POPULATION AND BIOMASS

ESTIMATES IN FOUR SPECIES

OF TERRESTRIAL PLETHODONTID SALAMANDERS

A Thesis

by

THAD ALAN HOWARD

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POPULATION AND BIOMASS

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ABSTRACT

POPULATION AND BIOMASS ESTIMATES IN FOUR SPECIES OF TERESTRIAL PLETHODONTID SALAMANDERS

(May 1987)

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In areas such as the Appalachian Mountains of North Carolina, woodland habitats provide a rich area for terrestrial, woodland salamanders of the Family Plethodontidae. To understand the relative abundance and biomass present, three separate but related studies were conducted: 1) a regeneration study, 2) an ecological study, and 3) a biomass determination.

A laboratory study of toe regeneration showed that toe clipping was acceptable for marking salamanders for a 13 week period since, even with regeneration, at least 95% of clipped toes could be identified with confidence. The 13 week time period was suitable for a mark recapture study taken over one active season. Toe nail clippers removed

toes quickly, accurately, and did not promote necrosis.

Population estimates were determined for Desmognathus ochrophaeus, Plethodon cinereus, Plethodon jordani, and Plethodon yonahlossee by harvest census, repeat census, and by two mark recapture techniques. Harvest census estimates ranged from 63 to 275 animals per quadrat (each 625 m^2) for a mean total of 3,052 per hectare. Repeat census estimates ranged from 307 to 508 animals per quadrat for a mean total of 6,560 per hectare. Mark recapture data were projected using the Schnabel and Schumacher methods. These methods were confined to a 15 week time period because salamanders can regenerate toes. Estimates were derived for Desmognathus ochrophaeus and Plethodon jordani only. Estimates for Desmognathus ochrophaeus ranged from 261 to 2,338 per quadrat. Values were not determined in two quadrats due to lack of recaptures. Estimates for Plethodon jordani were from 183 to 515 per quadrat. The combined means from both methods provided an estimate of 22,608 salamanders per hectare for the two species.

Total biomass, wet weight biomass, dry weight biomass, and calories were calculated for each species and for each population estimate. Total wet weight biomass ranged from 3.44 kg (Harvest Method) to 27.7 kg (Schnabel Method) per hectare. Total dry weight biomass ranged from 0.66 kg (Harvest Method) to 6.16 kg (Schnabel Method) per hectare.

Regressions for predicting wet weight biomass and dry weight biomass were slightly lower than actual values but were significant at the $P < 0.05$ level. Caloric content was projected from dry weight biomass estimates and the literature value of 5,176 calories per gram dry weight biomass given by Burton and Likens (1975a). Projected values ranged from 3.41 to 31.89 million calories per hectare and are much higher than any yet reported.

ACKNOWLEDGEMENTS

I would like to thank all those who encouraged and endured my studies while attending Appalachian State University. A special thanks to my Thesis Chairman, Dr. R. Wayne Van Devender, for the resources and hours of patience and guidance. Thanks also go to Dr. Mary Connell and Dr. Richard Henson for advice and care when I needed a hand and guidance in preparing this paper. Thanks go to Dr. Deanna Bowman who taught me the tedious, yet important, statistical analysis of data. I am grateful to Mr. and Mrs. Ed Hardy for use of their land and to Dr. Matthew Rowe, Jay Loftin, Heber Pittman, George Garrett, and Collette Tan for assistance in the field work.

DEDICATION

Words cannot express my love and gratitude to Mr. and Mrs. Julius F. Howard for their love, guidance, and support.

Please accept this dedication as a token of my gratitude.

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INTRODUCTION

Salamanders are abundant, diverse, and ubiquitous in the Appalachian Mountains; yet very little is known about their actual density and ecological importance in local communities or ecosystems. A better understanding of the role of these animals depends on knowledge of numbers present in an area and their energy content. The present study integrates field and laboratory data to obtain information on four species of terrestrial salamanders: *Desmognathus ochrophaeus*, *Plethodon cinereus*, *Plethodon jordani*, and *Plethodon yonahlossee*. Data were collected near Boone, Watauga County, North Carolina. This information is presented in four major segments. Relevant published information is reviewed. A laboratory study of the effectiveness of toe clipping as a salamander marking technique is presented. Harvest census, repeat census, and mark recapture data for estimates of population size are presented and compared. Laboratory analyses of mean salamander size, wet weight, and dry weight were used to project standing crop biomass and caloric content of salamander populations.

REVIEW OF LITERATURE

General

The Appalachian Mountains were the probable site of origin and radiation of the highly diverse Family Plethodontidae. Distribution of salamanders in the Family Plethodontidae have been reviewed for the eastern United States and Canada (Dunn, 1926; Conant, 1975), all of North America (Bishop, 1962), and for the Genus Plethodon in the eastern United States and Canada (Grobman, 1944; Highton, 1962b). Speciation in the Genus Plethodon was reviewed for North America (Hairston and Pope, 1948) and the Appalachian Mountains (Hairston, 1951, 1980). Elevation ranges for salamanders found in Watauga County, North Carolina were reported by Williams (1983).

Life history studies usually include estimates of population size, distribution, and interactions. These should serve as a basis for future studies such as community or behavioral ecology. Results of life histories studies have been reported for Desmognathus ochrophaeus (Tilley, 1980), Plethodon cinereus (Nagel, 1977), Plethodon glutinosus (Highton, 1956, 1962),

Plethodon glutinosus and Plethodon jordani (Hairston, 1980), Plethodon yonahlossee (Harris, 1981), and Notophthalmus viridescens (Healy, 1974; Gill, 1978). In forest communities species composition and observed density can be influenced by weather conditions. Gordon et al. (1962) described these influences on harvest size by day time and by seasonal activity for several plethodontid salamanders. Wells and Wells (1976) described movements of Plethodon glutinosus within a population. Taub (1961) described distribution of Plethodon cinereus in a soil profile.

Regeneration

An important component in a mark recapture study is the ability to recognize a mark on subsequent sample periods. Several marking techniques for amphibians and reptiles are described and discussed by Ferner (1979). One such technique is toe clipping, which has been used extensively in small mammal and reptile studies. However, its use with amphibians has been limited by their ability to regenerate tails, limbs, feet, and toes. A review by Hay (1966) describes several earlier limb regeneration studies (Hay, 1961; Rose, 1944). Heatwole (1961) reports controlling regeneration in Plethodon cinereus with beryllium nitrate. Efford and Mathias (1969) show inconclusive evidence of inhibition of regeneration and note that beryllium nitrate is carcinogenic to humans. Short term studies that have included toe clipping were a two week study with Plethodon cinereus (Klein, 1960), a seven month study of Plethodon cinereus and Desmognathus fuscus (Heatwole, 1961), and a six week study of Desmognathus ochrophaeus and Desmognathus fuscus (Hall, 1976). Highton (1956) reports a female Plethodon glutinosus was recaptured one year after marking. Other ways of marking salamanders include branding (Taber et al., 1975), freeze branding (Daugherty, 1976), and photographs (Hagstrom, 1973; Tilley, 1980). None of these seemed acceptable for the species studied here.

Ecological Studies

Two population parameters addressed in this study were size and biomass estimates. Early population studies used census or destructive harvest methods. Burger (1935) reports that 600 square yards may contain 100 or more red-backs, Plethodon cinereus. Test and Bingham (1948) using a repeat census found a density of one Plethodon cinereus per 21 square meters in Michigan. Jaegar (1969) used a repeat surface census after rainfall and found 2,100 to 2,500 Plethodon cinereus per hectare in Virgina. Plethodontid salamanders studied by mark recapture methods

include Plethodon cinereus (Klein, 1960; Merchant, 1972; Burton and Likens, 1975), Desmognathus ochrophaeus (Tilley, 1980), and Plethodon glutinosus (Semlitsch, 1980).

A variety of methods has been published for mark recapture studies. Lincoln (1930) expanded Peterson's (1896) method to form the original Lincoln-Peterson Index as described by Caughley (1977). The Lincoln-Peterson Index is a ratio of marked and nonnmarked individuals after a single marking period. Variations that have been developed include the Schnabel Method (Schnabel, 1935 as revised by Seber, 1973 and Ricker, 1975) and the Schumacher Method (Schumacher and Eschmeyer, 1943). Both methods employ multiple mark recapture samples to increase the number of recaptures and precision of the estimates. Clarifications of standard error, standard deviations, and confidence intervals for both methods were discussed by Seber (1973), Brower and Zar (1977), Caughley (1977), and Tanner (1978).

Biomass

Salamanders may play an important role as an energy resource in the forest community. The most extensively studied forest in reference to biomass, productivity, and energy flow has been the Hubbard Brook Ecosystem in New Hampshire. Studies include forest biomass and productivity

(Whittaker et al., 1974), herbaceous layer (Siccama et al., 1970), and atom or element flow as well as budgets in a deciduous forest (Likens et al., 1967). Limited data for fauna have been reported for birds (Holms and Sturges, 1973; Sturges et al., 1974), small mammals (Potter, 1974), and salamanders (Burton and Likens, 1975a,b).

Burton and Likens (1975b) estimated 2,950 salamanders per hectare and 1,770 grams wet weight biomass of salamanders per hectare in the Hubbard Brook forest. These values were about twice those for birds and approximately equal to small mammals in the same area. In another paper, Burton and Likens (1975a) estimated about 10,588 kcal per hectare per year of energy flow through salamanders. This represented approximately 0.02% of the total net primary productivity. Boyd and Goodyear (1971) listed the protein content, a potentially important biological attribute, for 23 species of reptiles and amphibians. The average for all species measured was 74.7% with ranges between 62.6% and 83.2% of dry weight biomass.

Several factors have been shown to influence biomass composition. Crump (1979) compared energy parameters of different age structures in Plethodon cinereus and observed that digestive efficiency did not differ significantly between age classes nor between males and nongravid females but did between gravid females and males. Crump (1979)

also found that water content decreased in percent with age, while ash content increased. Mean water content ranged from 80.1% to 84.7% of wet weight and mean ash content ranged from 9.8% to 13-14% of dry weight.

Burton and Likens (1975a) described energy flow through salamanders in the Hubbard Brook ecosystem. Salamanders appear to be more efficient than birds or mammals at incorporating protein and biomass. Since salamanders have restricted home ranges, they should not move biomass or nutrients into or out of an area. Burton and Likens (1975a) suggested that salamanders act as a sink for sodium but not for nutrients such as calcium, magnesium, potassium, phosphate, nitrogen, sulfur, and zinc. Thus, salamanders should be important food sources for predators.

MATERIALS AND METHODS

Regeneration

Plethodon glutinosus was used to study regeneration patterns following toe clipping. Two groups of salamanders were collected: 1) 21 animals from Powder Horn Mountain, Watauga County, North Carolina (34°37'91"N, 78°36'04"W) on 13 October and 9 November 1983; and 2) 28 salamanders from the Cape Fear River floodplain, Bladen County, North Carolina (36°10'18"N, 81°30'19"W) on 17 January 1984. Salamanders were housed in groups of two to four in plastic shoe boxes at Appalachian State University and fed a diet of mealworm larvae. Cages were cleaned weekly.

Fourteen toes on each salamander were suitable for clipping. A maximum of five toes per salamander and two toes per foot were clipped. In group one toes were amputated with a scalpel. Fingernail clippers were used on group two. In group one 81 toes were removed. Toes on the left side were cut transversely while those on the right were cut at an angle of 45° to determine if regeneration was affected by the angle of cut. In the second group 108 toes were clipped transversely. Toes were clipped in unique combinations for salamander identification. Weekly

observations were made on each toe as to appearance and progress in regeneration. Regeneration was monitored over a 20 week period. Afterwards, all surviving animals were anesthetized in 20% chlorotone, fixed in 10% formaldehyde, and stored in 70% ethanol in the vertebrate collection at Appalachian State University.

Ecological Studies

A study area was established on the north slope of Howards' Knob along a private road 1.6 to 1.9 miles west of N.C. 194 junction with secondary road #1318 and 0.9 miles south of secondary road #1318. The site was also 2.05 airline miles NNW from Boone City Hall, Watauga County, North Carolina. The study area was on a wooded hillside with moderate northerly slope at elevations between 3,875 feet (1,413m) and 4,125 feet (1,504m). Elevation was measured with an altimeter and checked against Boone 7.5 minute U.S.G.S. Topographic Map. No seepages were visible near each site. Four 625 meter^2 quadrats were set up between March and May of 1984 in the study area. Each quadrat was laid out, marked by a string around the periphery, and subdivided into 25 meter^2 subplots by reflective flags. Location of vegetation, trees, logs, debris, and exposed rocks was mapped in all quadrats. Importance values for canopy and subcanopy genera were determined using density, frequency, and tree girth (Krebs, 1978).

All salamander collections were made on warm, wet nights from early May until mid-November 1984. Each grid was searched systematically for surface active salamanders with a Wheat rechargeable headlamp. Animals were identified using Conant's (1975) field guide. Presence of mental gland or enlarged eggs allowed sex recognition of most animals. Measurements recorded for each salamander were snout to vent length (SVL in mm), snout to tail length (TL in mm), weight (grams), location of capture, and sequence of toes already marked or to be marked. Weight was obtained with a Pesola spring balance accurate to 0.1 grams in previously weighed Ziplock bags. Each salamander was marked in a specific sequence using nail clippers. Toes were reclipped on later observations if needed. When salamanders were abundant, those in a small area were bagged first and processed as a group to save time and to prevent escapes. Animals were usually released at site of capture within five to ten minutes. Four to six hours were required to search each quadrat. If a quadrat was not completed in one evening, it was finished the following evening. Whenever possible, all sites were sampled within 10-14 days. Each quadrat was sampled six to eight times. Climatological data were provided by the National Weather

Service's, Boone Substation and compared to data taken in the field.

Capture and recapture data were used to develop matrices and were analyzed by the Schnabel (Tanner, 1978) and Schumacher (Caughley, 1977) methods for population estimate. The Schnabel Method was based on the sum of the product of individuals marked and individuals captured divided by the sum of individuals recaptured (Appendix 1, equation 1). Ricker (1975) developed a formula for estimating the variance (s^2) of the population estimate ($\hat{N}$) based on its reciprocal (Appendix 1, equation 2). Seber (1973) also presented an equation for the standard error of the population estimate (Appendix 1, equation 3). Standard errors of ($1/\hat{N}$) were used to obtain 95% confidence intervals for the population estimates. Tanner (1978) gave descriptions and examples for each formula.

The Schumacher Method (Schumacher and Eschmeyer, 1943) also provided population estimates. It differed in being more dependent on the number of marked individuals recaptured. Estimates were calculated as the product of the sum of marked individuals (squared) and total captures divided by sum of the product of numbers of individuals marked and recaptured (Appendix 2, equation 4). The Schumacher Method also provided estimates of standard error and variance. The standard error (SE) of the estimate was calculated using the reciprocal of the population estimate (Appendix 2, equation 5). The standard error calculation was based on the standard deviation of the mean. The variance was based on equation 6 in Appendix 2.

Harvest censuses and repeat censuses gave absolute minimal population estimates for each quadrat. The three population estimates were used to extrapolate wet and dry biomass for each species and to predict total calories per hectare.

Biomass

The final sample in each quadrat was a destructive search of the entire leaf litter as well as under rocks and logs. Animals were stored in a refrigerator and processed within 12 hours. Salamanders were anesthetized in a 20% saturated solution of chlorotone, placed in freezer bags with water, and frozen for later analysis. These animals were used for both population estimation and biomass determination. Bags of specimens were thawed and processed separately. Each specimen was identified to species and sex, measured (SVL and TL), and weighed on a Ohaus Brainweigh B 1500 balance accurate to +/- 0.01g. Specimens were dried at 105 degrees Celsius in an oven for seven days. Dry specimens were removed, cooled in a desiccator, and weighed on a Mettler H-20 analytical balance to within

+/- 0.00001g. Salamanders were stored individually in vials. To reduce measurement error, salamanders with dry masses within +/- 0.001g were pooled (n = 2 to 5) for ash determination. Ash samples were burned in a muffle furnace at 600 degrees Celsius for one hour. Temperatures were monitored using a Fluke 77 multimeter and a nickel-chromium vs copper-nickel thermister. Microvolts were converted into degrees Celsius using an Omega reference table. Ash samples were removed, cooled in a desiccator for one hour, and weighed. Crucibles were cleaned using 6-molar HCL, rinsed in distilled water, dried for 24 hours in a drying oven, and stored in a desiccator.

Least square regressions were calculated separately for each species and within each quadrat for the following variables: SVL to wet weight, SVL to dry weight, wet weight to dry weight, dry weight to organic weight, and dry weight to ash free dry weight. Log natural transformations of data were used to test for linearity of regressions as described by Draper and Smith (1966). Regression calculations provided y-intercepts, slopes, and r^2 values. These regressions were used to develop formulae to predict wet weight biomass and dry weight biomass from a given SVL or wet weight of any common salamander in the study areas. Mean values for SVL and wet weight were calculated for all salamanders handled. Mean dry weight values were determined for salamanders collected in harvest samples only. These values were used to project total dry weight biomass per study area and hectare using each of the three population estimates.

Total dry weight biomass was used to project calories using the value 5,176 calories per gram dry mass (Burton and Likens, 1975b). Total calories per quadrat and hectare were compared with other published values.

Statistical tests were carried out using alpha values of $P < 0.05$ for significant (*) and $P < 0.01$ for highly significant (**) differences. Primary statistial sources were Draper and Smith (1966) and Steel and Torrie (1960).

RESULTS

Regeneration

Regeneration has often been considered an obstacle to marking salamanders and frogs since a mark must be permanent or identifiable over the sample period. The pilot study allowed recognition of marked toes throughout the regeneration process and provided a time schedule for use in a mark recapture study.

Several stages of regeneration were identified. Salamanders reacted very little when toes were removed, and little bleeding was observed. Within three days, the wound was closed over and a blastema developed at the site of injury. The blastema was a colorless, opaque ball of undifferentiated cells from which a new toe could develop. As toes regenerated, the colorless tissue elongated. Finally, pigmentation developed along the new digit. Once coloration was complete, identification was difficult if toes were normally shaped. Toes were considered as recognizably marked until pigmentation had returned.

Some toes in each group regenerated rapidly, but most toes were still incomplete after as many as 13 weeks

(Table 1). The first fully regenerated toes were noted on week eight in group one and on week three in group two. At least 95% of the marked toes were identifiable through week eight in group one and at the end of week 13 in group two.

Results from the two groups were somewhat different. In group one sample size was considered too small after six salamanders were lost by week six. These losses were attributed to necrosis and housing complications. On week eight the regeneration of the first toe reduced recognition below 95%. Additional toes were lost by necrosis which resulted in animal stress, limb loss, and animal loss. These conditions did not represent normal conditions for regeneration. Necrosis moved up the digit, on to the foot, and then up the arm. In all cases the animal died if necrosis reached the foot. Necrosis had several possible sources including: improper housing, intraspecific aggression by larger salamanders, and the marking procedure. In group two a larger sample size was maintained. Several possible reasons for this difference were: 1) cleaner, quicker amputation using nail clippers, 2) improved husbandry from experience, and 3) reduced crowding since animals were maintained in smaller groups. Toe recognition remained above 95% recognition through week 13 in group two. Proportion of marked toes recognizable

TABLE 1. Recognition of Toe Regeneration in the Salamander <u>Plethodon glutinosus</u>.

WEEK #	GROUP 1				GROUP 2			
	N	R	M	R/M	N	R	M	R/M
1	18	81	81	100	27	108	108	100
2	18	81	81	100	27	108	108	100
3	18	81	81	100	26	103	104	99
4	17	76	76	100	26	103	104	99
5	15	61	61	100	26	103	104	99
6	12	47	47	100	26	103	104	99
7	12	44	47	94	25	99	100	99
8	12	43	47	92	25	99	100	99
9	12	43	47	92	24	95	96	99
10	12	43	47	92	23	91	99	99
11	12	43	47	92	23	88	92	96
12	12	42	47	89	23	88	92	96
13	12	40	43	93	23	88	92	96
14	12	38	43	88				
15	12	38	43	88				
16	12	33	43	76				
17	12	32	43	74				
18	11	29	39	74				
19	11	29	39	74				
20	11	27	39	69				

N = Number of salamanders
M = Number of toes clipped
R = Toes recognizable
R/M = Percent recognizable
Group 1 = Power Horn Mountain sample
Group 2 = Cape Fear River sample

continued to fall as salamanders were lost through week 20 in group one.

Ecological Studies

The Area

The study area was a mixed Oak-Hickory forest along a gently sloping hill. Importance values for canopy species showed a dominance of *Quercus* and *Carya* (Table 2). The canopy was open in the spring but almost completely closed by summer. The subcanopy was composed mostly of *Acer* but was more mixed than the canopy (Table 2). The herbaceous layer was not sampled, however a dense layer of ferns existed throughout the summer. Each quadrat was mapped and evaluated for dead trees, stumps, logs, and rocks (Figures 1-4). Each 625 m^2 quadrat had an average of 6.6 m^2 of dead standing trees, 24.7 m^2 of stumps, 21.9 m^2 of logs, and 15.2 m^2 of exposed rock. The National Weather Service provided average monthly temperature and precipitation data for Boone, North Carolina between 1938 and 1971. These values were compared with 1984 data and presented in Figure 5.

Weather in Boone in 1984 varied from wet in early summer to very dry in late summer. Low precipitation in late spring resulted in a late start in field work.

TABLE 2. Importance Values[1] for Vegetation and Debris in Each Quadrat.

Quadrat	1	2	3	4	Mean	Rank
Canopy:						
Acer	38.3	23.9	16.3	16.2	23.8	3
Betula	8.9	--	--	--	2.2	8
Carya	50.0	50.4	56.7	92.1	62.3	2
Fagus	20.6	--	37.9	17.8	19.1	4
Juglans	--	--	--	17.3	4.3	6
Magnolia	24.5	--	--	--	6.1	5
Quercus	157.8	225.6	178.1	168.2	181.4	1
Ulmus	--	--	11.4	--	2.8	7
Subcanopy:						
Acer	121.0	103.1	642.4	155.3	255.4	1
Aesculus	--	--	9.2	--	2.3	8
Carya	--	78.9	24.1	48.7	37.9	2
Fagus	96.8	--	43.0	58.9	37.2	3
Magnolia	51.3	--	35.5	37.2	31.0	4
Quercus	--	60.1	--	--	15.2	6
Tilia	--	--	28.7	--	7.1	7
Ulmus	30.9	57.1	17.1	--	26.3	5
Others[2]:						
Trees	2.9	3.5	12.6	7.4	6.6	
Stumps	25.8	21.0	25.5	26.4	24.7	
Logs	18.6	16.4	28.1	24.6	21.9	
Rocks	16.9	--	34.3	9.6	15.2	

[1] Importance values were based on density, frequency and tree girth.
[2] Values were recorded in square meters.

FIGURE 1. Quadrat One of the Study Area. The total area was 625 m^2. The quadrat was divided into a 5m grid. Each 25 m^2 subplot was designated by numbers for North - South and by letters for East - West. Logs were designated by elongate structures, stumps and trees by hollow circles, and rocks by shaded areas. Total number of salamanders captured was 477.

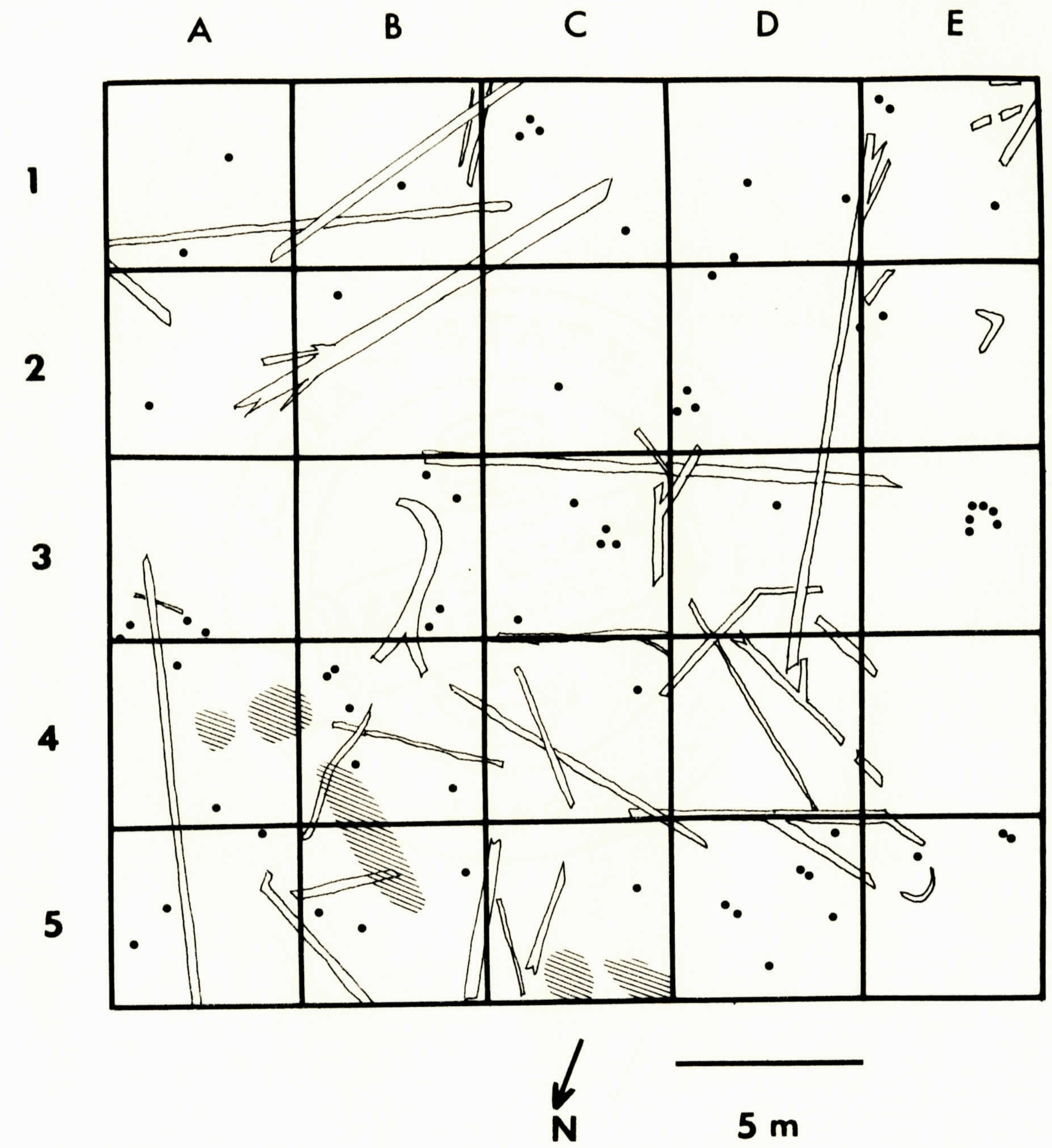


FIGURE 2. Quadrat Two of the Study Area. The total area was 625 m^2. The quadrat was divided into a 5m grid. Each 25 m^2 subplot was designated by numbers for North - South and by letters for East - West. Logs were designated by elongate structures, stumps and trees by hollow circles, and rocks by shaded areas. Total number of salamanders captured was 307.

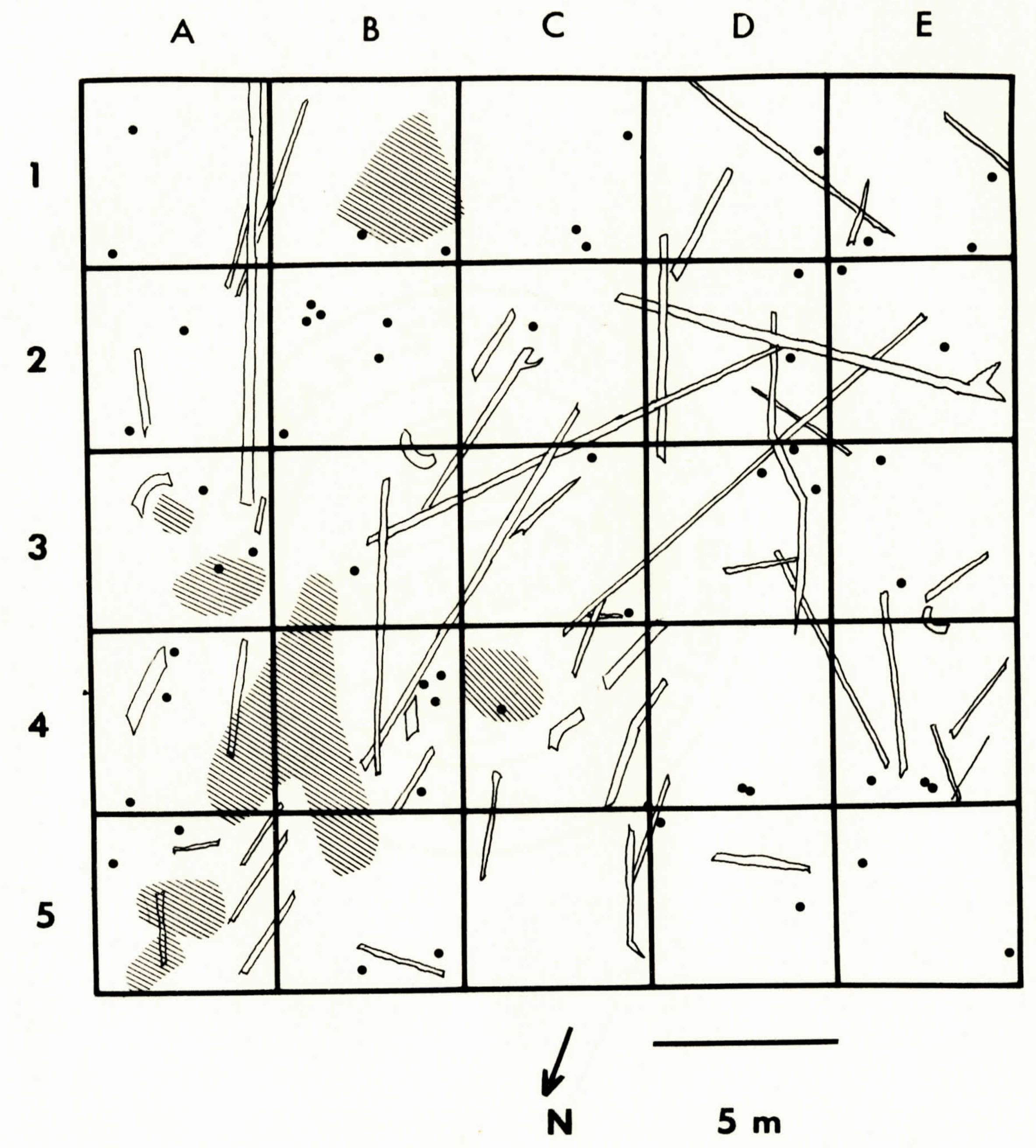


FIGURE 3. Quadrat Three of the Study Area. The total area was 625 m^2. The quadrat was divided into a 5m grid. Each 25 m^2 subplot was designated by numbers for North - South and by letters for East - West. Logs were designated by elongate structures, stumps and trees by hollow circles, and rocks by shaded areas. Total number of salamanders captured was 508.

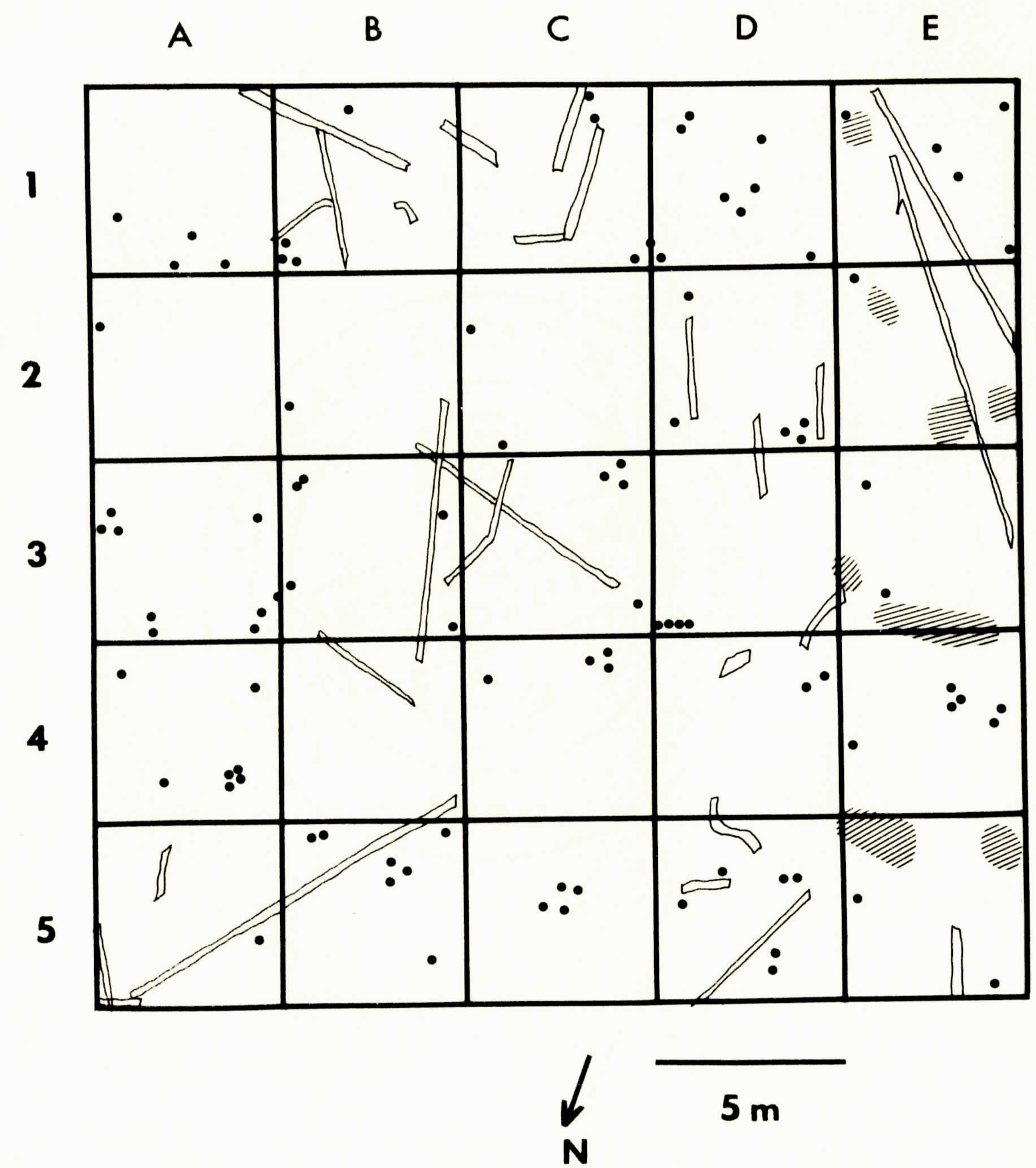


FIGURE 4. Quadrat Four of the Study Area. The total area was 625 m^2. The quadrat was divided into a 5m grid. Each 25 m^2 subplot grid was designated by North - South by numbers and by letters for East - West. Logs were designated by elongate structures, stumps and trees by hollow circles, and rocks by shaded areas. Total number of salamanders captured was 348.

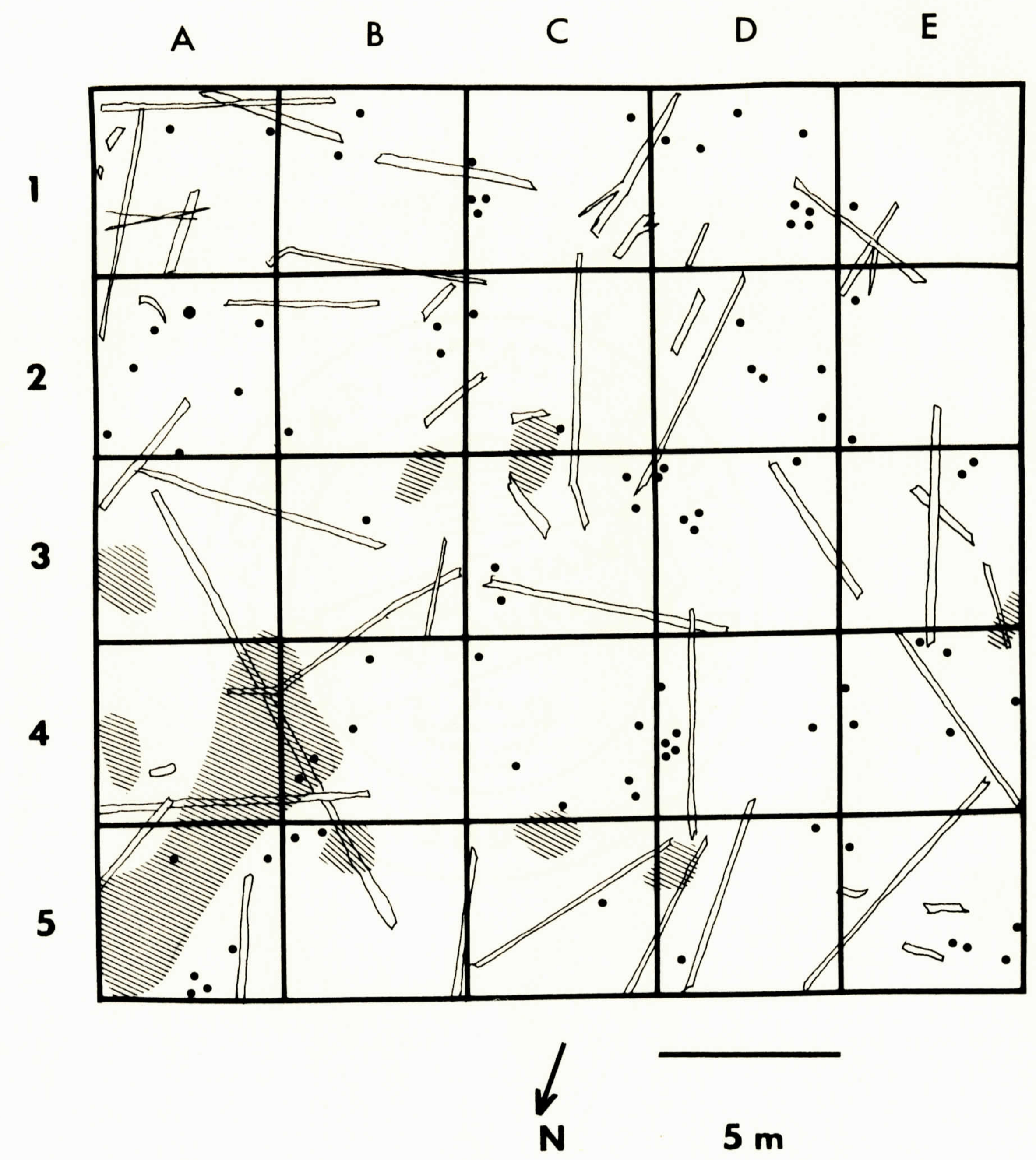
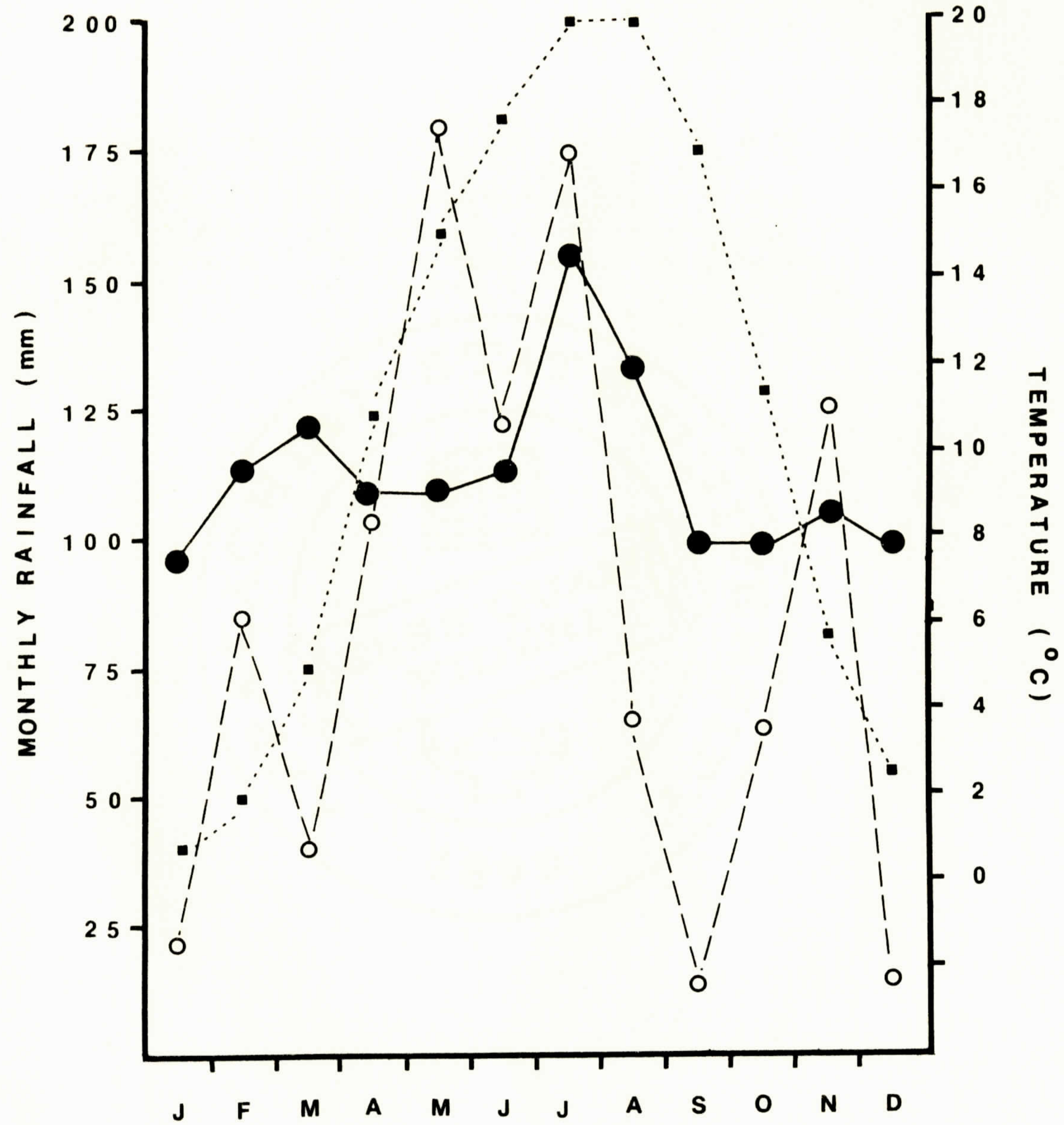


Figure 5. Temperature and Rainfall Data for Boone, Watauga County, North Carolina. Long term monthly temperature ■......■ (C°) were given from 1938 - 1971. Long term monthly rainfall O— —O were given in centimeters for 1938 - 1971. Average rainfall for 1984 ●——● given in centimeters.



Salamander activity increased as summer rains began, allowing considerable field work. Summer precipitation typically declines somewhat in late August and September. In 1984 only one day of field work was possible in September because of very dry conditions. Later in the fall slightly higher than normal precipitation allowed completion of field work.

Population Studies

Population results were obtained by harvest census, repeat census, and mark recapture techniques. Twenty-seven mark recapture samples were taken from 21 May through 1 September 1984, including six to eight visits per quadrat (Table 3). Seven species of salamanders were observed in the sites for a total of 1,640 captures. Relative frequencies of encountering these species were 41.5% Plethodon jordani, 25.8% Desmognathus ochrophaeus, 21.1% Plethodon cinereus, 10.1% Plethodon yonahlossee, 1.3% Eurycea bislineata, 0.1% Notophthalmus viridescens, and 0.1% Plethodon glutinosus (Table 3). A total of 196 man hours was spent in the quadrats.

Capture success per quadrat ranged from 14 to 96 salamanders per capture sample night and 63 to 275 salamanders per harvest night (Table 3). Micro-habitat for salamander captures was divided into five designations.

TABLE 3. Table of Collection Dates and Results for all Samples Taken in 1984. Species and abbrevations were Desmognathus ochrophaeus (Do), Eurycea bislineata (Eb), Notophthalamus viridescens (Nv), Plethodon cinereus (Pc), Plethodon glutinosus (Pg), Plethodon jordani (Pj), Plethodon yonahlossee (Py). R.S. refers to road side samples.

Date	Plot	Do	Eb	Nv	Pc	Pg	Pj	Py	Total
21 May	1	1	1	-	1	-	11	-	14
22 May	2	4	1	-	-	-	8	3	16
28 May	1	8	1	-	1	-	6	2	18
29 May	2	-	-	-	2	-	16	2	20
6 June	3	6	-	-	-	-	24	-	30
11 June	4	2	1	-	-	-	22	-	25
13 June	1	3	-	-	3	-	17	13	36
16 June	2	35	1	-	7	1	45	7	96
20 June	3	64	-	2	3	1	18	1	89
21 June	4	6	-	-	-	-	9	-	15
30 June	1	5	-	-	1	-	35	-	41
2 July	2	6	-	-	2	-	14	4	26
5 July	3	10	-	-	-	-	9	1	20
14 July	2	6	1	-	1	-	25	1	34
15 July	4	8	-	-	6	-	27	-	41
18 July	1	-	-	-	1	-	21	2	24
26 July	3	16	-	-	1	-	15	3	35
29 July	2	11	-	-	1	1	31	8	52
30 July	1	14	11	-	1	-	11	1	38
2 Aug.	4	17	-	-	3	-	37	-	57
14 Aug.	3	37	-	-	3	-	18	1	59
28 Aug.	1	29	1	-	2	-	11	3	46
1 Sept.	4	14	-	-	1	-	27	3	45
10 Oct.	1	68	-	-	127	-	65	-	260
10 Oct.	R.S.	-	-	-	-	-	-	76	76
22 Oct.	2	12	4	-	25	-	20	2	63
27 Oct.	3	54	1	-	89	-	131	-	275
1 Nov.	4	12	-	-	72	-	81	-	165
1 Nov.	R.S.	-	-	-	-	-	-	12	12
TOTAL		448	23	2	353	3	754	145	1727

Proportions of captures in each were: 64.5% in the leaf litter, 15.5% on vegetation, 12.6% near a dead log, 4.7% near a dead stump, and 2.9% near a rock. Success varied each night due to differences in ambient temperature and moisture conditions.

Each harvest census was a destructive sample that gave miminal estimates of salamanders present in the leaf litter (Table 4). Total captures for each species in the four quadrats and mean projections per hectare were 146 (584/ha) *Desmognathus ochrophaeus*, 313 (1,252/ha) *Plethodon cinereus*, 297 (1,188/ha) *Plethodon jordani*, 2 (8/ha) *Plethodon yonahlossee*, and 5 (20/ha) others. The total harvest was 733 (3,052/ha) animals. An additional 88 *Plethodon yonahlossee* were harvested outside the quadrats for biomass analysis.

Total number of animals handled in censuses also provided minimal population estimates (Table 5). Total number of salamanders handled and projection per hectare were 1,640 (6,560/ha). Totals for each species and projections per hectare were 448 (1,792/ha) *Desmognathus ochrophaeus*, 353 (1,412/ha) *Plethodon cinereus*, 754 (3,016/ha) *Plethodon jordani*, 57 (228/ha) *Plethodon yonahlossee*, and 28 (112/ha) others.

Capture and recapture data were recorded separately for each species, site, and sampling period. All data were

TABLE 4. Salamander Density Projections from Harvest Samples.

Quadrat number	1	2	3	4	Total
ANIMALS HARVESTED					
D. ochrophaeus	68	12	54	12	146
P. cinereus	127	25	89	72	313
P. jordani	65	20	131	81	297
P. yonahlossee	0	2	0	0	2
Others	0	4	1	0	5
TOTAL	260	63	275	165	733
ANIMALS PER HECTARE					Mean
D. ochrophaeus	1088	192	864	192	584
P. cinereus	2032	400	1424	1152	1252
P. jordani	1040	320	2096	1296	1188
P. yonahlossee	0	32	0	0	8
Others	0	64	16	0	20
TOTAL	4160	1008	4400	2640	3052

TABLE 5. Summary of Repeat Censuses throughout the Study and Projections of Density per Hectare.

Quadrat number	1	2	3	4	Total
# of visits	7	8	6	6	27
Man hours	76	51	47	22	196
INDIVIDUALS					
D. ochrophaeus	128	74	187	59	448
P. cinereus	137	38	96	82	353
P. jordani	177	159	215	203	754
P. yonahlossee	21	27	6	3	57
others	14	9	4	1	28
TOTAL	477	307	508	348	1640
INDIVIDUALS PER HECTARE					
D. ochrophaeus	2048	1184	2992	944	1792
P. cinereus	2192	608	1536	1312	1412
P. jordani	2832	2544	3440	3248	3016
P. yonahlossee	336	432	96	48	228
others	224	144	64	16	112
TOTAL	7632	4912	8128	5568	6560

included in matrix form for use in calculating population sizes. Data recorded for each species with each sampling interval (i) were: total individuals captured (Ci), new animals marked (Mi), and recaptures of individuals from previous intervals (Ri). Numbers of recaptures were inadequate for estimating population sizes in all species except *Plethodon jordani* and perhaps for *Desmognathus ochrophaeus* in two quadrats (Tables 6-8).

Population estimates for *Plethodon jordani* ranged from 183.2 to 486.1 with a mean of 297.8 per quadrat using the Schnabel Method and from 209.1 to 515.8 with a mean of 323.5 using the Schumacher Method (Table 9). The two methods gave similar results for *Plethodon jordani*, but confidence intervals were smaller with the Seber (1973) form of the Schnabel Method. Ricker's (1975) modification of the Schnabel Method was also used but resulted in larger confidence intervals. Similarities in the two estimates of population suggest equal chance of capture since differences in captures would be detected as changes in the Schumacher Method estimate compared to the Schnabel Method (Caughley, 1977).

Population estimates and ranges for *Desmognathus ochrophaeus* were from 2,338 (1,186.4 - 3,489.6) for quadrat three to 261 (122 - 399) for quadrat four for a mean of 1299.3 per 625 m^2 (Table 10) by the Schnabel Method

TABLE 6. Mark Recapture Matrices for *Desmognathus ochrophaeus* at Sites 3 and 4. Numbers in the diagonal are new animals (Mi). Recaptures from earlier periods (Ri) are listed below time first marked. Total captures (Ci) is the sum of the numbers in each row. Total number of captures in each quadrat (n) is given below each matrix.

Site 3:

Period (i)	1	2	3	4	5
1	6				
2	0	64			
3	0	0	10		
4	0	0	1	16	
5	0	0	1	0	37

n = 133
Ri = 2

Site 4:

Period (i)	1	2	3	4	5
1	2				
2	0	6			
3	0	0	8		
4	1	1	0	17	
5	0	0	0	1	14

n = 47
Ri = 3

TABLE 7. Mark Recapture Matrices for *Plethodon jordani* at Sites 1 and 2. Numbers in the diagonal are new animals (Mi). Recaptures from earlier periods (Ri) are listed below first time marked. Total captures (Ci) is the sum of the numbers in each row. Total number of captures in each quadrat (n) is given below each matrix.

Site 1:

Periods (i)	1	2	3	4	5	6
1	17					
2	3	17				
3	2	2	35			
4	2	1	3	21		
5	1	1	0	1	11	
6	1	1	1	0	0	11

n = 112
Ri = 19

Site 2:

Periods (i)	1	2	3	4	5	6
1	8					
2	0	16				
3	1	1	45			
4	0	0	4	14		
5	1	1	2	0	25	
6	0	0	3	0	0	31

n = 139
Ri = 13

TABLE 8. Mark Recapture Matrices for <u>Plethodon jordani</u> at Sites 3 and 4. Numbers in the diagonal are new animals (Mi). Recaptures from earlier periods (Ri) are listed below time first marked. Total captures (Ci) is the sum of the numbers in each row. Total number of captures in the quadrat (n) is given below each matrix.

Side 3:

Periods (i)	1	2	3	4	5
1	24				
2	3	18			
3	3	0	9		
4	1	1	0	15	
5	0	1	4	0	18

n = 85
Ri = 13

Site 4:

Period (i)	1	2	3	4	5
1	22				
2	0	9			
3	2	1	27		
4	5	2	1	37	
5	1	1	3	1	27

n = 122
Ri = 17

TABLE 9. Population Estimates and 95% Confidence Limits for <u>Plethodon jordani</u>. See Appendices 1 and 2 for calculation formulae.

Quadrat	n	R	Schumacher Method (1943) $\hat{N}$	CI	Schnabel Method Seber (1973) $\hat{N}$	CI	Schnabel Method Ricker (1975) $\hat{N}$	CI
1	83	19	226.4	135-700	194.4	168-220	194.4	134-353
2	126	14	515.8	283-2957	486.1	298-674	486.1	322-655
3	72	13	209.1	123-685	183.2	159-208	183.2	120-381
4	108	17	342.8	230-670	327.3	228-426	327.3	222-624
Average:			323.5		297.8		297.8	

n = Sample size
R = Number of recaptures
$\hat{N}$ = Population estimate
CI = Confidence intervals of the estimate N

TABLE 10. Population Estimates and 95% Confidence Limits for Desmognathus ochrophaeus[1]. See Appendices 1 and 2 for calculation formulae.

Quadrat	n	R	Schumacher Method (1943) $\hat{N}$	CI	Schnabel Method Seber (1973) $\hat{N}$	CI	Schnabel Method Ricker (1975) $\hat{N}$	CI
1	-	-	NA	NA	NA	NA	NA	NA
2	52	4	209	NA	NA	NA	NA	NA
3	119	2	2216	1116-15342	2338	1186-3490	2338	NA
4	44	3	291	28-359	261	122-399	261	NA
Average			905.3		1299.3		1299.3	

n = Sample size
R = Number of recaptures
$\hat{N}$ = Population estimate
CI = Confidence intervals of the estimate N
NA = Not available
[1] Values suspected due to small numbers of recaptures

(Seber 1973). Ricker's (1975) variance could not be calculated. Estimates and ranges using the Schumacher Method were 2,216 (1,106 - 1,5342) for quadrat three and 291 (28 - 359) for quadrat four for a mean of 1,263 per 625 m^2. Estimates were questionable in quadrats three and four because of the small number of recaptures and were not made in quadrats one and two. The population values for Plethodon jordani and Desmognathus ochrophaeus were multiplied by 16 to project numbers per hectare and divided by 625 to yield numbers per m^2.

The results provided two minimal population estimates ($\hat{N}$) and two estimates of population ($\hat{N}$) by mark recapture. All three values showed considerable variation among quadrats.

Biomass

Salamanders harvested in the destructive sample were used to determine the relationship between SVL to wet weight and dry weight biomass. Average size and mass for all salamanders were determined (Table 11). Differences among species were apparent for each measured descriptor. Plethodon cinereus and Desmognathus ochrophaeus were the smallest common salamanders. Plethodon yonahlossee was the largest, although the presence of many juveniles brought down the average values. Plethodon jordani was the most

TABLE 11. Mean Size and Mass for all Salamanders Handled.

Species	Measured SVL mm	Measured Wet mass gram	Measured Dry mass gram	Predicted Dry mass from wet
D. ochrophaeus	37.2 (461)	0.98 (446)	0.23054 (154)	0.19985
P. cinereus	36.7 (378)	0.82 (376)	0.14203 (333)	0.13729
P. jordani	41.9 (745)	1.53 (740)	0.28676 (275)	0.25417
P. yonahlossee	41.5 (181)	2.46 (169)	0.15886 (113)	0.41378
E. bislineata	34.1 (23)	0.78 (20)	-	-
N. viridescens	31.0 (2)	0.65 (2)	-	-
P. glutinosus	61.3 (3)	4.27 (3)	-	-

( ) = sample size

abundant species in the quadrats. *Desmognathus ochrophaeus* had the most variation in body size and weights as shown in least square regressions (Tables 12-14). Sample sizes were small and did not include all stages of the life cycle in *Eurycea bislineata*, *Notophthalmus viridescens*, and *Plethodon glutinosus*. Mean descriptors were not accurate representations of whole populations for these species.

Least square regressions were used to determine the relationship between wet and dry weight biomass to SVL, and wet weight biomass to dry weight biomass. Residual analyses of these variables indicated a curvilinear relationship between SVL to wet weight biomass and dry weight biomass. Natural logarithm transformations of SVL to wet weight biomass and dry weight biomass produced regression slopes of nearly three (2.69 to 3.19), which indicated cubic functions. Log natural regressions of wet weight biomass to dry weight biomass had slopes of 1.03 to 1.11, which indicated a linear relationship. Log natural regressions had higher r^2 values, that proportion of variance explained by the regression. All regressions were significant at a 0.01 level (**).

Regressions relating ash weight biomass to dry weight biomass and organic weight biomass to dry weight biomass were significant at the 0.05 level (*) with the exception of *Desmognathus ochrophaeus* and *Plethodon cinereus* for ash

TABLE 12. Biomass Regressions using Raw Data. Regressions are in the form y = a + b x. Where a is the y intercept and b is the slope. The square of the correlation coefficient (r^2) is a measure of the proportion of total variance that is explaned by the regression.

Dep./Indep. Variables	n	sig.	a	b	r	r^2
Desmognathus ochrophaeus						
SVL/Wet mass	437	**	- 1.40	0.064	0.8595	0.7388
SVL/Dry mass	154	**	- 0.40	0.017	0.8295	0.6880
Wet mass/Dry mass	154	**	- 0.01	0.220	0.9364	0.8765
Plethodon cinereus						
SVL/Wet mass	376	**	- 0.92	0.047	0.8731	0.7624
SVL/Dry mass	333	**	- 0.17	0.084	0.8572	0.7348
Wet mass/Dry mass	333	**	- 0.01	0.175	0.9749	0.9504
Plethodon jordani						
SVL/Wet mass	740	**	- 1.81	0.008	0.9231	0.8522
SVL/Dry mass	275	**	- 0.40	0.016	0.9238	0.8535
Wet mass/Dry mass	275	**	- 0.03	0.189	0.9847	0.9697
Plethodon yonahlossee						
SVL/Wet mass	169	**	- 4.18	0.155	0.9649	0.9311
SVL/Dry mass	113	**	- 0.93	0.033	0.9543	0.9106
Wet mass/Dry mass	113	**	- 0.04	0.199	0.9859	0.9720

TABLE 13. Biomass Regressions using Natural Logarithm Transformed Data. Symbols are as in Table 12.

Dep./Indep. Variables	n	sig.	a	b	r	r^2
Desmognathus ochrophaeus						
lnSVL/lnWet mass	437	**	- 9.82	2.690	0.8803	0.7750
lnSVL/lnDry mass	154	**	-12.38	2.986	0.8450	0.7141
lnWet mass/lnDry mass	154	**	- 1.59	1.114	0.9512	0.9049
Plethodon cinereus						
lnSVL/lnWet mass	376	**	-10.38	2.799	0.9513	0.9049
lnSVL/lnDry mass	333	**	-12.50	2.893	0.9473	0.8973
lnWet mass/lnDry mass	333	**	- 1.78	1.034	0.9885	0.9771
Plethodon jordani						
lnSVL/lnWet mass	740	**	-10.02	2.755	0.9581	0.9179
lnSVL/lnDry mass	275	**	-12.85	3.032	0.9843	0.9688
lnWet mass/lnDry mass	275	**	- 1.84	1.099	0.9965	0.9930
Plethodon yonahlossee						
lnSVL/lnWet mass	169	**	-10.45	2.881	0.9900	0.9781
lnSVL/lnDry mass	113	**	-13.44	3.193	0.9920	0.9841
lnWet mass/lnDry mass	113	**	- 1.87	1.095	0.9967	0.9935

TABLE 14. Regressions for Ash Biomass. Symbols are as in Table 12.

Dep./Indep. Variables	n	sig.	a	b	r	r^2
Desmognathus ochrophaeus						
Ash mass/Dry mass	3		-0.00376	0.123	0.8872	0.9418
Organic /Dry mass	3	*	+0.00376	0.877	0.9975	0.9987
Plethodon cinereus						
Ash mass/Dry mass	6		+0.02215	0.011	0.0540	0.2324
Organic/Dry mass	6	**	-0.02214	0.988	0.9976	0.9988
Plethodon jordani						
Ash mass/Dry mass	5	*	-0.00795	0.177	0.7550	0.8689
Organic/Dry mass	5	**	-0.03163	0.899	0.9673	0.9835
Plethodon yonahlossee						
Ash mass/Dry mass	3	*	-0.00813	0.175	0.9944	0.9971
Organic /Dry mass	3	**	-0.00510	0.824	0.9984	0.9999

weight biomass to dry weight biomass. Lack of significance was attributed to small sample size (n = 3 and n = 6) and to variance in weight of selected subsamples.

Regressions were used to predict wet and dry weight biomass from SVL, and dry weight biomass from wet weight biomass. Formulae were derived from raw data and from log natural transformed data (Table 15). Regressions of wet weight biomass to calculated wet weight biomass and dry weight biomass to calculated dry weight biomass were used to test validity of predictor formulae. All these regressions were significant (**) and had slopes between 0.998 and 1.000, and large r^2 values. Predicted values were closly and directly related to measured values and were used in further calculations. Formulae using log-natural transformed data were the best predictors of total biomass derived from SVL data, while formulae using raw data were adequate predictors of dry weight biomass from wet weight biomass.

Population biomass was estimated by multiplying population estimates by mean wet and dry animal weight (Table 16). Since different population estimates were used, more than one estimate of biomass was available for each species. Total biomass by repeat census was 8.24 kg/ha wet weight biomass and 1.51 kg/ha dry weight biomass. This total was composed primarily of Plethodon

TABLE 15. Regression Equations for Biomass.

Desmognathus ochrophaeus

Wet wt. biomass = $e^{(2.69044*\ln SVL - 9.82648)}$

Dry wt. biomass = $e^{(2.98594*\ln SVL - 12.38293)}$

Dry wt. biomass = 0.22004*Wet mass - 0.01259

Organic wt. biomass = 0.87667*Dry mass + 0.00376

Plethodon cinereus

Wet wt. biomass = $e^{(2.79940*\ln SVL - 10.38352)}$

Dry wt. biomass = $e^{(2.89273*\ln SVL - 12.50054)}$

Dry wt. biomass = 0.17528*Wet mass - 0.00517

Organic wt. biomass = 0.98848*Dry mass - 0.02215

Plethodon jordani

Wet wt. biomass = $e^{(2.75561*\ln SVL - 10.02470)}$

Dry wt. biomass = $e^{(3.03226*\ln SVL - 12.85232)}$

Dry wt. biomass = 0.18925*Wet mass - 0.002631

Organic wt. biomass = 0.89887*Dry mass - 0.03163

Plethodon yonahlossee

Wet wt. biomass = $e^{(2.88142*\ln SVL - 10.44732)}$

Dry wt. biomass = $e^{(3.19274*\ln SVL - 13.44375)}$

Dry wt. biomass = 0.19898*Wet mass - 0.03717

Organic wt. biomass = 0.82434*Dry mass - 0.00510

TABLE 16. Biomass and Caloric Estimates per hectare from Harvest Censuses, Repeat Censuses, and Mark Recapture Data.

Study	Population estimate	Wet Mass Kg/ha	Dry Mass Kg/ha	Million Calories/ha
HARVEST CENSUS:				
D. ochrophaeus	584	0.57	0.13	0.67
P. cinereus	1,252	1.03	0.18	0.93
P. jordani	1,188	1.82	0.34	1.76
P. yonahlossee	8	0.02	0.01	0.05
Total	3,032	3.44	0.66	3.41
REPEAT CENSUS:				
D. ochrophaeus	1,792	1.8	0.41	2.12
P. cinereus	1,412	1.2	0.20	1.04
P. jordani	3,016	4.6	0.86	4.45
P. yonahlossee	228	0.6	0.04	0.21
Total	6,448	8.2	1.51	7.82
MARK-RECAPTURE:				
Schnabel Method				
D. ochrophaeus[1]	20,789	20.4	4.79	24.80
P. jordani	4,765	7.3	1.37	7.09
Total	25,554	27.7	6.16	31.89
Schumacher Method				
D. ochrophaeus[1]	14,485	14.2	3.34	17.29
P. jordani	5,176	7.9	1.48	6.68
Total	19,661	22.1	4.94	23.97

[1] Values suspected due to small number of recaptures

jordani and *Desmognathus ochrophaeus*. Total biomass by harvest census was 3.44 kg/ha wet weight biomass and 0.66 kg/ha dry weight biomass. An increase in *Plethodon cinereus* availability in the fall resulted in higher biomass values for this species in the harvest sample. Both mark recapture estimates had the highest biomass values recorded. The Schumacher Method resulted in 27.7 kg/ha wet weight biomass and 6.16 kg/ha dry weight biomass for only two species. The Schnabel Method resulted in 22.1 kg/ha wet weight biomass and 4.94 kg/ha dry weight biomass. Both mark recapture estimates for *Desmognathus ochrophaeus* were considerably higher than harvest or repeat census estimates. The large values for *Desmognathus ochrophaeus* were attributable to large population estimates for this species. Calories were projected from mean dry weight biomass values using the conversion factor 5,176 calories per gram dry weight biomass given by Burton and Likens (1975a). Total calories per hectare by each method were: 3.41 million by harvest census, 7.82 million by repeat census, and 23.97 to 31.89 million by mark recapture (Table 16).

Regressions indicated several important relationships. Wet weight biomass could be predicted from SVL, and dry weight biomass could be predicted from SVL or wet weight biomass. Log transformations of each variable improved

predictions greatly for some relationships. Biomass measures approximated cubic functions of SVL. Mean dry weight biomass could be used to estimate total calories of these salamanders in wooded areas.

DISCUSSION

Knowledge of population structure, including density and standing crop biomass, can aid in understanding the importance of individual species in community structure. The present study was designed to obtain the data necessary for a better understanding of the role salamanders play in at least one local community. The study combined three phases: 1) a regeneration study to determine the suitability of toe clipping for marking salamanders; 2) an ecological study to estimate population size using harvest census, repeat census (animals handled), and mark recapture techniques; and 3) laboratory measurements of total wet and dry weight biomass of salamanders from quadrats located in the Blue Ridge Mountains near Boone, North Carolina.

Regeneration

The toe regeneration study was a necessary prerequisite for visual recognition of regenerating toes. It was assumed that the observed pattern of regeneration was a normal process for all species and that other patterns would not complicate recognition. All toes except one regenerated normally and were recognizable by small size or incomplete pigmentation. The unusual toe regenerated at an

angle from the normal axis and probably represented a permanent mark. Despite husbandry problems that resulted in salamander deaths and foot necrosis, the preliminary study did demonstrate that a large majority (96%) of toes clipped were still recognizable after thirteen weeks and that a smaller majority were recognizable after 20 weeks. These intervals were equivalent to those required in a one-season field study. A time scale for regeneration of digits was not available; however, several mark recapture studies suggested limitations. Highton (1965) reported 353 days, 77 days, and 68 days between marking and recaptures in *Plethodon glutinosus*. Intervals reported for *Plethodon cinereus* include seven months (Heatwole, 1961) and two weeks (Klein, 1960).

The pilot regeneration study provided three critical things: 1) skill in marking salamanders, 2) ability to recognize stages of toe regeneration, and 3) confidence in the reliability of toe clipping as a marking procedure over a reasonable time scale.

Ecological study

Woodland habitat provides an enormous area for exploitation by salamanders. As a result, woodland salamanders of the Family Plethodontidae have become abundant and diverse. In the present study, three procedures were used to reach population estimates for salamanders in the Blue Ridge Mountains: 1) harvest censuses, 2) repeat censuses of all animals handled in each quadrat, and 3) mark recapture estimates using the Schnabel and Schumacher methods.

The seven species observed were Desmognathus ochrophaeus, Eurycea bislineata, Notophthalmus viridescens, Plethodon cinereus, Plethodon jordani, Plethodon glutinosus, and Plethodon yonahlossee. Capture success varied seasonally and nightly. The species present and their abundance were dependent on ambient temperatures and precipitation. The best conditions for surface activity were warm, drizzly nights. Most salamanders were active in the leaf litter on the forest floor, near logs, and on stumps or trees. Plethodon jordani was the most common salamander throughout the summer. Desmognathus ochrophaeus was the second most common species captured, but densities seemed to be higher in the spring and fall. Desmognathus ochrophaeus and Plethodon jordani were the two most common species captured in this study area, as was found in Avery County, North Carolina (Gordon et al., 1962). Plethodon cinereus was the third most abundant salamander; however, almost all of observations were in the fall. Observations were in accordance to the activity patterns reported by

Taub (1961) for Plethodon cinereus with many spring captures followed by sharp reductions in the summer and then rapid increases in autumn. Plethodon jordani was typically found in the leaf litter, while Plethodon cinereus and Desmognathus ochrophaeus were found in the leaf litter and climbing on vegetation.

Censuses included nondestructive and destructive sampling. Nondestructive sampling was limited to surface activity animals only. The lowest census (n = 14) was the first night when conditions were partly cloudy. The largest census (n = 96) was a partly cloudy night with no moon following a heavy rain. Harvest samples were destructive since the entire leaf litter, forest debris, and vegetation were searched. The destructive samples maximized numbers of salamanders captured at the expense of habitat quality. The smallest harvest census (n = 63) was composed almost entirely of Plethodon cinereus and Plethodon jordani on a cool evening after an early morning rain. The largest harvest (n = 260) was composed of Plethodon jordani, Plethodon cinereus, and Desmognathus ochrophaeus on a cool night with intermittent showers after a rainy afternoon.

Harvest censuses provided minimal population estimates. Success varied from 63 to 275 salamanders per quadrat with a total of 733 in the four quadrats. Harvest of each species included 146 Desmognathus ochrophaeus, 313 Plethodon cinereus, 297 Plethodon jordani, 2 Plethodon yonahlossee, and 5 others. The total harvest was equivalent to a minimal density estimate of 0.30 salamanders per m^2. Harvest censuses reported in two other studies for Plethodon cinereus include 0.05 per m^2 (Test and Bingham, 1948) and 0.21 to 0.25 per m^2 (Jaegar, 1969).

Repeat censuses provided another way of estimating salamander densities. This cumulative method included all animals handled in the quadrats. The total of 1,640 salamanders included 448 Desmognathus ochrophaeus, 353 Plethodon cinereus, 754 Plethodon jordani, 57 Plethodon yonahlossee, and 28 others. The total repeat census was equivalent to 0.65 salamanders per m^2 as a minimal population density estimate for forested areas. Repeat census estimates were within the 0.16 to 2.72 per m^2 range calculated for Plethodon cinereus by Burton and Likens (1975a).

Since all salamanders were never active on the surface at the same time, it was necessary to provide realistic estimates of salamander abundance and density. Taub (1961) suggested that only 2% to 32% of the population would be on the surface at any given time; therefore, surface censuses were often underestimates of true population size. The

Schnabel and Schumacher mark recapture methods (Caughley, 1977) seemed the most appropriate ways to obtain realistic population estimates in the present study. These multiple mark recapture methods were separately derived from the Lincoln-Peterson methods and differ in methods of estimating variances.

Limitations and assumptions of any mark recapture study include the following: 1) the probability of capturing a salamander is the same for marked and non-marked salamanders, 2) no marks are lost, 3) no salamanders are born or immigrate into the area, and 4) no salamanders die or emigrate out of the area. Migrations and deaths can be allowed if marked and non-marked move or die at the same rate. The pilot study suggested that toe clips were appropriate marks for one season of activity and that toe nail clippers probably do not increase mortality via necrosis. It was assumed that if salamanders were lost during the study period, the loss was random with respect to marking. Several sources of differential loss which could have influenced data includes increased migration due to handling, increased predation by marking, or reduced foraging ability due to a "handicap" effect. No differential loss of marked salamanders was believed to have occurred.

The Schnabel and Schumacher methods were useful when dealing with small numbers of samples, small numbers of recaptures within each sample, and samples without recaptures. The Schnabel Method was the simpler form, but the Schumacher Method provided a test of equal chance of capture. If the two estimates were different, unequal chance of capture was a possible cause. Preliminary calculations using the harvest samples as part of the mark recapture study gave questionable results that suggested unequal chance of capture. Two sources of unequal chance of capture were loss of marks due to toe regeneration over the longer study period and species specific differences in seasonal activity patterns. Removal of harvest samples from calculations resulted in more homogeneous population estimates with narrower confidence intervals, a shorter sampling period of 15 weeks, and the removal of fall activity.

Disadvantages were associated with each of the three population estimators. Harvest samples were based on single samples taken within several weeks. These estimates could have been greatly influenced by differences in seasonal activity among the species present. In particular, Plethodon cinereus was much more active during this time period, and Plethodon yonahlossee was less active. Only an unknown proportion of the population was actually available for capture on any given night, so

censuses were underestimates of actual density. Also, it was clear that not all salamanders in the quadrats were eventually captured. Even the multiple capture censuses were underestimates by some unknown proportion. Mark recapture estimates were greatly influenced by numbers of recaptures of marked animals. Increased losses of marked salamanders would decrease the proportion of recaptures and inflate the population estimates.

Population estimates by mark recapture were completed only for Plethodon jordani and Desmognathus ochrophaeus. Estimates for Plethodon jordani ranged from 209.1 to 515.8 with a mean of 323.5 per 625 m^2 by the Schumacher Method and from 183.2 to 486.1 with a mean of 297.8 per 625 m^2 by the Schnabel Method. Estimates for Desmognathus ochrophaeus were calculated only in quadrats three and four. Values were 291.1 and 2216.0 using the Schumacher Method and 260.7 and 2,338 using the Schnabel Method. The large difference between population estimates for Desmognathus ochrophaeus was probably influenced by small numbers of recaptures at the two quadrats. This difference reduced confidence in all estimates for this species.

Three population estimates were used. Harvest samples and repeat censuses were both minimal estimates of population while the mark recapture analyses gave estimates of total population size based on proportions of marked and unmarked salamanders. Over all, results were in accord with expectations. Harvest samples gave the lowest mean estimate of 3,032 salamanders per hectare on or near the surface at one time. Repeat estimates were higher with a mean of 6,448/ha. Mark recapture estimates were the highest at 25,554/ha by the Schnabel and 19,661/ha by the Schumacher methods (Table 15).

Mark recapture estimates were four times larger than harvest estimates and 1.59 times larger than the repeat census for Plethodon jordani. These values suggested that only 25% of the population was out in the best conditions and that repeat censuses sampled only 63% of the population. Mark recapture estimates for Plethodon jordani were the most reliable due to the larger numbers marked and recaptured. Recaptures for Desmognathus ochrophaeus were probably inadequate for confidence in the estimates. If harvest estimates for the four most common species were expanded in proportion to Plethodon jordani, estimates would have been 2,336 Desmognathus ochrophaeus, 5,008 Plethodon cinereus, and 32 Plethodon yonahlossee for a total of 12,141 salamanders per hectare. If repeat censuses were expanded for all species as in Plethodon jordani, totals would have been 2,849 Desmognathus ochrophaeus, 2,245 Plethodon cinereus, and 363 Plethodon yonahlossee with a total of 10,222 salamanders per

hectare. Occasional species would have increased as well. Some seasonal differences in activity were increases in Plethodon cinereus in the fall and reductions in Desmognathus ochrophaeus and Plethodon yonahlossee by fall.

Estimates of density also have been variable in the literature (Table 17). Population estimates for Plethodon glutinosus in South Carolina (Semlitch, 1980) were higher than values presented here for Plethodon jordani. However, both these values were lower than estimates for Desmognathus ochrophaeus (Hall, 1976; Tilley, 1980). It should be noted that Tilley's (1980) work was at a rock face that had much larger population density than did nearby woodland habitats. The more powerful Jolly Seber Method mentioned in Table 17 was not useful for the present study due to the small number of recaptures.

Biomass

Population studies were necessary starting points for estimating standing crop biomass in the forms of wet weight biomass, dry weight biomass, and total calories per hectare. These estimates provided a more complete picture of the energy available for other species, energy flow, energy cycles, and distribution of energy at a community level.

TABLE 17. Comparison of Salamander Population Estimates.

Semlitch (1980) *Plethodon glutinosis*	Tilley (1980) *Desmognathus ochrophaeus*	Hall (1976) *Desmognathus fuscus*	Burton & Likens (1975) *Plethodon cinereus*
1 0.81/m^2 2 0.60/m^2 3 0.52/m^2 4 0.70/m^2 Avg. 0.66/m^2 Schumacher Method	1 2.71/m^2 1 3.10/m^2 2 3.80/m^2 2 3.10/m^2 Jolly-Seber Method	0.80/m^2 *Desmognathus ochrophaeus* 0.6 to 1.1/m^2 Jolly-Seber Method	0.26/m^2 mark-recapture 0.16 to 2.72/m^2 surface census expanded
Present study *Plethodon jordani*	Present study *Plethodon jordani*	Present study *Desmognathus ochrophaeus*	Present study *Desmognathus ochrophaeus*
1 0.31/m^2 2 0.78/m^2 3 0.29/m^2 4 0.52/m^2 Avg. 0.48/m^2 Schnabel Method	1 0.36/m^2 2 0.83/m^2 3 0.33/m^2 4 0.55/m^2 Avg. 0.52/m^2 Schumacher Method	1 NA 2 NA 3 3.74/m^2 4 0.42/m^2 Avg. 2.08/m^2 Schnabel Method	1 NA 2 0.33/m^2 3 3.55/m^2 4 0.47/m^2 Avg. 1.45/m^2 Schumacher Method

Wet weight biomass projections for each species were calculated as the product of population estimates and mean wet weight biomass for each species. The projections varied depending on the quadrat, species, and type of population estimator. Harvest sample and cumulative census data were available for all species, but mark recapture estimates were available only for *Plethodon jordani* and *Desmognathus ochrophaeus*. Harvest samples were miminal estimates of total kg wet weight biomass per hectare in salamanders. Total harvest estimates were equivalent to 3.44 kg of salamanders per hectare with a range of 0.57 to 1.82 kg/ha for common species. Of this total, *Desmognathus ochrophaeus* had a mean estimate of 0.57 kg/ha and a range of 0.19 to 1.07 kg/ha among different quadrats. *Plethodon jordani* had a mean of 1.28 kg/ha and ranged from 0.49 to 3.21 kg/ha among different quadrats. Repeat census increased total salamander wet weight biomass to 8.2 kg/ha with a range of 0.6 to 4.6 kg/ha for each species. Of this total, *Desmognathus ochrophaeus* had a mean of 1.8 kg/ha with a range of 0.93 to 2.93 kg/ha among different quadrats. *Plethodon jordani* had a mean of 4.6 kg/ha and a range of 3.98 to 4.97 kg/ha among different quadrats. The estimates of wet weight biomass were much higher than the 1.77 kg/ha value reported for the Hubbard Brook Forest in New Hampshire by Burton and Likens (1975a). The Hubbard

Brook estimate was the only other estimate available for total salamander biomass.

Dry weight biomass projections were obtained as the product of the population estimates and dry weight biomass estimates for average size animals. Overall mean values for dry weight biomass were not used since they reflected only the harvest samples. Total salamander dry weight biomass in the harvest was 0.66 kg/ha with a range of 0.01 to 0.34 kg/ha among species. Mean dry weight biomass for *Desmognathus ochrophaeus* was 0.13 with a range of 0.04 to 0.25 kg/ha. Mean dry weight biomass for *Plethodon jordani* was 0.34 with a range of 0.09 to 0.60 kg/ha. Repeat census total dry weight biomass was 1.51 kg/ha with a range of 0.04 to 0.86 kg/ha per species. Mean and ranges for dry weight biomass among the quadrats were 0.41 (0.22 to 0.69) kg/ha for *Desmognathus ochrophaeus* and 0.86 (0.73 to 0.99) kg/ha for *Plethodon jordani*. These values were minimal estimates and much larger than 0.24 kg/ha reported by Burton and Likens (1975a) for the Hubbard Brook Forest.

Mark recapture procedures allowed estimates of how many *Desmognathus ochrophaeus* and *Plethodon jordani* actually lived in each site instead of how many were available for capture at any one time. Population estimates suggested 14.2 to 20.4 wet kg/ha and 3.34 to 4.79 dry kg/ha of *Desmognathus ochrophaeus* and 7.3 to 7.9 wet kg/ha and 1.37

to 1.48 dry kg/ha of *Plethodon jordani*. These values were much larger than those of Burton and Likens (1975a).

Two values were available for converting salamander dry weight biomass into calories per gram dry weight. Merchant (1970) used 5,473 calories per gram dry weight, while Burton and Likens (1975a) used 5,176 calories per gram dry weight. The conservative value of Burton and Likens (1975a) was used to convert mean dry weight into salamander calories. Mean calories per species were 1,034 for *Desmognathus ochrophaeus*, 711 for *Plethodon cinereus*, 1,316 for *Plethodon jordani*, and 2,141 for *Plethodon yonahlossee*. Total calories per hectare for harvest samples was 3.41 million with a range of 0.05 to 1.76 million calories per species. Total calories per hectare for repeat census was 7.82 million with a range of 0.21 to 2.12 million calories per species. Projections using the mark recapture data were 17.29 to 24.80 million calories for *Desmognathus ochrophaeus* and 6.68 to 7.09 million calories for *Plethodon jordani*.

Estimates of standing crop biomass of salamanders allows a better understanding of the ecological role of those animals in their local community. The community with the most complete data so far is the Hubbard Brook Forest in New Hampshire which include data by Holms and Sturges (1973), Sturges *et al.* (1974), and Burton and Likens

(1975a,b). This area, however, has few species of terrestrial salamanders relative to the Appalachian Mountains. Salamanders in the Hubbard Brook Forest apparently consume about 10,588 kcal per hectare or 0.02 percent of total net primary productivity. Burton and Likens (1975b) reported that salamander biomass was 2.6 times that of breeding birds wet weight biomass and 1.9 times dry weight biomass. Also, salamander biomass was at least equal to that of small mammals.

The woodlands in the vicinity of Boone, North Carolina, have many more species of terrestrial salamanders than are found in New Hampshire. Wet weight biomass values for the Boone area exceed New Hampshire by 1.94 times (Harvest sample) to 15.65 times (Mark recapture - Schnabel Method). Dry weight mass estimates in North Carolina exceed New Hampshire by a factor of 2.75 (Harvest sample) to 25.66 (Mark recapture). Unfortunately, energy flow through the southern Appalachian Mountains woodland is not well known. The ecological role of the salamanders in the Appalachian Mountains is still unclear, but these animals must represent an important part of the energy flow through the community.

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APPENDIX 1. Schnabel Method for Population Estimation.

$$\hat{N} = \frac{\Sigma(Mi\ Ci)}{Ri} \qquad \text{Equation 1}$$

$$s^2 \text{ of } \frac{1}{\hat{N}} = \frac{\Sigma\ Ri}{(\Sigma\ Mi\ Ci)^2} \qquad \text{Equation 2}$$

$$SE \text{ of } \hat{N} = \frac{1}{\sqrt{\left(\frac{1}{\hat{N}-Mi} + \frac{K-1}{\hat{N}} + \frac{1}{\hat{N}-Ci}\right)}} \qquad \text{Equation 3}$$

Abbreviations used were:

- $\hat{N}$ = Population size
- Mi = Number of individual marked at visit (i)
- Ci = Number of captured individuals at visit (i)
- Ri = Number of individuals recaptured at visit (i)
- K = Number of visits per sample area
- j = Number of periods with recaptures
- i = Sample period
- s = Standard deviation of the sample
- s^2 = Sample variance
- SE = Standard error of mean of sample

APPENDIX 2. Schumacher Method for Population Estimation.

$$\hat{N} = \frac{\Sigma(Mi^2\ Ci)}{\Sigma(Mi\ Ri)} \qquad \text{Equation 4}$$

$$SE \text{ of } \frac{1}{\hat{N}} = \frac{s}{(Mi^2\ Ci)} \qquad \text{Equation 5}$$

$$s^2 \text{ of } \frac{1}{\hat{N}} = \frac{\frac{(Ri^2)}{(Ci)^2} - \frac{(\Sigma Mi\ Ri)^2}{(\Sigma Mi^2\ Ci)}}{j-1} \qquad \text{Equation 6}$$

Abbreviations used were:

- $\hat{N}$ = Population size
- Mi = Number of individual marked at visit (i)
- Ci = Number of captured individuals at visit (i)
- Ri = Number of individuals recaptured at visit (i)
- K = Number of visits per sample area
- j = Number of periods with recaptures
- i = Sample period
- s = Standard deviation of the sample
- s^2 = Sample variance
- SE = Standard error of mean of sample

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