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A Study on the Life History and Seasonal Foraging Habits of the Salamander Desmognathus quadramaculatus Holbrook, in WV

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A Study on the Life History and Seasonal Foraging Habits of the Salamander Desmognathus quadramaculatus Holbrook, in WV.

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ABSTRACT

A study was conducted on Desmognathus quadramaculatus in the northern periphery of its range with some aspects of its life history, surface density, and seasonal foraging habits. The results in this study are compared to studies done on D. quadramaculatus in the southern portion of its range.

Female D. quadramaculatus have been found tending egg clutches from June to September in the southern portion of its range and data collected in this study shows that egg deposition also occurs during this period in the northern population. Female size (SVL) at which D. quadramaculatus reach sexual maturity ranged from 57.6- 77.5 mm in the northern population where sexually mature females females were found to have SVL of 73-75 mm in the southern portion of the range.

Larval period and size class composition in the northern population also appeared to differ from studies done on southern populations. The smallest D. quadramaculatus found in the northern population had a SVL of 12.1 mm, whereas in the southern populations, it was 16 mm. Metamorphosis occurred anywhere from two, three, or even four years depending on the elevation and population studied. Other investigators estimated a 34-35 month larval period with some of the larvae having a fourth year. In this study, I found five size classes of larvae which indicated a 54-60 month larval period.

Substrate utilization was examined for D. quadramaculatus and D. monticola. Post-metamorphic D. monticola were almost entirely found foraging terrestrially. Post-metamorphic D. quadramaculatus were found foraging above the water surface 97.5% in June, 72.7% in July, 50.0% in August, and 40.0% in September. From October to April the post-metamorphic D. quadramaculatus foraged below the water surface.

Larval dipterans were found to be the most abundant invertebrate taxa and made up the largest percentage of the overall diet and occurred in the most stomachs of D. quadramaculatus. The diet of pre-metamorphic salamanders was made up of predominantly aquatic invertebrate taxa throughout the year while the post-metamorphic diet varied by season and contained large portions of terrestrial invertebrate taxa.

INTRODUCTION

In the last several decades, there has been a growing concern about the loss of amphibian species on a worldwide scale. Declines in populations or the extinction of species is mostly attributed to the destruction of habitats. Animals that can exist only in narrow environmental parameters (pristine conditions) are at most risk of being lost when the environment is altered.

Burton and Likens (1975) estimated that there were approximately 2,950 salamanders per hectare in New Hampshire. They also determined that salamanders made up twice the biomass of birds and equal to the biomass of small mammals. The great number of salamanders and the large percentage of biomass they represent indicate the importance of salamanders in forest and aquatic ecosystems.

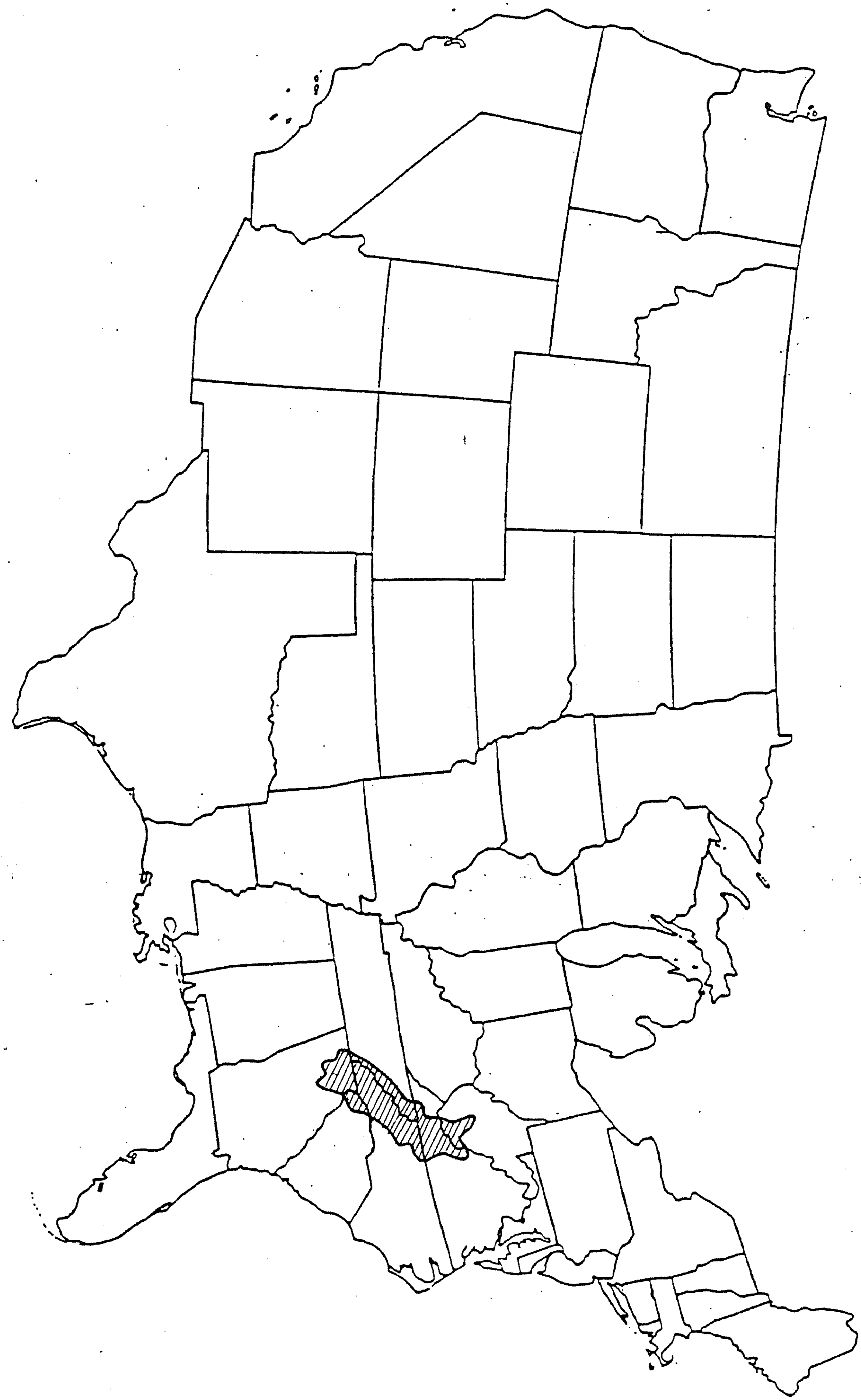
Salamanders, like most amphibians, are highly susceptible to environmental shifts due to their physiological requirements. Drastic environmental changes in pH, temperature, and moisture content can eradicate whole populations of amphibians. There are many species of salamanders that have widespread ranges and are found commonly throughout their range which demonstrates their ability to adapt to varying habitat conditions. However, there are some species that have limited ranges because of narrow habitat requirements. These animals are in the greatest peril of extinction due to man's activities.

The black-bellied salamander, Desmognathus quadramaculatus, is an example of an animal with a narrow range due to its environmental requirements. Desmognathus quadramaculatus is only found in high grade mountain streams that are covered by a dense deciduous or mixed canopy (Conant 1975; Organ 1961). Its range extends from south central West Virginia to Georgia, including the mountainous areas of western North and South Carolina, Virginia, and eastern Tennessee (Figure 1) (Conant 1975).

Desmognathus quadramaculatus belongs to the family Plethodontidae, lungless salamanders which respire by cutanial and bucocutanial absorption. Desmognathans must remain completely moist to achieve respiration at sufficient rates. This factor restricts areas which they can inhabit and also their seasonal and daily activity periods.

Hairston (1949) stated that D. quadramaculatus, D. monticola, D. fuscus, and D. ochrophaeus form the aquatic to terrestrial ecological and evolutionary series. Desmognathus quadramaculatus is the largest, most aquatic, and the most primitive while D. ochrophaeus is the smallest, most terrestrial, and furthest advanced of the three desmognathans mentioned above (Hairston 1949; Organ 1961; Conant 1975). This assemblage of salamanders was originally interpreted as a result of exploitative competition and niche partitioning (Hairston 1949). Hairston (1986) hypothesized the streamside guild structure was determined by predation interaction with the largest species, D. quadramaculatus, preying upon the smaller members of the genus. The result is a community of streamside species that exhibits a correlation between adult body

Figure 1. The known range of *Desmognathus quadramaculatus* in the United States (Conant 1975).



size and habitat use (Hairston 1986; Roudebush and Taylor 1987).

The purpose of this present study was to examine size classes, seasonal movements, diet, and reproductive periods of D. quadramaculatus in the northern most extent of its range and compare these findings with other studies.

Species Description

Blackbelly salamanders are robust and measure 10-20 cm (4-8in) in length and possess a characteristic black venter and a sharply keeled tail (Green and Pauley 1987). The dorsal surface of larger adults is brown to black but smaller adults or juveniles may have greenish or light brown dorsal blotches. Larval stages are also robust and have the distinctively keeled tail, but lack the characteristic black venter. The dorsal surface of the larva is marked with a double row of small dots beginning behind the head and extending above the hind legs (Green and Pauley 1987). The venter turns black around the time of metamorphosis.

Description of Study Site

The study site was located in a no name first order tributary of the New River approximately 0.9 miles North on ST. RT.41 from the town of Prince, WV in Fayette County. The stream consists of a series of cascades and plunge pools with small areas of riffles at the end of the pools (Figure 2). The study was conducted in a 100 m stretch of the stream. The entire length of the stream is covered by a moderate growth, dense, deciduous forest with the exception of a powerline in the lead waters of the watershed. The watershed contained coal stripmines on both facing slopes. The elevation

Figure 2. Study site from tansect one looking upstream toward transect 10.

ranges from 549 to 605 m.

Geomorphology of the Region

The New River starts in Blowing Rocks, North Carolina and ends when it meets the Gauley River in West Virginia where it becomes the Kanawha River. The geographical range of D.quadramaculatus follows the New River north inhabiting first to third order tributaries. The New River Gorge area is in the east-central part of the Appalachian basin where it is deeply entrenched in varied rock formations of late Mississippian to Middle Pennsylvanian age (Englund et al. 1982). The limestone basin of the New River Gorge gives the watershed a basic pH integrity.

The outcrops of resistant sandstone have maintained the New River in a narrow trench as it has eroded the plateau over the ages. This fact set the stage for the creation of high grade streams that flow off the plateau into the gorge. These streams form a series of spectacular waterfalls and cascades as the water makes its way to the river.

CHAPTER I

Life History and Surface Density of *Desmognathus quadramaculatus*

Introducion

A major contention of life history is that traits that determine life of an organism are "co-adapted and designed by natural selection to solve a particular ecological problem"(Stearns 1976). Berven and Gill (1983) implied that life history traits are genetically dictated and that they evolve under the influence of demographic selection. Bruce (1972) stated any feature of the life cycle evolved through natural selection is expected to contribute to the maximization of individual reproductive success. Bruce (1972) also suggested that selective pressures for life-cycle strategies vary with the habitat requirements of the organism and with the several components of its environment. Williams (1966) suggested selection of a life-cycle strategy as the achievement of an optimum balance of allocation of resources between immediate and future reproductive interests. Gadgil and Bossert (1970) determined the life history was the outcome of competition for available time and energy among the processes of maintenance, growth, and reproduction. In Chapter I, I discuss egg development, larval size classes, and sexual maturity of *D. quadramaculatus* in the northern periphery of its range and compare the findings to studies done in the southern portions.

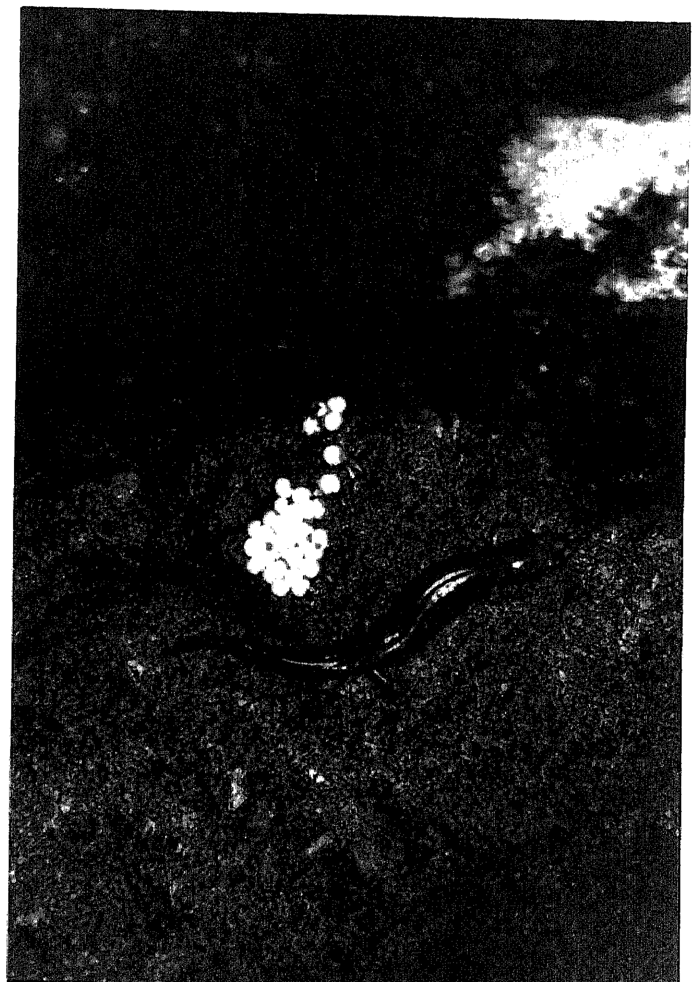
Egg Deposition

Organ (1961) found seven D. quadramaculatus egg clutches between June and September in southwestern Virginia at elevations between 1036 and 1524 m. The clutches were all attached on the underside of rocks embedded 15-30 cm in the streambed and were often associated with cascades (Organ 1961). Austin and Camp (1992) found egg clutches in May and hatchling larvae in July in the southern-most extent of the range in Georgia. Pauley (pers. comm.) found a single clutch of eggs in July in West Virginia in the northern-most extent of its range (Figure 3).

Materials and Methods

The reproductive period of D. quadramaculatus was determined by observation of egg clutches in the field or the measurement of egg volumes from preserved specimens. Gravid females were obtained from the West Virginia Biological Survey at Marshall University and from field collections over a period of a year from the study site described in the Introdunction. Females were killed in chlorotone upon capture, fixed in 10% formalin solution for two weeks, placed in water for one week, and then preserved in 70% ethyl alcohol. Specimens were kept in alcohol for at least two weeks before the ovaries were removed. Ovarian fat and extra tissue were carefully removed and total egg count was recorded per ovary. The entire ovary was then submerged in a 10 ml graduated volumetric flask and the displaced water was removed using a 10 ml syringe. The syringe reading was recorded

Figure 3. Female <u>Desmognathus quadramaculatus</u> found tending a clutch of eggs. Photo by Dr. T.K. Pauley.



in milliliters and individual egg volumes were calculated by taking the total number of eggs divided by the total volume displaced. When egg numbers could not be assessed due to immature sizes of eggs, salamanders were recorded as nongravid.

Results

In this study, 147 post-metamorphic females were examined and 33 of these were gravid (Table 1). Egg volumes of gravid females were measured in an attempt to estimate egg deposition. In January, two gravid females were collected and had mean egg volumes of 0.0021 ml and 0.0014 ml. In May, seven gravid females were collected and had mean egg volumes ranging from 0.0010-0.0186 ml. In June, nine gravid females were collected and had egg volumes ranging from 0.0033-0.0194 ml. In July, nine gravid females were examined and had mean egg volumes ranging from 0.0006-0.0102 ml. In August, three gravid salamanders were examined having a mean egg volume of 0.0037-0.0124 ml. In September, one gravid female was captured and had a mean egg volume of 0.0025 ml. In October, one gravid female was examined and had a mean egg volume of 0.0078 ml.

Table 1. Egg data from 33 *Desmognathus quadramaculatus* gravid females.

Date Collected	SVL (mm)	Egg No. Right Ovary	Egg Volume Right Ovary (ml)	Egg No. Left Ovary	Egg Volume Left Ovary (ml)	Total Egg Number	Total Egg Volume (ml)	Mean Egg Volume (ml)
1/29/93	75.2	18	0.04	21	0.04	39	0.08	0.0021
1/29/93	66.9	18	0.03	18	0.02	36	0.05	0.0014
2/28/93	69.5	21	0.06	25	0.06	46	0.12	0.0026
5/13/92	74.1	27	0.41	29	0.44	56	0.85	0.0152
5/13/91	71.1	24	0.48	27	0.47	51	0.95	0.0186
5/14/92	68.1	26	0.03	27	0.02	53	0.05	0.0009
5/14/91	64.2	24	0.10	26	0.12	50	0.22	0.0044
5/30/93	72.4	30	0.12	25	0.09	55	0.21	0.0038
5/30/93	77.5	25	0.42	28	0.48	53	0.90	0.0170
5/30/93	67.3	21	0.10	23	0.09	44	0.19	0.0043
6/12/91	70.9	21	0.07	22	0.07	43	0.14	0.0033
6/24/62	57.6	17	0.02	19	0.03	36	0.05	0.0014
6/24/62	67.4	15	0.23	12	0.24	27	0.47	0.0174
6/24/62	60.0	15	0.06	10	0.11	33	0.17	0.0052
6/24/62	68.0	21	0.30	19	0.27	40	0.57	0.0143
6/30/92	67.1	24	0.34	21	0.27	45	0.61	0.0136
6/30/92	66.6	25	0.42	16	0.29	41	0.71	0.0173
6/30/92	69.4	25	0.45	21	0.44	46	0.89	0.0194
6/30/92	63.5	21	0.22	23	0.20	44	0.42	0.0096
7/7/62	67.4	18	0.05	15	0.03	33	0.08	0.0024
7/9/91	64.9	25	0.09	20	0.08	55	0.17	0.0039
7/10/91	67.7	27	0.28	27	0.27	54	0.55	0.0102
7/15/91	66.4	26	0.16	29	0.17	55	0.33	0.0060
7/15/91	58.5	22	0.01	26	0.02	48	0.03	0.0006
7/16/91	71.3	38	0.33	29	0.25	67	0.58	0.0087
7/17/91	70.2	31	0.15	37	0.17	68	0.32	0.0047
7/25/92	64.9	22	0.07	22	0.07	44	0.14	0.0032
7/29/92	60.7	21	0.04	20	0.04	41	0.08	0.0020
8/29/92	67.5	23	0.30	27	0.32	50	0.62	0.0124
8/29/92	65.3	23	0.18	27	0.22	50	0.40	0.0080
8/29/92	67.1	14	0.05	16	0.06	30	0.11	0.0037
9/19/92	66.8	11	0.03	13	0.03	24	0.06	0.0025
10/31/92	73.0	32	0.26	39	0.30	71	0.56	0.0070

Discussion

Desmognathus quadramaculatus egg clutches have been found from June to September in previous studies. There are no discernable mean egg volume trends observed in this study perhaps due to the extended period of egg deposition. Another hypothesis may be that D. quadramaculatus only deposits a clutch of eggs every other year or as energy constraints allow. The production of ova is a considerable energy requirement and females may carry ova for an extended period until proper yolk volume is present. This is imperative for the first growth of larval salamanders and overall survival.

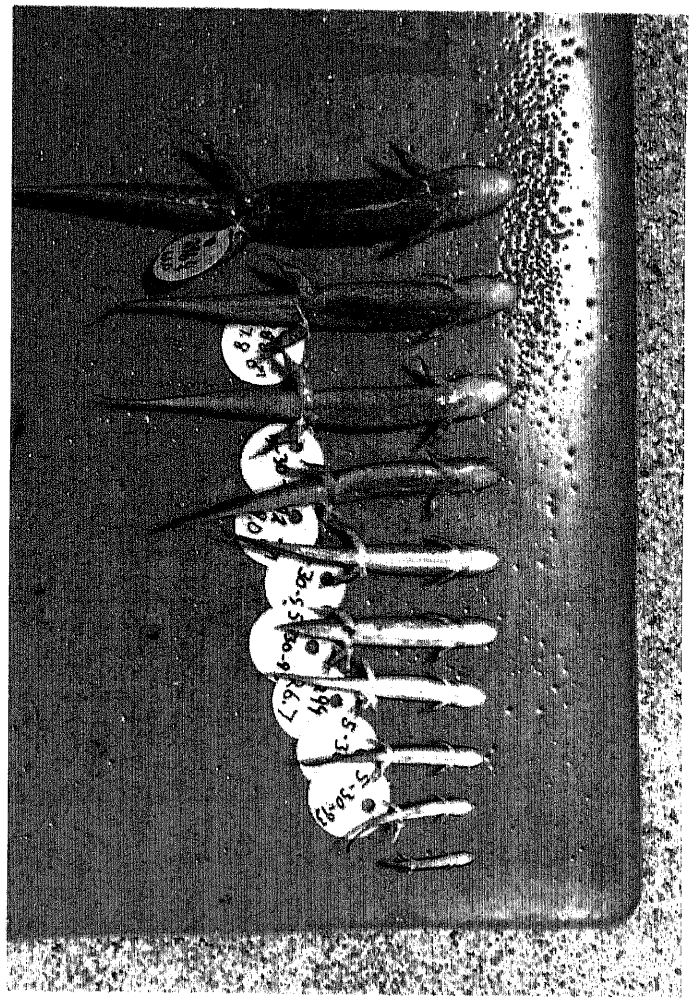
Larval Period

Environmental differences among localities account for a major portion of the observed variation in larval development (Berven and Gill 1983). Elevation can have a great effect on geographic variation in larval development of amphibians (Austin and Camp 1992). Sexton and Bizer (1978) proposed a temperature-controlled growth rate model that predicts longer larval periods and larger sizes at metamorphosis in populations that inhabit cooler thermal conditions. Juterbock (1990) pointed out that these predictions are not supported by studies of stream-dwelling salamanders and suggests that specific timing of resource availability may interact with temperature to complicate variations, especially when thermal differentials are relatively small and when individuals within a population may have alternative life histories. Breven and Gill (1983) found wood frog larvae from mountain sites had shorter larval periods than those from lowland sites and were morphologically larger at metamorphosis. A significant portion of observed variation in larval period length and larval body size among geographically separated populations is due to genetic determination (Berven and Gill 1983). Berven and Gill (1983) stated that larval patterns are locally adaptive and reflect differential selection pressures unique to each environment. Body size at metamorphosis is a result of the relative balance between growth rates and differentiation rates which, in turn, are a result of the prevailing environment such as temperature, density, and food availability (Smith-Gill and Berven 1979). High temperatures accelerate differentiation rates to a greater degree than they do growth rates, resulting in a shorter larval period and small body size, while differentiation rates at low temperatures are slowed relative to growth, resulting in prolonged larval period and relatively larger metamorphosis size (Berven and Gill 1983). Generally, fitness traits should have low levels of additive genetic variance (expression minimal compared to environmental influences), (Berven and Gill 1983).

The fact that D. quadramaculatus is found from West Virginia to Georgia and at a wide range of altitudes suggests that the larval periods vary greatly. They found D. quadramaculatus hatchlings with a SVL of 16 mm in July. Austin and Camp (1992) found no difference in male and female metamorphosis periods. Organ (1961) reported a two year larval period for D. quadramaculatus in populations from an elevational range of 900-1500 m in western Virginia. Bruce (1985b, 1988) reported both three and four-year larval periods in western North Carolina from sites ranging from 760-1200 m in elevation. In the southern-most extent of the range of D. quadramaculatus, Austin and Camp (1992) examined two populations. One population, found at 300 m of elevation was determined to have three larval size classes. They found hatchling larvae appearing during July with a SVL of 16 mm, while metamorphosing individuals were found in May and June, indicating a larval period of 34-35 months. The metamorphosing individuals had SVLs of 40-43 mm. The other population had a higher elevation (830 m) and was found to have a 4 year larval period with the mean metamorphosis of 54 mm. Although the study was conducted during the same time period, the higher elevation averaged 3.3°C lower in water temperature. Austin and Camp (1992) stated that the longer larval life and larger size at metamorphosis in cooler streams fit the predictions of Sexton and Bizer (1978). However, Austin and Camp (1992) stated that populations over a larger geographical and elevational range were considered, the variation in larval period and size at transformation in D. quadramaculatus did not meet these predictions.

Pre-metamorphic or larval blackbelly salamanders possess external gills and lack ventral pigmentation characteristic of the post-metamorphic blackbelly salamanders (Figure 4). Metamorphosis of the blackbelly salamander is characterized by the loss of external gills, a more terrestrial life, and the gradual pigmentation of the venter.

Figure 4. May collection of <u>Desmognathus</u> <u>quadramaculatus</u> from the study site. The collection demonstrates size varation within the population.



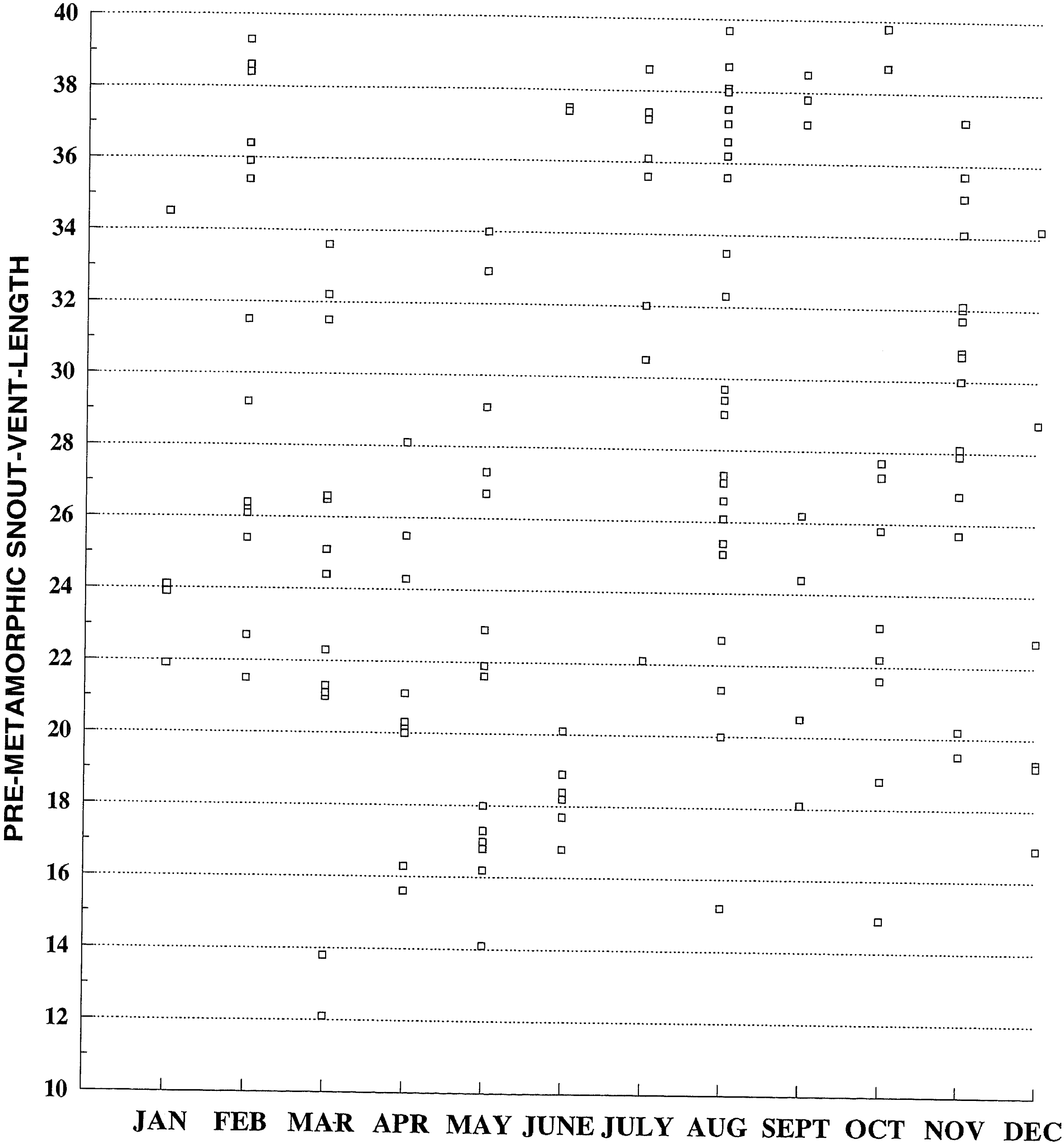
Materials and Methods

Specimens of blackbelly salamander were obtained from the West Virginia Biological Survey and supplemented by monthly collections for one year from my study site. They were killed in chlorotone upon capture, fixed in 10% formalin solution for two weeks, placed in water for one week, and then preserved in 70% ethyl alcohol. Morphological measurements including SVL(tip of the snout to the anterior portion of the cloaca) and headwidth (measurement of the head behind the eye and in front of the jaw musculature) were used in an attempt to track monthly growth and determine size classes.

Results

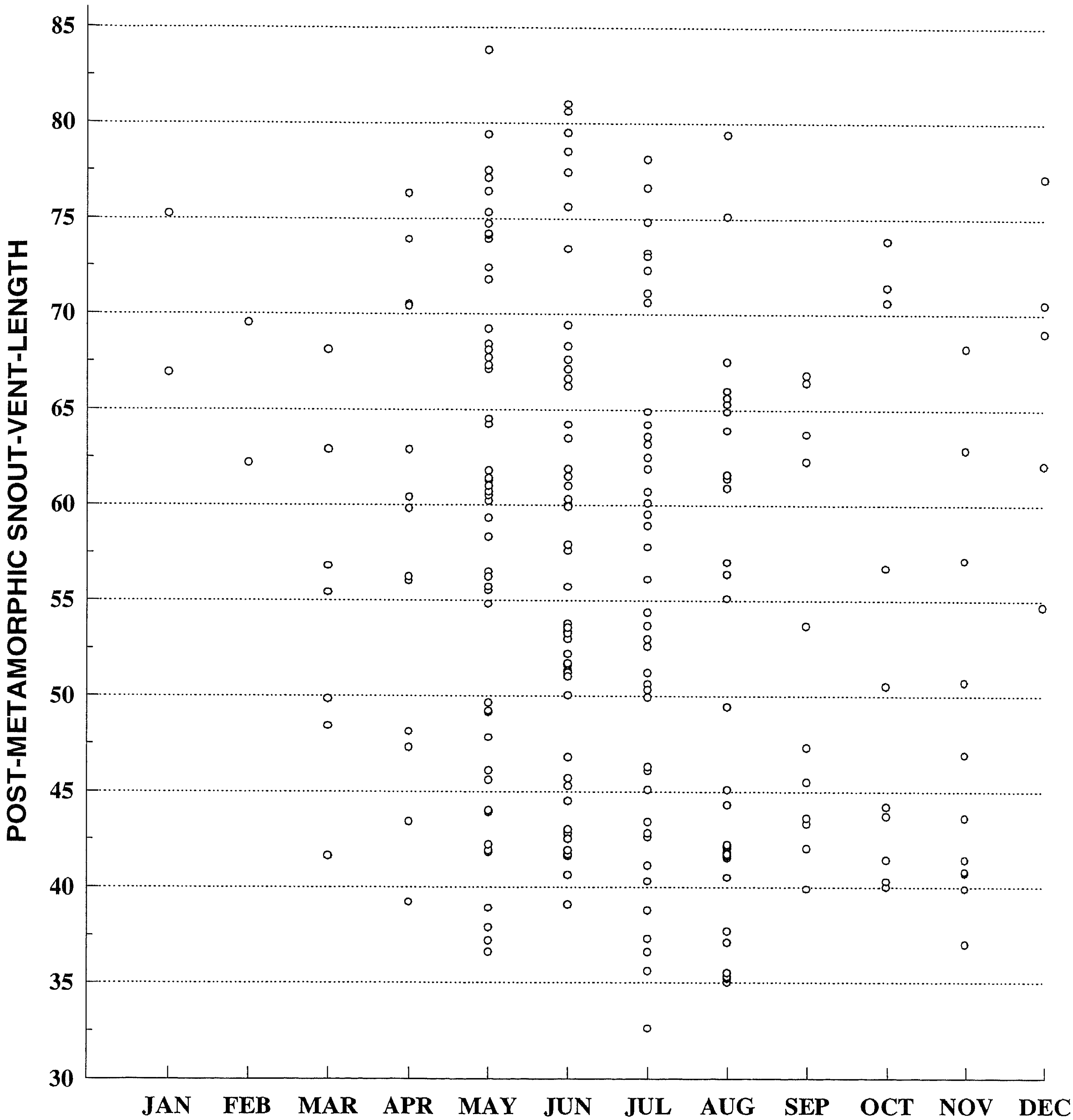
Larvae or pre-metamorphic individuals of D. quadramaculatus had a size range from 12.1 to 39.3 mm (Figures 5-6). Smallest individuals were more abundant in March. Small larvae captured had already absorbed the greatest proportion of the yolk sac and taken on the typical larval morphology for this species. Desmognathus quadramaculatus larval growth rate and size classes were charted using a scatter plot graph of their SVL versus month captured. In one calendar year from the estimated hatching period or second size class, larvae had a SVL of 14-16 mm. Larvae that comprised the third size class were more difficult to identify due to the extended time period in which the animals could have possibly hatched and the foraging success of the individual which directly affects the rate of growth. In the third calendar year from the time of hatching, larvae had SVLs ranging from 17-23 mm. They also started a rapid growth period which may be due to their

Figure 5. Snout-Vent-Length of pre-metamorphic *Desmognathus quadramaculatus* measured in milimeters versus month of capture.



PRE-METAMORPHIC SNOUT-VENT-LENGTH
40
38
36
34
32
30
28
26
24
22
20
18
16
14
12
10
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC

Figure 6. Snout-Vent-Length of post-metamorphic *D. quadramaculatus* versus month of capture.



POST-METAMORPHIC SNOUT-VENT-LENGTH
85
80
75
70
65
60
55
50
45
40
35
30
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC

larger head width that enables them to utilize a wider prey size and selection. The fourth year class had a greater size dispersal with animals ranging from 25-34 mm. Some metamorphosis may occur in this age group since a post-metamorphic individual with SVL of 32.6 mm was found. The fifth size class was made up of larvae with a SVL of 35-40 mm. These animals metamorphosed in the following spring, summer, or fall with a SVL of 35-39 mm. The SVL of pre-metamorphic and post-metamorphic individuals overlap extensively in this size range.

Discussion

Desmognathus quadramaculatus has a distinctively different larval size class composition in the northern-most extent of its range compared to its southern-most extent. Austin and Camp (1992) found newly hatched larvae in July with SVL of 16 mm and estimated metamorphosis at 34-35 months after finding post-metamorphic juveniles with SVL of 40.2 mm in the same population in Georgia. However, they also found populations of D. quadramaculatus in higher elevations in Georgia with four larval size classes and the largest pre-metamorphic individuals with SVL of 43.8 mm.

Bruce (1988) explored D. quadramaculatus size classes in North Carolina at three different elevations; Highlands Biological Station at 1170-1200 m, Wolf Creek at 975-1150 m, and Coweeta at 870-930 m. At the Highlands stream site, he found hatchlings SVL of approximately 15mm in September and April of the following year. Bruce (1988) found growth rates during the first year to be apparently slow, with the larvae increasing from

15-16 mm to 20-24 mm one year later. He noticed specimens from Coweeta and Highlands had a 4th year larval class that with SVL of 37-45 mm and Wolf Creek had only three size classes of larvae. However, Bruce (1988) found that post-metamorphic individuals measured 35-37 mm SVL at Highlands and Coweeta which indicated some metamorphosis had taken place in the third-year. He also noted Wolf Creek had fewer third-year larvae and a greater number of post-metamorphic salamanders that overlapped in SVL with the third-year larvae which had the smallest post-metamorphic salamanders SVL at 30 mm. This indicates some metamorphism occurred in the second year or early in the third year of life. Bruce (1988) summarized by saying, "based on the variation observed in three adjacent populations in this study, there is probably pronounced variation in length of larval period and metamorphic size among southern Appalachian populations of D. quadramaculatus."

In my study, the smallest SVL, 12.1 mm, was found in March. This individual had absorbed its yolk and its ventral surface was white. This indicated a smaller larval size class than was noted by Austin and Camp (1992) or by Bruce (1988). The pre-metamorphic period was perceived to be between 54-60 months and contained five size classes. Austin and Camp (1992) found metamorphosing individuals in May and June with a mean SVL of 40.2 mm. Bruce (1988) found pre- and post-metamorphic individuals SVL overlapping between 37-45 mm. I found the largest pre-metamorphic individual in October at 39.7 mm which falls into the size range Austin and Camp (1992) found at the Nancy Town Creek Site and

Bruce (1988) found at the Highland and Coweeta sites. A post-metamorphic individual was found with a SVL of 32.6 mm which may lend credence to some fourth-year larvae. The overall larger larval size at hatching and rapid growth rate of the southern D.quadramaculatus larvae may be attributed to geographic genetic variation, mean water temperature, or greater prey availability for extended periods of the year. Bruce (1985b) found larval growth rates to be slow in D. quadramaculatus which strengthens the concept of plethodontids as slow-growing, slow-developing amphibians.

Sexual Maturity

The developmental pattern of plethodontid salamanders puts adaptive emphasis on survivorship rather than reproduction, in response to the cool moist microclimates of the Appalachian mountains where they probably evolved (Feder 1983). This means an extended period of maturation and a long life occurs rather than a quick maturation and a short life. Bruce (1993) and Tilley (1968) agree that the age at first reproduction is positively correlated with adult body size in the genus Desmognathus. Desmognathus quadramaculatus, the largest desmognathan and thought to be the most primitive, has the longest larval period and the greatest age before becoming sexually mature (Bruce 1988). This is contrasted by the smaller and more terrestrial D. ochrophaeus, thought to be one of the more evolutionarily advanced desmognathans and to have the shortest larval period and quickest maturation time. Desmognathans are ectothermic and also require high relative humidity; as a result, periods of active foraging are controlled in part by climatic conditions. Within the geographic range of a species, body size and life history may greatly vary due to the climatic control over foraging periods or evolutionary genetic variation. Egg production is a considerable energy sink for female plethodontid salamanders and is regulated by resource availability and environmental factors. Tilley (1968) found in the genus Desmognathus that fecundity was intimately related to body size, both within and between species. He also established that selection is able to increase fecundity only by increasing body size, and that high fecundities are selectively advantageous in aquatic habitats. Desmognathus fuscus, from southwestern Virginia, was found to lay more eggs than those from Ohio which was attributed to their larger average size (Tilley 1968). Tilley (1968) surmised that D. fuscus larger size is an adaptation directed toward increased fecundity.

Bruce (1988) found D. quadramaculatus females to become sexually mature at seven years of age and at a SVL of 73-75mm (measured at the posterior portion of the cloaca). He conducted his study in North Carolina where he examined three sites ranging in elevations from 200 to 1200 m. It is the goal of my study to compare estimated age and size of maturation of female D. quadramaculatus in the northern-most extent of its range to those in the southern portions of its range.

Materials and Methods

Specimens were obtained from the West Virginia Biological Survey and supplemented by monthly collections for one year from the site previously described in West Virginia. Those that were collected were killed in chlorotone upon capture, fixed in 10% formalin solution for two weeks, placed in water for one week, and preserved in 70% ethyl alcohol. Sexual maturity in females was determined by the presence of eggs in the ovaries. Snout-vent length was measured from the tip of the snout to the anterior portion of the cloaca.

Results

The smallest gravid female examined had a SVL of 57.6 mm and the largest had a SVL of 77.5 mm (Table 1). The mean SVL, determined from the 33 gravid females, was 67.4 mm.

Discussion

There are distinct differences in the sizes at which female D. quadramaculatus become mature. Bruce (1988) found the smallest sexually mature females had a SVL of 73-75 mm, which is larger than the mean SVL (67.4 mm) of gravid females found in West Virginia. However, he measured SVL at the posterior portion of the cloaca, while I measured the SVL at the anterior portion of the cloaca. This would make a difference of about 2-3 mm in the SVL measurement. The smallest gravid female from this study had a SVL of 57.6 mm and the largest had a SVL of 77.5 mm.

Post-metamorphic individuals can be found with SVL measurements as small as 32.6 mm, but metamorphosis usually occurs in animals with SVLs ranging between 35-40 mm. Presuming that there is continued rapid growth after metamorphosis until maturation, it would take two to three years after metamorphosis to achieve the SVL of gravid females. This would result in a seven to eight year period from hatching to sexual maturity for female D. quadramaculatus.

CHAPTER II

Surface Density and Dispersal Mechanisms for *Desmognathus quadramaculatus*

Introduction

Home range is the area traversed by an animal during its normal daily activities (Barbour et al. 1969). However, the home range of an animal may change with the season (environmental conditions), energy demand (foraging), or during reproductive periods. Barbour et al.(1969) found home ranges in terrestrial salamanders were greatly affected by environmental stresses. Home range can best be determined by the long term observation and tracking of single individuals within a population for long periods of time. Observation of each individual should be accomplished with as little impact on the species' daily activity as possible. Ashton (1975) and Ashton and Ashton (1978) tagged *D. fuscus* and *Eurycea bislineata* subcutaneously with Co^{60} and tracked them throughout the year using a Geiger Counter. The radioactive tracking enabled him to find salamanders that had been previously marked even when they were not foraging on the surface (Ashton 1975). Modern biologists can monitor an individual in a population without disrupting its daily activities by a onetime attachment of a transmitter or microchip. However, this technology is expensive and most herpetologists use the toe clip method to identify individual salamanders within a population. This is done by placing the salamander venter up and designating the right hind foot as the tens and the left as the ones. The thumb is the number 10 position on the right and the number one position on the left. The remaining digits provide consecutive tens (20, 30, 40) on the right foot and ones (2, 3, 4) on the left foot. This method causes disruption in the animal's activity and habitat due to the constant search, capture, and handling required. Handling of salamanders removes the slime layer that acts as a protective seal from the outside environment and could leave the animal susceptible to bacterial or fungal infection.

Population structure and density of plethodontid salamanders along a streambed have been found to be influenced by environmental parameters, resource availability, migration, and by both intraspecific and interspecific competition (Bruce 1985; Stewart and Bellis 1970; Jaeger 1971; Formanowicz and Brodie,Jr. 1993; Jaeger and Gerits 1979; Keen 1982; Southerland 1986a,b,c). In the genus Desmognathus, there is a correlation between adult body size and habitat use, with larger species in a given geographic area occupying aquatic habitats (Beachy 1993). Hairston (1986) found that predation of the larger species of desmognathans on smaller members determined habitat partitioning. Southerland (1986a) found D. monticola was farther from water in streams that were inhabited by larger D. quadramaculatus. Beachy (1993) found larval cannibalism of first-year D. quardramaculatus by larger D. quadramaculatus is as frequent as their predation on other larval salamanders. He also stated that predation, not competition, was the important factor that served as a regulatory mechanism on stream-dwelling plethodontids.

Competition for substrate is also a determining factor in stream salamander guilds. Krzysik (1979) determined the plethodontid streamside community was governed by substrate size, frequency, quality, and the presence of interfering competitors. Keen (1985) stated that D. quadramaculatus restriction to a streambed microhabitat compared with the much more variable microhabitat selection of D. monticola resulted in spatial separation. He noticed D. fuscus altered its utilization of the physical habitat when influenced by the presence of D. monticola. Brandon and Huheey (1971) studied the spatial distributions and movements of D. quadramaculatus and D. monticola and concluded that substrate competition rather than predation was the partitioning factor. In a substrate-moisture experiment, Keen (1985) found D. monticola and D. quadramaculatus had the same preference for high moisture substrate. He suggested that selection of coarse substrates and large cover objects are behavioral characteristics that have evolved for predator avoidance as well as moisture retention.

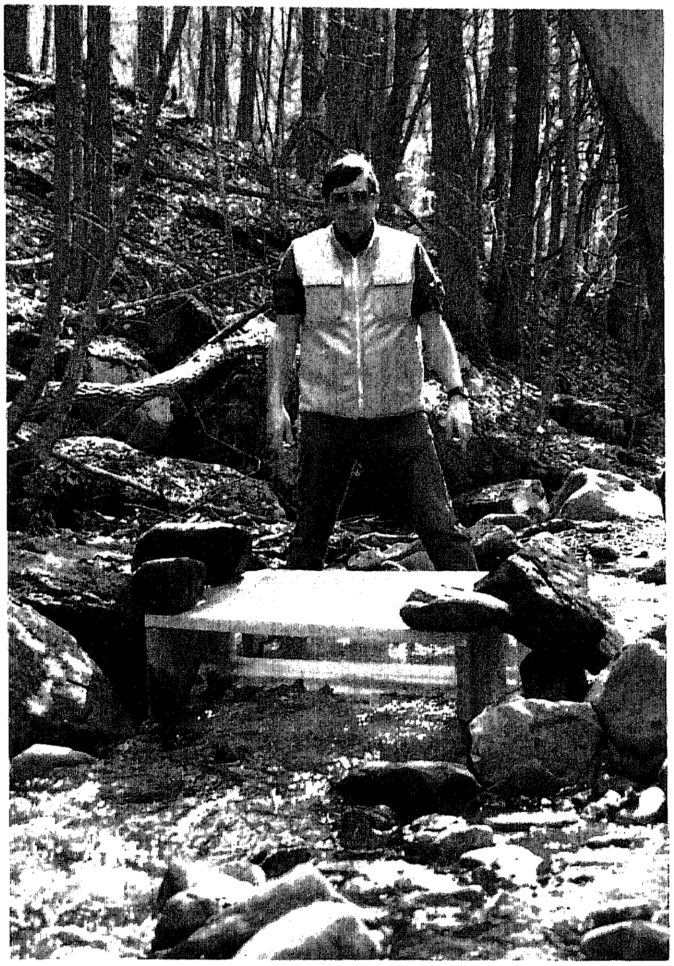
Materials and Methods

A 100 m section of stream at the study site was divided into ten quadrats at ecological habitat breaks i.e. cascades. Post-metamorphic individuals were captured by hand and with a net within the bankful zone, the area of the stream that is free of all vegetation and detritus due to the scouring affects of high water. This area entailed approximately 0.5 to 1.0 m from the edge of the stream. Collection of animals was restricted to bank full width area so that the main emphasis could be put on _D. quadramaculatus_ which rarely can be found more than a meter from the edge of the stream. Salamanders were toe clipped from June to September. Snout-vent length was measured by pressing the venter of the salamander against a clear metric ruler so that the tip of its snout was at the beginning of the calibrated portion of the metric scale. The salamander was then extended parallel to the ruler, and the anterior portion of the cloaca was observed through the ruler. The head width was taken by pressing the venter portion of the head of the salamander perpendicular to the ruler and measuring jaw width behind the eyes.

Each microhabitat was individually assessed by substrate type, substrate size, and quadrat found. Substrate type was recorded as either terrestrial or aquatic. Substrate size was recorded by grouping rock sizes in an arbitrary scale of one to four. Rock size one was approximately 15 cm^2 and rock size two 30 cm^2. Rock size three was approximately 45 cm^2 and rock size four included all rocks larger than rock size three rocks or rocks too large to be moved. Care was taken to replace the disturbed substrate in its original position. Captured individuals were returned to the original microhabitat once it was restored.

Adult migration and larval salamander population dispersal were assessed by using salamander traps (Figure 7). The salamander traps were a meter wide, a meter long, and 0.5 m high and covered with aluminum screen with the exception of one end that had an incline of 120° and was attached 18 inches from the front of the trap. One trap was placed at the end of the

Figure 7. Downstream migration trap in place at study site to monitor larval drift.



downstream portion of the study area with the open end facing up stream in an attempt to capture larvae being dispersed by stream drift. The other trap was placed at the end of the upstream reach with the open end facing down in an attempt to document any migration. The idea of stream drift and monitoring it by salamander traps was taken from a study by Bruce (1985b).

Results

The study site was visited once in June, twice in July, and once in both August and September. A total of 64 D. quadramaculatus and 25 D. monticola were captured, toe clipped, and released. In this period, seven D. quadramaculatus and one D. monticola were recaptured. In the June collection, only one (12.5%) of eight D. quadramaculatus captured was found foraging in the water. The three D. monticola captured in June were all found foraging terrestrially. In the June visit, an attempt to capture and release, without significantly altering the streams habitat, reduced the capture success rate and is reflected by the low numbers captured. In July, capture success rates were increased by using dipnets and a seine. In the first visit in July, 11 D. quadramaculatus and eight D. moticola were captured, examined and released. One D. quadramaculatus and one D. monticola were recaptured from the previous visit. In both cases, there was no movement from the previous capture site. Desmognathus quadramaculatus was found foraging on land 72.7% or eight of the 11 salamanders where D. monticola was found foraging 100% on land. In the second visit, five D. quadramaculatus and one D. monticola were examined with no recaptures. All species were found above the water surface. In August, 26 D. quadramaculatus and one D. monticola were found. Of these, four D. quadramaculatus were recaptures. The salamander designated as number three, which had been recaptured in the first visit in June, was recaptured a second time. However, it had moved from quadrat one to quadrat eight which encompasses approximately 80 meters up stream. The salamander designated as number 16 was found in quadrat four and was originally found at quadrat one on the first visit in July. The salamander designated as number seven, which was originally caught in June at quadrat five, was recaptured in August at quadrat three. Of the four salamanders recaptured in August, three had moved from their original positions. Of the D. quadramaculatus captured, 13 (50.0%) of 26 were found foraging above the surface of the water. The one D. monticola captured was found on land. The last visit, during which salamanders were toe clipped, was September 28-29. Salamanders were captured in the daylight hours of the 28th and throughout the night on the 29th. Fifteen D. quadramaculatus and 12 D. monticola were captured during this visit. Two D. quadramaculatus were recaptured from the August visit. The salamander designated as number 40 was found to have moved from quadrat six to quadrat seven, and the other recapture showed no movement. Captured D. quadramaculatus were found terrestrially six (40.0%) of the 15 while D. monticola were found terrestrially 11 (91.7%) of the 12. Substrate size was recorded for each salamander captured. However, I found that the size of the substrate was not a determining factor, but the positioning of the substrate in relationship to the surface of the water was a determining factor. It was observed that the closer the substrate was to the edge of the stream the more likely it was to have salamanders utilizing it as cover.

The first set of drift traps was put in place on 13 July 1992 and checked on 25 July 1992. In the down flow trap (the trap placed at the bottom of the study site with the open end facing up stream), 31 larvae were captured. They included two D. ochrophaeus, one D. fuscus, four D. monticola, 18 D. quadramaculatus, and six Eurycea bislineata, all young of the year. The traps were checked 20 August 1992 and both had unfortunately been disturbed by people. On the 28 September 1992 visit, the down flow trap contained three larvae between 16-18 mm SVL and one adult D. quadramaculatus along with one subadult Rana clamitans melanota. In the 24 October 1992 and 31 October 1992 visits, nothing was captured. The 14 November 1992 visit found both traps vandalized and destroyed beyond repair. I built two new traps exactly as the ones before and installed them on 29 January 1992 and by the next visit, they had also been destroyed.

Discussion:

The initial focus of the study was to estimate the population of desmognathans at the study site while monitoring their competition for substrate and foraging habits. Due to the low numbers of recaptures, an accurate estimate could not be made. However, there were differences in substrate utilization between D. quadramaculatus and D. monticola. Desmognathus monticola post-metamorphic individuals were almost entirely found foraging terrestrially, even though the study was restricted to the full bank width of the streambed. Desmognathus quadramaculatus adults were found to forage above the surface of the water at different degrees throughout the year. Of the D. quadramaculatus observed, 97.5% found in June, 72.7% found in July, 50.0% found in August, and 40% found in September were foraging above the surface of the water. From October to April, adult D. quadramaculatus were observed foraging totally in water. As the larger D. quadramaculatus foraged aquatically, the surface abundances of D. monticola along the edge of the stream increased. This may be an example of evolutionary niche partitioning through seasonal habitat utilization differences that allows the two competitors to inhabit the same habitat.

An interesting observation made during this study was that whereas D. quadramaculatus was overcollected by baitseekers and virtually eliminated, adult D. monticola replaced them. As I would move up or down the stream away from the accessibility of the highway and the collecting pressures of the bait collectors, D. quadramaculatus was found inhabiting its normal niche. This would indicate some interspecific interference for the optimum habitat which was the substrate along the stream. When D. quadramaclatus was present D. monticola was absent; however, when D. quadramaculatus was removed D. monticola inhabited the optimum habitat.

Rock size did not appear to be the selective force in habitat utilization for D. quadramaculatus. Substrate was selected by *D. quadramaculatus* according to its orientation to the edge of the stream. Rocks that were close to or on top of one another near the stream were used more. This may be due to moisture content of the microhabitat or escape route availability. *Desmognathus monticola* has a wider range of habitat preference which allows it to exist in the presence of a more dominant competitor. Keen (1985) found that *D. monticola* and *D. quadramaculatus* differ in microhabitat affinities which, instead of interspecific competition, accounts for their microhabitat distributions.

Chapter 3

Seasonal Foraging Habits of *Demognathus quadramaculatus*

Introduction

Utilization of prey items is a function of the size of a predator, the microhabitat preference of the predator, and the occurrence of prey (Davic 1991). He found that many vertebrate studies have shown that differential utilization of microhabitat and food resources were essential in minimizing intraspecific and interspecific competition. Davic (1991) noted an interspecific competition avoidance in prey selection between pre- and post-metamorphic *D. quadramaculatus*. Davic (1991) described the phenomenon as an ontogenetic shift from a predominately aquatic prey (82%) in the pre-metamorphic individuals to terrestrial prey in the post-metamorphic juvenile (64.4%) and adult (62.5%) diets. Davic (1991) also found 82% of pre-metamorphic *D. quadramaculatus* prey items to be aquatic where post-metamorphic juvenile diets were composed of 35.6% aquatic prey. He found the adult diet to be composed of 62.5% terrestrial prey. Davic (1991) summarized by stating that the type of interspecific competition avoidance may be the result of an evolutionary need to separate adults and larvae, which reduces interspecific predation and competition for a limited prey resource. Burton (1976) found the competition for prey items was reduced by different habitat requirements of larval forms leading to niche separation at all stages of life history. Wilbur (1980) found pre-metamorphic mortality due to predation in pond-breeding amphibians is an important population amphibians is an important population regulatory mechanism and affects habitat utilization and competition.

Desmognathus quadramaculatus can attain larval populations of 0.25-8 larvae/m^2 and differ greatly in mean body size (Beachy 1993). Beachy (1993) found that the presence of different size classes of larval D. quadramaculatus may cause interference competition or even cannibalism in a closed system. He found that cannibalism of first-year larval salamanders by larger size classes is more important to population dynamics and habitat utilization than intraspecific competition between classes. However, ecologists no longer believe that a single factor, such as competition or predation, controls the development and regulation of communities (Beachy 1993).

Ashton (1975) in Preble County, Ohio found that Desmognathus fuscus began to move into winter retreats when the stream temperature dropped below 7.0°C. He found that the D. fuscus were active and feeding throughout the winter. Ashton (1975) found all salamanders moved into springs, seepages, or crayfish burrows when the stream temperature rose above 22°C. Feeding occurred 24 hours a day, but salamanders were most active when relative humidity was 90% or more. Barbour et al. (1969) observed individuals on humid nights and just before or after a rain on the substrate along the stream. When the stream temperature was 1.5°C, D. fuscus was found to retreat underground 0.10 m or more and remained within an area of 0.25 m^2 (Ashton 1975). The winter retreats were 30 to 50 cm below the surface while the soil was frozen to a depth of 14 cm. The microhabitat salamanders inhabited was 4°C and probably warmed by ground water (Ashton 1975). The greatest period of movement for D. fuscus was in late fall, following the first freezing temperatures when the stream temperature dropped to 7°C or lower (Ashton 1975). Sixty-six per cent of the salamanders showed movement upstream, following what appeared to be a temperature gradient leading to ground water affluent. Desmognathus fuscus and Eurycea bislineata showed similarities in movements upstream, possibly following temperature gradients, into winter retreats when the stream temperature dropped below 7°C (Ashton and Ashton 1978). Under normal conditions throughout the winter, both E. bislineata and D. fuscus were found in active, feeding aggregations within areas of relative moderate temperatures. Feeding during the winter may have an important relationship to energy budgets and reproductive cycles (Ashton and Ashton 1978).

Ratios of snout-vent lengths and head widths between different desmognathan species on a body size gradient for both adults and juveniles have been found to be constant (Krzysik, 1979). Head width directly affects the size of the prey a salamander can utilize. Burton (1976) attributed this to the co-existence of different salamander species by stating gradation in the size of the adult salamanders leads to a divergence in the size of the prey taken. Therefore, as long as there are size differences between competing salamander species or young of the same species, competition will be reduced.

Materials and Methods

Seasonal and ontogenic changes in the foraging habits of D.

gudramaculatus were examined through gut analysis in conjunction with aquatic macroinvertebrate seasonal availability in terms of numbers and biomass. Salamanders were collected on monthly visits for one calendar year from the study site. They were killed in chlorotone upon capture and fixed in 10% formalin. Morphological measurements such as SVL and head width were documented using metric calipers. State of metamorphosis(pre or post), gender, and status of sexual maturity were examined for foraging differences. Upon capture of each salamander, its habitat was assessed by documenting substrate type. The place of foraging, in water or on land, was also documented. The physical habitat characteristics such as water temperature, air temperature, water pH, and relative humidity at water level were assessed at each visit.

Aquatic macroinvertebrates were collected monthly using a Surber sampler (Figure 8). Collections were made at ten sites that were chosen to exemplify the microhabitat diversity of the stream in an attempt to distinguish population differences in macroinvertebrates due to location.

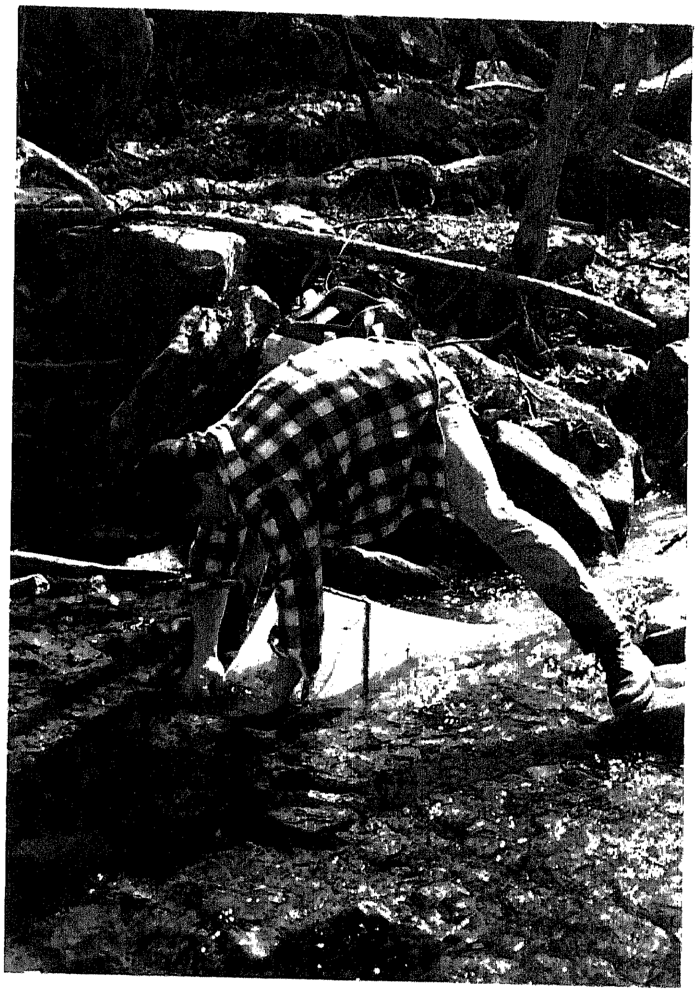
Below sites where macroinvertebrates were collected are described.

1) Surber Sampler: Riffle, wet width of 1 m, full bank width of 3 m, substrate size 15-25 cm^2, water depth 20-30 cm.

2) Surber Sampler: Riffle at the end of a plunge pool, wet width 0.5m, full bank width 1.5 m, substrate size 10-15 cm^2, water depth 30-40 cm.

3) Surber Sampler: Plunge Pool, wet width 1.5 m, full bank width 1.5 m, substrate size 2-5 cm^2, water depth 40-55 cm.

Figure 8. Collection of macrobenthos using a Surber sampler at study site.



4) Surber Sampler: Riffle, wet width 3 m, full bank width 4 m, substrate size 10-20 cm^2, water 10-15 cm.

5) Surber Sampler: Riffle, wet width 1 m, full bank width 1.5 m, substrate size 2-5 cm^2, water depth 45-50 cm.

6) Surber Sampler: Plunge pool, wet width 2 m, full bank width 2.5 m, substrate size fine to coarse sand, water depth 30-35 cm.

7) Surber Sampler: Lateral scour, wet width 0.5 m, full bank width 0.5 m, substrate size 2-5 cm^2, water depth 30-40 cm.

8) Surber Sampler: Glide at end of plunge pool, wet width 1 m, full bank width 1 m, substrate size 2-5 cm^2, water depth 30-45 cm.

9) Surber Sampler: Riffle, wet width 2 m, full bank width 3 m, substrate 2-10 cm^2, water depth 20-25 cm.

10) Surber Sampler: Riffle, wet width 1.5 m, full bank width 2 m, substrate size 20-25 cm, water depth 15-20 cm.

Samples were collected by placing the Surber sampler in the streambed and disturbing the substrate for a count of 60 (Figure 8). When the deciduous trees dropped their leaves, it was necessary to alter this procedure to cope with the detrital rafts. The Surber sampler was placed in the streambed and the detritus which fell within the parameter of the Surber was raked into the Surber net. The detritus within the net was placed in gallon plastic bags and a second sample was then taken from the same site following the previously described methodology. Samples were washed from the surber sampler with 70% ethyl alcohol into a gallon plastic bag (Figure 9). Samples were then double bagged

Figure 9. Demonstration of technique using 95% ethanol to remove macrobenthos and detitus from Surber sampler.

move

and immersed in 70% alcohol for transportation back to the lab. Macroinvertebrates were picked and identified to the generic level using Meritt and Cummins (1984), except dipteran and coleopteran larvae which were identified to the ordinal level. They were placed into petri dishes and dehydrated in a model 107801 Boekel Oven at 50°C for 6 hours. Samples were then weighed in their perspective groups on a Sartorius Analytical Balance to the 0.0000 g for biomass composition. These identifications resulted in 23 genera and 13 other taxonomic descriptions. Differences in the macroinvertebrate community in relation to microhabitat were mathematically evaluated using Newman-Keuls Multiple Comparison Summary.

The 10 monthly samples were grouped per month and then by season to be analyzed. The arbitarly designated seasons of winter and fall have three months or thirty Surber samples composing the season's invertebrate numbers and dry weight. The summer season is made up of four months while the spring season is composed of only two months.

Seasonal gut contents were analyzed by using the overall percent of invertebrate groups in the dietary composition and the frequency with which those groups occurred in the stomachs of the salamanders. This was first done by examining the overall diet of D. quadramaculatus as a population. Diet was then further dissected into seasonal gut contents with the seasons designated as spring (April and May), summer (June, July, August, and September), fall (October, November, and December), and winter

(January, February, and March). Seasons were grouped in this way due to the environmental similarities that occurred. Then diet was further separated into overall and seasonal pre- and post-metamorphic dietary analysis.

Results and Discussion: Seasonal Observations at Study Site

Desmognathus quadramaculatus was observed utilizing different microhabitats due to seasonal changes and resource availability. In late April, May, June, July, August, and September, the post-metamorphic D. quadramaculatus were found foraging terrestrially at the edge of the stream. Throughout the study, D. quadramaculatus was rarely found far from the safety of the water with the farthest specimen being 30 cm from the stream's edge. On days when relative humidity reached or exceeded 95%, the post-metamorphic individuals could be seen foraging on top of the substrate. Pre-metamorphic individuals remain totally aquatic throughout the year; however, it was observed that they demonstrated microhabitat partitioning of their environments by season and by individual size.

The pre-metamorphic D. quadramaculatus individuals were put into four to five size classes. The first two size classes consisted of individuals with SVLs of 12 to 14 mm and 14 to 16 mm, and were found predominately in coarse gravel in riffles or diverted stream cascades. The first size class was only found on the surface during late winter which indicates that they hatched and absorbed their yolk below the streambed. This may allow them to avoid predation and the threat of being washed downstream. The larger pre-metamorphs were found throughout the stream under substrate that was usually 25 cm^2 or larger.

Substrate utilization changed dramatically for both adults and larvae with the fall defoliation of the canopy. In late October, November, and December, salamander activity was significantly altered by the presence of deciduous detrital rafts. In October, large leaf rafts were found floating and clogging the stream and impeding the normal flow pattern. In much of the length of the stream, the detritus was so compiled, it completely concealed the stream. Both pre- and post-metamorphic individuals were found suspended in the leaf rafts and could be collected in great numbers by merely raking the detrital rafts into a net. At this time, a plecopteran emergence of Allocapnia occurred, presenting an abundance of prey for salamanders. Allocapnia was found in gut examinations to make up the largest portion of the diet in October.

In November, the leaf rafts had broken up and accumulated in pools or in large piles against rocks. The pre-metamorphic and juvenile salamanders could be readily captured by raking large clumps of detritus from the bottom of the pools into a seine. The larger adults were found under large rocks (45 cm^2 and larger) that were associated with a large leaf mass. By December, the leaf packs had further dissipated and could only be found at the end of pools and against large rocks. Pre- and post-metamorphic individuals could still be found in the leaf packs. Salamanders were found in the greatest concentrations when leaf packs were compiled on large rocks that made up a cascade.

Substrate used by salamanders had shifted from deciduous detritus back to rocks in January, Febuary, and March. In January, the leaf packs, for the most part, had been removed from the stream by heavy rains leaving only scattered masses against large rocks. Where these "islands" of detritus occurred, large adult D. quadamaculatus were usually present. The pre-metamorphic individuals could be found in abundance under rocks and in gravel, depending on the size of the individual. By February, the leaf packs were completely gone due to scouring floods, and the post-metamorphic individuals could not be found by conventional collecting techniques. The pre-metamorphic salamanders remained abundant under submerged rocks and buried in coarse gravel. In March, heavy rains further scoured the stream to such an extent that the composition of the whole study site had changed. Where there once was a plunge pool, a riffle existed in its place. After this major storm event, the pre-metamorphs could only be found under large rocks ($30 cm^2$ or larger) and the post-metamorphs could not be found at all.

In April, D. quadramaculatus adults began utilizing the terrestrial habitat once again. The emergence occurred with the blooming of Trillium (Trillium grandiflorum), Spring Beauty (Claytonia virginica), Jack-in-the-Pulpit (Arisaema triphyllum), and the refoliation of Yellow Buckeye (Aesculus octandra) and Sugar Maple (Acer saccharum). Flying dipterans and trichopterans were also emerging. However, May was a time of mass emergence for aquatic insects and salamanders alike. Post-metamorphic D. quadramaculatus were found in abundance foraging terrestrially on top of and under rocks at the edge of the water. Pre-metamorphic salamanders were dispersed among the substrate of the stream according to body size. The smallest individuals (12 to 16 mm) were found in coarse gravel that was located in immersed areas out of the direct stream channel. The other larvae were dispersed throughout the stream.

Results:(Surber Samples)

The number and dry weight of aquatic insect orders of Ephemeroptera, Plecoptera, Trichoptera, and Diptera fluctuated by month and season (Tables 2-5). The greatest dry weight of nymphal ephemeropterans was in April at 0.1914 g, and greatest number of individuals (273) was in February. They had the greatest occurrence and largest dry weight in the winter season with 678 individuals and 0.2408 g. Nymphal plecopterans were found in the greatest numbers in November with 958 individuals and its greatest dry weight in April with 0.3383 g. They were found to occur in the greatest numbers in the winter season with 1,237 individuals, but had the greatest dry weight in the spring with 0.3758 g. Larval trichopterans were found in the largest numbers in November with 137 individuals, but had the greatest dry weight in January with 0.0439 g. In the winter season, 255 nymphal trichopterans were found and had a dry weight of 0.0941 g which made it the season with both the greatest numbers of individuals and the largest dry weight.

Table 2. Spring invertebrates collected in Surber samples.

Taxonomy	April		May		Total Spring	
	Number	Biomass	Number	Biomass	Number	Biomass
Ephemeroptera	224	0.1914g	170	0.0342g	394	0.2256g
Ameletus	24	0.0365g	34	0.0092g	58	0.0457g
Baetus	19	0.0056g	86	0.0080g	105	0.0132g
Epeorus	91	0.0446g	20	0.0062g	111	0.0508g
Stenonema	19	0.0873g	2	0.0011g	21	0.0884g
Leptophlebia	18	0.0100g	4	0.0005g	22	0.0105g
Ephemera	0	0.0000g	0	0.0000g	0	0.0000g
Drunella	17	0.0008g	10	0.0026g	27	0.0034g
Ephemerella	36	0.0066g	14	0.0066g	50	0.0132g
Plecoptera	138	0.3383g	120	0.0375g	258	0.3758g
Peltoperla	0	0.0000g	0	0.0000g	0	0.0000g
Talloperla	0	0.0000g	1	0.0012g	1	0.0012g?
Allonarcys	1	0.2435g	0	0.0000g	1	0.2435g
Acroneuria	1	0.0005g	1	0.0009g	2	0.0014g
Isoperla	14	0.0679g	8	0.0210g	22	0.0889g
Hastoperla	47	0.0200g	36	0.0044g	83	0.0224g
Amphinemura	28	0.0015g	1	0.0003g	29	0.0018g
Allocapnia	46	0.0048g	47	0.0078g	93	0.0126g
Paracapnia	1	0.0001g	26	0.0019g	27	0.0020g
Trichoptera	102	0.0337g	62	0.0271g	164	0.0608g
Diplectrona	85	0.0328g	54	0.0227g	139	0.0555g
Rhyacophila	4	0.0005g	2	0.0016g	6	0.0021g
Macronema	3	0.0000g	1	0.0021g	4	0.0021g
Limnephilus	9	0.0003g	5	0.0007g	14	0.0010g
Pycnopsyche	0	0.0000g	0	0.0000g	0	0.0000g
Lepidostoma	1	0.0001g	0	0.0000g	1	0.0001

Table 2. Continued						
Taxonomy	April		May		Total Spring	
	Number	Biomass	Number	Biomass	Number	Biomass
Diptera	222	0.0488g	80	0.1762g	302	0.2250
Chironomidae	205	0.0264g	72	0.0060g	277	0.0324g
Tipulidae	17	0.0224g	8	0.1702g	25	0.1926g
Odonata	0	0.0000	1	0.0096g	1	0.0096g
Coleoptera	4	0.0005g	2	0.0020g	6	0.0025g
Decapoda	1	0.2050g	0	0.0000	1	0.2050g
Collembolla	1	0.0001g	0	0.0000	1	0.0001g
Arachnida	0	0.0000	2	0.0018g	2	0.0018g
Oligochaetes	12	0.0020g	2	0.0007g	14	0.0027g
Diplopoda	0	0.0000	0	0.0000	0	0.0000
Homoptera	0	0.0000	1	0.0001g	1	0.0001g
Hemiptera	0	0.0000	0	0.0000	0	0.0000
Megaloptera	0	0.0000	0	0.0000	0	0.0000
Hymenoptera	0	0.0000	17	0.0012g	17	0.0012g
Lepidoptera	1	0.0004g	1	0.0005g	2	0.0009

Table 3. Summer invertebrates collected in Surber samples.

	June		July		Augost		September		Total Summer	
Taxonomy	#	Bio.	#	Bio.	#	Bio.	#	Bio.	#	Bio.
Ephemeroptera	85	0.0291g	59	0.0115g	16	0.0125g	49	0.0102g	209	0.0633g
Ameletus	5	0.0013g	1	0.0005g	0	0.0000	3	0.0004g	9	0.0022g
Baetus	44	0.0067g	16	0.0018g	0	0.0000	18	0.0022g	78	0.0107g
Epeorus	17	0.0026g	11	0.0018g	5	0.0006g	4	0.0002g	37	0.0052g
Stenonema	2	0.0003g	24	0.0065g	6	0.0022g	12	0.0050g	44	0.0140g
Leptophlebia	9	0.0034g	3	0.0007g	1	0.0001g	9	0.0020g	22	0.0062g
Ephemera	0	0.0000	0	0.0000	4	0.0096g	3	0.0004g	7	0.0100g
Drunella	8	0.0148g	4	0.0002g	0	0.0000	0	0.0000	12	0.0150g
Ephemerella	0	0.0000	0	0.0000	0	0.0000	0	0.0000	0	0.0000
Plecoptera	54	0.0076g	84	0.0108g	69	0.0078g	57	0.0179g	264	0.0441g
Peltoperla	0	0.0000	0	0.0000	2	0.0002g	0	0.0000	2	0.0002g
Talloperla	1	0.0001g	0	0.0000	0	0.0000	0	0.0000	1	0.0001g
Allonarcys	0	0.0000	0	0.0000	0	0.0000	0	0.0000	0	0.0000
Acroneuria	0	0.0000	0	0.0000	4	0.0003g	1	0.0089g	5	0.0092g
Isoperla	1	0.0015g	3	0.0004g	6	0.0009g	3	0.0034g	13	0.0062g
Hastoperla	7	0.0018g	6	0.0017g	15	0.0028g	14	0.0019g	42	0.0082g
Amphinemura	1	0.0001g	2	0.0003g	0	0.0000	0	0.0000	3	0.0004g
Allocapnia	44	0.0041g	60	0.0071g	38	0.0033g	39	0.0037g	181	0.0182g
Paracapnia	0	0.0000	13	0.0013g	4	0.0003g	0	0.0000	17	0.0016g
Trichoptera	24	0.0151g	21	0.0036g	49	0.0031g	30	0.0052g	124	0.0270g
Diplectrona	14	0.0109g	16	0.0029g	45	0.0027g	22	0.0045g	97	0.0210g
Rhyacophila	4	0.0026g	1	0.0001g	4	0.0004g	8	0.0007g	17	0.0038g
Macronema	0	0.0000	4	0.0006g	0	0.0000	0	0.0000	4	0.0006g
Limnephilus	2	0.0001g	0	0.0000	0	0.0000	0	0.0000	2	0.0001g
Pycnopsyche	4	0.0015g	0	0.0000	0	0.0000	0	0.0000	4	0.0015g
Lepidostoma	0	0.0000	0	0.0000	0	0.0000	0	0.0000	0	0.0000

Table 3. Continued

	June		July		Augost		September		Total Summer	
Taxonomy	#	Bio.	#	Bio.	#	Bio.	#	Bio.	#	Bio.
Diptera	28	0.1177g	73	0.1505g	71	0.0058g	75	0.0124g	247	0.2864g
Chironomidae	23	0.0029g	68	0.0041g	68	0.0040g	68	0.0049g	227	0.0159g
Tipulidae	5	0.1148g	5	0.1464g	3	0.0018g	7	0.0075g	20	0.2705g
Odonata	1	0.0001g	0	0.0000	0	0.0000	0	0.0000	1	0.0001g
Coleoptera	2	0.0002g	3	0.0005g	2	0.0003g	1	0.0001g	8	0.0011g
Decapoda	0	0.0000	1	0.0264g	1	0.0415g	4	0.7919g	6	0.8598g
Collembolla	1	0.0001g	0	0.0000	0	0.0000	0	0.0000	1	0.0001g
Arachnida	1	0.0014g	0	0.0001g	1	0.0001g	0	0.0000	2	0.0016g
Oligochaetes	2	0.0010g	3	0.0002g	3	0.0007g	2	0.0008g	10	0.0027g
Diplopoda	1	0.1105g	0	0.0000	0	0.0000	0	0.0000	1	0.1105g
Homoptera	0	0.0000	0	0.0000	0	0.0000	0	0.0000	0	0.0000
Hemiptera	0	0.0000	6	0.0017g	5	0.0171g	0	0.0000	11	0.0188g
Megaloptera	0	0.0000	0	0.0000	2	0.0036g	1	0.0003g	3	0.0039g
Hymenoptera	0	0.0000	2	0.0004	4	0.0008g	0	0.0000	6	0.0000
Lepidoptera	0	0.0000	0	0.0000	0	0.0000	0	0.0000	0	0.0000

Table 4 . Fall invertebrates collected in Surber samples.

Taxonomy	October		November		December		Total Fall	
	#	Bio.	#	Bio.	#	Bio.	#	Bio.
Ephemeroptera	39	0.0274g	71	0.0456g	100	0.0236g	210	0.0965g
Ameletus	10	0.0006g	33	0.0059g	19	0.0015g	62	0.0080g
Baetus	2	0.0005g	5	0.0011g	23	0.0056g	30	0.0072g
Epeorus	5	0.0016g	11	0.0098g	33	0.0052g	49	0.0166g
Stenonema	9	0.0234g	13	0.0269g	13	0.0102g	35	0.0605g
Leptophlebia	10	0.0004g	7	0.0005g	9	0.0009g	26	0.0018g
Ephemera	3	0.0009g	2	0.0014g	1	0.0001g	6	0.0023g
Drunella	0	0.0000	0	0.0000	0	0.0000	0	0.0000
Ephemerella	0	0.0000	0	0.0000	2	0.0001g	2	0.0001g
Plecoptera	202	0.0288	958	0.01367	77	0.0690g	1237	0.2345g
Peltoperla	0	0.0000	0	0.0000	1	0.0002g	1	0.0002g
Talloperla	0	0.0000	0	0.0000	0	0.0000	0	0.0000
Allonarcys	0	0.0000	0	0.0000	5	0.0180g	5	0.0180g
Acroneuria	4	0.0104g	0	0.0000	2	0.0354g	6	0.0458g
Isoperla	3	0.0019g	11	0.0024g	2	0.0015g	16	0.0058g
Hastoperla	23	0.0028g	96	0.0176g	23	0.0042g	142	0.0246g
Amphinemura	0	0.0000	0	0.0000	0	0.0000	0	0.0000
Allocapnia	156	0.0127g	793	0.1088g	29	0.0060g	978	0.1275
Paracapnia	16	0.0010g	58	0.0079g	15	0.0037g	89	0.0126g
Trichoptera	21	0.0016g	137	0.0235g	61	0.0185g	219	0.0443g
Diplectrona	15	0.0016g	90	0.0123g	33	0.0067g	138	0.0206g
Rhyacophila	3	0.0003g	37	0.0057g	10	0.0021g	50	0.0081g
Macronema	2	0.0003g	7	0.0054g	9	0.0087g	18	0.0144g
Limnephilus	0	0.0000	3	0.0001g	5	0.0008g	8	0.0009g
Pycnopsyche	1	0.0001g	0	0.0000	2	0.0001g	3	0.0002g
Lepidostoma	0	0.0000	0	0.0000	2	0.0001g	2	0.0001g

Table 4. Continued								
Taxonomy	October		November		December		Total Fall	
	#	Bio.	#	Bio.	#	Bio.	#	Bio.
Diptera	93	0.0174g	295	0.3330g	406	0.6137g	794	0.9641g
Chironomidae	75	0.0027g	270	0.0163g	367	0.0289g	712	0.0479g
Tipulidae	18	0.0147g	25	0.3167g	39	0.5848g	82	0.9162g
Odonata	4	0.0467g	2	0.0333g	1	0.0034g	7	0.0834g
Coleoptera	2	0.0002g	0	0.0000	0	0.0000	2	0.0002g
Decapoda	1	0.0407g	1	0.1019g	2	0.1545g	4	0.2971g
Collembolla	0	0.0000	0	0.0000	0	0.0000	0	0.0000
Arachnida	1	0.0012g	0	0.0000	0	0.0000	1	0.0012g
Oligochaetes	12	0.0014g	1	0.0018g	17	0.0022g	30	0.0054g
Diplopoda	0	0.0000	0	0.0000	1	0.0043g	1	0.0043g
Homoptera	2	0.0006g	0	0.0000	0	0.0000	2	0.0006g
Hemiptera	5	0.0043g	0	0.0000	0	0.0000	5	0.0043g
Megaloptera	0	0.0000	0	0.0000	1	0.0064g	1	0.0064g
Hymenoptera	1	0.0001	0	0.0000	0	0.0000	1	0.0001g
Lepidoptera	0	0.0000	1	0.0010g	0	0.0000	1	0.0010

Table 5. Winter invertebrates collected in Surber samples.								
Taxonomy	January		Febuary		March		Total Winter	
	#	Bio.	#	Bio.	#	Bio.	#	Bio.
Ephemeroptera	252	0.0555g	273	0.0641g	153	0.1212g	678	0.2408g
Ameletus	59	0.0230g	50	0.0224g	18	0.0088g	127	0.0515g
Baetus	28	0.0045g	18	0.0071g	5	0.0037g	51	0.0153g
Epeorus	147	0.0238g	173	0.0322g	106	0.1044g	426	0.1564g
Stenonema	5	0.0010g	13	0.0010g	3	0.0002g	21	0.0022g
Leptophlebia	7	0.0031g	3	0.0003g	5	0.0025g	15	0.0059g
Ephemera	0	0.0000	0	0.0000	0	0.0000	0	0.0000
Drunella	0	0.0000	0	0.0000	0	0.0000	0	0.0000
Ephemerella	6	0.0001g	16	0.0011g	16	0.0016g	38	0.0028g
Plecoptera	150	0.0914g	82	0.0278g	53	0.0365g	285	0.1557g
Peltoperla	0	0.0000	0	0.0000	0	0.0000	0	0.0000
Talloperla	2	0.0023g	0	0.0000	0	0.0000	2	0.0023g
Allonarcys	0	0.0000	0	0.0000	0	0.0000	0	0.0000
Acroneuria	1	0.0003g	0	0.0000	0	0.0000	1	0.0003g
Isoperla	18	0.0615g	6	0.0188g	9	0.0271g	33	0.1074g
Hastoperla	57	0.0139g	34	0.0057g	14	0.0059g	162	0.0255g
Amphinemura	1	0.0001g	6	0.0004g	0	0.0000	7	0.0005g
Allocapnia	30	0.0042g	34	0.0024g	27	0.0030g	91	0.0096g
Paracapnia	41	0.0091g	2	0.0005g	3	0.0005g	46	0.0101g
Trichoptera	125	0.0439g	67	0.0264g	63	0.0238g	255	0.0941
Diplectrona	89	0.0242g	45	0.0132g	35	0.0082g	169	0.0456g
Rhyacophila	14	0.0034g	14	0.0022g	4	0.0002g	32	0.0058g
Macronema	7	0.0104g	6	0.0108g	18	0.0151g	31	0.0363g
Limnephilus	2	0.0002g	2	0.0002g	6	0.0003g	10	0.0007g
Pycnopsyche	13	0.0057g	0	0.0000	0	0.0000	13	0.0057g
Lepidostoma	0	0.0000	0	0.0000	0	0.0000	0	0.0000

Table 5. Continued

Taxonomy	January		Febuary		March		Total winter	
	#	Bio.	#	Bio.	#	Bio.	#	Bio.
Diptera	517	0.2444g	544	0.2648g	173	0.0315g	1234	0.5407g
Chironomidae	421	0.0460g	489	0.0562g	158	0.0227g	1068	0.1249g
Tipulidae	96	0.1984g	55	0.2086g	15	0.0088g	166	0.4158g
Odonata	2	0.0026g	1	0.0009g	0	0.0000	3	0.0035g
Coleoptera	0	0.0000	1	0.0001g	1	0.0001g	2	0.0002g
Decapoda	1	0.0108g	0	0.0000	0	0.0000	1	0.0108g
Collembolla	0	0.0000	0	0.0000	0	0.0000	0	0.0000
Arachnida	1	0.0003g	0	0.0000	0	0.0000	1	0.0003g
Oligochaetes	9	0.0035g	11	0.0033g	9	0.0129g	29	0.0197g
Diplopoda	0	0.0000	0	0.0000	0	0.0000	0	0.0000
Homoptera	0	0.0000	0	0.0000	0	0.0000	0	0.0000
Hemiptera	0	0.0000	0	0.0000	0	0.0000	0	0.0000
Megaloptera	0	0.0000	0	0.0000	0	0.0000	0	0.0000
Hymenoptera	0	0.0000	0	0.0000	0	0.0000	0	0.0000
Lepidoptera	0	0.0000	0	0.0000	0	0.0000	0	0.0000

The family Tipulidae occurred in the greatest numbers in January with 96, but had the greatest dry weight in December with 0.5848 g. While the winter season contained the greatest numbers of representatives of Tipulidae with 166, the fall season had the greatest dry weight 0.9162 g.

Odonata and Megaloptera are totally aquatic in their larval stages, but are not common in the stream and did not contribute significantly to the numbers of potential prey items or available biomass. Twelve nymphal odonates were identified from the Surber samples and had a dry weight of 0.0966 g. Four larval megalopterans were identified with a combined dry weight of 0.0103 g. Oligochaetes were found in the greatest numbers in December with 17 and the fall season with 30, but had the greatest dry weight in January with 0.0035 g and the winter season with 0.0197 g. Semi-aquatic order Collembolla was collected in the spring and fall, but only in one instance on both occasions. Decapods (crayfishes) were collected in greatest numbers and dry weight in September with 4 and 0.7919g and the summer season with 6 and 0.8598g.

Arachnida, Coleoptera, Diplopoda, Homoptera, Hemiptera, Hymenoptera, and Lepidoptera are terrestrial invertebrates that appeared in the Surber samples (Tables 2-5). These occurrences demonstrate that salamanders that forage aquatically may be exposed to terrestrial invertebrate groups and may rely on them for a large percentage of their diet in certain seasons. These terrestrial invertebrate groups were collected in the greatest numbers in the summer season.

Discussion

The invertebrate community was sampled in an attempt to identify population and biomass trends of the prey items of D. quadramaculatus throughout a year. By sampling 10 different aquatic microhabitats every month for a year, I was able to determine trends on invertebrate numbers, biomass, and habitat utilization. By knowing where specific invertebrate populations were found, salamander movements and foraging patterns could be determined by stomach contents. Newman-Keuls Multiple Comparison Summary found invertebrate species and numbers homogeneous throughout the stream. Differences in microhabitats sampled did not significantly alter the invertebrate community. However, the Newman-Keuls Multiple Comparison Summary found significant differences in invertebrate numbers by season.

Salamanders are known to eat any prey of proper size they can capture (Burton 1976). Desmognathus quadramaculatus was observed foraging primarily in or at the edge of the aquatic ecosystem in the study site. Therefore, the diet of D. quadramaculatus would reflect the invertebrate population fluctuations and may lead to an understanding of biomass utilization and seasonal movements of D. quadramaculatus.

In the summer season, the lowest numbers of aquatic invertebrates and aquatic invertebrate biomass were collected for the year, but the highest numbers of terrestrial invertebrate taxa and the highest terrestrial biomass were found in this period. The fall season was characterized by having the largest biomass of larval tipulids and the greatest number of Oligochaetes. November had the largest number of nymphal plecopterans and larval trichopterans of any month, while December had the largest biomass of larval tipulids and Oligochaetes. The winter season had the greatest numbers and biomass of nymphal ephemeropterans, larval trichopterans, and larval chironomids. It also had the greatest numbers of nymphal plecopterans and larval tipulids with the largest biomass of Oligochaetes. In January, the largest biomass for Oligochaetes and larval trichopterans was collected and also the greatest number of larval tipulids. In February, the largest numbers of nymphal ephemeropterans and larval chironomids were collected. Nymphal plecopterans were found in the largest biomass in the spring season. Nymphal ephemeropterans and nymphal plecopterans biomass reached its highest level in April.

Results: (Stomach Contents of *Desmognathus quadramaculatus*)

The percentage of salamanders, collected over a period of a year, found to contain a particular invertebrate group within their stomachs provide data on the dietary trends (Figure 10). Examination of the dietary items of *D. quadramaculatus* provides data on the importance of invertebrate taxa (Figure 11). Larval dipterans were found to occur most frequently and were found in 97(41.8%) of the 232 stomachs. Adult coleopterans, found in 56 (24.1%) of the 232 salamanders, were the second most frequently occurring taxa. Nymphal plecopterans were found in 49 (21.1%) of

Figure 10. Percent of *Desmognathus quadramaculatus* containing a given prey item.

STOMACH CONTENTS FOR

Desmognathus quadramaculatus

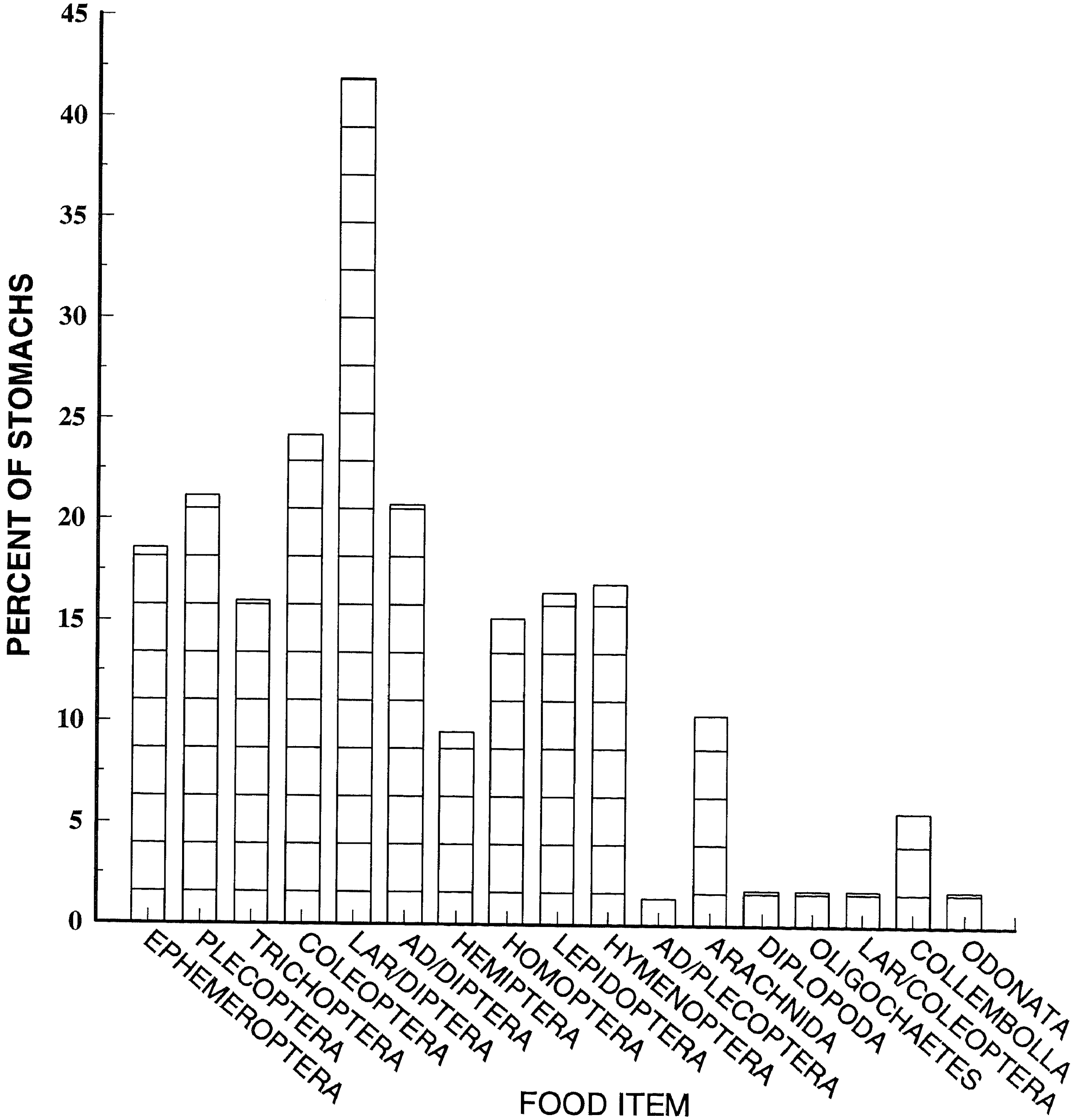
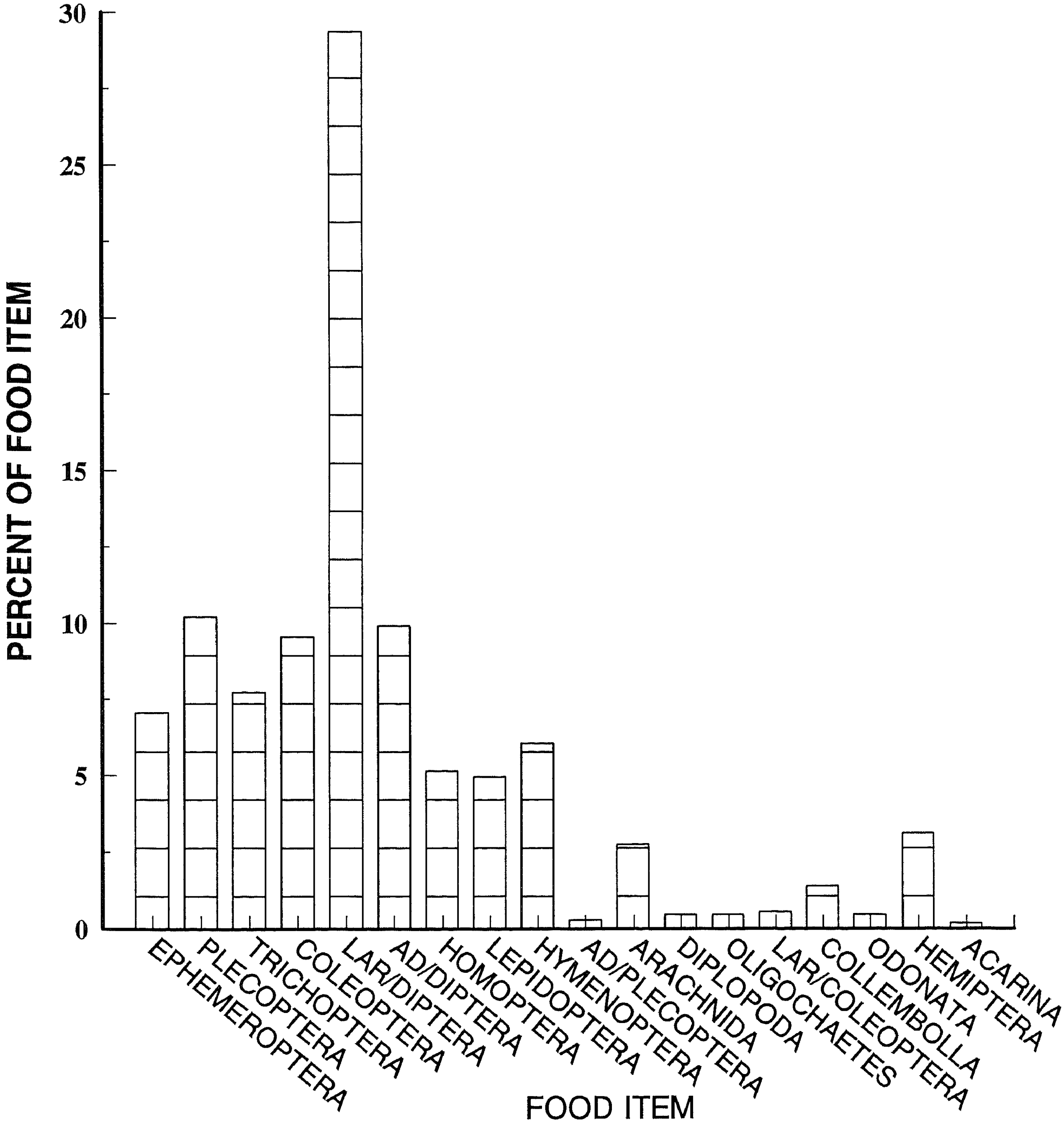


Figure 11. Invertebrate dietary composition for Desmognathus quadramaculatus.

FOOD ITEMS CONSUMED BY
Desmognathus quadramaculatus



the 232 salamanders, and adult dipterans were found in 48 (20.7%) salamanders. Nymphal ephemeropterans were found in 43 (18.5%) salamanders; hymenopterans, which were represented by wasps and ants, were found in 39 (16.8%) of the 232 salamanders. Lepidopterans were found in 38 (16.4%) of the total salamanders examined. Larval trichopterans were found in 37 (16.0%) salamanders while homopterans were found in 35 (15.1%). Arachnids were represented by the spiders and found in 24 (10.3%) salamanders. Hemipterans occurred in 22 (9.5%) of the salamanders collected and collembollans were found in 13 (5.6%). Diplopods, oligochaetes, aquatic coleopterans, and odonates each occurred in four (1.7%) of the salamanders examined. Adult plecopterans occurred in three (1.3%) of the salamanders while Acarins occurred in two (0.8%). Pseudoscorions, megalopterans, decapods, adult ephemeropterans, orthopterans all occurred in one or 0.4% of the salamanders.

The total dietary composition was determined by dividing the invertebrate group number by the total number of items found. Larval dipterans made up the greatest proportion of the overall diet at 320 (29.4%) items of the 1090 identified. Nymphal plecopterans made up 111 (10.2%) of the 1090 while adult dipterans comprised 108 (9.9%). Adult coleopterans made up 9.5% of the total items, while larval trichopterans composed 7.7%. Other food items included nymphal ephemeropterans (7.1%), hymenopterans (6.1%), homopterans (5.1%), lepidopterans (5.0%), hemipterans (3.1%), arachnids (2.8%), collembollans (1.4%), and aquatic coleopterans (0.6%). Odonates, oligochaetes, and diplopods each made up 0.5% of the diet. Megalopterans (0.1%), orthopterans (0.1%), decapods (0.1%), adult ephemeropterans (0.1%), pseudoscorpins (0.1%), and acarinids (0.2%) also were found to occur in the gut contents, but not significantly.

Spring Diet

The diet of D. quadramaculatus was also examined by season, comparing the number of stomachs within which each insect group occurred (Figure 12). In the spring season (April and May), 48 salamanders were dissected. Nineteen (40.0%) of the 48 salamanders contained representatives of terrestrial coleopterans. Adult and larval dipterans were second and third most commonly occurring groups. Adult dipterans were found in 14 (29.2%) of the 48 salamanders examined while larval dipterans were found in 13 (27.1%) of the 48 salamanders. Hymenopterans were found in 11 (22.9%) of the 48 salamanders examined while nymphal plecopterans were found in 10 (20.8%) salamanders. Nymphal ephemeropterans occurred in nine (18..8%) salamanders while lepidopterans were found in eight (16.7%) salamanders. The remainder of the insect groups are listed in descending occurrence: hemipterans (14.6%), arachnids(12.5%), and larval trichopterans(12.5%), homopterans (10.4%), collembollans (8.3%), diplopods (6.3%), odonates (2.2%), oligochaetes (2.1%), and adult ephemeropterans (2.2%).

In the spring, 235 dietary items were identified from the gut contents of D. quadramaculatus (Figure 13). Terrestrial

Figure 12. Percent of Desmognathus quadramaculatus containing a given invertebrate taxa in the spring season.

SPRING STOMACH CONTENTS FOR
Desmognathus quadramaculatus

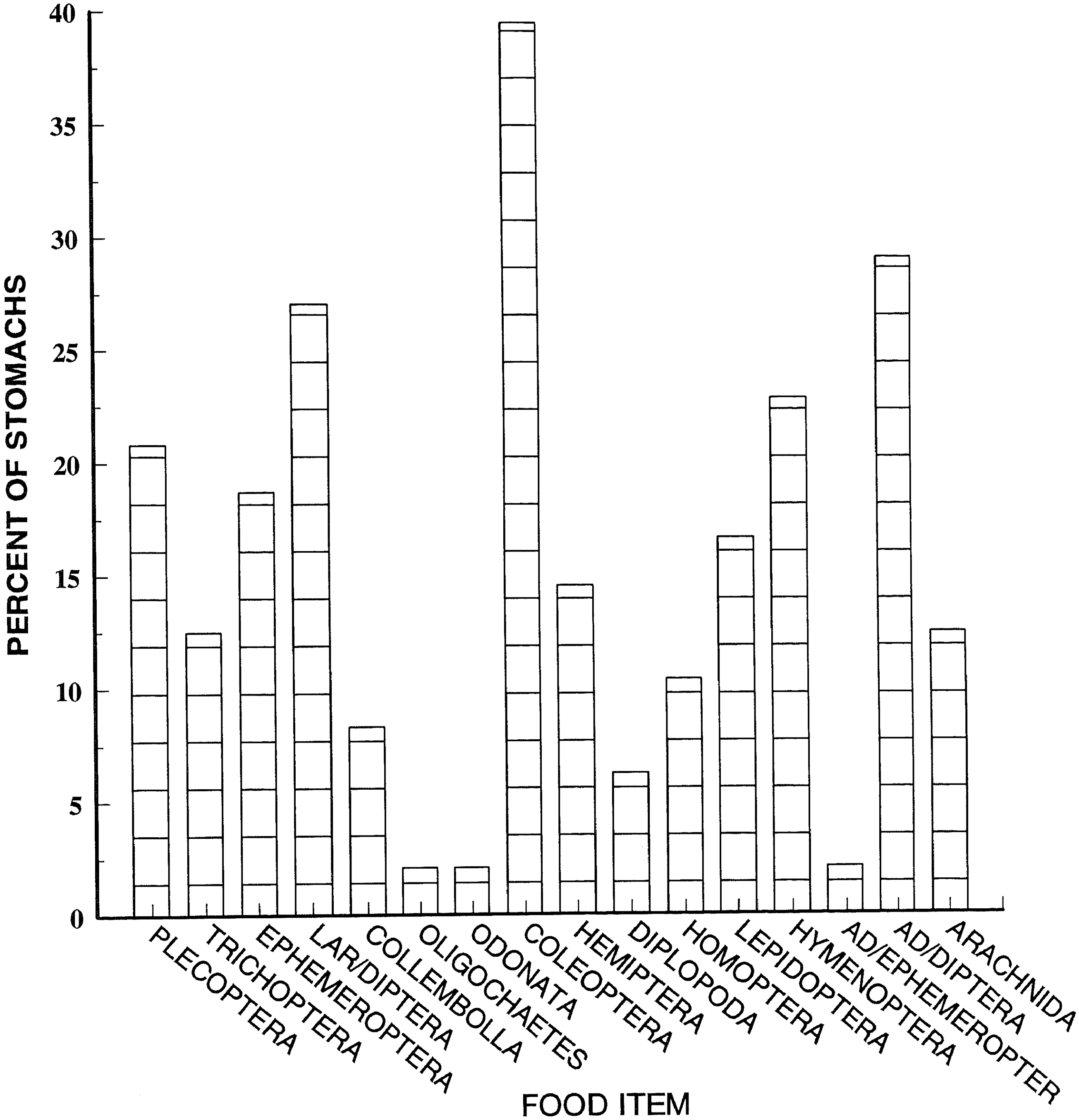
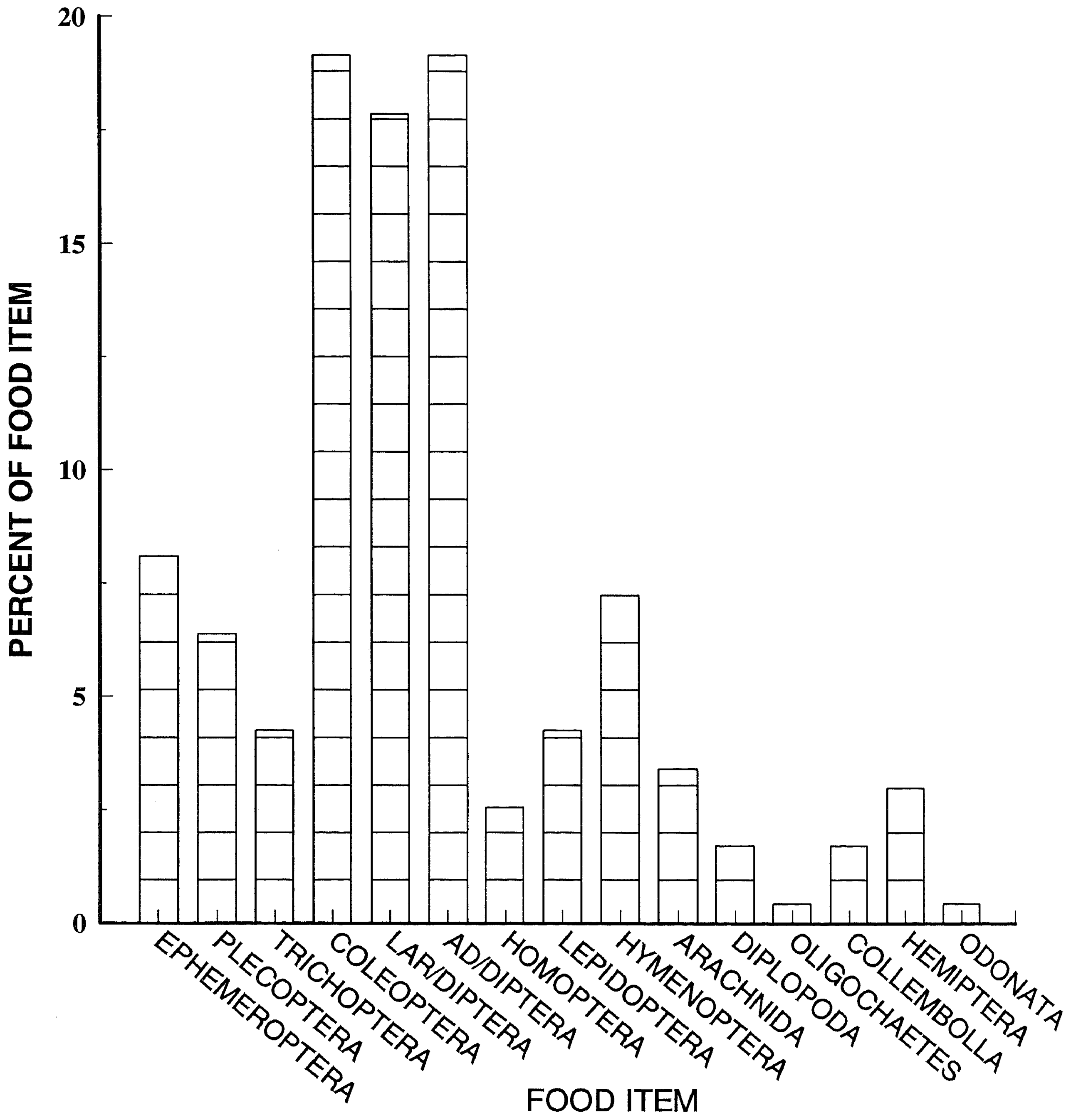


Figure 13. Spring invertebrate dietary composition for *Desmognathus quadramaculatus*.

FOOD ITEMS CONSUMED BY *Desmognathus quadramaculatus* IN THE SPRING SEASON



coleopterans and adult dipterans each had 45 (19.2%) of the 235 prey items observed. Larval dipterans comprised 42 (17.9%) items while nymphal ephemeropterans made up 19 (8.1%) items. Hymenopterans made up 17 (7.2%) items while nymphal plecopterans resulted in 15 (6.4%) items. Representatives from both larval trichopterans and lepidopterans each made up 4.3% of the diet. Arachnids (3.4), hemipterans (2.9%), homopterans (2.6%), diplopods (1.7%), and collembollans (1.7%) were found as multiple items in the spring diet of D. quadramaculatus. Odonates, adult ephemeropterans, and oligochaetes were found to be consumed each only in one instance.

Summer Diet

June, July, August, and September were designated as the summer season. In this period, larval dipterans were found in 31 (38.8%) of the 80 salamanders examined (Figure 14). The second most common prey item were lepidopterans which were found in 28 (35.0%) of the 80 salamanders. Adult dipterans were found in 24 (30.0%) of the salamanders surveyed while terrestrial coleopterans occurred in 23 (28.8%). Hymenopterans occurred in 19 (23.8%) salamanders while homopterans and arachnids both occurred in 14 (17.5%). Hemipterans, nymphal plecopterans, and nymphal ephemeropterans each occurred in 11 (13.8%) salamanders. Collembollans occurred at 8.8% with larval trichopterans at 7.5%. Odonates were found in 3.8% of the salamanders. Adult plecopterans occurred in 2.5% of the salamanders while orthopterans, megalopterans, pseudoscorpions, and aquatic

Figure 14. Percent of Desmognathus quadramaculatus containing a given invetebrate taxa in the summer season.

SUMMER STOMACH CONTENTS FOR

Desmognathus quadramaculatus

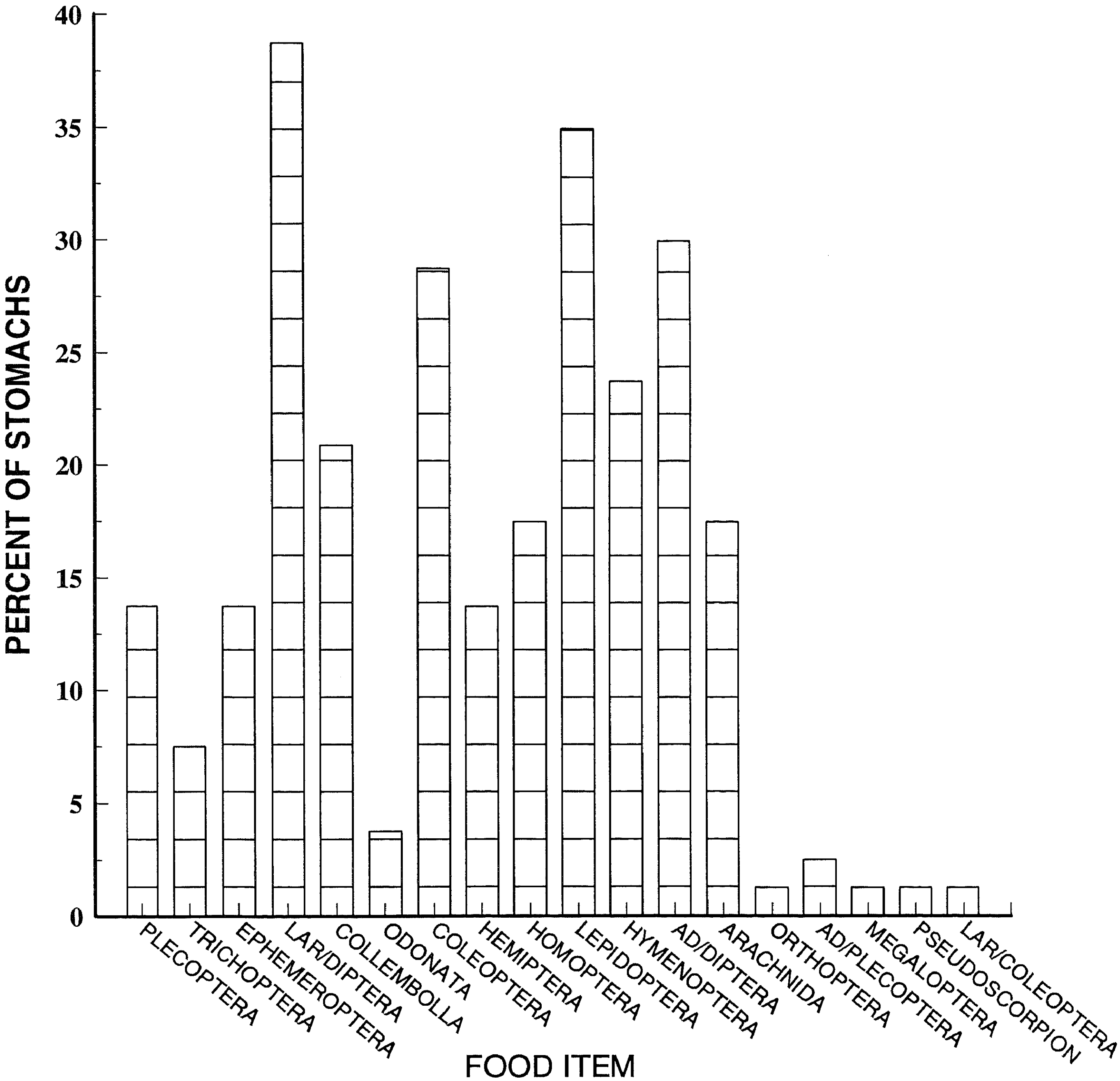
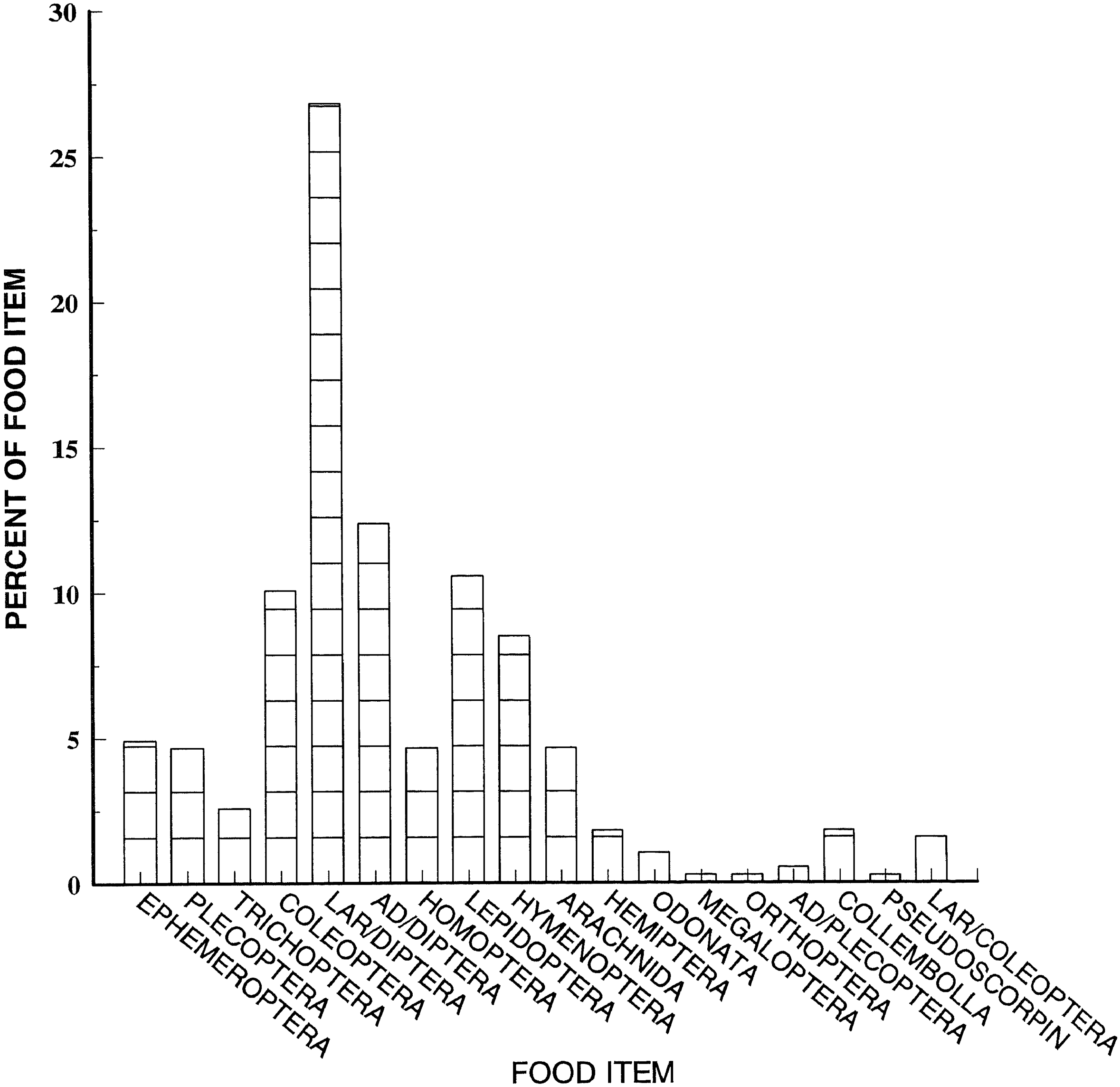


Figure 15. Summer invertebrate dietary composition for *Desmognathus quadramaculatus*.

FOOD ITEMS CONSUMED BY ***Desmognathus quadramaculatus***

IN THE SUMMER SEASON



coleopterans were found to occur only in one of the 80 salamanders.

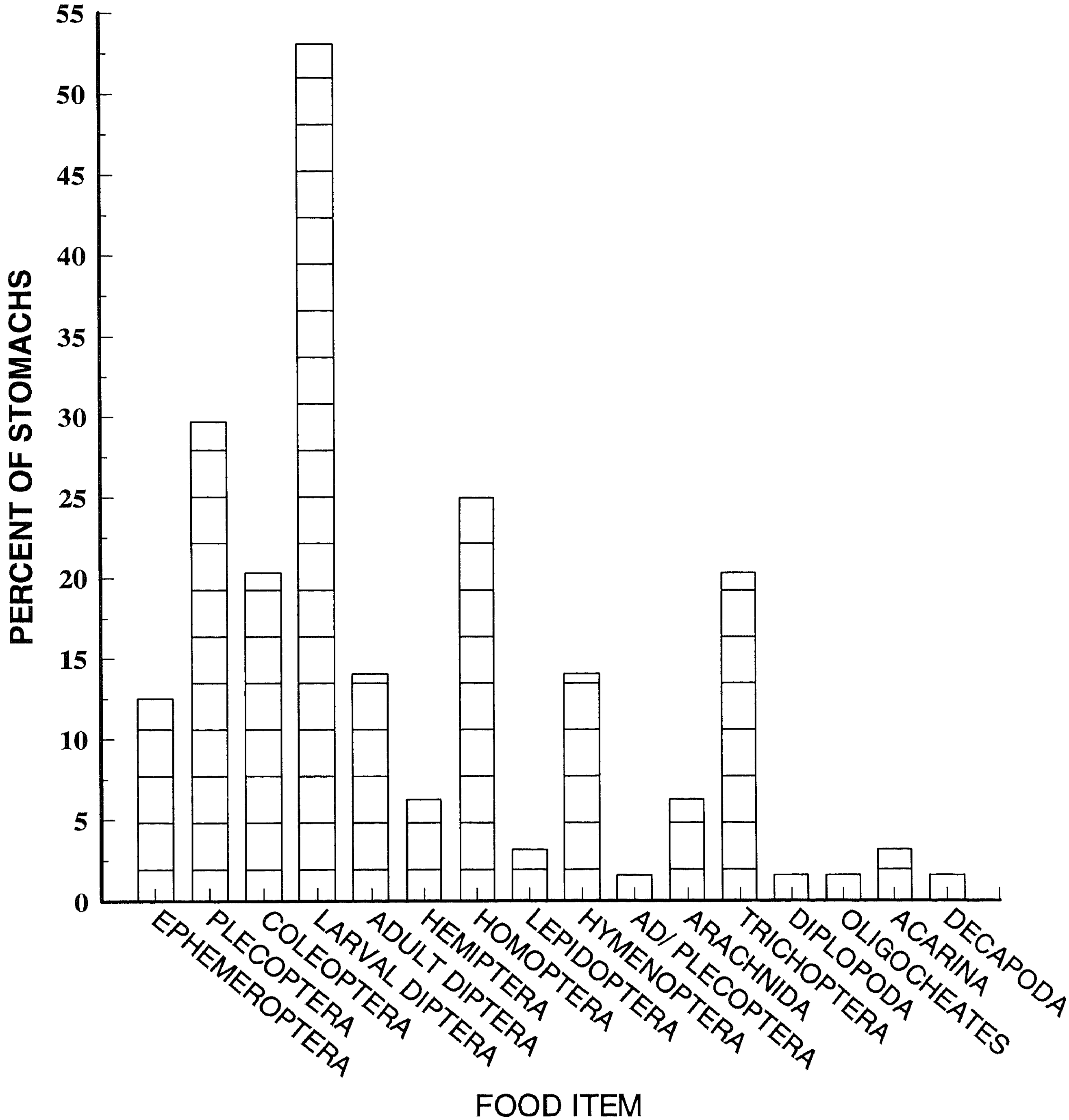
Larval dipterans made up the greatest overall dietary component of the summer season comprising 104 (26.9%) of the 387 items identified (Figure 15). Adult dipterans made up 48 (12.4%) items while representatives of lepidopterans numbered 41 (10.6%) of the dietary items. Terrestrial coleopterans made up 39(10.1%) of the 387 items while hymenopterans comprised 33 (8.5%) of the items. Nymphal ephemeropterans made up 4.9%. Nymphal plecopterans, homopterans, and arachnids each made up 4.7% of the diet in the summer season. Hemipterans 4.4%, larval trichopterans 2.6%, collembollans 1.8%, and aquatic coleopterans (1.6%) made up small percentages, but are still important aspects of the diet. Odonates (3.8%), megalopterans (1.3%), orthopterans (1.3%), adult plecopterans (1.3%), and pseudoscorpions (1.3%) each appeared in the diet, but infrequently.

Fall Diet

The fall season included October, November, and December. In this time period, 64 salamanders were collected, and of these, 34 (53.1%) salamanders had larval diptera within their stomach contents (Figure 16). Nymphal plecoptera were the next most frequently occurring insect group found in 19 (29.7%) of the salamanders examined. Homopterans were found in 16 (25.0%) salamanders while terrestrial coleopterans and larval trichopterans both occurred in 13 (20.3%) salamanders. Adult dipterans and hymenopterans were both found nine (14.1%)

Figure 16. Percent of *Desmognathus quadramaculatus* containing a given invertebrate taxa in the fall season.

FALL STOMACH CONTENTS FOR
Desmognathus quadramaculatus



salamanders and nymphal ephemeropterans were found in eight (12.5%). Arachnids and hemipterans each were found in four (6.3%) of the salamanders. Lepidopterans and Acarinids occurred in two (3.1%) salamanders while adult plecoptera, decapods, diplopod, and oligochaetes were each found in one.

The fall dietary composition was made up mainly of larval dipterans comprising 133 (37.8%) of the 352 items while nymphal plecopterans made up 64 (18.2%) items (Figure 17). Larval trichopterans made up 39 (11.1%) of the 352 items consumed while homopterans comprised 32 (9.09%) of the prey items. Hymenopterans (4.6%), adult dipterans (4.0%), nymphal ephemeropterans (3.1%), and hemipterans (2.8%), and arachnids (1.1%) made up the remaining portions of the diet. Decapods (0.3%), lepidopterans (0.9%), adult plectopterans (0.3%), acarinids (0.6%), oligochaetes (0.6%), and diplopods (0.3%) occurred in the diet, but in small numbers.

Winter Diet

The winter season included January, February, and March. Larval dipterans were found to occur in 19 (47.5%) of the 40 salamanders examined (Figure 18). Nymphal ephemeropterans were found in 15 (37.5%) salamander stomachs and larval trichopterans occurred in 12 (30.0%). Nymphal plecopterans were found in 9 (22.5%) salamanders. Oligachaetes and collembollans each were found in 2 (5.0%) salamanders. Adult dipterans and terrestrial coleopterans each occurred in one salamander stomach.

Larval dipterans comprised 41 (35.4%) of 116 items

Figure 17. Fall invertebrate dietary composition for Desmognathus quadramaculatus.

FOOD ITEMS CONSUMED BY ***Desmognathus quadramaculatus***

IN THE FALL SEASON

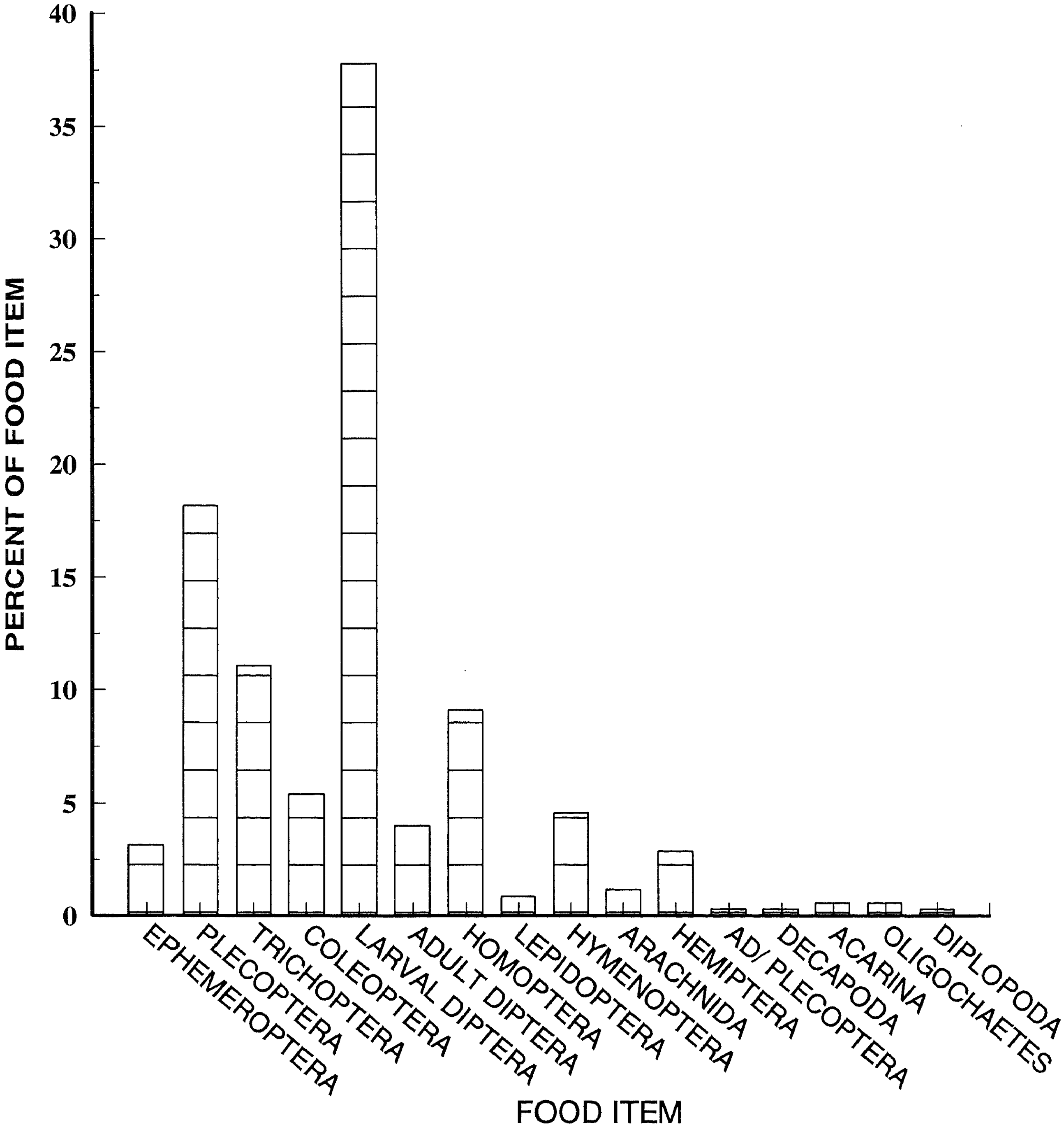


Figure 18. Percent of Desmognathus quadramaculatus containing a given invertebrate taxa in the winter season.

WINTER STOMACH CONTENTS FOR *Desmognathus quadramaculatus*

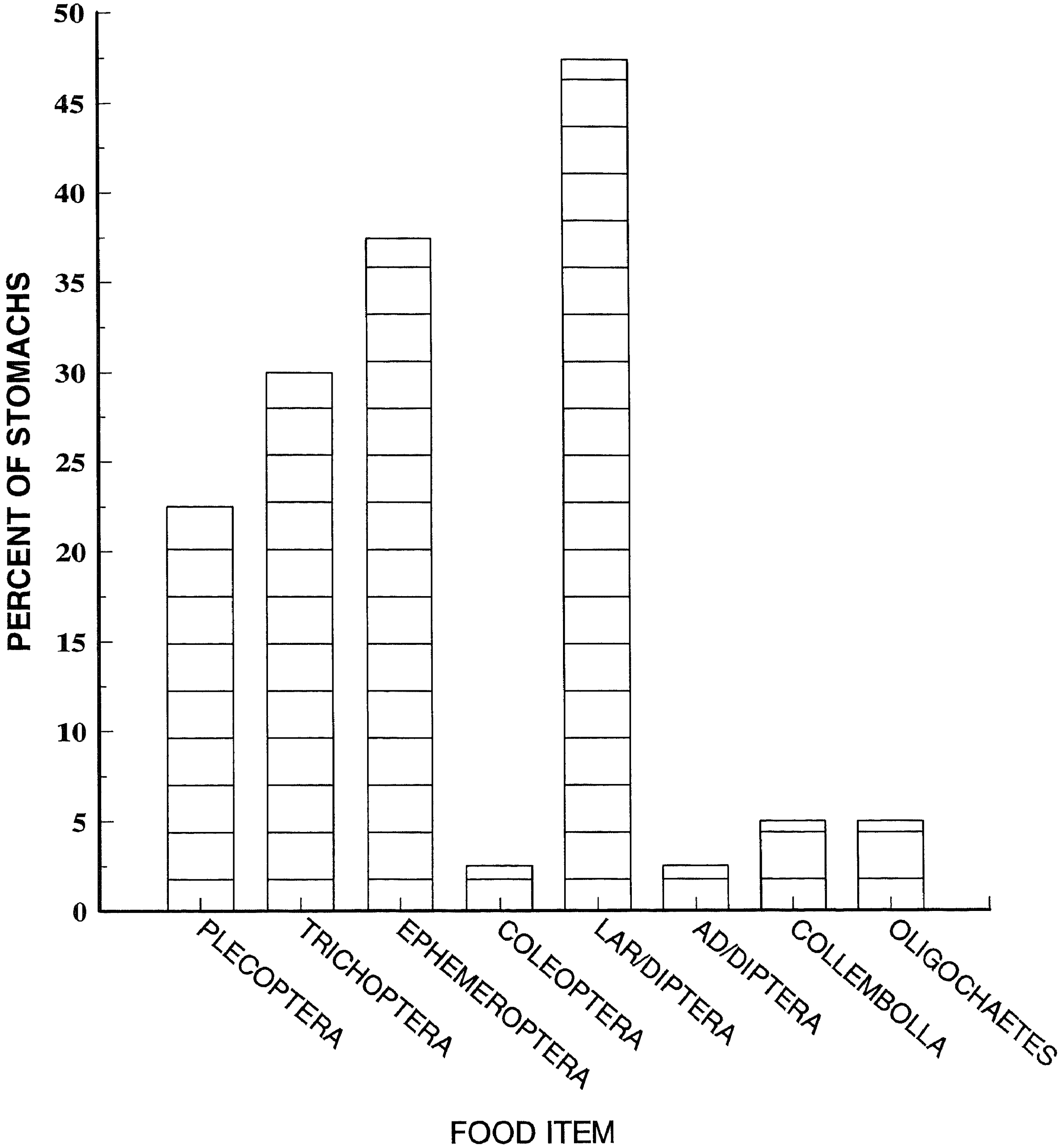
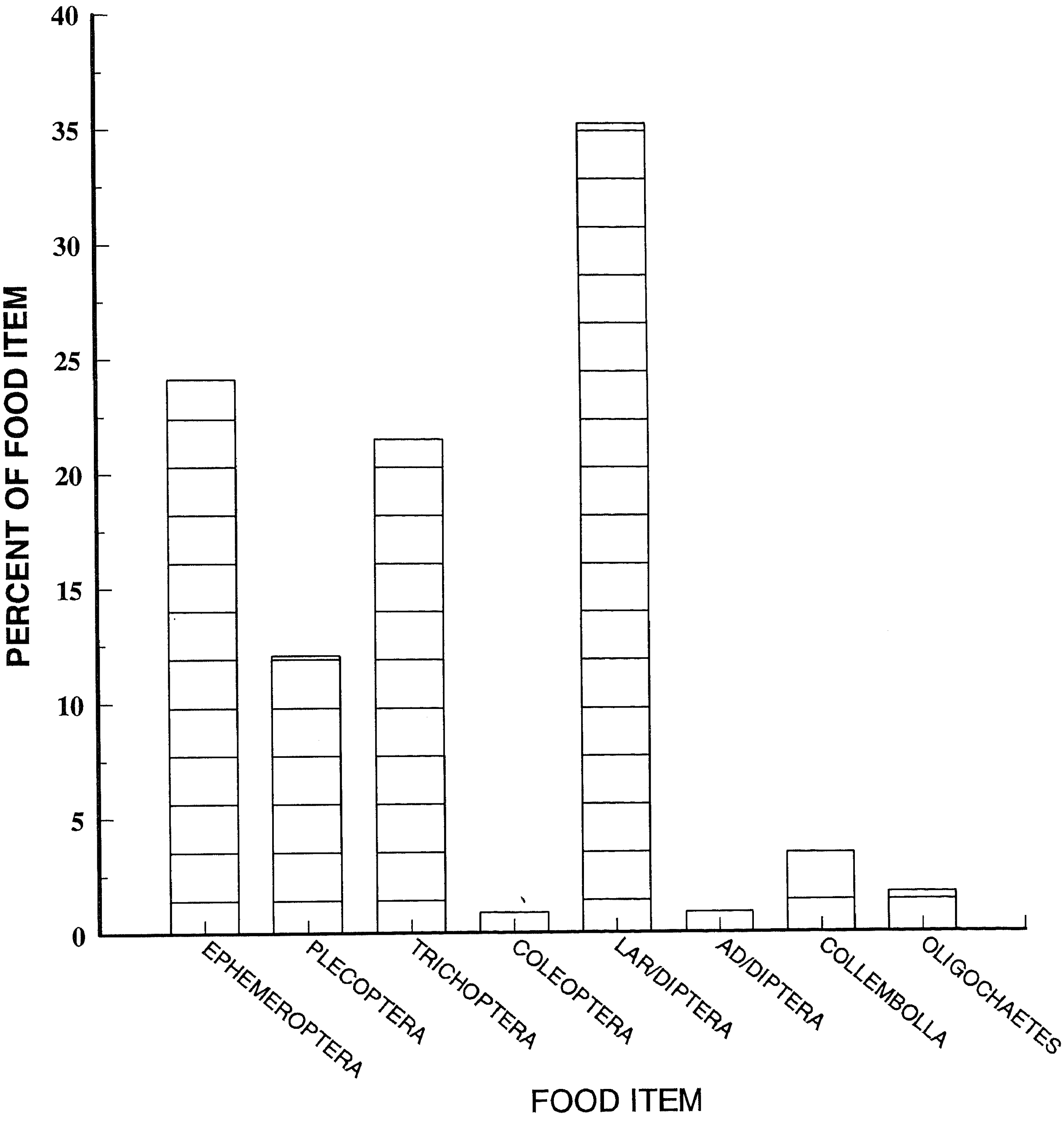


Figure 19. Winter invertebrate dietary composition for *Desmognathus quadramaculatus*.

FOOD ITEMS CONSUMED BY ***Desmognathus quadramaculatus***

in the Winter Season



identified in the winter diet (Figure 19). Nymphal plecopterans made up 14 (12.1%) of the 116 items consumed. Collembollans occurred 4 times composing 3.5% of the dietary items. Oligochaetes made up 1.7% of the diet, appearing 2 times while terrestrial coleopterans and adult dipterans each were consumed on one occasion.

Comparison of Pre- and Post-metamorphic Salamander Diets

Desmognathus quadramaculatus dietary components are best examined by splitting the species into pre- and post-metamorphic stages. Dietary differences were examined by looking at the overall and seasonal percent of occurrence and percent of diet composition the insect groups made up. When examining the total larval salamanders collected over one calendar year, it was found that larval dipterans occurred in 64 (48.9%) of the 131 salamanders examined (Figure 20). Nymphal ephemeropterans followed in frequency of occurrence with 36 (27.5%) of the salamanders examined. Larval trichopterans occurred in 30 (22.9%) salamanders and nymphal plecopterans in 25 (19.1%). Lepidopterans occurred in 10 (7.6%) pre-metamorphs while terrestrial coleopterans were found in 9 (6.9%) salamanders. Adult dipterans (6.8%), hymenopterans (6.1%), homopterans (6.1), and arachnids (4.6%) occurred frequently in the pre-metamorphic stomachs. Hemipterans (3.8%), collembollans (3.1%), adult plecopterans (1.5%), and oligochaetes (2.3%) occurred in small numbers of the pre-metamorphic individuals. Diplopods and pseudoscorpions each occurred in one salamander stomach.

Figure 20. Percent of pre-metamorphic *Desmognathus quadramaculatus* containing a given invertebrate taxa.

STOMACH CONTENTS FOR PRE-METAMORPHIC

Desmognathus quadramaculatus

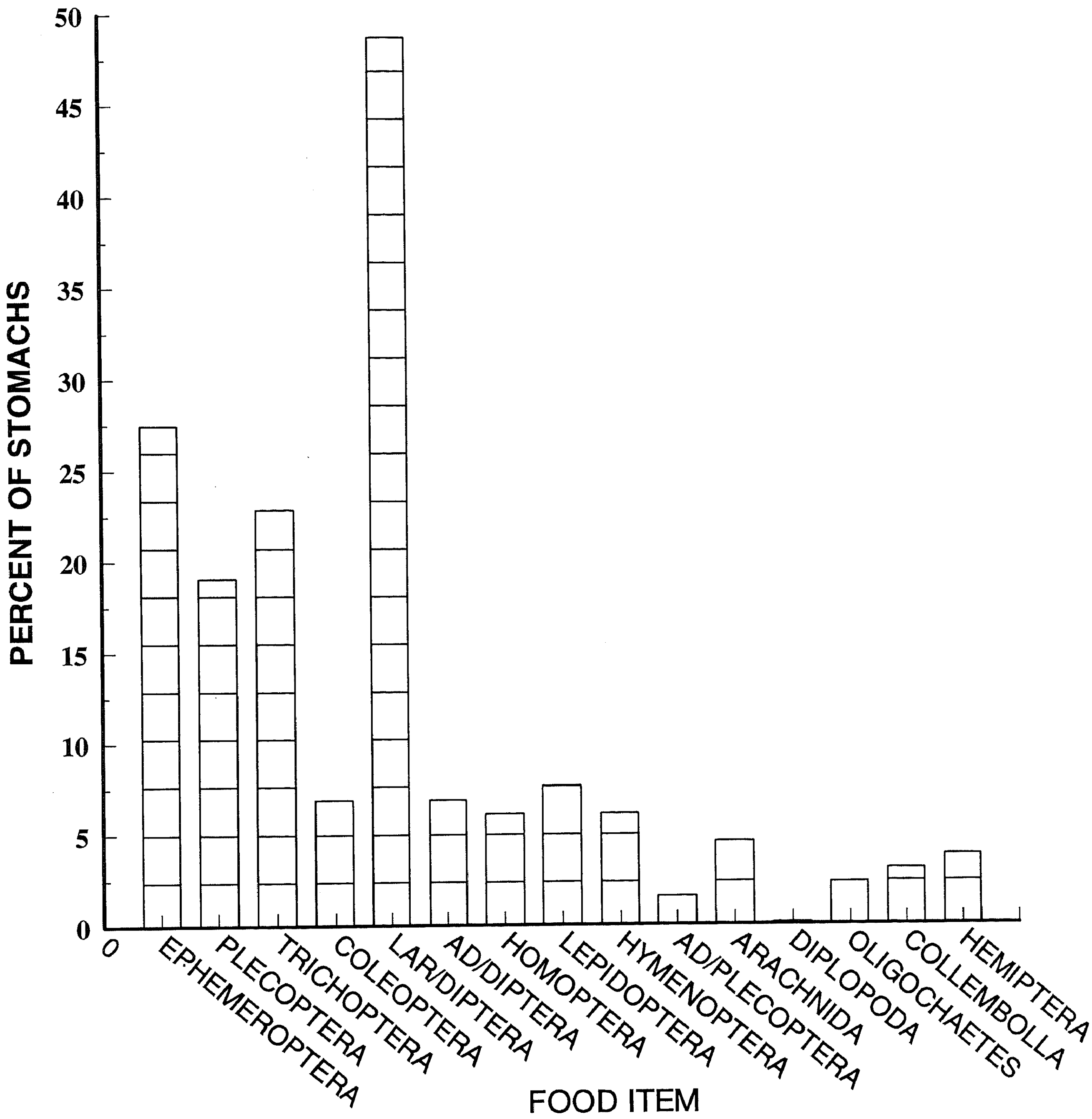
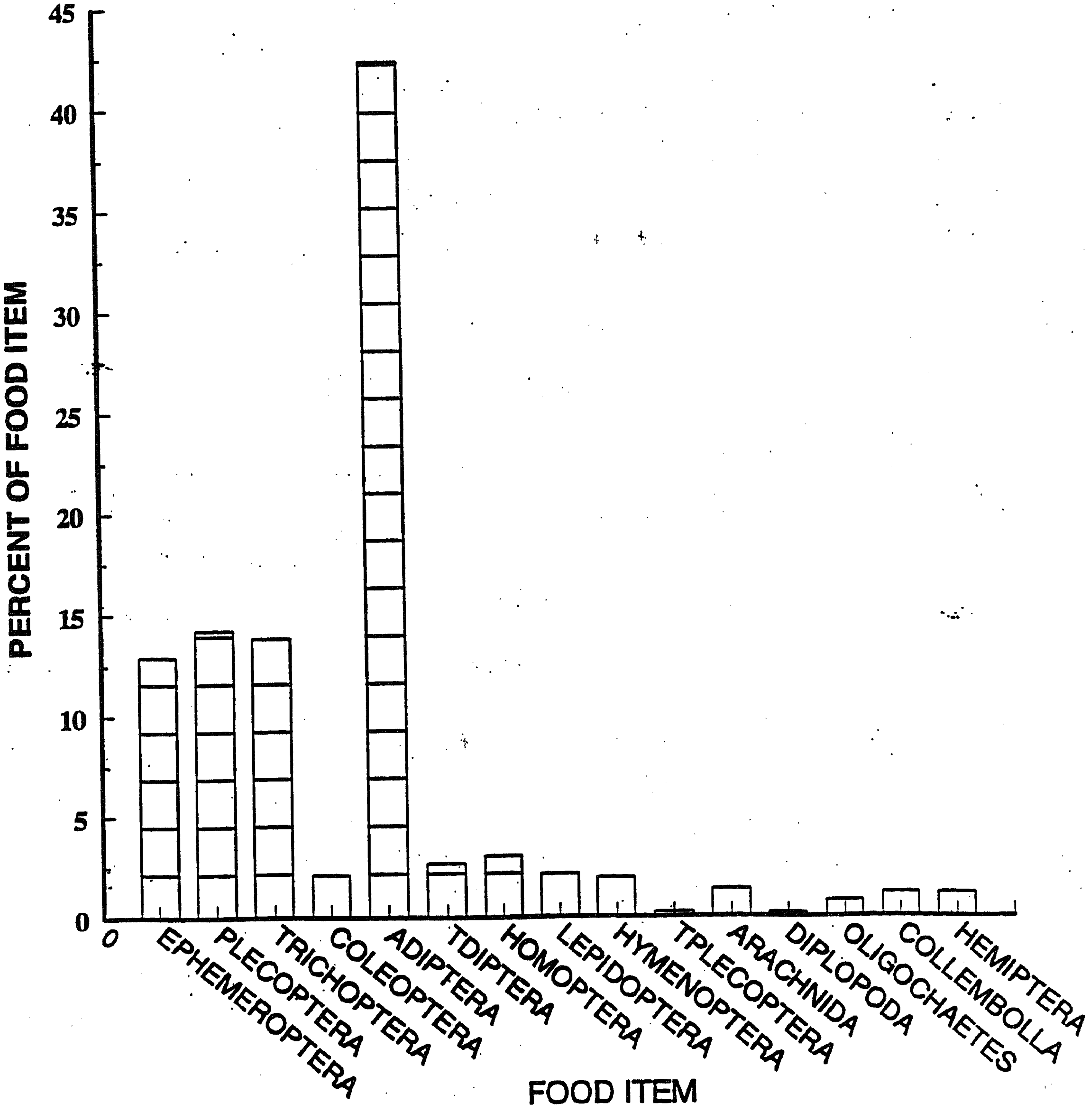


Figure 21. Pre-metamorphic _Desmognathus quadramaculatus_ invertebrate dietary composition.

FOOD ITEMS CONSUMED BY PRE-METAMORPHIC

Desmognathus quadramaculatus



The dietary composition of pre-metamorphic D. quadramaculatus was dominated by larval dipterans comprising 227 (42.7%) of the 535 items consumed (Figure 21). Nymphal plecopterans made up 76 (14.2%) items while larval trichopterans comprised 74 (13.8%) prey items. Nymphal ephemeropterans made up 69 (12.9%) prey items while homopterans comprised 3.0% of the items found. Representatives of adult dipterans made up 2.6% of the diet while terrestrial coleopterans and lepidopterans each comprised 2.1% of the dietary items. Hymenopterans were found to make up 1.9% while arachnids only comprised 1.3% of the total items identified. Hemipterans and collembollans each were found to comprise 1.1%. Oligochaetes (0.8%), nymphal plecopterans (0.4%), pseudoscorpions (0.2%), and diplopods (0.2%) were found in the diet infrequently.

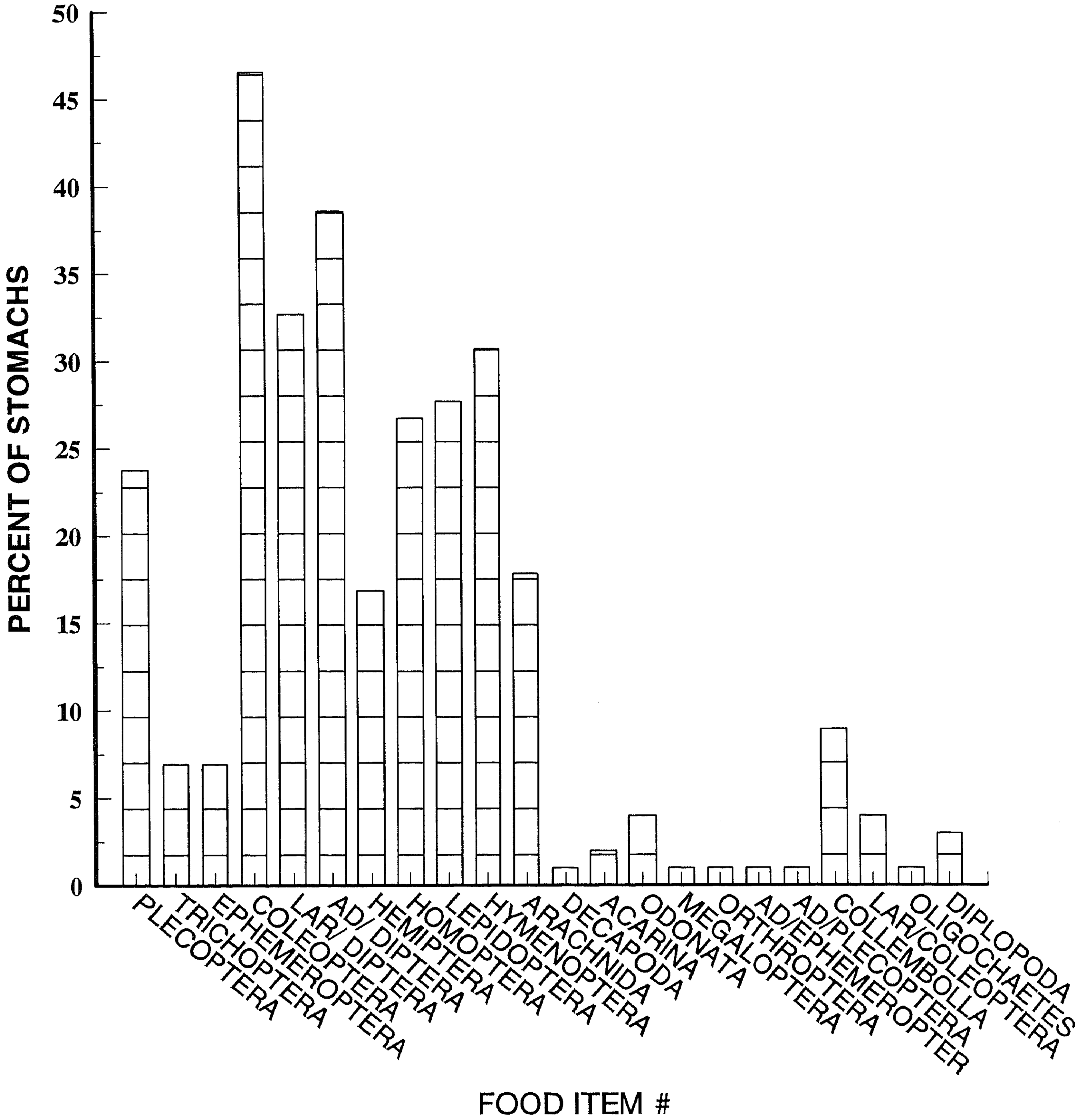
Post-metamorphic Diet

Examining the dietary differences of pre- and post-metamorphic D. quadramaculatus helped to highlight the intraspecific competitive avoidance Bruce (1988) defined. The largest component of post-metamorphic D. quadramaculatus was adult dipterans that made up 94 (16.9%) of the dietary items (Figure 22). Both terrestrial coleopterans and larval dipterans each made up 93 (16.8%) of the 555 items found. Hymenopterans had 56 (10.1%) of the 555 items of the post-metamorphic diet while lepidopterans had 43 (7.8%) items. Homopterans was found to contain 40 (7.2%) of the 555 items. Nymphal plecopterans contained 35 (6.3%) and hemipterans contained 28 (5.1%) of the dietary items identified. Arachnids made up 4.1% of the diet and

Figure 22. Percent of post-metamorphic <u>Desmognathus quadramaculatus</u> containing a given invertebrate taxa.

STOMACH CONTENTS FOR POST-METAMORPHIC

Desmognathus quadramaculatus



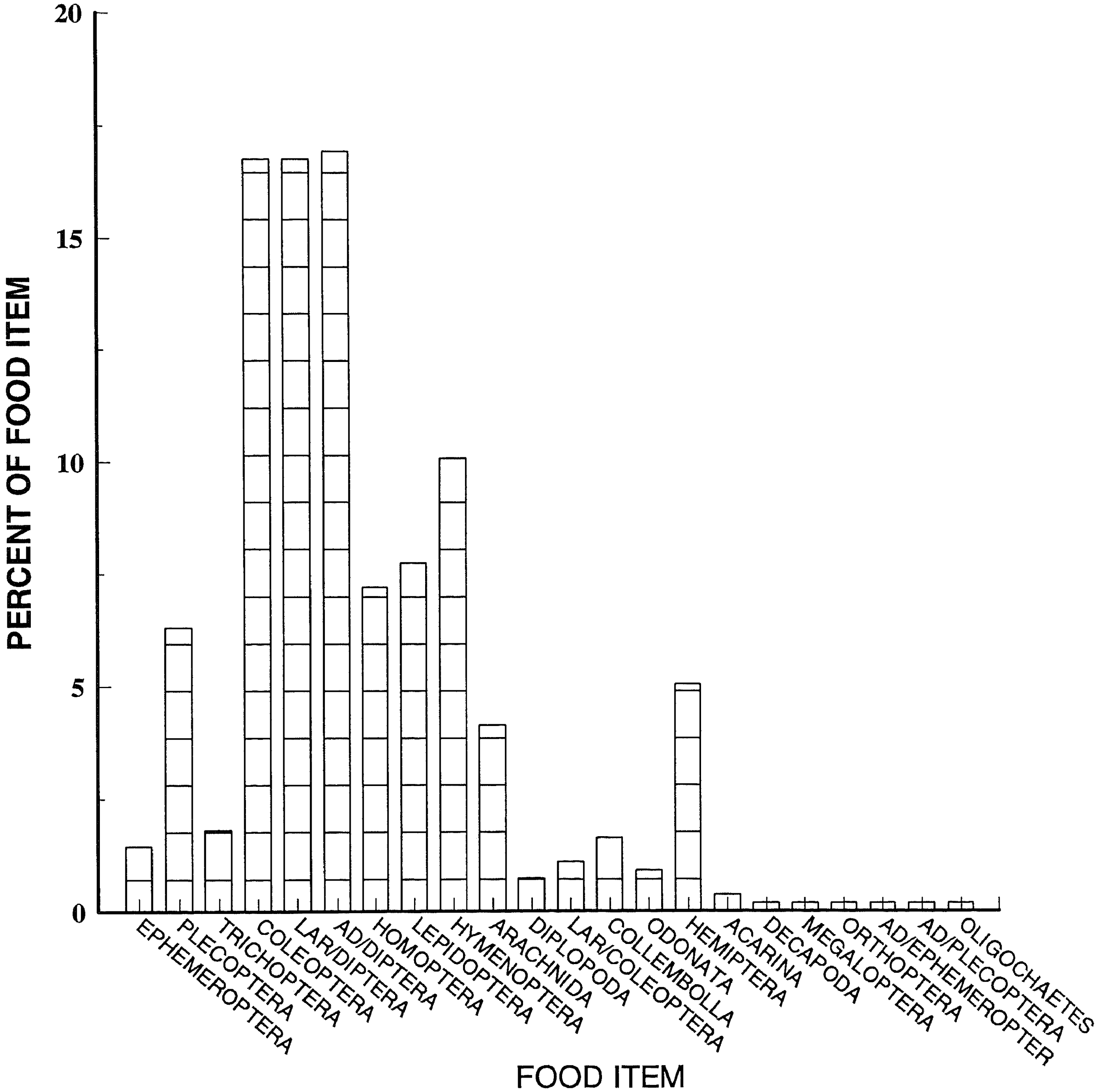
larval trichopterans made up 1.8%. Collembollans (1.6%), nymphal ephemeropterans (1.4%), aquatic coleopterans (1.1%), odonates (0.9%), diplopods (0.7%), and acarinids (0.4%) made up a small portion of the diet , but may be important in a seasonal perspective. Representatives of certain invertebrate taxa (decapods, megalopterans, orthopterans, adult ephemeropterans, adult plecopterans, and oligochaetes) were each found to occur only once in the diet of D. quadramaculatus.

The dietary composition of post-metamorphic D. quadramaculatus did not proportionally match the occurrence of the invertebrate groups in the guts (Figure 23). Adult dipterans composed the highest percentage of the dietary items, but was second most common in the number of specimens it occurred. Terrestrial coleopterans were found in 47 (46.5%) of the 101 specimens examined while adult dipterans were found in 39 (38.6%) of the 101 specimens. Larval dipterans occurred in 33 (32.7%) salamanders while hymenopterans were found in 31 (30.7%). Lepidopterans were found in 28 (27.7%) salamanders and homopterans were found in 27 (26.7%)salamanders. Nymphal plecopterans were found in 24 (23.8%) salamanders while arachnids occurred in 18 (17.8%). Hemipterans were found in 17 (16.8%) of the post-metamorphic D. quadramaculatus examined. Collembollans occurred in nine (8.9%) stomachs while both nymphal ephemeropterans and larval trichopterans were found in seven (6.9%). Odonates and aquatic coleopterans each occurred in four (4.0%) salamanders while diplopods occurred in three (3.0%).

Figure 23. Post-metamorphic <u>Desmognathus quadramaculatus</u> invertebrate dietary composition.

FOOD ITEMS CONSUMED BY POST-METAMORPHIC

Desmognathus quadramaculatus



Acarinids occurred in 2.0% of the post-metamorphic salamanders. Decapods, megalopterans, adult ephemeropterans, adult plecopterans, and oligochaetes were found in one salamander.

Spring Diet of Pre-metamorphic Salamanders

When looking at the dietary differences between pre- and post-metamorphic D. quadramaculatus, one must examine seasonal trends separately. Larval dipterans were found to occur in seven (35.0%) of the 20 pre-metamorphic D. quadramaculatus examined in the spring season(Figure 24). This was followed by nymphal ephemeropterans occurring in five (25%) pre-metamorphs while larval trichopterans were found in 4 (20%) salamanders of the total surveyed. Nymphal plecopterans occurred in three (15.0%) salamanders while hymenopterans were found in two (10.0%). Terrestrial coleopterans, adult dipterans, arachnids, oligochaetes each occurred in one of the pre-metamorphic salamanders collected.

The diet of the 20 pre-metamorphic D. quadramaculatus collected in the spring season consisted of 64 items (Figure 25). Larval dipterans comprised 30 (46.8%) items while nymphal ephemeropterans made up 14 (21.9%) items. Nymphal plecopterans and larval trichopterans each were found seven (10.9%) times in the diet. Hymenopterans were found to comprise two (3.1%) items of the diet while adult dipterans, arachnids, terrestrial coleopterans, and oligochaetes only occurred once.

Spring Diet of Post-metamorphic Salamanders

While the pre-metamorphic salamanders were found to have fed

Figure 24. Percent of pre-metamorphic Desmognathus quadramaculatus containing a given invertebrate taxa in the spring season.

SPRING STOMACH CONTENTS FOR PRE-METAMORPHIC *Desmognathus quadramaculatus*

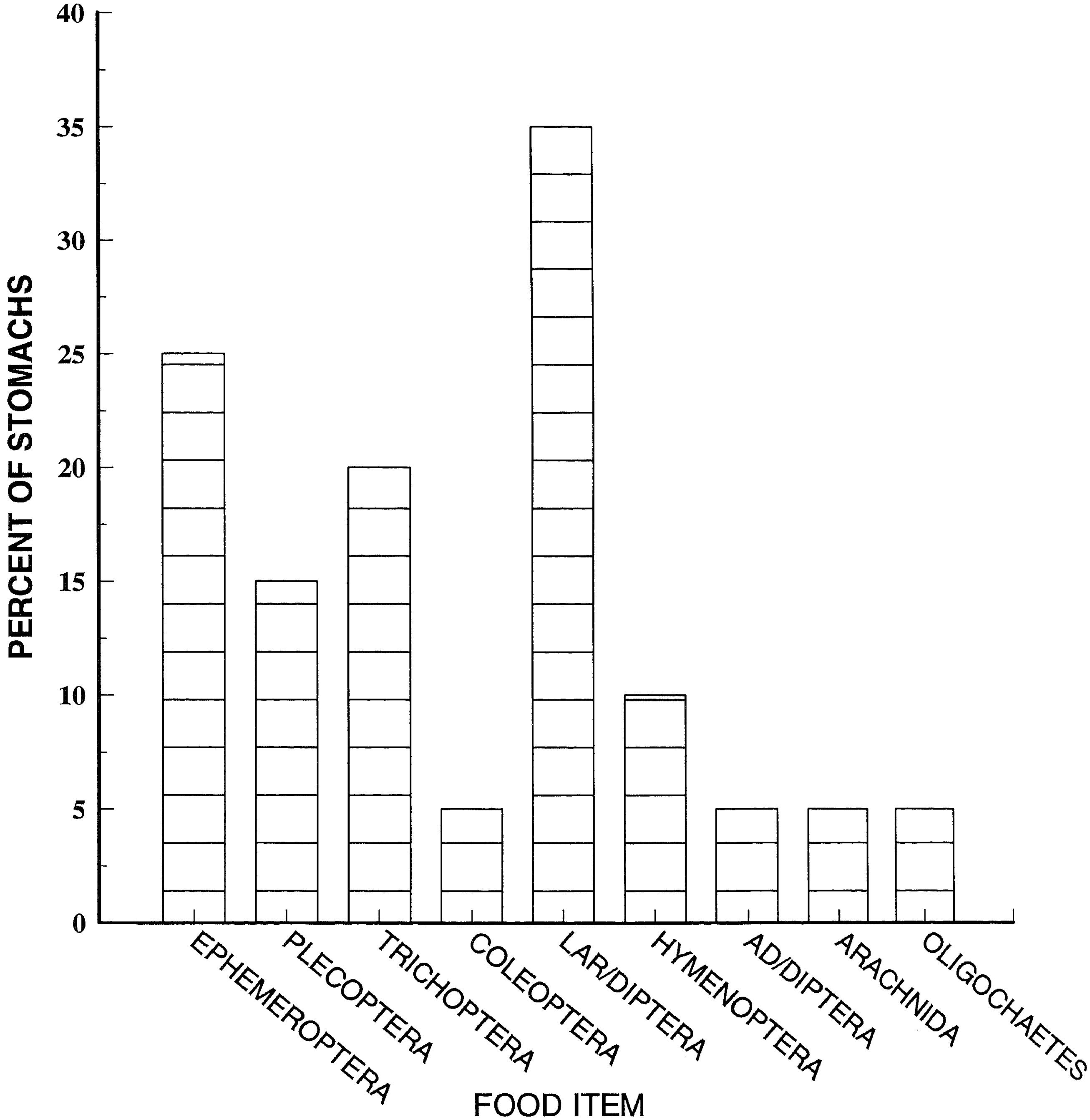
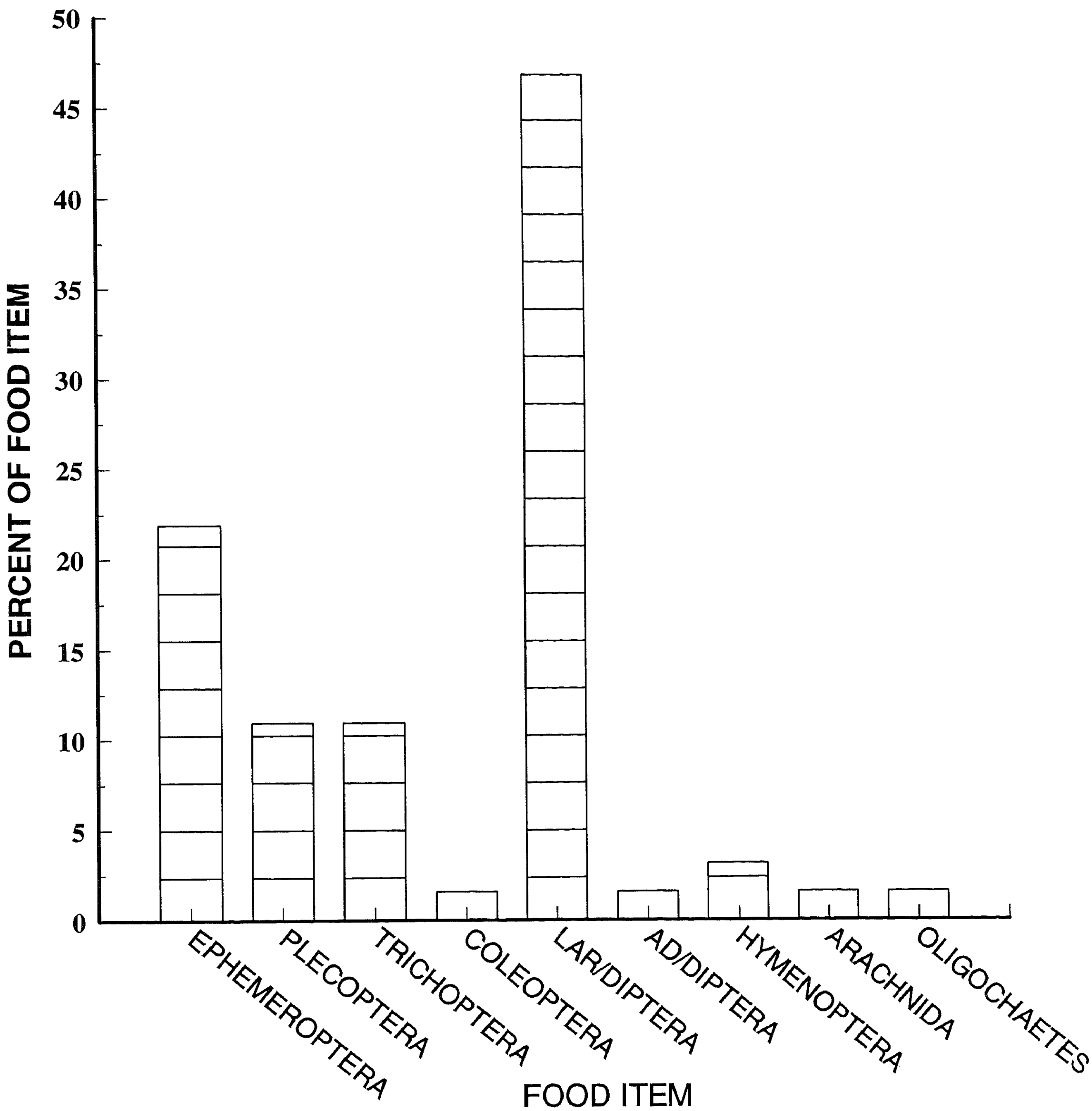


Figure 25. Pre-metamorphic *Desmognathus quadramaculatus* invertebrate dietary composition in the spring season.

FOOD ITEMS CONSUMED BY PRE-METAMORPHIC

Desmognathus quadramaculatus **IN THE SPRING SEASON**



on primarily aquatic invertebrate groups in the spring season, the post-metamorphic salamanders had terrestrial invertebrate groups composing the greatest portion of their diet during this season. Terrestrial coleopterans occurred in 18 (64.3%) of the 28 post-metamorphic D. quadramaculatus stomachs examined in the spring season (Figure 26). Adult dipterans occurred in 13 (46.4%) salamanders while hymenopterans were found in 9 (32.1%) guts. Lepidopterans occurred in eight (28.6%) of the 28 stomachs while hemipterans and nymphal plecopterans were found in seven (25.0%) salamanders. Larval dipterans occurred in six (21.4%) of the salamanders examined while homopterans and arachnids each occurred in five(17.9%). Collembollans and nymphal ephemeropterans each were found in four(14.4%) of the post-metamorphs while diplopods occurred in three(10.7%). Larval trichopterans representatives were found in two(7.1%) while nymphal ephemeropterans and odonates both occurred in one (3.6%) of the post-metamorphic salamanders examined.

The invertebrate groups that made up the diet of the post-metamorphic D. quadramaculatus in the spring season were predominately terrestrial (Figure 27). Of the 171 food items identified, Terrestrial coleopterans and adult dipterans each made up 44 (25.7%) items while hymenopterans comprised 15 (8.8%) items. Larval dipterans made up 7.0% of the dietary items while lepidopterans comprised 5.9% of the diet. Nymphal plecopterans made up 4.7% of the invertebrate items while hemipterans and arachnids each comprised 4.1%. Homopterans (3.5%), nymphal

Figure 26. Percent of post-metamorphic *Desmognathus quadramaculatus* containing a given invertebrate taxa in the spring season.

SPRING STOMACH CONTENTS FOR
POST-METAMORPHIC *Desmognathus quadramaculatus*

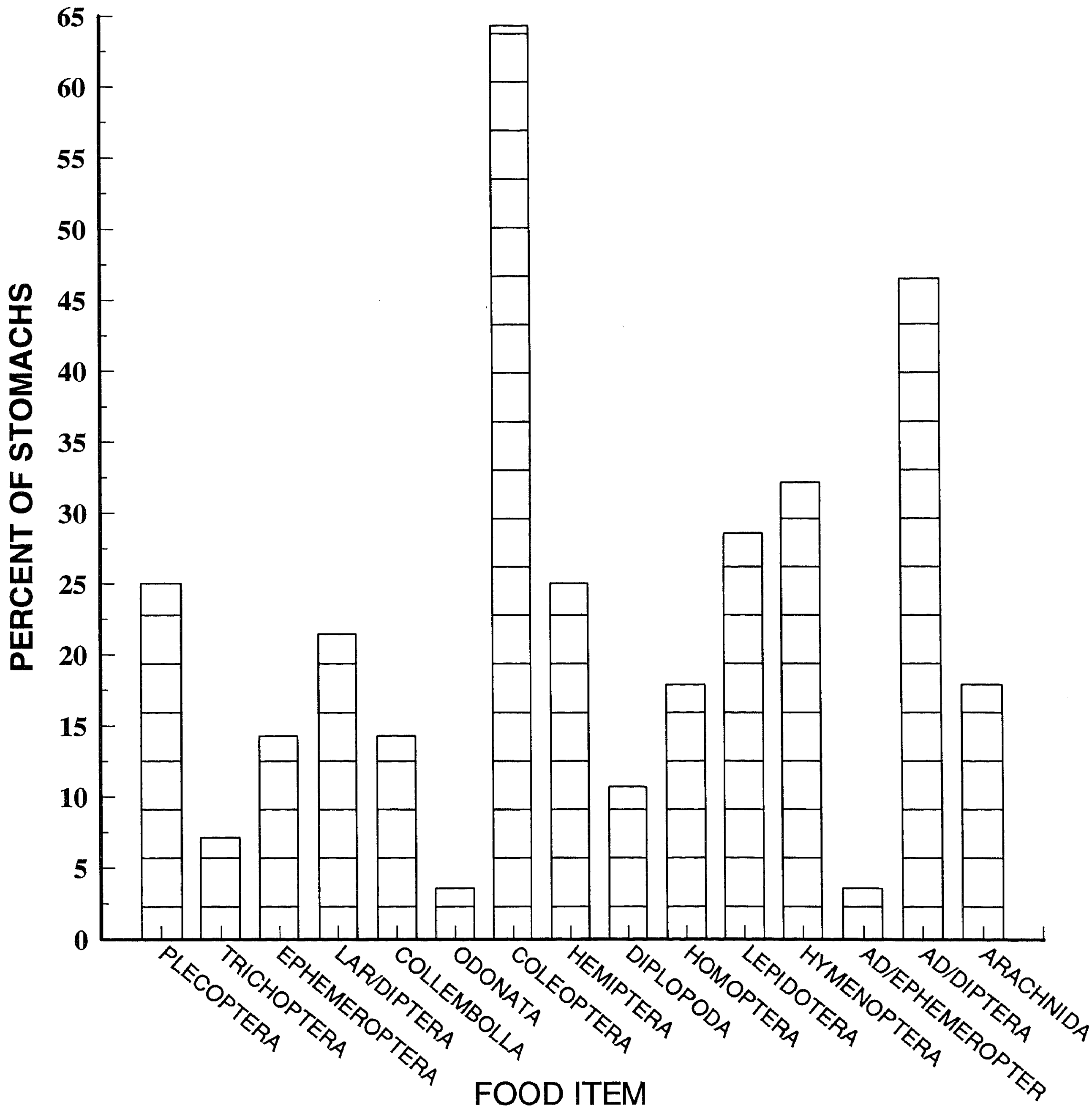
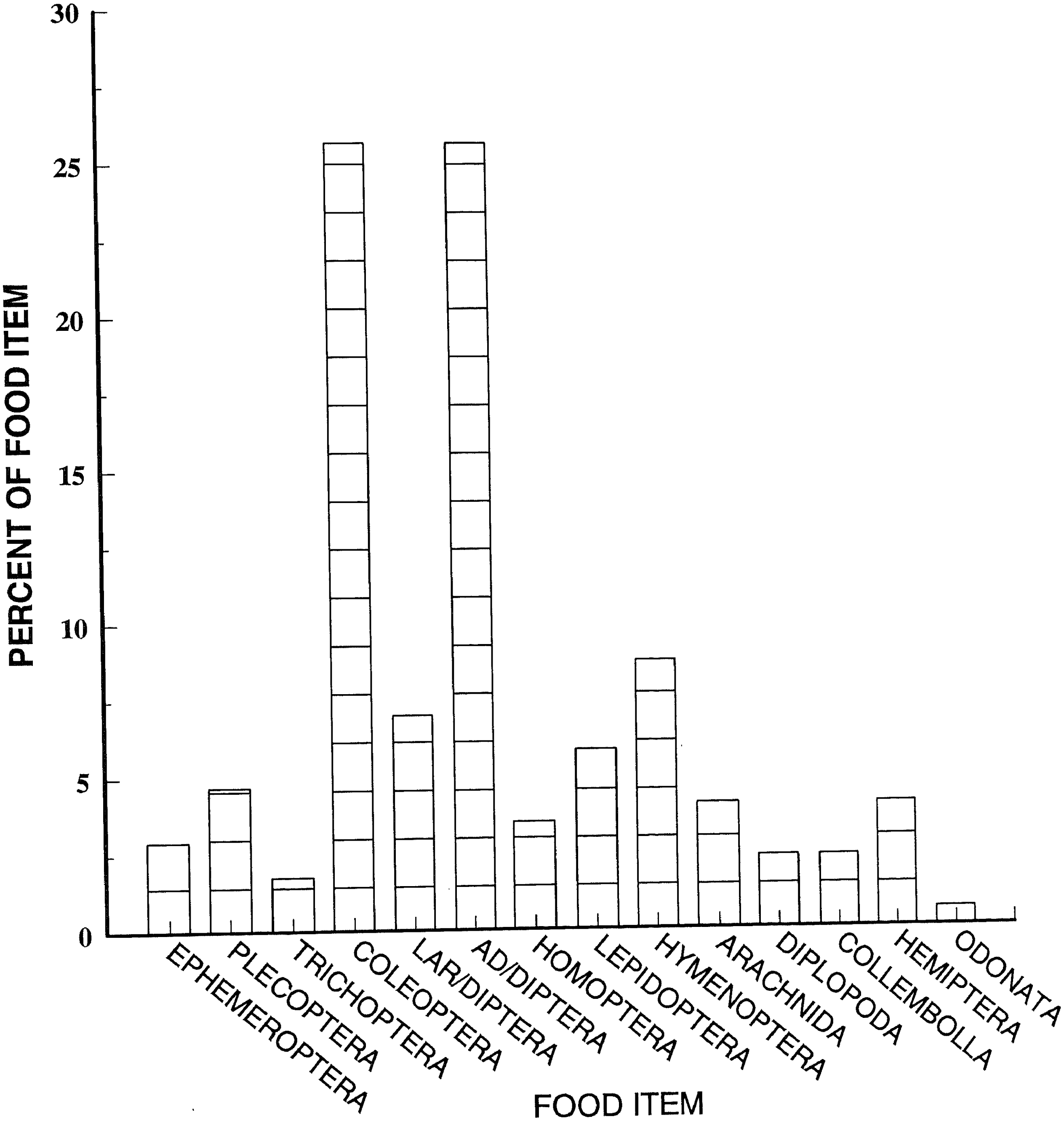


Figure 27. Post-metamorphic *Desmognathus quadramaculatus* invertebrate dietary composition in the spring season.

FOOD ITEMS CONSUMED BY POST-METAMORPHIC

***Desmognathus quadramaculatus* IN THE SPRING SEASON**



ephemeropterans (2.9%), collembollans (2.3%), diplopods (2.3%), larval trichopterans (1.8%). Odonates and nymphal ephemeropterans were found to occur once.

Summer Diet of Pre-metamorphic Salamanders

In the summer, larval dipterans were found in 16 (41.0%) of the 39 pre-metamorphic Desmognathus quadramaculatus examined (Figure 28). Nymphal ephemeropterans and lepidopterans each were found in nine (23.1%) of the 39 pre-metamorphic salamanders. Adult dipterans and aquatic trichopterans occurred in six (15.4%) of the pre-metamorphic salamanders examined, while terrestrial coleopterans, hymenopterans, and arachnids occurred in 12.8%. Hemipterans, collembollans, and homopterans were found in 7.7% of the summertime pre-metamorphic D. quadramaculatus. The invertebrate taxa of nymphal plecopterans, adult plecopterans, and pseudoscorpions occurred in 2.6% of the salamanders examined.

The summer diet of pre-metamorphic D. quadramaculatus, aquatic Diptera made up 50 (38.9%) of the 132 items of the overall organisms consumed (Figure 29). This was followed by nymphal ephemeropterans making up 17 (12.9%) items while adult dipterans comprised 11 (8.3%) items. Larval trichopterans and lepidopterans each comprised ten(7.6%) of the total items found while terrestrial coleopterans made up seven(5.3%). Hymenopterans and arachnids each made up six(4.6%) items while homopterans comprised five(3.8%). Hemipterans made up four(3.0%) items of the diet and collembollans comprised three(2.3%). Nymphal plecopterans, adult plecopterans, and pseudoscorpions were found

Figure 28. Percent of pre-metamorphic Desmognathus quadramaculatus containing a given invertebrate taxa in the summer season.

SUMMER STOMACH CONTENTS FOR PRE-METAMORPHIC *Desmognathus quadramaculatus*

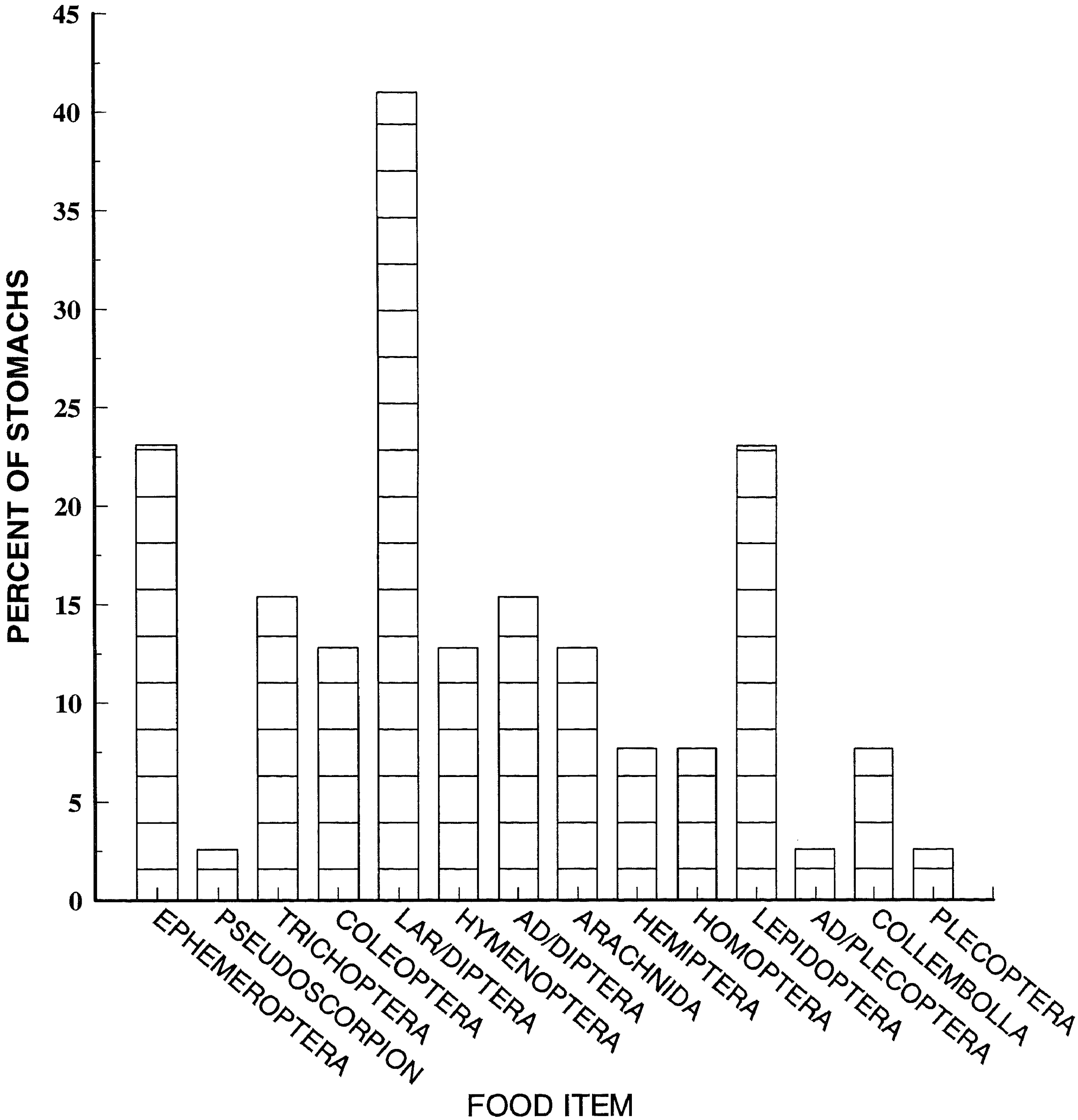
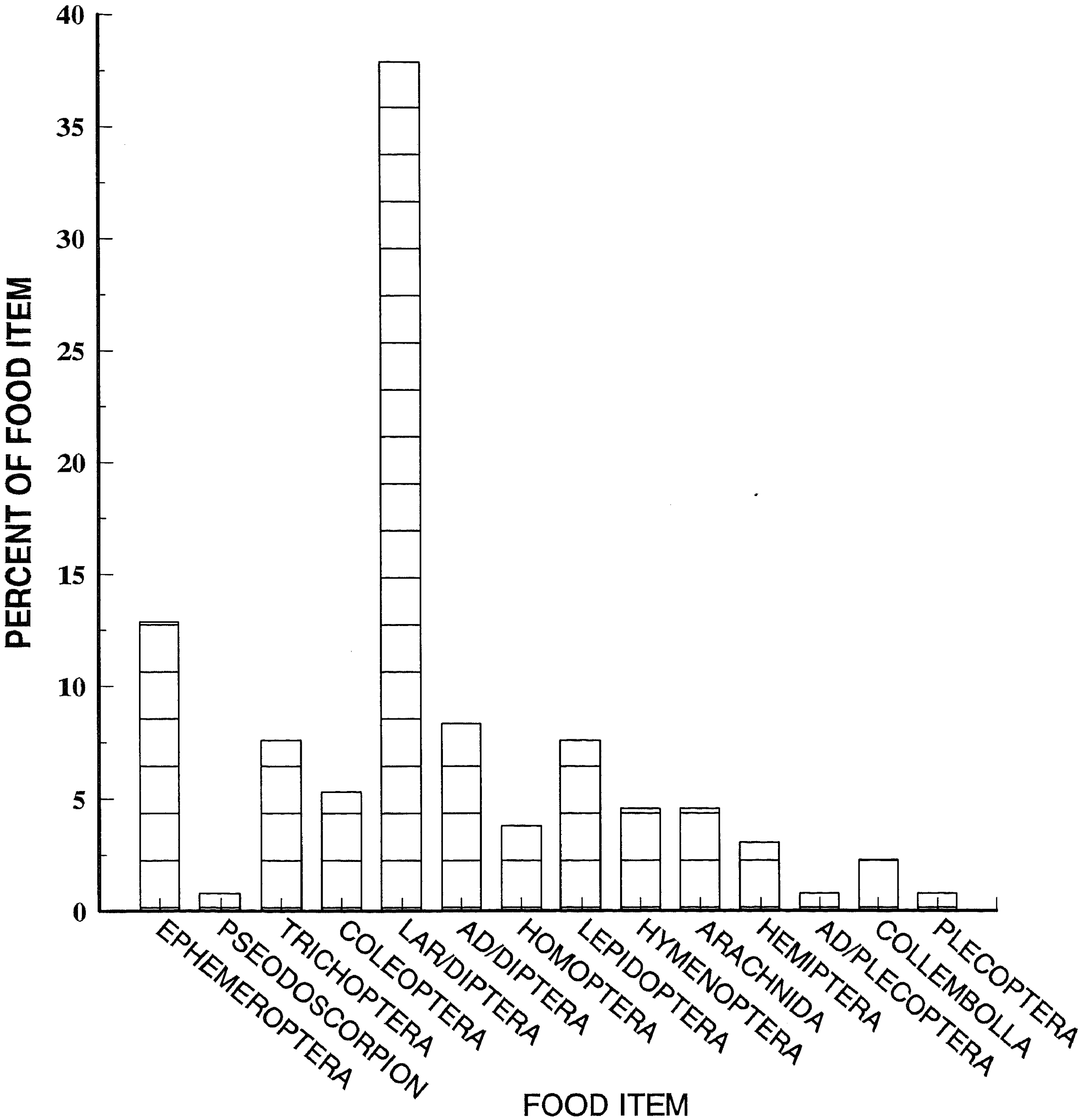


Figure 29. Pre-metamorphic *Desmognathus quadramaculatus* invertebrate dietary composition in the summer season.

FOOD ITEMS CONSUMED BY PRE-METAMORPHIC

Desmognathus quadramaculatus **IN THE SUMMER SEASON**



once in the diet making up 0.8% of the total organisms.

Summer Diet of Post-metamorphic Salamanders

During the summer months, the post-metamorphic D. quadramaculatus could be seen foraging terrestrially along the edge of the streams. This activity would lead one to believe that their diet would be made up of terrestrial insects. Dissection of salamanders from the summer season found lepidopterans to occur in 19 (46.3%) of the 41 specimens examined (Figure 30). This was closely followed by adult dipterans and terrestrial coleopterans, each occurring in 18 (43.9%) of the 41 post-metamorphs. Larval dipterans was found to occur in 15 (36.6%) of the post-metamorphs, while hymenopterans occurred in 14 (34.2%) specimens. The terrestrial insect order Homoptera was found in 11 (26.8%) of the post-metamorph stomachs while nymphal plecopterans occurred in 18 (24.4%) of the 41 salamanders. The following insect taxa are listed in descending order of occurrence in the post-metamorph stomachs: arachnids (22.0%), hemipterans (19.5%), aquatic coleopterans and collembollans each at 9.8%, odonates (7.3%), nymphal ephemeropterans (4.9%), adult plecopterans, orthopterans, and megalopterans each at 2.4%.

The summer diet of post-metamorphic D. quadramaculatus was a mixture of aquatic and terrestrial items (Figure 31). Larval dipterans made up 54 (21.2%) of the 255 items identified while adult dipterans comprised 37 (14.5%) items. Terrestrial coleopterans made up 32 (12.6%) items, while lepidopterans comprised 31 (12.2%) items. Hymenopterans made up 10.6%, while

Figure 30. Percent of post-metamorphic *Desmognathus quadramaculatus* containing a given invertebrate taxa in the summer season.

SUMMER STOMACH CONTENTS FOR

POST-METAMORPHIC *Desmognathus quadramaculatus*

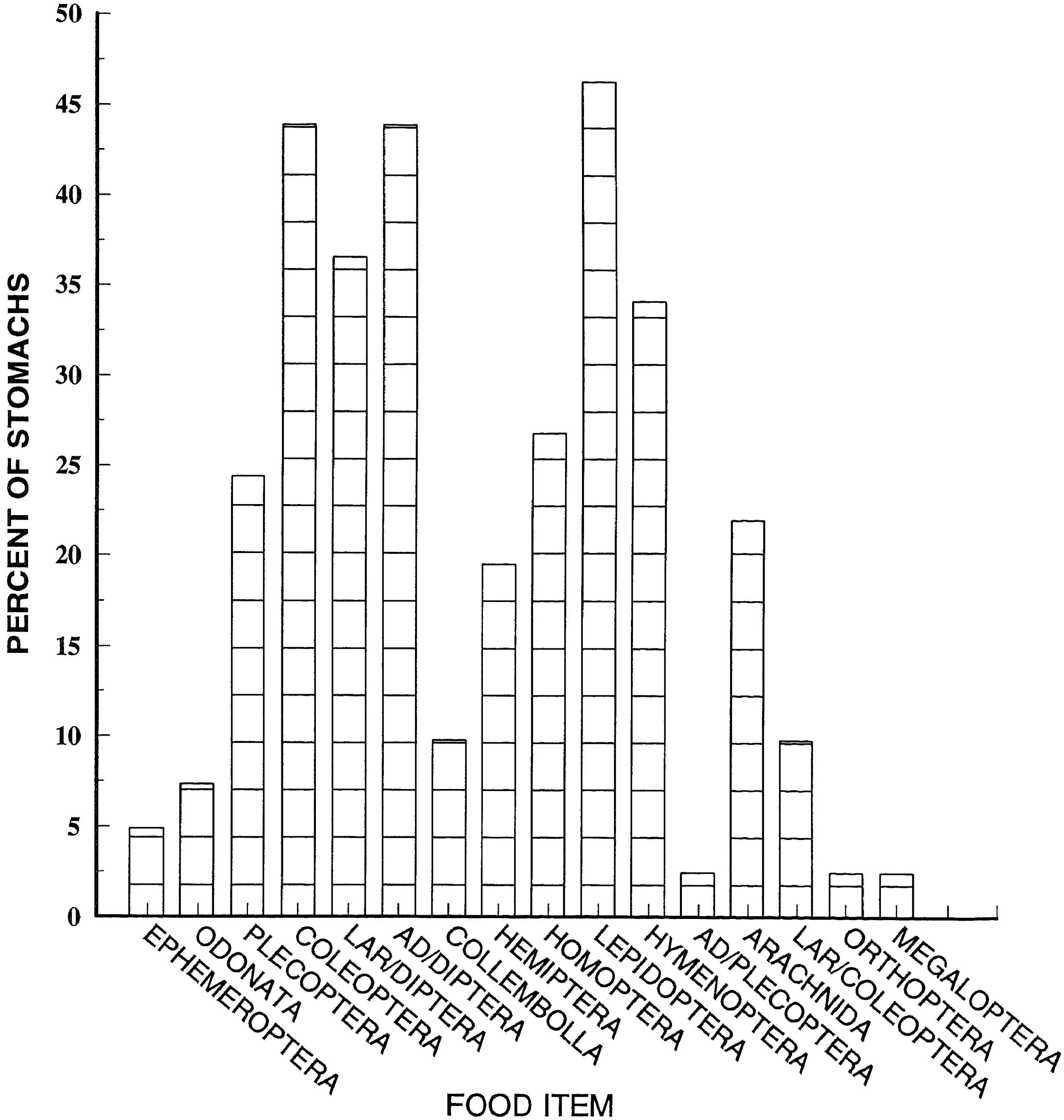
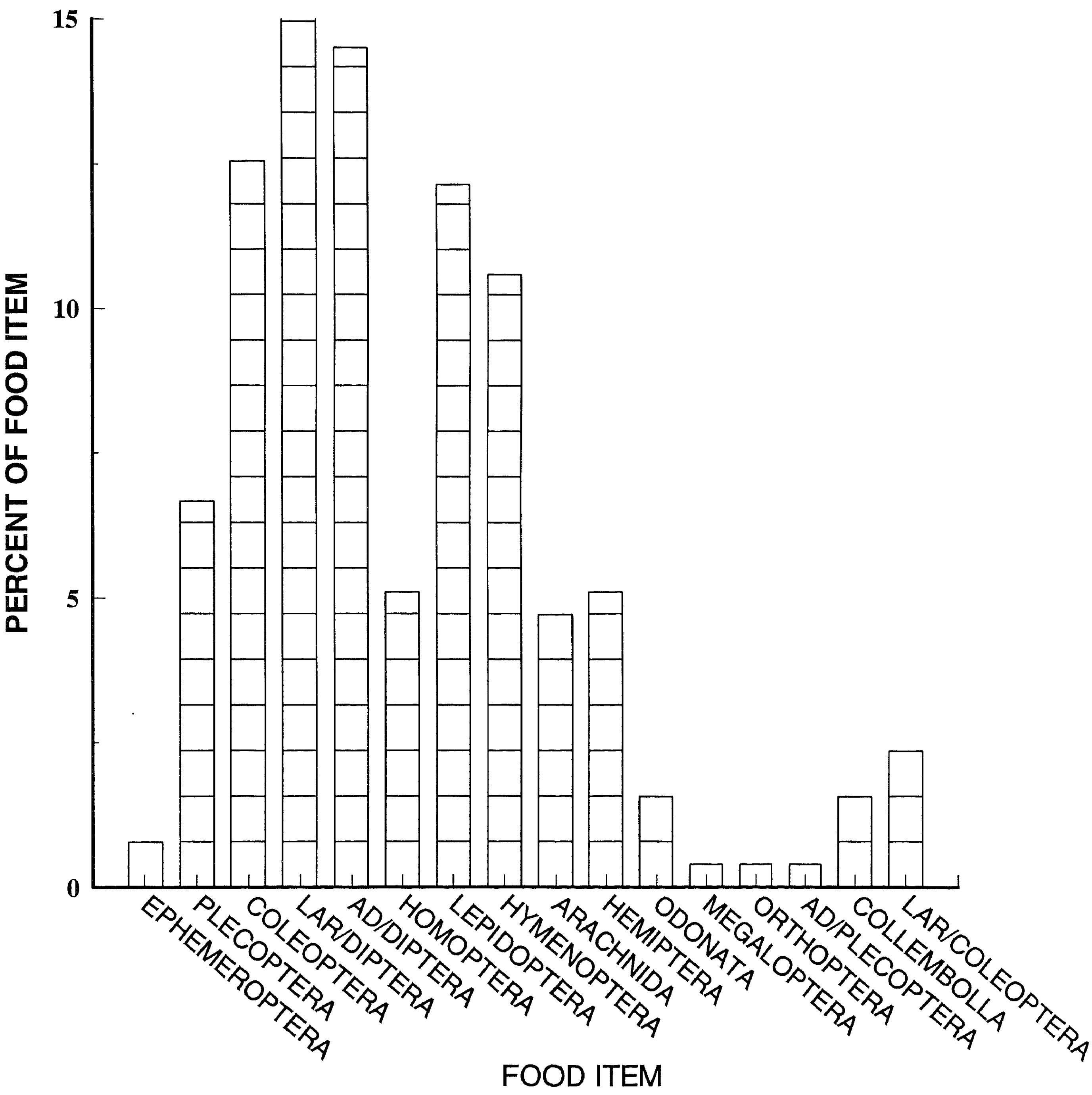


Figure 31. Post-metamorphic Desmognathus quadramaculatus invertebrate dietary composition in the summer season.

FOOD ITEMS CONSUMED BY POST-METAMORPHIC

Desmognathus quadramaculatus **IN THE SUMMER SEASON**



nymphal plecopterans comprised 6.7% of the dietary items. Hemipterans and homopterans each made up 5.1% of the total items while, arachnids comprised 4.7%. Larval coleopterans made up 2.4%, while collembollans and odonates were found to compose 1.6% of the post-metamorphic diet. Nymphal ephemeropterans at 0.8% along with megalopterans, orthropterans, and adult plecopterans each at 0.4% made up the smallest portion of the dietary items.

Fall Diet of Pre-metamorphic Salamanders

In the fall season, both pre-metamorphic and post-metamorphic D. quadramaculatus were observed foraging in water which would lead to the greatest degree of intraspecific competition. For this reason, this time period will be analyzed by season and then by months. Larval dipterans were found to occur in 24 (63.2%) of the 38 pre-metamorphic salamanders (Figure 32). This was followed by nymphal plecopterans occurring in 13 (34.2%) pre-metamorphs while larval trichopterans were found in nine (23.7%). Nymphal ephemeropterans occurred in eight (21.1%) of the 38 pre-metamorphs collected in the fall. Homopterans were found in 13.2% of the pre-metamorphic salamanders examined while terrestrial coleopterans and hemipterans were found in 5.3%. Lepidopterans, Hymenopterans, adult plecopterans, adult dipterans, diplopods, and oligochaetes were found in 2.6% of the pre-metamorphic salamanders dissected.

Larval dipterans made up 108 (47.0%) of the 230 total prey items found in the gut contents of pre-metamorphic D. quadramaculatus that were collected in the fall (Figure 33).

Figure 32. Percent of pre-metamorphic <u>Desmognathus quadramaculatus</u> containing a given invertebrate taxa in the fall season.

FALL STOMACH CONTENTS FOR

Pre-metamorphic *Desmognathus quadramaculatus*

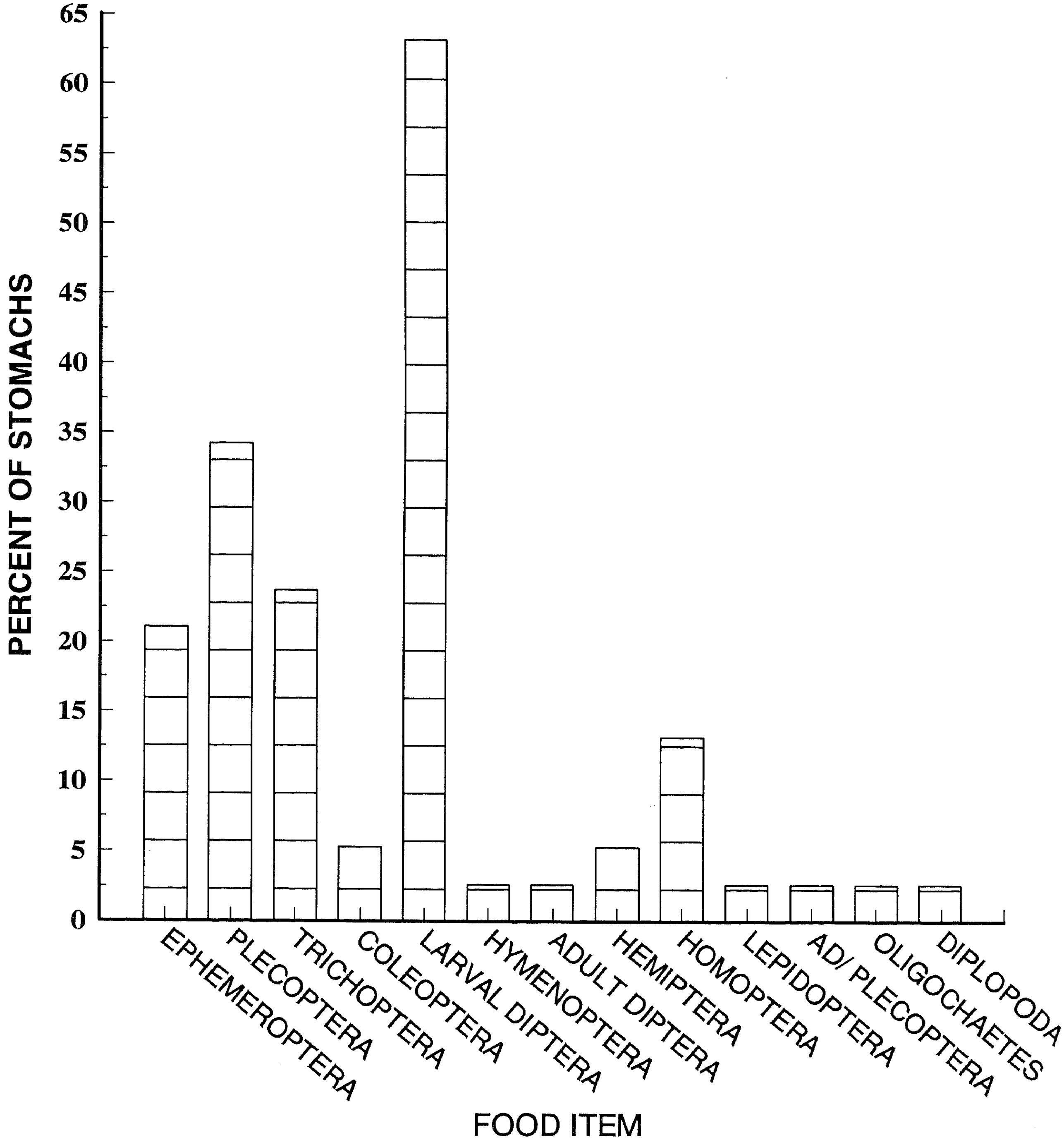
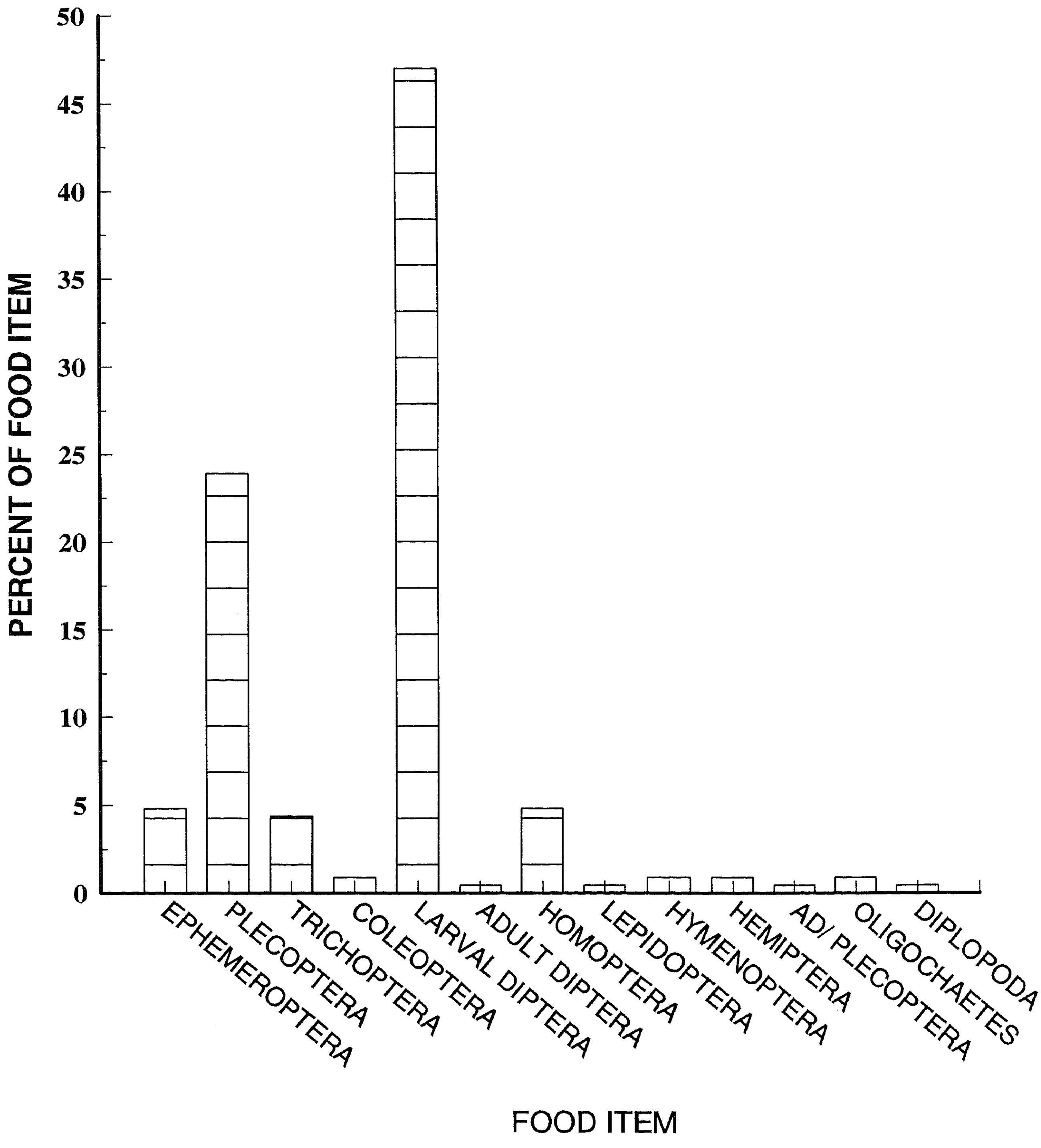


Figure 33. Pre-metamorphic <u>Desmognathus</u> <u>quadramaculatus</u> invertebrate dietary composition in the fall season.

FOOD ITEMS CONSUMED BY PRE-METAMORPHIC
Desmognathus quadramaculatus **IN THE FALL SEASON**



Nymphal plecopterans comprised 55 (23.9%) items while larval trichopterans made up 33 (14.4%) items. Nymphal ephemeropterans and homopterans each comprised 4.8% of the diet while terrestrial coleopterans, hemipterans, oligochaetes, and hymenopterans composed 0.9% of the diet. Lepidopterans, adult plecopterans, adult dipterans, and diplopods made up 0.4% individually which composed the remaining percentage of the gut contents from the fall collected pre-metamorphic D. quadramaculatus.

Fall Diet of Post-metamorphic Salamanders

In the fall, terrestrial coleopterans and homopterans were both found in 11 (42.3%) of the 26 post-metamorphic salamanders examined (Figure 34). Larval dipterans were found in 10 (38.5%) of the 26 post-metamorphs while hymenopterans and adult dipterans were found in eight (30.8%) of post-metamorphic D. quadramaculatus . Nymphal plecopterans occurred in six (23.1%) guts while arachnids and larval trichopterans were found in 15.4%. Hemipterans and acarinids occurred in 7.7%, while decapods and lepidopterans were found in 3.9%.

Larval dipterans comprised the greatest percentage of the fall diet of the post-metamorphic D. quadramaculatus making up 25 (20.5%) of the 122 items (35). It was closely followed by homopterans comprising 21 (17.2%), items while terrestrial coleopterans made up 17 (13.9%) items. Hymenopterans made up 14 (11.5%) items and adult dipterans comprised 10.7%. The remaining portion was made up of nymphal plecopterans (7.4%), hemipterans (6.6%), larval trichopterans (4.9%), arachnids (3.3%), acarinids

Figure 34. Percent of post-metamorphic *Desmognathus quadramaculatus* containing a given invertebrate taxa in the fall season.

FALL STOMACH CONTENTS FOR POST-METAMORPHIC

Desmognathus quadramaculatus

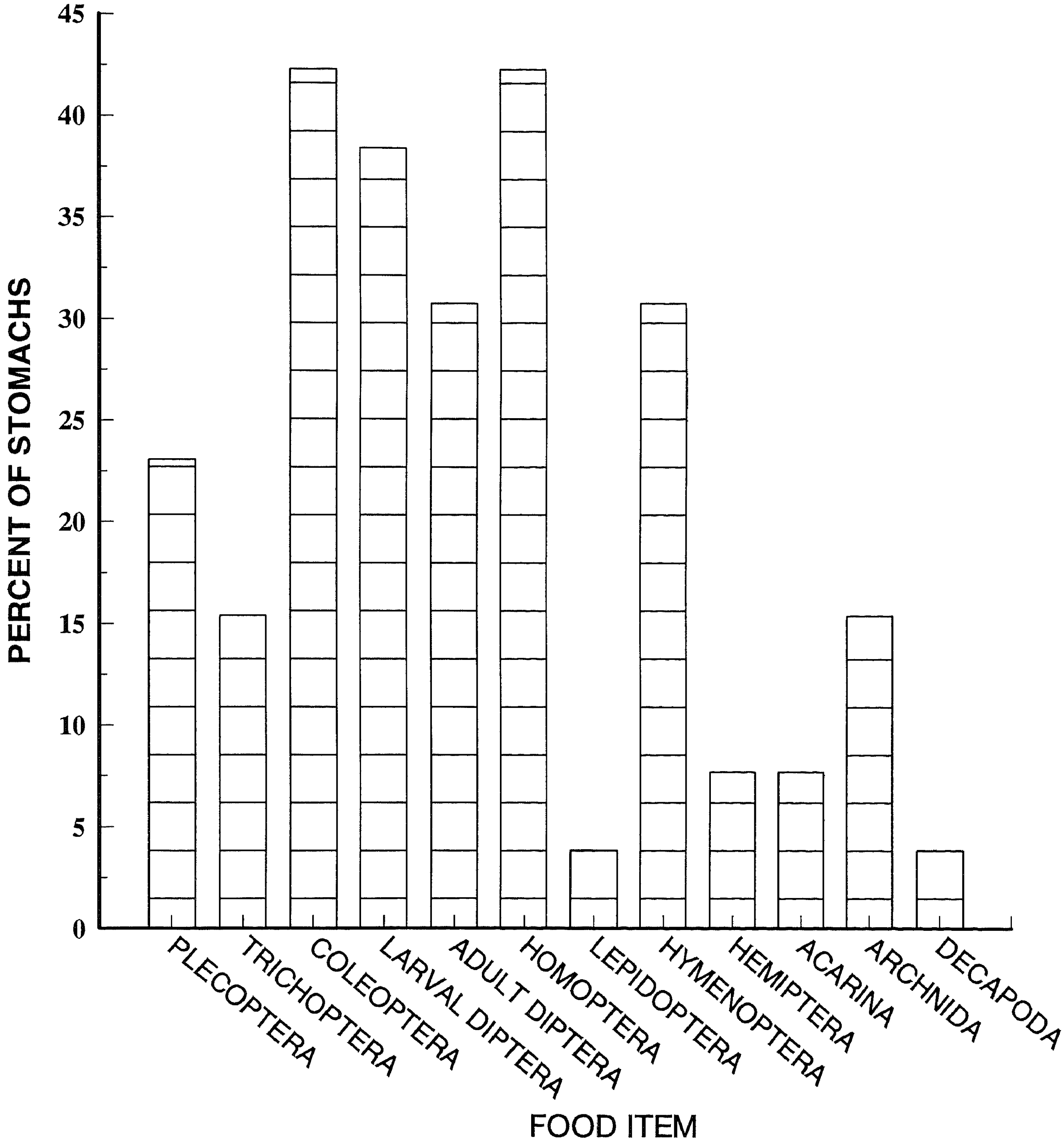
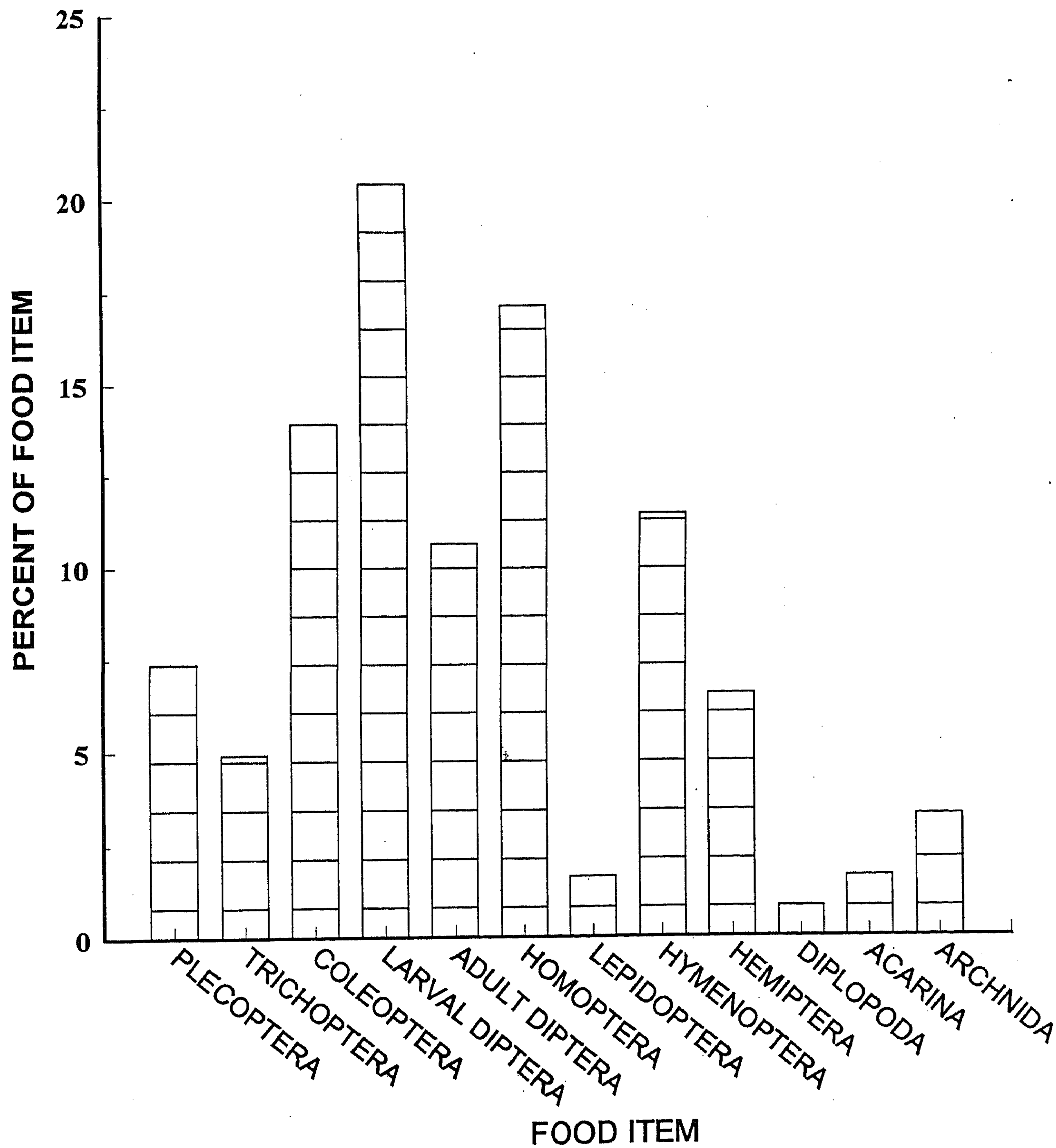


Figure 35. Post-metamorphic Desmognathus quadramaculatus invertebrate dietary composition in the fall season.

FOOD ITEMS CONSUMED BY POST-METAMORPHIC

D. quadramaculatus IN THE FALL SEASON



and lepidopterans each at 1.6%, and decapods 0.8% of the items.

Fall Season Monthly Breakdown of Diet

Analyzing the fall diets of the pre- and post-metamorphic D. quadramaculatus by seasons and months aides in the identification of the intraspecific competitive avoidance that occurred. In October, nine pre-metamorphic salamanders were collected ranging in SVL from 14.9 to 27.6 mm with a mean of 22.4 mm. The smallest of the nine salamanders had no gut contents. The remaining eight had consumed 78 organisms which were made up of 63 larval dipterans, 14 nymphal plecopterans, and one larval trichopterans. The larval dipterans can be further separated into tipulids(10) and larval chironomids(53).

There were two common genera of tipulids, Hexatoma and Tipula, inhabiting the stream. There were at least two cohorts of these genera which made them available for predation from the small pre-metamorphic salamanders and also the larger post-metamorphic salamanders. On October 9, post-metamorphic salamanders were collected with SVL ranging from 38.7- 56.7 mm with a mean of 43.9 mm. These post-metamorphic individuals consumed 26 invertebrates which included six homopterans, five terrestrial coleopterans, three hymenopterans (ants), two lepidopterans, two oligochaetes, one nymphal plecopterans, one larval dipterans, one adult dipterans, one acarinids, one diplopods, one hemipteran, one nymphal ephemeropteran, and one adult plecopteran. This can be summed up by stating that 100% of the pre-metamorphic diet was aquatic while the post-metamorphic diet was only 19.2% aquatic in October.

In November, the SVL's of pre-metamorphic salamanders ranged in size from 16.5- 37.2 mm with a mean of 28.7 mm and had a sample size of 21. Of 21 pre-metamorphic salamanders examined, three had no stomach contents. Eighteen pre-metamorphic D. quadramaculatus examined in November consumed 98 organisms, 40 of which were larval dipterans. Larval dipterans were further broken down to 37 larval chironomids and three tipulids. Nymphal plecopterans were next in abundance at 38. The remaining pre-metamorphic diet consisted of eight larval trichopterans, five homopterans, five nymphal ephemeropterans, one diplopods and one lepidopterans. In November, the pre-metamorphic diet consisted of 92.9% aquatic prey.

On November 10, post-metamorphic salamanders were collected with the SVL's ranging from 37.0- 57.1 mm with a mean of 43.5 mm. Of 10 post-metamorphs examined, one had no gut contents. The remaining nine post-metamorphic salamanders consumed 50 invertebrates and of these, 15 were dipterans. This included six adult dipterans, eight chironomids, and one tipulids. The remaining items identified were 10 hymenopterans, seven homopterans, four nymphal plecopterans, four larval trichopterans, four terrestrial coleopterans, three arachnids, one aquatic coleopteran, one acarinid, and one hemipteran. Terrestrial invertebrates made up 64.0% of the diet of post-metamorphic D. quadramaculatus in November.

In December, five pre-metamorphic salamanders and five post-metamorphic salamanders were examined and two of the pre-metamorphs had no gut contents. The pre-metamorphic salamanders' SVL's ranged from 16.9- 28.8 mm with a mean of 21.4 mm. The three remaining pre-metamorphic salamanders' diets consisted of 22 larval trichopterans, one adult dipteran, and one chironomid which is 95.8% aquatic prey. The post-metamorphic SVL ranged from 54.7- 77.1 mm with a mean of 66.7 mm. They were found to consume six homopterans, three chironomids, three terrestrial coleopterans, two nymphal plecopterans, two hymenopterans, two tipulids, one adult dipterans, one decapod, and one arachnid thus showing that 61.9% of the post-metamorphic diet was made up of terrestrial invertebrates.

Winter Diet of Pre-metamorphic Salamanders

In the winter season, 17 (50%) pre-metamorphic D. quadramaculatus out of 34 examined were found to have larval dipterans within their gut contents (Figure 36). In this season, many of the regularly occurring insect orders were missing from the stomach contents. Nymphal ephemeropterans were found in 14 (41.2%) of the pre-metamorphic salamanders while larval trichopterans were found in 11 (32.4%). Nymphal plecopterans were found in 8 (23.5%) of pre-metamorphic D. quadramaculatus. Terrestrial coleopterans, adult dipterans, collembollans, and oligochaetes were all found in 2.9% of the pre-metamorphic salamanders.

Larval dipterans composed 39 (35.8%) of the 109 organisms found in the guts of the pre-metamorphs (Figure 37). Nymphal

Figure 36. Percent of pre-metamorphic *Desmognathus quadramaculatus* containing a given invertebrate taxa in the winter season.

WINTER STOMACH CONTENTS FOR

PRE-METAMORPHIC *Desmognathus quadramaculatus*

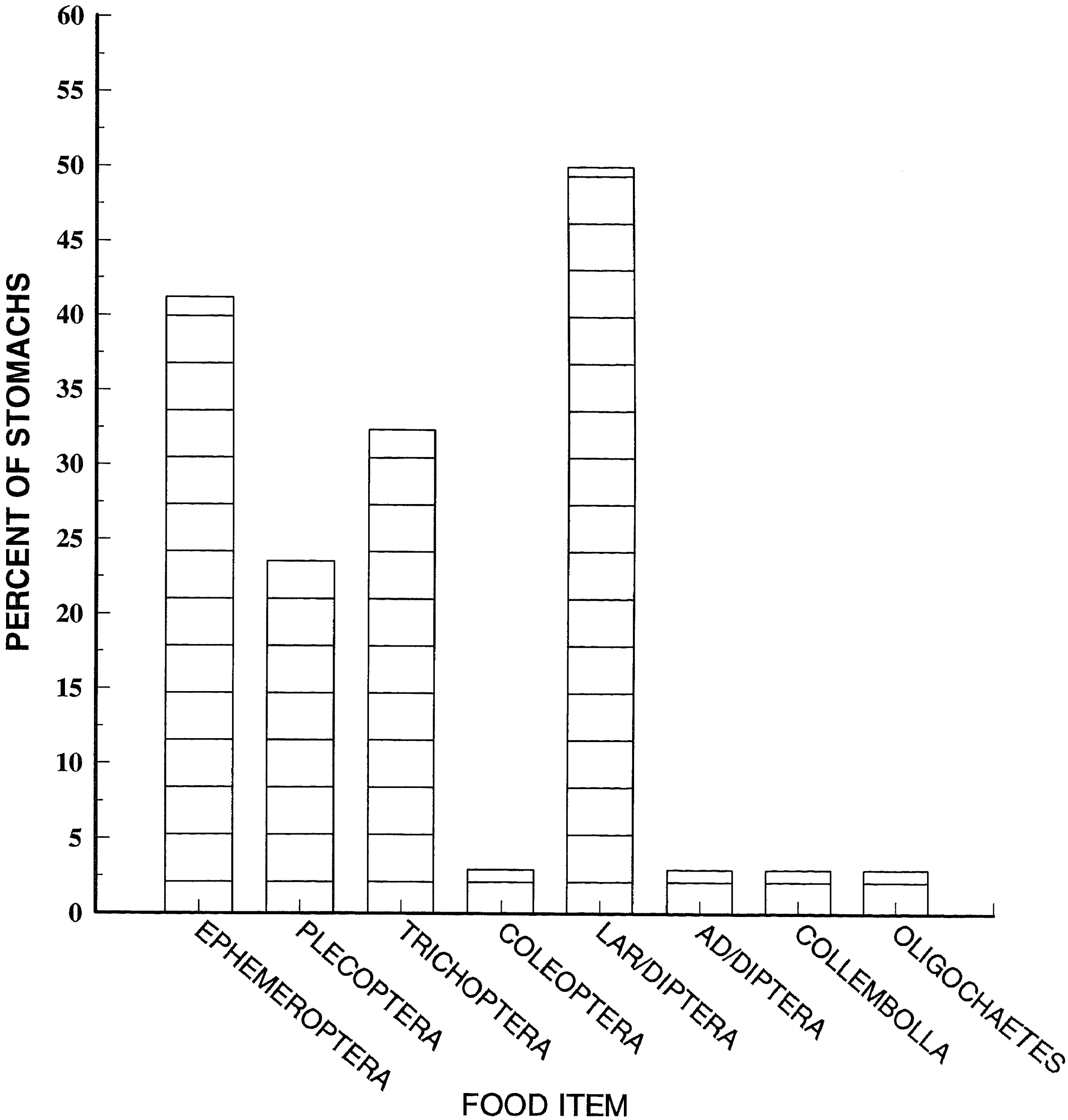
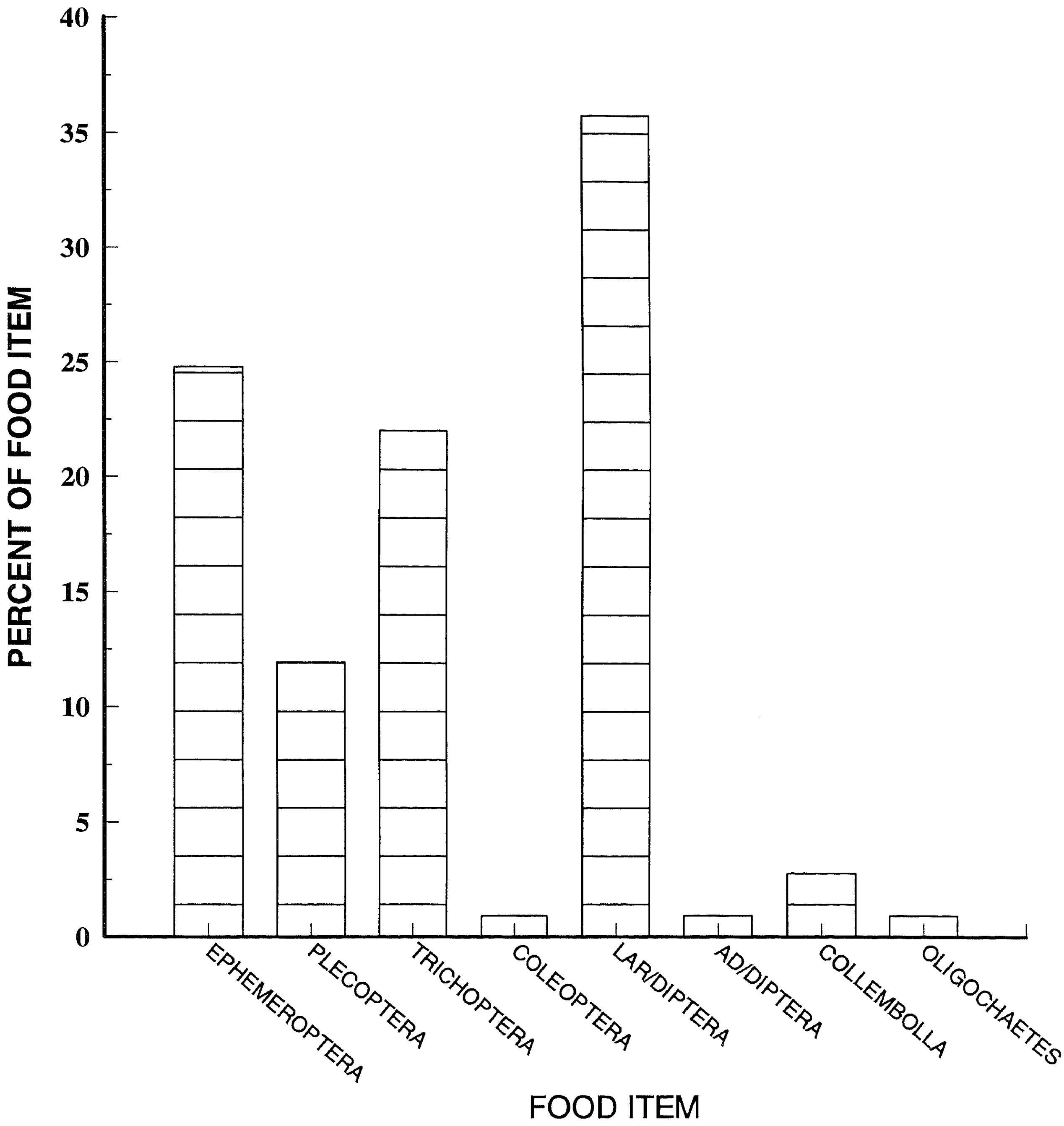


Figure 37. Pre-metamorphic *Desmognathus quadramaculatus* invertebrate dietary composition in the winter season.

FOOD ITEMS CONSUMED BY PRE-METAMORPHIC
Desmognathus quadramaculatus **IN THE WINTER SEASON**



ephemeropterans made up 27 (24.8%) items while larval trichopterans comprised 24 (22%)items of the diet. Nymphal plecopterans made up 13 (11.9%) of the diet of 109 items, while collembollans made up 2.8%. Terrestrial coleopterans, adult dipterans, oligochaetes each occurred once(0.9% of the total diet).

Winter Diet of Post-metamorphic Salamanders

The winter season found the post-metamorphic D. quadramaculatus absent or unattainable using conventional collection methods. For this reason, the sample was only made up of six post-metamorphic salamanders. Larval dipterans occurred in two (33.3%) of the six salamanders (Figure 38). Oligochaetes, collembollans, larval trichopterans, nymphal plecopterans, and nymphal ephemeropterans each occurred in one (16.7%) post-metamorphic salamander.

Larval dipterans made up two (28.6%) of the seven items of the diet while nymphal ephemeropterans, nymphal plecopterans, larval trichopterans, collembollans, and oligochaetes occurred once(14.3%) (Figure 39).

Figure 38. Percent of post-metamorphic *Desmognathus quadramaculatus* containing a given invertebrate taxa in the winter season.

WINTER STOMACH CONTENTS FOR POST-METAMORPHIC *Desmognathus quadramaculatus*

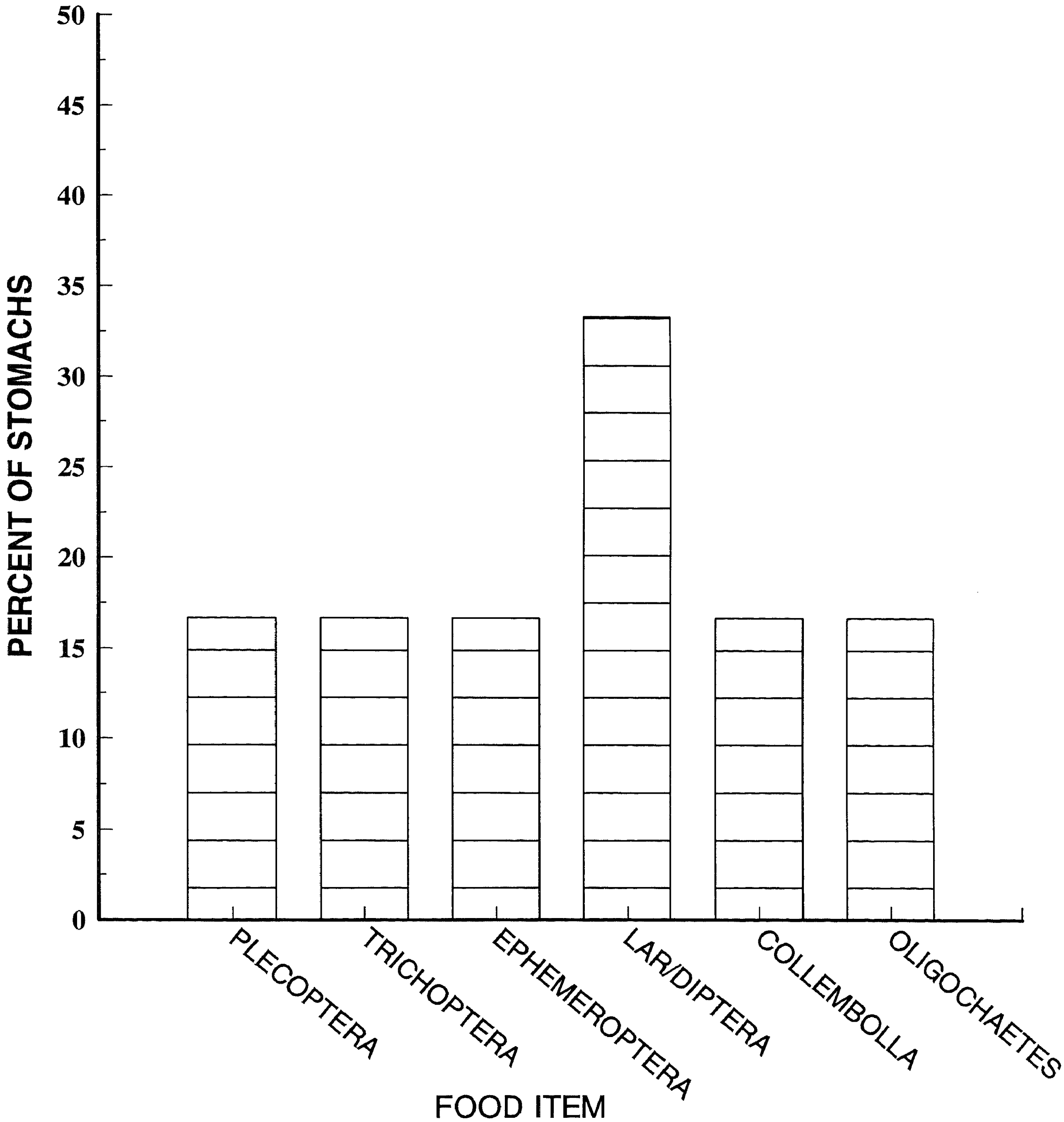
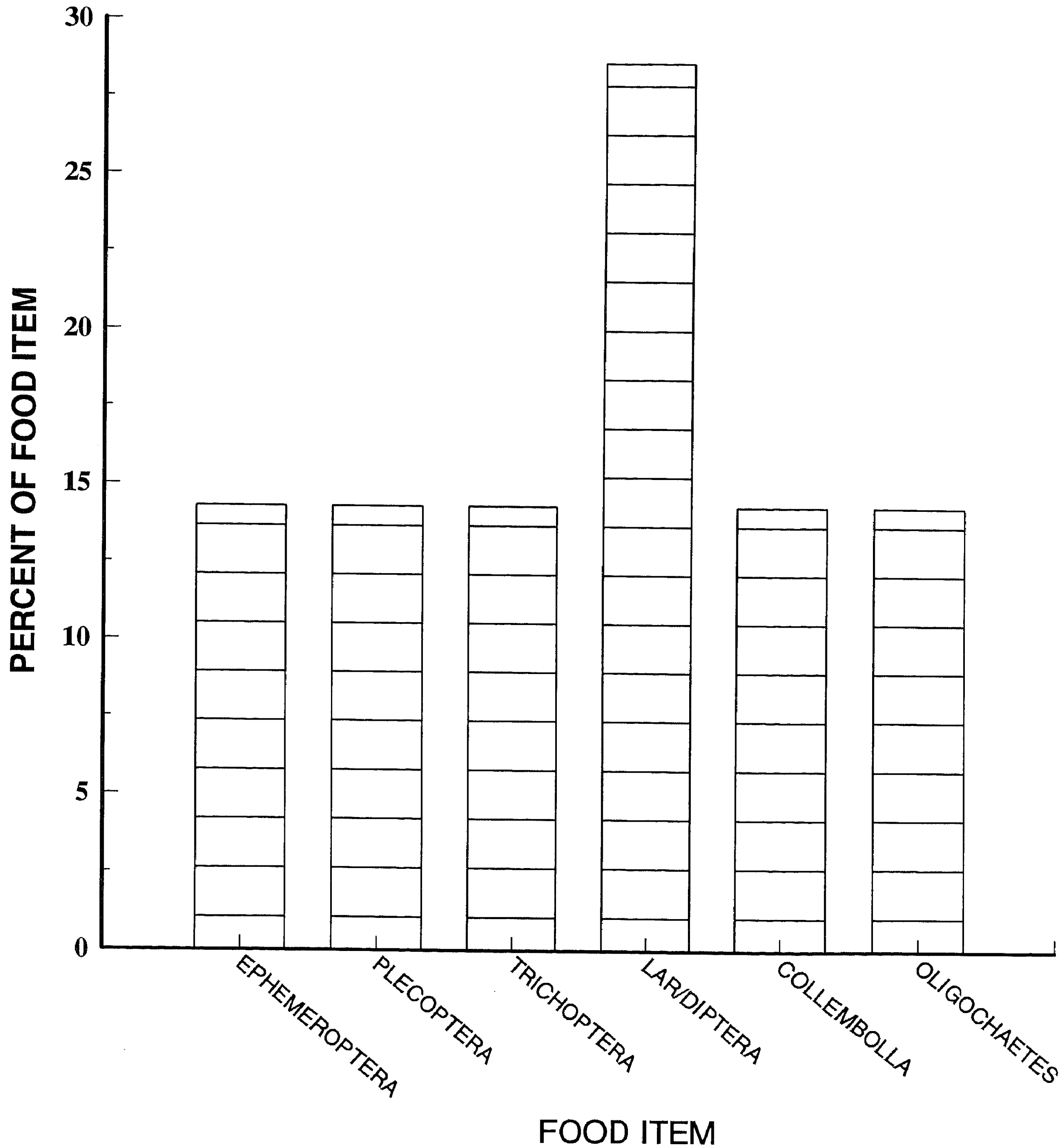


Figure 39. Post-metamorphic Desmognathus quadramaculatus invertebrate dietary composition in the winter season.

FOOD ITEMS CONSUMED BY POST-METAMORPHIC *Desmognathus quadramaculatus* IN THE WINTER SEASON



Discussion

In analyzing the importance of a particular insect group in the energy requirements of D. quadramaculatus, it is important to examine two things. First, the dietary composition of prey items is important. Second, the frequency of salamanders that consumed the prey items is relevant. When one only looks at the total composition of diet from a small number of salamanders, individual salamander foraging and encounters with prey groups may bias the data. However, when coupled with the frequency of stomachs in which they were found, an insect taxa's importance in dietary composition can actually be assessed. For this gives one an idea of the frequency of encounters with the insect taxa an individual may experience in a normal foraging day. By looking at both diet composition and percent of salamanders, one can see trends in foraging strategies for a particular species. These data can further be used to examine the intraspecific competition avoidance strategies used between pre- and post-metamorphic D. quadramaculatus in partitioning its habitat. If dietary shifts are examined seasonally, one can follow D. quadramaculatus movements throughout the year by the prey items it has ingested and indirectly the foraging area and substrate it has utilized.

Larval dipterans were found to make up the greatest portion of the overall diet of D. quadramaculatus and this taxon occurred in the greatest number of stomachs. Larval dipterans made up the largest percentage of the diet and occurred in more stomachs in the summer, fall, and winter seasons. This indicates the importance of larval dipterans in the energy regime of _D. quadramaculatus_. This also indicates that _D. quadramaculatus_ spends much of its foraging time submerged, which results in direct competition between pre- and post-metamorphic individuals.

Larval dipterans made up the greatest component of the pre-metamorphic diet and also occurred in the greatest number of stomachs. Terrestrial coleopterans were found to occur in the greatest number of post-metamorphic stomachs and adult dipterans made up the largest portion of the overall diet. This partitioning of the prey resource was noted by Bruce (1988) and referred to as a ontogenic shift in the diet of the pre- and post-metamorphic _D. quadramaculatus_. The concept of ontogenic shift in diet is further strengthened by comparing the four most commonly occurring invertebrate groups in the pre- and post-metamorphic diet for the entire year. Pre-metamorphs were found to consume 42.4% larval dipterans, 14.2% nymphal plecopterans, 13.8% larval trichopterans, and 12.9% nymphal ephemeropterans, while post-metamorphs consumed 16.9% adult dipterans, 16.7% larval dipterans, 16.7% terrestrial coleopterans, and 10.1% hymenopterans. The significant portion of the pre-metamorphic diet is made up entirely of aquatic taxa where the post-metamorphic diet is made up of three terrestrial and one aquatic taxa. It is not indicated in the results above, however, that many of the larval dipterans found in the post-metamorphic diet were tipulids belonging to the genera _Tipula_ and _Hexatoma_. These two genera become quite large and out of the gape capacity of the pre-metamorphic size guild. It was observed that the post-metamorphic salamanders had a tendency to feed on larger aquatic dipterans which also reduces intraspecific resource competition.

Nymphal plecopterans made up 10.2% of the overall diet and occurred in 21.1% of the stomachs examined. Terrestrial coleopterans were found in 24.1% of the stomachs examined, but only made up 9.5% of the total diet. Nymphal plecopterans made up a larger portion of the overall diet than terrestrial coleopterans, but occurred in a fewer number of stomachs. This is the result of a few salamanders consuming a great number of nymphal plecopterans during an emergence. Terrestrial coleopterans did not make up a large portion of the items consumed in any season, but was present in the gut contents for most of the year. This resulted in the appearance of terrestrial coleopterans in more of the D. quadramaculatus stomachs, but lacked the numbers of individual insects found in the gut contents to compose a significant portion of the overall diet.

Adult dipterans made up 9.9% of the prey items consumed and occurred in 20.7% of the stomachs examined. Nymphal ephemeropterans occurred in 18.5% of the salamanders and made up 7.1% of the prey items consumed. Hymenopterans occurred in 16.8% of the stomachs dissected and composed 6.1% of the diet. Collembollans was found in 5.6% of salamanders dissected and made up only 1.38% of the total ingested items identified. Collembollans and acarinids are invertebrate orders that are semiaquatic, being found on the moss and liverworts along the stream and also on the submerged substrate. Out of the 23 invertebrate taxa found in the stomach contents of D. quadramaculatus, 13 were considered terrestrial and nine were aquatic. However, if one only examines the invertebrate taxa that composed 5.0% or more of the total diet composition, it is found that four aquatic groups composed 54.3% and five terrestrial groups made up 35.6% of the overall diet.

The terrestrial invertebrate dietary composition of D. quadramaculatus was an unexpected and interesting discovery. A salamander that rarely can be found more than half a meter from the edge of the stream in the post-metamorphic stage and has an extended pre-metamorphic stage that is totally aquatic, would be presumed to have a mainly aquatic diet. As noted in the observations section, post-metamorphic individuals could be observed foraging on top of stream-side substrate on rainy days and at night. However, this only occurred during months when a dense deciduous canopy along with warm temperatures maintained a near 100% relative humidity at stream level. This would apply to the seasons of spring (April-May) and summer (June- September) in the New River Gorge Area of West Virginia. The significant (>5%) spring diet of D. quadramaculatus contained six terrestrial invertebrate taxa composing 55.9% of items found in the 48 salamanders collected during this period. The occurrence rate of an insect taxon in the stomach, as stated before, indicates the successful encounters the foraging salamander had a short time before the animal was collected. This gives one an idea of what is abundant in prey resource and where the animal is foraging by the type of prey it has consumed. By examining the invertebrate taxa's occurrence rates, one can hypothesize the majority of the prey biomass available is terrestrial and/or most foraging time is spent terrestrially. Examining the dietary composition of the pre-metamorphic salamanders along with the number of stomachs within which the invertebrate taxon occurred, one can conclude the salamanders in the spring were only foraging in water. The occurrence rates in the salamanders and total composition of the invertebrate taxa are proportional which means the larval salamanders are foraging in the same habitat and the invertebrate populations are homogeneous. The terrestrial taxa are represented in low numbers and are probably "drop-ins" from the canopy or "wash-ins".

The spring diet of the post-metamorphic salamanders is markedly different than that of the pre-metamorphic individuals. Where the pre-metamorphs fed on predominantly aquatic prey, the post-metamorphs fed on terrestrial invertebrates. Terrestrial coleopterans, adult dipterans, and hymenopterans fit the proportional trends of dietary occurrence and composition. However, the remaining invertebrate groups do not follow the expected pattern of abundance probably due to individual salamander foraging strategies and substrate utilization.

In the summer season, the significant invertebrate groups that made up the diet of D. quadramaculatus in the spring remained the same. However, they shifted in the degree of composition. Larval dipterans was the most frequently occurring invertebrate taxon in the pre-metamorphic salamanders collected in the summer season. When one compares the proportionality of occurrence and dietary composition, it is found that adult dipterans made up a greater percentage of the items consumed than lepidopterans, but lepidopterans occurred in more salamanders. This can be attributed to a single salamander consuming many adult dipterans. The occurrence of collembollans is also an anomaly, as it was found in 20.9% of the salamanders, but only composed 1.8% of the diet. Collembollans were found in 7 different salamanders which each had consumed only one. It can be concluded that collembollans were part of the regular diet, but are encountered infrequently and not in great numbers. Aquatic invertebrate taxa such as odonates and megalopterans are predatory insect taxa and make up 10% of the insect population (River Continuum Theory) and encounters with them are infrequent.

Terrestrial invertebrate taxa such as orthopterans, pseudoscorpions, and diplopods are those that are not thought to be associated with water and are probably infrequently encountered. Terrestrial taxa such as terrestrial coleopterans, hemipterans, adult dipterans, and arachnids have some families within the taxon considered to be associated with water by their feeding habits or have larval life stages tied to the aquatic environment. Since these groups spend large amounts of time in the stream or near the edge of the stream, they appear frequently in the diet of D. quadramaculatus. Terrestrial groups such as homopterans, hymenopterans, and lepidopterans occur frequently in the diet of D. quadramaculatus due to the sheer numbers of these taxa that occur in the deciduous canopy.

The summer diet of D. quadramaculatus demonstrates the greatest degree of ontogenic shift between the pre- and post-metamorphic categories. In the summer season, 41.0% of the pre-metamorphic salamanders had larval dipterans within their stomach contents. Larval dipterans made up 38.9% of the prey items consumed by the 39 pre-metamorphic salamanders. Nymphal ephemeropterans and lepidopterans were each found in 23.1% of the 39 pre-metamorphic salamanders examined. Nymphal ephemeropterans composed 12.9% of the total prey items identified, while lepidopterans only made up 7.6%. Lepidopterans were found in as many salamanders as the nymphal ephemeropterans, but did not occur in the same magnitude. The lepidopterans were all terrestrial, but were common along and in the stream because of the great numbers falling out of the canopy. Adult dipterans and larval trichopterans both occurred in 15.4% of the salamanders. Adult dipterans comprised 8.3% of the organisms found in the gut contents while larval trichopterans made up 7.6%. Adult dipterans are dipterans that have reached the winged stage of their life cycle. The appearance of these winged adults in the diet of totally aquatic larval salamanders can be explained in three ways. First, the larval salamanders may be ambushing the young adults before they can fly from the aquatic habitat. Second, the larval salamanders may be capturing adults that are depositing eggs along or in the aquatic system. Third, they may be capturing individuals that have fallen into the stream.

The post-metamorphic summer foraging time was focused on terrestrial prey. Lepidopterans, adult dipterans, and terrestrial coleopterans where the top three most occurring invertebrate taxa in the summer. Larval dipterans were found in fewer post-metamorphic salamanders, but made up the greatest portion of the diet at in the summer. Again, this may be the result of a few salamanders exclusively foraging aquatically and may not express the trends of the entire population.

In comparing the pre- and post-metamorphic diets in the summer months, one can easily identify the ontogenetic shift of prey that composes the diet even though the diets include many of the same invertebrate taxa. The post-metamorphic diet was made up of 65.6% terrestrial organisms from ten invertebrate taxa and 31.1% aquatic organisms from 6 invertebrate taxa with the remaining portion of the diet being semiaquatic. This is contrasted by the pre-metamorphic diet being composed of 60.2% aquatic organisms from four taxa and 38.8% terrestrial organisms from nine invertebrate groups. The feeding shifts are easily distinguished when the significant invertebrate taxa are compared by using the percentage of salamanders in which they appeared. If one only examines the organisms that occurred in 20% or more of the salamanders collected, the post-metamorphic diet would be composed of seven terrestrial and two aquatic invertebrate groups whereas the diet of the pre-metamorphic salamanders would be made up of two aquatic and one terrestrial.

The designated fall season (Oct.-Dec.) began with the defoliation of the deciduous canopy which created conditions along the streams edge that forced the post-metamorphic salamanders to forage in the water. During this time intraspecific competition for prey resources would hypothetically have its maximum effect. The pre-metamorphic diet was made up of 91.0% aquatic prey in the fall season.

Although larval dipterans made up a greater percentage of the diet of post-metamorphic salamanders in the fall, both terrestrial coleopterans and homopterans also occurred in the diet. The sample size in this season was very small and led to the unrelatedness of percent consumed and percent occurred. Individual foraging habitats within the sample of post-metamorphic salamanders is expressed which would be diluted by a larger sample. However, prey items and foraging emphasis can be detected by the gut contents listed. The diet of the fall post-metamorphic salamanders was 64.8% terrestrial.

By analyzing the fall diets of pre- and post-metamorphic D. quadramaculatus the intraspecific competitive and ontogenetic shift in diet Bruce (1988) described is easily observed . While the pre- and post-metamorphic salamanders both were observed foraging in water, their dietary composition was different.

When examining the diet of pre- and post-metamorphic individuals by season and by invertebrate taxa, some of the essential intraspecific avoidance mechanisms are lost. In

October, the pre-metamorphic diet based on a sample of nine with a mean SVL of 22.4 mm was 100% aquatic prey while the post-metamorphic diet based on a sample of nine with a mean SVL of 43.9 mm was composed of only 19.2% aquatic prey. The November collection of D. quadramaculatus was 21 pre-metamorphic salamanders with a mean SVL of 28.7 mm and 10 post-metamorphic salamanders with a mean SVL of 43.5 mm. The diet of the pre-metamorphic salamanders was 92.9% aquatic while the post-metamorphic diet was 36.0% aquatic prey items. Only five pre-metamorphic and five post-metamorphic D. quadramaculatus were captured in December. The pre-metamorphic salamanders had a mean SVL of 21.4 mm and diet consisted of 95.8% aquatic prey while the post-metamorphs had a mean SVL of 66.7 mm with a diet consisting of 38.1% aquatic prey.

The winter (Jan.-Mar.) season, 34 pre-metamorphic individuals were collected. Larval dipterans were found in 17 (50%) of the salamanders sampled and comprised 39 (35.8%) of the 109 items found in the guts. Nymphal ephemeropterans were found in 14 salamanders and comprised 27 (24.8%) of the dietary items while larval trichopterans were found in 11 (32.4%) of the pre-metamorphic salamanders and made up 24 (22.0%) items in the diet. Nymphal plecopterans occurred in 8 (23.5%) salamanders and comprised 11.9% of the diet. Collembollans occurred in one salamander, but made up 2.8% of the diet. This is an example of the foraging preferences of a single salamander consuming several representatives of an invertebrate group which, in a small sample, distorts the dietary trends of the population. Oligochaeta were found in one salamander and made up 0.9% of the diet or one item. Adult Coleoptera and terrestrial Diptera are the only terrestrial invertebrate groups that occurred in the winter season and both occurred in one record and comprised 0.9% of the diet. In the winter season, the pre-metamorphic diet was made up of 98.2% aquatic prey items.

The post-metamorphic winter sample consisted of 6 specimens. Aquatic Diptera occurred in 2 guts and made up two (28.6%) of the seven items. Oligochaeta, Collembolla, aquatic Trichoptera, aquatic Plecoptera, and aquatic Ephemeroptera occurred in one salamander and made up 14.3% or one of the seven items. In the winter season, the diet of post-metamorphic salamanders was 100% aquatic, but the surface abundance of these salamanders was limited.

CONCLUSION

The life history characteristics of Desmognathus quadramaculatus in the New River Gorge, WV, the northern-most periphery of its range, were found to differ in several aspects when compared to the southern populations. The size at which sexual maturity is achieved by females is markedly smaller and the length of the larval period seems to be extended.

The surface density sampling of the desmognathan community along the stream study site showed distinct shifts in species utilization of the substrate. In months when D. quadramaculatus post-metamorphs were utilizing the rocky substrate along the edge of the water, D. monticola were scarce, if not entirely absent. However, during periods when D. quadramaculatus post-metamorphs foraged exclusively in water, the D. monticola were found using the substrate along the edge of the water. Also, in areas of the stream where bait collectors removed large numbers of D. quadramaculatus, the smaller and presumably more mobile D. monticola would be found utilizing the optimum substrate. Krzysik (1979) found the mechanism of the shifts, as well as the selective forces that molded the organization of the desmognathan community, appears to be interspecific interference competition.

The foraging and dietary shifts of D. quadramaculatus were examined by sampling the invertebrate populations in the aquatic system and gut contents of the individual salamanders collected over a period of one year. Salamanders are thought to be opportunistic feeders and therefore would prey upon what is present in the proper size range, greatest numbers, and biomass. Larval dipterans were found to be the most abundant aquatic invertebrate taxon and made up the largest percentage of the overall diet and occurred in the most guts of D. quadramaculatus. Nymphal plecopterans were the second most occurring aquatic invertebrate taxon and were found to be the second most consumed invertebrate prey item in the overall diet. However, it did not occur in as many guts as terrestrial coleopterans which demonstrated ontogenetic shift or intraspecific avoidance between pre- and post-metamorphic salamanders. The diet of pre-metamorphic salamanders was made up of predominantly aquatic invertebrate groups throughout the year while the post-metamorphic diet varied with the season and contained large portions of terrestrial invertebrate groups. In fact, when the post-metamorphic diet is examined separately from the pre-metamorphic diet, the post-metamorphs consumed more terrestrial or adult dipterans than larval dipterans. This factor supports Davic's (1991) theory of the ontogenetic shift in diet.

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