ABSTRACT

Joe H. Clayton. SEASONAL DISPERSION PATTERNS OF THE DUSKY SALAMANDER, DESMOGNATHUS FUSCUS, IN THE COASTAL PLAIN. (Under the direction of Susan J. McDaniel) Department of Biology, May 1974.

The dispersion patterns of the dusky salamander, Desmognathus fuscus, from primary seepages in Pitt County, North Carolina, were determined during a period from September 22, 1972, to September 16, 1973. One thousand quadrats, 0.6 meters square, were established in a natural area and a randomly selected ten percent were collected once a week for the 52 weeks. In the 5,200 quadrats sampled, 784 dusky salamanders were observed. Correlations of dispersion to several measured environmental factors were analyzed.

The dispersion pattern of D. fuscus was found to be clumped on a yearly and seasonal basis. The monthly analysis of dispersion found the duskies clumped except for the months of January and May. As the density of the sample population increased, so did the number of clumped quadrats. Clumped quadrats generally contained salamanders of different sexes and sizes during all parts of the year.

Field studies indicated that environmental temperature was an important factor in determining relative abundance and dispersion patterns. In general, the sample population dispersions were not correlated with moisture gradients from rainfall or cloud cover. It was not easily determined whether the clumping of the salamanders was due to temperature changes, the result of the changing of the

seasons, or a combination of the two. *D. fuscus* does seem to have a longer activity period in the milder climate of the coastal plain compared to the same species in mountain areas.

Although no vigorous test for territoriality was maintained, existence of territoriality other than that of the possible nesting and mating behavior is doubtful. Mating and nesting behavior probably influenced the dispersion patterns in spring reducing clumping relative to abundance.

Cover was considered a very important factor in determining the dispersion patterns of *D. fuscus*. The general consensus from past and present research is that as cover increases, the salamanders tend to disperse at random.

SEASONAL DISPERSION PATTERNS OF THE

DUSKY SALAMANDER, *DESMOGNATHUS FUSCUS*,

IN THE COASTAL PLAIN

A Thesis

Presented to

the Faculty of the Department of Biology

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In Partial Fulfillment

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Master of Arts in Biology

by

Joe H. Clayton

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INTRODUCTION

Spacing patterns among animals are known to vary. Spacing is brought about by the manner in which different individuals of a species react to each other and to features of the environment. The dispersion pattern of a species has important effects on the population dynamics, population genetics and evolution of a species (Brown and Orians, 1970).

Studies on dispersion patterns have shown species in which individuals actively avoid each other, have only chance meetings or are present in aggregations (Brown and Orians, 1970). When animals avoid each other and actively defend an area, they are displaying territorial behavior. Animals that express strong territorial behavior usually have dispersion patterns that are negatively contagious or uniform. When a habitat is uniform and environmental conditions such as temperature, moisture and food availability permit, animals tend to disperse randomly if social behavior does not serve to alter the pattern. If the habitat is not uniform and/or environmental factors cause stressful situations then aggregations of animals may occur, depending again upon social behavior.

Previous research on spacing patterns includes invertebrates, fish, amphibians, reptiles, birds and mammals (Brown and Orians, 1970). Animal populations rarely appear to exhibit random dispersion within their habitats. More often they form aggregations or disperse evenly as in the case of territorial animals.

Brookside salamanders appear to be likely species for random distributions because the habitat area is relatively uniform. Aggressive behavior which might result in uniform spacing of males has also been reported in salamanders (Grant, 1955; Hutchison, 1959; Organ, 1961). In all of these cases, the defended areas are very small and agonistic responses do not occur until the intruding individual is close to the resident. The function of the defense may be mating, resting, hiding or foraging space.

Studies on the dispersion patterns of *Desmognathus fuscus* in the mountains of Pennsylvania were done by Sherbine (1969) and Stewart and Bellis (1970). They concluded that *D. fuscus* was distributed randomly except for possible hibernation aggregations. The differences between the mountains and coastal plain in geography, climate and other environmental variables might be sufficient to change dispersion patterns or their seasonal variations. The objective of the present study was to determine the dispersion patterns of the dusky salamander, *Desmognathus fuscus* Rafinesque, in the coastal plain.

A living system reacts to the quality and quantity of environmental conditions by producing a response which is a function of those conditions. Previous research on the effects of temperature on salamanders (Blanchard, 1933; Vernberg, 1953; Rosenthal, 1957; Fitzpatrick, Bristol and Stokes, 1972; Spotila, 1972) indicated that temperature was an important factor in determining behavior and dispersion patterns. Barbour, et al. (1969) found that *D. fuscus* moved during wet weather, but did not find a significant correlation with rainfall and maximum or minimum activity. Sherbine (1969) found *D. fuscus* clumped under boards on overcast days and randomly dispersed on non-overcast days.

The present study was also designed to determine the effects of several environmental variables such as those above on the dispersion pattern of *D. fuscus*.

Study Area

The two test locations, located within 600 meters of each other, were two kilometers north of Falkland, Pitt County, North Carolina, 1000 meters off North Carolina State Highway 43 (Figure 1).

The collecting areas were spring-fed, uniformly poorly drained, primary seepages of clear water, with a flow that did not fluctuate widely throughout the year. Both areas were in steep-sided gorges with the open end facing north and feeding water to Otter Creek, a tributary of the Tar River. Although both areas were located within 30 meters of Otter Creek, they were not flooded when flood conditions prevailed several times during the study period. Elevation of the collecting sites was approximately 16 meters above sea level (Powell, 1968).

The sponge-like floor of the forest was comprised of vegetative debris which varied in depth from two cm. to 20 cm. during the year. The soil was silt or muck with silt-stone and clay as the subsoil substrate.

Forest structure was typical of the sand hill swamp forest (Wells, 1967). The upland portion was composed primarily of swamp oak (*Quercus michauxii* Nuttall) and beech (*Fagus grandifolia* Ehrhart) and the flood plain portion of bald cypress (*Taxodium districhum* Richard). The shrub layer, averaging two to three meters in height, was dominated by mountain laurel (*Kalmia latifolia* Linnaeus) and holly (*Ilex opaca* Aiton). The herb layer was best developed in the spring and early summer and was best characterized by chain fern (*Woodwardia areolata* Moore), jewel-weed (*Impatiens capensis* Meerb), jack-in-the-pulpit (*Arisaema triphyllum* Schott) and lizards tail (*Saururus cernuus* Linnaeus).

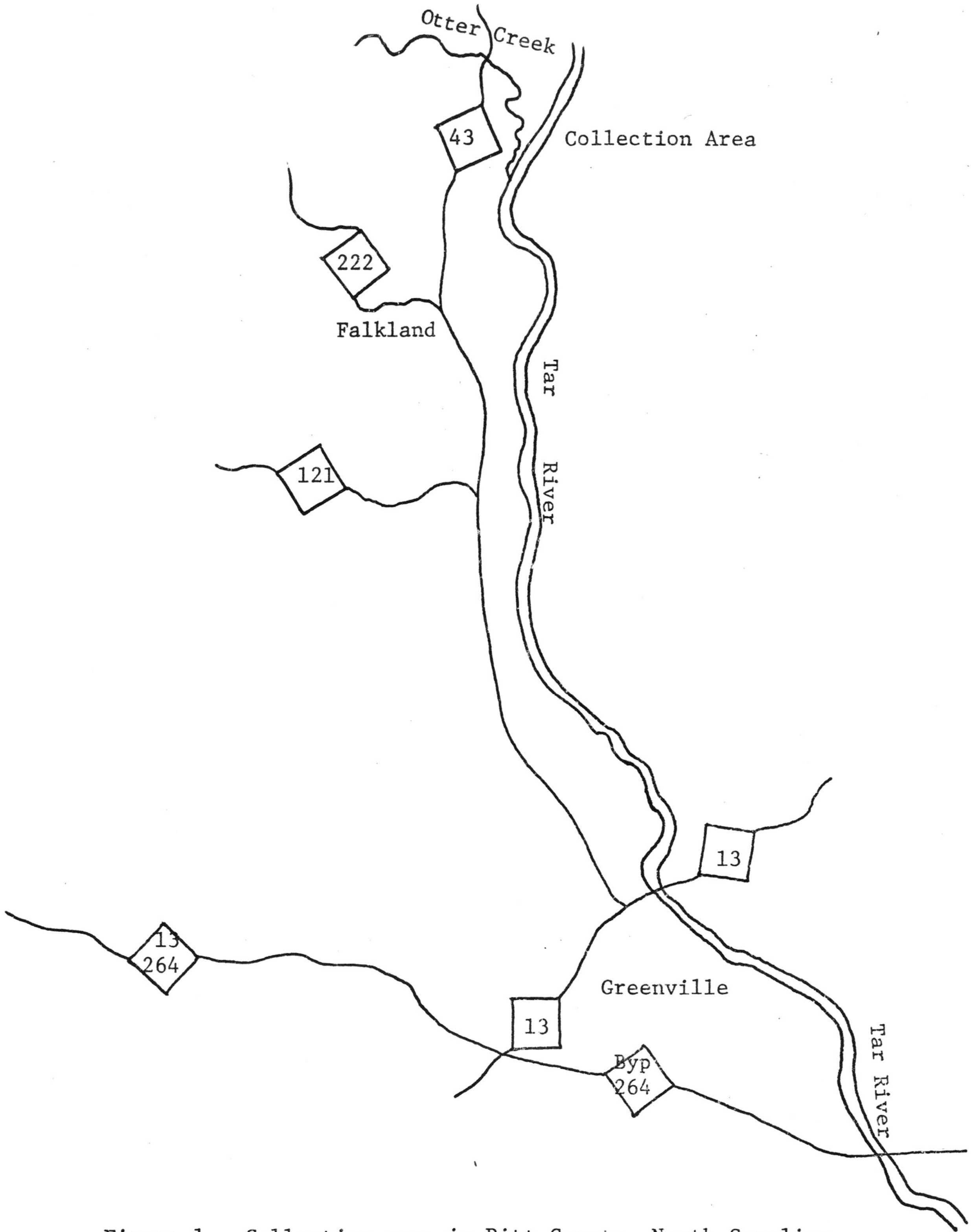

Figure 1. Collecting area in Pitt County, North Carolina (from Pitt County map: N. C. State Highway Commission, Raleigh, North Carolina)

MATERIALS AND METHODS

Salamanders were collected from quadrats. Large macroquadrats, six meters square, which contained one-hundred smaller quadrats, six-tenths meters square, were identified (Figure 2). String was tied to stakes to form these macroquadrats and was left standing throughout the test year. Each of the two major areas had five macroquadrats. Every attempt was made to place the macroquadrats in areas where each would have an equal opportunity to represent breeding, feeding and hibernating habitats for the dusky salamander. Both seepage areas and slightly drier areas were included to ensure habitat coverage.

Fifty-two collections were made every four to ten days (generally seven days apart) from September 22, 1972, to September 16, 1973. Collections were made no more than once a week to reduce movement through the area, handling of the test populations and possible disturbance to the population's distribution patterns. Collections were made during the morning (1000) and afternoon (1300) with the majority being around noon (1200) to take advantage of the period of best light in which to find the salamanders.

Macroquadrats were represented by letters (A and B) for each area and numbers (one through five) while quadrats within each were represented by numbers one through 100. Ten quadrats were selected randomly using a random table of numbers for each of the ten macroquadrats (Shefler, 1969; Sokal and Rohlf, 1969a). In all, 100 quadrats were sampled on each collecting date by placing a wooden frame, 0.6m square, on the ground at each selected test quadrat and carefully examining the surrounded area.

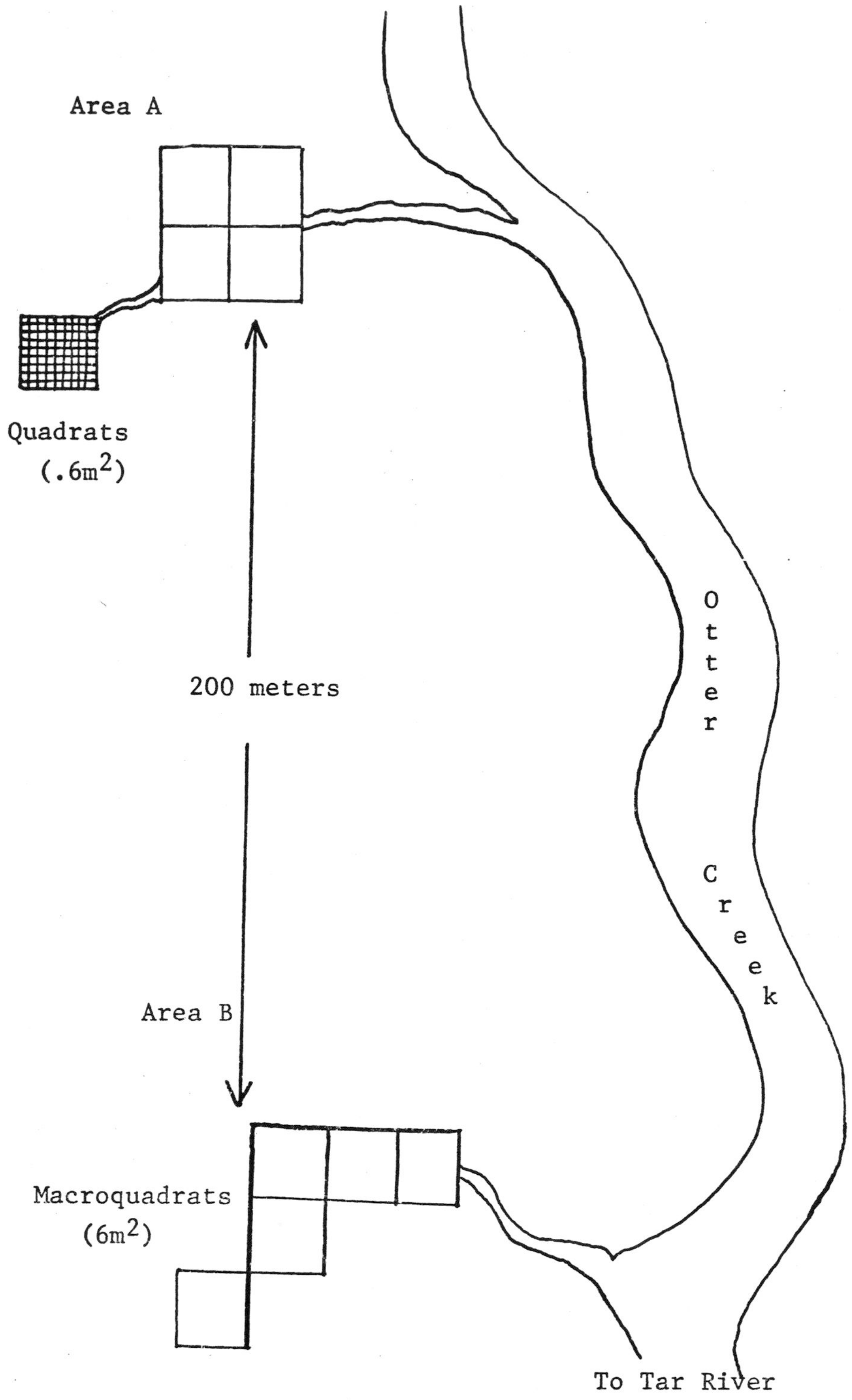

Figure 2. Collection macroquadrats and quadrats

The number of salamanders of each species collected in each quadrat was recorded. Snout-vent length was recorded for all salamanders observed as well as the sex of salamanders over three centimeters long. All macroquadrats and microquadrats randomly selected and surveyed over the period were recorded.

A marking system was initiated at the onset with clipping of the toes of the test populations. This later proved to be unsatisfactory as the population was growing back toes at a faster rate than reported by Schauble (1972). The excess handling necessary for the marking procedure was thought to influence some of the handled salamanders to move away from the test area. To make conditions as natural as possible, every attempt was made to handle the specimens as little as possible. If a specimen was handled, it was released in the same quadrat in which it was found.

On each collection date various environmental factors were observed and recorded. Air temperature was recorded outside the canopy and under the canopy at the collecting site at the time of collection. Maximum and minimum air temperatures at the collecting site since the previous collection were also noted. The water temperature of the streams at both collection sites was recorded. General climatic conditions of wind and weather were noted as well as the rainfall accumulation on the forest floor since the previous collection date. Cloud cover was described as overcast or non-overcast and given numerical values of 5 and 0 respectively for later statistical analysis. A ground description of water accumulation was determined for each collection date. The description was quantified using one of the following five values.

(1) Standing water.

(2) Upper leaves wet.

(3) Upper leaves damp and lower leaves wet.

(4) Upper leaves dry and lower leaves damp.

(5) Very dry.

Ground cover variation whether it involved increased vegetative growth, falling leaves, dead limbs or other debris was noted. Other factors thought to influence the behavior of salamanders such as food availability, predators, etc. were also recorded.

A preliminary study was made on April 23 and 29, 1972. The results from that study indicated a feasible study.

Statistical determination of the distribution of the population studied used the Poisson distribution to derive expected distribution and Chi square to test goodness of fit. The completely randomized method of collecting salamanders allowed observed data to be compared to Poisson distributions calculated from sample means. The .05 level of significance was used. Coefficients of dispersion were also calculated aiding determination of the degree of dispersion. Data were pooled and treated to determine monthly, seasonal and annual dispersion patterns.

Product-moment correlation analysis of associations between two variables was used to determine the degree of association of various environmental variables with the frequency of occurrence of the study animal.

RESULTS

In the 5,200 microquadrats observed during the study, 784 dusky salamanders (*Desmognathus fuscus* Rafinesque) were observed. Three other species of salamanders were observed in the quadrats studied. *Eurycea bislineata cirrigera* (Green) was the most frequent with 79 reported; *Plethodon cinereus cinereus* (Green) and *Ambystoma maculatum* (Shaw) were each found on only one occasion. The total number of duskies observed per trip ranged from 1 (January 14, 1973) to 39 (September 16, 1973) with an average of 15.07 duskies per trip.

The observed dispersion pattern of *Desmognathus fuscus* is presented in Table I with the frequency of salamanders per quadrat (0-5). Using the Poisson distribution, an expected frequency was estimated from the mean of the sample population (Sokal and Rohlf, 1969b). Expected frequencies for the quadrats observed are also presented in Table I. Expected and observed frequencies on a seasonal basis are displayed in Table II where fall (collections during the months of October, November and December), winter (January, February, March), spring (April, May, June) and summer (July, August, September) are the seasons. A total for the year is also given in Table II.

The degree to which the sample population was randomly dispersed was determined by the relationship of the observed data to the Poisson distribution. Chi square was used to test the goodness of fit (Sokal and Rohlf, 1969b).

That the observed frequency did not deviate significantly from the expected (Poisson) frequency constituted the null hypothesis.

TABLE I

MONTHLY DISPERSION OF DUSKY SALAMANDERS

Month	No. of quadrats sampled	Observed number of quadrats with various frequencies						Total observed	Total clumped quadrats[1]	Expected number of quadrats with various frequencies[3]						Chi-square	C.D.[2]
		frequencies								frequencies							
		0	1	2	3	4	5			0	1	2	3	4	5		
Oct.	400	335	40	16	4	5	0	104	25	308	80	13.2	.90	.035	.0031	738.02*	1.86
Nov.	400	360	31	5	3	0	1	55	9	349	47	3.1	.14	.004	.0001	10,062.67*	1.73
Dec.	500	447	42	9	2	0	0	66	11	438	58	3.8	.16	.005	.0001	31.67*	1.32
Jan.	400	374	24	2	0	0	0	28	2	373	27	.9	.02	.000	.0000	1.70	1.07
Feb.	400	368	27	4	0	1	0	39	5	363	35	1.6	.05	.001	.0000	764.82*	1.42
March	400	370	21	8	0	0	1	42	9	358	39	2.1	.07	.002	.0000	21,762.23*	1.75
April	500	458	32	6	4	0	0	56	10	447	50	2.8	.09	.002	.0000	170.47*	1.67
May	400	355	41	3	1	0	0	50	4	353	44	2.7	.11	.003	.0000	7.40	1.11
June	500	439	46	14	1	0	0	77	15	428	66	5.0	.26	.009	.0003	24.82*	1.29
July	400	345	41	9	4	1	0	75	14	331	62	5.8	.36	.017	.0006	104.31*	1.53
Aug.	400	355	33	10	2	0	0	59	12	345	51	3.7	.18	.006	.0002	34.72*	1.39
Sept.	500	412	56	23	6	2	1	133	32	383	102	13.5	.86	.067	.0042	337.44*	1.68

*Indicates significant deviation from $H_o = f = \hat{f}$ $P_{(.05)} \geq 9.48$ with df=4

[1]A clumped quadrat contains two or more salamanders.

[2]Coefficients of Dispersion.

[3]Determined by Poisson distribution.

TABLE II

SEASONAL DISPERSION OF DUSKY SALAMANDERS

Season	No. of quadrats sampled	Observed number of quadrats with various frequencies						Total observed	Total clumped quadrats	Expected number of quadrats with various frequencies[2]						Chi-square	C.D.[1]
		frequencies								frequencies							
		0	1	2	3	4	5			0	1	2	3	4	5		
Fall	1300	1142	113	30	9	5	1	225	45	1093	189	16.3	.93	.039	.0014	1,452.2*	1.51
Winter	1200	1112	72	14	0	1	1	109	16	1096	99	4.4	.13	.002	.0001	10,454.2*	1.46
Spring	1400	1252	119	23	6	0	0	183	29	1229	160	10.4	.45	.014	.0001	94.4*	1.31
Summer	1300	1112	130	42	12	3	1	267	58	1059	217	22.3	2.27	.104	.0033	478.5*	1.58
Year	5200	4618	434	109	27	9	3	784	148	4477	665	53.4	3.78	.159	.0049	2,607.52*	1.54

*Indicates significant deviation from $H_o = f = \hat{f}$ $P_{(.05)} \geq 9.48$ with df=4

[1]Coefficients of Dispersion

[2]Determined by Poisson distribution

Significance was indicated at the .05 level with four degrees of freedom. Results of the significance tests are displayed in Table I.

When comparing distribution data pooled by months to the Poisson distribution it was found that the Chi-square values were significant in all but May and January. On these two months the null hypothesis of randomness of dispersion was accepted. As shown by significant Chi square values, observed frequencies deviated significantly from expected frequencies; during all other months and periods this indicated a contagious or clumped dispersion.

If a contagious distribution was present, as indicated by the majority of Chi square values, then there would be an excess of quadrats with zero and more than two organisms as compared with the expected values. This would result in a large variance in the study population. Using a sample variance and the sample mean, the coefficient of dispersion was estimated (Sokal and Rohlf, 1969b). The ratio of the variance to the mean is close to unity or one if the observed data follow the Poisson distribution. As this ratio becomes greater than one the dispersion pattern is more contagious or clumped. Calculations for the coefficients of dispersion are also indicated in Table I. This statistic also indicates that the only two months during which dispersion approached random were January and May. Coefficients of dispersion in Table II indicate that both on a seasonal and yearly basis the salamanders had a contagious dispersion.

Some indication of the population age structure was gained from the recorded snout-vent measurements (Spight, 1967). A catch-curve representing the frequency of various sizes of salamanders for the entire year is presented in Figure 3. Size-specific survivorship for the year is represented in Figure 4. This curve represents the percent survivors from the juvenile population for each size specific group for the collection (Barns and Stanbury, 1951). The frequency of occurrence of juveniles (snout-vent length less than 25 mm), transforming juveniles (25 to 36 mm) and adults (greater than 36 mm) during each month is represented in Figure 5.

No estimates of birth and death rates were made. There were several occasions when eggs of dusky salamanders were observed. On April 1, 26 to 30 eggs hatching larvae of 10 to 11 mm were found under a large siltstone. In that instance, a male (59 mm) was found in the same quadrat. On September 9, a clutch of 14 eggs was found in a quadrat with a female (37 mm) and a male (42 mm) salamander. These eggs were later observed hatching on September 21. Another clutch observed on September 16 had 14 to 16 eggs accompanied by a female (45 mm) and a male (50 mm) in the same quadrat.

There were only two instances of finding dead dusky salamanders. One was found on March 2 (15 mm) and another on March 18 (16 mm).

Food in the form of worms (Oligochaeta), various crustaceans (Copepoda, Isopoda) and insect larva (Coleoptera, Diptera) was available all year. During the coldest days of winter (January, February), insect larvae were plentiful beneath the debris of litter.

Potential predators, water snakes (Natrix sipedon Linnaeus) were observed on June 15 and 29, 1973. After one of these snakes was brought to the laboratory, it readily consumed dusky salamanders.

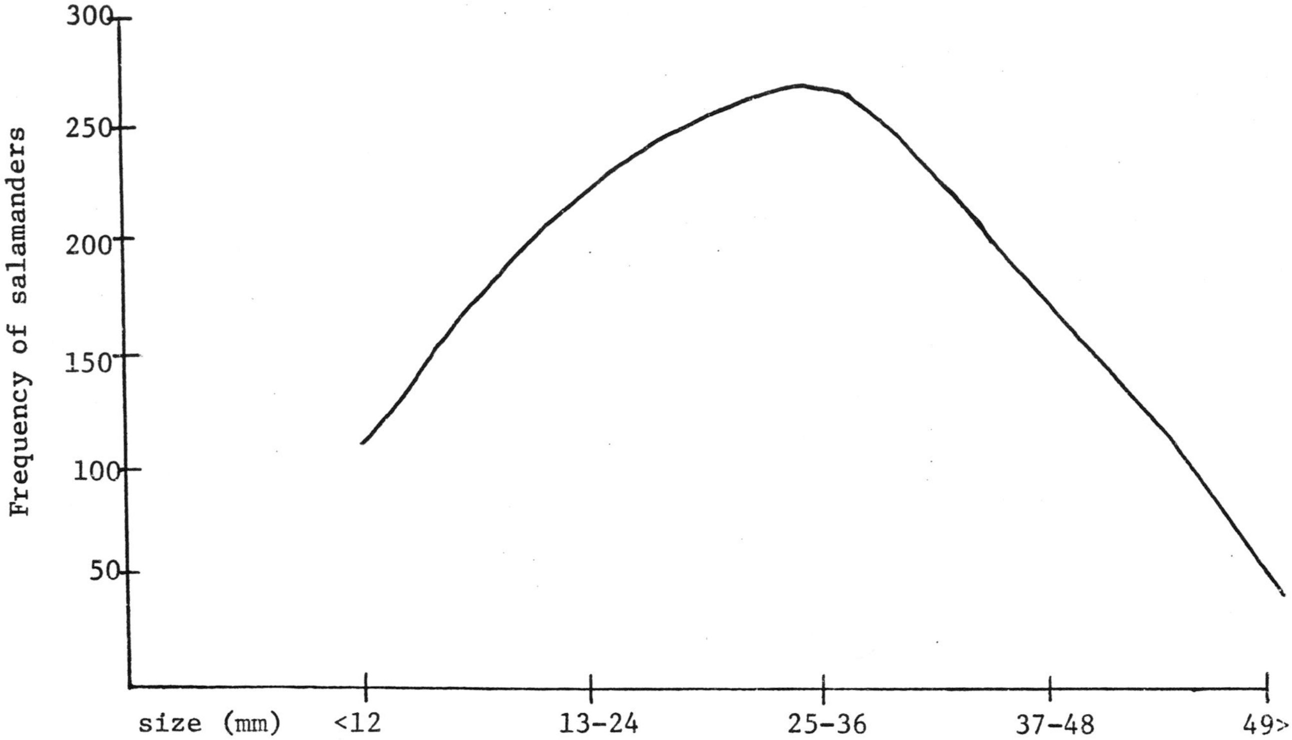

Figure 3. Size Catch Curve

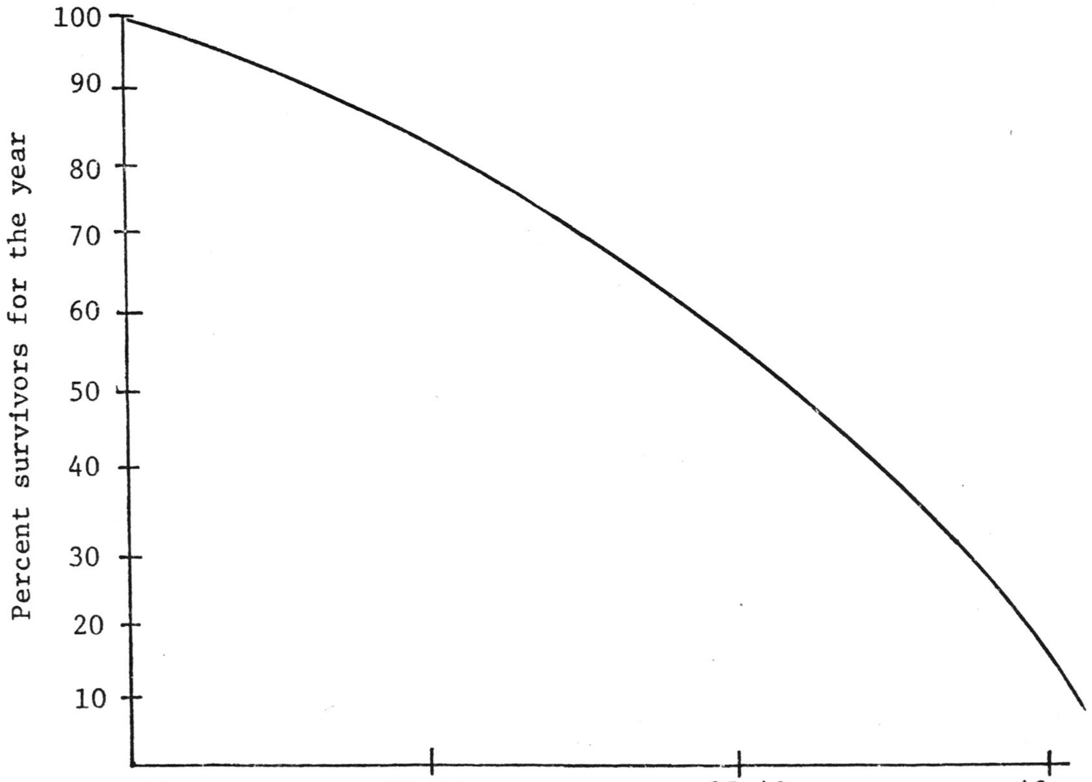

Figure 4. Survivorship Curve

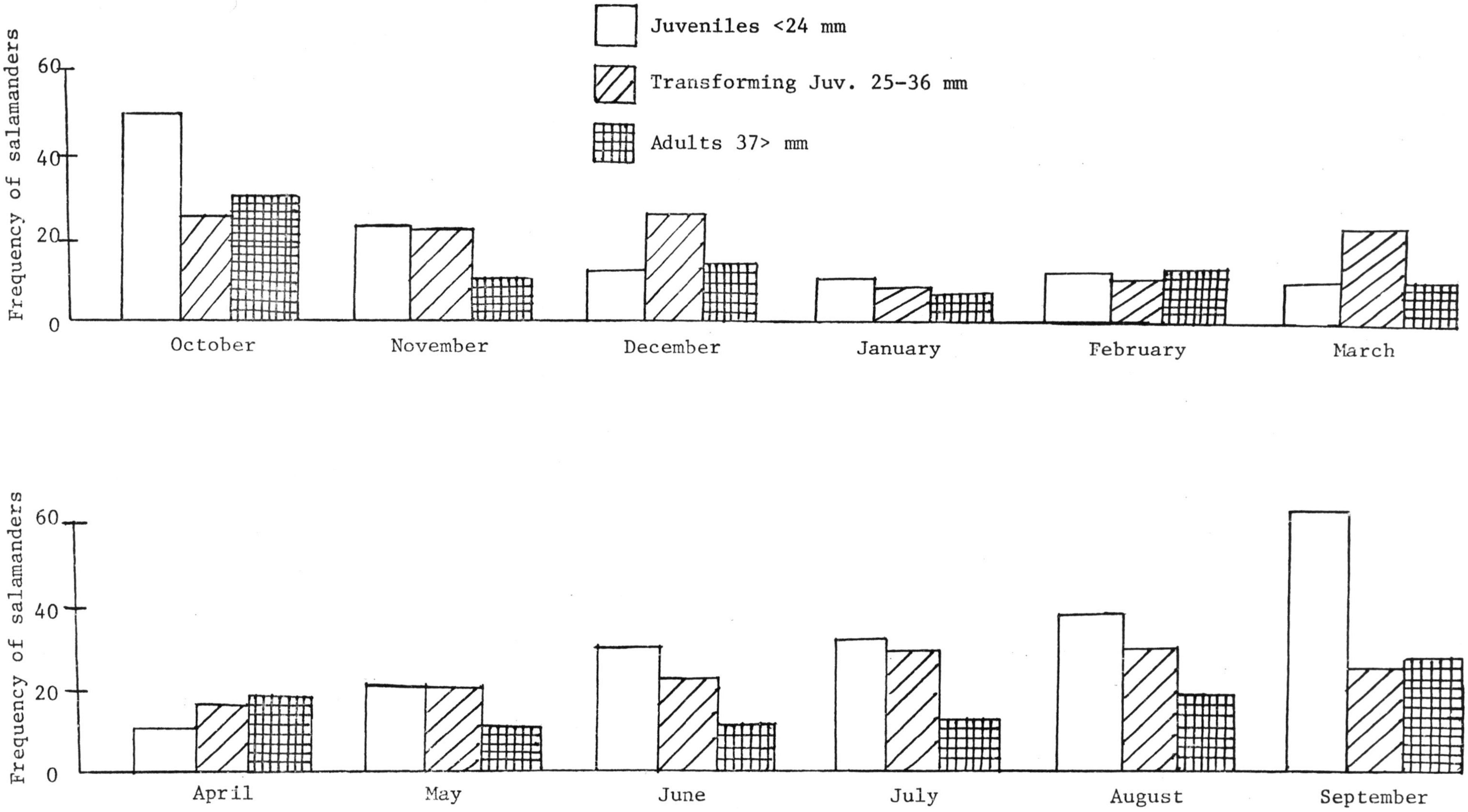

Figure 5. Monthly Trend of Frequency of Salamanders

Data collected weekly on frequency of salamanders, frequency of clumped quadrats (those containing two or more salamanders), air temperature, water temperature, cloud cover, rainfall and description of ground water accumulation were converted to moving averages as follows. Weekly data for each parameter were placed in order of occurrence from the first collecting date on September 22, 1972, till the last collecting date on September 16, 1973. The mean of the first four numbers was computed; this mean and the next three numbers were averaged; this second mean and the next three numbers were averaged to compute the third moving average and so on through the 52 measurements (Pollack and Sterling, 1968). The mathematical representation of the above is:

$$\bar{x}_1 = \Sigma\frac{(a+b+c+d)}{4} \qquad \bar{x}_2 = \Sigma\frac{(x_1+e+f+g)}{4} \qquad \bar{x}_3 = \Sigma\frac{(x_2+h+i+j)}{4}$$

(first moving average) (second moving average) (third moving average)

This procedure developed 17 points (moving averages) representing 52 collecting dates starting with the month of October. Figure 6 displays the moving averages for air temperature, water temperature, frequency of clumped quadrats and frequency of salamanders. Figure 7 displays the moving averages for rainfall and ground description of water accumulation.

To find the degree of association between pairs of variables in the sample population, product-moment correlation analysis was conducted (see Table III) (Sokal and Rohlf, 1969b).

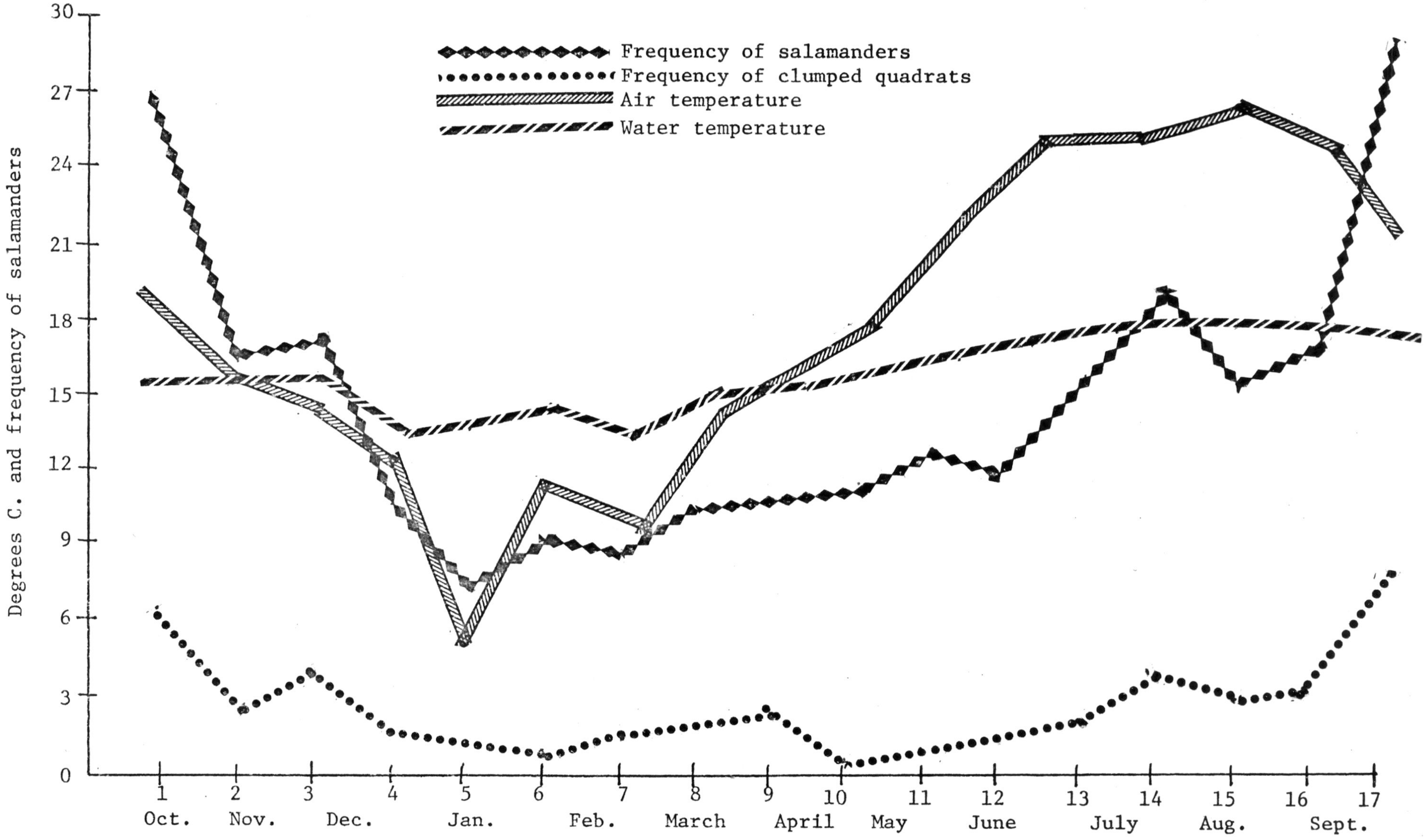

Figure 6. Moving averages representing 52 collection dates for the test year

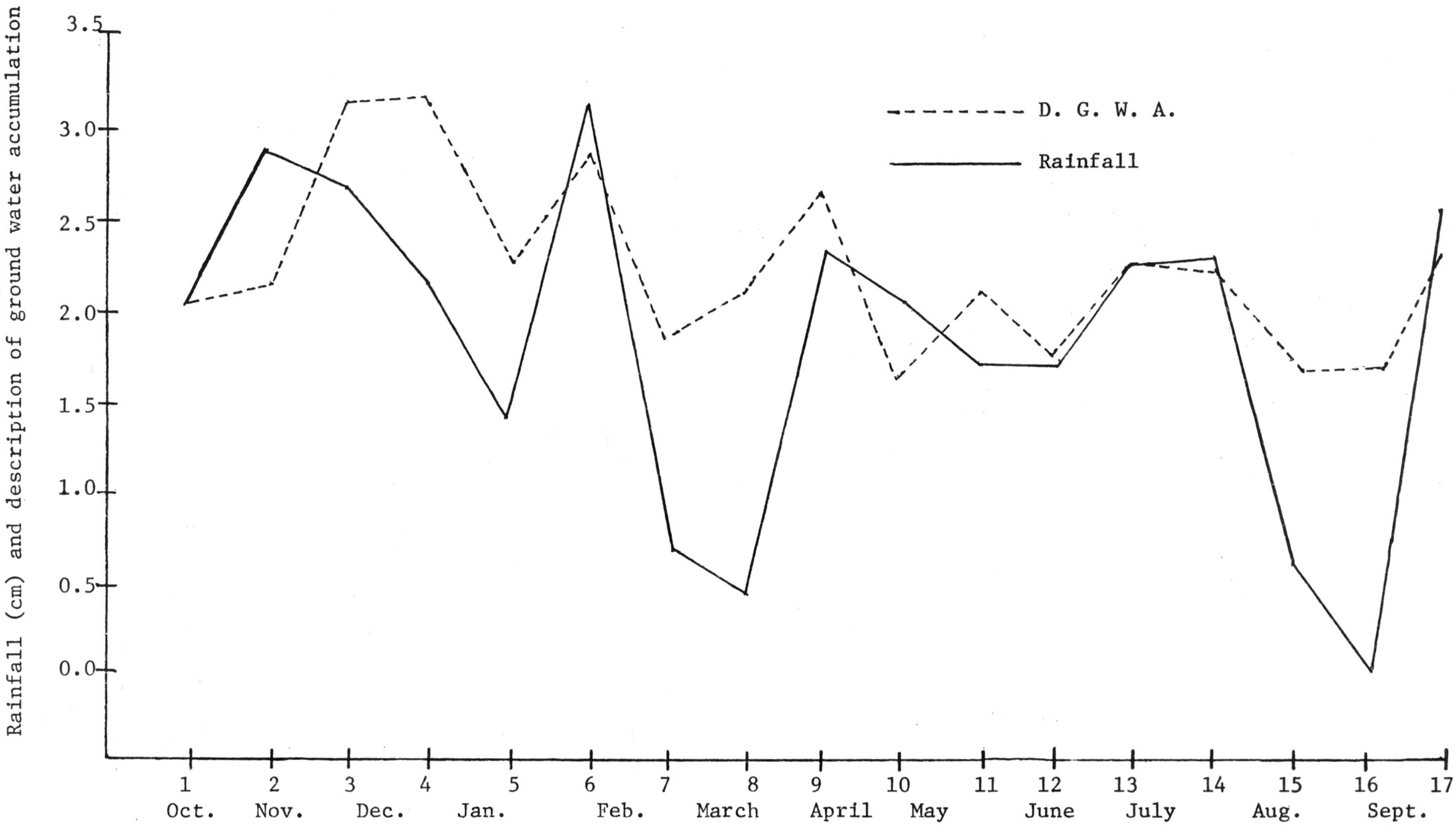

Figure 7. Moving averages for description of ground water accumulation and rainfall throughout the test year

TABLE III

CORRELATION COEFFICIENTS BETWEEN VARIOUS PARAMETERS MEASURED OVER THE COURSE OF THE EXPERIMENT

	Frequency of duskies	Frequency of clumped quadrats
Water accumulation	.44	.21
Description of ground water accumulation	.47	-.05
Air temperature	.58*	.52
Water temperature	.64*	.59*
Overcast vs non overcast days	.12	.17

*Indicates significance for correlation between the parameters compared

$H_o = r \not> r_t$ $P_{(.05)} > .578$ with df=15

The null hypothesis was that the observed r was not greater than the tabulated r and therefore that the variables are independent of each other. Significance was allowed at the .05 level with 15 degrees of freedom (see Table III). If the value of the observed was greater than .574, the null hypothesis was rejected and the two parameters significantly correlated. Both air and water temperature were significantly correlated with frequency of dusky salamanders; the frequency of clumped quadrats and water temperature were correlated.

Randomness of occurrence within each macroquadrat was tested. Occurrence was defined as observation of one or more salamanders in a specific quadrat of a macroquadrat. For example, three occurrences in macroquadrat A_1-quadrat 26 would mean that on three separate occasions three salamanders were found in quadrat 26 of macroquadrat A_1. The basic assumption required for the statistical analysis of the data generated from the random collecting technique used in this study was that the collecting area was uniform. It was assumed that there was no clumpness due to habitat preference within the area tested. From the observed frequencies of number of quadrats with 0, 1, 2, 3, 4 and 5 occurrences, the Poisson distribution was calculated (Sokal and Rohlf, 1969b). Observed and expected frequencies of salamanders within macroquadrats are in Table IV.

The null hypothesis was that the observed frequency did not deviate significantly from the predicted frequency. The significance level was .05 with four degrees of freedom for all macroquadrats but B_1; it had five degrees of freedom. The results of these Chi Square tests are

TABLE IV

DISPERSION PATTERNS OF OCCURRENCES WITHIN THE MACROQUADRATS

THROUGHOUT THE TEST YEAR

Macro-quadrat	Observed no. of quadrats with the freq. of occ.[1] frequencies							Expected no. of quadrats with the freq. of occ.[2] frequencies							Chi square	C.D.[3]
	0	1	2	3	4	5	6	0	1	2	3	4	5	6		
A_1	76	19	4	1	0	0		74	22	3.3	.34	.02	.00		1.94	1.17
A_2	46	32	15	4	3	0		42	36	15.6	4.50	.98	.17		5.29	1.19
A_3	59	23	11	7	0	0		52	34	11.0	2.40	.00	.00		20.25*	1.32
A_4	74	20	5	1	0	0		72	23	3.7	.43	.03	.00		1.81	1.15
A_5	55	33	11	1	0	0		56	32	9.4	1.78	.25	.02		.88	.91
B_1	54	30	13	2	0	0	1	54	33	10.3	2.07	.32	.03	.004	249.38*	1.58
B_2	54	31	12	2	0	1		54	33	9.9	2.02	.32	.04		23.60*	1.39
B_3	49	34	10	3	3	1		45	40	14.3	3.73	.76	.12		15.76*	1.38
B_4	57	31	9	3	0	0		56	32	9.4	1.03	.26	.02		4.15	1.05
B_5	66	23	8	3	0	0		62	29	7.1	1.18	.13	.01		4.83	1.24

*Indicates significant deviation from $H_o = f = \hat{f}$ $\quad P_{(.05)} \geq 9.48$ with df=4

$P_{(.05)} \geq 11.87$ with df=5

[1]Occurrences are the number of times collections of salamanders were made within a quadrat

[2]Determined by Poisson distribution

[3]Coefficients of dispersion

in Table IV. Coefficients of dispersions calculated for each macroquadrat are included in Table IV. In macroquadrats A_1, A_2, A_4, A_5, B_4 and B_5 occurrences were randomly distributed. Macroquadrats A_3, B_1, B_2 and B_3 had contagious or clumped dispersion patterns of occurrences.

DISCUSSION

The dusky salamanders were found not to be distributed randomly; they tended to occur in clumps. These contagious patterns may be explained by one or a combination of the following.

(1) Genetically determined capacity (range of tolerance of biological response to temperature, water and/or cloud cover).

(2) General behavior and population dynamics.

(3) Habitat preference.

Temperature Response

From the fluctuation in frequency of occurrence of the dusky salamanders, it was indicated that temperature plays an important role in salamander activity and would therefore limit the activity of the animal (Prosser, 1973). These animals are seldom totally immersed in water and often are completely out of it. The fact that a high correlation existed between frequency of occurrence and water temperature may relate more to the temperature of the microhabitat of the study animal. Air temperature was measured approximately one meter above the ground surface. Field observations showed that the duskies were found at or near the surface of the soil in the moderately warmer months; as temperature decreased or increased to the extremes, they apparently burrowed further down into the soil or remained closer to moving water. Compensatory acclimation during the days or weeks of exposure to cold enabled the duskies to maintain relatively constant activity during sudden temperature changes. The effects of undercompensation under laboratory conditions at 5° C. have been demonstrated in *D. fuscus* (Fitzpatrick, Bristol and Stokes, 1972; Spotila, 1972). Through compensation, the members of the sample population were able to forage for food during early spring and fall evenings when temperatures dropped below 10° C. Because of the milder climate, more easterly populations of *D. fuscus* are felt to have a substantially longer annual period of activity (Spight, 1967).

Clumping was positively correlated with water temperature. Clumping to reduce heat loss was suggested by Rosenthal (1957). Movement to microhabitats that offer optimum thermal protection from extremes of cold and heat was indicated in the sample population. Blanchard (1933) reported aggregations of *Hemidactylium scutatum* during hibernation. Vernberg (1953) found *Plethodon cinereus cinereus* and *Eurycea bislineata bislineata* in contagious distributions in early fall. Sherbine (1969) found *D. f. fuscus* contagiously dispersed under boards at lower temperatures. He also postulated that changing day length in the fall of the year along with lowering temperatures accounted for clumping of salamanders prior to hibernation.

Water

Correlation between frequency of salamanders and clumping with water accumulation or rainfall was not significant. As the temperature and moisture conditions reached extremes, the salamanders would move underground or closer to the streams. Previous research on the time of occurrence of maximum and minimum activity related to rainfall showed no correlation (Barbour, et al., 1969). However, Barbour did state that a large percentage of the population moved during wet weather. Relative humidity (Barbour, et al., 1969), skin temperature (Hattingh, 1972), and body weight (Houck and Bellis, 1973) are considered important in transepidermal water regulation. Because the study area was generally wet or soggy all year, individuals of the study population were thought to be able to maintain effective water regulation. Although measurements of microhabitat humidity and soil moisture were not made in this study, neither appeared to affect the dispersion pattern of dusky salamanders. In general, these brookside salamanders are probably not as sensitive to moisture gradients as are their more terrestrial relatives.

Cloud Cover

Light (within its normal range in the brookside habitat) is an important factor in stimulating salamanders to seek cover. Sherbine (1969) reported *D. f. fuscus* clumped under boards on overcast days and randomly dispersed on non-overcast days. Higher relative humidity associated with overcast days generally increased activity in *Rana sylvatica* (Bellis, 1962). No significant correlation between clumping and degree of cloud cover was found in the data of this study (see Table III). Dusky salamanders are generally more active at low levels of light (Barbour, et al., 1969). Light may influence salamanders to seek cover, but does not influence the dispersion pattern (Sherbine, 1969).

Behavior and Population Dynamics

The observed distribution pattern of a species can be considered a function of the biological characteristics of a species as influenced by environment (Barns and Stanbury, 1951). Environmental variables such as temperature, moisture, quality and quantity of food, and disease organisms present can at some times change part of a population's dispersion pattern and affect its abundance. The survivorship curve gives a good indication of how well the sample population was able to cope with its environment and fill its niche (see Figure 4). The curve indicates a gradual drop in number of salamanders as they become older.

Monthly peaks of emergence of juveniles, transforming juveniles, and adults indicate the cyclic pattern of population structure (Figure 5). Eggs were found hatching early in April and late in September. Eaton (1953) found eggs and hatching larva of *Desmognathus fuscus auriculatus* Holbrook early in January and late in October in the same county. These data indicate a long mating season; it is likely then that no rare aggregations occur for breeding purposes. Notes on nesting habits of alpine *D. fuscus* suggest much shorter breeding seasons (Organ, 1961; Spight, 1967; Sherbine, 1969; Tilley, 1969). The seasonal trend in abundance increasing from March to September and decreasing from October to February, suggested that the population grew as environmental conditions and resources allowed (Table I). Eventually only a small percentage of the population remained to start the cycle over again. The annual density in the study area was .25 salamanders per square meter. As the abundance and density increased, so did the number of clumped quadrats.

Field data were analyzed to determine similarity of size (snout-vent lengths within 2 mm of each other) of salamanders in clumped quadrats. A considerably larger number of clumped quadrats (95) contained salamanders that were not the same size as compared with quadrats with salamanders the same size (53). Seasonal comparisons gave comparable results to this annual consideration.

Data were analyzed to determine whether clumped quadrats contained animals of the same or of different sexes. The sex of approximately ten percent of the sample population was established. The ratio of clumped quadrats with salamanders of different sexes to clumped quadrats with salamanders of the same sex was three to one on both an annual and seasonal basis. Chi square was used to determine whether the ratio of males to females was significantly close to one to one. The results indicated that there was indeed a one to one ratio of animals sampled on both an annual and a seasonal basis. Winter and spring collections generally had fewer females (percentage of population collected) compared to summer and fall collections. Fewer females may be present in winter and spring due to a higher mortality rate of brooding females during summer and fall (Organ, 1961).

Although the study generally indicated clumping, randomness was found during several periods, notably the months of January and May. The month of January was one of the coldest. This in itself could have sent the salamanders to deeper ground for protection from the elements and where they were not collected. A sharp decline in the number of clumped quadrats relative to abundance was noted in the spring of the collecting year, notably May. This temporary, more random-like dispersion may be due to their spring migrations from the winter hibernacula. Organ (1961) reported that salamanders of the genus Desmognathus are not able to make sexual distinctions and that males will attempt courtship with any adult of their own species. It is likely, therefore, that no attraction mechanism exists and that courtship meetings occur by chance. The probability of such meetings occurring would be increased by movement of the populations in the spring.

Territoriality

Territoriality in salamanders has been reported (Grant, 1955). Grant stated that both Hemidactylium scutatum and E. b. bislineata actively defended an area with the latter defending by biting. No such territoriality was observed in the sample population.

Existence of territories smaller than the study quadrat sizes (.6 m^2) is possible. In a test for territoriality in relation to cover size by Sherbine (1969), three board sizes of one inch thickness were used: 12 x 7 5/8 inches (.06 m^2), 6 x 7 5/8 inches (.03 m^2), and 6 x 3 13/16 inches (.014 m^2). Sherbine's distribution of D. f. fuscus under the three different board sizes did not support the existence of territories. If such exists, the size may be expected to be between 0.6 m^2, the quadrat size used here, and 0.06 m^2, the largest of Sherbine's areas.

A nesting behavior of females occurred as the author examined the eggs; they would not move from the eggs. When eggs were not present, females readily attempted to escape from view. Males courted during breeding season are known to bite and chase other courting males (Sherbine, 1969). These nesting and courting behaviors are thought to reduce the clumping tendency during the breeding seasons.

Intraspecific and Interspecific Competition

Competition for space, food, etc. should generally limit the number of animals in a specific area. The more highly populated areas sampled were areas with high concentrations of food and/or good protection from the elements. But within these areas, there were quadrats which contained no salamanders and other quadrats which contained a large number of salamanders for no apparent reason. Interspecific competition with *D. fuscus* and *E. bislineata* was not considered to be significant considering the relatively small number (79) of *Eurycea* found compared with the large number (784) of *Desmognathus*. Clumped quadrats were found containing both *D. fuscus* and *E. bislineata* as well as clumped quadrats with only one species. There was no trend of clumped quadrats of *D. fuscus* in the absence or presence of *E. bislineata*. Sherbine (1969) found associations between *D. f. fuscus*, *D. o. ochrophaeus* and *E. b. bislineata* not significantly non-random; they seemed to occur by chance. He found that the dispersion pattern for each species was distinctive. Although all three species did occupy overlapping areas the presence of one species did not significantly affect the dispersion of another.

Activity and Home Range

Considerable research has been done on activity and home range (Barbour, 1969; Barthalmus and Bellis, 1969; and Barthalmus, 1973). They concluded that the home range was small (3 meters) and that activity was at its peaks at mid-morning (0600-0900 hrs.) and late evening (2200-2400 hrs.). From this information, it is likely that the sample population did not move far from the test area, nor did a large number of other salamanders move through the area during the test period. Because most sampling was done at low activity periods, the population density was probably a conservative estimate as many salamanders may have been inactive at this time.

Habitat and Cover

In the developing community there is a continuous modification of the habitat and consequent movement of animals. As the salamander seeks food and protection from the elements and predators, it is more prone to be constantly moving to meet these new demands. From Table IV it is seen that the occurrences of salamanders were generally randomly dispersed with the macroquadrats. When the dispersion of occurrences in the macroquadrats was found to be clumped, generally just one or two quadrats having a large number of occurrences in each were found (B_1, B_2, B_3 in Table IV).

Suitable cover is considered a very important factor governing the dispersion of salamanders (Sherbine, 1969). The general consensus is that as cover becomes more abundant salamanders tend to disperse at random. Monthly analysis of Sherbine's study found D. f. fuscus to be randomly distributed with the exception of November (contagious) and May (non-contagious or uniform). Sherbine's study was made in the mountains of Pennsylvania where the study area had streams with rocky beds. As there are very few, if any, rocks to supply suitable cover in the coastal plain, the dispersion patterns tended to indicate aggregations of salamanders. Both living and dying vegetation provided the substrate under which the coastal plain salamanders hid and sought food.

It was difficult during early December and January to collect salamanders beneath the leaf cover of 5-8 inches. During late May and June, the living herb layer was fully developed and as high as 1.5 meters in some areas. This thick vegetative growth obstructed vision and hampered collection. These difficulties may have accentuated the lack of clumped dispersion patterns at these times.

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