FEEDING HABITS OF SEEPAGE-DWELLING DUSKY SALAMANDERS (DESMOGNATHUS FUSCUS) OF SHORT MOUNTAIN, CANNON COUNTY, TENNESSEE

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ABSTRACT—Salamanders inhabiting splash zones of seepage areas have access to both aquatic and terrestrial prey. Stomach-content analyses of Cannon County dusky salamander populations indicate that postmetamorphic individuals consume a variety of invertebrate prey, and the diet varies with prey seasonal availability and abundance. Of the 958 prey items identified from 100 salamanders, 52% of the prey were aerial insects, 29% aquatic insects and other arthropods, and 19% terrestrial arthropods. The aquatic portion of the diet was greatest during autumn (42%) and early winter (43%) and decreased through early and late spring (31% and 10%, respectively). Although a large body of evidence indicates that desmognathine salamanders feed on aquatic prey, little is known about the mechanism of prey capture for most species, including *D. fuscus*.

Habitat preferences among species of the plethodontid subfamily Desmognathinae are varied, ranging from fully aquatic (Desmognathus marmoratus) and semiaquatic stream-dwelling species (Desmognathus quadramaculatus) to inhabitants of the forest floor (Desmognathus wrighti, Desmognathus aeneus; Hairston, 1984). Although several species of Desmognathus often inhabit the same general area, food resources potentially are partitioned by a species preference for different habitats (Hairston, 1949; Organ 1961; Krzysik, 1976). Such an assumption implies that the postmetamorphic desmognathine feeding system functions efficiently in different habitats, such as underwater or on land. The morphological and functional features associated with this feeding system are considered the most generally adapted for tongue protrusion among plethodontids and are similar among all members of the subfamily (Dalrymple et al., 1985; Dunn, 1926; Larsen and Beneski, 1988; Lombard and Wake, 1976; 1977). Nonetheless, laboratory maintained postmetamorphic Desmognathus of several species (D. quadramaculatus, D. fuscus, and D. ocoee) readily feed both on land and in water (personal observations). Also, several studies indicate that aquatic prey is a routine component of the diet of postmetamorphic desmognathines (Barbour and Lancaster, 1946; Burton, 1976; Davic, 1991; Donovan and Folkerts, 1972; Hamilton, 1932; Hairston, 1949; Keen, 1979; Krzysik, 1976; Sites, 1978).

Information on the diet of *D. fuscus* is well documented. However, in Tennessee such information is limited to the report by Sites (1978) who studied populations from the western Highland Rim in Montgomery County. Sites (1978) reported that *D. fuscus* consumed a variety of prey items and that seasonal shifts in diet occurred. Although aquatic prey formed a relatively small proportion of the diet in these populations, the data are suggestive that Montgomery County populations of *D. fuscus* feed predominantly on terrestrial prey during the late summer and early autumn and shift to aquatic prey during the spring (Petranka, 1998). The purpose of this study was twofold: 1) to characterize the diet of seepage-dwelling populations of the Dusky salamander from

the eastern Highland Rim of middle Tennessee, and 2) to examine seasonal variation regarding use of aquatic and terrestrial food resources.

MATERIALS AND METHODS

One hundred eleven postmetamorphic *D. fuscus* were collected from three seeps located on the southeastern slope of Short Mountain, Cannon County Tennessee from October 1990 to June 1991. Short Mountain, located 35°52′N, 85°58′W, attains a height of 638 meters above sea level and lies within the transitional zone of the Eastern Highland Rim and Cumberland Plateau geographical regions. All three seepage areas of the study were located along an abandoned logging road at an altitude of 550 meters and were created by contact springs (Fetter, 1980) originating in bedrock located above the road.

The relatively small size of the seepage areas prevented us from establishing transects along which salamanders could be systematically collected. Rather, random searches were conducted by overturning rocks, logs and wet leaf litter. An attempt was made to capture all desmognathine salamanders encountered. Captured animals were kept chilled to inhibit digestion, transported to the laboratory and individually anesthetized in a weak solution of tricaine methyl sulfonate (MS222). The stomach contents were obtained using a modified version of a flushing method described by Legler and Sullivan (1979). Anesthetized animals were placed on a dampened towel-lined tray and small diameter tubing was inserted into the stomach via the mouth and esophagus. A syringe attached to the tube was used to pump water into the stomach with sufficient force to expel the contents from the gut onto the tray. Prey items were removed from the tray and preserved in individual vials of 70% ethanol. Fully recovered animals were returned to the seeps at Short Mountain. Gut contents were identified and classified as aquatic, terrestrial, or aerial using Pennak (1953) and Merrit and Cummins (1984).

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RESULTS

The stomachs were either empty or their contents were well-digested and unidentifiable in eleven (11%) salamanders. A total of 958 prey items were identified from the stomachs of 100 *D. fuscus* (Table 1).

Desmognathus fuscus fed predominantly on arthropods (99% of the prey), with insects forming the bulk (87%) of the diet (Table 1). The invertebrate taxa identified in the diet varied among the collection periods and presumably reflect seasonal prey availability. For example, adult plecoptera were not a component of the diet during autumn, but comprised 37% of the diet during the winter collection period. Adult winged diptera and hymenoptera formed substantial proportions of the diet during the early and late spring collection periods, but were a minor component of the diet during autumn (Table 1). Desmognathus fuscus consumed a variety of aquatic prey, which included both neustonic and benthic organisms, indicating that dusky salamanders were able to capture prey from various aquatic zones. The proportion of aquatic prey varied seasonally. Overall, 29% of the prey items were identified as aquatic invertebrates. More than 40% of the prey items from salamanders collected during the early autumn and late winter months consisted of aquatic invertebrates. In contrast, the percentage of aquatic prey in the diet dropped to 30% and 10% during the early spring or late spring months, respectively (Table 1). However, the relatively low percentage of aquatic prey observed during late spring should be viewed with caution; the stomachs were flushed from only six salamanders during early June.

DISCUSSION

Desmognathus fuscus typically inhabits intermediate zones, such as streambanks, springs, and seeps (Hairston, 1949; Organ, 1961) and in this study demonstrated an ability to effectively exploit the resources of the seeps. Desmognathus fuscus is considered a feeding generalist that consumes any available resource in the proper size category (Orser, 1974; Burton, 1976; Sites, 1978; Keen, 1979). Certainly, the diet of D. fuscus at Short Mountain supports this generalist contention. Indeed, the diet of D. fuscus reflects the diversity and seasonally abundant invertebrate fauna found in both the terrestrial and aquatic microhabitats contained within the seeps studied. Considering the different invertebrate communities present at different regions, the diet of D. fuscus at Short Mountain is similar to that reported for conspecifics from seeps at other locales (Pennsylvania-Bennett and Bellis, 1972; New Hamphsire—Burton, 1976; Tennessee—Sites, 1978). At each of these localities the diet of D. fuscus consists predominantly of terrestrial prey, but aquatic invertebrates are a significant proportion of the diet (37, 26, and 14% respectively).

Sites (1978) reported that the diet of dusky salamanders from the western Highland Rim varied seasonally and that aquatic prey formed a relatively small proportion of the diet. His data are suggestive that Montgomery County populations of *D. fuscus* feed predominantly on terrestrial prey during the late summer and early autumn and shift to aquatic prey during the spring (Petranka, 1998). Our data support the contention that the diet of *D. fuscus* varies seasonally, but not that the aquatic proportion is greatest during the spring. Indeed, in the eastern Highland Rim populations studied, the aquatic proportion of the diet was less during the spring sampling period than during the autumn peri-

TABLE 1. Seasonal variation of prey items flushed from the stomachs of 100 *Desmognathus fuscus* from Short Mountain, Cannon County, Tennessee.

Prey	Number of prey items/percentage of total items			
	Oct/		Mar/ Apr $n = 73$	June n = 6
	Nov $n = 13$	Feb $n = 8$		
Amphipoda	02/04		07/01	
Ephemeroptera naiads			14/02	_
Plecoptera naiads	03/06	08/17	41/06	01/01
Hemiptera		_	04/*	01/01
Megaloptera larvae	_			01/01
Trichoptera larvae		01/02	32/04	
Diptera larvae	15/31	11/24	130/18	09/07
Terrestrial prey	22/46	09/20	135/18	08/06
Oligochaeta	01/02	_	01/*	
Pulmonata			01/*	
Phalangida	_	_	03/*	
Acarina		01/02	05/02	01/01
Aranae	04/08	_	09/01	
Isopoda	_	02/04	08/01	01/01
Diplopoda	_		01/*	_
Collembolla	04/08	01/02	42/06	02/02
Diplura	01/02	01/02		
Thysanura			03/*	_
Homoptera		_	03/*	
Coleoptera larvae			03/*	
Coleoptera adults	04/08	01/02	25/03	02/02
Lepidoptera larvae	_	_	14/02	_
Diptera pupae	01/02	_	04/*	01/01
Hymenoptera: wingless	07/15	03/07	13/02	01/01
Aerial prey	06/13	17/37	374/51	107/84
Ephemeroptera adults			03/*	_
Plecoptera adults	_	17/37	86/12	03/02
Diptera adults	04/08	_	70/09	103/81
Hymenoptera: winged		_	205/28	01/01
Unidentifiable items	02/04	_	10/01	
Total prey items	48	46	737	127

^{*} Value is < 0.5%.

ods. We suggest that in association with their opportunistic feeding habits, *D. fuscus* select any available food source. The extent to which aquatic prey is utilized will vary spatially and temporally and is determined by local environmental conditions that control local invertebrate densities and, consequently, availability.

Other desmognathine salamanders that inhabit seepage areas exhibit similar feeding habits. For example, the diet of seepage dwelling *D. monticola* (Hairston, 1949), *D. ochrophaeus* (Hairston, 1949; Keen, 1979) and *D. aeneus* (Donovan and Folkerts, 1972) consist of both aquatic and terrestrial prey. Although the diets of desmognathine salamanders consist largely of terrestrial

prey, the proportion of aquatic organisms composing their diet is significant. The feeding system of the desmognathine salamanders apparently allows them to capture prey both on land and in water—two media that impose distinctly different biophysical constraints on the feeding system.

Until recently, little was known regarding aquatic prey capture mechanisms in transformed plethodontids and, in terms of vertebrate feeding mechanisms, filter and suction feeding were thought to be the primary modes of capturing aquatic prey (Lauder, 1985). Although oropharyngeal suction has not been reported for this group, lingual projection, typically thought of as a terrestrial mode of prey capture, is utilized by *Desmognathus marmoratus* feeding in water (Schwenk and Wake, 1988). Evidence presented here and by others (Hairston, 1949; Burton, 1976; Davic, 1991) indicate that species of the genus *Desmognathus*, including *D. fuscus*, capture benthic prey, but little is known regarding how these prey are captured in nature.

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