STOMACH CONTENTS OF TWO ROCKFACE AND STREAMBANK SALAMANDERS OF THE GENUS DESMOGNATHUS: A COMPARATIVE ANALYSIS

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STOMACH CONTENTS OF TWO ROCKFACE AND STREAMBANK SALAMANDERS OF THE GENUS *DESMOGNATHUS*: A COMPARATIVE ANALYSIS

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In Partial Fulfillment
of the Requirements for the Degree
Master of Science

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by

Sallie McCain McReynolds Noel

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To the Graduate and Research Council:

I am submitting herewith a Research Paper, written by Sallie M. Noel entitled "Stomach Contents of Two Rockface and Streambank Salamanders of the Genus *Desmognathus*: A Comparative Analysis." I have examined the final copy of this paper for form and content, and I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in biology.

David Snyder
Major Professor

Accepted for the Graduate and Research Council:

Linda B Rudolph
Dean of Graduate School

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CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

The food contained in an animal's stomach often proclaims much of the lifestyle of that animal. An accurate interpretation of this proclamation depends equally upon a thorough knowledge of extrinsic factors, such as the nature of the species' habitat, and upon the cognitive ability of the researcher. Unfortunately a fully integrated analysis of the ecology of any plethodontid species is rarely available and fragments from many authors must be assembled before a meaningful mosaic begins to appear. This study contributes a shard of information to the resolution of the enigmatic question of how a salamander selects its prey.

Comparative studies of the feeding ecology of various salamanders have been done and the middens of herpetological literature have been inundated by a plethora of data as a result. Some findings suggest a slight degree of prey selectivity, but the bulk of evidence indicates that salamanders are generally opportunistic euryphagic feeders (Donavan and Folkerts 1972, Jaeger 1972, Shealy 1975, Burton 1976). When selectivity has been observed, it has occurred as a function of increased rainfall (Jaeger 1972, Sites 1978, Keen 1979), increased body size of salamander (Lynch 1973, Camp and Bozeman 1981), or has been an obligate dietary difference resulting from seasonal competition, as noted by Powders and Tietjen (1974) between *Plethodon jordani* and *P. glutinosus*. Synchronous foraging, correlated with the peak activity of the potential prey, is suggested by Holomuzki (1980) as a means of lessening such interspecific competition for food despite the overall similarity of diet. Montague and Poinski (1978) report that opportunistic feeding will occur, even in brooding females, if suitable prey items are available and that brooding does not necessarily entail a specific disinclination to feed.

A comparison of feeding habits of two sympatric species is especially useful, since there is always the possibility that niche diversification or some other type of habitat partitioning might be seen through their patterns of feeding and their selection of prey (Lynch 1973, Burton 1976). A comparative analysis of the stomach contents of 38 *Desmognathus quadramaculatus*, the Blackbelly Salamander, and 39 *D. monticola*, the Seal Salamander, from rockface and streambank habitats, provides the basis for this study. The purpose of this comparison is to draw general conclusions about the feeding habits and diversity of diet of two sympatric desmognathine species and to relate these findings to those of researchers in the field. The depth of analysis was limited by the brief duration of the study, the relatively small sample size, and the lack of recent data on prey availability at the two sites studied.

CHAPTER II

METHODS AND MATERIALS

Description of Species

Desmognathus quadramaculatus is a robust salamander with a dark venter and two distinctive rows of lateral white dots. Its sharply keeled tail is typical of aquatic species. This species will feed nocturnally some distance from the streamside and frequently a large percent of its food intake is terrestrial. *Desmognathus monticola* is also a relatively large salamander, although somewhat smaller than *quadramaculatus* at maturity. Its boldly patterned dorsal markings and whitish venter readily distinguish it from the Blackbelly. Young Seal Salamanders can be distinguished from similar species by the presence of three or four pairs of dorsal chestnut spots. The name Seal is derived from the noticeably seal-like profile when *monticola* is perched upon a wet rock or at the mouth of its burrow when foraging (Conant 1958, Martof, *et al*. 1980).

Both *quadramaculatus* and *monticola* are essentially aquatic to semi-aquatic forms. *Desmognathus quadramaculatus* is considered by Hairston (1949) to most closely resemble the ancestral form, and the remaining *Desmognathus* species represent increasing morphological specializations, such as decreased body size, paralleling an increasing degree of terrestriality. *Desmognathus monticola*, the next most advanced evolutionarily, occupies banks and streams in seepage areas. It is found in slightly more terrestrial sites than those occupied by quadramaculatus and body size reduction in monticola reflects the trend toward terrestriality seen in the smallest and most terrestrial of the Desmognathus species, D. wrighti (Organ 1961, Tilley 1968).

Both quadramaculatus and monticola forage openly at night and Shealy (1975) records moderate diurnal activity of monticola. Dunn (1926) felt that the amount of water and the rate of flow separated the two species somewhat, with quadramaculatus selecting the wetter and swifter sites. This was confirmed by Hairston (1980), who found quadramaculatus unable to extend its range by crossing the forest floor between isolated seepage areas.

Description of Sites

The rockface site was at the foot of Scaly Mountain on highway N. C. 106, Macon County, North Carolina, at Blue Valley Vista, and will hereafter be referred to as BV. This site is 7.4 km west-southwest of Highlands, North Carolina, at an elevation of 1134 m above sea level and lies 84°29'5" W and 35°2'30" N on the Knoxville, Tennessee, Topographic Quadrangle (USGS 1972). The BV rockface, formed during road construction in 1936, extends for about 40 m along the highway, and is composed of continuous black biotite gneiss. The rockface surface has a variable and abundant cover of vegetation and the amount of water present varies from a thin film to a brisk flow (Huheey and Brandon 1973). Dry Falls (hereafter referred to as DF), 4.8 km west-northwest of Highlands, North Carolina, on highway U. S. 64, was selected as the second site. This site, in Cullasaja Gorge, is a combination rockface and streambank habitat and is formed by the cascading waters of the Cullasaja River, which converge below the falls as a stream flowing over the richly vegetated mountainside. The melanized soils of the region are typical of the central deciduous forest (Braun 1950). Dry Falls is located at 1265 m above sea level and lies 84°29'30" W and 35°4'30" N on the Knoxville, Tennessee, Topographic Quadrangle (USGS 1972). Both sites lie within the Mixed Mesophytic Forest region of Braun (1950) and the Southern section of the Blue Ridge Province of Fenneman (1938).

Collection and Preparation of Specimens

Collections of quadramaculatus and monticola at BV and DF sites were made on the nights of 30 June 1983 through 4 July 1983 from 2130 to 2330 hours. Despite light rainfall on most afternoons, all collecting nights were relatively clear and temperatures ranged from 18° to 21° C. Specimens were collected, identified and placed with damp moss into plastic bags and returned to the laboratory. They were immediately anesthetized with tricaine methane-sulfonate. Measurements of head width and snout-vent length (SVL) were recorded and stomachs were flushed with water injected into the mouth through plastic tubing with a small syringe. Each stomach was flushed four times to make certain all contents were removed. Dissection was also performed on several specimens to check the technique, which was found to be quite effective.

The stomach contents were then placed in plastic vials of 40% isopropyl alcohol and labeled with appropriate number and SVL of the corresponding specimen. Identification and measurements of stomach contents were made by using a Wild M3 Heerbrugg microscope (10 x 6.4 power) with a Lasico digital micrometer and scaler accurate to 0.001 mm. Identification of prey was aided by Pratt (1935), Jaques (1947), Chu (1949), Usinger (1956) and Milne and Milne (1980). The specimens were revived, refrigerated overnight and returned to collection sites.

Analysis of Data

Statistical analysis of stomach contents included calculations of percent frequency (number of a specific type of prey divided by total prey number) and percent occurrence (number of stomachs in which a prey type occurred divided by total number of stomachs). Volume of each prey item was calculated by taking measurements and assuming the prey shape to be a cylinder, using the equation, $V = \pi r^2 h$. Total volume percents for each prey taxonomic order were determined. Coefficients of diversity were calculated by the Shannon-Weiner Diversity Index, $H = -\sum_{i=1}^{n} pi \log_e pi$, with the higher H values indicating a more diverse diet (Ricklefs 1979). The Mann-Whitney U test was used to determine if prey diversity (H values) differed significantly at the two sites (Campbell 1974).

CHAPTER III

RESULTS

Data from Blue Valley

At BV (Table 1), Desmognathus quadramaculatus and D. monticola were well matched in size, with a SVL range from 31-69 mm for quadramaculatus and 31-66 mm for monticola. When stomach contents of quadramaculatus and monticola were compared at BV, it was found that Diptera species were the most numerous in the diet of both salamanders. The 41 dipterans taken from quadramaculatus were consumed by seven individuals with a 29 percent occurrence. Diptera species composed 46 percent of quadramaculatus' diet by percent frequency, but only 28 percent of monticola's diet by percent frequency at BV.

Leeches (Hirudinea) were found in the stomachs of six quadramaculatus and none were found in stomachs of monticola. Coleopterans were second in importance to both monticola and quadramaculatus at BV in both number and percent frequency. Ants (Formicidae) were also an important prey item to both species. Other prey of less importance were mites (Acarina), spiders (Araneae), grasshopper nymphs (Orthoptera), aphids and leafhoppers (Homoptera), moths (Lepidoptera), wasps (Vespidae), and one species each of Hemiptera and Plecoptera.

A comparison by percent volume of prey taken at BV by quadramaculatus (Fig. 1) and monticola (Fig. 2) indicated

Table I. Stomach Contents of 24 Desmognathus quadramaculatus and 16 Desmognathus monticola from Blue Valley Vista in Macon County, North Carolina N = Number of Prey Items; %oc = Percent of Stomachs in which Prey Occurred; %fr = Percent Frequency of Prey; SVL = Snout-Vent Length; R = Range.

	D. quadramaculatus			D. monticola		
	$\bar{x}$ SVL = 46.78 mm R = 31-69 mm			$\bar{x}$ SVL = 44.75 mm R = 31-66 mm		
Prey Item	N	%oc	%fr	N	%oc	%fr
Annelida						
Hirudinea	16	25.0	17.8			
Arthropoda						
Arachnida						
Acarina	1	4.0	1.0	2	13.0	6.3
Araneae	1	4.0	1.0	2	13.0	6.3
Insecta						
Coleoptera	12	38.0	13.0	8	44.0	25.0
Diptera	41	29.0	46.0	9	44.0	28.1
Hemiptera				1	6.0	3.1
Homoptera	1	4.0	1.0	2	13.0	6.3
Hymenoptera						
Formicidae	7	17.0	7.8	4	25.0	12.5
Vespidae	4	13.0	4.4	2	13.0	6.3
Lepidoptera	3	13.0	4.4	2	6.0	3.1
Orthoptera	2	8.0	2.2			
Plecoptera	2	8.0	2.2	1	6.0	3.1

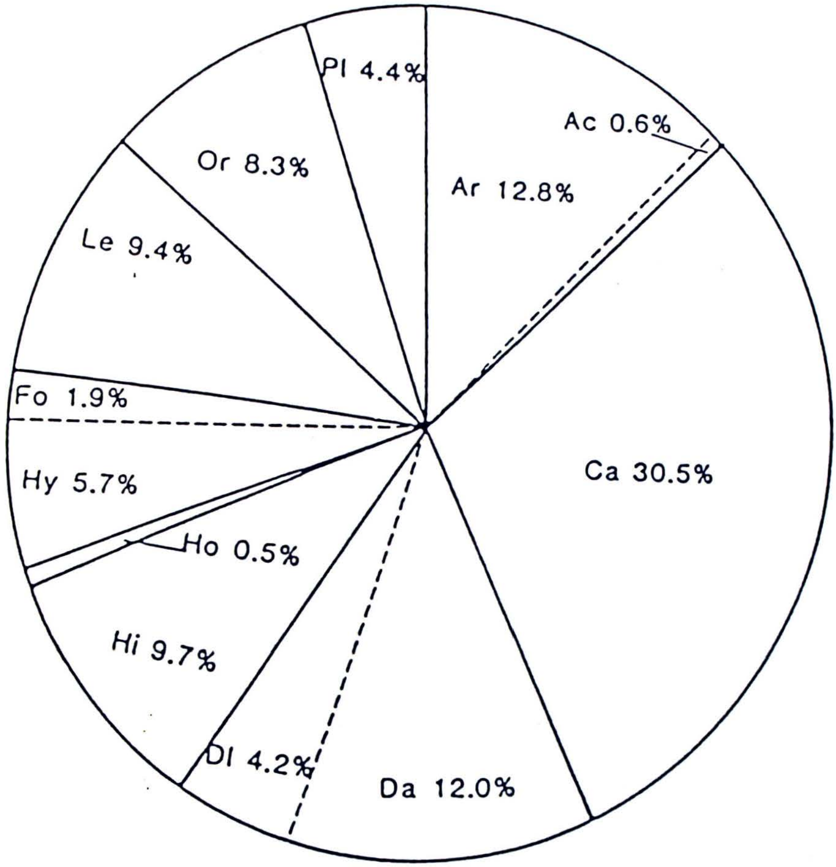

Figure 1. Comparison by Percent Volume of Prey Taken by <u>Desmognathus quadramaculatus</u> at Blue Valley Vista, Macon County, North Carolina

Explanation of Symbols: Phylum Annelida: Hirudinea (Hi). Phylum Arthropoda: Arachnida; Araneae (Ar), Acarina (Ac); Insecta; Coleoptera adults (Ca), Diptera adults (Da), Diptera larvae (Dl), Homoptera (Ho), Hymenoptera other than Formicidae (Hy), Formicidae (Fo), Lepidoptera (Le), Orthoptera (Or), Plecoptera (Pl) Dotted lines separate maturity levels or closely related taxonomic groups.

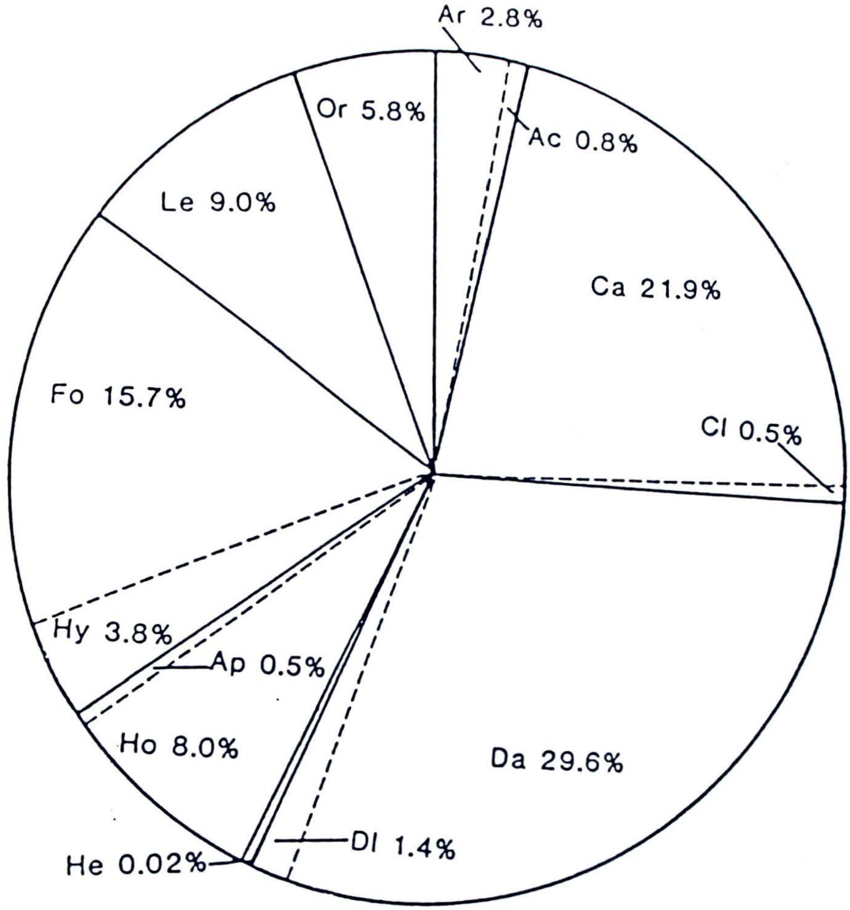

Figure 2. Comparison by Percent Volume of Prey Taken by Desmognathus monticola at Blue Valley Vista, Macon County, North Carolina

Explanation of Symbols: Phylum Arthropoda: Arachnida; Araneae (Ar), Acarina (Ac); Insecta; Coleoptera adults (Ca), Coleoptera larvae (Cl), Diptera adults (Da), Diptera larvae (Dl), Hemiptera (He), Homoptera other than aphids (Ho), Aphididae (Ap), Hymenoptera other than Formicidae (Hy), Formicidae (Fo), Lepidoptera (Le), Orthoptera (Or) Dotted lines separate maturity levels or closely related taxonomic groups.

the importance of Diptera and Coleoptera as food items, but suggested too that size of prey was more significant than number. For example, the four large carpenter ants (Formicidae) taken by monticola (Fig. 2) composed 15.7 percent of the total food volume, while seven small red ants consumed by quadramaculatus (Fig. 1) amounted to only 1.9 percent of the prey by volume. One large spider (Araneae) composed 12.8 percent of the quadramacuatus diet by volume (Fig. 1). Diptera larvae comprised a greater volume of the diet for quadramaculatus than for monticola.

A determination of number of prey items per stomach (Fig. 3) revealed a range from 0-10 prey items for quadramaculatus with a $\bar{x}$ number of 2.95 prey items per stomach. Prey items per stomach for monticola ranged in number from 0-6 with a $\bar{x}$ of 1.87 prey items per stomach. Twenty five percent of the quadramaculatus stomachs were empty as compared with only 12.5 percent of the stomachs of monticola at the same site.

In determining the number of insect orders per stomach (Fig. 4), it was found that despite the six empty stomachs of quadramaculatus, those that had fed generally contained more orders of prey than did monticola. A $\bar{x}$ of 2.0 prey orders per stomach was found for quadramaculatus and a $\bar{x}$ of 1.75 prey orders per stomach for monticola.

Figure five at BV indicated a slightly more diverse diet among the quadramaculatus, with the highest H value for the entire study, 1.8, occurring in quadramaculatus from

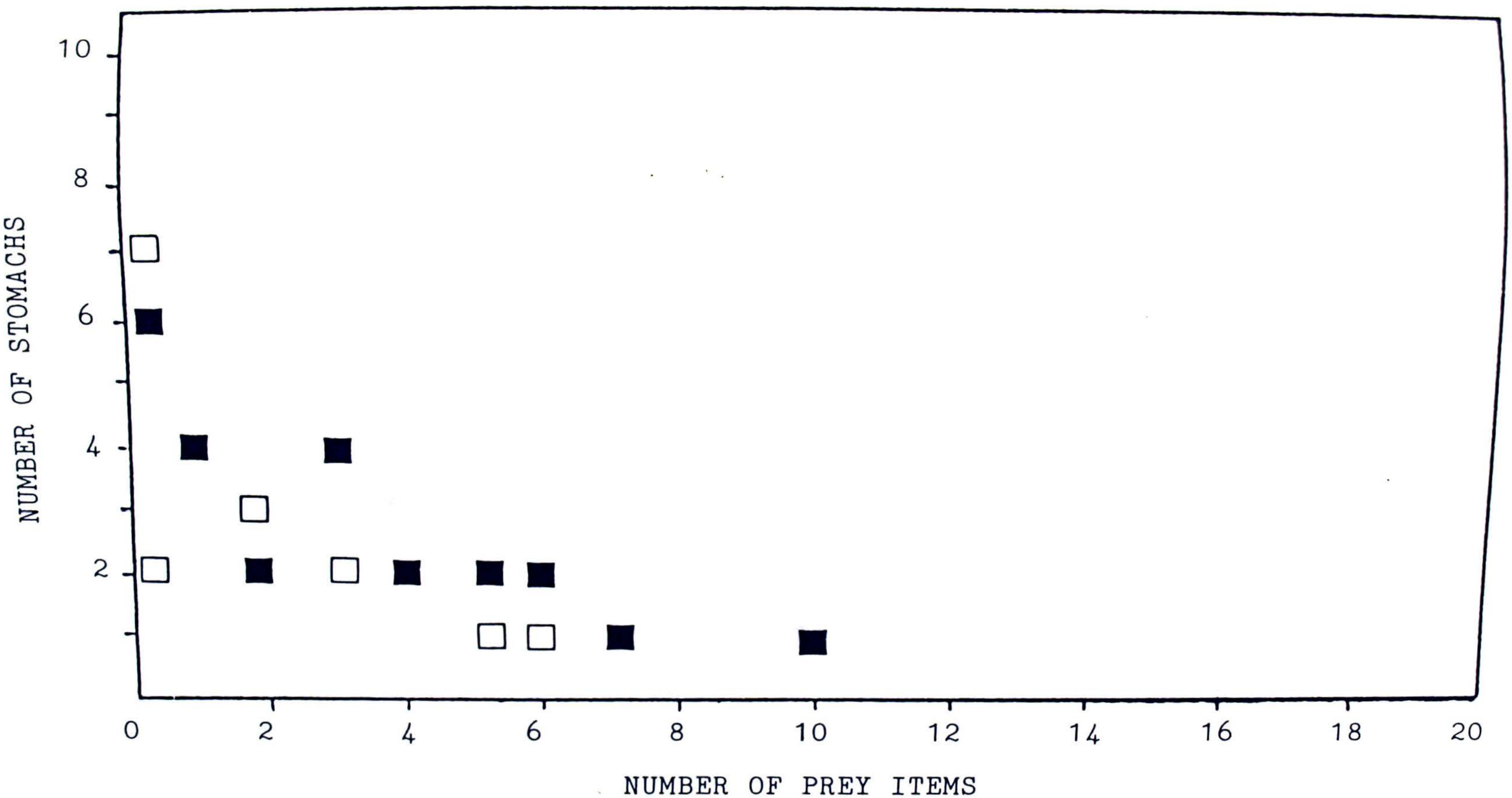

Figure 3. Number of Prey Items per Stomach in 24 *Desmognathus quadramaculatus* and 16 *Desmognathus monticola* from Blue Valley Vista in Macon County, North Carolina Symbols: ■ = *Desmognathus quadramaculatus* □ = *Desmognathus monticola*

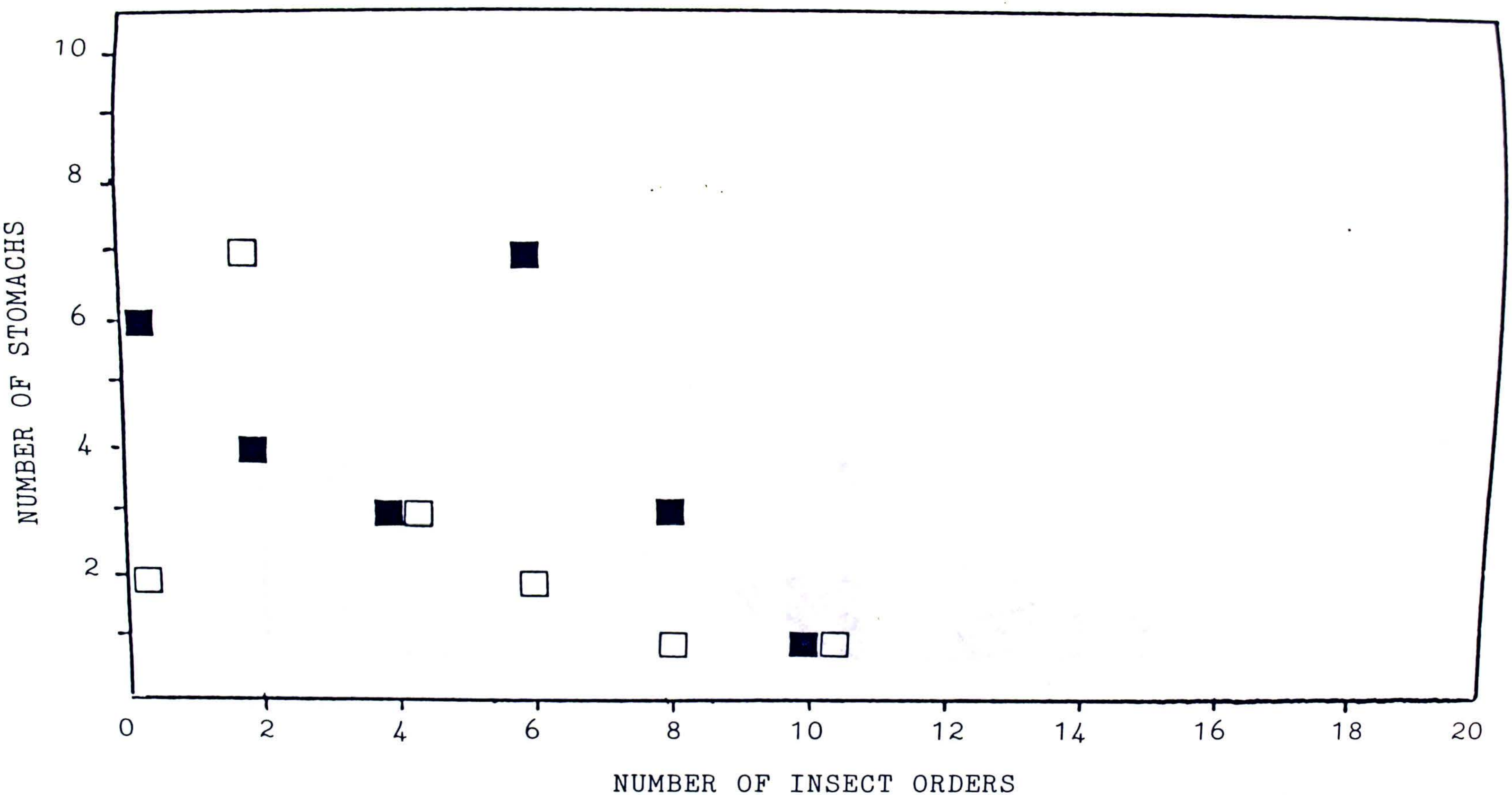

Figure 4. Number of Orders of Insect Prey per Stomach in 24 *Desmognathus quadramaculatus* and 16 *Desmognathus monticola* from Blue Valley Vista in Macon County, North Carolina Symbols: ■ = *Desmognathus quadramaculatus* □ = *Desmognathus monticola*

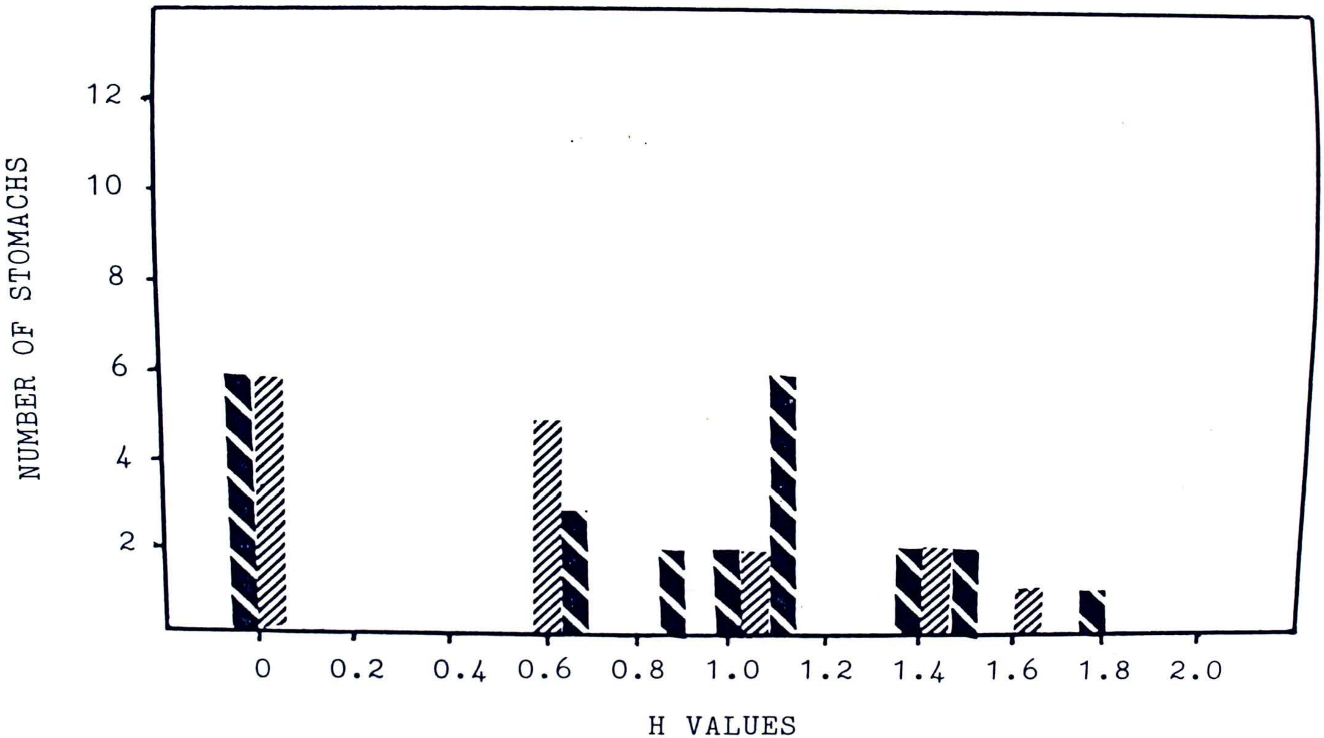

Figure 5. Prey Diversity of Desmognathus quadramaculatus and Desmognathus monticola at Blue Valley Vista in Macon County, North Carolina Symbols: = Desmognathus quadramaculatus = Desmognathus monticola H values represent coefficients of diversity calculated by the Shannon-Weiner Diversity Index,

$$H = -\sum_{i=1}^{n} pi \log_e pi$$

that site. Six individuals of each species at BV showed no prey diversity. Despite a wide range of H values, there was no statistically significant difference in prey diversity of the two species when the Mann-Whitney U test was applied. At the 95 percent confidence level, critical values of U under 1.96 indicate no significant difference (Campbell 1974). A calculated U value of 1.37 was determined for the BV sample.

Data from Dry Falls

Both species were larger at DF than at BV (Table II). At DF quadramaculatus ranged from a SVL of 46 mm to a very large 105 mm and monticola ranged from 32-78 mm SVL. Head widths, recorded only for the DF specimens, indicated a $\bar{x}$ of 10.5 mm for quadramaculatus and 7.21 mm for monticola.

At DF, Diptera species were again the most important food item for both salamanders, by both number and percent occurrence (Table II). By number, diplopods and collembolans were second in importance in the diet of quadramaculatus, while beetles (Coleoptera), ants (Formicidae), and sowbugs (Isopoda) were the most frequent prey items of monticola. The only vertebrate food item, a salamander, was consumed by a quadramaculatus at DF. The remainder of prey consumed were earthworms (Lumbricidae), spiders (Araneae), moths (Lepidoptera), and a negligible number of prey from Diplura, Homoptera, and Orthoptera.

Percent volumes of prey (Figures 6 and 7) indicated the importance of size of prey in the diet. At DF, seven

Table II. Stomach Contents of 14 *Desmognathus quadramaculatus* and 23 *Desmognathus monticola* from Dry Falls in Macon County, North Carolina N = Number of Prey Items; %oc = Percent of Stomachs in which Prey Occurred; %fr = Percent Frequency of Prey; SVL = Snout-Vent Length; R = Range

	D. quadramaculatus $\bar{x}$ SVL = 74.07 mm R = 46-105 mm			*D. monticola* $\bar{x}$ SVL = 48 mm R = 32-78 mm		
Prey Item	N	%oc	%fr	N	%oc	%fr
Annelida						
Lumbricidae	1	7.1	2.7	1	4.3	2.0
Arthropoda						
Arachnida						
Araneae	2	14.3	5.5	2	8.6	4.0
Diplopoda	7	35.7	19.4			
Isopoda				9	4.3	18.0
Insecta						
Coleoptera	4	28.5	11.1	7	8.6	14.0
Collembola	7	7.1	19.4	7	17.4	14.0
Diplura				1	4.3	2.0
Diptera	12	35.7	33.3	10	30.3	20.0
Homoptera	1	7.1	2.7			
Hymenoptera						
Formicidae	1	7.1	2.7	8	17.4	16.0
Vespidae				2	8.6	4.0
Lepidoptera				2	8.6	4.0
Orthoptera				1	4.3	2.0
Chordata						
Urodela	1	7.1	2.7			

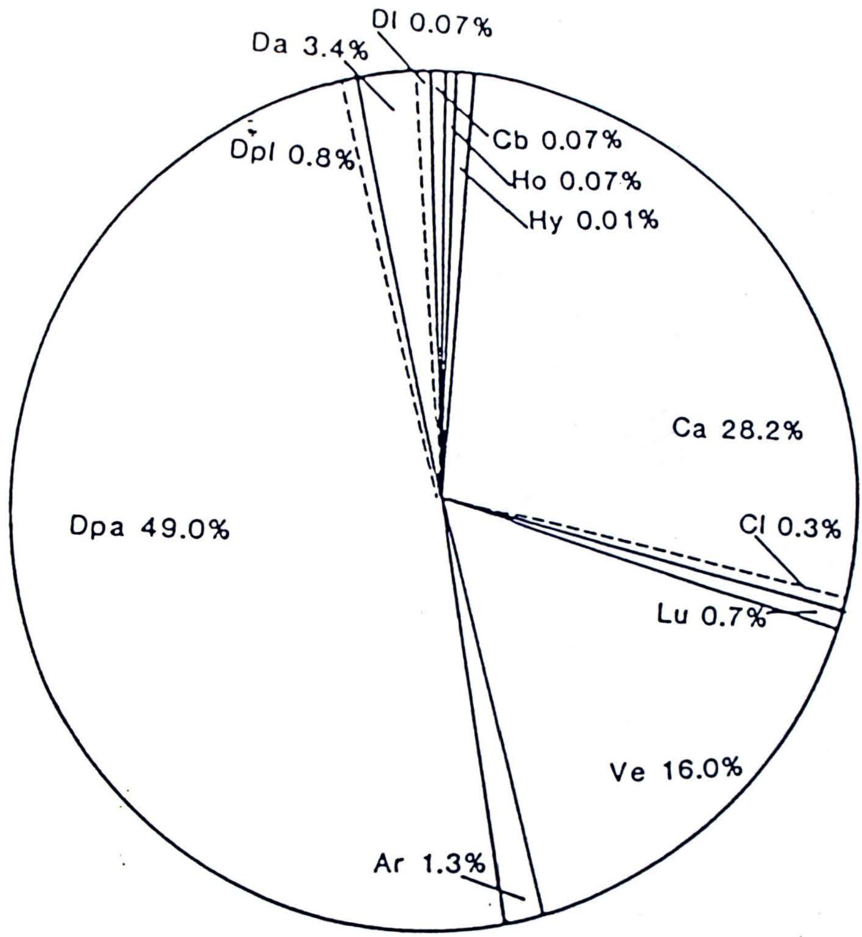

Figure 6. Comparison by Percent Volume of Prey Taken by <u>Desmognathus quadramaculatus</u> at Dry Falls in Macon County, North Carolina

Explanation of Symbols: Phylum Annelida: Lumbricidae (Lu); Phylum Chordata: Urodela (Ve); Phylum Arthropoda: Arachnida, Araneae (Ar), Diplopoda adults (Dpa), Diplopoda larvae (Dpl); Insecta; Coleoptera adults (Ca), Coleoptera larvae (Cl), Diptera adults (Da), Diptera larvae (Dl), Hymenoptera (Hy), Homoptera (Ho), Collembola (Cb) Dotted lines separate maturity levels.

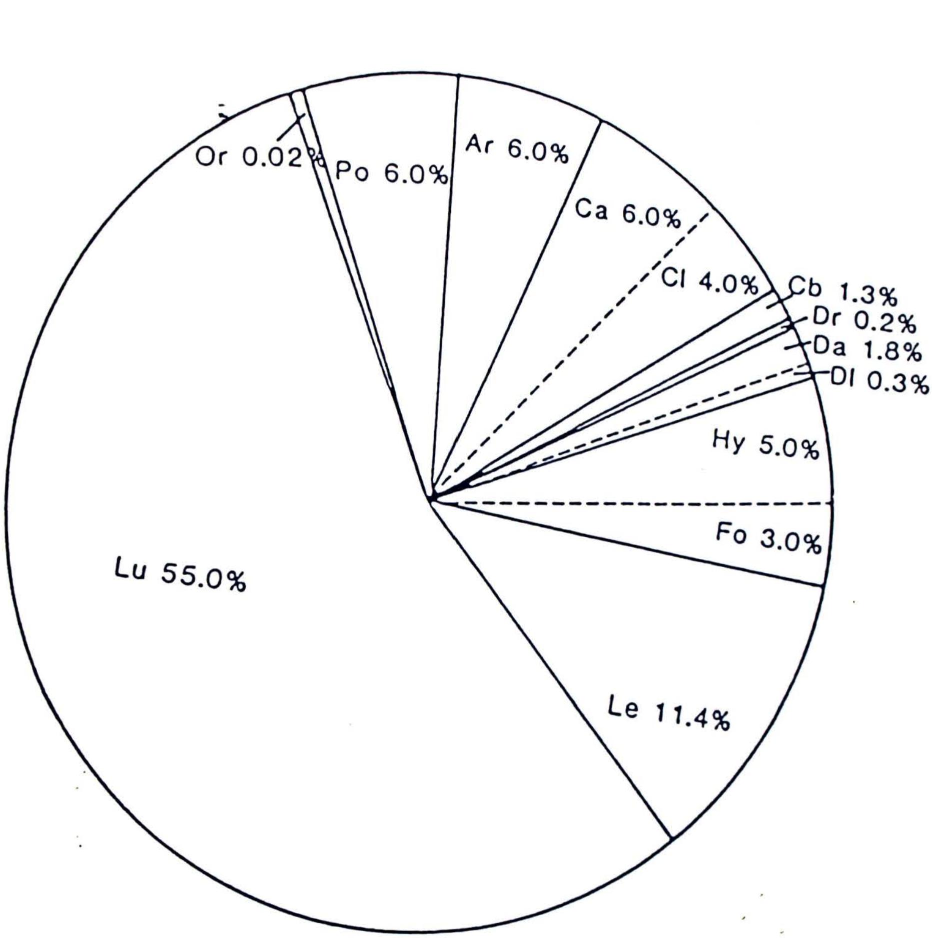

Figure 7. Comparison by Percent Volume of Prey Taken by <u>Desmognathus monticola</u> at Dry Falls in Macon County, North Carolina

Explanation of Symbols: Phylum Annelida: Lumbricidae (Lu); Phylum Arthropoda: Isopoda (Po); Arachnida, Araneae (Ar); Insecta; Coleoptera adults (Ca), Coleoptera larvae (Cl), Diptera adults (Da), Diptera larvae (Dl), Hymenoptera other than Formicidae (Hy), Formicidae (Fo); Collembola (Cb), Diplura (Dr), Lepidoptera (Le), Orthoptera (Or) Dotted lines separate maturity levels or closely related taxonomic groups.

diplopods consumed by five quadramaculatus made up 49.8 percent of the total volume of prey for quadramaculatus at that site. The one earthworm consumed by one monticola accounted for 55.0 percent of the total food volume for the entire sample of monticola at DF. Coleoptera adults were far more significant dietary items for quadramaculatus (Fig. 6) than for monticola (Fig. 7) if significance is assessed strictly by volume.

Considerable variation was found in number of prey items per stomach (Fig. 8) at DF, with seven quadramaculatus having only one item per stomach and one containing 17 prey items. Monticola also showed a wide variation, with six individuals containing only one prey item and one having consumed ten prey items. Quadramaculatus at DF contained a $\bar{x}$ of 2.71 prey items while monticola contained a $\bar{x}$ of 2.56 prey items, with less variance occurring in the monticola sample.

Less variation was encountered when number of insect orders per stomach was examined (Fig. 9). The majority of the salamanders, 19 monticola and 12 quadramaculatus, had consumed prey from no more than two orders. The greatest number of orders seen in one stomach was five in quadramaculatus at DF. Monticola at DF generally contained slightly more insect orders of prey than did quadramaculatus, with a $\bar{x}$ of 1.69 orders per stomach for monticola and a $\bar{x}$ of 1.57 orders of prey per stomach for quadramaculatus.

Figure 10 reveals that half of both samples at DF

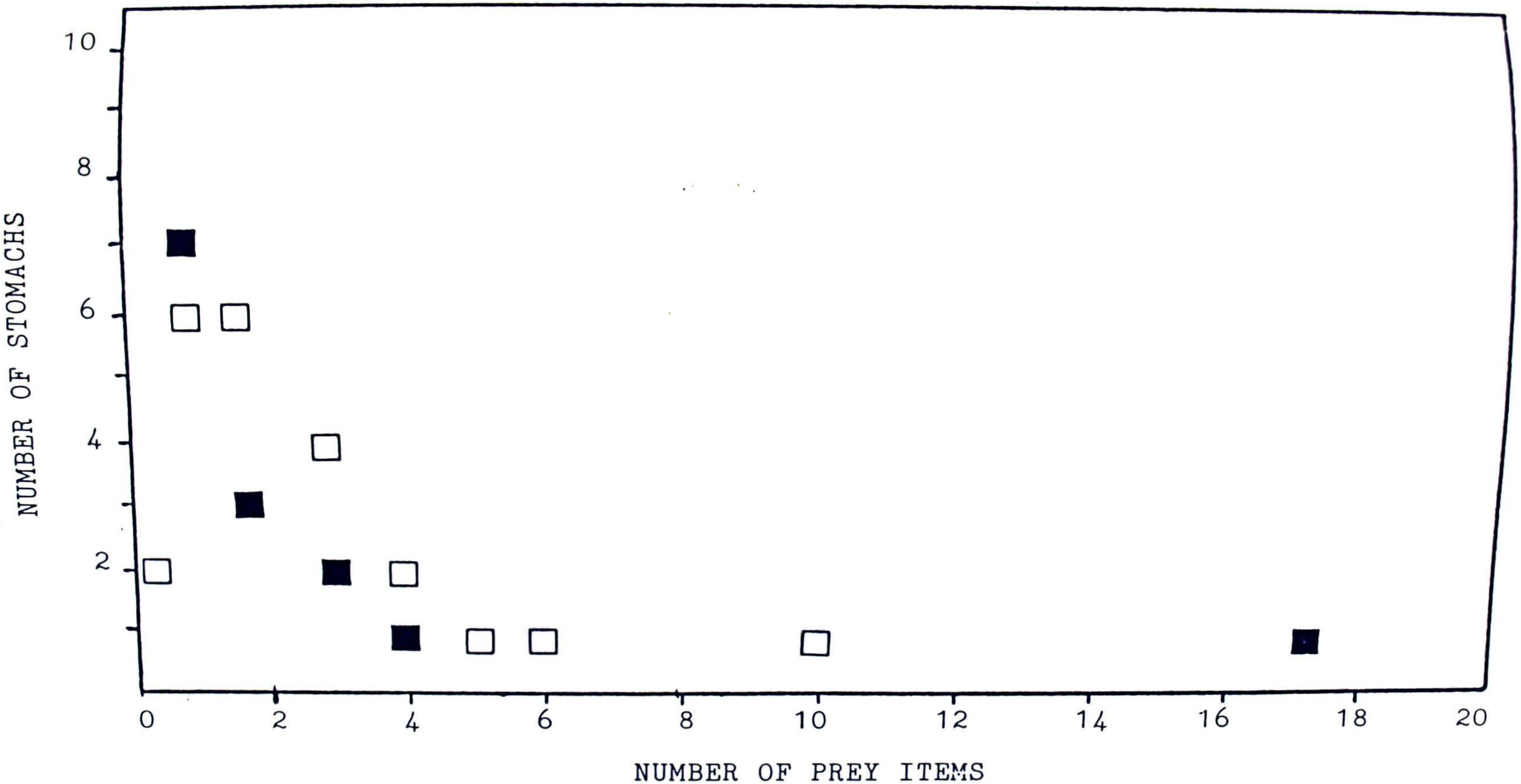

Figure 8. Number of Prey Items per Stomach in 14 *Desmognathus quadramaculatus* and 23 *Desmognathus monticola* from Dry Falls in Macon County, North Carolina Symbols: ■ = *Desmognathus quadramaculatus* □ = *Desmognathus monticola*

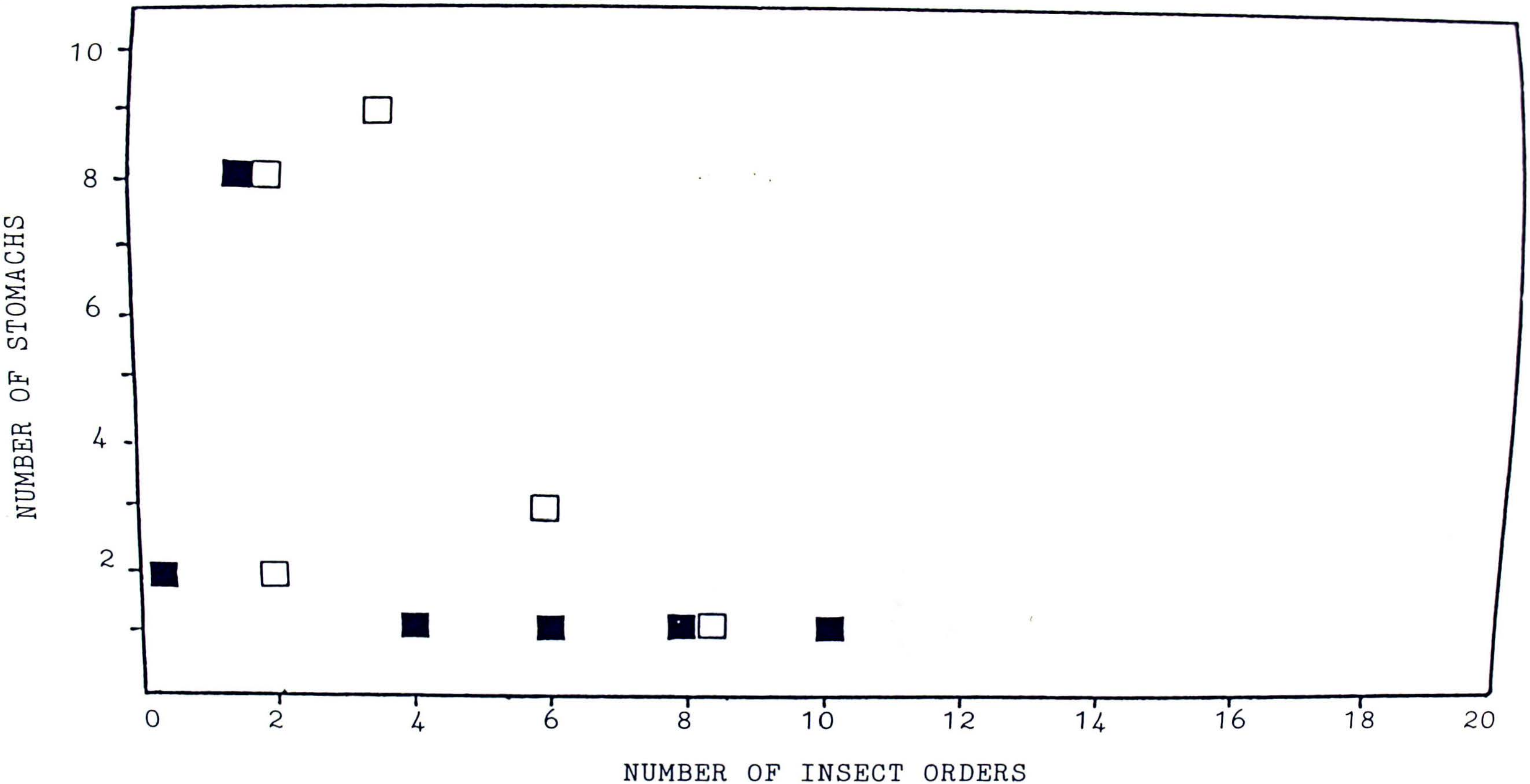

Figure 9. Number of Orders of Insect Prey per Stomach in 14 _Desmognathus quadramaculatus_ and 23 _Desmognathus monticola_ from Dry Falls in Macon County, North Carolina Symbols: ■ = _Desmognathus quadramaculatus_ □ = _Desmognathus monticola_

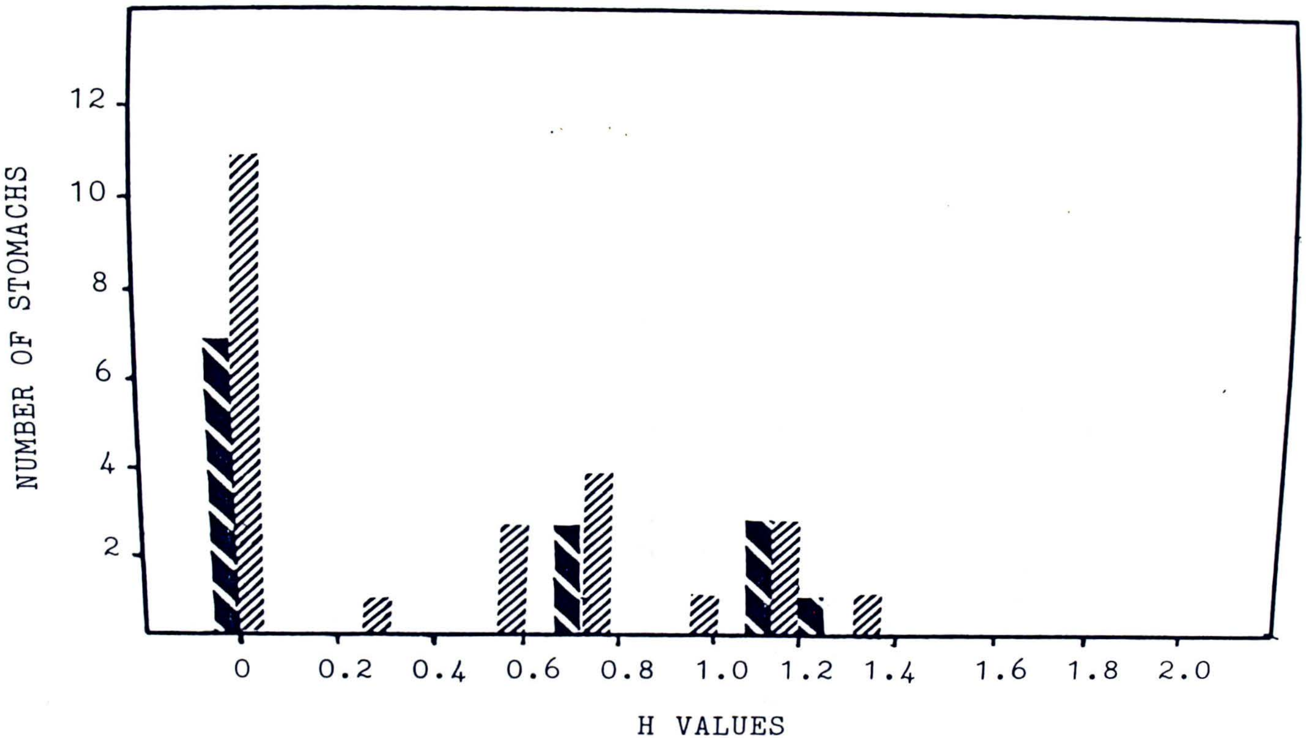

Figure 10. Prey Diversity of _Desmognathus quadramaculatus_ and _Desmognathus monticola_ at Dry Falls in Macon County, North Carolina Symbols: ◣= _Desmognathus quadramaculatus_ ▨ = _Desmognathus monticola_ H values represent coefficients of diversity calculated by the Shannon-Weiner Diversity Index,

$$H = -\sum_{i=1}^{n} pi \log_e pi$$

had no diversity of prey in their stomachs. No significant difference was found in the diets of _quadramaculatus_ and _monticola_ when H values were compared by the Mann-Whitney U test. Values of U under 1.96 indicate no statistically significant difference at the 95 percent confidence level (Campbell 1974). When the DF data were analyzed, a calculated value of 0.17 was obtained for U.

A single (but different) prey item dominated in each population when percent volume was calculated. At DF, one earthworm (Lumbricidae) composed 55.0 percent of the entire prey volume of the sample of _monticola_ (Fig. 7) and one adult diplopod accounted for 49.0 percent of the total prey volume of _quadramaculatus_ (Fig. 6). By volume, diplopods, coleoptera adults, and a salamander were the most important food items to _quadramaculatus_ at DF. If the one large earthworm taken by _monticola_ at DF (Fig. 7) is discounted, other percents by volume are fairly well distributed, ranging from 6-11 percent contributed by Isopoda, Arachnida, Hymenoptera, Coleoptera, and Lepidoptera. The remaining 3.6 percent was contributed by Collembola, Diptera, Diplura, and Orthoptera.

CHAPTER IV

DISCUSSION

Though many carnivores face evolutionarily imposed dietary restrictions, which reduce their ability to consume a wide range of prey types, such limitations are less apparent among plethodontid salamanders. Many studies have revealed that salamanders will eat almost any prey that is available and of edible size. Noble (1927) and Hairston (1949) found that no species of urodele was known to restrict its diet to a particular kind of animal food. Davidson (1956) and Powders and Tietjen (1974) felt availability was the most important factor governing a salamander's feeding habits. If these assumptions are valid, the prey taken by these forms are more a representation of what is available than what their "preference" might be. The variety of food items found in this study was similar to that found by Donavan and Folkerts (1972) in a study of *Desmognathus aeneus*. Snails, found by Donavan and Folkerts (1972) to be a significant dietary item to *aeneus*, were not found in the diets of *Desmognathus quadramaculatus* or *D. monticola* at BV or DF. Because a determination of prey availability was not attempted in my study, I could not determine the degree to which the species I observed were selectively exploiting their habitats. It was, however, possible to compare the diets of the two species at each site and to look for significant trends.

Both species were frequently found to ingest both inorganic and plant material as well as living invertebrate forms. Some have proposed that the inorganic matter, such as sand grains, could aid in macerating food, but it seems probable that sand, as well as leaves, bark and other bits of detritus were taken incidentally with prey. Similar conclusions were reached by Martof and Scott (1957) in a study of the feeding habits of Leurognathus marmoratus. I observed monticola swallowing a small clump of soil when failing to capture a moth. Nematodes were found in the stomachs of several quadramaculatus. Since the nematodes were alive and not even slightly digested, I assumed they were parasites rather than food. Donavan and Folkerts (1972) considered a partially digested nematode found in the gut of D. aeneus to be food.

The annelids which made up nearly 10% of the diet of quadramaculatus were leeches (Fig. 1) and were found on almost all of the quadramaculatus collected, as well as in the stomachs of six specimens. No monticola were found with leeches attached externally or in their stomachs. Whether quadramaculatus was selected over monticola by the leeches is uncertain. It is unclear whether the quadramaculatus were plucking the leeches from their own bodies or selecting them as prey from the rockface.

There seemed to be no significant relationship between the size of prey and head width of the salamanders (data for DF site only), since all prey items were small enough to have been swallowed by even the smallest salamander in the sample. The $\bar{x}$ head width of the sample of *monticola* was 7.21 mm and the $\bar{x}$ head width of the *quadramaculatus* sample was 10.5 mm, while the $\bar{x}$ prey widths were 1.77 mm and 1.86 mm respectively, somewhat smaller than found by Hairston (1949) in a similar study. The fact that smaller prey were frequently taken by the larger animals suggests that the salamanders were eating what was available rather than being selective. This is somewhat contrary to the findings of Burton (1976), who found that the larger predators took fewer and larger prey. This discrepancy could reflect the supposedly more limited food supply on a rockface (Tilley 1968, 1974), or be due to my small sample sizes.

Martof and Rose (1962) reported the coexistence of *quadramaculatus* and *monticola*, but I noticed a slight tendency toward spatial separation at BV, with *monticola* feeding lower on the rockface than did *quadramaculatus*. This could well be a reflection of *quadramaculatus*' slightly more aquatic nature, since at higher levels on the BV rockface they were in more direct water flow. It could also account for the higher volume of Diptera larvae (Fig. 1) as opposed to Diptera adults in the *quadramaculatus* diet, since fragile dipteran adults would have been less abundant in the heavy spray and splashing water at higher levels of the rockface at BV. The predominance of dipterans in the desmognathine diet was noted by Krzysik (1979). The putative stratification noted in my study could also explain the greater volume of Formicidae (Fig. 2) consumed by monticola, which tended to feed lower on the rockface and had better access to insects climbing up from the ground. Whitaker and Rubin (1971) found that as salamanders increased in size, ants became less significant in their diets and did not as a rule compose a great percent of desmognathine diets.

Prey such as mites and collembolans, which are often ingested in large numbers but compose a negligible percent of the diet by volume, may be more significant in the salamander's diet than their volume would suggest. Burton and Likens (1975) hypothesized that small or rare prey in a diet may be nutritionally important in ways other than furnishing bulk nutrients for energy. Ants and beetles, sizeable prey items when consumed, frequently pass through the animal only partially digested and thus may be of less dietary significance than their bulk might indicate (Sites 1978, Keen 1979). Insect larvae were considered by Sites (1978) to be the most beneficial prey nutritionally. The taking of invertebrate prey, often in the form of salamanders, is not uncommon. Although this is more often recorded for Gyrinophilus porphyriticus danielsi, it has also been reported for quadramaculatus by Martof and Scott (1957).

In his discussion of feeding strategies of Desmognathus fuscus, Sites (1978) presents a model first introduced by Schoener (1971). It is interesting that data in this study conform quite well to Schoener's (1971) observations. It is suggested that in the trend from aquatic to terrestrial existence there will be a concurrent trend toward more active prey search (Schoener 1971). In my study, I observed that quadramaculatus, more aquatic than monticola, assumed the sit-and-wait predator role and monticola foraged more actively. According to Schoener's model, the sit-and-wait predator consumes a more diverse diet and shows more variation in stomach contents (Schoener 1971). A slightly more varied diet was confirmed in the quadramaculatus samples at both BV and DF.

Jaeger (1972) also noted that it is seldom advantageous for large salamanders to forage in periods of dry weather, since the energy expended is likely to be greater than that taken in as prey found during the search. The dry conditions behind the falls at DF could have imposed this restriction on the quadramaculatus in which six empty stomachs were encountered. Time spent exposed on the surface in dry weather also resulted in increased exposure to predation by shrews, according to Jaeger (1972), thus making the sit-and-wait strategy preferable despite the occasional empty stomach. I found monticola, also conforming to the Schoener model, to be a noticeably more active forager than quadramaculatus, with the majority of the monticola specimens being captured in open areas away from their burrows. Quadramaculatus had to be forced from crevices or enticed into the open by simulated prey movement.

CHAPTER V

SUMMARY AND CONCLUSIONS

Two series of rockface and streambank salamanders, *Desmognathus quadramaculatus* and *D. monticola*, were collected in Macon County, North Carolina. Stomach contents were removed, measured, and identified. Appropriate statistical analysis was performed and the results were evaluated after consideration of other similar research.

Although qualitative and quantitative differences in prey consumed were found, a lack of prey-availability data prevented attributing the observed differences to definite selection of prey by size or taxon. Statistical analysis indicated that differences in diversity of prey consumed were not significant.

Despite the small sample size, possible foraging strategies were observed. There were indications of spatial stratification of the two species at the rockface site, and foraging strategies conforming to theoretical predictions based on the degree of terrestriality of each were noted at the rockface/streambank site. The data collected best conform, however, to the opportunistic euryphagic feeding model for these salamanders, since no statistically significant pattern of prey selection was evident.

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