

**FORAGING STRATEGY OF THE DUSKY SALAMANDER,
DESMOGNATHUS FUSCUS: A FIELD STUDY**



JACK WALTER SITES, JR.

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An Abstract
Presented to
the Graduate Council of
Austin Peay State University

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

by
Jack Walter Sites, Jr.

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ABSTRACT

The indirect approach developed by Maiorana (1971) was employed to study foraging strategy of the dusky salamander, Desmognathus fuscus, in three populations and at two seasons, in Montgomery County, Tennessee. Theoretical predictions of predator feeding activity (Schoener, 1969a, 1969b, among others) were considered empirically in analyzing features of the salamanders' diets, and inferences were made from these data, and from salamander activity patterns as influenced by rainfall, in postulating a mode of foraging for this species.

Desmognathus fuscus shifts from a sit-and-wait predator (Schoener, 1971) during periods of dryness, to a more actively searching predator as substrate moisture increases. Selectivity for both prey species and size increases with an increase in the frequency of rainfall. Litter samples show that most prey items are consistently abundant, so that they are probably limited in relative rather than absolute availability to the salamanders. As the substrate dries, salamanders retreat beneath moisture-retaining objects, and their foraging range shrinks to the limited space beneath the object. There they may either feed or await the next rain, after which they may disperse widely. Some sexual partitioning of food items occurs, and this may be an adaptation to increase the total energy available to the species and reduce intra-specific competition. Possibly complimentary feeding niches are sustained where D. fuscus shares a habitat with one or more species of Eurycea.

The significance of the foraging strategy in the life history of D. fuscus is discussed, as are some of the difficulties involved in conducting such a study. Laboratory experiments are proposed for critically testing the influence of many variables, such as temperature, atmospheric relative humidity, and the nutritional state of the predator itself, on the foraging behavior of this species.

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To the Graduate Council:

I am submitting herewith a thesis written by Jack W. Sites, Jr. entitled "Foraging Strategy of the Dusky Salamander, Desmognathus fuscus : A Field Study." 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 H. Snyder
Major Professor

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CHAPTER I

INTRODUCTION AND REVIEW OF THE LITERATURE

The concept of species diversity has aroused considerable interest among biologists in recent years, and many workers have focused their attention on evaluating factors that regulate the species diversity achieved by a given lineage. Particularly important are the constraints placed on that lineage regulating the number of species that coexist within a community. The phyletic history of any group places constraints on the degree of ecological divergence among its species and, thus, on the number of species that the lineage may pack into a given community (MacArthur and Levins, 1967). Those constraints generally considered important in regulating the species diversity of a particular lineage are: (1) the structural configuration of the community inhabited by the lineage, (2) potential competitors for vital resources, and (3) the biology of the lineage.

There is now strong evidence supporting the idea that community structure is important in the vertical and horizontal partitioning of space among cohabiting species of the same lineage. Studies of birds (Cody, 1968; MacArthur, 1958; MacArthur and MacArthur, 1961; Morse, 1967, 1971; Orians and Horn, 1969) and lizards (Andrews, 1971; Pianka, 1966, 1967, 1969, 1973; Schoener, 1968, 1970; Schoener and Gorman, 1968) show that, within these groups, coexistence is achieved and competitive exclusion is avoided to some degree by a separation

of structural niches among many species. Many lizards and birds exhibit species-specific affinities for perches of a certain height and/or diameter and utilize different foraging areas on the same tree (near the trunk, on the periphery, etc.), and this is an important basis for food resource partitioning. Alternatives to this type of niche segregation might be the utilization of different sets of resources (such as different predator species feeding on different prey species) or the exploitation of certain patch types within the environmental mosaic, utilizing all resources within these patches (feeding in certain types of trees). The problem then becomes one of defining the evolutionary channels by which these two diverse and independently evolving groups (lizards and birds) arrived at a common means of resource division—spatial separation. No doubt the biology of these two lineages, the nature of the food resource, and potential competitors interacted to favor one method of resource partitioning over another.

Among species of a group not occupying separate structural niches, selection would favor a reduction of competitive interactions along other major niche dimensions. Many studies (Ashmole, 1968; Bury and Martin, 1973; Hespenheide, 1973; Jaeger, 1971, 1972; Lynch, 1973; Menge, 1972b; Root, 1967; Schoener, 1965; Spotila, 1972) have shown that differences in body size, trophic appendages, physiological requirements, environmental tolerances and other features of the biology of any lineage may be important in the separation of niches of sympatric species. Since ecological compatibility is a prime requirement for sympatry, and the shape of a species' niche is related to the proximity and abundance of competing species (MacArthur and Levins,

1967), the diversity attained by a lineage often depends on the size of the resource base that that lineage can command for its use under competitive pressures. The more finely a lineage can subdivide critical resources, the more species it can pack into a community until a point is reached where all available resources are utilized. The packing of species may be closer when niche dimensionality decreases and if niche breadth is small. For example, most amphibians have a tongue feeding apparatus specialized for capturing small terrestrial invertebrates; they have been unable to exploit plant foods. All else being equal, the diversity achieved by this group depends on how finely it can subdivide a food base of small invertebrates while competing with other lineages for this resource. Additional features of their biology, such as a water-dependent reproductive mode and a highly vascularized integument requiring moisture, further restrict amphibians to specific types of communities.

Of the many phyletic groups available for the investigation of community structure and species diversity, salamanders of the family Plethodontidae offer some advantages. Representatives of three major groups within this family (Desmognathines, Plethodontines, and Bolitoglossines) have left the ancestral mountain stream habitat on three separate occasions (Wake, 1966). Attendant modifications in the feeding structure suggest that partitioning of food resources may have been important in developing the diversity achieved by this family. Of the three major groups mentioned above, the Desmognathines possess the most generalized tongue feeding apparatus and display the least species diversity, while the Bolitoglossines, possessing a highly

specialized tongue feeding apparatus, display the greatest species diversity. This development follows a general functional trend toward increased extensibility and greater protrusion of the tongue from the mouth, associated with an increasingly terrestrial existence (Regal, 1966).

Of the feeding specializations that have accompanied adoption of a terrestrial mode of life by these salamanders, studies of foraging strategies have been largely ignored, due no doubt to the cryptic and nocturnal habits of these animals. Maiorana (1971), working with Batrachoseps attenuatus, developed an indirect approach of analyzing the foraging strategy of natural populations of this salamander through inferences made from observations of diet and behavior.

I have followed Maiorana's approach in my investigation of the foraging strategy of Desmognathus fuscus. Though no such studies have been previously conducted on any species in this genus, it should be well suited to such studies since the genus displays an evolutionary trend toward an increasingly terrestrial mode of life paralleled by decreasing body size (Organ, 1961; Tilley, 1968). This trend from an aquatic to terrestrial existence is also correlated with an increasing trend toward active prey search (Stewart, 1970). Food habit studies of various members of this genus have shown that the feeding niche is more terrestrial than aquatic (Donavan and Folkerts, 1972; Hairston, 1949; Huheey, 1966).

Desmognathus fuscus is the most widespread member of its genus, suggesting that it may be the most flexible along one or more critical dimensions of its niche. Its feeding niche is semi-aquatic

to terrestrial (Barbour and Lancaster, 1946; Bennett and Bellis, 1972; Hamilton, 1932), and, though it has a restricted home range (Ashton, 1975; Barthalmus and Bellis, 1972), the size of the home range may fluctuate widely (Barbour et al., 1969). This varying home range size may allow the adoption of seasonally varying foraging strategies, making a seasonal analysis imperative.

The foraging strategy concept—how a predator locates and selects its prey—represents a relatively recent approach to predation theory. Models formulated by some workers (Emlen, 1966, 1968; Pulliam, 1974; Rapport, 1971; Schoener, 1969a, 1969b) go beyond descriptions of predator-prey systems in an attempt to predict the optimal diet (that which maximizes net energy gain per unit foraging time) of a predator under a given set of conditions. A basic assumption made in these models is that a predator has certain food preferences (that a predator will, if given a choice, choose prey items representing the highest caloric value, nutrient gain, ease of acquisition, etc.) that have been established through natural selection acting to maximize energy gain per unit foraging time. Within the framework of the proposed models, the optimal diet of a predator may be influenced by: (1) changes in environmental conditions, (2) changes in the predator's condition (hungry or satiated), (3) changes in prey abundance or availability, and (4) competition for available food. A number of testable predictions emerge from these models that lend themselves to an empirical approach.

Schoener (1971) summarizes previous discussions of two basic types of predators. The first is a sit-and-wait predator (time mini-

mizer) that, while watching for food, simultaneously monitors mates, territorial invaders, and predators of itself. It expends no more energy searching for food than it would have expended in other activities. Conversely, an actively foraging predator (energy maximizer) expends considerable time and energy searching for food as well as expending energy for other activities. All else being equal, actively foraging predators tend to be more specialized than sit-and-wait predators either in their diets or foraging areas or some combination of the two. Table I illustrates features of the diets, derived from theoretical expectations, of these two modes of foraging.

One prediction derived from the models is that searching predators (energy maximizers) will show less diversity of stomach contents than will sit-and-wait predators. The argument is that the former cover a larger area of the environment, thus encountering more items from which to choose, and can spend more time searching in areas of the more favorable prey (Schoener, 1969a). A sit-and-wait predator is expected to reflect in its diet the patchiness of the microhabitat distribution of prey. Since the actively foraging predator will chance to encounter more of the preferred prey types, it is expected to take fewer of the less preferred prey types than is the stationary predator (MacArthur and Pianka, 1966). Also, since the active predator expends more energy in searching than does the stationary predator, it should have a more restricted range of potential prey items representing a net energy gain, given that the methods of capturing, handling, and assimilating prey are similar. This prediction can be tested by quantifying the diets of a population of predators in a giv-

TABLE I. Theoretical characteristics of stomach contents, based on two modes of foraging (modified from Maiorana, 1971)

Sit-and-wait predator (time minimizer)		Actively foraging predator (energy maximizer)
Prey species	Diverse, many taxa taken, large numbers of less preferred prey types	Not as diverse, fewer taxa taken, large numbers of more preferred prey types
	Much individual variation in stomach contents, reflecting patchy distribution of most prey types	Less individual variation, reflecting wider areas covered in search of preferred prey types
	Diets show small deviation from proportions of prey species as they are available in the habitat	Diets deviate considerably from the proportions of prey species as they are available in the habitat
Prey size	Wide range of prey sizes taken	More restricted range of prey sizes taken
	Proportionally smaller prey items taken	Proportionally larger prey items taken

en habitat, quantifying the prey items available in that habitat, and comparing prey ingested by the predators with prey available in the habitat.

A second important prediction is that the width of a predator's feeding niche is an inverse function of prey availability. When prey items are scarce, optimal feeding calls for essentially all potential food items encountered to be taken, and as prey become more available or as the predator becomes more satiated, selectivity should increase (Emlen, 1966, 1968; Rapport, 1971; Schoener, 1971). Where prey are regularly available, specialization should be favored, but in unstable environments where prey species fluctuate unpredictably in availability, generalists should be at an advantage (Schoener, 1969b). The intensity of competitive pressures must be considered as a factor influencing the width of a predator's feeding niche. Competition, if it affects the diets of competitors at all, will tend to cause greater generalization over a brief period of time, although the long range evolutionary effect might be increased feeding specialization and thereby reduction of direct competition. To test these ideas I have compared the diets of salamanders and prey populations in habitats that differed in the density of potential competitors. Seasonality was also considered as a factor possibly influencing prey availability.

In the absence of heterospecific competitors, a species may increase the breadth of certain critical dimensions of its niche by developing pronounced sexual differences in size or morphology associated with differences in structural niches occupied and/or prey sizes

taken (Jackson, 1970; Ligon, 1968; Morse, 1968; Robins, 1971; Schoener, 1967, 1969a; Storer, 1966). This implies that the sexes are utilizing different sets of resources, thus reducing intraspecific competition while increasing the total energy available to the species. I have looked for sexual dimorphism in the salamander populations sampled, and assessed the degree of food resource partitioning present.

Several models also predict that larger predators with higher energy requirements should take larger prey items than smaller individuals when feeding optimally, but unless prey are very abundant, larger animals should take a greater range of food sizes than smaller ones (Schoener, 1971). During periods of environmental stress, low prey availability, or intense competition for food, large individuals within the population are expected to take a proportionally greater number of smaller prey items, indicating a sub-optimal foraging mode. I have correlated salamander size with prey size taken in all populations sampled to determine which population was most size-selective of its prey.

CHAPTER II

METHODS AND MATERIALS

To test some of the predictions of the models and determine some of the factors that might influence the foraging mode of Desmognathus fuscus, I have taken advantage of its occurrence in different habitats and seasons. This provided samples of individuals believed to have come from environments varying with regard to such factors as substrate moisture, competitive pressures, and species composition and density of the prey community. Three different habitats were selected for study, all located in Montgomery County, Tennessee on the western Highland Rim. The physiography of these areas was broadly similar; each was a small wooded ravine bisected by a stream of slight gradient. The slopes exhibited loose talus outcrops of limestone, and in places the streams had cut down to limestone bedrock. The dominant vegetation in all areas was the Western Mesophytic Forest type of Braun (1950), composed primarily of oaks (Quercus) and hickories (Carya).

Of the three areas, I worked Tank Hollow (hereinafter referred to as site I) most extensively. It was located about 22.5 km by road SW of the Austin Peay State University campus, where a spring emanated from a limestone outcrop and flowed 150-200 m to its confluence with the Cumberland River. The stream was clear, with a limestone substrate, moderately swift, and in most places less than one m wide and

from 1 to 12 cm deep. Stream flow was relatively stable throughout the year and the stream supported an aquatic invertebrate fauna.

Desmognathus fuscus was by far the most common salamander in this habitat. Plethodon glutinosus, P. dorsalis, Eurycea lucifuga, and E. bislineata were also present but were not encountered in sufficient numbers to be taken for comparative purposes.

Salamanders were taken from site I during three separate periods. On 28 September 1974, 51 animals were collected. This collection immediately followed a heavy rain, and many of the salamanders had dispersed widely from the stream bed. No samples of the invertebrate community were taken on that date. Salamanders were again collected during a four week interval beginning on 16 October and ending on 9 November 1974. Five salamanders were taken during each of the four weeks and the invertebrate community was sampled twice each week throughout this time. During this interval rain fell only twice (slight both times), and the substrate was dry excepting the microhabitats beneath rocks and logs; the salamanders were therefore confined to a narrow corridor within one m of the stream. Since substrate moisture may greatly affect the mode of foraging adopted by this salamander, I sampled the population again when rainfall was more frequent. From 1 April to 12 April, 1975, I collected 30 D. fuscus (15/week) and sampled the invertebrate community of potential prey items twice each week. I shortened the collecting interval from four to two weeks to reduce the unmeasured effect of the time lapse between weeks (since only seasonal trends were analyzed) and to minimize disturbance to this habitat, which was very limited in size. During this

spring sampling rainfall was more frequent than it had been in the autumn sampling period and the salamanders were not as confined, though most were still within one or two m of the water's edge.

The second habitat selected for analysis was located on the Austin Peay State University farm (site II) about 4.0 km by road NE of the APSU campus. This area differed from site I in that the degrading stream flowed only intermittently and supported no significant aquatic invertebrate community. For much of the year part of the streambed was normally dry with only one or two deep pools retaining water, while other sections were kept moist by minute seepages from overhanging limestone outcrops. Very little limestone bedrock was exposed; most of the creekbed was chert gravel, the moister parts of which supported dense populations of earthworms. A small population of D. fuscus inhabited a section of this streambed approximately 100 m long. Other species of salamanders encountered there were Plethodon dorsalis, Pseudotriton ruber, and Eurycea longicauda. Eurycea longicauda was common and often found in the same microhabitat as D. fuscus. I considered it to be a potential competitor for food and collected ten specimens for comparative purposes. This habitat was sampled during the same four week time interval as was site I and collections of both salamanders and invertebrates were made as at site I. Unfortunately I had to abandon this habitat before making spring collections due to a depleted population.

A third habitat (site III) was selected with which to compare the spring collections made at site I. Site III was located just off Simpson Drive 6.6 km by road SE of the APSU campus. The area was sim-

ilar to site I except that the stream carried a slightly greater volume of water (it was up to 20 cm deep). The stream was clear with a limestone substrate and supported an aquatic invertebrate fauna. The section of ravine that I studied was approximately 200 m long and supported a stable population of D. fuscus as well as a number of Eurycea bislineata and E. longicauda. I collected from this area during the same two week period as for the spring sample at site I, collecting 30 D. fuscus and sampling the invertebrate community twice weekly. Eighteen Eurycea (seven E. longicauda and 11 E. bislineata) were collected for comparative purposes.

Table II summarizes the numbers of D. fuscus taken from each habitat and the periods during which they were collected.

TABLE II. Summary of sample sizes and dates of collection of Desmognathus fuscus taken from three habitats differing in stream flow, potential prey available, and density of potential competitors

Site	major habitat differences	numbers of salamanders collected		
		28 Sept. 1974	16 Oct.- 9 Nov., '74	1-12 April 1975
I	permanent stream, few heterospecifics present	51 animals	20 animals (5/week)	30 animals (15/week)
II	temporary stream, habitat shared with <u>Eurycea</u>	—	20 animals (5/week)	—
III	permanent stream, habitat shared with <u>Eurycea</u>	—	—	30 animals (15/week)

In summary, my collecting effort yielded enough material for comparisons of populations of salamanders feeding in the presence and absence of potential heterospecific competitors, and under the influence of differing moisture regimes.

All salamanders were collected before noon by turning stones, rocks, and other objects in the stream, on its banks, and on bordering wooded slopes. Captured animals were put singly in numbered plastic bags and placed on ice to arrest digestion. In the laboratory, each specimen was weighed and then frozen, and subsequent morphological measurements were taken from specimens preserved in formalin. Measurements routinely taken were body length (measured from the tip of the snout to the posterior angle of the vent), total length, and greatest head width. All measurements were recorded to the nearest 0.5 mm. Each individual was dissected and its sex determined, and the entire digestive tract was removed and stored in 70 percent ethyl alcohol.

When analyzing stomach contents I first determined the total volume of all food items present, using a smaller version of the volumeter described by Inglis and Barstow (1960). If large enough to be measured ($\geq .005 \text{ cm}^3$), I determined the volume of the single largest prey item. I then measured prey items (length x greatest width) under a dissecting microscope fitted with an ocular micrometer calibrated to 0.1 mm. Only intact prey items were measured, their being intact implying that they had been recently ingested (Jaeger, 1972; Maiorana, 1971).

Most valid tests of the predictions of feeding theory carried

out in a field situation must be made on organisms for which it is feasible to estimate with reasonable accuracy the relative abundance of potential prey. Using animals that select prey from a food base of small invertebrates presents some problems, since there is no single technique available that allows sampling of the various groups of soil and litter fauna with equal efficiencies (MacFayden, 1962).

I utilized four methods of sampling the habitats for available prey that I believe were adequate for determining the relative abundance of those invertebrates most likely to be encountered by a foraging salamander. Leaf litter and loose top soil were collected from 25 cm square plots for separation in Berlese funnels. To sample invertebrates too large to be separated by the funnels, larger plots (50 cm squares) were carefully raked and the invertebrates picked out with forceps. Stream bed samples were made within 15 cm square plots. Each of these techniques was repeated five times on each sampling day, and each habitat was sampled twice weekly during the sampling periods. To capture flying and fast-moving invertebrates that might not be taken by the other three techniques, I set out tanglefoot traps once a week at each habitat during the designated collecting periods. Insect tanglefoot was spread on 22 x 14 cm sheets of rag paper, and 15 of these were then left scattered throughout a habitat for 24 hrs.

The invertebrates taken by these techniques were separated by taxa, and in most cases animals were identified to the familial level. Classifications followed were those of Borror and White (1970) for terrestrial insects, Pennak (1953) for aquatic invertebrates, and Pratt (1935) for terrestrial invertebrates other than insects. Prey

densities were routinely expressed as the number of a particular taxon per m^2 , thus allowing a determination of the relative abundance of all taxa in the different habitat types. The densities calculated were undoubtedly conservative estimates, as some groups of litter animals are always under-represented in the samples, even when elaborate techniques are used (Kempson, Lloyd, and Ghelardi, 1963). Since the insect tanglefoot attracted many flies, precluding an unbiased sample, no estimates were made of the densities of prey items collected by that technique.

Because salamanders may select a prey item by size as well as by taxon, the litter animals were also measured and grouped into size classes for analysis. Prey items were measured under a dissecting microscope fitted with an ocular micrometer calibrated to 0.1 mm. Up to 100 individuals from each major taxon were measured. The frequency distribution of prey sizes in the litter could then be compared with the frequency distribution of prey sizes taken by the salamanders.

CHAPTER III

RESULTS

A necessary assumption made in this study is that the foraging strategy is an adaptation of the species achieved through natural selection. I have also assumed that the predator has a hierarchy of preferences for the prey species and, if given a choice, selects certain prey types over others. These favored prey species may be ranked in order of decreasing importance to the predator in terms of net energy and nutrient gain per unit foraging time. Prey features that possibly influence their position in the predator's hierarchy of food preferences include size, color, hardness of integument, defense mechanisms, locomotory mode, etc. The degree of selectivity shown by Desmognathus fuscus has been measured in two ways: (1) selection of prey by species and (2) selection of prey by size.

SELECTION OF PREY BY SPECIES

The preference for certain prey taxa exhibited by D. fuscus was measured by the difference of the stomach contents from the prey items available in the habitats. Most of the prey availability data used in this study may be found in the appendixes.

Table III shows the percentages of different prey taxa consumed by D. fuscus at all collecting sites and through different seasons. Eurycea bislineata and E. longicauda are included there for

TABLE III. Percent of prey (by number of items) found in the stomachs of Desmognathus fuscus and Eurycea (including E. longicauda under the site II column, and both E. longicauda and E. bislineata under the site III column) from three sites (I, II, and III) in Montgomery County, Tennessee. Percents are of total number of items for all samples

prey	date taxon site	Sept.	Oct.-Nov.		April		
		<u>D. fuscus</u> I	<u>D. fuscus</u> I	<u>Eurycea</u> II	<u>D. fuscus</u> I	<u>Eurycea</u> III	
Pulmonata		2.5	2.4	--	10.3	--	--
Oligochaeta							
Lumbricidae		1.0	2.4	27.3	--	9.8	4.3
Araneae		4.0	--	--	--	2.4	--
Acarina		2.5	--	--	13.8	--	4.3
Diplopoda							37.5
Callipodidae		2.0	--	--	--	2.4	13.0
Chilopoda							12.5
Scolopendridae		1.5	--	9.1	--	2.4	4.3
Chelonethida							--
Chernetidae		0.5	--	--	3.4	--	--
Insect larvae		54.3	31.7	18.2	6.9	24.4	4.3
Lepidoptera		--	--	--	--	2.4	--
Diptera							12.5
Lonchopteridae		--	--	9.1	--	--	--
other flies		--	2.4	9.1	--	--	--
Collembola							--
Poduridae		1.0	--	--	--	--	--
Sminthuridae		6.0	2.4	--	44.8	--	--
Entomobryidae		5.5	12.2	9.1	3.4	--	4.3
							25.0

TABLE III (continued)

prey	date taxon site	Sept.	Oct.-Nov.		April		
		<u>D. fuscus</u>	<u>D. fuscus</u>	<u>Eurycea</u>	<u>D. fuscus</u>	<u>Eurycea</u>	
		I	I	II	I	III	III
<hr/>							
Coleoptera							
Pselaphidae		--	9.8	--	--	--	--
Staphylinidae		0.5	2.4	--	3.4	2.4	4.3
Carabidae		0.5	--	--	--	9.8	4.3
Tenebrionidae		0.5	--	--	--	--	--
Curculionidae		1.0	--	--	--	2.4	--
Elateridae		0.5	--	--	--	--	--
Hydrophidae		--	--	--	--	2.4	--
Scarabaeidae		--	--	--	--	--	4.3
other beetles		1.0	--	--	--	--	4.3
Homoptera							
Aphididae		0.5	4.9	--	10.3	--	--
Cicadellidae		--	2.4	--	--	2.4	--
Hemiptera							
Cydnidae		0.5	--	--	--	--	--
Nabidae		--	--	--	3.4	--	--
other bugs		1.0	--	--	--	--	--
Hymenoptera							
Formicidae		6.0	4.9	--	--	2.4	4.3
Braconidae		--	2.4	--	--	--	--
Eulophidae		--	2.4	--	--	--	--
Cynipidae		--	2.4	--	--	--	--
Platygasteridae		0.5	--	--	--	--	4.3

TABLE III (continued)

prey	date taxon site	Sept.	Oct.-Nov.		April		
		<u>D. fuscus</u> I	<u>D. fuscus</u> I	<u>Eurycea</u> II	<u>D. fuscus</u> I	<u>Eurycea</u> III	<u>Eurycea</u> III
Orthoptera							
Blattidae		0.5	--	--	--	--	--
Gryllidae		0.5	--	--	--	--	--
Isopoda							
Asellidae		1.5	9.8	9.1	--	19.5	43.4
Oniscidae		1.0	2.4	9.1	--	--	--
Amphipoda							
Gammaridae		0.5	2.4	--	--	14.6	--
number of stomachs containing food		45	17	10	9	20	10
total number of prey items found in all stomachs		199	41	11	29	41	23
average number of prey items/stomach excluding empty guts		4.4	2.4	1.1	3.2	2.0	2.3

comparative purposes. Because of wide variation among the samples in the number of stomachs containing food, the percentages must be considered relative to the sample size within each group. For example, the data suggest that a wide diversity of prey taxa were routinely consumed. In fact much of the prey diversity was contributed by the large sample of salamanders taken from site I in September, many of which contained only one item (0.5 percent of the total number of items) of an uncommon taxon. When a sample that large (relative to the other samples) is considered, the range of individual variation is expected to be greater, and this might account for some of the greater taxonomic breadth of the food base consumed by that group. Some of the other samples may be inadequate for revealing the diversity of the food base, but, despite the unequal sample sizes, certain trends were evident.

Most of the common litter inhabitants were represented in the diets, but in proportions that did not correlate well with the litter samples. Much more frequently exploited by D. fuscus than expected from their abundance in the litter were the insect larvae. Only in the sample from site III was this not the case. All three samples of D. fuscus taken from site I contained a higher percentage of insect larvae than any other single prey type. Since this taxon was generally poorly represented in the litter community throughout the year in all habitats, the possibility exists that D. fuscus was selectively feeding on larvae at sites I and II. The predator population at site II may also have selected for earthworms, though those items were more common there than at the other two sites, while the population at site

III consumed more asellid isopods and callipodid millipedes than was expected based on the occurrence of those two taxa in the litter and stream samples. Collembolans and mites, by far the most abundant animals in the leaf litter, were under-represented in the stomach contents of all samples of D. fuscus. This represented a second deviation from what was expected of a predator indiscriminate in its food preferences.

Seasonal variation in the diet is shown in Table III for the population of salamanders at site I. Salamanders taken in September (the day after a heavy rain) consumed more insect larvae than anything else, with sminthurid and entomobryid collembolans, and ants constituting the bulk of the remainder of the diet. In the October-November sample, insect larvae were still the most frequently eaten prey, but there was an increase in the proportion of entomobryid collembolans, pselaphid beetles, and asellid isopods consumed and a corresponding decrease in the proportion of ants ingested. These differences may have resulted from a shift in the foraging strategies employed by the salamanders (there was very little rainfall during the October-November collecting period), or changes in the population structure of the prey community, but since no prey availability data are available for the September sample, this point cannot be resolved.

Seasonal variation can best be analyzed by a comparison of the October-November and April samples of D. fuscus from site I, for which prey availability data were taken. There was a decreased feeding on insect larvae, entomobryid collembolans and pselaphid beetles in April even though all these groups increased in density in the litter. The

decreased representation of the above three taxa in the diets of the salamanders collected in April correlated with an increase in the proportion of earthworms, carabid beetles, asellid isopods, and gammarid amphipods consumed. Earthworms increased in density from November to April at site I; carabid beetles decreased slightly, and isopods and amphipods decreased tremendously. April was the wetter of these two periods, and this may have facilitated this population's seasonal shift in prey selectivity.

Variation between populations from different habitats also occurred. In the October-November samples, the salamanders from site II took a smaller proportion of insect larvae than did those from site I, even though insect larvae were about equally abundant at both sites. Earthworms were consumed in greater proportion by the animals at site II, but these were the most abundant prey in the streambed samples taken at that site.

Samples of salamanders taken from two different habitats in April also differed in their diets. Asellid isopods comprised almost half of all prey items ingested by the animals at site III, and that taxon made up just over half (50.5 percent) of all prey individuals appearing in the streambed samples. This suggests that individuals foraging within the stream or at the water's edge were feeding opportunistically, taking the most frequently encountered prey. The salamanders from site I consumed more insect larvae than any other single taxon, but asellid isopods and gammarid amphipods were the second and third most abundant taxa taken, respectively. Insect larvae were most abundantly collected in the streambed samples at site I in April

(37.5 percent of all prey individuals), followed by gammarid amphipods (31.8 percent) and asellid isopods (19.2 percent). The salamanders at this site appeared to ignore the aquatic insect larvae while consuming isopods more frequently and amphipods less frequently than expected on the basis of the occurrence of those prey types in the stream.

The Eurycea inhabiting sites II and III showed little dietary competition with D. fuscus. At both sites, the former were mostly opportunistic feeders, taking the most abundant taxa (mites and collembolans) in the litter.

The proportions of different taxa observed in the diets of a sample of salamanders may speciously suggest a particular mode of foraging utilized by the group, since a few individuals gorging themselves on a single prey type can account for a relatively high percentage of that type in the entire sample when the dietary data of all individuals are lumped. If the population was foraging widely and selectively feeding on certain taxa, then those taxa should be common to many individuals. Table IV gives the frequency of occurrence of the prey taxa taken from the stomachs of D. fuscus collected from all habitats and during both sampling periods. Eurycea are again included for comparison.

Among the three samples taken from site I, insect larvae were consumed by more individual salamanders than any other taxon, although the percentage of individuals exploiting this food source had decreased by April. The most abundant (and presumably the most frequently encountered) taxa in the litter generally did not occur in

TABLE IV. Percent of stomachs of Desmognathus fuscus and Eurycea (including E. longicauda at site II, and both E. longicauda and E. bislineata at site III) which contained at least one item of the designated prey taxon. Animals were collected from three sites (I, II, and III) in Montgomery County, Tennessee

prey	date taxon site	Sept.	Oct.-Nov.		April		
		<u>D. fuscus</u> I	<u>D. fuscus</u> I	<u>Eurycea</u> II	<u>D. fuscus</u> I	<u>Eurycea</u> III	<u>Eurycea</u> III
Pulmonata		9.8	5.0	--	20.0	--	--
Oligochaeta							
Lumbricidae		3.9	5.0	15.0	--	10.0	3.3
Araneae		15.7	--	--	3.3	--	--
Acarina		9.8	--	--	40.0	--	3.3
Diplopoda							16.7
Callipodidae		7.8	--	--	--	3.3	6.7
Chilopoda							5.6
Scolopendridae		5.9	--	5.0	--	3.3	3.3
Chelonethida							--
Chernetidae		2.0	--	--	10.0	--	--
Insect larvae		58.8	35.0	10.0	20.0	26.7	3.3
Lepidoptera		--	--	--	--	3.3	--
Diptera							--
Lonchopteridae		--	--	5.0	--	--	--
other flies		--	5.0	5.0	--	--	--
Collembola							
Poduridae		3.9	--	--	--	--	--
Sminthuridae		17.6	5.0	--	60.0	--	--
Entomobryidae		7.8	10.0	5.0	10.0	--	3.3
							11.1

TABLE IV (continued)

prey	date taxon site	Sept.	Oct.-Nov.		April			
		<u>D. fuscus</u> I	<u>D. fuscus</u> I	II	<u>Eurycea</u> II	<u>D. fuscus</u> I	III	<u>Eurycea</u> III
<hr/>								
Coleoptera								
Pselaphidae		--	20.0	--	--	--	--	--
Staphylinidae		2.0	5.0	--	10.0	3.3	3.3	--
Carabidae		2.0	--	--	--	13.3	--	--
Tenebrionidae		2.0	--	--	--	--	--	--
Curculionidae		3.9	--	--	--	3.3	--	--
Elateridae		2.0	--	--	--	--	--	--
Hydrophidae		--	--	--	--	3.3	--	--
Scarabaeidae		--	--	--	--	--	3.3	--
other beetles		3.9	--	--	--	--	3.3	--
Homoptera								
Aphididae		2.0	10.0	--	10.0	--	--	--
Cicadellidae		--	5.0	--	--	3.3	--	--
Hemiptera								
Cydnidae		2.0	--	--	--	--	--	--
Nabidae		--	--	--	10.0	--	--	--
other bugs		3.9	--	--	--	--	--	--
Hymenoptera								
Formicidae		25.5	10.0	--	--	3.3	--	--
Braconidae		--	5.0	--	--	--	--	--
Eulophidae		--	5.0	--	--	--	--	--
Cynipidae		--	5.0	--	--	--	--	--
Platygasteridae		2.0	--	--	--	--	3.3	--

TABLE IV (continued)

prey	date taxon site	Sept.	Oct.-Nov.		April		
		<u>D. fuscus</u> I	<u>D. fuscus</u> I	<u>Eurycea</u> II	<u>D. fuscus</u> I	<u>Eurycea</u> III	<u>Eurycea</u> III
Orthoptera							
Blattidae		2.0	--	--	--	--	--
Gryllidae		2.0	--	--	--	--	--
Isopoda							
Asellidae		5.9	5.0	5.0	--	10.0	--
Oniscidae		3.9	5.0	5.0	--	--	--
Amphipoda							
Gammaridae		2.0	5.0	--	3.3	--	--
<hr/>							
total number of sto-							
machs in sample		51	20	20	10	30	10
percentage of							
empty stomachs		11.8	15.0	50.0	10.0	43.3	61.1

many individual D. fuscus except at site I in September. There collembolans and ants were taken often, but collembolans were still under-represented when compared to their abundance in the litter.

As would be expected of a non-selective predator, Eurycea showed a high frequency of occurrence of the common litter animals, again supporting the idea that this salamander probably consumes what is most readily available.

In summary then, selectivity by D. fuscus for certain prey types appears high in all three habitats when diets are compared against prey in the litter and against the diets of sympatric Eurycea. At site I, D. fuscus favored insect larvae above all other available taxa, while the second and third most important taxa in the diets varied seasonally. There was a noticeable increase in the proportion of semi-aquatic prey animals taken in April by the population at site I. The salamanders taken in the fall from site II took more earthworms than any other taxon, while those collected from site III favored semi-aquatic prey. At all three sites and during all sampling periods D. fuscus appeared to selectively ignore the most abundant prey taxa in the litter, while these taxa (mites and collembolans) constituted the bulk of the diets of both species of Eurycea.

SELECTION OF PREY BY SIZE

Theory predicts that size of prey might also be a feature for which the predator discriminates in its selection of food (Schoener, 1969a, 1971). Since size correlates approximately with caloric content, especially among closely related taxa, a predator is

expected to take the larger prey items within the size range it is capable of handling, if a choice is presented. If the predator is hungry and/or prey are scarce, then the predator must be less size-selective if it fails to encounter the preferred prey sizes often enough to meet its energy requirements.

I have analyzed the degree of size-selectivity in D. fuscus by comparing the frequency distribution of prey sizes consumed by the salamander against the spectrum of prey sizes distinguished in the litter. I divided all prey (those from the samples and those consumed by salamanders) into three size classes based on body length.

In my analysis the streambed samples and the few salamanders that had ingested aquatic prey were not considered, nor were the prey taken in the tanglefoot traps, due to biased sampling techniques or inadequate numbers of animals. Figures 1 and 2 show the frequency distributions of prey sizes as they occurred in the leaf litter at all habitats and as they were found in the diets of all D. fuscus and Eurycea samples except those collected in September at site I (for which no prey availability data were gathered).

Prey of the largest size class were more frequently exploited by all salamander populations than was expected from their abundance in the litter. The most abundant but smaller prey items (<1.0 mm) were selectively ignored by D. fuscus in all habitats and during both seasons. In the two habitats shared with Eurycea, the latter took prey of all sizes, but selected more of the largest and especially the intermediate sized prey than expected. Fewer of the smallest prey were eaten by Eurycea, but the smaller Eurycea definitely took some

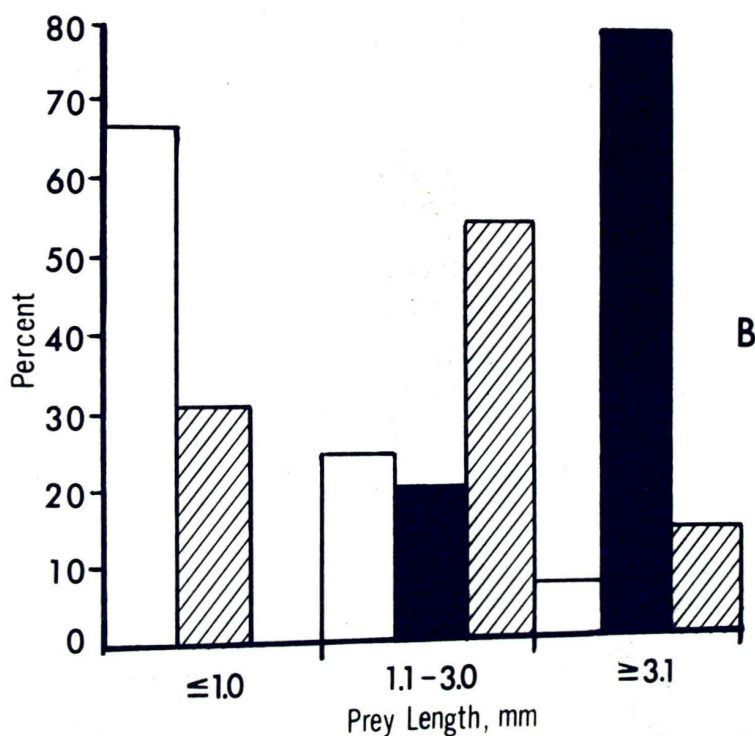
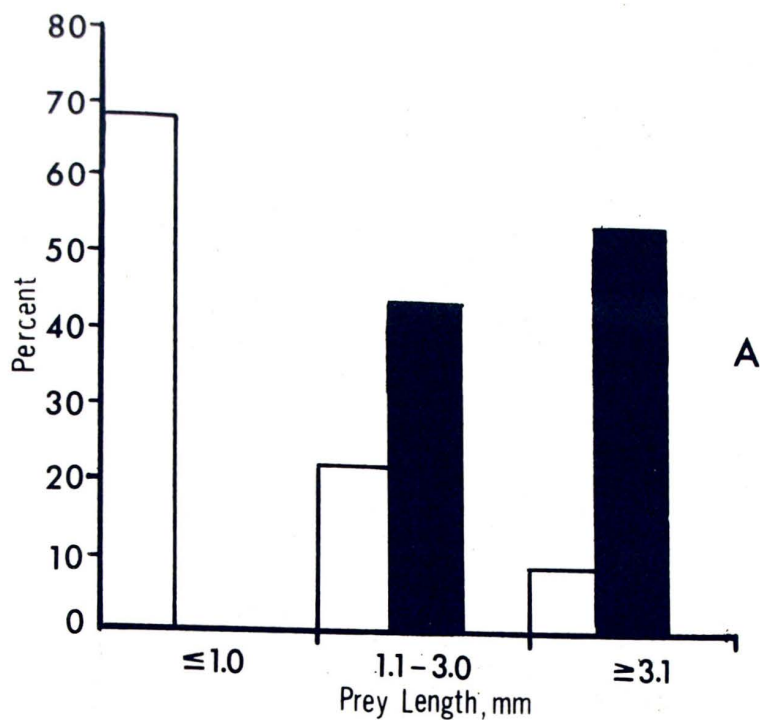


Figure 1. Distribution of prey sizes (percent by number of items) found in the stomachs of *Desmognathus fuscus* (solid bars, N= 16 in A, found in 9 in B), *Eurycea longicauda* (striped bars, N= 9), and encountered in the litter samples (open bars). A. Site I, October-November, 1974. B. Site II, October-November, 1974. Both sites are described in the text.

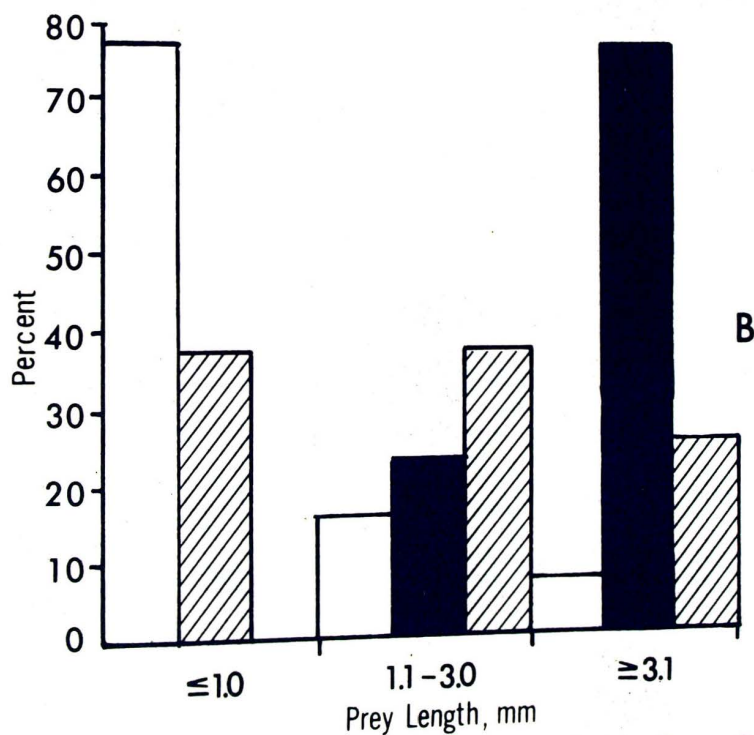
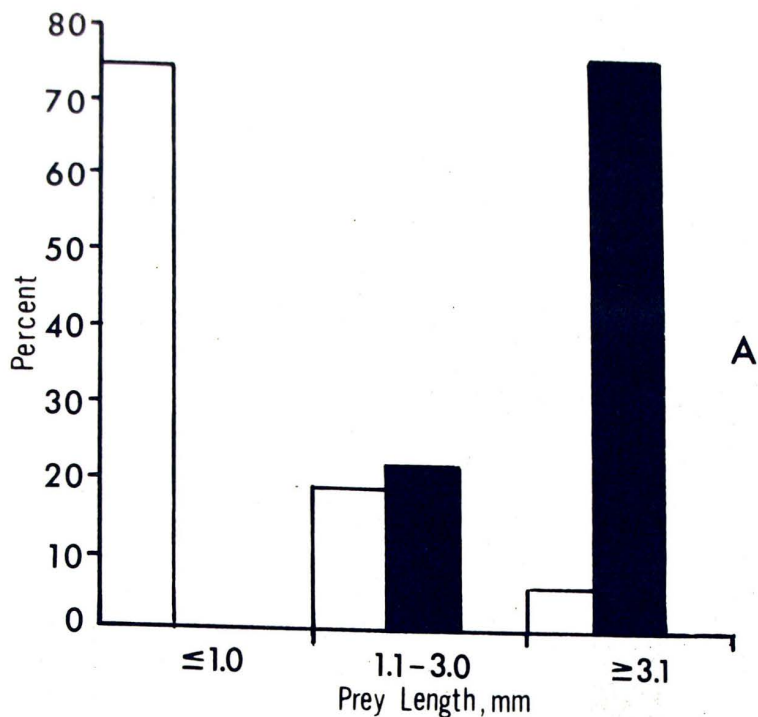


Figure 2. Distribution of prey sizes (percent by number of items) found in the stomachs of *Desmognathus fuscus* (solid bars, N= 18 in A, 8 in B), *Eurycea* (both *longicauda* and *bilineata*, striped bars, N= 5), and encountered in the litter samples (open bars). A. Site I, April, 1975. B. Site III, April, 1975. Both sites are described in the text.

of the smallest prey.

A statistical comparison of the prey lengths taken by D. fuscus from site I ($\bar{X} = 4.3 \pm 2.4$ mm, $N = 36$) with those from site II ($\bar{X} = 5.6 \pm 4.3$ mm, $N = 8$) in the fall showed no significant difference ($t = -0.624$ with 42 df, $\alpha > .05$, Wilcoxon 2-sample test). The same test used for a comparison of prey lengths taken by the salamanders from sites I ($\bar{X} = 6.2 \pm 5.1$ mm, $N = 37$) and III ($\bar{X} = 6.1 \pm 3.0$ mm, $N = 22$) showed no significant difference ($t = 0.063$ with 57 df, $\alpha > .05$).

A seasonal shift in prey size selectivity occurred between autumn and spring in the D. fuscus population sampled from site I (compare figures 1A and 2A). During the October-November collecting interval, D. fuscus selectively exploited the largest size class of prey but also took a considerable proportion of intermediate-sized prey (55.5 and 45.5 percent, respectively). In April, a much greater proportion (78 percent) of the prey items was taken from the larger size class, even though this size class had declined in abundance in the litter. This trend, correlated with an increase in rainfall, represents a considerable deviation from what is expected of an indiscriminate predator that exploits prey proportional to their occurrence in the habitat. This argues that D. fuscus is highly selective of the prey sizes it consumes and that this selectivity increases with an increase in rainfall. Further, a statistical comparison of the prey lengths taken by D. fuscus in the October-November sample from site I ($\bar{X} = 4.3 \pm 2.4$) with the April sample from the same site ($\bar{X} = 6.1 \pm 5.1$) showed a difference significant at the 95 percent confidence level with the Wilcoxon 2-sample test ($t = 2.58$ with 71 df, $\alpha < .05$) and at the

99 percent confidence level with the Student's-t test ($t = 2.88$ with 71 df, $\alpha < .01$). Not only was the population taking a greater proportion of the larger prey items, but the salamanders were exploiting significantly fewer intermediate-sized prey.

If D. fuscus is a size-selective feeder, then the size of the prey ingested should increase with salamander size, since a greater nutrient gain would be necessary to maintain the larger individuals (Schoener, 1971). All else being equal, the larger salamanders would be expected to take larger individual prey items under optimal feeding conditions. Because the very small prey items are usually by far the most abundant, the larger predators would be expected to occasionally take some of these smaller prey unless large prey were readily available. The smaller salamanders within the population would then be afforded the opportunity of selecting proportionally larger prey items within the size range of prey that they could handle, simply because they generally have a larger range of prey sizes available to them that represents a net energy gain. Thus the smaller individuals are expected to exhibit a more restricted range of prey sizes ingested. When large individuals are forced to feed sub-optimally, they are expected to increasingly take the smaller prey. Thus the degree of selectivity within a predator population may be measured by the extent to which its largest individuals continue to exploit the smallest prey.

Since head width and body length are highly correlated in D. fuscus (with Spearman rank correlation coefficient, $r_s = 0.885$, $\alpha < .01$, $N = 40$), I employed head width as a measure of the size at-

tained by individuals within a population. I have drawn regression lines of prey size on salamander head width for all D. fuscus taken from sites I and II during the October-November sampling period, and for the animals taken from sites I and III during the April sampling period (figure 3). All regression lines are of the largest (by length) prey item ingested per individual on that individual's head width. The differences in the slopes of these lines suggest which populations were feeding most selectively with respect to prey size. For example, the large individuals in the population represented by line Ia were consuming prey much smaller than the maximum size they could handle, while maximum prey size consumed increased significantly with salamander size in the population represented by line II.

The raw data for prey length and head width were statistically analyzed for significance of the differences noted above, and the results are shown in Table V, along with results of analyses for mean prey size on salamander head width, volume of food in the stomach on salamander head width, and volume of the largest single prey item ingested on salamander head width. The Spearman rank correlation coefficient (r_s) was employed and showed that in most cases correlation between salamander head width and maximum prey size consumed was low. Salamander head width correlated significantly with both maximum and mean prey size ingested at site II, and with mean prey size ingested at site III.

The significance of observed correlations between volume of prey consumed and volume of the largest single prey item ingested with salamander size was determined statistically (Table V), since

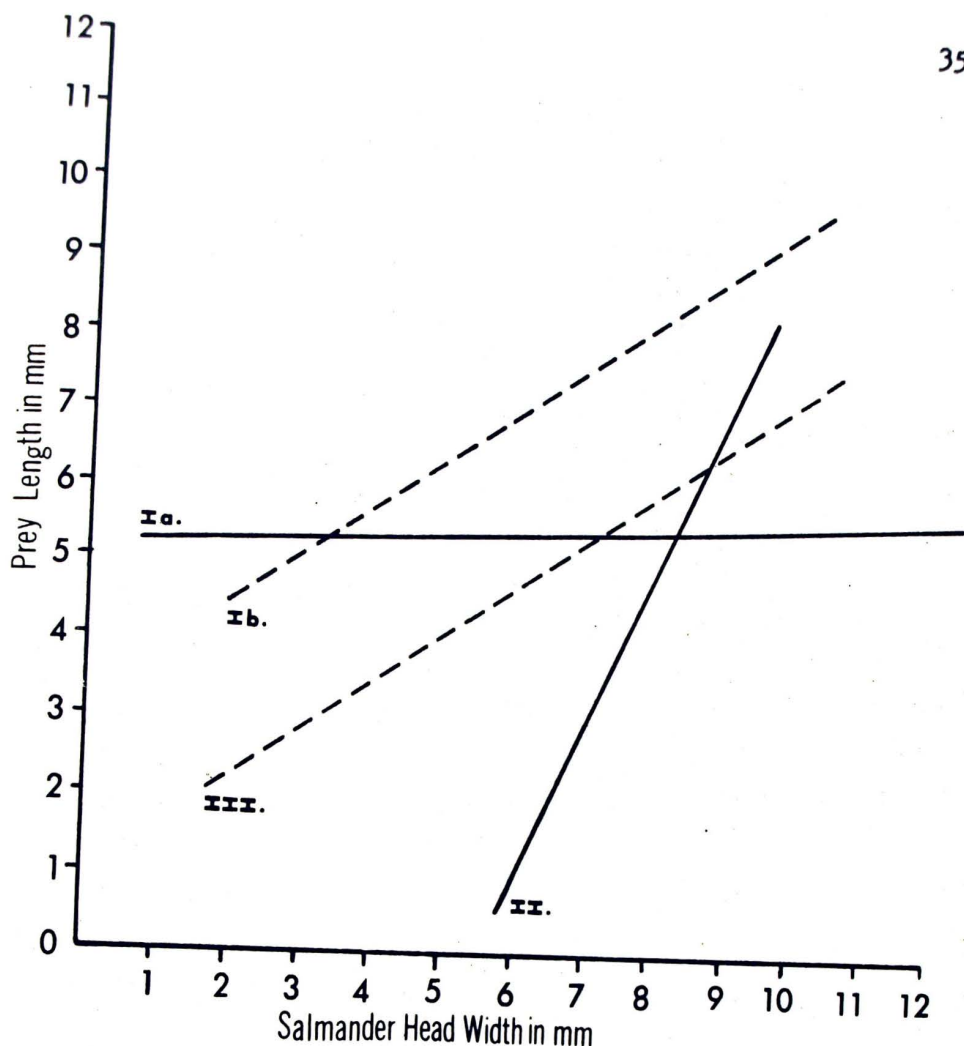


Figure 3. Regression of prey length on head width of Desmognathus fuscus taken from sites I, II, and III. Solid lines represent October-November samples, while broken lines represent April samples. The lines represent regressions of the largest single prey item (by length) taken by each individual salamander on that animal's head width. Regression formulas and sample sizes are as follows: Ia. $Y = 5.03 + .064X$, $N = 16$. Ib. $Y = 3.25 + .643X$, $N = 18$. II. $Y = -11.8 + 2.1X$, $N = 8$. III. $Y = .97 + .646X$, $N = 9$.

TABLE V. Spearman rank correlation coefficients (r_s) between head width of Desmognathus fuscus and (1) mean size of prey items ingested, (2) size of the largest single prey item ingested, (3) volume of food in the stomach, and (4) volume of the largest single prey item ingested. The number (N) of individuals used in the sample and the range of head widths (HW) in mm for that sample are included

site	comparison (key above)	sampling period			
		October-November (r_s)	(N)	April (r_s)	(N)
I	(1)	0.314	(16)	0.138	(18)
	(2)	0.226	(16)	-0.014	(18)
	(3)	0.062	(17)	0.112	(25)
	(4)	0.171	(17)	-0.035	(20)
	HW	4.1 — 11.0		6.0 — 12.0	
II	(1)	0.923**	(8)		
	(2)	0.923**	(8)		
	(3)	0.730*	(9)		
	(4)	0.804**	(10)		
	HW	6.4 — 12.0			
III	(1)			0.658*	(9)
	(2)			0.350	(9)
	(3)			0.079	(15)
	(4)			0.504	(9)
	HW			7.0 — 15.0	

** represents significance at the 99 percent level of confidence

* represents significance at the 95 percent level of confidence

some prey items (earthworms) were not measured by length. Again, with the exception of the animals from site II, there was little or no correlation between the size of the salamander and the size of or the amount of food ingested.

SEXUAL DIFFERENCES IN FEEDING

The sample of D. fuscus collected from site I in September was large enough for a comparison of the feeding ecologies of adult males and females. The mean body length of 14 females was 44.7 ± 6.7 mm, and of 30 males was 55.6 ± 11.5 mm. Statistically (Wilcoxon 2-sample test), this difference in body size was highly significant ($t = 4.0$ with 42 df, $\alpha < .01$). This same test was used to test the significance of the difference between prey lengths consumed by males and females of that sample. The mean prey length taken by 27 males was 6.3 ± 6.4 mm, while for 11 females it was 5.1 ± 3.2 mm. The difference between these sizes was highly significant ($t = 4.78$ with 36 df, $\alpha < .01$). In this instance then, there was a significant sexual partitioning of food resources by size.

The Spearman rank statistic was again employed to test for significant correlation between head width and prey length for the two sexes. In the males, $r_s = .324$, which just missed significance at the 95 percent level of confidence ($r_s .05 = .329$ with 27 df, $0.1 > \alpha > 0.05$). In the females, correlation between prey length and head width was low ($r_s = .278$ with 11 df, $\alpha > .05$). This sample thus resembled the sample taken from site II in that the males showed a trend toward increased prey size being taken by larger individuals.

The fact that the females showed no such significant trend may reflect the difference in sample size.

CHAPTER IV

DISCUSSION AND CONCLUSIONS

Although the restricted size of the collecting sites necessitated taking small samples and the results presented in the previous section may need further substantiation, they strongly suggest that foraging Desmognathus fuscus, when compared to sympatric Eurycea, is a specialist in terms of prey sizes and taxa. This leads to the question of what is the adaptive significance of the feeding ecology in the life history of this species, and what set of factors has interacted to favor this mode of foraging over a more specialized or a more generalized one?

My results suggested that D. fuscus shifted its foraging strategy in different habitats and under different moisture regimes. Most noticeable was an increase in size selectivity of prey with an increase in the frequency of rainfall, implying that rainfall is a critical climatic influence, and that the feeding of D. fuscus may be patterned by the spacing of rains. Evidence for this may be seen in the following; (1) an increase in the size selectivity and mean prey size taken by the salamanders collected from site I in April (wet), when compared with those taken from that site during October and November (dry), (2) the fact that salamanders taken from site I immediately after a rain displayed the greatest prey species selection, (3) the ingestion by salamanders from site I immediately after a rain

of the greatest number of items and the greatest volume of food per individual, and (4) the fact that the same group referred to in items 2 and 3 had the lowest percentage of empty stomachs. Many individuals taken from site I following a heavy rain were collected well up on the wooded ravine slopes 50-60 m from the stream, while those taken in the October-November samples were mostly restricted to a narrow corridor along the stream within one m of the water's edge. Salamanders collected from this site in April, when rainfall was more frequent, were again widely dispersed. Thus, scant rainfall apparently restricted movement of this salamander, which resulted in a reduction of food intake. D. fuscus, constrained by the nature of its integument to a moist microhabitat, was forced to retreat beneath objects serving as moisture traps and heat shields as the litter dried between rains. To the salamander, prey may therefore differ only in relative rather than absolute availability because the animal's feeding range is gradually reduced with the loss of substrate moisture to small patches beneath rocks and logs. The salamander then has two choices: it can forage beneath the object and try to satisfy its energy requirements, or it can expend minimal energy and wait until the next rain.

The fact that many of the larger individuals taken from beneath rocks and logs in dry weather had empty stomachs argues that it may not be energetically feasible for these large salamanders to feed at all between rains. This idea could be critically tested by documenting prey consumed by D. fuscus at established time intervals after a rain (such as the day after, three days after, and one week after a rain). I predict that the number of prey items (and perhaps

their size) consumed by individual D. fuscus would decrease with increasing substrate dryness, and that this would be correlated with decreased movement of the salamanders. Jaeger (1972) sampled the diets of Plethodon cinereus under these three conditions and found that the mean number of prey per salamander was inversely proportional to time lapse since the last rain.

A salamander faced with a drying substrate has at least one other option: it can retreat to the stream and exploit the aquatic invertebrate fauna. The large percentage and small frequency of occurrence of isopods in the diets of salamanders taken at site III indicates that some individuals did this, but why did these prey, which are easily digested and probably high in nutrient content, not figure more prominently in the diets? One explanation may be found in the streambed samples taken from site I in the fall and in the spring (see appendixes). There was a drastic decrease in the numbers of the most common prey species (including isopods) found in the streams, and this extreme fluctuation in the prey population may have acted to maintain a mostly terrestrial foraging mode in this otherwise semi-aquatic salamander.

If a rain-dependent feeding periodicity does exist for D. fuscus, as is postulated here, then it assumedly is advantageous for this predator to maximize energy and nutrient intake during the brief periods when the predator has access to the prey. Since salamanders typically swallow their prey whole, and this limits the size of the items they can handle, it is conceivable that prey with an elongate body shape might yield more energy for the predator's effort than a

less elongate prey item. This might explain the apparent selectivity exhibited by D. fuscus for insect larvae and earthworms, as these soft-bodied prey are undoubtedly high in nutrient content. More heavily armored prey, such as ants and beetles, frequently passed through the gastrointestinal tract nearly intact, implying that the total contribution of those prey items to the salamander's energy budget was low. Since chitin doesn't appear to be digested, a salamander limited in its feeding time would assumedly benefit by ignoring chitinous prey in favor of more readily digested forms. The salamander could still occasionally eat a low ranking prey item as long as the total energy gained exceeded that spent in foraging, but these lower ranking items should decrease in frequency in the animal's diet as foraging opportunities improve, i. e. as the predator is afforded more choices of prey.

The foraging strategy of D. fuscus can be analyzed in another context by its comparison to a plethodontid salamander with a different foraging mode. Maiorana (1971) has documented this aspect of the ecology of Batrachoseps attenuatus in California. This species has adopted a rather indiscriminate foraging mode and apparently maximizes its energy intake by feeding at regular intervals on all prey within striking range rather than selecting only certain prey taxa (the species does show some size selectivity). Batrachoseps attenuatus inhabits semi-arid regions with restricted time available for surface activity and feeding, but its fossorial mode of life allows it to feed under an object in the sit-and-wait predation style. There was little or no prey-species-selectivity shown by this salamander; generally

the most abundant animals in the litter were most frequently consumed. Individuals examined a month after a rain contained as much food as those taken the day after a rain, suggesting the species is not restricted to feeding on rainy nights, as is presumed for D. fuscus. The fact that B. attenuatus is the most abundant species of salamander in southern California (Maiorana, 1971) bespeaks the success of this mode of foraging.

Desmognathus fuscus, being larger and more robust than B. attenuatus, undoubtedly has higher energy requirements. If it exploited the most abundant prey it would necessarily consume a great number of these tiny prey to satisfy its energy requirements. By searching for and taking larger prey, however, it satisfies its needs during an optimal foraging period with a smaller energy expenditure than would be possible if it confined its feeding to the most numerous items in the litter. Over most of the range occupied by D. fuscus rain is predictably frequent, possibly occurring often enough to offset any need to feed heavily between rains.

An obvious question to raise at this point is: why is D. fuscus less efficient at feeding when confined to an area beneath an object that is B. attenuatus? I have discussed above the conditions under which D. fuscus might not need to feed extensively while confined in space, but it may also be that it is morphologically incapable of feeding efficiently while beneath an object. B. attenuatus possesses a highly specialized tongue which may be extended proportionally farther from the mouth than that of D. fuscus (Wake, 1966).

In a confined space, this might enlarge the effective prey capture zone of B. attenuatus. Since it exploits the most abundant prey species, the distance between prey items would be effectively reduced, the feeding range restricted, and the salamander still able to satisfy all of its energy requirements while feeding beneath one object. It is perhaps energetically more feasible for D. fuscus, possessing a more primitive tongue and selecting larger prey items, to avoid wasting energy pursuing swift prey (such as collembolans).

Data given in the previous section show that Eurycea longicauda and E. bislineata—also possessing specialized tongues—concentrate their feeding on smaller prey. These salamanders were common only at sites II and III, where D. fuscus were larger and not as numerous as at site I. The scarcity of Eurycea at site I might be explained by interspecific competition with the large population of D. fuscus. At sites II and III, Eurycea (both longicauda and bislineata) and D. fuscus may have shared complimentary feeding niches. Size-selective predation may thus affect salamander diversity in a woodland, as Dodson (1970) found it influencing predator diversity in freshwater planktonic communities. Just exactly how these salamanders exploit the same prey pool, and to what degree similar-sized individuals of the two genera overlap in their feeding niches might best be determined experimentally.

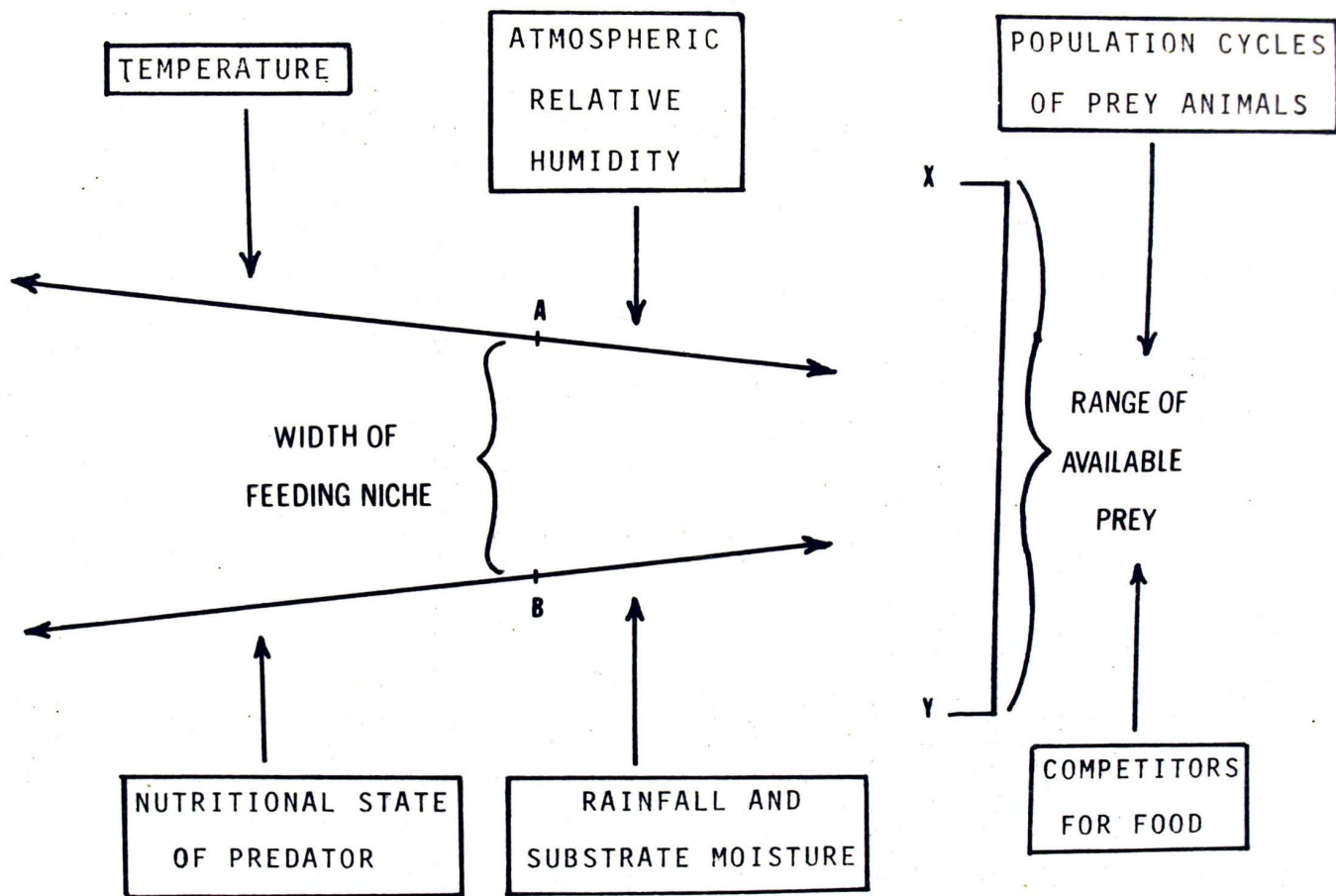
The question of sexual differences in feeding by D. fuscus needs further investigation in view of the limited data gathered during this study. The observed difference in body size between adult males and females may reflect a collecting bias, due to the fact that

larger females were yolking eggs and were generally better hidden (almost twice as many males were collected). If the difference is real, then the sexes might logically be expected to partition prey by size when in a situation offering optimal foraging opportunities, as is believed to be the case on rainy nights. The finding that males took larger prey items and exhibited a positive correlation between body size and mean prey size ingested, significant at greater than the 90 percent level, is consistent with work of Orser and Shure (1975) showing that adult males are the most active and mobile individuals within the population.

Landerberger (1968) has pointed out some of the problems involved in field studies concerning selective feeding predators. Among them are the difficulties in sampling prey availability and determining the effects of environmental influences, especially temperature, on the feeding activities of poikilothermic predators. Unlike most other predators, by the nature of their integument salamanders are further restricted in foraging activities to moist areas. Thus atmospheric relative humidities and substrate moistures also undoubtedly influence their activities. With the influence of these variables not fully known, a profitable approach to the salamander foraging strategy problem might be undertaken in the laboratory.

In figure 5 I have diagrammatically illustrated the feeding niche of D. fuscus and some physical and biotic factors that I believe exert major influences on the foraging behavior of this salamander. The distance between points A and B on the two converging lines can be considered as the width of the animal's feeding niche. A decrease

Figure 4. Diagram representing the feeding niche of Desmognathus fuscus and the factors thought to exert a major influence on the width of this predator's feeding niche. Arrows on which points A and B lie indicate possible effects and no significance is meant by their length or slope.



in this distance indicates increasing specialization (on prey size and/or species), while greater generalization may be shown by an increase in the distance between A and B. The distance between points X and Y represents the total range of prey physically accessible and susceptible to D. fuscus in a given habitat, and this distance may also vary under different conditions. The exact influence of each of the variables depicted isn't known, but under proper laboratory conditions all could be controlled so that each's influence might be determined. A test for prey size selectivity, for example, might be set up as follows.

Terraria could be set up with substrates containing no prey items, and salamanders introduced into these and allowed to acclimate to their conditions. Temperature, relative humidity, and substrate moisture would be kept constant. Hemi-metabolic insects could then be raised and fed to the salamanders in known proportions of different size classes. By subjecting salamanders to different ratios of prey size densities, data could be gathered on what type of "decision" a salamander would make when prey size densities changed. Other types of motivational factors and responses could be observed under varying degrees of satiation of the salamander, or different gradients of relative humidity, substrate moisture, temperature, and in the presence or absence of competitors. This approach was used successfully by Werner and Hall (1974) in their study of the sunfish Lepomis macrochirus and Menge (1972a) in his study of two intertidal starfishes. Selection of prey species could be tested in a similar manner. Maiorana (1971) considered the behavior of ants and the biology of

Salamanders in the discussion of a specific interaction between these prey and their potential predators. Ants, being social insects, are patchily distributed and concentrated in clusters, so a predator can spend a lot of time and energy locating a nest and specialize on these prey. Salamanders of the genus Plethodon are thought to be active foragers (Stewart, 1970), and some literature regarding food habits of members of this genus (Davidson, 1956; Rubin, 1969; Whitaker and Rubin, 1971) shows that ants compose a large proportion of their diet. Now a detailed investigation is needed to help confirm this salamander-ant interaction or suggest a new one. Ants are not prominent in the diets of most Desmognathus, suggesting that this group doesn't forage as actively as Plethodon, or that ants are ranked as a low priority item. The latter idea is amenable to laboratory testing. Species of both genera could be confined in terraria and offered known proportions of ants and alternate prey items

This approach of interplaying theoretical modelling and experimentation has been used productively by Menge (1972a), Murdoch (1969, 1971), Murdoch and Marks (1973), Salt (1967), and Werner and Hall (1974). All of these investigations involved the experimental analysis of various components of predation under laboratory conditions. Only when these components are fully understood can the predator be meaningfully studied in its natural context. Then the problem may be attacked at the level of natural populations and a generalized approach developed that, with occasional modifications, would be applicable to diverse groups of predators. Studies of foraging strategies of different species within any particular lineage might then be integrated

with other features of the biology of that lineage and its evolutionary history in an attempt to explain the diversity realized by that lineage in any community.

CHAPTER V

SUMMARY

An empirical approach to the foraging strategy problem was utilized to test predictions concerning the feeding behavior of a predator under various environmental stresses. The dusky salamander, Desmognathus fuscus, a semi-aquatic species common in Montgomery County, Tennessee, was used as the study animal. Natural populations were studied seasonally and in differing habitats to determine the effects of moisture, potential competitors, and fluctuations in the prey populations on the foraging mode of this species.

Collections were made from two populations of salamanders during October and November (dry season) of 1974 and again in April of 1975 (wet season). One of the areas sampled in April was a new habitat; thus three different areas were actually studied. The leaf litter and stream beds were sampled in all habitats to determine what types of prey were potentially available to D. fuscus.

Results showed that this salamander was both size and species selective of the prey it consumed. Proportions of prey species found in the diets of the salamanders did not correlate well with the proportions of prey as they occurred in the litter. Specifically, D. fuscus exhibited a marked selectivity for insect larvae, and this selectivity increased with an increase in the frequency of rainfall. Salamanders of the genus Eurycea (longicauda and bislineata), with

which D. fuscus shared two of the habitats, were found to be non-selective of prey and consumed the most abundant items found in the litter—mites and collembolans.

Desmognathus fuscus took considerably more of the larger prey (≥ 3.1 mm in length) than expected on the basis of the range of prey sizes observed in the litter samples. This size selectivity increased from November to April, correlated with an increase in rainfall.

Eurycea exhibited less prey-size selectivity, exploiting more of the intermediate-sized prey items (1.1 - 3.0 mm in length).

With one exception (salamanders at site II), predictions of larger individuals consuming larger prey items were not confirmed. This was attributed to the fact that the larger animals were feeding sub-optimally and continued to exploit the smaller prey, probably because the larger prey were less abundant.

One sample was large enough to permit analysis of sexual differences in feeding and a significant sexual partitioning of food resources by size was detected. This occurred in the dense population of D. fuscus (site I) with few heterospecifics and is interpreted as a means of reducing intraspecific competition.

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APPENDIX A. AVAILABILITY DATA FOR
PREY COLLECTED DURING THE OCTOBER-
NOVEMBER 1974 SAMPLING PERIOD AT SITE I

Table VI. Prey collected in streambed samples taken from site I during October and November. Samples were taken twice weekly for four weeks, and all sample data were lumped to determine mean percents and densities. Mean percent is from total number of prey

taxon	frequency of occurrence	\bar{X} % of sample	\bar{X} density/m ²
Coleoptera			
Dryopidae	.50	0.5	15.6/m ²
Trichoptera			
Hydropsychidae	.50	0.5	15.6/m ²
Ephemoptera			
Baetidae	.13	0.6	17.8/m ²
Insect larvae	.63	0.8	33.8/m ²
Isopoda			
Asellidae	1.00	31.5	896.2/m ²
Amphipoda			
Gammaridae	1.00	51.9	1625.5/m ²
Decapoda			
Astacidae	.13	0.5	8.9/m ²
Tricladida			
Planariidae	1.00	15.5	511.0/m ²

Table VII. Prey collected by raking leaf litter at site I during October and November. Samples were taken twice weekly for four weeks, and all sample data were lumped to determine mean percents and densities. Mean percent is from total number of prey

taxon	frequency of occurrence	\bar{X} % of sample	\bar{X} density/m ²
Coleoptera			
Carabidae	.75	3.8	1.3/m ²
Scarabaeidae	.13	1.3	.8/m ²
Staphylinidae	.50	1.8	.8/m ²
Melyridae	.13	2.2	.8/m ²
Hymenoptera			
Formicidae	.50	9.2	5.4/m ²
Isoptera			
Rhinotermitidae	.13	9.6	4.8/m ²
Orthoptera			
Gryllidae	.13	1.3	.8/m ²
Gryllacricidae	.13	2.2	.8/m ²
Thysanura			
Iapygidae	.25	4.2	.8/m ²
Hemiptera			
Cydnidae	.25	3.6	1.6/m ²
Nabidae	.25	1.8	.8/m ²
Pentatomidae	.13	2.0	.8/m ²
Insect larvae	1.00	12.8	4.3/m ²
Diplopoda			
Julidae	.88	4.4	1.5/m ²
Polydesmidae	1.00	12.0	3.9/m ²
Chilopoda			
Scolopendridae	.75	4.4	1.7/m ²
Scutigerae	.38	2.8	1.1/m ²
Geophilidae	.50	3.1	1.2/m ²
Isopoda			
Oniscidae	1.00	7.6	2.2/m ²
Oligochaeta			
Lumbricidae	1.00	24.1	9.0/m ²
Araneae	.88	4.1	1.6/m ²
Pulmonata	1.00	15.6	5.0/m ²

Table VIII. Prey separated in Berlese funnel samples taken from site I during October and November. Samples were taken twice weekly for four weeks, and all sample data were lumped to determine mean percents and densities. Mean percent is from total number of prey

taxon	frequency of occurrence	\bar{X} % of sample	\bar{X} density/m ²
Coleoptera			
Cerambycidae	.75	0.3	7.0/m ²
Staphylinidae	.75	0.4	6.4/m ²
Pselaphidae	.13	0.3	3.2/m ²
Erotylidae	.13	0.3	3.2/m ²
Carabidae	.13	0.2	3.2/m ²
Hemiptera			
Cydnidae	.25	0.2	3.2/m ²
Homoptera			
Cicadidae	.38	0.2	3.2/m ²
Cicadellidae	.75	1.4	22.9/m ²
Aphididae	.75	0.8	16.6/m ²
Psyllidae	.13	0.1	3.2/m ²
Hymenoptera			
Mymaridae	.13	0.1	3.2/m ²
Formicidae	.75	0.3	5.1/m ²
Eulophidae	.25	0.2	4.8/m ²
Platygasteridae	.38	0.2	3.2/m ²
other wasps	.13	0.3	6.4/m ²
Collembola			
Entomobryidae	1.00	9.3	177.8/m ²
Poduridae	1.00	39.3	786.3/m ²
Sminthuridae	1.00	8.0	177.8/m ²
Diptera			
Phoridae	.50	0.4	3.4/m ²
Culicidae	.13	0.1	3.2/m ²
Mycetophyllidae	.25	0.1	4.8/m ²
Tipulidae	.13	0.1	3.2/m ²
other flies	.25	0.3	4.8/m ²
Orthoptera			
Tetrigidae	.13	0.5	3.2/m ²
Blattidae	.13	0.5	6.4/m ²
Insect larvae	1.00	3.4	37.5/m ²

Table VIII. (continued)

taxon	frequency of occurrence	\bar{X} % of sample	\bar{X} density/m ²
Isopoda			
Armadillidiidae	.13	0.5	3.2/m ²
Oligochaeta			
Lumbricidae	1.00	1.6	26.5/m ²
Acarina			
Galumnidae	1.00	8.6	140.0/m ²
Trombidiidae	1.00	2.1	23.3/m ²
Tetranychidae	.38	1.0	17.1/m ²
other mites	.88	19.7	350.7/m ²
Chelonethida			
Chernetidae	.88	0.5	9.1/m ²
Symphyla			
Scolopendrellidae	.63	0.7	10.4/m ²
Chilopoda			
Lithobiidae	.38	0.4	3.2/m ²
Scutigerae	.13	0.2	3.2/m ²
Scolopendridae	.13	0.5	6.4/m ²
Diplopoda			
Julidae	.25	0.2	3.2/m ²
Polydesmidae	.13	0.3	3.2/m ²
Callipodidae	.13	0.5	9.6/m ²

Table IX. Prey taken in tanglefoot traps at site I during October and November. Samples were taken once a week for four weeks, and all sample data were lumped to determine mean percent. Mean percent is from total number of prey.

taxon	frequency of occurrence	\bar{X} % of sample
Diptera		
Tipulidae	.75	2.9
Pipunculidae	.50	1.1
Drosophilidae	.50	4.5
Phoridae	1.00	6.1
Dolichopodidae	1.00	3.7
Empididae	.50	1.1
Muscidae	.75	2.7
Syrphidae	.75	0.6
Ptychopteridae	.50	1.8
Culicidae	.50	0.7
Chironomidae	.50	0.6
Tachinidae	.50	1.3
Bombyliidae	.25	0.6
Lonchopteridae	.25	14.8
Sarcophagidae	.50	5.3
Platypezidae	.50	4.6
other flies	1.00	29.9
Orthoptera		5.2
Gryllacricidae	1.00	0.6
Tettigoniidae	.25	
Coleoptera		1.0
Erotylidae	.50	0.6
Elatерidae	.25	2.3
Pselaphidae	.25	
Lepidoptera		0.8
Hesperiidae	.50	
Homoptera		3.1
Aphididae	1.00	8.7
Cicadellidae	1.00	
Collembola		12.6
Entomobryidae	1.00	1.0
Sminthuridae	.75	

Table IX. (continued)

taxon	frequency of occurrence	\bar{X} % of sample
Hymenoptera		
Braconidae	1.00	2.1
Platygasteridae	.50	0.9
Colletidae	.25	0.6
Ichneumonidae	.50	1.1
Pteromalidae	.25	1.1
Diapriidae	.25	1.8
Megachilidae	.25	0.8
Insect larvae	.50	1.9
Isopoda		
Oniscidae	.25	0.6
Araneae	.75	2.0

APPENDIX B. AVAILABILITY DATA FOR
PREY COLLECTED DURING THE APRIL 1975
SAMPLING PERIOD AT SITE I

Table X. Prey collected in streambed samples taken from site I during April. Samples were taken twice weekly for two weeks, and all sample data were lumped to determine mean percents and densities. Mean percent is from total number of prey

taxon	frequency of occurrence	\bar{X} % of sample	\bar{X} density/m ²
Coleoptera			
Dryopidae	.25	0.9	8.8/m ²
Trichoptera			
Hydropsychidae	.50	2.9	26.7/m ²
Insect larvae	1.00	37.5	283.6/m ²
Naiads	.50	3.3	26.7/m ²
Amphipoda			
Gammaridae	1.00	31.8	268.8/m ²
Isopoda			
Asellidae	1.00	19.2	131.2/m ²
Tricladida			
Planariidae	.75	11.1	71.2/m ²

Table XI. Prey collected by raking leaf litter at site I during April. Samples were taken twice weekly for two weeks, and all sample data lumped to determine percents and densities. Mean percent is from total number of prey

taxon	frequency of occurrence	\bar{X} % of sample	\bar{X} density/m ²
Coleoptera			
Staphylinidae	.25	2.9	.8/m ²
Carabidae	.75	4.8	1.1/m ²
Chrysomelidae	.25	3.4	.8/m ²
Scarabaeidae	.25	3.4	.8/m ²
other beetles	.25	3.6	.8/m ²
Hymenoptera			
Formicidae	.75	5.0	1.1/m ²
Hemiptera			
Cydnidae	.25	3.4	.8/m ²
Insect larvae	1.00	12.3	2.6/m ²
Chilopoda			
Scolopendridae	.25	11.4	3.2/m ²
Geophilidae	.50	3.3	.8/m ²
Lithobiidae	.25	2.9	.8/m ²
Diplopoda			
Julidae	.75	7.8	1.7/m ²
Polydesmidae	.75	5.6	1.3/m ²
Isopoda			
Oniscidae	1.00	10.6	2.2/m ²
Oligochaeta			
Lumbricidae	1.00	38.9	9.2/m ²
Araneae	1.00	3.6	.8/m ²
Pulmonata	.75	10.4	2.1/m ²

Table XII. Prey separated in Berlese funnel samples taken from site I during April. Samples were taken twice weekly for two weeks, and all sample data were lumped to determine mean percents and densities. Mean percent is from total number of prey

taxon	frequency of occurrence	\bar{X} % of sample	\bar{X} density/m ²
Coleoptera			
Staphylinidae	.75	0.2	7.5/m ²
Curculionidae	.50	0.1	3.2/m ²
Cerambycidae	.50	0.2	9.6/m ²
Pselaphidae	.25	0.2	9.6/m ²
Carabidae	.50	0.1	3.2/m ²
other beetles	.25	0.2	6.4/m ²
Homoptera			
Cicadellidae	1.00	0.4	13.6/m ²
Aphididae	1.00	1.0	30.4/m ²
Hymenoptera			
Formicidae	1.00	0.5	12.0/m ²
Platygasteridae	.25	0.2	6.4/m ²
Collembola			
Entomobryidae	1.00	8.6	279.2/m ²
Sminthuridae	1.00	17.0	502.4/m ²
Poduridae	1.00	27.4	826.4/m ²
Diptera			
Psychodidae	.25	0.2	3.2/m ²
Chironomidae	.25	0.1	6.4/m ²
Sciaridae	.25	0.2	3.2/m ²
other flies	.50	0.3	4.8/m ²
Insect larvae	1.00	3.1	93.6/m ²
Oligochaeta			
Lumbricidae	1.00	2.6	80.0/m ²
Chelonethida			
Chernetidae	.75	0.2	14.9/m ²
Acarina			
Galumnidae	1.00	2.8	88.0/m ²
Tetranychidae	1.00	0.7	28.0/m ²
Trombididae	1.00	1.5	40.0/m ²
other mites	1.00	32.2	1136.0/m ²

Table XII. (continued)

taxon	frequency of occurrence	\bar{X} % of sample	\bar{X} density/m ²
Symphyla			
Scolopendrellidae	1.00	0.4	9.6/m ²
Chilopoda			
Scolopendridae	.25	0.2	3.2/m ²
Lithobiidae	.25	0.4	6.4/m ²
Geophilidae	.25	0.1	3.2/m ²
Diplopoda			
Callipodidae	.75	0.2	7.5/m ²

Table XIII. Prey taken in tanglefoot traps at site I during April. Samples were taken once a week for two weeks, and all sample data were lumped to determine mean percent. Mean percent is from total number of prey

taxon	frequency of occurrence	\bar{X} % of sample
Diptera		
Syrphidae	1.00	1.2
Muscidae	.50	1.6
Tachinidae	1.00	0.6
Dolichopodidae	1.00	3.2
Empididae	1.00	2.7
Tipulidae	1.00	1.0
Drosophilidae	.50	1.7
Lonchaeidae	.50	1.1
Phoridae	.50	0.6
Mycetophilidae	.50	0.8
other flies	1.00	53.0
Orthoptera		
Gryllicircidae	.50	0.3
Coleoptera		
Carabidae	.50	0.8
other beetles	.50	0.8
Homoptera		
Aphididae	1.00	0.6
Cicadellidae	1.00	12.1
Collembola		
Entomobryidae	1.00	16.4
Sminthuridae	1.00	2.8
Hymenoptera		
Andrenidae	.50	2.5
Ichneumonidae	.50	0.3
Colletidae	.50	0.8
Apidae	.50	0.3
Araneae	1.00	1.0

APPENDIX C. AVAILABILITY DATA FOR
PREY COLLECTED DURING THE OCTOBER-
NOVEMBER 1974 SAMPLING PERIOD AT SITE II

Table XIV. Prey collected in streambed samples taken from site II during October and November. Samples were taken twice weekly for four weeks, and all sample data were lumped to determine mean percents and densities. Mean percent is from total number of prey

taxon	frequency of occurrence	\bar{X} % of sample	\bar{X} density/m ²
Coleoptera			
Staphylinidae	.13	14.2	8.9/m ²
Cucujidae	.13	6.2	8.9/m ²
Thysanura			
Iapygidae	.25	9.8	11.1/m ²
Insect larvae	.38	6.6	8.9/m ²
Oligochaeta			
Lumbricidae	1.00	86.2	121.2/m ²
Isopoda			
Oniscidae	.13	7.1	8.9/m ²
Diplopoda			
Polydesmidae	.25	9.0	13.4/m ²
Chilopoda			
Lithobiidae	.13	7.1	8.9/m ²
Pulmonata	.13	8.3	8.9/m ²

Table XV. Prey collected by raking leaf litter at site II during October and November. Samples were taken twice weekly for four weeks, and all sample data were lumped to determine mean percents and densities. Mean percent is from total number of prey

taxon	frequency of occurrence	\bar{X} % of sample	\bar{X} density/m ²
Coleoptera			
Carabidae	.38	3.0	1.3/m ²
Scarabaeidae	.13	4.4	2.4/m ²
Chrysomelidae	.13	2.8	.8/m ²
Staphylinidae	.13	2.0	.8/m ²
Orthoptera			
Gryllacricidae	.25	1.6	.8/m ²
Gryllidae	.13	2.8	.8/m ²
Blattidae	.13	3.7	1.6/m ²
Hymenoptera			
Formicidae	.13	1.4	.8/m ²
Thysanura			
Iapygidae	.50	3.9	2.7/m ²
Hemiptera			
Lygaeidae	.13	1.4	.8/m ²
Insect larvae	1.00	7.6	3.2/m ²
Diplopoda			
Julidae	.88	3.3	1.7/m ²
Polydesmidae	1.00	33.3	10.6/m ²
Chilopoda			
Geophilidae	.50	4.3	1.4/m ²
Scolopendridae	.63	2.0	.8/m ²
Oligochaeta			
Lumbricidae	1.00	39.6	13.1/m ²
Araneae	.38	4.0	1.6/m ²
Pulmonata	.88	7.1	2.6/m ²

Table XVI. Prey separated in Berlese funnel samples taken from site II during October and November. Samples were taken twice weekly for four weeks, and all sample data were lumped to determine mean percents and densities. Mean percent is from total number of prey

taxon	frequency of occurrence	\bar{X} % of sample	\bar{X} density/m ²
Coleoptera			
Cerambycidae	1.00	2.1	15.6/m ²
Pselaphidae	.38	0.5	3.2/m ²
Staphylinidae	.50	0.8	7.2/m ²
Scarabaeidae	.13	0.1	3.2/m ²
Curculionidae	.25	0.5	3.2/m ²
Erotylidae	.13	0.1	3.2/m ²
Homoptera			
Aphididae	.38	0.4	6.4/m ²
Hemiptera			
Aradidae	.13	0.3	3.2/m ²
Hymenoptera			
Formicidae	.75	2.0	10.7/m ²
Mutillidae	.13	0.3	3.2/m ²
Braconidae	.13	1.0	3.2/m ²
Cynipidae	.13	1.0	3.2/m ²
Platygasteridae	.25	0.2	3.2/m ²
other wasps	.13	0.2	6.4/m ²
Collembola			
Entomobryidae	1.00	6.6	56.8/m ²
Poduridae	1.00	41.8	758.4/m ²
Sminthuridae	1.00	9.8	110.4/m ²
Diptera			
Mycetophilidae	.13	0.1	3.2/m ²
Agromyzidae	.13	0.3	3.2/m ²
Phoridae	.13	0.9	3.2/m ²
Simuliidae	.13	1.0	3.2/m ²
Orthoptera			
Blattidae	.50	0.5	4.0/m ²
Insect larvae	1.00	5.7	37.2/m ²
Oligochaeta			
Lumbricidae	.88	5.7	37.2/m ²

Table XVI. (continued)

taxon	frequency of occurrence	\bar{X} % of sample	\bar{X} density/m ²
Chelonethida			
Chernetidae	.63	0.5	3.8/m ²
Acarina			
Galumnidae	.88	5.1	65.8/m ²
Trombidiidae	.75	1.6	13.3/m ²
Tetranychidae	.25	5.5	30.4/m ²
other mites	1.00	26.8	595.8/m ²
Araneae	1.00	2.6	23.6/m ²
Symphyla			
Scolopendrellidae	.25	2.2	4.8/m ²
Chilopoda			
Geophilidae	.38	0.4	4.3/m ²
Diplopoda			
Callipodidae	.25	0.2	3.2/m ²

Table XVII. Prey taken in tanglefoot traps at site II during October and November. Samples were taken once a week for four weeks, and all sample data were lumped to determine mean percents. Mean percent is from total number of prey

taxon	frequency of occurrence	\bar{X} % of sample
Diptera		
Asilidae	.25	0.3
Calliphoridae	.75	1.3
Dixidae	.25	2.2
Dolichopodidae	1.00	12.2
Drosophilidae	.25	2.2
Empididae	.25	0.9
Muscidae	1.00	10.2
Mycetophilidae	.25	5.4
Phoridae	.25	8.0
Pipunculidae	.25	1.3
Sarcophagidae	1.00	8.1
Syrphidae	1.00	2.6
Tachinidae	1.00	5.2
Tipulidae	.25	1.1
other flies	1.00	25.0
Orthoptera		1.1
Acrididae	.25	0.3
Gryllidae	.25	0.3
Gryllacricidae	.25	
Coleoptera		0.3
Carabidae	.25	0.3
Erotylidae	.50	1.8
Pselaphidae	.25	1.1
Scarabaeidae	.25	
Lepidoptera	.50	0.3
Hesperiidae		
Homoptera	1.00	1.8
Aphididae	1.00	4.0
Cicadellidae		
Thysanura	.25	0.3
Lepismatidae		

Table XVII. (continued)

taxon	frequency of occurrence	\bar{X} % of sample
Collembola		
Entomobryidae	1.00	8.1
Poduridae	.25	1.1
Sminthuridae	.50	5.1
Hymenoptera		
Apidae	.25	1.1
Braconidae	1.00	1.7
Colletidae	.25	1.1
Formicidae	.50	2.0
Platygasteridae	.75	0.9
Vespidae	.50	1.6
other wasps	.25	1.3
Insect larvae	.50	0.7
Araneae	.75	1.7

APPENDIX D. AVAILABILITY DATA FOR
PREY COLLECTED DURING THE APRIL 1975
SAMPLING PERIOD AT SITE III

Table XVIII. Prey collected in streambed samples taken from site III during April. Samples were taken twice weekly for two weeks, and sample data were lumped to determine mean percents and densities. Mean percent is from total number of prey

taxon	frequency of occurrence	\bar{X} % of sample	\bar{X} density/m ²
Coleoptera			
Dryopidae	.25	0.7	8.9/m ²
Trichoptera			
Hydropsychidae	.75	0.7	27.0/m ²
Insect larvae	1.00	31.3	193.3/m ²
Naiads	1.00	6.4	48.9/m ²
Decapoda			
Astacidae	.25	0.7	8.9/m ²
Isopoda			
Asellidae	1.00	50.5	408.7/m ²
Tricladida			
Planariidae	1.00	13.4	80.0/m ²

Table XIX. Prey collected by raking leaf litter at site III during April. Samples were taken twice weekly for two weeks, and all sample data were lumped to determine percents and densities. Mean percent is from total number of prey

taxon	frequency of occurrence	\bar{X} % of sample	\bar{X} density/m ²
Coleoptera			
Carabidae	.25	2.6	.8/m ²
Scarabaeidae	.50	2.7	.8/m ²
Endomychidae	.25	2.0	.8/m ²
Hymenoptera			
Formicidae	.50	41.1	12.0/m ²
Homoptera			
Cicadellidae	.25	2.0	.8/m ²
Insect larvae	1.00	19.0	5.8/m ²
Chilopoda			
Scolopendridae	.75	2.6	.8/m ²
Geophilidae	.50	5.4	1.6/m ²
Diplopoda			
Polydesmidae	1.00	9.4	2.8/m ²
Julidae	.25	2.0	.8/m ²
Oligochaeta			
Lumbricidae	1.00	35.2	16.3/m ²
Araneae	.50	4.5	1.2/m ²
Pulmonata	1.00	5.5	1.6/m ²

Table XX. Prey separated in Berlese funnel samples taken from site III during April. Samples were taken twice weekly for two weeks, and all sample data were lumped to determine mean percents and densities. Mean percent is from total number of prey

taxon	frequency of occurrence	\bar{X} % of sample	\bar{X} density/m ²
Coleoptera			
Pselaphidae	.25	0.1	3.2/m ²
Cerambycidae	.50	0.2	3.2/m ²
Curculionidae	.50	1.0	3.2/m ²
Staphylinidae	.50	0.1	3.2/m ²
Chrysomelidae	.25	0.1	3.2/m ²
other beetles	.25	0.1	3.2/m ²
Homoptera			
Aphididae	.25	0.3	9.6/m ²
Cicadellidae	.50	0.3	8.0/m ²
other homopterans	.50	0.1	3.2/m ²
Hymenoptera			
Formicidae	1.00	4.4	115.2/m ²
Platygasteridae	.50	1.0	3.2/m ²
Collembola			
Entomobryidae	1.00	14.8	454.4/m ²
Sminthuridae	1.00	8.1	302.4/m ²
Poduridae	1.00	28.7	840.8/m ²
Diptera			
Dixidae	.50	0.4	8.0/m ²
Drosophilidae	.25	0.1	3.2/m ²
Phoridae	.25	0.1	3.2/m ²
Chironomidae	.25	0.2	3.2/m ²
other flies	.50	1.5	6.4/m ²
Insect larvae	1.00	3.2	63.1/m ²
Oligochaeta			
Lumbricidae	1.00	2.6	68.8/m ²
Isopoda			
Armadillidiidae	.25	0.1	3.2/m ²
Chelonethida			
Chernetidae	.50	0.3	14.4/m ²
Acarina			
Calumnidae	1.00	1.3	38.4/m ²

Table XX. (continued)

taxon	frequency of occurrence	\bar{X} % of sample	\bar{X} density/m ²
Trombididae	1.00	1.3	44.0/m ²
Tetranychidae	1.00	1.4	42.4/m ²
other mites	1.00	31.0	1043.7/m ²
Symphyla			
Scolopendrellidae	.75	0.2	7.5/m ²
Chilopoda			
Geophilidae	.25	0.2	3.2/m ²
Scolopendridae	.25	0.1	3.2/m ²
Lithobiidae	.50	0.1	4.8/m ²
Diplopoda			
Polydesmidae	.25	0.1	3.2/m ²
Callipodidae	1.00	0.2	7.2/m ²
Araneae	1.00	1.1	29.6/m ²
Pulmonata	.50	0.1	4.8/m ²

Table XXI. Prey taken in tanglefoot traps at site III during April. Samples were taken once a week for two weeks, and all sample data were lumped to determine mean percent. Mean percent is from total number of prey

taxon	frequency of occurrence	\bar{X} % of sample
Diptera	1.00	1.4
Syrphidae	1.00	1.7
Tachinidae	1.00	3.4
Muscidae	.50	1.1
Calliphoridae	1.00	2.4
Dolichopodidae	1.00	0.7
Empididae	.50	1.1
Tipulidae	.50	3.3
Drosophilidae	.50	0.3
Lonchaeidae	.50	2.4
Anthomyzidae	.50	2.4
Phoridae	1.00	44.2
other flies		
Orthoptera	.50	1.1
Tetrigidae	1.00	0.7
Gryllacricidae		0.3
Coleoptera	.50	
Erotylidae		6.9
Homoptera	1.00	
Cicadellidae		2.1
Collembola	1.00	
Sminthuridae		0.3
Hymenoptera	.50	4.4
Apidae	.50	1.1
Braconidae	.50	1.4
Trichoptera	1.00	0.3
Araneae	.50	
Acarina		