (ed.). 1990. Freshwater Macroinvertebrates of Northeastern North America. Cornell University Press, Ithaca, New York. 442 pp.

Petranka, J. W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, D.C. 587 pp.

———, and S. M. Murray. 2001. Effectiveness of removal sampling for determining salamander density and biomass: A case study in an Appalachian streamside community. J. Herpetol. 35:36–44.

Powell, R., J. S. Parmerlee Jr., M. A. Rice, and D. D Smith. 1990. Ecological observations of *Hemidactylus brookii haitianus* Meerwarth (Sauria: Gekkonidae) from Hispaniola. Caribb. J. Sci. 26:67–70.

Redmond, W. H. 1980. Notes on the distribution and ecology of the Black Mountain dusky salamander *Desmognathus welteri* Barbour (Amphibia: Plethodontidae) in Tennessee. Brimleyana 4:123–131.

Shipman, P., D. L. Crosswhite, and S. F. Fox. 1999. Diet of the Ouachita dusky salamander (*Desmognathus brimleyorum*) in southeastern Oklahoma. Am. Midl. Nat. 141:398–401.

Sites, J. W., Jr. 1978. The foraging strategy of the dusky salamander, *Desmognathus fuscus* (Amphibia, Urodela, Plethodontidae): an empirical approach to predation theory. J. Herpetol. 12:373–383.

Stone, A., C. W. Sabrosky, W. W. Wirth, R. H. Foote, and J. R. Coulson. 1965. A Catalog of the Diptera of America North of Mexico. United States Department of Agriculture Handbook No. 276. Washington, D.C. 1696 pp.

Tilley, S. G., R. B. Merritt, B. Wu, and R. Highton. 1978. Genetic differentiation in salamanders of the *Desmognathus ochrophaeus* complex (Plethodontidae). Evolution 32:93–111.

Vanni, M. J. 2002. Nutrient cycling by animals in freshwater ecosystems. Annu. Rev. Ecol. Evol. Syst. 33:341–370.

Wagner, D. L. 2005. Caterpillars of Eastern North America: A Guide to Identification and Natural History. Princeton University Press, Princeton, New Jersey. 512 pp.

Weichert, C. K. 1945. Seasonal variation in the mental gland and reproductive organs of the male *Eurycea bislineata*. Copeia 1945:78–84.

Wilder, I. W. 1913. The life history of *Desmognathus fuscus*. Biol. Bull. 24:251–292.