To the Graduate Council:

I am submitting herewith a thesis written by Robert L. Jones entitled "Resource Partitioning Among Six Species of the Salamander Family Plethodontidae." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

Arthur C. Echternacht

Arthur C. Echternacht, Major Professor

We have read this thesis
and recommend its acceptance:

Susan E. Reichert

James T. Tanner

Accepted for the Council:

L. Evans Roth

Vice Chancellor
Graduate Studies and Research

RESOURCE PARTITIONING AMONG SIX SPECIES OF THE SALAMANDER FAMILY PLETHODONTIDAE

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Robert L. Jones

August 1977

ACKNOWLEDGMENTS

Many people have contributed to the completion of this study. To them I would like to express my appreciation.

Dr. James T. Tanner originally suggested a study of salamander competition. W.M. Post III, Dr. H.H. Shugart, and Dr. Susan E. Riechert offered much needed statistical advice. Dr. George W. Folkerts and Dr. Stephen G. Tilley provided advice on salamander identification. I would especially like to thank Dr. Arthur C. Echternacht for his assistance, encouragement, and patience during the course of this study.

Finally, I would like to thank the genus Desmognathus for being morphologically distinct in at least one part of its range.

ABSTRACT

Resource partitioning is a means by which similar species divide community resources. This may occur in terms of spatial, temporal, or trophic partitioning. Six species of salamanders (Desmognathus aeneus, D. ochrophaeus, D. fuscus, D. monticola, D. quadramaculatus, and Plethodon glutinosus) occur sympatrically in Cherokee National Forest of southeastern Tennessee in sufficient abundance for quantitative studies. This study was designed to investigate temporal and spatial partitioning among these six species.

Thirteen microhabitat and five activity variables were measured in the field. In addition, salamanders found during the microhabitat sampling were collected, aged, and measured. Due to problems with correlations and distributions, the microhabitat data set was reduced to eight variables; the activity set to three. These data sets were analyzed using a stepwise multiple discriminant analysis.

Differences in size are often cited as facilitating food partitioning. For this reason, a size variable, snout-vent length, was added to the microhabitat data set to determine its effects in species separation when considered with the microhabitat variables.

The multiple discriminant analysis indicated that in both adults and juvenile salamanders, separation of microhabitats was primarily a function of the mean distance of each species from water. However, the microhabitat variables were only able to place approximately 50% of all individuals into the correct species. With the addition of a size variable to the microhabitat variables, approximately 80% were

correctly predicted. Temporal partitioning apparently did not occur, as only about 40% of all observations were correctly predicted.

This study indicates that if food size is related to body size, then resource partitioning among the six species of salamanders apparently has both a trophic and a spatial aspect. This follows from the fact that the microhabitat and size variables taken together provide the best method of separating species. This is thought to be a result of physiological constraints related to water loss limiting the extent to which habitat partitioning can occur. Other factors that may have important effects on the local distribution of salamanders are age-class competition and predation.

TABLE OF CONTENTS

LIST OF TABLES

TABLE PAGE

LIST OF FIGURES

I. INTRODUCTION

The ecological niche of a species may be described by that species' utilization of or occurance along environmental axes important to its biology (Hutchinson, 1957). Geometrically, this describes a hypervolume of n dimensions, each of which represents one of those axes. Many of these dimensions represent types of resources in the community. The particular area or distribution of elements utilized by a species from a resource gradient is represented by a utilization curve, which is a picture of the niche in that dimension (Cody, 1974). The geometric configuration of all curves taken together describes the hypervolume. According to current theory, there are two ways of conceptualizing the niche. The Eltonian niche (Elton, 1927) deals with the functional role of a species within a community. The Hutchinsonian niche (Hutchinson, 1957), described above, has a functional aspect plus habitat or spatial parameters. In the original formulation of the n-dimensional hypervolume, Hutchinson specified that the model referred to a single instant in time, but stated that time must also be considered a variable.

Resource partitioning is concerned with how similar species divide community resources. In particular, it deals with the limits interspecific competition places on the number of species present in the community (Schoener, 1974). Animals are thought to partition resources in three basic ways: temporally, trophically, and spatially (Pianka, 1973). This resource division serves to separate niches and to

reduce competition (Hutchinson, 1957; MacArthur, 1972). However, not all cases of resource division are the result of competition. In some situations, separation between species along resource gradients may result from the effects of predation (Grant, 1972) or from reproductive isolation (Schoener, 1974).

In situations where competition occurs, there should result an overdispersion of niches in niche space; ie. niches should be regularly and widely spaced over one or more dimensions. Overdispersion of niches may fall into one of three categories (Schoener, 1974):

1. Regular spacing along a single dimension.
2. Increase in number of important dimensions with increase in species number.
3. Separation of species along complementary dimensions, which indicates that similarity of resource use along one dimension should imply dissimilarity along another.

Resource partitioning has been an area of increasing interest to ecologists (review in Schoener, 1974). However, little attention directly dealing with partitioning has been given amphibians, although related research has been done (Avery, 1968; Crump, 1974; Dumas, 1956; Fraser, 1976; Hairston, 1949; Heyer, 1976; Jaegar, 1971; Inger and Greenburg, 1967; Means, 1975).

Studies of competition in salamanders by Fraser (1976), Jaegar (1971), and Dumas (1956) have concentrated on two-species interactions within the genus Plethodon. Fraser found differences in seasonal activity patterns which, along with food size differences, were suggested as means of reducing competition between P. hoffmani and P. punctatus. Jaegar suggested that differences in food and microhabitat allowed the coexistence of P. cinereus and P. nettingi in Virginia,

although later (Jaegar, 1974) he indicated evidence of behavioral interactions between the two species. Dumas felt that competition between P. vehiculum and P. dunni did not occur due to differences in secondary prey type, microhabitat utilization, and because population levels never reached carrying capacity.

Hairston (1949) and Organ (1961) studied the local distribution and ecology of the genus Desmognathus in North Carolina and in Virginia, respectively. Hairston found an aquatic to terrestrial gradient among the four species he worked with (D. wrighti, D. ochrophaeus, D. monticola, and D. quadramaculatus) as well as differences in prey size for a small sample of stomach contents from each species. Organ added a species to the series (D. fuscus) and indicated that D. fuscus was probably unable to compete successfully against D. quadramaculatus and D. monticola when both were present in sites utilized by D. fuscus.

Nine species of plethodontid salamanders are known to occur in the Tellico Wildlife Management Area of southeastern Tennessee (pers. obs.). Six of these, D. quadramaculatus, D. monticola, D. fuscus, D. ochrophaeus, D. aeneus, and P. glutinosus, are sufficiently abundant for quantitative ecological studies. Pseudotriton ruber, Gyrinophilus porphyriticus, and Eurycea bislineata are encountered infrequently or show seasonal changes in abundance.

Desmognathus quadramaculatus, the largest member of the genus (total length for adults, 10-17 cm, Conant, 1975), is usually found in mountain streams at elevations above 500 meters (Valentine, 1974). Hairston (1949) reported it to be 78% aquatic, 90% nocturnal, and restricted to aquatic sites continuous at the surface.

Desmognathus monticola is a moderately large (8-13 cm), semiaquatic species characterized as a stream bank species by Organ (1961), and Hairston (1949), who found 54% of all specimens collected in this type of habitat. This species was found restricted to elevations of less than approximately 1300 meters in Virginia (Organ, 1961) and 1100 meters in North Carolina (Hairston, 1949), where it was reported to be 93% nocturnal.

Desmognathus fuscus is a medium-sized (6-11 cm), semiaquatic species, also characterized as a stream bank species by Organ (1961), who considered it to be slightly more terrestrial than D. monticola. In Virginia, D. fuscus was found restricted to seepage areas at low elevations where it occurred with D. monticola; stream sites were occupied by D. monticola and D. quadramaculatus (Organ, 1961). At higher elevations where D. monticola was absent, D. fuscus was found in seepage areas by itself and in streams with D. quadramaculatus. From this evidence Organ concluded that D. fuscus was able to coexist with either D. quadramaculatus or D. monticola, but not with both species at the same time.

Desmognathus ochrophaeus is a medium-sized (7-10 cm), semi-terrestrial species that inhabits stream margins and seepage areas, but which may move considerable distances into adjacent woodland (Tilley, 1973). Hairston (1949) found it to be 99% nocturnal and 76% terrestrial in North Carolina. In Alabama, D. ochrophaeus inhabits moist cliff faces and talus areas, and in such areas, D. fuscus is usually absent (Mount, 1975).

Desmognathus aeneus, the smallest member of the genus found in this study (4.4-5.7 cm), is restricted to surface cover near seepage areas and small streams (Brown and Bishop, 1947; Martof and Humphries, 1955). It is also one of the most terrestrial species in the genus (Harrison, 1967).

Plethodon glutinosus is a large (12-17 cm), wide-ranging species that is completely terrestrial throughout its life cycle. These salamanders were found to be completely nocturnal in North Carolina (Hairston, 1949).

The above evidence indicates that these six species are potential competitors in areas of sympatry, yet apparently coexist. For this reason, microhabitat and temporal factors affecting local distribution and activity of these salamanders were studied to determine how these species are able to coexist, what resources are most important in separating their niches, and if complementarity along resource axes is present.

II. METHODS AND MATERIALS

Study Area

The study area coordinates were 35° 25' and 35° 30' north latitude, 84° 00' 00" and 84° 07' 30" west longitude, Cherokee National Forest, Monroe County, Tennessee. All collections were made within the Citico Creek watershed of the Tellico Wildlife Management Area. This area is managed for hunting, trout fishing, and timber production. Floristics and a short history of the area were summarized by Malter (1977). Place names used in this paper are from the United States Geological Survey May of the "Whiteoak Flats Quadrangle," 1957 edition.

Samples (described below) were taken from streams and seepage areas within the study area. Most of these were along Citico Creek, which flows into the Little Tennessee River, and Doublecamp Creek, the major eastern tributary of Citico Creek. Smaller streams and tributaries of both Citico Creek and Doublecamp Creek were also sampled. Doublecamp Creek is the major stream in a cove formed by Cowcamp Ridge to the north and by Pine Ridge to the south. Two tributaries of Doublecamp Creek, Crowder Branch and Mill Branch, were extensively sampled. These two streams drain the northern slope of Big Fodderstack Mountain, the summit of which is the highest elevation (1325 meters) in the immediate vicinity.

Citico Creek and Doublecamp Creek are large streams, ranging on the average from approximately 8 to 20 meters in width. The beds and

banks of these streams are usually composed of sand, coarse gravel, and large rocks, and in areas where the stream has cut down to it, of solid bedrock. These streams run continuously, and at higher elevations, usually have a strong current. The banks of these streams are devoid of large amounts of leaf litter and vegetation.

The smaller tributaries, including both Crowder Branch and Mill Branch, range from less than 1 to approximately 4 meters in width. These streams usually have a slower current and a mixture of mud and rock or gravel composing their beds and banks. Leaf litter and vegetation are also commonly found along the banks of the smaller streams. At higher elevations, the smallest streams have seasonal periods of flow, usually drying up during the late summer.

Seepage areas are areas that generally have a detectable water flow, but that are not connected on the surface with any streams in the area. These range from vertical rockfaces to areas that are almost flat. Rockfaces usually have large amounts of mosses growing over them, while the flatter areas have deep layers of leaf litter.

Microhabitat Samples

Microhabitat sampling was begun on 15 June, 1976 and continued through 15 September, 1976. Sampling was conducted during the daylight hours for an average of four days per week, except during the week of August 8 to 14.

Streams were sampled by extending 5 meter wide transects 50 meters into the forest on both sides of the stream at 50 meter elevation intervals between 300 and 950 meters. Seepage areas were sampled in the same manner as streams; however, elevation interval varied depending on the

availability of the seepage areas, which were found between 300 and 980 meters. An attempt was made to search all potential salamander shelters and to capture all transformed individuals seen. Thirteen variables associated with the microhabitat were measured for each salamander captured. The thirteen variables and the method and equipment used to measure them are listed below:

1. Aspect, defined as the facing direction of the sample site, was measured with a compass to the nearest degree.
2. Slope, defined as the slope of the seepage area or stream, was measured with an Abney level to the nearest half degree.
3. Width, the distance across the stream or seepage area parallel to the transect at the sample site, was measured with a meter tape to the nearest .1 meter.
4. Distance from water, defined as the distance in meters of the salamander from the nearest open water, was measured in the same manner as width.
5. Elevation was measured with an altimeter, which was corrected daily at bench marks or by using landmarks on a topographic map.
6. Water temperature was measured at the midpoint of the stream or seepage area.
7. Water pH was measured for two samples of water from the stream or seepage area with a portable water pH meter. The mean of these two samples was recorded as water pH.
8. Air temperature at 6 cm was measured 6 cm above the point where the salamander was first seen.

9. Air temperature at 1 cm was measured 1 cm above the point where the salamander was first seen.
10. Substrate moisture content was measured at the point where the salamander was first seen with a portable soil pH-moisture meter. On some occasions, the nature of the substrate (eg. rock) made it impossible to measure this variable.
11. Substrate pH was measured at the point where the salamander was first seen with a portable soil pH-moisture meter. On some occasions, as with substrate moisture, no measurement was possible.
12. Substrate temperature, taken at the point where the salamander was first seen, was measured with a soil thermometer to the nearest degree.
13. Foliage cover was estimated at the point of capture to the nearest 5%, based on the amount of unobstructed sky visible above the point of capture.

Each salamander represented in the analysis of microhabitat was killed in a solution of Chlorotone and weighed on a gram scale to the nearest .1 gram. After death, snout-vent length (SVL) was recorded with a metal rule to the nearest .1 cm. The stomach and contents were removed and placed in a labeled 2-dram vial containing 70% ethyl alcohol. Salamanders were tagged and fixed in a 10% formalin solution for approximately 24 hours. After hardening, the salamanders were stored in a 70% solution of ethyl alchol. Sexing of each individual, if possible, was done after preservation and based on the presence of papillae or folds in the cloaca (Bishop, 1947). The presence of these structures also indicated sexual maturity (Bishop, 1947). All specimens were

deposited in the Vertebrate Zoology Collection of the University of Tennessee, Knoxville.

Diel Activity Pattern

Activity samples were taken July 22, July 28, August 3, August 19, August 26, and September 2. Transects similar to those for microhabitat were constructed at selected localities and monitored hourly for 24 consecutive hours. Sample localities were selected if certain species were known to occur there in order to obtain as many observations on as many species as possible.

Six variables thought to influence activity in salamanders were recorded each hour:

1. Air temperature at 6 cm above the substrate.
2. Air temperature at 1 cm above the substrate.
3. Substrate temperature, which included both soil and water temperatures, depending upon the location of the observation.
4. Relative humidity, measured with a sling psychrometer.
5. Time since sunset, sunset being defined as the time when light conditions were such that artificial light was required for species identification.
6. Illumination. A qualitative method for judging illumination, developed by Sealy (1968), was used to estimate the relative amount of light. Light conditions were estimated on a scale from 1 to 10. A score of 1 indicated no perceptible light, 5 or 6 indicated conditions equivalent to those at dawn or

dusk, depending upon weather conditions, and a score of 10 indicated clear skys and direct sunlight.

Salamanders were scored as being 100% active if the entire animal was visible, 50% active if it was partially within a shelter (Hairston, 1949). Specific identifications and scoring were made without disturbing the salamanders with the aid of a battery powered head lamp. Individuals not readily identifiable were not recorded.

Data Analysis

The data sets for activity and microhabitat were analyzed using a stepwise multiple discriminant analysis. Multiple discriminant analysis (Afifi and Azen, 1972; Cooley and Lohnes, 1971; Klecka, 1975) reduces a data set of n measurements on m variables to n measurements on p new variables. Each measurement is associated with an individual of one of s groups. These new variables, the discriminant functions, are orthogonal, additive functions of the original variables. The maximum number of discriminant functions which can be derived is s-1 if the number of variables is greater than the number of groups ($m>s$), or is equal to the number of variables if that number is less than the number of groups ($m<s$).

The objective of the discriminant analysis is to weight and linearly combine the variables of the data set so that the groups are as statistically distinct as possible. This is done by forming the discriminant functions, which are of the form (Klecka, 1975)

$$D_i = d_{i1}Z_1 + d_{i2}Z_2 + \ldots + d_{im}Z_m$$

where D_i is the score on the ith discriminant function, d_i's are weighting coefficients, and Z's are the standardized values of the m

variables in the analysis. A discriminant score is calculated for each individual in each group. The weighting coefficients (d_i's) represent the relative contributions of their associated variables to each discriminant function. The relative importance of each discriminant function, expressed as the relative percentage of the eigenvalue associated with it, gives a measure of the total variation existing in the original data set. Centroids, which are the means of the discriminant scores for each group on each discriminant function, can be used to locate groups along the appropriate discriminant function axes.

The stepwise procedure used maximizes the Mahalonobis distance, the ordinary Euclidean distance in space defined by a set of oblique axes (Rao, 1952), between the two closest groups. The stepwise process first chooses the single variable which yields the largest Mahalonobis distance between the two closest groups. The initial variable is then paired with each of the other available variables until the pair that maximizes the Mahalonobis distance is found. These two variables are then combined with the remaining available variables until the triplet which maximizes the Mahalonobis distance is found. This process continues until all variables are selected or until no additional variables provide an adequate increase in the Mahalonobis distance, determined by an F test, between the two closest groups.

Classification coefficients are derived from the pooled within-groups covariance matrix and the group centroids. The coefficients are used to classify the group members, based on the scores on each variable of the original data set. In this way, a check is made on the effectiveness of the data set in separating groups (Klecka, 1975).

For this analysis, a high percentage of correct classifications indicates that species are partitioning resources correlated with the variables measured. A low percentage indicates that the variables are not effective in species separation; ie, resource partitioning is not taking place, at least in terms of the variables considered.

The assumptions for the use of the multiple discriminant analysis on ecological data are (Green, 1971):

1. The groups can be defined a priori. There is much morphological variation in the genus Desmognathus throughout its range; however, in the study area the five species are distinct and readily identifiable. Plethodon glutinosus, the only member of its genus found in the study area, is readily separable from the Desmognathus species.
2. The ecological variables are sampled from a multivariate normal distribution and are, in fact, additive linear functions. Each variable used in the analysis was tested for kurtosis and skewness. Those that exhibited distributions aberrant for these two parameters were transformed. The angular transformation was used for proportions (Sokal and Rohlf, 1969), the logarithmic transformation for continuous variables.
3. The group covariance matrices are estimates of a common covariance matrix. If this pooled matrix is estimated on a large number of degrees of freedom, the total variation is approximately distributed as a chi-square (Rao, 1952), and may serve as a test for overall group

differences if the group covariance matrices are homogeneous. Since this assumption is unlikely to be satisfied with ecological data (Green, 1971), the overall chi-square is biased. However, if the chi-square test is significant and the discriminant analysis is ecologically interpretable, then it is reasonable to assume that the species differences are greater than would result from random sampling of a multivariate swarm (Green, 1971).

The original set of 13 microhabitat variables was reduced to eight that were used in the analysis. The variable "aspect" was deleted because samples were taken primarily from north and northwest facing slopes, which did not provide enough variation to discriminate between species' distributions on the basis of aspect selection. The variables "water temperature" and "water pH" were eliminated for two reasons. Terrestrial salamanders, such as Plethodon glutinosus, are not directly affected by these stream parameters, since they rarely, if ever, enter water. Secondly, salamanders found in water were recorded as having a substrate temperature equivalent to the stream's temperature and a substrate pH equivalent to the stream's pH. Including the stream parameters in the analysis would in effect result in recording the same variable twice for those salamanders found in contact with water. Strong correlations among variables tend to amplify the effects of those variables in a discriminant analysis (Sokal and Sneath, 1963; W.M. Post III, pers. comm.). The variables "air at 1 cm," "air at 6 cm," and "substrate temperature" were all strongly correlated (air 6 cm - air 1 cm, r = .93; air 6 cm - substrate temperature, r = .91; air 1 cm -

substrate temperature, r = .96). Since the air temperatures were subject to the greatest modification due to air movements and to the disturbance of salamander shelters during the searching phase, substrate temperature was judged the most accurately measured of the three and was retained in the analysis. The eight microhabitat variables remaining and the mnemonic used to identify them in the analysis were slope (SLOPE), stream width (WIDTH), elevation (ELEVATE), distance from water (DFHOH), substrate pH (SUBPH), substrate moisture (SUBHOH), substrate temperature (SUBTEM), and percent foliage cover (FOL). Strong correlations among the activity variables caused the elimination of "air at 6 cm" and "air at 1 cm" (air 6 cm - air 1 cm, r = .96; air 1 cm - substrate temperature, r = .86; air 6 cm - substrate temperature, r = .95) and "time since sunset," which was strongly correlated with "illumination" (r = .70). The three remaining variables and the mnemonic used to identify them in the analysis were substrate temperature (SUBTEMP), relative humidity (HUMIDITY), and illumination (LIGHT).

As mentioned earlier, values for substrate pH and substrate moisture were not obtainable for several individuals. In order to retain these individuals in the data set, the means of these variables over all species and individuals were substituted for missing values. This does not bias the results of the discriminant analysis if the appropriate degrees of freedom, in this case, two, are subtracted from the overall chi-square (H.H. Shugart, pers. comm.).

All data analyses were done using the SPSS multiple discriminant analysis subprogram (Klecka, 1975) on an IBM 360/65 computer at the University of Tennessee Computer Center, Knoxville. Separate analyses

for adults and juveniles were conducted in order to eliminate age or size class differences within a species.

III. RESULTS AND DISCUSSION

The overall test of significance of the discriminant analysis of adult microhabitat selection yielded $\chi^2 = 506.75$, which was significant at a probability level of .005 ($\chi^2_{.005,\ 38\ df} = 64.182$). Fewer microhabitat variables had a significant F value for entry into the stepwise analysis of the juveniles. The overall test of significance for among species differences in the juveniles yielded $\chi^2 = 175.436$, also significant at a probability level of .005 ($\chi^2_{.005,\ 33\ df} = 57.649$). The untransformed means for adults and juveniles of each species on the microhabitat variables, plus a size variable, snout-vent length, are given in Table 1. Ranges for the same variables are given in Tables 2 and 3.

Adult Microhabitat Analysis

The results of the microhabitat discriminant analysis for adults are given in Table 4. The first three discriminant functions accounted for 94.36% of the relative variability among adult salamanders. The first discriminant function (DF I), accounting for 64.07% of the among species variance, was largely a function of the mean distance from water for each species. This function separated species along an aquatic to terrestrial gradient, with the primarily aquatic *D. quadramaculatus* at one extreme and the terrestrial *P. glutinosus* at the other.

The second discriminant function, accounting for 22.03% of the relative variability, separated species largely on the basis of slope.

Table 1. Untransformed means of microhabitat variables and snout-vent length for adults and juveniles of six salamander species. See text for explanations of variables.

Species	SLOPE (deg)	WIDTH (M)	ELEVATE (M)	DFHOH (M)	SUBHOH (%)	SUBPH (pH)	SUBTEM (°C)	FOL (%)	SVL (cm)
P. glutinosus									
Adults	8.9	3.98	746.4	18.22	37.2	6.8	18.3	77.4	5.55
Juveniles	9.1	3.28	775.0	18.98	31.9	6.9	18.7	80.0	3.21
D. aeneus									
Adults	8.2	3.17	685.0	8.11	49.4	6.8	18.7	78.0	2.35
Juveniles	3.9	4.58	630.0	4.28	55.0	6.7	18.9	80.6	1.83
D. ochrophaeus									
Adults	40.1	4.61	666.0	2.98	61.6	6.9	18.4	73.5	3.73
Juveniles	42.5	4.71	687.8	1.78	65.4	7.0	18.9	74.6	2.18
D. Fuscus									
Adults	7.2	3.86	450.5	1.18	62.9	6.9	18.4	76.1	4.57
Juveniles	5.4	3.54	546.2	1.74	67.4	6.9	18.3	73.8	2.65
D. monticola									
Adults	12.2	4.41	592.3	1.09	64.7	7.0	18.3	76.9	5.87
Juveniles	15.6	4.05	627.4	0.84	72.9	7.0	17.8	75.5	3.35
D. quadramaculatus									
Adults	12.9	4.33	623.6	0.58	86.2	7.2	17.0	77.1	7.74
Juveniles	7.9	3.59	750.0	0.08	95.3	7.2	15.4	74.7	5.05

Table 2. Untransformed ranges of five microhabitat variables for adults and juveniles of six salamander species. See text for explanation of variables.

Species	SLOPE (deg)	WIDTH (M)	ELEVATE (M)	DFHOH (M)	SUBHOH (%)
P. glutinosus					
Adults	1.0-12.5	2.2-8.7	500-980	1.9-47.0	10-65
Juveniles	4.5-12.5	1.6-5.0	600-950	2.5-32.6	20-45
D. aeneus					
Adults	0.0-90.0	1.6-8.7	300-980	0.3-30.1	15-80
Juveniles	2.0- 6.0	2.2-6.6	600-900	2.0-10.7	20-70
D. ochrophaeus					
Adults	3.0-90.0	1.6-8.0	450-980	.05-13.9	5-100
Juveniles	3.0-90.0	2.0-8.0	450-850	.05- 6.9	5-100
D. fuscus					
Adults	3.0-21.0	1.6-21.1	300-980	0.0- 9.7	30-100
Juveniles	3.0-12.5	1.6- 5.8	300-980	0.0-10.4	30-100
D. monticola					
Adults	1.0-90.0	0.9- 8.8	300-980	0.0- 6.8	20-100
Juveniles	1.0-90.0	1.6- 8.8	300-980	0.0- 7.9	15-100
D. quadramaculatus					
Adults	1.0-90.0	1.9-8.8	300-980	0.0-5.4	30-100
Juveniles	1.0-21.0	1.6-8.8	350-950	0.0-0.9	20-100

Table 3. Untransformed ranges of three microhabitat variables and snout-vent length for adults and juveniles of six salamander species. See text for explanation of variables.

Species	SUBPH (pH)	SUBTEM (°C)	FOL (%)	SVL (cm)
P. glutinosus				
Adults	6.2-7.0	13.5-23.0	60-95	4.0-8.3
Juveniles	6.8-7.0	17.0-20.5	70-90	2.3-3.8
D. aeneus				
Adults	5.6-7.0	12.5-22.5	60-95	1.9-3.1
Juveniles	6.6-6.8	17.0-20.0	70-90	1.7-2.0
D. ochrophaeus				
Adults	6.4-7.5	12.5-21.5	60-95	2.5-4.8
Juveniles	6.6-7.5	15.0-23.5	60-85	1.6-2.8
D. fuscus				
Adults	6.6-7.3	12.5-22.0	60-100	3.0-6.3
Juveniles	6.7-7.3	13.0-23.0	60-90	1.6-3.7
D. monticola				
Adults	6.6-7.6	12.5-23.0	50-100	4.2-7.2
Juveniles	6.6-7.6	12.5-22.0	50-95	1.6-5.4
D. quadramaculatus				
Adults	6.8-7.6	12.0-21.4	50-95	5.9-11.0
Juveniles	6.7-7.6	13.4-20.6	50-85	4.2-5.6

Table 4. Standardized discriminant function coefficients (d_j's) showing the relative contribution of the original variables to each discriminant function for the adult microhabitat analysis.

	Discriminant Functions				
	I	II	III	IV	V
Percentage of among species variance	64.07	22.03	8.26	3.78	1.86
Cumulative percentage	64.07	86.10	94.36	98.14	100.00
Variables:					
SLOPE	-0.046	0.820	0.520	-0.026	0.054
WIDTH	0.022	0.473	-0.019	0.399	0.053
ELEVATE	-0.350	0.423	-0.631	-0.466	0.715
DFHOH	-0.939	-0.032	-0.228	0.180	-0.841
SUBPH	-0.005	0.387	-0.763	0.860	-0.174
SUBTEM	-0.133	-0.083	-0.143	0.018	1.084
SUBHOH	-0.157	-0.012	-0.096	-1.051	-0.373
FOL	-0.066	0.180	-0.336	0.077	0.078

Desmognathus ochrophaeus, abundant on rockfaces in the study area, was at one extreme of the discriminant axis, while D. aeneus, characteristic of banks of slow moving streams and seepage areas, was at the other. The locations of the centroids for all species on the first two discriminant axes are shown in Figure 1.

The third discriminant function, accounting for 8.26% of the relative variability, was a contrast between substrate pH and elevation relative to slope, as indicated by the opposite signs of the coefficients of these variables (Table 4). This function separated D. fuscus, which had a low mean elevation and slope, from D. quadramaculatus, which had a relatively high mean elevation and slope (Table 1).

The fourth and fifth discriminant functions accounted for a total of 5.64% of the relative variability in the data set. The fourth discriminant function separated the two most terrestrial species, D. aeneus and P. glutinosus, on the basis of substrate moisture content relative to substrate pH. The fifth discriminant function contrasted elevation and substrate temperature relative to distance from water, and served to separate D. fuscus and D. monticola. Since no statistical tests were conducted on the individual discriminant functions, the significance of the last two was unknown. However, since together they provide less than 10% of the discriminating power of DF I, their value appeared limited and they were not considered further.

The results of the classification phase of the discriminant analysis for adults are given in Table 5. Only 51.35% of all adults were correctly classified. The most distinct species, based on the

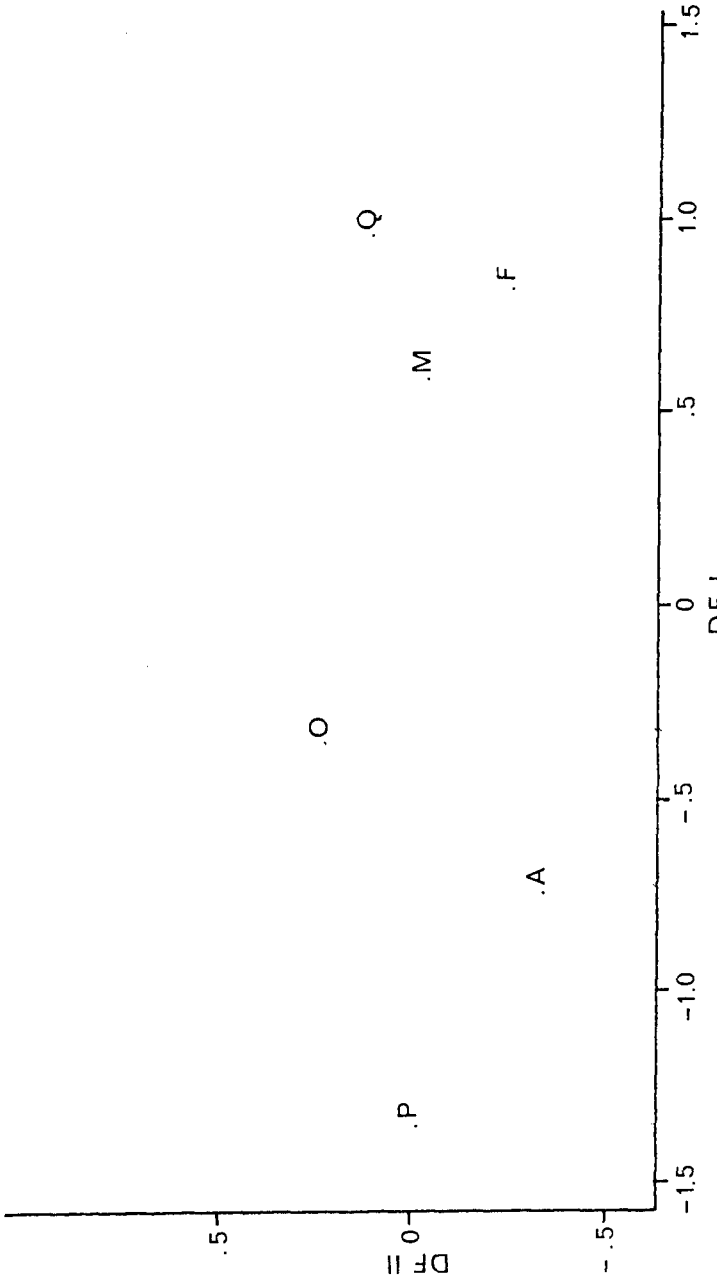

Figure 1. Centroids of species on the first two discriminant axes for the adult microhabitat analysis. P - Plethodon glutinosus, A - Desmognathus aeneus, O - D. ochrophaeus, F - D. fuscus, M - D. monticola, Q - D. quadramaculatus.

Table 5. Classification results of the discriminant analysis for adult salamanders using microhabitat variables. Numbers in parentheses represent actual number of individuals placed in each group. Percent of all individuals correctly classified: 51.35.

Actual species	n	Predicted group membership					
		Plethodon glutinosus	D. aeneus	D. ochrophaeus	D. fuscus	D. monticola	D. quadra-maculatus
P. glutinosus	33	84.8(28)	9.1(3)	3.0(1)	3.0(1)	0.0(0)	0.0(0)
D. aeneus	48	22.9(11)	50.0(24)	6.2(3)	12.5(6)	6.2(3)	2.1(1)
D. ochrophaeus	73	21.9(16)	8.2(6)	53.4(39)	1.4(1)	12.3(9)	2.7(2)
D. fuscus	40	0.0(0)	5.0(2)	0.0(0)	60.0(8)	20.0(8)	15.0(6)
D. monticola	97	2.1(2)	5.2(5)	12.4(12)	17.5(17)	28.9(28)	34.0(33)
D. quadramaculatus	42	2.4(1)	0.0(0)	11.9(5)	2.4(1)	16.7(7)	66.7(28)

classification scores of each individual, was P. glutinosus, with 28 of 33 (84.8%) correctly classified. The least distinct species, D. monticola, had 28 of 97 (28.9%) correctly classified.

Juvenile Microhabitat Analysis

The results of the microhabitat discriminant analysis for juveniles are given in Table 6. The discriminant analysis for the juveniles showed results similar to those for the adults on the first two discriminant functions. As with the adults, DF I separated species along an aquatic to terrestrial gradient, accounting for a slightly smaller percentage of the relative variability than in the adults (59.94 vs. 62.07%). The second discriminant function separated species by slope, and, to a lesser degree, by elevation. This discriminant function accounted for a slightly greater percentage of the relative variability than did DF II for adults (26.54 vs 23.03%). There was also a reversal in position along the discriminant function axis between juvenile P. glutinosus and D. monticola, relative to that of the adults (Fig. 2). This may have been due to small sample size for P. glutinosus rather than a qualitative shift in slope preferences or added importance of elevation in the juvenile salamanders.

The third discriminant function separated species by distance from water and substrate pH relative to substrate temperature. This function separated P. glutinosus, with a low mean pH and high mean distance from water, from D. fuscus, a semiaquatic species with a relatively high mean substrate temperature.

Table 6. Standardized discriminant function coefficients (d_i's) showing the relative contribution of the original variables to each discriminant function for the juvenile microhabitat analysis.

	Discriminant Functions				
	I	II	III	IV	V
Percentage of among species variance	59.94	26.54	8.95	3.88	0.69
Cumulative percentage	59.94	86.48	95.43	99.31	100.00
Variables:					
SLOPE	-0.143	-0.961	-0.198	0.091	0.498
WIDTH	-0.169	-0.320	-0.283	0.211	-0.648
ELEVATE	0.058	-0.500	0.426	0.450	-0.511
DFHOH	-0.992	0.277	0.695	0.008	0.119
SUBPH	-0.088	-0.331	0.563	-1.026	-0.458
SUBTEM	-0.012	-0.151	-0.623	0.149	-0.495
SUBHOH	0.050	0.209	0.148	0.915	0.125

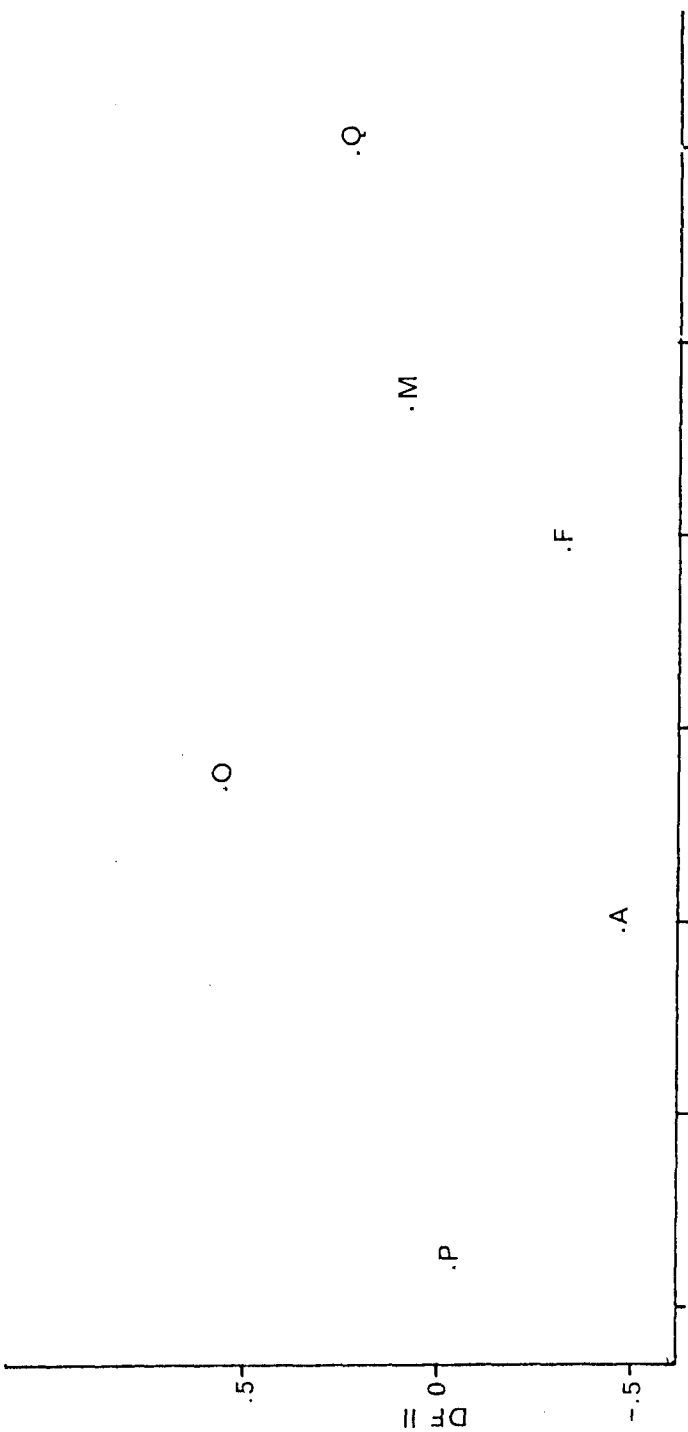

Figure 2. Centroids of species on the first two discriminant axes for the juvenile microhabitat analysis. P - Plethodon glutinosus, A - Desmognathus aeneus, O - D. ochrophaeus, F - D. fuscus, M - D. monticola, Q - D. quadramaculatus.

The fourth and fifth discriminant functions, as in the adults, explained little of the variability in the data set. The fourth discriminant function separated the two most terrestrial species, D. aeneus and P. glutinosus, on the basis of substrate pH relative to substrate moisture content. The fifth discriminant function, based on a combination of stream width, substrate pH, and substrate temperature, all relative to slope, accounted for less than 1% of the relative variability. As in the adults, the last two discriminant functions appeared to be of little value in separating species, and were not considered further.

Based on the values of the microhabitat variables for each individual, 51.94% of the juvenile salamanders were correctly classified (Table 7). Four species (D. aeneus, D. ochrophaeus, D. quadramaculatus, and P. glutinosus) had classification scores greater than 80%. As in the adults, D. monticola had the lowest number of correct classifications, 17 of 65, for 26.2%.

Discussion: Microhabitat Partitioning

The major separation of the six salamander species, as indicated by the first discriminant function, was along an aquatic to terrestrial gradient. The first discriminant function divided the six species into two groups; those that were relatively more aquatic, consisting of D. quadramaculatus, D. monticola, and D. fuscus; and those that were relatively more terrestrial, consisting of P. glutinosus, D. ochrophaeus, and D. aeneus. These groups were evident when group centroids were plotted along the first two discriminant function axes in both adults (Fig. 1) and juveniles (Fig. 2), but were less distinct in the latter. This may have been due to small sample sizes for juveniles of some species. The

Table 7. Classification results of the discriminant analysis for juvenile salamanders using microhabitat variables. Numbers in parentheses represent actual number of individuals placed in each group. Percent of all individuals correctly classified: 51.94.

		Predicted group membership					
Actual species	n	Plethodon glutinosus	D. aeneus	D. ochrophaeus	D. fuscus	D. monticola	D. quadra-maculatus
P. glutinosus	8	87.5(7)	0.0(0)	12.5(1)	0.0(0)	0.0(0)	0.0(0)
D. aeneus	8	12.5(1)	87.5(7)	0.0(0)	0.0(0)	0.0(0)	0.0(0)
D. ochrophaeus	18	5.6(1)	0.0(0)	83.3(15)	5.6(1)	0.0(0)	5.6(1)
D. fuscus	13	7.7(1)	7.7(1)	0.0(0)	53.8(7)	7.7(1)	23.1(3)
D. monticola	65	3.1(2)	12.3(8)	15.4(10)	18.5(12)	26.2(17)	24.6(16)
D. quadramaculatus	17	0.0(0)	0.0(0)	0.0(0)	0.0(0)	17.6(3)	82.4(14)

aquatic to terrestrial gradient was similar to that found in other studies of the genus Desmognathus by Hairston (1949) and Organ (1961). Plethodon glutinosus undoubtedly extends further into the woodland that was indicated by the microhabitat samples. However, the analysis did indicate its position relative to the species in the genus Desmognathus.

The second discriminant function acted to further separate the species within each group. This function was measuring primarily the slope of the seepage or stream where samples were taken, and was therefore roughly an indication of the general relief of the sample site.

Separation of species was greater in the terrestrial group than in the aquatic (Figs. 1 and 2, pages 23 and 27) for both adults and juveniles. There are several possible explanations for this. The terrestrial group included two different genera, Plethodon and Desmognathus, while the aquatic group contained only Desmognathus species, which are more similar in morphology and physiology, and thus, possibly more similar in their ecological requirements. The second discriminant function was largely a function of slope. Since the terrestrial group contains the species with the largest mean slope (D. ochrophaeus) and the two species with the fourth and fifth smallest mean slopes (D. aeneus and P. glutinosus), greater separation of the terrestrial species could be simply an artifact of the analysis. Terrestrial environments are generally more rigorous for amphibians than are aquatic ones due to the problems amphibians have with water loss (Spight, 1967; Spotila, 1972). The greater separation of the terrestrial

species may reflect specialization on the part of the species involved for distinct microhabitats correlated with slope. This appears to have been the case in both species of terrestrial Desmognathus. Desmognathus aeneus was found commonly in seepage areas, which have poor drainage in part reflected by slope. Desmognathus ochrophaeus was particularly abundant on rockfaces that had a detectable movement of water over them.

The classification statistics showed a significant amount of microhabitat overlap among the six species of salamanders, since only slightly over 50% of all adults and juveniles were assignable to the correct species on the basis of the microhabitat variables measured (Tables 5 and 7, pages 24 and 29). In the adults the two most extreme groups on the aquatic to terrestrial gradient, P. glutinosus and D. quadramaculatus, had the highest classification scores, with 84.8% of the former and 66.7% of the latter correctly classified. Desmognathus aeneus, D. ochrophaeus, and D. fuscus were intermediate in this respect, with scores ranging from 50 to 60%. Desmognathus monticola had the lowest score among the adults, with less than 30% of all individuals correctly classified.

Among the juveniles, four species (D. aeneus, D. ochrophaeus, D. quadramaculatus, and P. glutinosus) had classification scores greater than 80%. Desmognathus fuscus and D. monticola had scores similar to the adults, with slightly more than 50% correct in D. fuscus juveniles and less than 30% correctly classified in D. monticola. The high scores were probably a reflection of small sample size rather than a smaller overlap in microhabitat among juvenile salamanders.

The classification scores indicate that adult P. glutinosus and D. quadramaculatus were fairly distinct in terms of the microhabitat variables measured. A consideration of the misclassifications shows that most occurred among species within either the aquatic or terrestrial groups. For example, slightly over 20% of D. aeneus and D. ochrophaeus were predicted to be P. glutinosus. Similarily, most of the misclassified D. fuscus and D. monticola were placed either in D. quadramaculatus or the remaining member of the group. This was to be expected, since the classification statistics were based on each individual's scores on the microhabitat variables, but further emphasizes the relative similarity of species within each group.

The classification statistics of D. monticola warrant special attention. This species had the lowest number of individuals correctly predicted of all species in the analysis; in fact, more D. monticola were classified as D. quadramaculatus than as D. monticola. This may be explained in one of two ways. A particular microhabitat variable that would have separated D. monticola was not measured, although none immediately suggests itself. Another possibility is that D. monticola is a habitat generalist, apparently more like D. quadramaculatus in this respect than any other species in the analysis, although the number of D. monticola predicted to be D. ochrophaeus and D. fuscus each exceeded 10%. Although no quantitative population estimates were made, D. monticola appeared to be the most common species in the study area, as indicated by the number captured and by the fact that it appeared in all but three of the samples. One reason for its apparent abundance may be that it is able to survive in almost any semiaquatic microhabitat within the confines of the study area.

Microhabitat Plus Size

The six species of salamanders included in the study represent a gradient of increasing body size from D. aeneus through D. quadramaculatus (Table 1, page 18). Differences in size, especially in trophic structures, are often cited as facilitating food partitioning (Pianka, 1969, 1973; Schoener, 1968). For this reason, snout-vent length was included with the microhabitat variables to examine size effects in conjunction with the effects of microhabitat selection. Weight is probably a better estimate of true body size differences, but was not used because of variation due to missing limbs and tails in many specimens.

Results of these analyses are given in Table 8 for adults and in Table 9 for juveniles. The overall chi-square test for adults yielded $\chi^2 = 948.63$, which was significant at a probability level of .005 ($\chi^2_{.005,\ 33\ df} = 70.616$). For the juveniles, the overall chi-square test yielded $\chi^2 = 248.38$, which was also significant at a probability level of .005 ($\chi^2_{.005,\ 28\ df} = 50.993$).

The first three discriminant functions accounted for 97.57% of the total variation in the adult salamanders. The first discriminant function, accounting for 78.94% of the relative variability, separated the adults on the basis of size. The second discriminant function, accounting for 12.64% of the relative variability, separated the species on a basis of distance from water and elevation, placing the low elevation, semiaquatic D. fuscus at one extreme of the axis and the terrestrial, high elevation P. glutinosus at the other. The third discriminant

Table 8. Standardized discriminant function coefficients (di's) showing the relative contribution of the original variables to each discriminant function for the adult microhabitat plus size analysis.

	Discriminant Functions				
	I	II	III	IV	V
Percentage of among species variance	78.94	12.64	5.99	1.56	0.87
Cumulative percentage	78.94	91.58	97.57	99.13	100.00
Variables:					
SLOPE	0.019	0.251	-0.900	0.191	-0.080
WIDTH	-0.004	0.150	-0.412	0.199	0.321
ELEVATE	-0.034	0.566	-0.108	-0.862	0.459
DFHOH	-0.288	0.916	0.442	0.285	-0.511
SUBPH	0.079	0.330	-0.025	0.098	0.759
SUBTEM	-0.026	0.094	0.121	-0.249	0.796
SVL	0.821	0.488	0.306	0.216	-0.219
SUBHOH	-0.050	0.122	0.037	-0.735	-0.828
FOL	0.026	0.196	-0.023	-0.197	0.266

Table 9. Standardized discriminant function coefficients (di's) showing the relative contribution of the original variables to each discriminant function for the juvenile microhabitat plus size analysis.

	Discriminant Functions				
	I	II	III	IV	V
Percentage of among species variance	71.36	14.86	12.04	1.37	0.37
Cumulative percentage	71.36	86.22	98.26	99.63	100.00
Variables:					
SLOPE	-0.004	-0.839	-0.254	-0.100	-0.537
WIDTH	-0.090	-0.301	-0.112	-0.306	0.369
ELEVATE	0.090	-0.517	0.125	-0.449	0.447
DFHOH	-0.601	-0.224	0.896	0.436	0.120
SUBPH	-0.175	-0.310	0.036	0.930	0.717
SVL	0.687	-0.206	0.687	-0.057	-0.277

function, accounting for 5.99% of the variability, separated species by slope. The fourth and fifth discriminant functions accounted for only 2.43% of the relative variability, and therefore were not considered further.

Classification statistics for the adult salamanders are given in Table 10. Approximately 80% of all individuals were correctly predicted. Desmognathus aeneus, with 46 of 48 individuals (95.8%) was the most distinct species in the analysis. Desmognathus monticola, with 65 of 97 (67%) was the least distinct species. All species except D. monticola had greater than 80% correct classification.

In the analysis of the juvenile salamanders, the first three discriminant functions accounted for 98.26% of the relative variability. The first discriminant function, accounting for 71.36% of the variability, separated species on the basis of snout-vent length relative to distance from water. This function separated the small, terrestrial D. aeneus from the large, aquatic D. quadramaculatus. The second discriminant function, accounting for 14.86% of the relative variability, separated species on the basis of slope and elevation, placing the species with the highest mean slope, D. ochrophaeus, at one extreme of the axis and the relatively high elevation species D. aeneus at the other. The third discriminant function, accounting for 12.04% of the relative variability, separated species on the basis of distance from water and size, representing residual variation in these two variables given the effects of the first two discriminant functions. In this case, however, the sizes of the coefficients of the two variables were reversed. This separated the relatively large, terrestrial P. glutinosus from the smaller, semi-terrestrial D. ochrophaeus. As in the adults, the fourth

Table 10. Classification results of the discriminant analysis for adult salamanders using microhabitat variables plus size. Numbers in parentheses represent actual number of individuals placed in each group. Percent of all individuals correctly classified: 79.88.

		Predicted group membership					
Actual species	n	*Plethodon glutinosus*	*D. aeneus*	*D. ochrophaeus*	*D. fuscus*	*D. monticola*	*D. quadra-maculatus*
P. glutinosus	33	87.9(29)	0.0(0)	3.0(1)	3.0(1)	3.0(1)	3.0(1)
D. aeneus	48	0.0(0)	95.8(46)	4.2(1)	0.0(0)	0.0(0)	0.0(0)
D. ochrophaeus	73	9.6(7)	5.5(4)	82.6(60)	2.7(2)	0.0(0)	0.0(0)
D. fuscus	40	5.0(2)	2.5(1)	2.5(1)	80.0(32)	10.0(4)	0.0(0)
D. monticola	97	7.2(7)	0.0(0)	4.1(4)	11.3(11)	67.0(65)	10.3(10)
D. quadramaculatus	42	4.8(2)	0.0(0)	0.0(0)	0.0(0)	14.3(6)	81.9(34)

and fifth discriminant functions explained very little of the relative variability and were not considered further.

Classification statistics for the juvenile salamanders are given in Table 11. Two-thirds (66.67%) of all juveniles were correctly classified. Desmognathus aeneus, D. quadramaculatus, and P. glutinosus were the most distinct. Desmognathus monticola, with 29 of 65 (44.6%) correctly classified, was again the least distinct species.

Discussion: Microhabitat Plus Size

When snout-vent length was added to the analysis, it became the most important variable in separating both adults and juveniles. Figure 3 shows the locations of the centroids for adults of each species along the first two discriminant axes. Instead of a clustering of species into groups, there was almost a linear progression along the first discriminant axis, based primarily on size. The second discriminant function separated species along the aquatic to terrestrial gradient in reference to elevation. This served to separate the two most similar species along the first discriminant axis, D. fuscus and P. glutinosus.

Among the juveniles, the three terrestrial species in the first analysis were still moderately clustered (Fig. 4). The juvenile aquatic species separation was similar to that in the adults. The clustering of the three terrestrial species may have been due to either smaller sample sizes, as mentioned earlier, or may indicate the effects of different age classes within the juvenile classification. This is indicated by the fact that size was not as efficient in separating juveniles, since the first discriminant function included effects of distance from water as well as size.

Table 11. Classification results of the discriminant analysis for juvenile salamanders using microhabitat variables plus size. Numbers in parentheses represent actual number of individuals placed in each group. Percent of all individuals correctly classified: 66.67.

		Predicted group membership					
Actual species	n	Plethodon glutinosus	D. aeneus	D. ochrophaeus	D. fuscus	D. monticola	D. quadra-maculatus
P. glutinosus	8	100.0(8)	0.0(0)	0.0(0)	0.0(0)	0.0(0)	0.0(0)
D. aeneus	8	0.0(0)	100.0(8)	0.0(0)	0.0(0)	0.0(0)	0.0(0)
D. ochrophaeus	18	11.1(2)	0.0(0)	83.3(15)	5.6(1)	0.0(0)	0.0(0)
D. fuscus	13	7.7(1)	0.0(0)	0.0(0)	69.2(9)	23.1(3)	0.0(0)
D. monticola	65	4.6(3)	1.5(1)	10.8(7)	26.2(17)	44.6(29)	12.3(8)
D. quadramaculatus	17	0.0(0)	0.0(0)	0,0(0)	0.0(0)	0.0(0)	100.0(17)

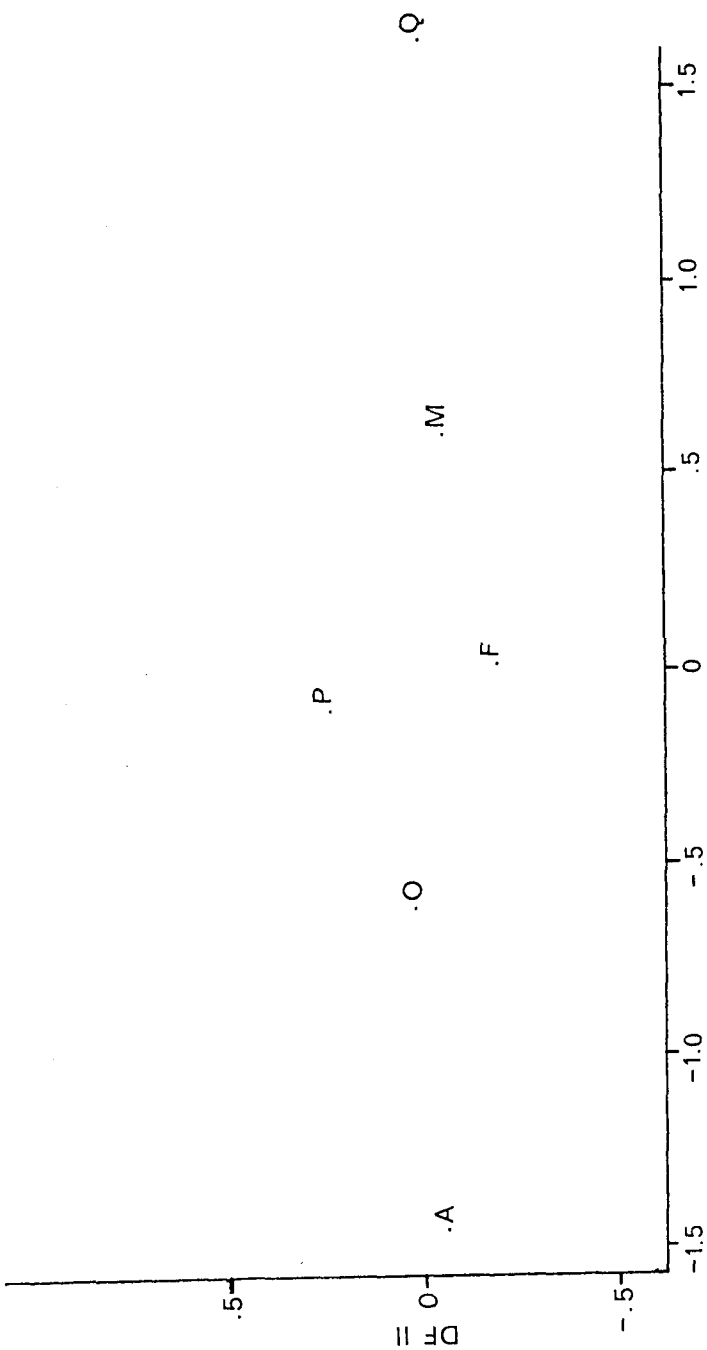

Figure 3. Centroids of species on the first two discriminant axes for the adult microhabitat plus size analysis. P - Plethodon glutinosus, A - Desmognathus aeneus, O - D. ochrophaeus, F - D. fuscus, M - D. monticola, Q - D. quadramaculatus.

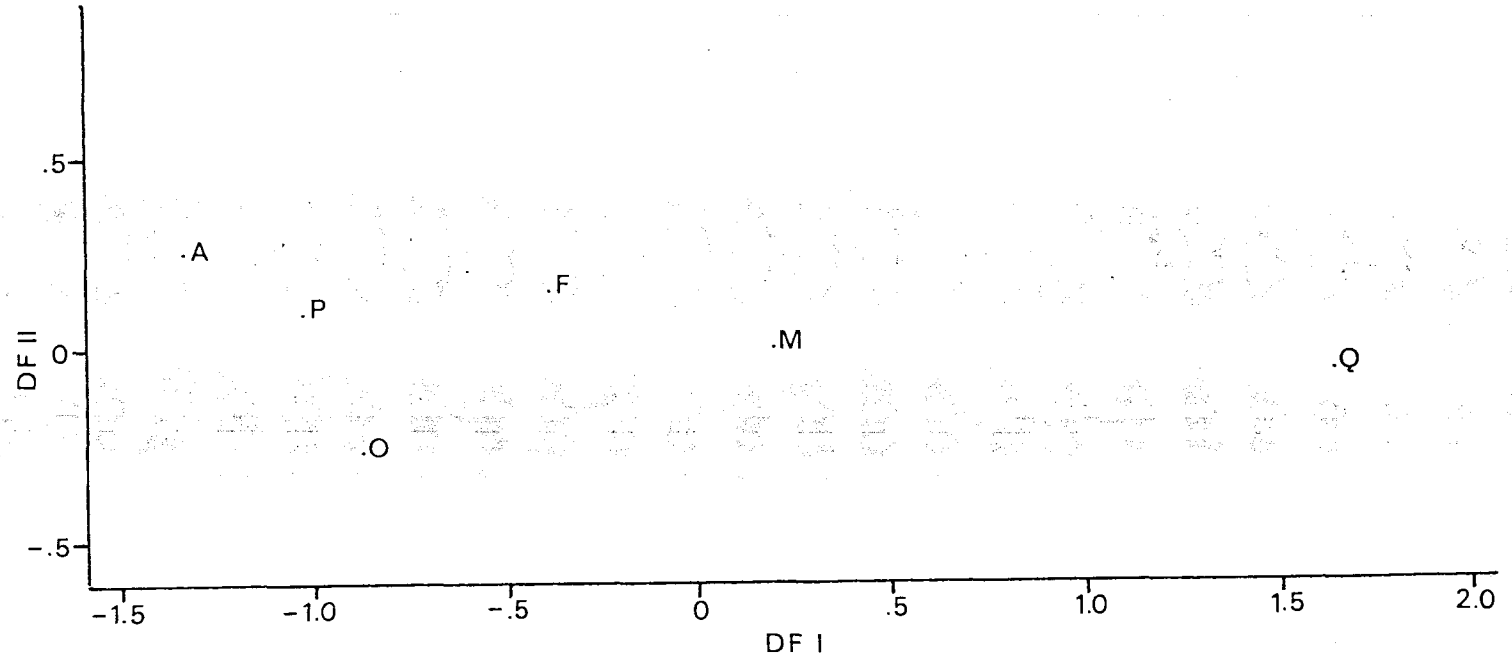

Figure 4. Centroids of species on the first two discriminant axes for the juvenile microhabitat plus size analysis. P - Plethodon glutinosus, A - Desmognathus aeneus O - D. ochrophaeus, F - D. fuscus, M - D. monticola, Q - D. quadramaculatus.

Classification statistics for adults (Table 10, page 36) indicate the effectiveness of separation when a size variable was included in the discriminant analysis. Five of the six species had greater than 80% of all individuals correctly identified. The greatest improvement of classification scores was for those species which were relatively indistinct when only microhabitat variables were considered. For example, the classification score for D. monticola improved from 26.8 to 67%, while P. glutinosus, the most distinct species in terms of microhabitat, improved by only 4.3%.

Size is probably related to resouce partitioning in terms of prey size selection. All of these species are carnivores, eating mostly invertebrates and occasionally other salamanders. Most references to salamander food habits indicate that salamanders are generalists in terms of prey taxa (Barbour and Lancaster, 1946; Burton, 1976; Fraser, 1976), but Hairston (1949) indicated differences in prey sizes among the species he examined in North Carolina.

The microhabitat and combined discriminant analyses indicate that for some species, such as P. glutinosus and D. quadramaculatus, the microhabitat variables measured are sufficient for separation. In other species, the addition of a size variable tends to improve separation. This may indicate partitioning of resources for some species in terms of space, and in others by food, if body size is strongly correlated with prey size.

Activity Analysis

Five of the six species included in the microhabitat analysis were also eaxmined in relation to activity period. Desmognathus

aeneus was not seen active on the surface during any part of either the microhabitat or activity sampling, even though areas where it was known to be abundant were sampled. Mount (1975) stated that this species apparently never leaves the leaf litter.

The results of the activity analysis are given in Table 12. The overall chi-square for significance of separation among species yielded $\chi^2 = 333.56$, which is significant at a probability level of .005 ($\chi^2_{.005,\ 10\ df} = 25.188$). Since aging the individuals was not possible without disrupting their activity, separation into adults and juveniles was not possible. In order to quantify degree of activity, each individual that was found to be 100% active was counted twice; those only 50% active were counted once.

The untransformed means and ranges of the activity variables are given in Table 13. The first discriminant function explained 68.76% of the among species variability. This discriminant function was largely a function of the effects of substrate temperature and humidity on activity of the five species included in the analysis. The second discriminant function accounted for an additional 29.11% of the relative variability among groups, and appeared to be measuring the effects of substrate temperature relative to the effects of humidity. The third discriminant function, accounting for the remaining 2.13% of the variability was a function of illumination.

The classification statistics (Table 14) indicated that only 41.67% of all observations were correctly predicted. The lowest scores were for D. fuscus, D. monticola, and D. quadramaculatus, each of which had less than 25% of its members correctly identified. The two highest

Table 12. Standardized discriminant function coefficients (di's) showing the relative contribution of the original variables to each discriminant function for the activity analysis.

	Discriminant Functions		
	I	II	III
Percentage of among species variance	68.76	29.11	2.13
Cumulative percentage	68.76	97.87	100.00
Variables:			
LIGHT	0.238	-0.209	-1.205
SUBTEMP	0.586	0.815	0.083
HUMIDITY	0.879	-0.752	-0.462

Table 13. Untransformed means and ranges (in parentheses) of activity variables for five salamander species. See text for explanations of variables.

Species	LIGHT	SUBTEMP(^{o}C)	HUMIDITY(%)
P. glutinosus	2.3(2-3)	17.7(14.5-20.0)	94.5(86-100)
D. ochrophaeus	3.7(1-9)	18.3(13.0-20.0)	92.8(53-100)
D. fuscus	4.1(2-9)	17.6(15.5-21.5)	88.5(80-100)
D. monticola	4.2(1-9)	18.3(13.0-21.0)	83.8(53-100)
D. quadramaculatus	4.1(2-9)	17.6(13.0-20.5)	87.9(75-100)

Table 14. Classification results of the discriminant analysis using activity variables. Numbers in parentheses represent actual number of observations placed in each group. Percent of all observations correctly classified: 41.62.

Actual species	n	Predicted group membership				
		Plethodon glutinosus	D. ochrophaeus	D. fuscus	D. monticola	D. quadra-maculatus
P. glutinosus	31	48.4(15)	9.7(3)	3.2(1)	38.7(12)	0.0(0)
D. ochrophaeus	493	14.0(69)	62.5(308)	0.0(0)	16.8(83)	6.7(33)
D. fuscus	64	26.6(17)	7.8(5)	21.9(14)	40.6(26)	3.1(2)
D. monticola	365	3.3(12)	41.9(153)	4.1(15)	26.8(98)	23.8(87)
D. quadramaculatus	186	11.8(22)	4.8(9)	29.6(55)	32.8(61)	21.0(39)

scores were for D. ochrophaeus, with 62.5% accurately predicted, and P. glutinosus, with a score of 48.4%.

Discussion: Temporal Partitioning

The time-related variables showed that the two most distinct species in terms of activity were P. glutinosus and D. ochrophaeus. These were also the two most terrestrial species in the activity analysis. Most of this distinctness was based on the first discriminant function, which was largely measuring activity in terms of relative humidity. Several studies have indicated that relative humidity was probably the most important microenvironmental factor affecting diel activity in salamanders (Barbour, et al., 1969; Heatwole, 1962; Orser and Shure, 1975). However, Sealy (1968) found that light was the primary factor influencing daily activity of D. monticola and D. ochrophaeus on a seepage area in South Carolina.

Hairston (1949) stated that relative humidity had more marked effects on two terrestrial species of Desmognathus than it did on the primarily aquatic D. quadramaculatus. The present study seems to support this, in that relative humidity was the most important variable in the discriminant analysis, and that the two most terrestrial species, P. glutinosus and D. ochrophaeus, were moderately predictable in terms of this variable.

If temporal partitioning occurred among the five species studied, then the levels of one of the three variables included should be correlated with activity periods for the five species. However, this did not appear to be the case. Percent of total activity vs. time since sunset for the five salamander species is shown in Figure 5. This

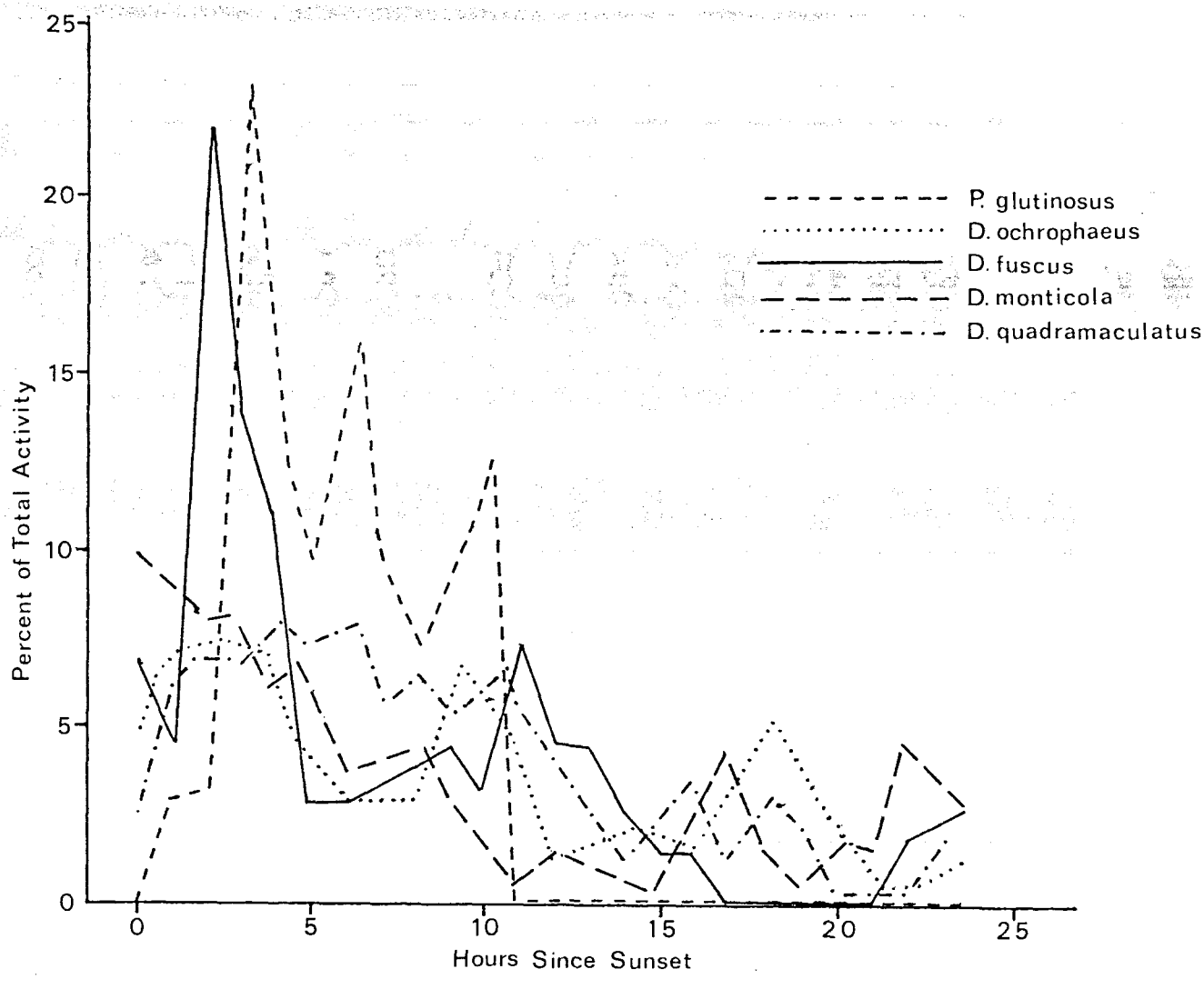

Figure 5. Activity patterns of the five salamander species.

figure indicates that all species were primarily nocturnal, and that extensive overlap in activity occurs for all species pairs. The peaks in activity for D. fuscus and P. glutinosus were probably due to small sample size rather than restricted activity periods, although P. glutinosus does seem to be totally nocturnal.

IV. GENERAL DISCUSSION AND CONCLUSIONS

Patterns of Resource Partitioning

This analysis of microhabitat indicates that a separation of species along environmental axes does occur, but that much overlap between species pairs is present. Diel activity patterns show that some species respond differently to certain environmental variables, but that overlap of activity periods is extensive for all species examined. This does not support Schoener's (1974) contention that terrestrial poikilotherms frequently partition time on a daily basis as a result of their sensitivity to diel weather variation. However, seasonal activity patterns may help to alleviate potential competition between species, as indicated by Fraser (1976) for P. punctatus and P. hoffmani. Life history data indicate that there is at least some variation in time of egg production and nesting among species of Desmognathus (Organ, 1961) which may indicate seasonal differences in activity.

Both Hairston (1949) and Organ (1961) found zones of salamander distribution in relation to streams, as well as elevational replacement between species. Although elevational differences in distribution occurred in the study area, the limited range of elevations and sites sampled does not permit definitive statements regarding this variable. For example, P. glutinosus was found primarily at the higher elevations in the study area (Table 1, page 18). One reason for this may be that

many of the low elevation samples were through areas with a substantial growth of various Pinus species. The presence of these trees indicates relatively xeric conditions. This plus the fact that pine needles apparently provide little in the way of adequate salamander shelter probably indicates that the sample sites were not suitable for P. glutinosus, rather than the absence of this species at low elevations. This study does support Hairston's and Organ's data on stream zone distribution, but indicates extensive overlap between species pairs. Some species, notably P. glutinosus and D. quadramaculatus, are apparently more isolated in terms of space than are others, such as D. monticola, which shows extensive overlap with D. fuscus and D. quadramaculatus. This stream zone distribution was thought to be a function of a physiological tolerance to desiccation (Hairston, 1949). If this were actually the case, then it was hypothesized that soil moisture content might be a critical resource in terms of microhabitat partitioning. However, after the study was completed, it was found that percent soil moisture was not sufficient for predicting salamander distribution unless soil mositure tension curves are also obtained (Spight, 1967).

Other studies of salamanders (Burton, 1976; Dumas, 1956; Fraser, 1976; Hairston, 1949) indicated that food partitioning occurred among the species considered, although the effectiveness of this partitioning in separating species was not indicated. Burton (1976) stated that food partitioning was related to a gradation in size among six species of salamanders in New Hampshire. The present study indicates that if food size is related to body size, then partitioning may occur, since the addition of a body size variable to the microhabitat variables led

to a much better separation of species. An analysis of the stomach contents of the salamanders collected should help to clarify matters.

If, as speculated above, food partitioning is important to salamanders, the greatest effects should be among the three more aquatic species, since microhabitat overlap is more pronounced among them than in the more terrestrial species. Organ (1961) felt that competition among D. fuscus, D. monticola, and D. quadramaculatus led to exclusion of D. fuscus whenever D. monticola and D. quadramaculatus occurred together. In this study, D. monticola and D. quadramaculatus were found in all samples that contained D. fuscus, but, where D. fuscus was found, it was more common than either of the other two species. The distribution of D. fuscus in the study area is problematic, since it was generally limited to below 500 meters elevation. However, populations at 530 meters and in a seepage area at 980 meters were found. This may indicate that relatively intense competition among the three relatively aquatic species of Desmognathus is occurring.

A logical question at this point is why should only partial species separation occur when microhabitat is considered, while a much greater separation occurs when a food related variable is added, assuming that salamander size is actually related to food size. Schoener (1974) found that, for a variety of animal species, partitioning of habitat was important more often than food partitioning, which was important more often than temporal partitioning. The likelihood of habitat partitioning relative to food partitioning was explained using the MacArthur-Pianka (1966) foraging-strategy model. Briefly, competition would change the value per-unit-time of feeding in different habitats

once they were entered, but would not affect the value per-unit-time of eating food types once they were found. This was thought to indicate that habitat partitioning would occur before food partitioning. Another factor suggested dealt with the way habitat and food are distributed in space and are encountered by consumers. If an individual was too selective in its foraging it would lose too much energy and time in searching relative to its energy intake. Macrohabitats are more continuously distributed than food and are large relative to an individual's ability to range through them. Therefore, an individual could possibly spend most of its time in a single macrohabitat. This was suggested as indicating that when it became impossible to further partition food macrohabitat partitioning would still be possible.

If food partitioning is more important than habitat partitioning among the salamander species studied, then this may be a reflection of physiological constraints on habitat partitioning in these amphibians. Several studies (Littleford, et al. 1947; Spight, 1968; Spotila, 1972) have indicated that water loss rates are important to salamander survival, and, in effect, these species are limited in their distributions by the availability of water as a critical resource. As shown earlier, a certain degree of habitat partitioning did occur, which appeared to be related to water availability. However, this was apparently not sufficient for a complete separation of species, as indicated by the classification analyses. Further species separation and coexistance may only be possible if some other resource is partitioned. Temporal partitioning appears to be uneconomical in many respects, since it involves trading what would be a small energy gain in the time period utilized by competitors for no yield at all, if these periods are

avoided (Schoener, 1974). Among these six salamander species, it would probably require that some become primarily diurnal, exposing them to diurnal predators and to a greater physiological stress in terms of water loss, since relative humidity is lower in the study area during the daylight hours (pers. obs.). Food then is the major resource type remaining that may be partitioned.

Other Factors

In studies of resource partitioning in vertebrates with long development times, the problem of different size classes and interspecific competition has been given little attention. Fraser (1976) addressed this problem, indicating that adults of P. hoffmani and juveniles of P. punctatus could possibly compete for food. He further speculated that differences in seasonal activity probably helped to reduce this competition. In this study, the analysis of juveniles and adults of each species indicated a general similarity in microhabitat requirements, although differences are evident and may stem in part from the small sample sizes for juveniles. Whether the smaller size classes of larger species compete with adults of smaller species is not known. Another aspect of competition concerning different life history stages is larvae competition. Two of the species studied, P. glutinosus and D. aeneus, have completely terrestrial development. The remaining four have aquatic larvae stages. Competition between larvae of these four species may be more important than competition in adults, since development occurs in a spatially restricted part of the environment. Rates of development of the larvae of the four species

differ, as shown by Organ (1961); however, data on competition for food and space is lacking.

Predation was not examined in this study, but its effects on resource utilization may be of some importance. On several occasions, superficial examination of salamander stomach contents revealed the presence of salamander remains. On other occasions, smaller salamanders were eaten by larger ones when both were kept in the same collecting bag. Predation by other salamanders may be more important than competition in influencing the distribution of some salamander species, as implied by Organ (1961) for D. wrighti, another small, terrestrial species of Desmognathus. The fact that D. aeneus apparently remains within the leaf litter most of the time also supports this, since surface foraging would mean greater exposure to predators, including other salamanders. Predator pressure may also explain the tendency for large populations of D. ochrophaeus to occur on rockfaces, which do not appear to be readily accessible to some of the larger salamander species.

In conclusion, distinct resource partitioning did not appear to occur among the salamander species represented in this study. Predation, age class differences, and physiological factors may all contribute to the observed relationships among the six species. The ecological relationships among these species may be more complex than previously imagined, due to the interactions of several factors rather than to the effects of any single factor.

differ, as shown by Organ (1961); however, data on competition for food and space is lacking.

Predation was not examined in this study, but its effects on resource utilization may be of some importance. On several occasions, superficial examination of salamander stomach contents revealed the presence of salamander remains. On other occasions, smaller salamanders were eaten by larger ones when both were kept in the same collecting bag. Predation by other salamanders may be more important than competition in influencing the distribution of some salamander species, as implied by Organ (1961) for D. wrighti, another small, terrestrial species of Desmognathus. The fact that D. aeneus apparently remains within the leaf litter most of the time also supports this, since surface foraging would mean greater exposure to predators, including other salamanders. Predator pressure may also explain the tendency for large populations of D. ochrophaeus to occur on rockfaces, which do not appear to be readily accessible to some of the larger salamander species.

In conclusion, distinct resource partitioning did not appear to occur among the salamander species represented in this study. Predation, age class differences, and physiological factors may all contribute to the observed relationships among the six species. The ecological relationships among these species may be more complex than previously imagined, due to the interactions of several factors rather than to the effects of any single factor.

LITERATURE CITED

LITERATURE CITED

Afifi, A.F. and S.P. Azen. 1972. Statistical Analysis: A Computer Oriented Approach. Academic Press, New York. 366 p.

Avery, R.A. 1968. Food and Feeding relations of three species of Triturus (Amphibia, Urodela) during the aquatic phase. Oikos 19: 408-412.

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

Barbour, R.W., J.W. Hardin, J.P. Shafer, and M.J. Harvey. 1969. Home range, movements, and activity of the dusky salamander Desmognathus fuscus. Copeia 1969:263-279.

Bishop, S.C. 1947. Handbook of Salamanders. Comstock Press, New York. 555 p.

Brown, W.C. and S.C. Bishop. 1947. A new species of Desmognathus from North Carolina. Copeia 1947:163-166.

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

Cody, M.L. 1974. Competition and the Structure of Bird Communities. Princeton Univ. Press, Princeton. 318 p.

Conant, R. 1975. A Field Guide to Reptiles and Amphibians of Eastern and Central North America. Houghton Mifflen Co., Boston. 429 p.

Cooley, W.W. and P.R. Lohnes. 1971. Multivariate Data Analysis. Wiley, New York. 364 p.

Crump, M.L. 1974. Reproductive strategies in a tropical anuran community. Univ. Kansas Mus., Misc. Publ. 61.

Dumas, P. 1956. The ecological relations of sympatry in Plethodon dunni and P. vehiculum. Ecology 37:484-495.

Elton, C.S. 1927. Animal Ecology. Sidgwick and Jackson, London. 209 p.

Fraser, D.F. 1976. Coexistance of salamanders in the genus Plethodon: A variation of the Santa Rosalia theme. Ecology 57:238-251.

Grant, P.R. 1972. Interspecific competition among rodents. Ann. Rev. Ecol. Syst. 3:79-106.

Green, R.H. 1971. A multivariate statistical approach to the Hutchinsonian niche: Bivalve molluscs of central Canada. Ecology 52:543-556.

Hairston, N.G. 1949. The local distribution and ecology of the plethodontid salamanders of the Southern Applachians. Ecol. Monogr. 19:47-73.

Harrison, J.R. 1967. Observations on the life history, ecology, and distribution of Desmognathus aeneus aeneus. Brown and Bishop. Amer. Midl. Nat. 77:356-370.

Heatwole, H. 1962. Environmental factors influencing local distribution and activity of the salamander Plethodon cinereus. Ecology 43:460-472.

Heyer, W.R. 1976. Studies in larval amphibian habitat partitioning. Smithsonian Contr. Zool. 242.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22:746-759.

Inger, R.F. and B. Greenburg. 1967. Ecological and competitive relations among three species of frogs (genus Rana). Ecology 47:746-759.

Jaegar, R.G. 1971. Moisture as a factor influencing the distribution of two species of terrestrial salamanders. Oecologia 6:191-207.

Jaegar, R.G. 1974. Interference of exploitation? A second look at competition between salamanders. J. Herpetology 8:191-194.

Klecka, W.R. 1975. Discriminant Analysis. In H.H. Nie, et al. (eds) SPSS Manual, second Ed. McGraw-Hill, New York.

Littleford, R.A., W.F. Keller, and N.E. Phillips. 1947. Studies on the vital limits of water loss in the plethodont salamanders. Ecology 28:440-447.

MacArthur, R.H. 1972. Geographical Ecology. Harper and Row, New York. 267 p.

MacArthur, R.H. and E.R. Pianka. 1966. On the optimal use of a patchy environment. Amer. Natur. 100:603-609.

Malter, J.L. 1977. The flora and wilderness history of Citico Creek Nature Study Area, Cherokee National Forest, Monroe County, Tennessee. Unpubl. Master's Thesis, Univ. of Tennessee, Knoxville.

Martof, B.S. and R.L. Humphries. 1955. Observations on some amphibians from Georgia. Copeia 1955:245-248.

Means, D.B. 1975. Competitive exclusion along a habitat gradient between two species of salamanders (Desmognathus) in western Florida. J. Biogeography 2:253-263.

Mount, R.H. 1975. The Reptiles and Amphibians of Alabama. Auburn Univ. Ag. Exp. Sta. 347 p.

Organ, J.A. 1961. The local distribution, life history, and population dynamics of the salamander genus Desmognathus in Virginia. Ecol. Monogr. 37:189-220.

Orser, P.N. and D.J. Shure. 1975. Population cycles and activity patterns of the dusky salamander, Desmognathus fuscus fuscus. Amer. Midl. Nat. 93:402-410.

Pianka, E.R. 1969. Sympatry of desert lizards (Ctenotus) in Western Australia. Ecology 50:1012-1031.

Pianka, E.R. 1973. The structure of lizard communities. Ann. Rev. Ecol. Syst. 4:53-74.

Rao, C.R. 1952. Advanced Statistical Methods in Biometrical Research. Wiley, New York. 390 p.

Schoener, T.W. 1968. The Anolis lizards of Bimini: Resource partitioning in a complex fauna. Ecology 49:704-726.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science 185:27-39.

Sealy, R.M. 1968. Factors influencing activity of two species of the salamander genus Desmognathus. Unpubl. Master's Thesis, Clemson Univ.

Sokal, R.R. and F.J. Rohlf. 1969. Biometry. W.H. Freeman Co., San Francisco. 776 p.

Sokal, R.R. and P.H.A. Sneath. 1963. Principles of Numerical Taxonomy. W.H. Freeman Co., San Francisco. 359 p.

Spight, T.M. 1967. The water economy of salamanders: Exchange of water with the soil. Biol. Bull. 132:126-132.

Spight, T.M. 1968. The water economy of salamanders: Evaporative water loss. Physiol. Zool. 41:195-203.

Spotila, J.R. 1972. Role of temperature and water in the ecology of lungless salamanders. Ecol. Monogr. 42:95-125.

Tilley, S.F. 1973. Desmognathus ochrophaeus. Cat. Amer. Amphib. Rept. 129.1-129.4.

VITA

Robert L. Jones was born in Louisville, Kentucky on October 13, 1951. He attended elementary schools in Harrison County, Indiana and was graduated from South Central High School in June 1969. The following September he entered Indiana University, and in May, 1973 received a Bachelor of Arts degree in Zoology.

After working in a chemical plant in Louisville, Kentucky for fifteen months, the author entered the Graduate School of The University of Tennessee, Knoxville, in September, 1974. He received the Master of Science degree with a major in Ecology in August, 1977.