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To the Graduate Council:

I am submitting herewith a thesis written by David Henry Bickner entitled "A Study of Possible Factors Controlling Individual Growth and Population Size of the Slimy Salamander, Plethodon glutinosus glutinosus (Green)." I recommend that it be accepted for nine quarter hours of credit in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

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A STUDY OF POSSIBLE FACTORS CONTROLLING INDIVIDUAL GROWTH AND POPULATION SIZE OF THE SLIMY SALAMANDER, PLETHODON GLUTINOSUS GLUTINOSUS (GREEN)

A Thesis

Presented to

the Graduate Council of

The University of Tennessee

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

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by

David Henry Bickner

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ABSTRACT

There has long been a controversy in population ecology regarding which factors govern the size of animal populations. Both physical and biological control mechanisms have been proposed. Among the latter, a popular theory of control was proposed in a paper by Hairston, Smith and Slobodkin (1960), who credited the control of herbivore populations to predation and the control of both predator and decomposer populations to food shortage.

An attempt is made here to deduce factors which might limit the size of a population of slimy salamanders (Plethodon glutinosus glutinosus Green). The limiting factors studied were food and atmospheric moisture.

A population of slimy salamanders was maintained in a simulated natural habitat provided with abundant food. Weekly measurements were made of their increase in weight and length. Similar measurements were taken at the same time of a wild, unfed population of slimy salamanders. The experiment lasted for a period of 65 days in late summer and fall of 1971. Upon comparison of the changes between the two populations, the controlled population was found to have increased in both weight and length significantly above the wild population.

A second experiment was performed to determine the effects of moisture upon two populations of slimy salamanders maintained in the laboratory under simulated natural conditions. One group was maintained

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in a high-moisture environment, the other in a low-moisture environment. Both populations were provided with abundant food. Weekly measurements were made of their change in weight and length. The experiment lasted 57 days during the winter of 1972. Comparison of the measured parameters between the two groups showed that the high-moisture population's weight differed significantly from the low-moisture population. Comparison of their lengths showed no significant difference between them.

Observations of caged, fed salamanders in the late summer and fall of 1970 and during the course of the feeding experiment showed the definite possibility that slimy salamanders are territorial during the breeding season, but not at other times. The observations cannot be stated to show that territoriality positively exists in this species, however. It is concluded from the literature that predation may also be a factor in population control, but probably not the principal factor in this case.

The conclusions of this paper are that wild slimy salamanders receive insufficient food to attain their maximum growth potential. Since food limits growth of individual salamanders, its lack is seen to be a probable factor in limiting the population size as well. This is based on the theory that an increase in population size would only serve to further reduce an already inadequate food supply. Moisture does not affect individual growth or population size where it does not become extreme, but where extreme, it limits species range as well. Territoriality and predation may also be limiting factors upon population size of slimy salamanders.

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I. INTRODUCTION

Literature Review

Populations of organisms expand and contract, sometimes explode into great numbers and at other times decline toward extinction, but at times their numbers remain in a rhythmic oscillation about an equilibrium. What regulates these populations? Thomas Malthus, writing in his famous work, Essay on the Principle of Population, expounded the theory that food, or its lack, would ultimately be the final control of human expansion. To the black horseman of famine, he appended as auxillary controls poverty, disease and war. This theory, modified somewhat, was given application to other life-forms besides man by Darwin in his work on evolution. In chapter 3 of his Origin of Species he stated,

> . . . every single organic being may be said to be striving to the utmost to increase in numbers . . . heavy destruction inevitably falls either on the young or old, during each generation or at recurrent intervals. Lighten any check, mitigate the destruction ever so little, and the number of species will almost instantaneously increase to any amount.

Darwin defines these checks as,

> The amount of food for each species of course gives the extreme limit to which each can increase; but very frequently it is not the obtaining food, but the serving as prey to other animals, which determines the average numbers of a species. . . . Climate plays an important part in determining the average number of a species, and periodical seasons of extreme cold or drought seem to be the most effective of all checks.

Population ecology since Darwin's day has been concerned with the essential dichotomy he expressed, to wit: populations are regulated by biotic and/or physical (abiotic) factors. Darwin, in the quotation

above, seemed of two minds as to which was more important and so, often enough, were his successors. Various researchers have championed one or the other of these factors as the primary method of control. Over the course of time the number of population biologists preferring abiotic factors has become secondary to the number preferring biotic factors of control, but the issue is not yet finally resolved.

An example of theories of abiotic population control may be seen in the works of Davidson, Andrewartha and Birch. Davidson and Andrewartha published two papers (1948 a, b) concerning the populations of Thrips imaginis in Australia in which the ultimate population size was linked to the coming of the dry season. Andrewartha and Birch's work of 1954 continued and expanded this climate theory of population control. Birch (1957 b) again noted the role of weather in regulating animal abundance, though he no longer thought it to be the only regulator of these numbers. In this paper he admitted other factors to be important, but these were still primarily physical in nature. A restatement of this point of view may be found in Ehrlich and Birch (1967).

Theories of biotic factors of population control were discussed by Elton (1927), who elaborated the Malthusian theory:

> The regulation of numbers of most animals would appear, therefore, to take place along the following lines. Each species has certain hereditary powers of increase which are more or less fixed in amount for any particular conditions. It is usually also kept down in numbers by factors which affect breeding. . . . It is further controlled by its enemies, and if these fail, by starvation. But the latter condition is seldom reached.

All of the researchers probing into biotic theories of control, even when these included abiotic methods as well, eventually came upon the fact that as a population grew larger, its rate of mortality often increased. This would seem to indicate that most of the biotic and perhaps many of the abiotic controls become more limiting as population pressure grows. This has given rise to the labelling of such controls as density-dependent. When such controls do not take a higher casualty rate in denser populations, they are said to be density-independent. These terms were first coined by Smith (1935). This is especially well treated in a paper by Varley and Gradwell (1970). Some researchers do not feel that density-dependent controls exist, and others often become involved in the problem of whether a given control is density-dependent or -independent, and how to tell the difference. Andrewartha and Birch (1954) seemed to deny all density-dependent controls, preferring pure chance, or density-independence, to be the true condition of control factors. Elton (1955) disagreed severely with this, saying in part,

> But I cannot believe that the natural communities of the world will be found to have evolved solely "by guess and by chaos", or that the inter-relations of animal populations have not introduced a gradual order into the structure of animal communities.

Andrewartha (1957) reviewed his position by noting that by proper reasoning it would often be difficult or even impossible to decide when some factors of the environment were exerting density-dependent or density-independent forces upon animal populations. At present, theories denying the existence of density-dependent factors are very much in the minority (Varley and Gradwell, 1970).

If density-dependent factors exert at least some control upon animal populations, then it may be seen that this often comes about by means of a surplus of animals all desiring an insufficiency of resources, the situation becoming more critical with each increase in the numbers of these animals. The resulting phenomenon is called competition. As it is presently used, competition may mean a group of animals of the same or different species seeking to utilize a common, insufficiently supplied resource and harming one another in the process; it may mean a group of animals interfering with one another even when there is no desire for a common resource; it may be taken to indicate a predator-prey relationship; or it may be used to mean natural selection (Birch, 1957a). Of these meanings, Birch (1957 a) prefers the first as being the only true definition in the strictest etymological sense.

One of the earliest mentions of density-dependent factors was by Thompson (1929), who developed these as a primary factor of control. Specifically, he stated that as the density of an animal population became greater, animals were forced to migrate into less favorable habitats where they were largely exterminated by physical factors. Smith (1935) further developed this theory and considered all physical factors to be density-independent and biotic factors to be density-dependent. He separated density-dependent factors from competition, however, though he did consider that the former were instrumental in causing the latter when the density-dependent factors were limiting. In this conclusion Smith was also drawing upon the work by Nicholson

(1933), who recognized competition but did not relate it to density-dependence. Nicholson also concluded that all population control could be finally traced back to climate, which affects plants upon which all animal life ultimately depends. He felt, therefore, that animal life was affected indirectly by physical factors and directly by competition for such things as food and shelter.

Competition became more prominent in the theories of many authors. As it did so, the question arose as to which type of competition could be considered more important, interspecific or intraspecific. Interspecific competition is competition between individuals of two separate species for the same goal; interspecific competition is competition between two individuals of the same species for that goal. This question reflected upon the idea first demonstrated by Gause (1934), which has come to be known as Gause's principal. In essence, if two different animals share similar ecological niche requirements in the same place, they are in competition. Only one species may ultimately fill any one ecological niche in a given location and time. It could follow, therefore, that two individuals of the same species would also be in competition. Milne (1957) stated that the ultimate population control would be intraspecific competition, even though it rarely gets to operate and is replaced imperfectly by interspecific competition and predation. It may be shown in the laboratory that intraspecific competition does exercise a marked influence on populations. One such experiment by Nicholson (1950) showed that intraspecific competition for food among individuals of the fly Lucilia cuprica

caused definite oscillations in the population size. Similar experiments have been done with the flour beetle Tribolium confusum (Chapman, 1928).

Elton (1946) noted considerable evidence that interspecific competition exerts a large amount of control over which animals will be found in a given habitat, although he did not apply this to a control of population size. It is of interest to note that he found that species of the same genus seem to compete more than those belonging to separate genera. Hairston (1949, 1951, 1964) has written a number of papers dealing with competition. In his work on competition among Appalachian salamanders (1951), he found that the two species Plethodon glutinosus and Plethodon jordani are vertically distributed in separate zones on mountain sides due to competition between them. Hairston stated that each species was capable of existing normally in at least part of the habitat of the other, but that the two are seldom found occupying the same area at the same time. Bogert (1952) found a similar competition between Plethodon glutinosus and Plethodon cinereus in Virginia.

One of the main difficulties with the theory of density-dependent factors was noted above in the objections of Andrewartha (1957). Another is that casual observation often sees competition as occurring where it is not. This problem was noted by Gause (1934). Lack (1945) wrote that two particular species of closely related birds which appear to be in competition actually are not. Bogert (1952) found that although Plethodon glutinosus and Plethodon cinereus appear to compete for some environmental needs, they do not for others,

especially shelter. Reynoldson (1957) observed that density-dependent factors exercised their regulation only in habitats where physical conditions were favorable, and that in less optimum areas physical conditions became the regulators of animal populations. The data presented by Birch (1957 b) indicates the same conclusions. Blair (1957) found that the populations of four species of herptiles existing at the edge of their natural range under unfavorable conditions were strongly regulated by physical factors, in this case drought.

One occurrence in some natural populations which may be density-dependent was discussed by Chitty (1957). He noted data concerning wild field mouse (Microtus spp.) populations which experience periodic population crashes occurring when the populations reach sufficient density. The exact mechanism responsible for this die-off is unknown, but it appears to be in part related to a genetic change which occurs in the population. This would appear to be a classical case of suppression as defined by Solomon (1949).

Along with the physical and biotic theories of population control, another, more encompassing idea was formulated by researchers. Chapman (1928) stated that, ". . . the potential rate of reproduction of the animal is pitted against the resistance of the environment . . ." He included as a part of the environmental resistence both physical and biotic aspects. This idea was modified by Thompson (1929) and Smith (1935), who emphasized density-dependent factors, but was restated in an almost pure form by Crombie (1947). This holistic concept was expanded by Thompson (1939), who felt that population

control was due to a broad complex of factors, different ones of which act under differing circumstances. Solomon (1949) generally adopted this theory, stating,

> The level of abundance depends ultimately on all the major elements of the ecosystem, although the density-related, controlling factors are the immediate determinants. Only in regard to particular types of situations, or of animals, can more precise statements be made.

Nicholson (1957) also endorsed this position when he determined that,

> . . . it is the innate ability of animals to produce a surplus of offspring which enables populations to persist in spite of adverse environmental factors which cause heavy mortality. . . .

Hairston, Smith and Slobodkin (1960) attempted to combine and simplify the biotic, abiotic, and holistic theories of population control by integrating parts of each into a rather simple whole. The conclusions of this paper were as follows: as a group, (1) Producers (plants) are resource (water, minerals, climate) limited; (2) Herbivores are rarely food limited, but instead are kept in check by predation, which includes parasitism, predation and disease; (3) Predators are limited by their supply of food; and (4) Decomposers are also limited by food. These conclusions apply only to terrestrial ecosystems. Interspecific competition exists among the members of each group.

Murdoch (1966) and Ehrlich and Birch (1967) disagreed with these findings, but were unable to seriously challenge them. In a reply to the criticisms of these authors, Hairston, Smith and Slobodkin restated their conclusions at greater length and with more supporting evidence, and offered ideas on how their statements could be tested

(Slobodkin, Smith and Hairston, 1967). Other authors also noted exceptions to Hairston et al. Edwards (1969) found that soil arthropods nominally filling a decomposer niche were more limited by predation by soil mites than by lack of food. Eisenberg (1966) observed that predators seemed to have little effect upon populations of a herbivorous aquatic snail. Instead, this snail was limited by available food quality. Although this applied to a nonterrestrial ecosystem, it is reminiscent of the food-limited Thrips imaginis studied by Davidson and Andrewartha (1948 a, b). The work by Odum, Connell and Davenport (1962) seems to indicate that a similar situation may exist in the case of many herbivorous insects. This study also found granivorous vertebrates to most likely be food limited. Tanner (1966) found that in vertebrates which establish and defend a territory, lack of this territory may increase the animal's chance of being eaten. Thus, this territory seems to play a large part in regulating the population size.

On the other hand, there has been support of Hairston et al. Their work contributes much to the understanding of the findings of Lindeman (1942). Lindeman noted that in the biological transfer of energy from trophic level to trophic level, some energy is always lost. At higher (consumer) trophic levels organisms become more efficient at obtaining and conserving energy. At the same time the amount of energy lost due to respiration also increases with increasing trophic levels. These facts imply that the higher trophic levels (second and third level consumers) are far more limited by available energy than the lower consumer and producer levels. For consumers,

energy comes packaged in the form of food; therefore, the higher trophic levels are more concerned with the obtaining, efficient digestion of and retention of energy from this food.

Also, it may be necessary to reconsider the trophic levels to which many animals are assigned. The soil arthropods cited by Edwards (1969) are labelled decomposers, but tropho-dynamically speaking they may not be decomposers at all. Many decomposers feed upon the same material that is eaten by vertebrate herbivores. What, then, is the trophic difference?

Probably the most spectacular evidence for the conclusions of Hairston et al. may be seen in the case of the deer herd of the Kaibab Plateau, Arizona. Deer, of course, are herbivores and should be predator-limited rather than food-limited. As the natural predators of this herd were removed by man, the herd size increased from about 4,000 in 1907 to greater than 100,000 by 1925. Then the population "crashed," due to starvation, to a low of 20,000 in 1932 and 10,000 by 1938 (Kormondy, 1969). Similar situations have been found when pesticides destroy the natural predators of herbivorous arthropods (Edwards, 1969). Odum, Connell and Davenport (1962) noted that herbivorous insects did not seem to be limited by lack of food, although they did not speculate on what factor did limit these insects. Schaller (1972) found that African vertebrate herbivores are limited entirely by predation and disease, with no sign of food limitation. Tanner (1966) found that populations of herbivorous insects at low and moderate levels are regulated primarily by disease, parasitism and predation. He also found non-territorial vertebrates controlled

mainly by predation, this falling most heavily upon the juvenile individuals. Studies upon mites by Huffaker, and Huffaker and Kennet, cited by Slobodkin (1962) show clearly that predators can control the population size of their prey. Similarly, predators and diseases of the evergreen bagworm, Thyridopteryx ephemeraeformis, have been found to exercise a definite control over population size of this insect (Kangas, 1972).

Studies of population control have been performed on a variety of vertebrates and non-vertebrates. A group of animals which have been little studied from this aspect are the salamanders. As a general order, the salamanders are a widespread group, occurring over a large part of the earth's surface in its wetter areas. Salamanders have proven fascinating to humans throughout time and many fanciful properties have been attributed to them, causing their use in a number of magical charms and potions (Grillot de Givry, 1963). Their true life cycles and attributes have been shown to be quite complicated. Many salamanders exhibit complex courtship and reproductive behavior, including elaborate mating dances (Noble and Brady, 1930; Organ, 1968; Salthe and Salthe, 1964; Sayler, 1966). They are all carnivorous and generally exhibit few food preferences, save that they primarily eat arthropods (Bogert, 1952; Hamilton, 1932). Due to their varied habitats, some being primarily aquatic, others terrestrial, they exhibit a variety of breathing methods, including gills, lungs, skin and buccopharyngeal mucosa (Whitford and Hutchinson, 1963). Generally, salamander ecology is unknown, although it has been worked out for several species of the Plethodontidae (Gordon, 1952; Hairston, 1949).

Salamanders have, with few exceptions, moist, somewhat slimy skins and cannot endure xeric conditions. Experiments performed with a variety of salamanders have shown them to vary widely in their ability to tolerate drying, however, and this is reflected in their choice of habitat (Littleford, Keller and Phillip, 1947; Ray, 1958; Spight, 1967 b; Stebbins, 1945). Other factors which influence their choice of habitat include temperature, slope of the ground, aspect of hillsides and available cover (Bogert, 1952; McKenzie and Storm, 1970; Stewart and Bellis, 1970). Some salamanders exhibit territoriality. Among these are two plethodontid salamanders, the four-toed and the two-lined salamanders (Hemidactylium scutatum, Eurycea bislineata), with some others in the Plethodontidae giving indication of not being territorial at all (Grant, 1955; Stewart and Bellis, 1970). Since territoriality has been found in other amphibians, it might be expected to turn up in some other salamanders as well (Dole, 1965; Martoff, 1953).

Besides occasionally being territorial, most salamanders establish a definable home range to which they will return if removed (Barbour, Hardin, Schafer and Harvey, 1969; Barthalmus and Bellis, 1969; Grant, Anderson and Twitty, 1968; Madison and Shoop, 1970). Their homing mechanisms would appear to vary only slightly; smell has been partially indicated (Barthalmus and Bellis, 1969; Grant, Anderson and Twitty, 1968; Madison and Shoop, 1970), but the commonest method seems to be a "sun-compass" (Adler, 1969; Landreth and Ferguson, 1967 a, b; Madison and Shoop, 1970). This is literally orientation of the animal by use of sunlight, and is a method of photoreception which is accomplished directly by the pineal body.

Some information on population dynamics is available for a few species. Bogert (1952) made a study of numbers and habitat selection of several species of terrestrial plethodontid salamanders. Hairston has studied the patterns of habitat selection in several species of Desmognathus (1949) and Plethodon (1951). He found what he believed at the time to be the only known instance of geographical variation due to interspecies competition occurring between Plethodon glutinosus and Plethodon jordani (1951). Stewart and Bellis (1970) studied patterns of habitat selection among three species of plethodontid salamanders. Spight (1967 a) has performed a census and biomass study on Desmognathus fuscus, while Test and Bingham (1948) did a similar study on Plethodon cinereus. Vernberg (1953) noted that winter mortality was high among the plethodontid salamanders Plethodon cinereus and Eurycea bislineata, giving the first real data on a means of population control. Orr (1962) discussed predation on Plethodon jordani and Desmognathus ochrophaeus, and Powders (1970) observed levels of parasitism among Plethodon jordani and Plethodon glutinosus.

One of the most common eastern salamanders is the slimy salamander, Plethodon glutinosus glutinosus (Green). This animal belongs to the family Plethodontidae (the lungless salamanders) of the suborder Salamandroidea, order Caudata (tailed amphibia, or salamanders). Plethodon glutinosus glutinosus is a relatively small vertebrate, although large for a salamander. Bishop (1943) gives its size being between 121 and 188 mm (4 3/4 to 7 7/16 inches) with the males averaging larger than the females. Orton (1946) disagrees with this, however,

seeing no significant size differences between the sexes. Huheey and Stupka (1967) note a larger record found by Highton to be eight inches (203 mm), but such large sizes are rare. This is the widest ranging eastern salamander, being found from New York to central Florida and westward to Texas, Oklahoma and Missouri (Conant, 1958). Its normal habitat is in moist woods, especially along the hillsides of gullies and ravines (Bishop, 1943). Its life cycle is entirely terrestrial; it rarely enters water voluntarily. The eggs are laid in moist locations on land and have been found in caves (Brode and Gunter, 1958), in nests in logs (Highton, 1956) and even under damp cement bags (Wood and Rageot, 1955). The eggs hatch on land and the young are born fully formed for terrestrial life (Noble, 1931; Bishop, 1943; Highton, 1956). The season of egg laying varies with the locality, being earlier in the year in more southern locations (Highton, 1962). There are often two occasions of egg laying, one in spring and one in early autumn (Highton, 1956, 1962). Like other plethodontid salamanders, Plethodon glutinosus has an involved courtship behavior, featuring a nuptual dance (Noble and Brady, 1930; Organ, 1960). It is also extremely difficult to breed in laboratory conditions. Dr. Paul Zahl, in an article in the National Geographic Magazine, discussed a method for breeding captive Plethodon cinereus which might be applicable to Plethodon glutinosus (Zahl, 1972). It is cited here if anyone should wish the reference in the future.

Being a lungless salamander, Plethodon glutinosus breathes mainly with its skin and bucco-pharyngeal mucosa (Whitford and Hutchinson, 1963). Like other plethodontid salamanders, it prefers

a moist habitat (Bogert, 1952). It is much more resistant to drying than more aquatic salamanders, though not so much as is Plethodon cinereus (Littleford, Keller and Phillips, 1947; Shelford, 1914). Plethodon glutinosus is capable of recovering from a severe drying, and gains its body water from the soil through its skin, both much like other terrestrial salamanders (Littleford, Keller and Phillips, 1947; Stebbins, 1945; Spight, 1967 b). Its behavior is much influenced by light and it homes by means of an extra-optic sun compass (Adler, 1969; Barbour, 1963). It is active primarily at night, though it may move about in daylight, principally on cool, cloudy days (Barbour, 1963). Plethodon glutinosus is relatively easy to maintain in captivity, especially since it will eat virtually any animal small enough to catch and swallow (Davidson, 1956; Hamilton, 1932; Huheey and Stupka, 1967), including the juveniles of its own species.

An interesting sidelight is that although lungless, Plethodon glutinosus can vocalize to some extent. This is a rare occurence, however (Neill, 1952).

Purpose of the Experiment

The objective of this experiment was to study the population control mechanisms of a predatory species of animal. The species selected for the study was the slimy salamander, Plethodon glutinosus glutinosus (Green).

As has been mentioned, it is very difficult to breed slimy salamanders in captivity. In the wild, their secretive habits and relatively long life cycle mean that the study of a natural population

and its fluctuations would be open to considerable error and would involve many years of observation. It was resolved, therefore, to attempt to draw some conclusions concerning the mechanisms of salamander population control through indirect means. It was decided to use the growth rates of individual salamanders as an indicator of population trends. The theory behind this decision was that many factors which limit population growth should affect the growth rates of individual salamanders as well. The factors which could be exercising this control could be food, climatic factors, predation on the salamanders, and territoriality. The author set out to study food, working on the theory that if these animals were getting enough to eat in the wild, they would be growing near their maximum possible rate, and overfeeding them in captivity would not significantly change this growth rate. The author set out also to study the effect of moisture variance upon growth rate in the presence of abundent food. In the case of moisture, effects upon individual growth would be indirect, in that salamanders in a dry habitat would tend to move about less and thus have less chance of finding food. Predation and territoriality would have more subtle effects upon the growth rates of individuals, if these factors affected growth rates at all. Predation could not be studied in the wild, but this aspect was researched in the literature. Lastly, observations were made concerning territoriality. Coincidentally, the hunting and feeding activities of the salamanders were observed, and a brief description of these is included.

II. GENERAL METHODS AND MATERIALS

Indoor Environment

The indoor salamander population was set up in the Ecology Building at 408 Tenth Street, Knoxville, Tennessee. The exact area used was a blind hallway in the rear of the building. The blind portion of this hallway comprises a floor area measuring about 532 square feet. To block this area off from the rest of the hall, the hallway was partially closed off with a large steel shelf assembly measuring 24 inches by 38 inches by 84 inches. The remaining area was then 88 inches long by 56.5 inches wide.

To support the cages for the indoor population, a bleacher-style, two step rack was constructed from plywood and 2 inch by 4 inch boards. This rack was 28.5 inches high and 88 inches long, and projected out into the hallway some 40 inches from the wall. The rack was a self-contained structure, not anchored to the wall in any way. Eight cages were placed on this rack, four on the top shelf and four on the bottom shelf. In addition, a sheet of 1/2 inch plywood measuring 20 inches by 50.5 inches was anchored to the blind end wall at a height of 54 inches from the floor by use of four 14 inch shelf brackets. Two cages were placed on this shelf. Two other cages were placed, one per shelf, on two steel shelves of the assembly blocking the hallway. These two cages were 27 inches and 54 inches above the floor. All cages faced into the laboratory

and received equal amounts of light from a fluorescent light fixture suspended above.

The cages were constructed entirely of plywood with a pine board and screen lid. The floor of each cage was made of a plank of 3/4 inch plywood measuring 20 inches by 20 inches. The sides were nailed to this board and to each other, all joints were caulked with Sears Tile Repair and Tub Caulk, and the entire inner surface of the cage was given two coats of waterproof varnish to waterproof the cages. The back of each cage was twice as high as the front, giving the top a slope. This was done to try and allow as much light penetration as possible. The top of each cage measured 21 inches by 20.5 inches and was constructed of 1 1/2 inch by 1/4 inch pine screen lath strips. When it was found that this top permitted too rapid evaporation of moisture from the cages, the author covered the screen portion with strips of clear plastic, leaving four 3-inch square openings for air transfer.

To prepare the cages for the salamanders, the author tried to reconstruct, as nearly as possible, the habitat from which they had come. For the feeding experiment, each cage bottom was filled with soil, litter, and larger debris (logs, planks, and so forth) from the ravine in I. C. King Park. This ravine is described in Section III. The soil depth was made to be about 1 1/2 inches in each cage. Leaf litter and three or four rotting log fragments for cover were distributed over the soil in each cage. For the moisture experiment this environment was changed slightly.

Rough measurements taken with a photographic light meter in I. C. King Park at ground level under a dense canopy cover and in the laboratory revealed the intensity of light received by the salamanders to be similar under both conditions. In order to achieve a day-night light cycle, a fluorescent assembly was plugged into an Ingram Do-All 24 hour light timer. This regulator was found to be both inexpensive ($5.00 cost) and sufficiently accurate for these purposes.

Moisture in the cages was controlled by means of the plastic strips over the tops of the cages, as mentioned above. In order to maintain suitable relative humidity in the cages, the cages were watered at least once a week with tapwater. Measurement of the relative humidity in the cages was accomplished by means of a Durotherm Hygrometer.

The temperature in the cages was the same as that within the building, about 72° F. This factor was monitored weekly in the cages by means of a mercury thermometer.

Measurement Techniques

The parameter the author wanted to measure on each salamander was growth, expressed as increases in weight and snout-vent length. To measure weight, a two pan balance made by the Torsion Balance Company, Clifton, New Jersey was used. He selected this balance because it is extremely rugged, simply constructed, and precise. In addition, any repairs which might be normally necessary could be made by the author. It is an ideal field balance. Its maximum capacity

is 200 grams, and it is precise to a hundreth of a gram. Its self-contained stand is a box with three small feet, two of the three feet being adjustable screws for leveling.

The torsion balance was used for all weight measurements, both in the field and in the laboratory. It was found that the best way of immobilizing the salamanders for weighing and measuring was to place them in plastic sandwich bags. Hefty bags were used because they are made of very thin plastic and are light.

All length measurements of the salamanders to the nearest millimeter were made with a Post 15 cm. flexible plastic ruler. Snout-vent length was measured rather than total length because these salamanders were often caught without tails, this species having an easily detached tail.

Feeding

As was mentioned above, Plethodon glutinosus will feed naturally on a wide variety of small organisms, including other, smaller Plethodon glutinosus. As the food supply the author used crickets distributed by Selph's Cricket Ranch, Box 2123 DeSoto Station, Memphis, Tennessee 38102. Because the salamanders varied widely in size, small Australian grey Crickets (Gryllus asimilis) 1/2 inch long were ordered. These cost $9.00 per thousand. The laboratory population was fed 1,000 of these crickets per week.

III. FIRST EXPERIMENT: FOOD AS A VARIABLE

General Feeding Observations

During the course of the territoriality observations described under Section V and during the course of the feeding experiment the opportunity to observe Plethodon glutinosus feeding occurred many times. Since no description of their feeding behavior was encountered in the literature, it seemed that it might be useful to include it in this paper.

Plethodon glutinosus is largely a nocturnal creature, although the author has occasionally seen them wandering about in the wild in the daylight hours. They become active hunters at night, but will take food at almost any time. The feeding method which they seem to use with the most success is an ambush. A salamander will often come out onto the surface of the ground and wait, immobile, for some prey to appear. When the prey is about half an inch away, the salamander strikes out suddenly and quite swiftly, grasping the prey in its mouth. There is very little attempt at chewing the prey, instead it is swallowed whole. Plethodon glutinosus strikes out at motion only. The author has seen these animals while hunting ignore unmoving prey and take that which is moving. They will strike at any moving object, including twigs and one another. The strikes at other Plethodon glutinosus generally do not seem to be territory defense, as the author has seen salamanders strike at other salamanders which have been sharing the same cover.

The other feeding technique employed by Plethodon glutinosus

is an active seeking of prey. Often, if prey is moving about several inches from the salamander it will actively chase the prey. While the ambush technique with its sudden strike is usually accurate and successful, the chase is not. These salamanders seem to have very poor eyesight, and during a chase they often run into objects and miss their prey altogether.

Radioactive Tracing Method

One of the biggest problems encountered with this experiment was that of marking and recapturing the wild population. Toe-clipping, an old standby method, is difficult to use because salamanders regenerate toes quite rapidly. Since Plethodon glutinosus has no lungs and uses its skin in their place, nothing like dye or paint may be applied to the salamander without killing it. Tags or bands would inhibit the salamanders' movements and throw a bias into the experiment.

It seemed that the ideal solution to these difficulties was found in the form of radioactive tagging. This is a relatively new method of tagging and tracing animals, having been developed by Tomes and Brian in 1946. In their work and a subsequent work by Brian (1947) the material used was radium sulphate. Elaboration of radioactive marking and detection techniques was published by Griffin in 1952. Subsequent improvements of methods and materials for radioactive tagging and detection have been recorded by Godfrey (1954 b), Pendleton (1956), and Harvey (1965). With all of the possible isotopes to chose from, very few have been found to be suitable for marking

wild animals under natural conditions. Cobalt-60 has become one of the preferred materials, being first used by Godfrey for voles (1954 a) and moles (1955). This same isotope was utilized by Karlstrom in 1957 to tag amphibians in the field. Kaye (1960) has preferred gold-198 because of its short half-life.

In many ways radioactive tags are superior to trapping for various aspects of ecological sampling. In the case of salamanders they are virtually the only way of permanently marking an individual. They also facilitate recapture by making the salamander easy to locate. Ambrose (1969) found that radioactive tagging and tracing of field mice gave a better idea of home range than live trapping. Radioactive tags generally do not inhibit or impede the normal movements of wild animals as do many other methods of tagging (Barbour and Harvey, 1968). They do have a drawback in that too strong a tag may eventually cause tumors to form in the animal (Cosgrove, Dunaway and Story, 1969).

Most of the tagging techniques used were based upon work done at the University of Kentucky (Barbour, Hardin, et al., 1969 and Barbour, Harvey, et al., 1969) and on personal communication with the above Dr. Roger W. Barbour. To complement this information there were consultations with Dr. Stephen Kaye and Mr. Paul Dunaway at the Oak Ridge National Laboratory, Ecological Sciences Division. The sum total of this preparation was that it was decided to use small wires of tantalum-182 as the radioactive tag. Tantalum-182 was selected because of its half-life (115 days) which was long enough for the experiment but short enough that if any of the tags were lost they would lose energy fairly quickly and be of little hazard to the

environment. Other considerations involved were a fairly strong, easily detectable gamma emission and low-energy beta emission by this isotope. The tags were shaped into small sections of wire 3 to 4 mm long by .75 mm in diameter each having an activity of 50 microcuries. Tags of this same material and similar specifications have been used by Madison and Shoop (1970) on Plethodon jordani.

Seventy-five tags were obtained from the Research Reactor Facility, University of Missouri, Columbia, Missouri, in early summer of 1971. The cost for the tags, shipping, and so forth, was $75.00. The tags were stored in a lead container in the Ecology Building while they were being inserted into salamanders. It was planned to detect the tagged salamanders in the field by means of a Geiger-Müller counter. The actual device to be used was a Victoreen Instrument Company Model 6A Radiological Survey Meter which was obtained from the Civil Defense Headquarters located at The University of Tennessee. Because of possible beta-induced damage to the salamanders, the tags were shielded by placing them in sections of capillary tubes and sealing the tubes with heat from a bunsen burner. The tags implanted into smaller salamanders could not be shielded because the increased tag size would badly damage the smaller animals.

All of the sources consulted, published and not, indicated that they had implanted their tags in animals by putting each tag into a hypodermic needle (not a syringe) and injecting the tag subdermally, in the case of small mammals, or intramuscularly, in the case of amphibians, which have no loose skin. No form of anesthesia was ever mentioned, but it is virtually impossible to hold on to

a squirming slimy salamander so they were tranquilized before being injected. The salamanders seemed to suffer no extended after effects from tranquilization. The tags were injected into the abdominal muscles of each animal, as was done by Madison and Shoop (1970). After tagging, the salamanders were kept in the laboratory for a week in order to check on their recovery from the operation. All but one or two healed without visible complications.

Due to the nature of the experimental technique, it was impossible to set the wild population close to The University of Tennessee. Oak Ridge National Laboratory gave permission to work on their reservation, however, and the field populations were established in three locations on the reservation. This was done in mid-summer 1971. The population were given a week of unmolested equilibration in the field to become used to their surroundings and then an attempt was made to find them.

Most of these animals were never found. The author did find some of the tags, usually without any sign of the salamanders. At about this same time, a group of tagged salamanders that had been kept in the laboratory for purposes of comparison with the wild population began dying off also. What caused this sudden death in both populations is not known. At any rate, there was now insufficient time and tags to begin this method again.

Mark-Recapture Method

At this time, the largest single problem facing the researcher was that while there was a fairly-well established laboratory population,

there was no wild population to comapre it with. Due to the lateness of the season and the lack of radioactive tags, it was decided to abandon this method and change over to the old standby, toe-clipping. The biggest problem with this technique is that salamanders regenerate lost members fairly quickly. Various substances have been found to retard this process, primarily by damaging or destroying the nerves in the remaining portion of the amputated member (Hui and Smith, 1970). Most of these chemicals are not readily available, however. Woodbury (1956) has given an excellent review of conventional methods of tagging amphibians. He notes that toe-clipping is perhaps the only practicable method of marking salamanders (aside from radioactive tags as reviewed above), and feels that the regeneration process is sufficiently slow that the clipping period is useful in at least some experiments. It was felt that since there would no longer be as long a duration to the experiment as had been originally planned, regeneration of lost toes would not become a serious problem in the experiment.

The experiment as it was set up now was as follows: Two populations were to be identified, one experimental population (the laboratory population) and the other the control (the wild population). The experimental population was to be subjected to control of only one variable, food. This population had available as much food as it could eat. Certain other variables between the experimental and control populations were similar. From each population 30 animals, selected strictly at random, would be weighed and measured each week. The reason for this was that it was found to be very difficult to

find more than 30 salamanders at any one time from the wild population. The weights and lengths from each population were to be averaged each week and the resulting means plotted against each other.

The wild population was located in a ravine beside the I. C. King Park. This park is about five miles south of Knoxville, Tennessee, just off of the Alcoa Highway (U.S. 129). The ravine in which the work was done is a 700 meter long valley which terminates in the I. C. King Park at the bank of the Tennessee River. The orientation of this ravine is northwest. It has a small intermittent stream running from its head to the Tennessee River; the lower portion of this stream is usually running water, the upper portion is usually dry. The area of the ravine is well forested in second-growth timber and the ravine floor is usually in deep shade. Dominant canopy species include Acer rubrum (L.), Acer saccharum (Marsh), Fagus grandifolia (Ehrh.), Carya spp., Quercus spp., Celtis occidentalis (L.) and Plantanus occidentalis (L.). No attempt was made to catalogue all of the vegetation in this ravine, it was simply noted to be a rather typical mixed hardwood forest common to this area. The forest floor is usually very moist and littered with abundant cover for small animals.

Marking of salamanders in this ravine was begun in August, 1970, which is a little late in the year to begin an outdoor experiment in Tennessee. Two toes were clipped from a hind foot of each salamander marked. No attempt was made to distinguish individuals because it was felt that it would be difficult to recapture the same

salamanders consistently on a weekly basis for two or three months. All told, about 100 salamanders were marked in this ravine, and unmarked individuals were still captured each week. There is really no good trapping method for salamanders, so it was necessary to search the ravine each week, rolling over stones, logs, and so forth, to find enough salamanders to measure. It was soon found that it was a full day's work to find 35 salamanders in this ravine, even though it was known that there were several hundred there.

Originally it was planned to have 60 salamanders in the indoor or experimental population. Half of these were tagged with radioactive isotopes. These, however, died when the ones in the field died. With extras which were in a spare cage in the ecology building, there remained some 40 untagged salamanders to distribute throughout 12 cages. This increased the work in maintaining the population, so the number of cages was reduced to ten with four animals in each cage. They did not seem overly crowded. Later on, the entire population of one cage was eliminated by some disease, bringing the total number of salamanders to 36.

As mentioned above, an attempt was made to reduce the number of variables in this experiment by duplicating the natural environment insofar as possible in the laboratory. It was somewhat cooler inside, but not appreciably for the time of year. Moisture was very similar. Light was duplicated with the timer mechanism; the photoperiod indoors and out were similar.

Data on both populations was gathered on a weekly basis. For the outdoor population all measurements were performed in

the field on the 30 salamanders. All salamanders in the laboratory were measured and then 30 were picked at random for the final numbers. In both cases the weights and lengths were averaged and the averages graphed.

Results

The actual results of weighing and measuring appear in Figures 1 and 2.

In both cases the average measurements of the populations are plotted versus time, and a linear regression line calculated from these measurements by the least squares method is plotted on the graph. The time scale occupies a period of three months, from September 15 through November 20, 1971.

There is a marked divergence in weight change between the two populations, as may be seen in Figure 1. The average weight of the caged populations increased at a rate of 0.018 grams per day, as opposed to that of the wild population, which increased at a rate of 0.007 grams per day. A t-test was made on these regression coefficients to determine if they were significantly different. The value of t was calculated to be 11.5985 with 16 degrees of freedom, significant at the 99 percent level of confidence. Thus, the weight of the caged population is increasing at a rate significantly greater than than of the wild population.

Little divergence is seen between the average lengths (Figure 2). The average length of the caged population increased at a rate of 0.0088 centimeters per day, while that of the wild population increased 0.0074

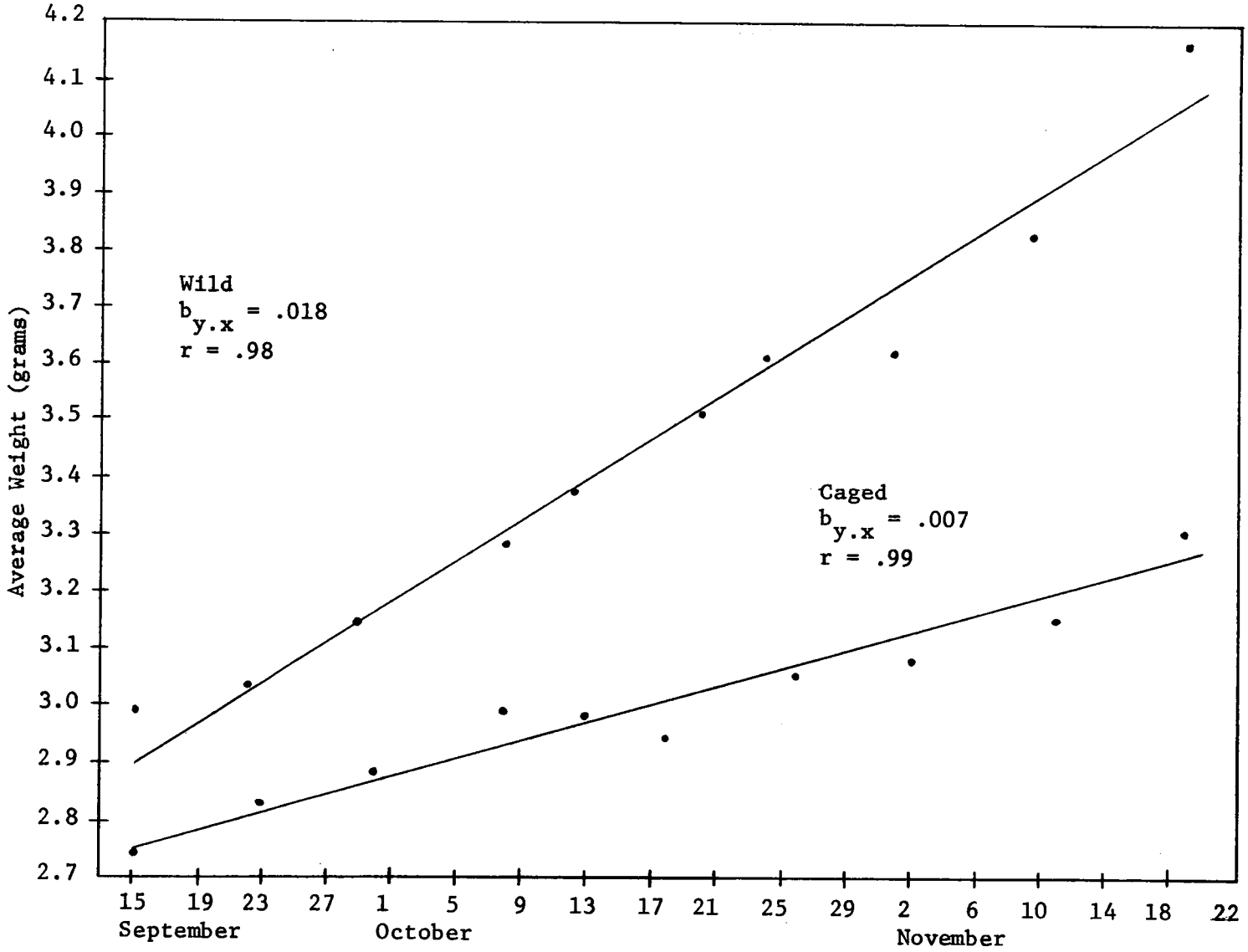


Figure 1. Weight gain of caged and wild salamanders.

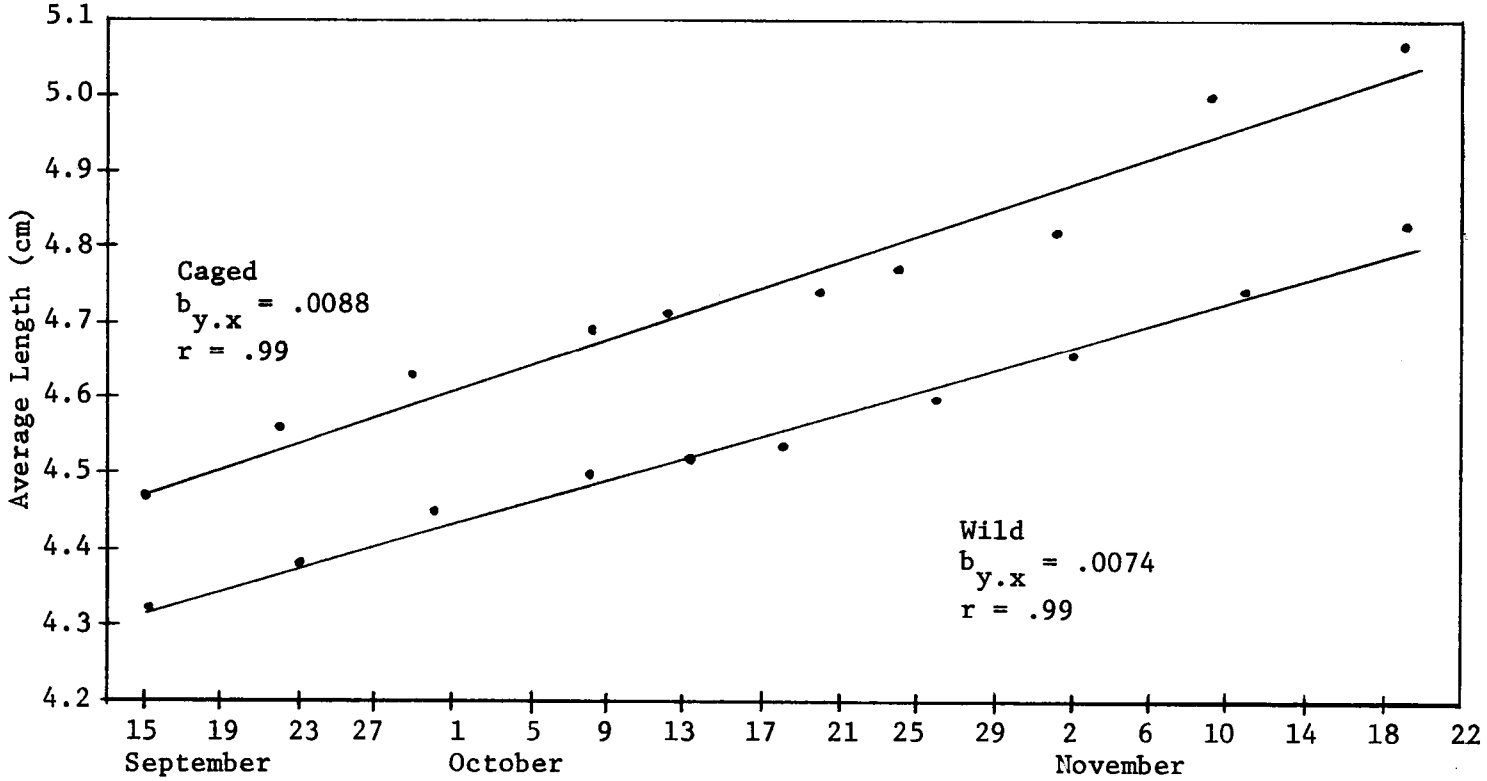


Figure 2. Length increase of caged and wild salamanders.

centimeters per day. The value of t in this case was calculated to be 1.4737, significant at the 80 percent level of confidence with 16 degrees of freedom. Although this is a much smaller level of confidence, the author would be inclined to place more emphasis on length measurements, since weight gain may be of a less permanent nature than length gain.

References used for the statistical analysis of this data were Snedecor and Cochran (1967), and Steel and Torrie (1960).

IV. SECOND EXPERIMENT: MOISTURE AS A VARIABLE

Moisture as a Population Control

In testing the possibility that physical (abiotic) factors were the chief controls of the population of Plethodon glutinosus, it was first necessary to decide which of the possible factors should be considered. One possibility was the variable of temperature. Being poikilothermic animals, salamanders' body temperatures vary directly with those of their environment. Bogert (1952) noted that terrestrial salamanders, including Plethodon glutinosus, in Virginia were found in surroundings where temperatures varied from 13.2° C. to 20.0° C. Each salamander species studied had a preferred temperature regime. Test and Bingham (1948) found the temperatures beneath logs inhabited by Plethodon cinereus in Michigan to range from 9.5° C. to 17.5° C. in the spring. Hairston (1951) has noted that Plethodon glutinosus ranges from sea level to elevations as great as 5,340 feet in the Tennessee mountains, although it is more commonly found at altitudes below 5,000 feet. This embraces a wide range of temperatures. Generally speaking, these salamanders prefer habitats in which temperatures remain below 26.7° C., but they do exist in areas where temperatures are higher.

In at least some areas, winter temperatures might be critical in the control of salamander populations. Vernberg (1953) found the salamanders Plethodon cinereus and Eurycea bislineata experienced mortality rates of 57 percent and 50 percent, respectively, during winter hibernation. Soil temperatures recorded at a depth of 15 inches

during this winter study, which took place at Purdue University, reached lows of 3° C., which is much colder than those at lower elevations in East Tennessee. The winter, also, lasts much longer in Indiana. While this area is in the center of the range of Plethodon cinereus, it is very close to the edge of the range of Plethodon glutinosus (Conant, 1958); it is likely that winter mortality of the latter is much greater than the former in Indiana. Vernberg noted that neither of the salamander species studied utilized rotting logs placed in their encaged area as hibernaculae. This contrasts with Plethodon glutinosus which is often found in such logs in the winter. In any case, it is highly doubtful that low winter temperatures exert a significant amount of population control in the more southerly portions of the range of Plethodon glutinosus, especially in such areas as Georgia and Florida.

Water plays an important role in range limitation of virtually all amphibians. Thorson and Svihla (1943) in an experiment to determine vital limits of water loss in ten species of frogs and toads found that aquatic and terrestrial species with wet skins (Hyla spp., Rana spp.) could become dehydrated beyond recovery in four to eight minutes. Losses of greater than 40 percent of their body water were almost invariably fatal to frogs, as opposed to the terrestrial toads with dry skins (Bufo spp., Scaphiopus spp.) which could survive losses of better than 50 percent of their body water and periods of extreme drying for more than 20 minutes.

By and large, salamanders are similar to wet-skinned frogs in their ability to survive drying. For example, one of the least

drought-tolerant frogs, Rana pipiens (common leopard frog), has a vital limit of dessication of about 45 percent loss of its body water (Thorson and Svihla, 1943). For one of the most drought-tolerant plethodontid salamanders, Plethodon cinereus, this same vital limit is between 23 and 35 percent loss of body water (Littleford, Keller and Phillips, 1947).

Salamanders' content of body water is strongly related to the environment in which they live. Littleford, Keller and Phillips (1947) noted that salamanders absorb water directly through their skin. This has been demonstrated also by Stebbins (1945) and Spight (1967 b). Spight found salamanders to be capable of complete rehydration after some water loss by taking up water directly from the soil when moisture tension in the soil was not too great.

Ray (1958) performed desiccation experiments upon eight species of salamanders and was able to relate their abilities to withstand water loss to their general choices of habitat. He noted that all of the salamanders tested seemed to lose water at the same general rate; some, however, could stand more loss than others. These more tolerant species preferred drier habitats than the less tolerant, but it should be pointed out that no salamander inhabits a truly xeric or even dry mesic location. All are found in water or moist woodlands and hillsides, although some may venture into drier locales such as rock outcroppings or into trees for short periods. Ray noted that few of the salamanders tested showed "special protective behavior" to drying, by which he meant body postures.

Since moisture plays such an important part in range limitations of salamanders it might also play a role in population control. The question was how much drought would affect these animals. Obviously, a strong drought would eliminate a population entirely. Would mesic conditions prevent the salamanders from feeding and cause them to gain less weight than those in moister habitats? This was the proposition to be tested.

Methods

Due to the epidemic mentioned in Section III, and the possibility of spreading it to other cages in the laboratory, it was thought to be wise to clean and sterilize all of the cages before beginning the new experiment. All of the salamanders were placed in a holding cage in the ecology building and all 12 experimental cages were cleaned thoroughly with hot water and Alconox detergent, followed by a thorough spraying of Lysol. The cages were allowed to dry completely for a week after this treatment.

All of the soil, litter and logs that had been in the cages were thrown out. A new, artificial soil which consisted of one part sand, two parts clay loam and one part sawdust was then prepared. This soil was sterilized three times in a large autoclave located in the Microbiology Department in Hesler Biology Building at The University of Tennessee. This sterile soil was put into each cage to a depth of 1 inch. For litter a bag of pine bark mulch was procured and this was added to a depth of about 1/2 inch. The logs were replaced with new logs from an area where there were no salamanders or other

amphibians. These measures seemed to work, as there was no recurrence of the disease.

Moisture was regulated by watering the cages with a sprinkling can. Moisture measurement of the soil was by sight, and of the humidity in the cages by the Durotherm Hygrometer. It was felt that the relative humidity in the cages would well reflect the moisture tension of the soil. The humidity in the high moisture cages was maintained at about 95 percent, that of the low moisture cages at 55 percent to 65 percent.

The laboratory light cycle was set at 12 hours of light and 12 hours of darkness.

Utilizing the table of random numbers in Snedecor and Cochran (1967) six cages were chosen to serve as high moisture cages. Six others were low moisture cages. All of the plastic was stripped from the screening covering the lids of the low moisture cages. The plastic covering the high moisture cage lids was replaced with a more efficient method consisting of a single large sheet of plastic with two circular holes 2 inches in diameter. The sheet covered the entire screen surface of each lid, with the holes to allow gas transfer.

The cages were completely set up by December 16, 1971. The cages were allowed to stand empty until the first week of January, 1972, to reach equilibrium.

During November and December of 1971 the wild population was revisited and 14 salamanders were captured. These were added to the 36 already in the laboratory. These 50 salamanders remained in the holding cage until January 17, when they were all placed into

the cages in the laboratory. There were four salamanders per cage, with five each in cages 5 and 10. Cage 5 was a high moisture cage and Cage 10 a low moisture cage. The salamanders were placed in the cages at random; as each salamander was removed from the holding cage, it was put in a cage until there were four salamanders in each cage. There was no particular reason for placing the extra salamanders in cages 5 and 10; they needed to be put somewhere and these cages were convenient to remember.

During the course of the experiment the salamanders were fed 1,000 crickets per week. These were of the same size and from the same source as in the feeding experiment. An initial feeding of 2,000 crickets was placed in the cages to overcome any effects of hibernation and starvation in the salamanders.

Measurements were taken in the same manner and with the same tools as in the feeding experiment. Measurements were taken at one-week intervals beginning on March 6, 1972. The cages had been allowed to stand unmolested for the month of February in order to allow the salamanders to become used to their environments. During this period both low and high moisture cages were kept at the same humidity, around 90 to 95 percent. Five salamanders died, for reasons unknown, and the remainder were slightly redistributed to try to keep numbers as even as possible. It has been found to be best to allow this one to two month adjustment period, because some of the salamanders always die.

Results

The actual results of the weighting and measurings may be seen on the graphs, Figures 3 and 4. Figure 3 represents average weights plotted versus time, Figure 4 average lengths versus time. The experiment ran from March 6 to May 2, 1972.

As in the feeding experiment, the divergence between the two populations in weight is greater than that in length. The average weight of the high-moisture population increased at a rate of 0.009 grams per day. That of the low-moisture population increased at a rate of 0.0197 grams per day, contrary to what would be expected if moisture were a regulating factor of growth rate. A t-test was performed, as in the feeding experiment, to see if the regression coefficients of the two populations' weights were significant. The value of t was calculated to be 3.057 at 12 degrees of freedom, significant at the 90 percent level of confidence.

The regressions of length show a similar relationship to the weights, in that once again individuals in the low-moisture population seem to be growing faster than those of the high moisture population. The high-moisture individuals are growing at an average rate of 0.006 centimeters per day, those of the low-moisture population at a rate of 0.008 centimeters per day. The value of t between these two regression coefficients was calculated to be 0.4255, not significant at any level of confidence with 12 degrees of freedom.

There may be some question as to how valid the results of this experiment are in view of the wide discrepancy between the initial sizes of the two populations compared. There is some indication

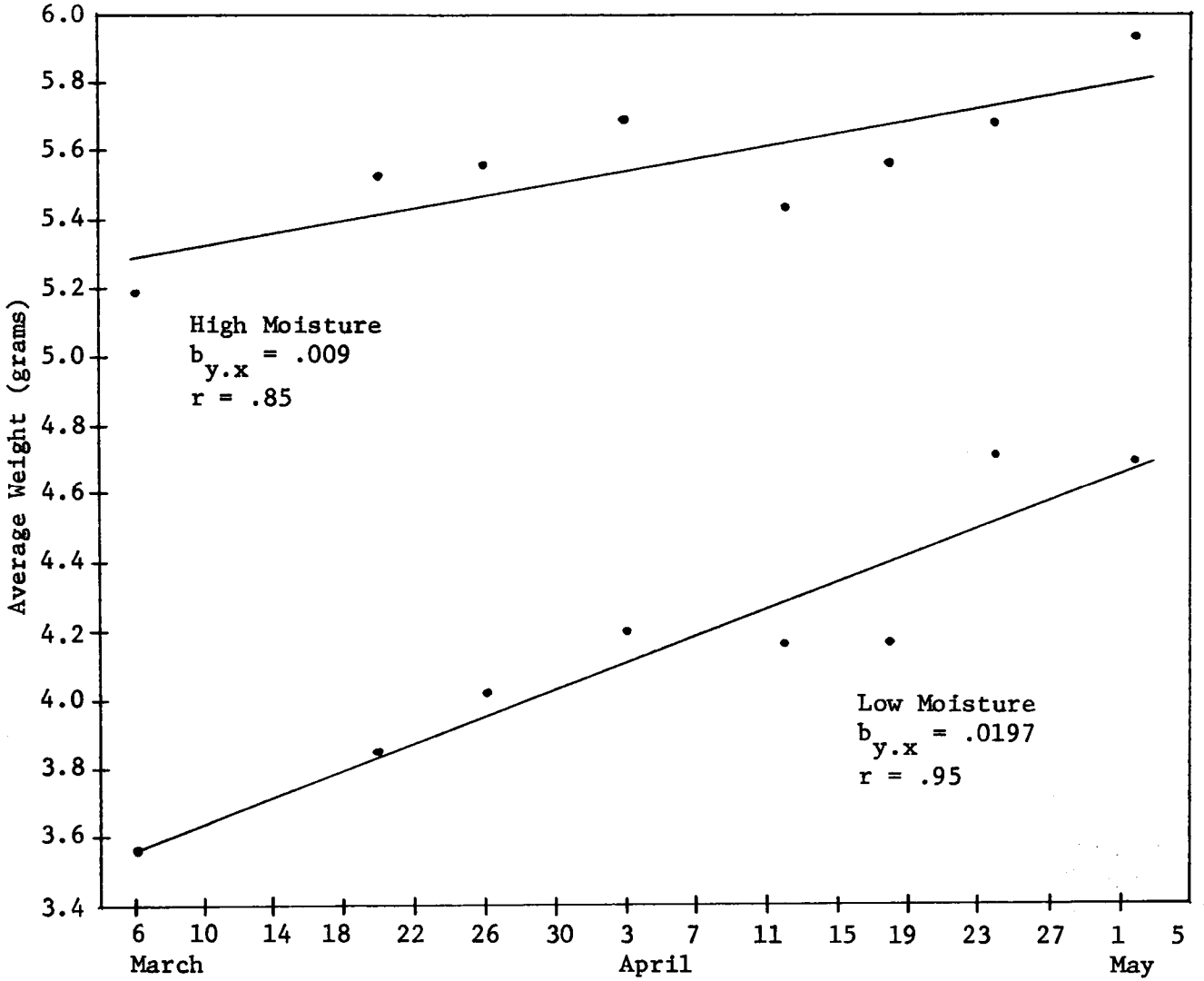


Figure 3. Weight gains of salamanders under high and low moisture conditions.

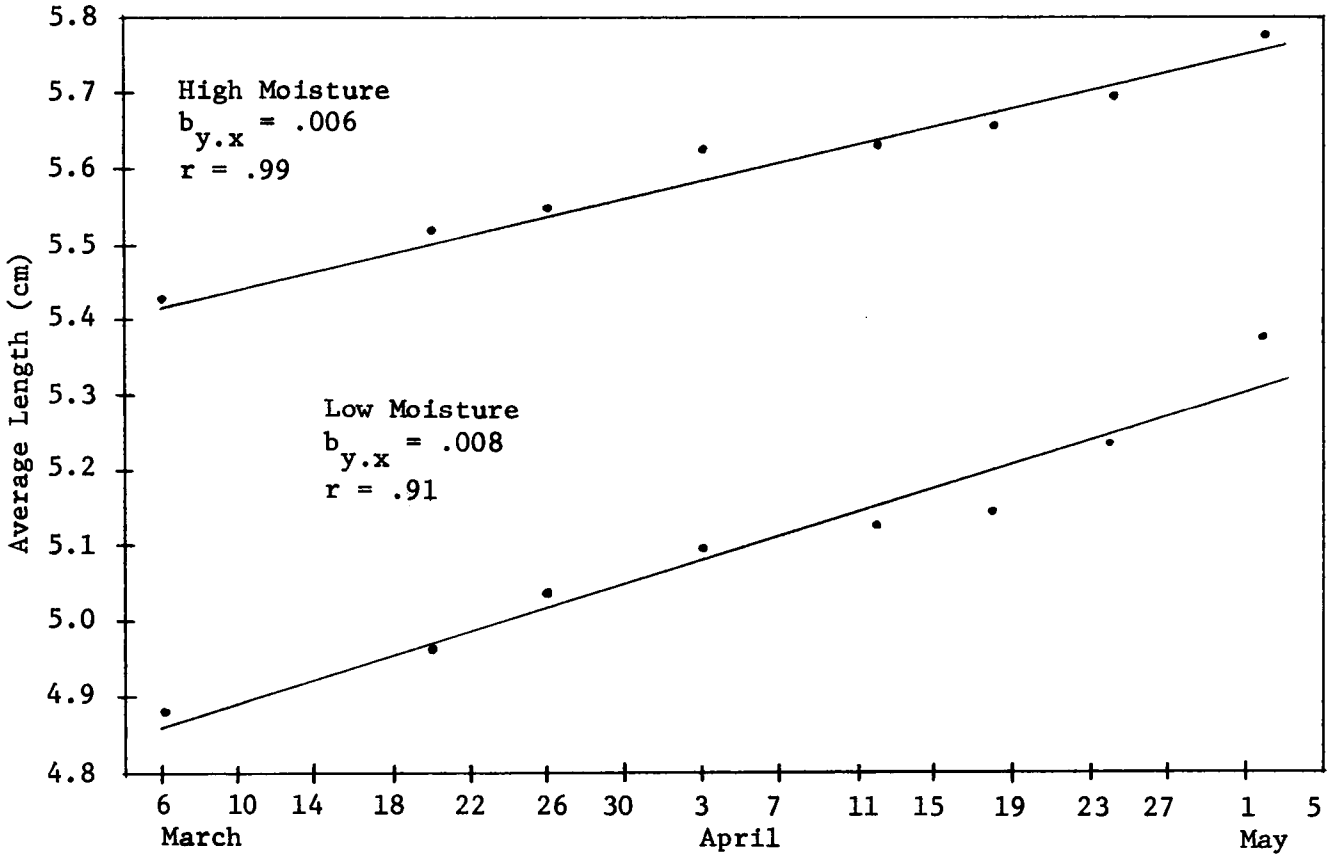


Figure 4. Length increase of salamanders under high and low moisture conditions.

that the low-moisture population was increasing in both weight and length at a faster rate than the high-moisture population. This could be due to the fact that the majority of the individuals in the low-moisture population were smaller than those of the high-moisture population. Smaller animals often grow faster than larger, more mature animals of the same species. If the sizes of the two populations had initially been more nearly similar such a growth rate difference might not have been evident.

However, it should also be noted that there was no significant difference between the two populations in length increase. Insofar as the greater weight increase rate is concerned, by the theories of control by climate the animals existing under high-moisture conditions should have been showing the greater increase. This did not happen. Therefore, it is probably safe to say that in this instance, at least, low moisture is not affecting the growth rate of Plethodon glutinosus.

V. OTHER OBSERVATIONS

Territory as a Population Control

The establishment and maintenance of territories by some animals has long been seen as a method of population control. Elton (1927), when faced with the problem of control factors for "top predators" in the pyramid of life, postulated that territoriality would prove to be a major control. It is true enough that many animals, from fish to fowl, establish and defend territories. These may be temporary or permanent, solely for breeding or also as a living space. Such behavior has attracted the attention of a number of researchers; among the better, more recent compilations of territorial behavior are the works by Lorenz (1952, 1967). Tanner (1966) has found that competition for territories is the ultimate biotic control in territorial vertebrates, superseding even predation and other forms of competition.

In light of these findings it seemed worthwhile to find if Plethodon glutinosus was territorial. Other amphibians have been found to establish territories. Martoff (1963) found the green frog (Rana clamitans) to be territorial in the breeding season. Grant (1955) tested two species of salamanders, Hemidactylium scutatum and Eurycea bislineata for territoriality. He found the latter to be quite aggressive in its territorial defense. The former salamander was not nearly as aggressive, but it too established and defended territories. Stewart and Bellis (1970) were unable to definitely

establish territoriality for Desmognathus fuscus and Desmognathus ochropheaus. The fact that these salamanders tended to congregate in groups of two individuals under each bit of overhead cover tends to cause one to doubt territoriality as a constant mechanism. It might be a seasonal phenomenon, however.

Methods

This experiment was performed during the period of August - October, 1970, before either of the experiments noted in this paper had begun. At this time, the primary interest was in observing the general behavior of Plethodon glutinosus, in order to know what sort of occurrences to expect when the cages were set up for later experiments.

The cage which was built was square, 2 feet on a side. The sides were 8 inches high. The top was a single pane of glass. Holes 1 inch in diameter were bored in the sides and then covered with screen in order to allow air transfer. The bottom of the cage was 3/4 inch thick plywood. The inside of the cage was lined with plastic to make it waterproof.

This cage was set up much like the ones in the feeding experiment, in that an attempt was made to duplicate the natural habitat with materials from that habitat. The soil depth was made to be about 2 inches; this was covered with leaf litter, moss polsters, logs, bark and other material. The cage was stocked with nine salamanders which had been caught in an area near where the wild population in the feeding experiment was later located. Since Plethodon glutinosus

is primarily nocturnal, it was necessary to watch them at night. The cage was placed in a laboratory in the ecology building and the salamanders were observed by the light of a small red light. Red light is often invisible to nocturnal animals; it is definitely not invisible to Plethodon glutinosus. At first they hid from it. After about a week they came to accept it and it was possible to observe feeding and other behavior.

Results

As to whether Plethodon glutinosus is truly territorial, the evidence is somewhat debatable. Often as many as five salamanders would take up residence in a log, if it were large enough. Up to four were found under a single log in the wild. More important, they have been found together, that is, actually in contact with one another, often enough that such behavior could not be called rare. It is hardly the rule, however.

On the other hand, the researcher has seen behavior which might be termed territorial defense. Although he never witnessed the pushing away of intruding salamanders by the defending salamander as was recorded by Grant (1955) for his two species, the author has seen slimy salamanders attack others of their own species by biting. Many of the caged salamanders showed bites in the fall, but less often at other times. Fall is the mating season of Plethodon glutinosus. It was also noted that more males than females exhibited such bites. This observation was thought sufficiently important to place more than enough shelter logs in each cage for the number of salamanders.

Before this was done, two male salamanders were found dead from what appeared to be bites. It is believed, therefore, that territoriality in Plethodon glutinosus may occur in the breeding season, a one or two month period in early fall.

Predation as a Population Control

Predation of Plethodon glutinosus was not actually studied, and no first hand data is offered on it. Some light can be shed on it from a literature review aspect, however.

Hairston (1949) gave as a general rule that ". . . salamanders are fed upon by almost any carnivorous species that is able to catch them." Orr (1962), in his work on possible mimicry between Plethodon jordani jordani and Desmognathus ochrophaeus carolinensis, narrowed the list of possible predators of these two species to the garter snake Thamnophis sirtalis sirtalis, the short-tailed shrew Blarina brevicauda, and two species of salamanders which are not present in the I. C. King Park area. The author has observed in this area the southern ring-necked snake (Diadophis punctatus punctatus), toads (Bufo spp.), an unidentified owl, and the common opossum (Didelphis marsupialis). All of these, plus the short-tailed shrew, which the author has also seen in this area, may be listed as potential predators on Plethodon glutinosus. In addition, Plethodon glutinosus is a cannibal. There might also be other predators in the area. If, in fact, predation does play a significant part in population control of salamanders, there are certainly sufficient predators present in I. C. King Park to affect the population of Plethodon glutinosus there.

VI. DISCUSSION AND CONCLUSIONS

As stated in the introduction to this paper, it was the researcher's purpose to study the population control mechanisms of Plethodon glutinosus through indirect means. In the two experiments performed, these indirect means were the measurement of individual growth parameters of increase of length and weight versus time. The researcher feels that length-versus-time relationships are a more accurate reflection of individual growth than weight-versus-time. The reason for this is that weight increase is a reversible phenomenon, whereas length increase is largely permanent. A salamander cannot substantially decrease in snout-vent (head and body) length without incurring severe injury or death.

In the first experiment, a comparison of the fed and unfed populations as to weight and length in the form of their respective regression coefficients shows a definite significant difference between the populations. This difference is significant only at the 80 percent confidence level in the case of length, but such a large margin of error is not unusual in biological studies. It may be stated with some feeling of assurance, therefore, that the very abundant food supply available to the captive salamanders caused them to increase in both length and weight at a rate which was far superior to the salamanders in their natural habitat. A similar study in which the quality, rather than the quantity, of food available was insufficient was that of Eisenberg (1966) in his work on pond snails. Many

authors, including Odum (1971), have noted that certain freshwater fish, especially the common bluegill, Lepomis macrochirus (Rafinesque), grow at a poor rate and often become stunted when their biomass approaches the carrying capacity of the habitat.

In the second experiment, the physical factor which was felt to be most likely to affect Plethodon glutinosus populations in this area was moisture stress. From the experiment performed, it may be seen that a relative humidity of 90 to 95 percent is probably not the optimum, since the salamanders living at a lower relative humidity showed a greater weight gain. This weight gain was statistically significant. Neither population, however, grew significantly faster than the other in body length. For salamanders to increase in size they must be actively consuming food. When moisture becomes critical, however, these animals employ a variety of "special protective behavior" actions to avoid drying out (Ray, 1958). Severely dried salamanders do not move about (Littleford, Keller, and Phillips, 1947; Ray, 1958; Stebbins, 1945). In the case of Plethodon glutinosus, the researcher has noticed that they construct elaborate tunnel networks in the litter and soil. These tunnels resemble mouse runs and could easily be mistaken for them; however, salamanders maintained in the laboratory also constructed such tunnels. This construction might conceivably be a protective adaptation against drying since such tunnels usually feel moist to the touch. They might also be a protection against predation. Another "protective behavior" is estivation. None of the salamanders in the laboratory estivated.

One of the observations made was that this salamander may be territorial in the breeding season. If territories are set up, observations indicate that they are not permanent. Such temporary territoriality may have an effect on population size. The work by Tanner (1966) indicates that while non-territorial vertebrates may experience their most severe predation pressure as juveniles, territorial vertebrates which do not possess territories become the more hunted prey. A census of wild populations of the salamander Plethodon cinereus by Test and Bingham (1948), found the relationship of juveniles to mature animals to average about 50-50. A census taken of the salamanders in I. C. King Park in 1970 showed a similar relationship to exist for this population. Test and Bingham conclude that their figures indicate that there is little differential mortality between the two classes of salamanders. While there has been no work done on possible territoriality in Plethodon cinereus, this salamander is similar enough to Plethodon glutinosus that findings made upon one may be applied with caution to the other. Thus, the populations of both may be affected by territory. Grant (1955) has shown that in the case of two species of salamanders, territories consist largely of overhead cover. Those individuals not possessing a territory are denied the protection of such cover, which greatly increases their vulnerability to predators and weather.

Lastly, Plethodon glutinosus is a prey as well as a predator. A large number of other creatures eat these salamanders if they can obtain them (Hairston, 1949; Orr, 1962). However, Plethodon glutinosus is probably not the mainstay of any creature's diet. It is rather

hard to catch. It is both nocturnal and largely subterranean in habit, and constructs its own tunnel system which may or may not connect to the tunnels of other creatures. In addition, catching a slimy salamander is not always keeping it. They are very slippery and have a "break-away" tail. How much control is exercised over Plethodon glutinosus populations by predation is unknown.

By the above experiments, it has been shown that captive individual slimy salamanders, when given abundant food, increase in size faster than wild individual slimy salamanders. It has also been shown that variations in habitat moisture above the point at which these salamanders cease activity or die does not affect this growth rate appreciably when the salamanders have abundant food. The question now becomes, what relationship, if any, does an increase in the body size of individual salamanders have to an increase in the size of the population as a whole? Gause (1934) believed that a relationship did exist, and he formulated an equation to express this relationship. His conclusion was that as the number of individuals in a population increased, the rate of growth of each individual in the population decreased. He ascribed this decrease in growth rate to competition for an increasingly limited quantity of food. This harks back to the writings of Darwin (1859) and Elton (1927), who postulated food to be the ultimate limiting factor, but unlike their conclusions Gause's idea does not necessitate that starvation be reached before food becomes a limiting factor on population growth. If no other limiting factor were present, of course, the ultimate fate of a complete cessation of both individual and population growth

due to starvation would occur. This was seen in the case of the deer of the Kaibab Plateau (Kormandy, 1969). Odum (1971) has noted the similarity between the graphical expressions of population growth forms and the individual growth patterns as shown by Bertalanffy (1957). Odum is cautious about drawing any conclusions from this similarity and is content only to call attention to it.

For the researcher's own point of view, he tends to agree with Gause. In a population of animals small enough to be well below the carrying capacity of the habitat, the individual animals should have abundant food available to them and should be able to grow at a high rate. In addition, the chances are that each individual well-fed animal will be healthier, or at least stronger, than a less well-fed animal. As the numbers of animals increase, however, the amount of food available to each will be necessity decrease and the growth rate should decrease as well. At some point this decreasing food will begin to affect the health of the population and could cause a decline in the survival chances of the individuals and the population numbers. If the animals of a wild population are seen to be growing at a distinctly submaximal rate due to lack of food, additional animals of the same species can only serve to increase this lack of food for all. At this time either an out-migration should occur or the individuals will become stunted and possibly a die-back of some proportion of the population will be observed. It is most likely, however, that before such starvation effects occur the numbers of animals will be thinned somewhat by disease or predation. Therefore, it is most likely that food is limiting to both the individual growth

and the population size not only through the mechanism of starvation, but also by lowering reproduction and the general survivability of the animals and increasing the population's susceptibility to disease, parasitism, and predation. The same reasoning applies to moisture: if moisture limits individual growth in the presence of abundant food, it will most likely limit the size of the population under the same conditions. This is even more probable since the population numbers can increase only up to the amount of moist shelter available in a dry habitat.

The conclusions drawn from these experiments are as follows: food is limiting to individual growth potential and probably to population growth in a like manner. The salamander Plethodon glutinosus is not achieving its full growth potential in the ravine at I. C. King Park, indicating that the population is sufficiently large to be competing among itself for a less than abundant food supply. The general level of health prevailing among the salamanders in I. C. King Park indicates that this competition has not become severe, however, which could mean that the population is being kept in check by out-migration, predation, or simply has not had time enough to grow sufficiently large to deplete its food supply. Where moisture levels of the habitat are not so low as to cause incapacitation or death of the salamanders, moisture is not a limitation on individual growth. In the presence of sufficient moist habitat and cover moisture is not a limitation on the population size either. Moisture is probably not a limiting factor on the population in I. C. King Park. Territory is probably a limiting factor to the population size of Plethodon

glutinosus adults, at least in the breeding season, in an area where available territories are limited. Predation is probably a limiting factor to population size where predators are abundant and shelter is limited. Predation pressure may be most severe in the breeding season of Plethodon glutinosus. Work by Test and Bingham (1948) indicates that it is extremely difficult to obtain reliable census figures for a population of terrestrial plethodontid salamanders; the census of the population in the ravine at I. C. King Park was undoubtedly imperfect for the same reasons as that done by Test and Bingham. In the absence of a truly accurate census of the wild population studied it is impossible to say how great a part territoriality or predation are playing in the control of this population.

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