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THE DISTRIBUTION OF THE RED-BACKED SALAMANDER, *PLETHODON C. CINEREUS*, WITHIN THE SOIL[1]

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INTRODUCTION

Salamanders have been the subjects of many ecological studies but little is known of their population ecology. It has been estimated by Conant (1952) that they are among the most abundant terrestrial animals, yet they, and any effects which they may have on their environment, are often ignored.

The purpose of this work has been to study the distribution of *Plethodon c. cinereus* within the soil as a means of interpreting field captures. Most field studies of salamanders have been based upon captures made beneath superficial shelter objects such as logs and stones, although it has been known that the salamanders thus captured might not constitute a major part of the population (Test and Bingham 1948). Seasonal differences in the surface captures may reflect differences in the behavior of individuals rather than changes in the population as by death or dispersal (Test 1955). While the mineral soil has been frequently suggested as a refuge (Conant 1952, Test and Bingham 1948, Vernberg 1953), it has not been adequately studied as a habitat. An understanding of the vertical distribution within the soil and the factors which influence this distribution is needed to interpret the surface captures. This study was intended as one step toward the prediction of the parameters of a population when the parameters of the surface population and the appropriate environmental factors are measured.

Three approaches were used: (1) a field plot in which a study of the surface captures of *Plethodon* was made under natural conditions, (2) underground cages, in which the vertical distribution could be measured under partially natural conditions, and (3) mazes, in which the

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vertical distribution could be measured under controlled, simulated soil conditions.

Methods

The animal

The red-backed salamander, *Plethodon c. cinereus*, is common in the northeastern part of the United States. The natural history of the lungless family Plethodontidae has been summarized by Dunn (1926). In this species the entire life cycle is completed on land. Breeding takes place during the summer, and the eggs are laid in crannies in logs; the female, and occasionally also the male, remain with the eggs. At hatching, during late summer or autumn, the young have lost their gills and are adapted for the terrestrial habitat (Noble 1954). The species feeds upon small invertebrates, primarily insects (Jameson 1944).

Location

The field studies were done in the William L. Hutcheson Memorial Forest, formerly known as Mettler's Woods, located on the eastern edge of East Millstone, Somerset County, New Jersey. The plot and underground cage studies were done in a portion of the woods which has never been cleared. The woods is the least disturbed forest stand on the piedmont plain in New Jersey.

The canopy over most of the forest consists of white oak (*Quercus alba*), black oak (*Q. velutina*), and red oak (*Q. rubra*), along with some red hickory (*Carya ovalis*), and shagbark victory (*C. ovata*). White ash (*Fraxinus americana*), beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), Norway maple (*A. platanoides*), and sweet cherry (*Prunus avium*) contribute to the discontinuous subcanopy between the canopy and the understory. The understory layer consists of a continuous cover of flowering dogwood (*Cornus florida*). The shrub cover is markedly influenced by drainage. On the well-drained areas (*ca.* 50% of the plot) maple-leaved viburnum (*Viburnum acerifolium*) is the principal shrubs; the herb stratum is composed of May apple (*Podophyllum peltatum*), spring beauty (*Claytonia virginica*), rueanemone (*Anemonella thalictroides*), spring cleavers (*Galium aparine*), false Solomon's seal (*Smilacina racemosa*), Solomon's seal (*Polygonatum biflorum*), jack-in-the-pulpit (*Arisaema triphyllum*), *Carex* spp., and enchanter's nightshade (*Circaea quadrisulcata*). The moss stratum is poorly developed. The poorly-drained area along the stream has a shrub stratum of spicebush (*Lindera benzoin*) and arrow-wood (*Viburnum dentatum*). This area differs from the main body of the forest by the absence of a definable understory tree stratum and by the sparseness of the canopy due to the greater concentration of blown-down trees. Several species of *Rubus*, greenbrier (*Smilax rotundifolia*), and numerous saplings occur here. Herbs are abundant. Skunk-cabbage (*Symplocarpus foetidus*), spotted touch-me-not (*Impatients capensis*), and clearweed (*Pilea pumila*) are characteristic (Monk 1957).

The soil is classified in the Penn series and is weathered from a red shale (Brunswick formation) of Triassic origin (Balloni 1958). One profile was described from an upland, well drained area as follows: A_{00} 1 in., leaf litter of deciduous trees; A_0 1 in., partially decomposed plant residues, very friable; A_1 2 in., dark gray, not continuous, rather erratic, rich in organic matter; A_2 8 in., brown, silt loam, worm holes (and mammal burrows) and roots abundant; A_3 2 in., transition zone, no abrupt change in the horizons; B_1 8 in., reddish yellow, silt loam; B2 or B-D 4 in., yellowish-red, loam; C or D, at 24 in., red, sandy loam, bedrock. The soil of the stream flood plain, and in particular at the location of the underground cages, has a different nature. The A_{00} and A_0 are thinner, the soil is very poorly drained and genetic profile development is lacking. The soil is dark gray to a depth of 10 in. where a 2 in. stone-like porous layer of clay and iron is present due to the interaction of the shifting water table and the iron from the red shale bedrock. Beneath this layer, steel-blue clay is found at least to a depth of 14 in. below the surface. Animal burrows are abundant in the upper layers.

One notably variable climatic factor during the field work was precipitation. The year 1957 was dry with rainfall of 35.27 in. or 8.76 in. below normal. In contrast, 1958 was unusually wet, with 49.81 in., 5.78 in. higher than normal. (Rainfall and temperatures are shown in Fig. 5.)

The field plot

A 70 × 90 ft plot, set up paralleling "Spooky Brook," a small intermittent stream that dries up almost every summer, was marked off in a 10-ft grid system (*cf.* Figs. 1 and 4).

Natural cover for salamanders consisted of pieces of logs of all sizes and in all states of decay, and leaf litter which almost completely covered the soil except where washed away by the occasionally-swollen stream. The pieces of logs were considered to be shelter objects and were arbitrarily classified as movable or non-movable. Those classified as non-movable were logs too heavy to be moved, pieces of dead roots partially on the surface and partially imbedded in deep

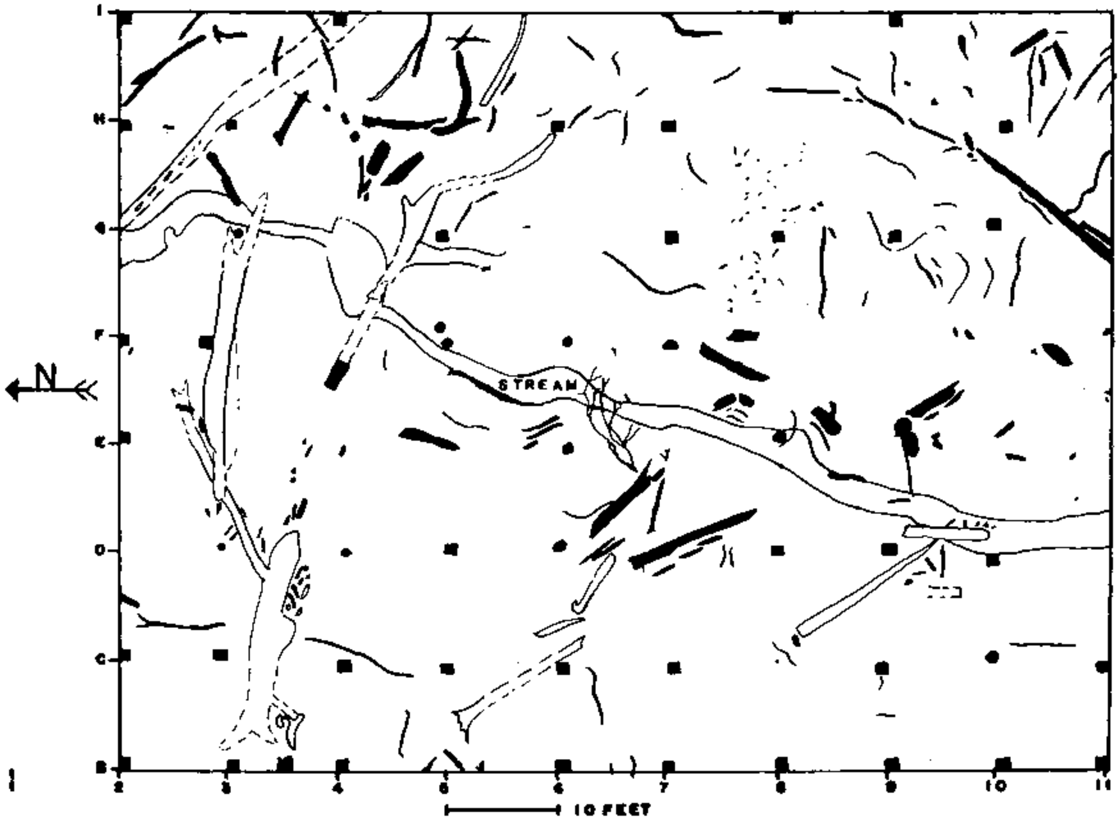

FIG. 1. Map of the research plot showing the grid system and the cover. Solid forms represent movable shelter objects and open forms represent non-movable shelter objects. Dotted lines represent logs which are suspended above the soil. The sizes and shapes of natural shelter objects are shown. Squares represent experimental shelter boards, circles represent experimentally placed rocks.

soil, and fragments too small and too numerous to move; this totaled 153 ft² within the plot. Movable cover, which could be turned for routine examination, totaled 187.5 ft². The distribution of movable and non-movable cover is shown in Figure 1. Leaf litter was not mapped because the amount varied from place to place seasonally. Roots of living plants were not counted as cover although there is no reason to suspect that they could not serve in this capacity. Logs suspended over the soil, but not touching the surface, were not counted as cover.

To this natural cover were added 39 pine boards 12 × 10 × 1 in., and one similarly-sized piece of tar paper. These were placed at grid points throughout the plot but especially in the areas deficient of natural cover. Eight stones, each approximately ½ ft² in area, were used along the stream in place of boards. These experimental shelter objects were placed during October and November 1955. Thus a total of 340.5 ft² of natural, and approximately 44 ft² of experimental, shelter occurred in the area during th study.

Between November 1955 and November 195 119 searches of the plot were made. A singl search consisted of over-turning the movable nat ural shelter objects and the experimental shelte objects and examining the surface of the objec and the litter beneath it for salamanders. Th entire plot was searched in a minimum length o time, usually one to 2 hours. These searches wer made during all hours of the day and night.

Other areas were sampled less frequently thar the plot. An area immediately outside of th plot, designated as I-1 was searched as completel and frequently as the plot after the spring of 1956 This area measured approxmiately 500 ft² anc contained 37 ft² of cover, all natural and movable The periphery of the plot was frequently searched Occasionally searches were made in the remainde of the forest.

Adults from the plot were measured, marked and released. A salamander was measured by placing it on a card and prodding it gently into a suitable position. The position of the head, vent (estimated) and tip of tail were marked on the card and measured in the laboratory. This proved to be as accurate as stretching the animal along a ruler edge and it was less time consuming and required less handling. The method was accurate to within ±2 or 3 mm for an 80 mm salamander. At this time the general condition of the animal, the location, and time of capture were noted.

Each individual was numbered by means of toe clipping. All but the smallest *Plethodon* could be marked in this manner. Despite the possibility of non-recognition of a marked animal because of the regeneration of clipped toes, toe clipping is the method recommended by Woodbury (1956) after a review of marking methods. A method of suturing was attempted, but abandoned. The animals were released at the point of capture within 5 minutes of capture.

The temperature was measured at the beginning and/or end of each search. These readings were taken at grid position A_2 at the base of a tree and on the surface of the litter. From November, 1955 to June, 1956 a thermistor was used; later a rapid-reading mercury thermometer was used. Temperatures were also taken at many of the capture sites by means of a rapid-reading thermometer. A set of maximum and minimum thermometers was left in the plot or in the cages to measure the range of temperature on the floor of the forest.

From September, 1956 to the end of the study, soil samples were taken from the majority of the capture sites. This was done by collecting 20-30 grams of soil from the exact location of the salamander capture. The soil was placed in a small vial, corked, brought to the laboratory, uncorked, weighed, dried in an oven slightly above 100°C for at least 24 hours, and reweighed. The soil moisture was expressed in terms of weight of water per weight of dry soil.

Underground field cages

Four underground cages were installed approximately 15 ft from "Spooky Brook" near the research plot. The soil in this area was that of the stream flood plain. The cages were buried to a depth of 12 in. and extended 6 in. above the soil. The cages (Figure 2) were made of plastic Saran mesh (16 threads per in.) with wooden supports. Originally the tops were fastened with eyelets and hooks around the wooden edges, but later heavy duty brass zippers were used and found to be more satisfactory. To prevent mammals from burrowing through the sides, the 4 cages were

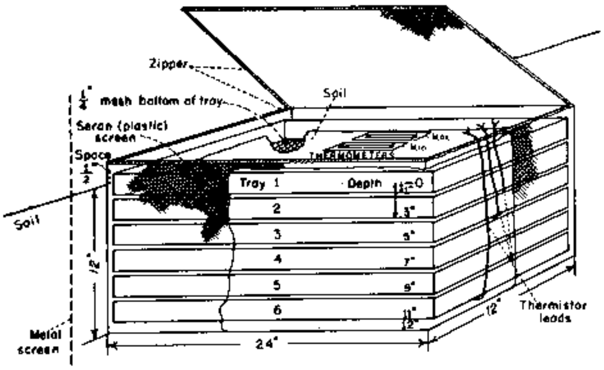

FIG. 2. Underground field cages used to study vertical *Plethodon* distribution under semi-natural conditions.

placed within an enclosure of hardware cloth that extended 14 in. below ground and 10 in. above ground level. The cages were arranged 6 inches apart in the form of a square.

Two of the cages were fitted with trays through which salamanders could pass but which would support the soil. Each tray was made of wooden sides, 2 in. high and ½ in. in thickness, with an open mesh bottom. Originally a rayon "fish net" curtain material was used, but this had to be replaced each month because of rotting. In 1958 galvanized hardware cloth of ¼ in. mesh was used after it was ascertained that the metal was not toxic to *Plethodon*. The length and width of each tray was such that it fit somewhat loosely into the plastic mesh cage. Six such trays were fitted one on top of another into the bottom of each of the cages. The cage and tray design is shown in Fig. 2. The salamanders were able to move about, between, and along the sides of the trays with little difficulty. Thus they had access to the depths of the soil either by burrowing through soil and mesh or by moving down the sides between the Saran mesh and the tray sides.

Instruments were buried in one of the trayless and one of the trayed cages when they were filled with soil. Thermistor elements were buried at the 3 in., 6 in., and 12 in. levels. During 1957 gypsum soil blocks were buried at the 3 in. and 12 in. levels to measure vertical moisture gradients. The thermistor elements and gypsum blocks were read with an A. C. ohmmeter. In 1958 soil samples were taken to measure the soil moisture in place of the gypsum blocks.

Ten *Plethodon cinereus*, collected from other locations in New Jersey, were placed in each of the four cages. These were replaced as animals died or escaped.

The trayless cages were sampled by quietly opening the lid, searching the top inch of soil and litter, recording any captures, and taking instrument readings. The trayed cages were sampled as follows: a large sheet of plastic was spread on the ground beside the cage; the trays were removed as rapidly as possible, and stacked with plastic interleaves; the trays were then individually searched and salamander captures were recorded as to tray number. The mean depth was calculated on the basis of the tray numbers in which the salamanders were found. Thus all salamanders found in the top tray, whether on top or under the litter were counted as being in tray 1. The salamanders were replaced in the trays in which they were found, and the trays were replaced in their original order.

The cages were sampled immediately before and/or after the natural plot was searched during the fall of 1957 and during the summer and fall of 1958, and once during April, 1959. Hibernation survival was measured for the winters of 1957 and 1958.

Mazes—an experimental substrate

Plaster of Paris mazes were constructed as a means of observing the vertical distribution of *Plethodon* within a simulated soil environment which required neither handling of the animals nor destroying the environment for each observation (Figure 3). The surface was exposed to light and dark cycles while tunnels below the surface were dark except for brief periods during observations. Within the mazes the changes in salamander distribution in response to various moisture and temperature gradients were measured.

Each maze was molded and used in a 10 in. diameter battery jar coated with a thin layer (*ca.*

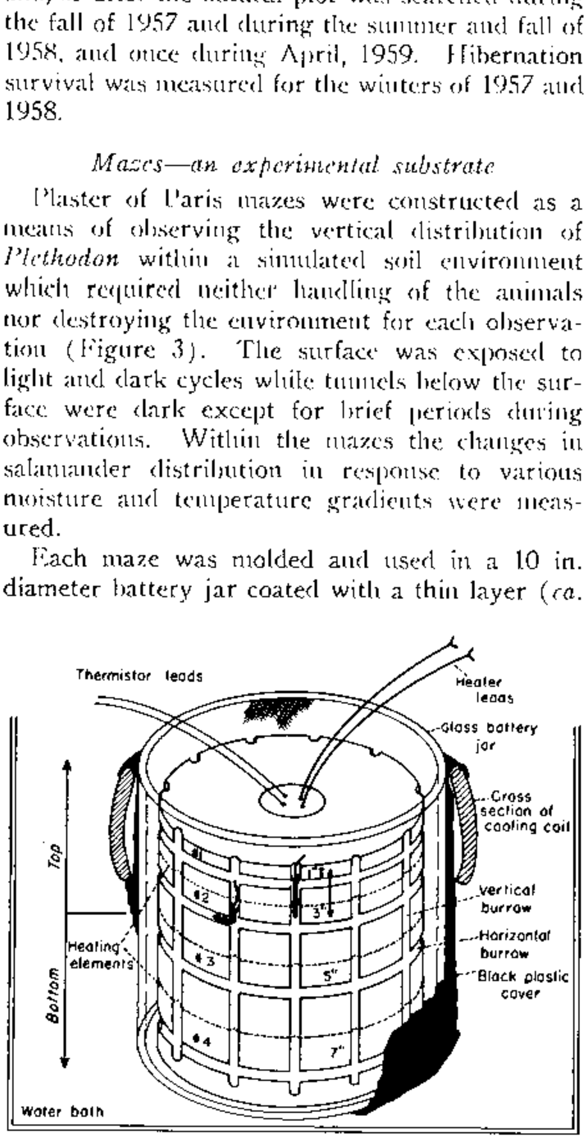

FIG. 3. Experimental mazes used to study vertical *Plethodon* distribution under controlled simulated soil conditions.

mm) of paraffin. A tall jar of 6 in. diameter was coated with petroleum jelly and placed in the center of the battery jar. Small plugs of plaster (molded from wax casts of size 2 rubber stoppers) were attached to the center jar and covered with petroleum jelly. (These plugs were intended as a means of measuring the percentage of moisture). Plaster of Paris was mixed with half its volume of water and poured into the battery jar to a depth of 2 in. This was permitted to harden, and the surface was coated with petroleum jelly. Three additional layers were poured in this manner so that the depth of the maze was 8 in. The battery jar was then turned upside down and heated so that the paraffin melted. Thus the plaster layers were removed from the glass jar. The 4 layers were then separated and cleaned. Grooves of approximately 1 cm diameter were gouged around the circumference so that they formed tunnels, or burrows. The glass formed one wall of the burrows when the mazes were placed in the battery jars. A horizontal groove was gouged in the center of each of the 4 layers and 11 vertical grooves were gouged the depth of the 4 layers. The center cavity, which remained after the inner jar was removed, provided access for instruments. This was covered with a thin layer of plaster which provided a complete surface for the salamanders. The small plaster plugs were removed, cleaned, and replaced. In use, the battery jar was covered by a black plastic cover up to the top of the plaster. The mouth of the jar was covered with a fine netting of nylon and, in later experiments, with hardware cloth.

Moisture gradients were determined at the time the mazes were set up. Two qualities of moisture were used. "Wet" was a layer soaked to take up a maximum amount of water, which required 10-15 minutes, and drained for at least 30 minutes, until it no longer dripped. "Dry" was air-dried for greater than 1 month after construction. During the course of an experiment there was a slight tendency for the dry layers to gain water while the wet layers lost water. The tendency to gain water was greater for the bottom layers.

Moisture conditions were as follows:

wet/wet	Uniformly wet—all 4 layers soaked.
wet/dry	Top 2 layers wet, bottom 2 dry.
dry/wet	Top 2 layers dry, bottom wet.

The heating equipment, installed in 3 of the mazes consisted of 660 watt Nichrome heating elements placed in heat resistant and waterproof plastic tubes. Two were placed in each maze, one between the first and 2nd layers, and the other between the 3rd and 4th layers. Canals were gouged out to hold the tubes so that the layers fitted snugly together again. Electricity was supplied through a transformer, usually at 10 to 15 volts, to either the top or bottom heaters of the 3 mazes in parallel.

Two types of cooling equipment were used. For bottom cooling the battery jars were placed in a running cold water bath to a level between layers 2 and 3. For cooling the tops of the mazes, plastic tubes of 2 in. diameter (made by heat sealing sheet plastic) were held against the battery jars by hardware cloth frames. The frames were covered with black plastic and the usual black cover came up to the bottom of the cooling frame. The temperature conditions were designated as follows:

TA	seasonal temperature, no superimposed gradient.
hot/cool	hot on top, cool on the bottom.
cool/hot	cool on top, hot on the bottom.
TB	seasonal temperature, no superimposed gradient.

Two thermistor elements were placed in one of the mazes at the top and bottom layers. Occasional checks were taken with mercury thermometers in the other mazes.

The 3 mazes with heating equipment were kept in a greenhouse and were subject to seasonal light cycles and temperature conditions, as a base upon which temperature gradients were superimposed. For each experimental run one of these mazes was set up under wet/wet, one under wet/dry and one under dry/wet moisture conditions.

One maze, which served as a control, was kept under the same temperature, lighting conditions, and moisture wet/wet, during all experimental runs. Temperature control was maintained by a constant temperature incubator placed within a constant temperature coldroom. The temperature within the incubator was maintained at 18° ± 2°C. The light cycle was regulated by a time switch to give 12 hours of light beginning at 0600 EST and 12 hours of dark. The light was supplied by a 6 watt Westinghouse bulb. (The November control sample was run with a 6 watt General Electric bulb which gave off more heat; for this reason the November control data have not been used). During the "day" the top of the maze was a few degrees warmer than the bottom, where the temperature was measured.

For each experimental run 12 salamanders were put on the surface of each of the 4 mazes on day zero, and left without the superimposition of temperature gradients (TA), until day 3, at which time observations were made at 1400 and 2000 EST. At the end of the 2000 EST observation, the 3 greenhouse mazes were subjected to cooling on the bottom and heating toward the top to produce the hot/cool condition. The mazes were maintained in this condition from the evening of day 3 through the evening of day 5, when observations were made at 1400 and 2000 EST. After the 2000 EST observation, the greenhouse mazes were subjected to heating on the bottom and cooling toward the top to produce the cool/hot condition. Observations were made of the T3 condition on day 7 at 1400 and 2000 EST. At the conclusion of T3 condition all temperature regulation was ended, and greenhouse mazes were permitted to obtain a uniform temperature (TB), which was usually similar to the first temperature condition. This was maintained until day 10 when the final pair of observations took place. Observations of the control were made immediately after observations of the greenhouse mazes. Thus each moisture condition was subjected to the same regime of temperature conditions, and the control and the 3 moisture conditions in the greenhouse were observed almost simultaneously.

Observations were made by lowering the black plastic cover and gently rotating the maze. The position of each salamander was sketched on a data sheet. Temperature conditions within the mazes were measured immediately after the observations. At night a 6 volt headlight was used for observations. The horizontal burrows were used as depth indicators, level one being 1 in. below the surface; level two, 3 in. below the surface; level three, 5 in. below the surface; and level four, 7 in. below the surface. Thus a depth of 2.5 indicates that the center of a salamander's body was between the 2nd and 3rd horizontal layers, or 4 in. below the surface.

The mazes were cleaned and soaked for each month's run. The following runs were made: 2 simultaneous runs in February (wet/wet, without temperature gradients); early May; late May; July; August; September; October; November; and December. With 2 exceptions the salamanders for each run were captured within 2 days of beginning of the run. The salamanders used in the February runs had been in captivity all winter, and the animals used in the December run were mostly those that had been used in November. The salamanders for each maze were selected randomly from the fresh captures of *Plethodon* of more than 40 mm head to tail length taken from various parts of New Jersey.

Results

Horizontal distribution and movement in litter

One hundred nineteen routine searches of the research plot yielded 145 captures of *Plethodon c. cinereus*, 118 *Eurycea b. bislineata*, and 3 *Pseudotriton r. ruber*. Within the I-1 and peripheral areas 83 *Plethodon*, 24 *Eurycea*, and 4 *Pseudotriton* captures occurred. These were the only species of salamanders found in the forest. Of the *Plethodon* captures, 5.4% were of the red phase and the remainder were of the dark phase.

The horizontal distribution of captures within the plot is analyzed with respect to the stream in Figure 4. The plot has been divided into two areas, (1) the stream and vicinity, a strip 30 ft in width which constitutes 43% of the plot, and (2) the area away from the stream, which is 57% of the plot. If the salamander distribution was independent of the stream, approximately 43% (62) of the captures should be in the vicinity of the stream, whereas only 49 of the 145 *Plethodon* captures actually occurred near the stream. A Chi-Ssquare test, showed significant differences between observed and expected frequencies ($\chi^2 = 4.8$, d.f.$= 1$, $p < 0.05$).

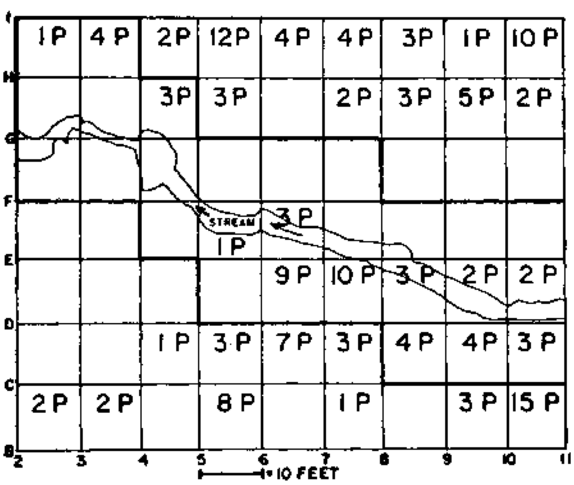

FIG. 4. Chart of the research plot showing the horizontal distribution of captures.

One hundred fifty-four *Plethodon* were marked. Twenty-four individuals were recaptured; 20 were recaptured only once, 1 was recaptured twice, 2 were recaptured 3 times; and 1 was recaptured 4 times. At the conclusion of the study the majority of the salamanders captured showed no signs of having been marked.

The horizontal movements of the animals are shown by the distances moved between captures of marked animals. Twenty-seven measurements were taken between capture sites of 20 *Plethodon* individuals. There were 14 distances of less than 1 ft (usually under the same object as the previous capture), 4 of 1-5 ft, 5 of 6-10 ft, 1 of 11-15 ft, and 3 of greater than 16 ft distance moved between captures. There was no correlation between the number of captures of an individual and the greatest distance between captures. The direction of the movements and the searches of the peripheral area gave no indication of immigration into, nor emigration from the plot.

Several searches of the plot frequently occurred between recaptures of marked individuals. A mean of 10 searches occurred between successive captures, the maximum being 56 searches of the plot; on the 57th search this specimen was found under the same object from which it had originally been captured 11 months previously. There was no correlation between the length of disappearance and the distance moved.

Effects of environmental factors on occurrence in the litter

Under natural conditions the vertical movements and resulting distribution can best be inferred by the abundance of litter captures (assuming a stationary population size). The captures are shown in control chart form in Figure 5 along with the temperature of the forest floor and the rainfall as recorded at the New Brunswick Station of the U. S. Weather Bureau. The control chart method is a statistical means of deciding whether variation is due to "chance" or are larger than would be expected due to chance alone. A point falling outside of the control limits at ± 3 standard deviations has a probability of occurrence of less than 0.01 and is said to be due to an "assignable cause." The chart here is based on a Poisson distribution because, according to Dice (1955), frequency of capture data best fit this kind of curve. For example, if the distribution is random, the number of samples in which 0, 1, 2, . . . are counted will fall into a Poisson series. This method is number 16 as described in the ASTM manual on Quality Control of Materials (1951).

Plethodon captures increased through spring, sharply decreased through the summer, and then increased sharply in the autmn in 1956 and 1958. The higher *Plethodon* captures/search tended to be made as the temperature increased during spring and as it decreased during autumn. Temperature readings taken by a rapid-reading thermometer at salamander capture sites were usually within 1°C and never more than 2°C of the temperature taken at the surface of the litter at the A_2 grid position. Therefore the A_2 grid temperature is an approximate measure of the tem-

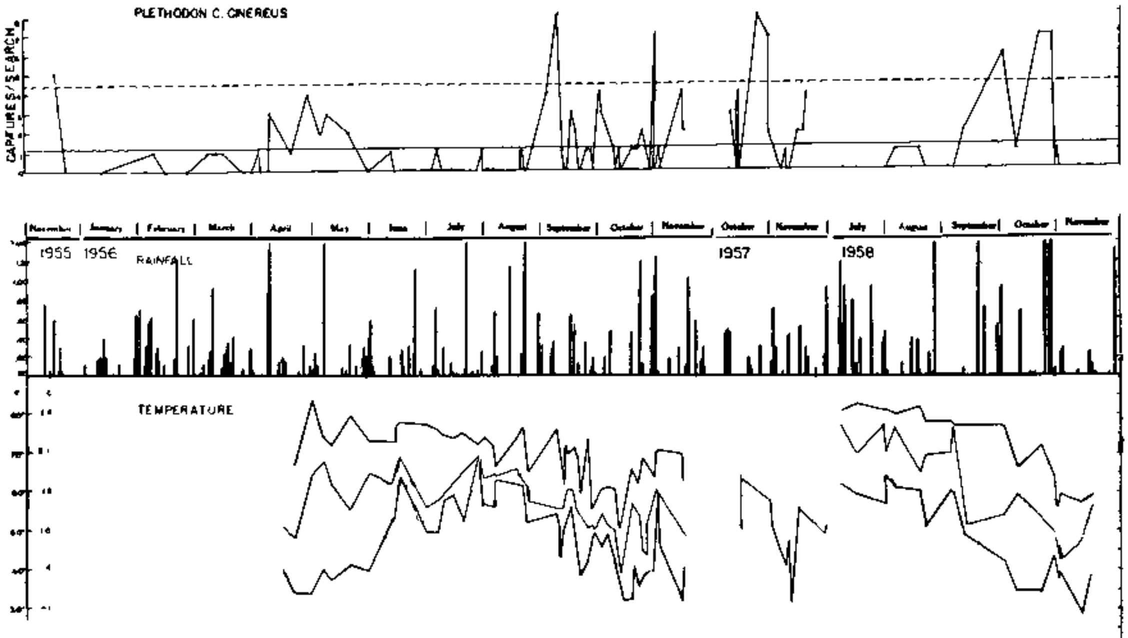

FIG. 5. Control chart of *Plethodon* captures, compared with daily rainfall, from U.S. Weather Bureau summaries, and temperature on the forest floor. The control chart refers to the numbers of captures made during each search. The center line represents the mean. The dotted line is the upper control limit at +3 standard deviations. The lower control limit for both species is 0 captures /search. In the temperature graph, the heavy lines are the maximum and minimum temperatures; the lighter line represents the temperatures at which the searches were made.

perature of all the captures made during a given search. When the number of salamanders captured at each temperature is divided by the number of searches at that temperature, any bias is removed which might have been introduced by sampling any temperature a disproportionate number of times (Figure 6). Captures occurred from 5°C to 25°C with a mean of 13.3°C (s = 9.7, n = 135). The distribution is skewed toward the lower temperatures.

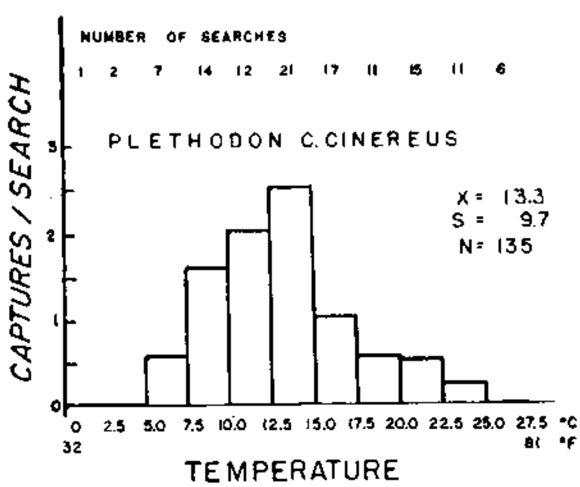

FIG. 6. Average captures per search with respect to temperature. The number of animals found at each temperature has been divided by the number of searches at that temperature.

It may be noted in Figure 5 that heavy rainfalls frequently, but not invariably, preceded unusually high numbers of captures/search. For example the heavy rains during July and August did not result in high captures of *Plethodon* during 1956 nor during 1958.

The soil moisture (weight of water × 100/ weight of dry soil) of salamander capture sites

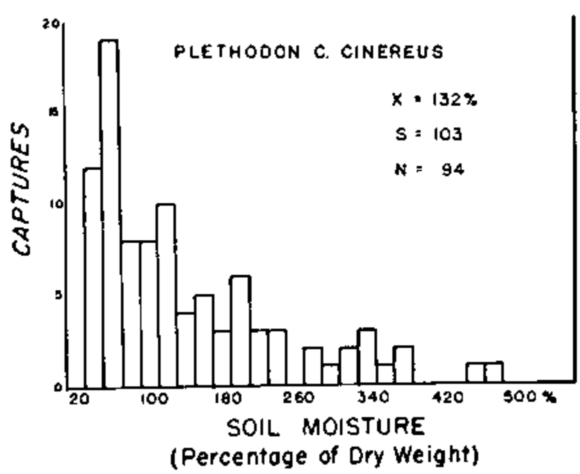

FIG. 7. Histogram of captures with regard to soil moisture.

(Figure 7) had a mean of 132% (s = 103, n = 94). The very great amounts of water reflect the high organic content of the surface soils.

The data show a mean of 1.129 captures/search (s = 1.74, n = 77) during the day as compared to 1.38 captures/search (s = 2.19, n = 41) during the night. These means were not significantly different (z = 0.72, P = 0.22).

Twenty % of the 1956 *Plethodon* captures were estimated as having hatched that year on the basis of size distribution. In 1957, an unusually dry year, only 6.5% of the captures were in the first year class. In 1958, 30% of the captures were estimated as being in the first year class.

The experimental cover yielded more salamanders per square foot (mean of 1.20) than the natural cover (.50).

Vertical distribution

Within the trayed cages *Plethodon* moved downward to the full depth of 12 inches. The average depth for the entire study was 5 in. (tray level 3.5). The mean depth for 1957 was 7 in. (tray level 4.6) while that of 1958 was 2.8 in.

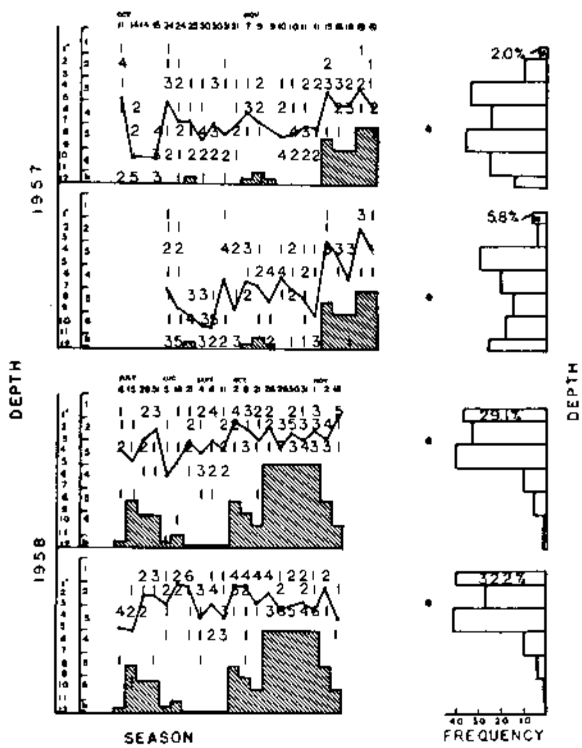

FIG. 8. Vertical distributions of *Plethodon* in the trayed underground cages. Two cages were run simultaneously. Each number represents the number of salamanders found in that tray during a single observation. The circled dot represents the average depth for each cage for each year. Summated distributions are shown to the right. The percentage of salamanders found in the surface tray (top inch of litter and soil) is indicated. The slanted lines represent the water table.

(tray level 2.3). As shown in Figure 8, the overall pattern of distribution was higher in 1958 than in 1957. The known differences between the 2 years were: (1) rainfall and therefore water table level, and (2) the addition in 1958 of bark to the natural leaf litter. Environmental factors appeared to influence the vertical distribution since trends, as shown by the changes in the means, frequently corresponded in the 2 trayed cages that were run simultaneously. The environmental factors considered were daily light-dark cycle, temperature, water table level, and soil moisture.

There was no diurnal difference in vertical distribution as shown by the means of night and day searches, both means being 3.5. More *Plethodon* were found on top of the litter at night, but there was no shift toward the surface in the overall vertical distribution. During part of 1957, equal numbers of searches were made during 4 time periods, 0000-0550; 0600-1150; 1200-1750; 1800-2350 EST (Table I). A slight tendency was noted for the distribution to be nearer the surface during the 0000-0550 period.

TABLE I. Vertical distribution of *Plethodon* during 4 time periods. Several searches have been summed for each time period

Depth in.	Tray no.	Time Period, EST			
		0000-0550	0600-1150	1200-1750	1800-2350
1	1	3	1	0	1
3	2	5	5	0	1
5	3	20	13	12	10
7	4	8	12	15	14
9	5	11	15	14	15
11	6	10	14	15	15
12	b	15	14	11	0

However, the vertical distributions of these time periods were not significantly different as tested by a Chi-square test of homogeneity ($\chi^2 = 15.66$, d.f. = 9, P = 0.07). The temperature range studied was −6°C to 25°C. Temperature seemed to have an effect only at the lower end of this range, as shown in Figure 9. No salamanders were ever found at temperatures below 4°C although such temperatures were sampled 15 times. Immediately above 4°C captures were common, although there was a tendency for salamanders to avoid all temperatures below 10°C if a higher temperature occurred in the cage. No avoidance was noted at the upper end of the temperature range studied. The temperature range over which *Plethodon* were found here, 4°-25°C, agrees almost exactly with the range over which *Plethodon* were captured in the research plot, 5°-25°C.

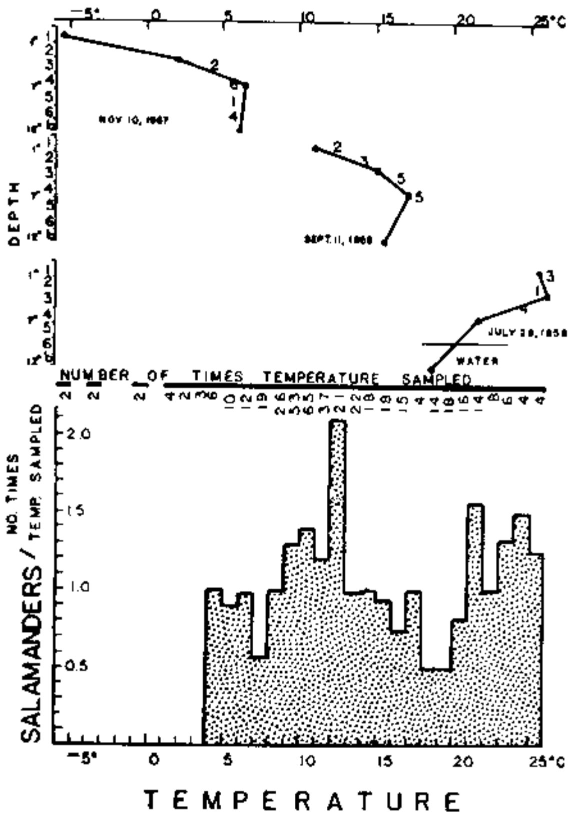

FIG. 9. *Plethodon* distribution in the trayed cages with respect to temperature. The histogram shows the frequency of capture at each temperature divided by the number of times that temperature was sampled. The temperatures sampled and the number of times each temperature was sampled is illustrated above the histogram. The salamander distributions over 3 temperature ranges are shown in the upper half of the Figure as samples of the raw data. Each number represents the number of salamanders found at that depth and temperature. The line represents the range of temperatures as measured at the surface, 3 in., 6 in., and 12 in. levels.

There was a definite avoidance of levels which were below the water table (Fig. 8). As the water table rose, in both 1957 and 1958, the entire distribution was shifted upward. Even after the water table dropped in November, 1958 the salamanders did not rapidly reoccupy the formerly inundated soil. Occasionally salamanders dropped from the sides of the trays into the water and remained there for several minutes but they always returned if the cages were not disturbed for a few minutes.

Study of the vertical distribution of soil moisture is a complex problem. Soil moisture is best discussed in terms of the tenacity with which soil water is held or the force necessary to remove water from the soil (Lutz and Chandler 1946). The percentage of water found in the soil is not necessarily a meaningful measure, since soils of different locations and of different depths at the same location are saturated at different percentages and will hold soil water with different tenacities. Thus at the site of the cages, the soil of the first 5 in. is saturated at 61.2% soil water, while the soils at depths of 6-10 in. and 11-15 in. are saturated at 35.5% and 28.6% respectively. The surface soils will also yield water more readily than the lower layers as shown in Table II. The soil in the cages was almost always saturated and the methods used here did not give as sensitive a measure as would be necessary to relate slight changes in the vertical pattern of soil moisture to the salamander distribution.

TABLE II. Water relations of the soil at the cage site (poorly drained). The percent of moisture is the amount of soil moisture remaining in the soil after extractions at tensions indicated by pF. pF is the logarithm of the height in centimeters of a column of water equivalent to the force with which moisture is held at the air-soil surface. Each value is the mean of 6 samples

Depth (in.)	% Soil Water			
	at saturation	pF 1.8 (60 cm.)	pF 2.5 ($\frac{1}{3}$ atm.)	pF 3.0 (1 atm.)
1- 5	61.2%	46.0%	44.4%	43.1%
6-10	35.5	27.0	25.7	24.1
11-15	28.6	27.1	26.5	26.0

Population estimates based on litter captures

Population estimates based on litter, results of the trayed and trayless cages during a one week period, were analyzed as described by Hayne (1949). This uses a mark and release method to estimate the population by following the increase of the proportion marked in samples drawn from the popluation as additional animals are marked. The data and calculations are shown in Table III. In the 2 trayless cages, estimates of 11.8 and 9.9 salamanders were obtained when 10 *Plethodon* had been placed in each of the cages at the beginning of the study and 9 were recovered from each of the cages at the end of the study. In the trayed cages, estimates of 4 and 4.4 salamanders were obtained when 10 *Plethodon* had been placed in each of the cages at the beginning and 8 and 9 respectively, were recovered in each at the end of the study. The low estimates result from the fact that some individuals tended to remain on or near the surface while others were not captured on the surface at all. Thus in each of the trayed cages only 3 individuals were found on the surface during the 4 searches, while 5 and

TABLE III. Record of surface captures in trayed and trayless cages, and calculation of population size estimates (estimated population, $P = \frac{wx^2}{wxy}$

Cage number	Number of Captures: Total (w)	New	Old	Proportion of catch previously handled (y)	Total no. previously handled (x)
#1 (trayless)	6	6	0	0	—
true population = 9-10	3	1	2	.50	6
	9	2	7	.78	7
	3	1	2	.33	9
		P = 11.8			
#2 (trayless)	2	2	0	0	—
true population = 9-10	2	1	1	.50	2
	1	1	0	0	4
	3	2	1	.33	5
		P = 9.9			
#3 (trayed)	0	0	0	0	—
true population = 8-10	2	2	0	0	0
	1	0	1	1.00	2
	3	1	2	.33	2
		P = 4.0			
#4 (trayed)	1	1	0	0	—
true population = 9-10	2	1	1	.50	1
	2	1	1	.50	2
	1	0	1	1.00	5
		P = 4.4			

6 individuals were not found on the surface. In the trayless cages, which gave fairly accurate estimates, 10 individuals were captured on the surface of one, and 6 were captured on the surface of the other.

Comparison of plot and cage distributions

In an attempt to see if there was a relationship between the results in the experimental field plot and the results in the experimental field cages, the plot results were compared (1) with the surface results of the trayed cages, and (2) with the mean depth of salamanders in the trayed cages. For each day of observations, the number of captures of *Plethodon* within the plot was charted against the percentage of salamanders found near the surface in the trayed cages. A table of frequencies was prepared from this chart, Table IV, and the frequencies were compared by a Chi-square test of associaion (Simpson and Roe 1939). The data do not suggest that a large number of captures in the plot are associated with a large percentage of salamanders on the surface in the cages ($\chi^2 = 0.118$, df. = 1, P = 0.85). A similar test between the number of captures in the plot with the mean depth in the cages also failed to suggest that a mean depth near the surface was associated with large numbers of captures of *Plethodon* in the plot, Table 5 ($\chi^2 = 0.238$, d.f. = 1, P = 0.60).

TABLE IV. Comparison of the number of searches of the plot with and without captures with the percentage of the trayed cage population found on the surface

Plot	Cage: % of population found in surface tray — Less than 10%	10% or more
0 captures	9	10
Greater than 0 captures	8	7

TABLE V. Comparison of the number of searches of the plot with and without captures with the mean depth of the salamanders in the trayed cages

Plot	Cage: $\bar{x}$ lower than 5 in.	$\bar{x}$ higher than 5 in.
0 captures	8	8
Greater than 0 captures	10	7

Winter survival

Four and 6 *Plethodon* respectively, survived the winter in the 2 trayed cages. Ten salamanders had been left in each of the cages from November 22, 1957 to June 1958. The vertical temperature distribution was found to range from —6°C to 2°C during 2 checks in February, 1958. No salamanders survived the 1958 winter, which was colder with less snow.

Vertical distribution under controlled environmental conditions

When the salamanders were placed on the surfaces of the mazes, they wandered about briefly and then entered the tunnels, usually within 10 minutes. Preliminary studies showed that they were spread throughout the mazes at the end of 2 days. The overall distribution of the salamanders was measured by the mean depth in terms of tunnel levels. The mean depth values at each observation of each of the mazes are shown in Figure 10. The trends can best be seen in the results of July, August, and September. Under uniform temperature (TA) the salamanders were close to the surface in the wet/dry maze (wet top, dry bottom), near the bottom in the dry/wet maze and spread throughout the entire maze in the wet/wet maze. After the hot/cool condition had been superimposed for 1-½ days, the salamanders had moved downward in all of the mazes. After the temperature gradient was reversed, cool/hot, the salamanders moved upward. After all the temperature gradients were removed

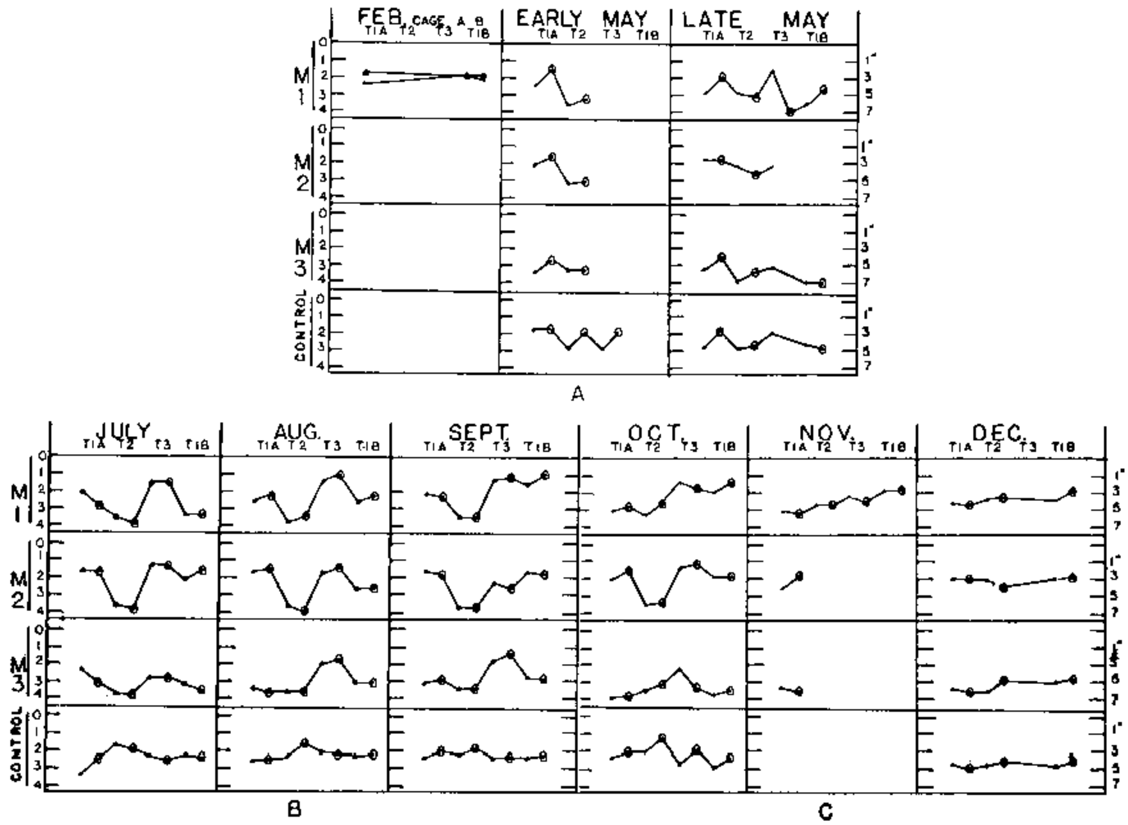

FIG. 10. Mean depth of each observation of each run of salamanders in the mazes. Dots represent day observations, and circled dots represent night observation. All points within a vertical line were taken within one hour. The depths are given both in inches (right) and in terms of the horizontal burrows (left). The environmental conditions are indicated as follows: TIA seasonal temperature, no superimposed gradient; T_2, hot/cool; T_3, cool/hot; TIB seasonal temperature, no superimposed gradient (10 days after TIB); MI, wet/wet; M_2, wet/dry; M_3, dry/wet.

(TB) and the mazes left for 2-½ days, the distribution shifted toward the original TA pattern, but was typically nearer the surface, showing some lag from the cool/hot condition. During the cooler months (spring and fall) the temperature effects were less extreme. The distributions of salamanders in the control maze were relatively constant.

The effects of the 10 day captivity, season, temperature, moisture, and light have been analyzed. The data have been presented and analyzed in an analysis of means (Figure 11), as described by Ott (1958), but slightly modified to handle unequal sample sizes as given in the ASTM manual (1951). One use of this method is to compare the effects of different factors and/or different levels of factors upon the variation in results. The method consists of summing the results of all runs under each condition and comparing the means of each condition by a control chart. The control limits are based upon the normal distribution and are drawn at X ± 3 standard deviations of the means.

To test whether there was any effect upon the vertical distribution due to the salamanders being in the mazes for 10 days, the first day observations in the control maze were compared with the observations of the 10th day. No significant differences were found.

The overall analysis for seasonal effect is somewhat misleading because the experiments in several of the months lacked the complete series of temperature gradients (February, early May, late May, November, and December); this tended to skew the results. Thus February and May results appear to be significantly higher and lower, respectively, than the rest of the means largely because no temperature gradients were imposed during the February run, and each of the May runs lacked a complete cool/hot gradient for both day and night. To remove the effect of incomplete runs, the seasonal effects were compared under the TA, uniform temperature, wet/wet, light condition, which was taken for each of the months studied. Using these data the monthly mean vertical distributions are not significantly

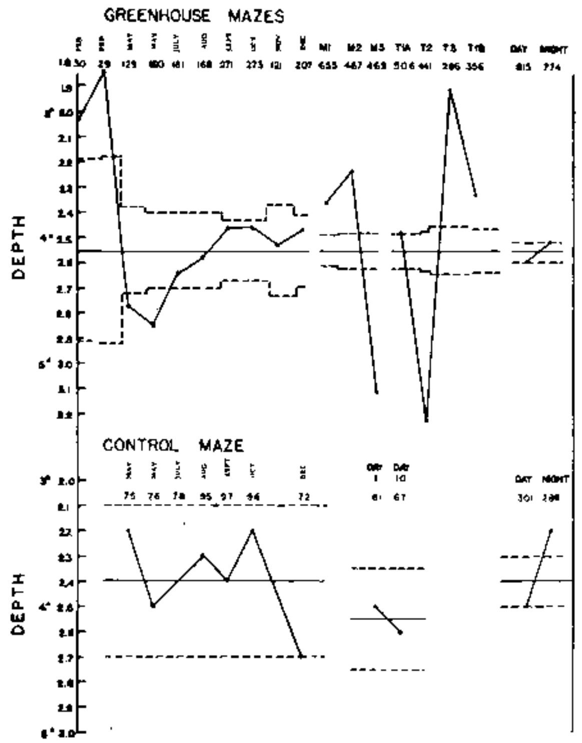

Fig. 11. Control chart of mean depth of salmanders for total maze data. Letter symbols as in Fig. 10. The heavy center line is the mean. The dotted lines are the control limits at ± 3 standard deviations. The number above each point represents the salamander observations upon which that point is based.

different from each other. Under the control conditions, no significant differences were found in the vertical distributions of the various months.

A seasonal difference was seen in the surface occurrence, although not at a significant level. Occurrences tended to be high in spring and fall, and low in summer in both the greenhouse and the control mazes. This is especially noteworthy in the control maze since only the animals, but not the environmental conditions, varied seasonally.

Moisture gradients significantly affected the vertical distribution of *Plethodon*. The salamanders avoided the dry layers if no temperature gradients were superimposed. This is most evident under uniform temperature (*i.e.*, seasonal temperature, with no vertical gradient). The wet/dry maze had a significantly higher distribution (2.6 in., n = 161) and the dry/wet had a significantly lower distribution (5.5 in., n = 166) than did the wet/wet maze (3.9 in., n = 192).

Temperature gradients also significantly affected the vertical distribution. The effect of temperature alone is most evident when the wet/wet condition is considered, the average depths being, TA 4.0 in. (n = 192); hot/cool 5.3 in. (n = 166); cool/hot 2.5 in. (n = 126); TB, 3.1 in. (n = 171). Under most of the temperature ranges used, the salamanders moved toward the cooler end whether it was in the upward or downward direction. Because seasonal, and therefore different, temperatures were used in the greenhouse mazes, it is necessary to examine each temperature range separately (Fig. 12). Here the results of the hot/cool condition are shown because the temperature ranges used were wider than under the cool/hot condition. When the temperature exceeded 18°C the salamander distribution was skewed toward the lower temperature. The higher the temperatures, the more sharply the distribution was skewed. *Plethodon* was never found above 27°C although the ranges of July, August, and September extended up to or beyond this temperature. When the minimum temperature was below 15°C, there was a slight tendency to move away from the cool end. Essentially the same results were seen when the direction of the gradient was reversed. Thus there was no indication that the salamanders moved downward any more readily than upward in response to similar temperature gradients.

As an indication of the sensitivity of *Plethodon* to temperature, the distribution was skewed when the gradient had a range of only 1.5 and 2.0°, and where the lowest temperature was above 18°C under cool/hot conditions.

The distribution under TB tended to be significantly higher than at TA although similar temperatures prevailed under both conditions (Fig. 11). It appears that the raised distribution due to heating the bottom under cool/hot conditions carried over for the 3 day period after the temperature gradient was removed.

The wet/dry and dry/wet mazes measured the interaction between moisture and temperature gradients. In these mazes salamanders avoided the dry layers if no temperature gradient existed or if the temperature of the dry layers was above than that of the wet layers. Under both moisture conditions there were a tendency to move onto the dry layers if they were cooler and if the wet blocks exceeded 18°-20°C. Thus the same temperature which caused movement from hot-wet layers to cool wet layers sufficed to cause movement from hot-wet layers to cool-dry layers. No salamanders were found on layers which exceeded 27°C. (Condensed water on the glass somewhat alleviated the dry condition, but the plaster gained very little water. Occasionally condensed water collected at the bottom of the mazes). When the temperature gradients were re-

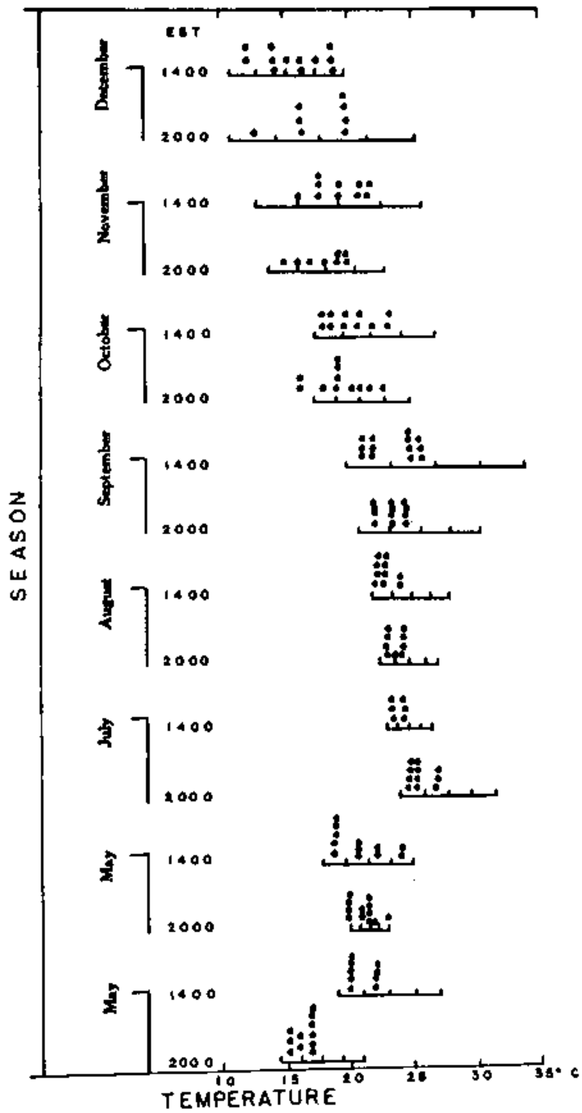

FIG. 12. Distribution of *Plethodon* under different temperature ranges. All gradients were cooler toward the bottom of the maze. The maze was uniformly wet. The horizontal line represents the range of temperature over the 4 layers of the maze. Each dot represents the position of a salamander.

moved, the salmanders went back to the wet layers.

Salamanders were seen on the surface almost exclusively at night. Of 815 day time salamander observations, only two were on the surface (0.24%) as compared to 29 surface observations of 774 night salamander observations (3.7%) in the greenhouse mazes. A similar result was noted in the control maze; no surface observations were noted during 301 day time salamander observations as compared to 12 surface observations during 288 night salamander observations (2.0%). Moisture and temperature gradients seem to affect the occurrences on the surface, but not a significant level.

The mean vertical distributions of day and night were significantly different, although the magnitude of the difference was slight. Salamanders were distributed throughout the mazes both at night and during the day under uniform temperature and moisture. Summing all of the night and day observations in the greenhouse mazes, the mean depth for the day observations was 4.18 in. while that of the night observations was 4.02 in. Thus the night observations averaged 0.16 in. closer to the surface than the day observations. A similar result was noted in the control maze; the night observations averaged 0.6 in. closer to the surface than the day observations. The slightly higher night distribution is almost completely due to surface occurrence during the night observations.

During the November run the wet/dry and dry/wet mazes were inadvertently filled with water. They were drained to the middle of the mazes, and the salamander distributions were noted during the remaining observations. None of the 124 salamander observations were of submerged individuals, although the very tips of the tails were occasionally in the water. The temperature conditions observed were air 16°C, water 12°C; air 11°C, water 12°C; air 12.5°C, water 11.5°C; air 8°C, water 9°C; air 9.5°C, water 8°C; air 14°C, water 10.5°C; and air 4°C, water 4°C. Shaking the mazes did not induce the salamanders to enter the water, but dismantling the mazes did drive them into the water until the disturbance ceased.

Discussion

Litter as part of the total habitat

It has been found in this study that the litter is but a part of the total habitat of these salamanders. While the litter is the most convenient portion of their habitat for study—and therefore where they are most frequently captured—it must not be assumed that such captures are an adequate measure of the ecology of these organisms. The following data support this conclusion:

One hundred nineteen intensive searches of a 70 × 90 ft field plot together with somewhat fewer searches of adjacent and peripheral areas yielded 228 captures of *Plethodon c. cinereus*. Of these, 154 individuals were marked and released. At the conclusion of study the majority of animals captured showed no signs of having been marked. It may therefore be concluded that the total salamander population is considerably larger than the sample size.

Three lines of evidence indicate that the high number of captures within the plot was due to long-term residents and not immigrants. (1) Measurements of distance moved between recaptures showed very restricted horizontal movements. (2) The direction of these movements and searches of the peripheral areas gave no indication of migration. (3) Salamanders frequently disappeared from the surface and later reappeared under the same object as their original capture, an average of 10 searches later.

Since it appears that the population within the plot exceeded the total number captured on the surface, and since the average number of captures/search was 1.2, only a very small proportion of the population was sampled during rather intensive searches of the plot. This agrees with the findings of Test and Bingham (1948) when they failed to deplete a *Plethodon cinereus* population by the removal of all *Plethodon* found under surface objects. Within experimental field cages, 2% to 32% of the total observations occurred in the top inch of the soil. The proportion found near the surface apparently depended upon temperature, level of the water table, and type of surface shelter available. Within the mazes only a small minority of the observations were made on the surface.

That the surface captures may not be an adequate nor a random sample of the total population has been reported by Test (1955) and is supported by this study. The population sizes within the underground field cages were estimated on the basis of surface captures by a mark and release technique. The surface captures gave an adequate estimate only when undreground passageways were not available, as in the trayless cages. In the trayed cages, where underground passageways were available, part of the population remained on the surface while part was never found on the surface. This led to erroneously low estimates. The numerous animal burrows and the disappearance of marked animals indicate that the natural soil provides numerous passageways as do the trayed cages. The non-random movements of *Plethodon* severely limit the use of statistical estimates which assume random mixing. Most authors choose to call the surface captures "abundance," (*e.g.* Hendrickson 1954, Stebbins 1954) but Gordon (1952) uses the term "visible population." This latter term is more descriptive and less subject to misinterpretation.

It therefore appears that the litter is only a minor part of the salamander's habitat even under favorable conditions, in contrast to the comment of Vernberg (1953) and the inference of Test (1955) that salamanders use the depths of the soil primarily under unfavorable conditions. Given an opportunity to utilize underground passageways, as in the trayed cages, *Plethodon* penetrated to the full depth of 12 in. Within the mazes, *Plethodon* readily entered darkened burrows. Test (1946) found that the behavior pattern reponsible for the well-known tendency for *Plethodon cinereus* to be found under objects is dependent on their negative response to light, but not to dorsal contact. Such a behavior pattern could result in the utilization of burrows as readily as the utilization of superficial shelter objects. Thus the habitat is best described in terms of volume rather than surface area.

The vertical distribution is predictable to some extent, as shown by the responses in the cages and mazes. Additional work along these lines to improve the predictability could yield estimates of total population parameters by measuring soil conditions and observing litter occurrence. This general method should be applicable to any cryptic population that has at least some part of its habitat convenient for study. One caution must be observed: because of the lag effect, shown by the slowness of the return of individuals to areas from which they had previously been driven out by unfavorable conditions, the distribution at a particular time may reflect previous conditions as well as present conditions. Therefore, frequent environmental measurements must be taken.

Seasonal distribution

Captures varied seasonally being high during the spring and autumn and low during the summer. Seasonal changes in captures could be due to seasonal climatic conditions and/or seasonal behavior patterns. The occurrence of more *Plethodon* on the surface of the plaster mazes during the spring and fall indicates that seasonal behavior patterns may exist. This was true both in the greenhouse mazes under semi-natural seasonal conditions, and in the control maze under constant conditions, although not at a statistically significant level. Test (1955) stated that the decrease in the captures of mature females during the summer may be due to their being in nursery chambers. No significant seasonal changes in the mean vertical distributions were found in the mazes.

Temperature

Temperature had a limited effect on the distribution. The highest captures/search were made as the surface temperatures increased during the spring and as they decreased during the fall. Either the temperatures or the change in temperature may influence surface occurrence. The range of surface temperatures for *Plethodon* captures in the plot was from 5°C to 25°C. Within the underground cages, *Plethodon* were found over approximately the same range, 4°C to 25°C, although temperatures as low as −6°C were sampled. The range here is much wider than that shown for this species by Bogert (1952) of 16°C to 21°C. This wide range is in partial accord with Bogert's conclusion that salamanders do not exercise control over the thermal level of their bodies by their activities and choices of their immediate environment as he has found in lizards. However, his statement that salamanders are insensitive to temperatures within their environment must be modified, for *Plethodon* sharply avoids temperatures below 4°C. The data here are in accord with Vernberg's findings (1953) that *Plethodon cinereus* and *Eurycea bislineata* will avoid air temperatures of 0°C by burrowing into warmer sand. In the mazes, the vertical distribution was markedly influenced by temperature ranges which extended above 18°C; at temperatures above this, the distribution was skewed toward the cooler end. Under the maze conditions the salamanders were sensitive to temperature differences as small as 1.5°C if the temperature was above 18°C. In the cages no temperature avoidance was noted at the higher temperatures up to 25°C, which was the highest temperature sampled. In the field plot captures were made up to 25°C although slightly higher temperatures were sampled, and the distribution of captures was skewed away from the higher temperatures. Thus it appears that the *Plethodon* were more sensitive to temperature under the maze conditions than under field conditions. The complete avoidance of temperatures exceeding 27°C is in keeping with the report (Zweifel 1957) that the maximum lethal temperatures for numerous species of salamanders are between 30° and 36°C.

Moisture

There is particular interest in the moisture relationships of amphibians because they represent a transitional stage between terrestrial and aquatic organisms. It has been shown that at constant temperature, salamanders will lose water through evaporation at a rate inversely related to the relative humidity but will eventually desiccate even in saturated air, so that water in a liquid form is occasionally necessary (Ray 1958, Hall 1922). The water relationships within the soil are therefore of interest. Within soil cavities, the air will be saturated with water vapor if the soil is wetter than the hygroscopic coefficient (Lutz 1946). Since this was the case in the cage experiments, lowered relative humidities were not studied here; nor could the reactions to soil moisture be studied in the field. The soil within the cages was almost always saturated, and the percentage of water in the soil samples taken from the capture sites is more an indication of high organic content of the soil than of moisture available to salamanders. In the mazes the salamanders avoided dry layers unless the wet layers were warmer than 18°C and the dry layers cooler.

In both the mazes and cages *Plethodon* showed a clear avoidance of standing water. As the water table rose in the cages, the salamanders abandoned the inundated layers. It was noted that high captures/search frequently, but not always, followed heavy rains. It may be that when the soil is saturated, additional rain fills the underground passageways and the salamanders are driven upward.

Diel periodicity

While salmanders appeared on the surface only when it was dark, the vertical distribution within the soil was only very slightly affected by light and dark cycles both in the cages and the mazes. Nor were the number of captures under superficial shelter objects significantly higher at night than during the day in the research plot as might be expected of nocturnal animals. Since salamanders can avoid light by retreating under superficial shelter objects, it is not necessary to retreat deeply into the soil. It appears that the salamanders near the surface may move onto the surface when it is not light, for they are photonegative (Vernberg 1955, Test 1946), but no indications of daily vertical migrations were seen in the plot, the cages, or the mazes.

Comparison of experimental and plot results

It must be concluded that the results of the cage experiments were a poor measure of the plot results. Yet the temperature data of the two areas had almost identical ranges. At least part of this failure was probably due to the location of the cages near the stream, since *Plethodon* tended to be found away from the stream. Had the cages not been so close to the stream where the water table level was the major controlling factor, the results of the cages might have been in better agreement with the plot results. Within the cages, *Plethodon* reacted to environmental conditions and thus gave some measure of the vertical distribution under these conditions. In a similar manner, the mazes showed that salamanders do react to temperature and moisture gradients in a predictable manner. The extent to which such experimental results can be applied to field interpretations requires additional studies.

Home range

The restricted horizontal movements of marked animals illustrates that they have a restricted home range. Restricted home ranges have been shown for numerous amphibians, *e.g. Rana clamitans* (Martoff 1953), *Scaphiopus holbrooki* (Pearson 1955), and *Batrachoseps* (Hendrickson 1954). Since no defense was noted in this study they cannot properly be termed territories.

Hibernation survival

Hibernation survival in the cages was 50% for the winter of 1957 and 0% for the winter of 1958. The 1957 results compare closely with those of Vernberg (1953) of 43% survival. Survival undoubtedly depends upon the severity of the winter, for 1958 was a colder winter with less snow.

Experimental shelter objects

Experimentally placed objects, pine boards, rocks, and tar paper, were found to yield approximately twice as many captures as naturally occurring logs and rocks per foot of cover. One factor relating to this efficiency is the ease of scanning the one square foot under the experimental objects as compared to scanning several square feet under logs, especially at night.

Summary

1. The distribution of *Plethodon c. cinereus* within the soil was studied as a means of interpeting field captures.

2. Three approaches were used: (1) a mark and release method in a field plot for a study of the surface captures of *Plethodon* under natural conditions, (2) underground field cages, in which the vertical distribution could be measured under partially natural conditions, and (3) mazes, in which the vertical distribution could be measured under controlled simulated soil conditions.

3. It was found that *Plethodon* captures (1) varied seasonally, captures occurring more frequently during spring and fall (2) tended to occur away from the stream, and (3) occurred from 5°C to 25°C. Recapture data indicated restricted home ranges.

4. It appears that the litter of the soil is only a minor part of the salamander's habitat even under favorable conditions. With the underground field cages it was found that *Plethodon* are distributed within the soil, at least to a depth of 12 inches if they are given the opportunity to utilize water-free underground passageways. Those found on the surface or within the first inch of soil were but a small part of the population under plot, cage, and maze conditions. The vertical distribution is affected mostly by water relationships, especially water table level, temperature, and to a limited extent, by light. *Plethodon* avoided inundated soil, but preferred a moist substrate. Within the plot, cages, and mazes, an avoidance of low temperature was found. In the mazes, an avoidance of high temperature was also found. Light had little affect on the vertical distribution within the soil, but did affect exposure on the surface, and thus affected average vertical distribution to a limited extent. Light did not affect the frequency of captures under superficial surface objects in the field plot. A lag was shown in the return of *Plethodon* to areas where they had previously been driven out by unfavorable conditions.

5. Thus a *Plethodon* population reacts toward environmental conditions in a somewhat predictable manner. Additional work along these lines to improve the predictability could yield estimates of total population parameters by measuring soil conditions and observing litter occurrence. This general method should be applicable to any cryptic population that has at least some part of its habitat convenient for study. Numerous environmental measurements must be taken over a period of time since the distribution of the organism may reflect previous conditions as well as present conditions.

6. Hibernation survival depends upon the severity of the winter, 50% of the caged *Plethodon* survived during the winter of 1957 while none survived the winter of 1958 which was colder with less snow.

7. Experimentally-placed shelter objects, pine boards, rocks, and tar paper had approximately twice the efficiency of naturally occurring logs and rocks in yielding salamander captures.

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A POPULATION SURVEY OF RHESUS MONKEYS IN NORTHERN INDIA: II. TRANSPORTATION ROUTES AND FOREST AREAS[1]

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This paper presents data on the abundance and population structure of rhesus monkeys (*Macaca mulatta* Zimmerman) observed along roadsides, canal banks, railroad rights-of-way, and forest areas of northern India from September, 1959, to June, 1960. A previous paper presented population data on rhesus monkeys in villages, towns, and temples in the same region (Southwick, Beg and Siddiqi 1961). These several types of habitat and survey categories were selected because they represented logical categories in the habitat distribution of rhesus monkeys, and they provided a convenient system of data classification for the

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