POPULATION ECOLOGY OF THE SPADEFOOT TOAD, *Scaphiopus h. holbrooki.*

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By

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INTRODUCTION*

The spadefoot toad of eastern United States (Scaphiopus h. holbrooki) has aroused keen interest among biologists since before the middle of the 19th Century. It has received attention from scientists because of its secretive habits, because of its amazingly sudden appearances in very large breeding groups during periods of heavy rainfall, and because of its interesting embryonic development. Much has been written about this secretive behavior and the sudden but sporadic breeding choruses, and the literature has been well summarized by A. H. Wright (1932). The spadefoot breeds only in temporary water, and probably correlated with this larval habitat is its rapid embryonic development, which has been studied in other species by A. H. and M. S. Trowbridge (1937) and M. S. Trowbridge (1941, 1942). The latter in 1941 (p. 522) said, "In Scaphiopus bombifrons, the rate of development

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*Many individuals have given generously of helpful suggestions and criticisms, and for this I wish to thank Olive and Coleman J. Goin, Archie Carr, H. T. Odum, R. A. Edwards, and W. L. Jennings. Many have helped physically in construction of field projects and I gratefully acknowledge the help of W. Auffenberg, J. Crenshaw, K. Hansen, W. McLane, B. B. Leavitt, A. Carr, and A. M. Laessle, who also aided in plant identification. Doctors A. B. Grobman and Warren Hansen gave advice on statistical matters, although I take full responsibility for any errors in theory or detail found herein. Doctors A. Carr and J. C. Dickinson kindly offered the use of their respective ranches for study and the College of Arts and Sciences gave a fellowship for the summer of 1953. Two persons deserve most special acknowledgement. My teacher, Dr. W. C. Allee, has guided my academic program, has wisely led my research, and has given me inspiration. My wife, Winifred Pearson, has helped physically in the field study, has given aid and suggestions in writing this report, and she has provided, most ably, financial and moral support.

throughout the entire embryonic and larval period is more rapid than that which has been reported for any other amphibian. The cleavages in particular take place with surprising speed; they are among the most rapid cell divisions ever recorded." A comprehensive study of the larvae of S. holbrooki was made by Richmond (1947) that opened vistas for further study of the social phenomena in the tadpole aggregations.

The spadefoot toad is quite abundant in Florida, especially in the upland forests. It spends much of its life in underground burrows from which it emerges during nights of optimal toad environment. The toad is not nearly as secretive as reported in the literature and in the Gainesville region it can be observed on a majority of the nights of the year. The abundance of this animal, the ease with which it is captured, and the obvious need for further study of its habits make it an ideal animal for a population study.

In a recent book, The Principles of Animal Ecology, by Allee, Emerson, Park, Park and Schmidt (1949), one large section was devoted to populations and their study. This section of the book illustrated that (1) the main part, and in some cases, all of the data supporting the principles of population ecology has been obtained in artificial laboratory experiments, and (2) that terrestrial, cold-blooded vertebrates have not been utilized as observational or experimental material in careful studies of population biology. However, at least two good field studies of reptile populations have appeared recently. Stickel (1950) made an extensive study of the home range and population factors of the box turtle and more recently Carpenter (1952) made a comparative study of three garter snake populations. Dice (1952) in a book on natural communities states (p. 180), "At the present time thorough and long continued quantitative studies of the rates of increase, rates of mortality, and fluctuations of populations living under natural conditions are very much needed."

The first objective of the present project was to test some ideas current in population studies, using a terrestrial, poikilothermic vertebrate in its native habitat. For example, observations were made relative to the density and age group distribution and their effect on individual growth and mortality rates. Likewise, data on the relationship between the physical environment and the activities of the toads were gathered.

A second objective of this work was to attempt a determination of the extent or level of social behavior of this amphibian, with special reference to its home range, in its natural surroundings. It should be remembered, however, that a firm foundation of sound observations concerning the life history and habits of an animal is needed before general principles can be wisely formulated. An important part of the research was to raise, by observation and experiment, the base level of factual information about this animal.

DESCRIPTION OF SCAPHIOPUS HABITATS

The Gainesville region is on the center of an elongated ridge section of Florida, designated as the Central Highlands topographic division by Cooke (1939, 1945). Surface features north of Gainesville include a relatively flat area with elevations of 150 feet and higher dominated mainly by pine forests. To the south of the city are gently rolling hills between 70 and 130 feet in elevation with much of the surface about 80 feet above sea level. A mantle of Pleistocene sands covers some 4,000 feet or more of sedimentary bedrock, of which most is limestone. These rocks are eroded by subsurface solution producing typical Karst characteristics of solution lakes, prairies, and sink holes. A number of large level prairies are found south and southwest of Gainesville and most are at about 60 feet in elevation; in this region the mantle is thin enough to permit frequent outcrops of bedrock,

According to Carr (1940) adult *Scaphiopus* is a characteristic element of upland hammocks, is frequently found in high pine woods, and is occasionally seen in rosemary scrub, low and mesophytic hammocks, and palmetto flatwoods. Of these communities it appears that the following serve as major spadefoot habitats: (1) high pine, (2) upland hammocks, and mesophytic hammocks.

The habitat nomenclature was later changed by Laessle (1942) when he discussed and defined the plant communities near Welaka, Florida in great detail. The community classification used here is that of Laessle (*ibid*). The *Pinus palustris* - *Quercus laevis* Association (High pine of Carr, *op. cit.*) occurs on hilly to gently rolling topography having deep well drained and leached soils. Longleaf pine (*Pinus palustris*) and turkey oak (*Q. laevis*) are dominant in this often burned, xeromorphic habitat that exhibits extreme variations in climate. In it no large or extensive populations of toads were studied by the author.

Spadefoot toads are found in greater densities in xeric hammocks (upland hammocks of Carr, op. cit.). The canopy of the dominant live oak (Q. virginiana) with the characteristic Spanish moss on its limbs, catches much of the rainfall, especially during light showers. Winds move freely under the canopy of the live oaks, and reduce atmospheric moisture so that it is not surprising to find dry soils and xermorphic conditions. Shrub and herbaceous vegetation is sparse and no great amount of leaf mold accumulates on the forest floor.

The climax association of north Florida is characterized by the magnolia (Magnolia grandiflora) and American Holly (Ilex opaca) (mesophytic hammock of Carr, op. cit.). The canopy considerably reduces wind movement and penetration of light to the floor of the habitat. Humidities are generally higher and more stable in this community than in other spadefoot habitats and a more stable general environment is found here than in other communities (Rogers, 1933). Shrub and herbaceous plants are more common than in the xeric hammock, and leaf mold and other organic materials collect in greater quantities on the floor of this habitat than in the others mentioned.

Spadefoots are also observed in old fields, pastures, and other ruderal plant communities that are usually areas cleared of one of the major habitats mentioned above. They are also recorded infrequently in others described by Laessle (op. cit.) as P. clausa - Quercus spp. scrub (Rosemary scrub of Carr, op. cit.) and in longleaf pine flatwoods (partly the palmetto flatwoods of Carr, op. cit.).

The soils of the major toad habitats are alike in that they are all well drained, they are generally loose and friable, they are derived from surficial sands, and there is no extensive accumulation of organic materials. Lakeland fine sand, the leached soil of the high pine community, is characterized by gray fine sand in the top six inches with a yellow fine sand occurring below this to a depth of about six feet. The xeric and mesic hammocks have Kanapaha or Blichten soils. Those of the mesic hammock are generally more moist and darker in color and there is a greater proportion of organic material than in the more leached soils.

The climate of north Florida is most influenced by three pressure systems known as the maritime polar (MP), the continental polar (CP) and the maritime tropical (MT) air masses. The source region of the MP is in the north Pacific and it is more humid and not as cold as the CP air mass that moves southward from the Hudson Bay region. Both of these masses usually move southward and eastward across the continent. The MT air originates in the Caribbean and the southerly winds bring warm, moist weather to Gainesville.

During the summer the polar air moves into Florida more slowly and is considerably modified in the meantime. Under the influence of the Bermuda high pressure system, occasionally polar air masses stagnate and assume the hot, dry characteristics typical of continental tropical (CT) weather; however, because of its secondary source region this is not truly a CT mass. Maritime tropical air holds forth in Florida during much of the summer giving a hot and usually humid environment. There is little variation of temperature during the summer months as is shown by the maximum and minimum daily temperatures given in Figure 1.

In October the first polar air mass bringing lower temperatures usually penetrates as far south as Gainesville. From fall through spring there is a continual variation between several days of polar air mass domination and several days of MT weather. This is illustrated by the variations shown in maximum and minimum temperatures of the fall and winter period in Figure 1. Polar air masses (MP and CP) passing over the continent southward during the winter become dry and if these circulations are situated so that north or northwesterly winds occur in Gainesville, cold and dry weather exists with cloudless blue skies and high evaporation rates. On the other hand, if these polar circulations move further eastward, and north to easterly winds strike north Florida, they pick up much moisture over the Atlantic and bring a moist, raw, but not as cold type of weather.

The average rainfall for the Gainesville region is 49.11 inches, but the rainfall is quite unequally distributed. Convectional precipitation occurs from June to September (MT weather) and accounts for about half of the annual precipitation. Cyclonic rainfall occurs from October to April as centers of extratropical storms moving northeastward, while front weather in advance of polar air masses is primarily responsible for the winter rainfall. Comparatively long droughts are common in winter and spring and not infrequently occur during the normally wet summer period, as for example July through August, 1952.

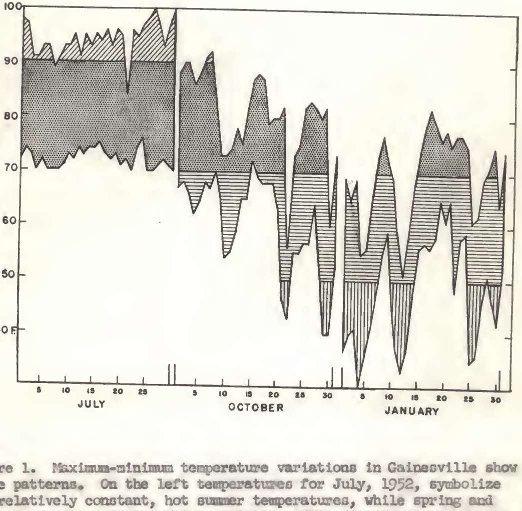


Figure 1. Maximum-minimum temperature variations in Gainesville show three patterns. On the left temperatures for July, 1952, symbolize the relatively constant, hot summer temperatures, while spring and fall seasons are illustrated by October, 1952, records that show the sudden change of pattern from the summer type to the variable winter type. On the right January, 1953, weather shows the variations from several days of warm to several days of colder climate.

The hytherograph shown in Figure 2 summarizes in pictorial form the average temperature and rainfall for the months of the year.

The relative humidity of north Florida fluctuates with recorded extremes of 20 to 100 per cent. Rogers (op. cit.) says that humidities may fall in the mesophytic habitats during mid-afternoon to as low as 30 per cent in even the driest habitats. Rogers, comparing evaporation rates in five major communities of the Gainesville region, observes that the mesic hammock has the lowest and least variable evaporation rates, while the high pine community has high and quite variable evaporation. The humidity of the xeric hammock is lower and more variable than the mesic hammock.

DESCRIPTION OF SPECIFIC RESEARCH PLOTS

The present study was started in June, 1951, and was continued through November, 1953. Three plots were selected as sites for the population studies, and these areas were chosen with regard to the size of the spadefoot population, the plant communities, the expected permanency of the habitat, and the convenience of travel to the site. The plots will hereafter be referred to and described as plots 1, 2, and 3.

Plot 1. Dickinson Ranch. Plot 1 is located about five miles southwest of Gainesville in Range 19 E, Township 10 S. Section 16, and its elevation is 60 feet. This plot was studied as nearly as possible once each week from July 19, 1951, until September, 1953. However, if the weather was such that toads were inactive, as during cold, dry winter periods, these weekly visits to the plot were not regularly made. This plot as

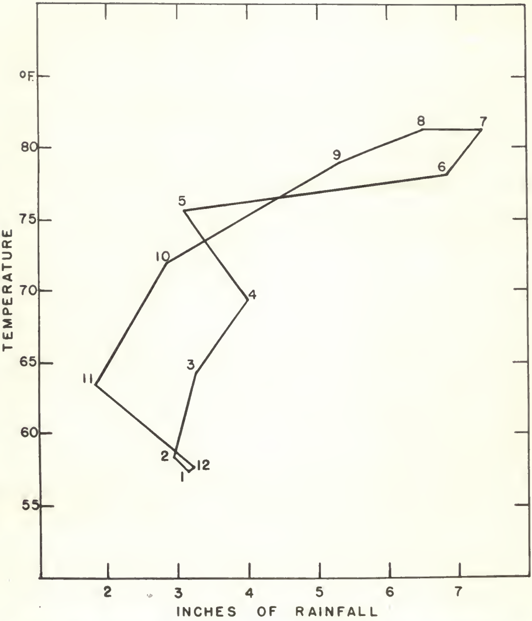


Figure 2. A hytherograph showing the annual variation in average monthly temperature and rainfall at Gainesville, Florida.

originally surveyed measured 200 by 300 feet with the longer axis paralleling an ecotone between a xeric hammock community and a grass prairie, as shown in Figure 3. As this figure shows, a 100-foot grid system and three 10-foot grid systems were used and that grid lines were numbered and lettered. The intersections of the grid lines were made plainly visible for the nocturnal research by the insertion of white stakes at these points.

The canopy of the forested portion of this plot is dominated by large live oaks and an occasional sweet gum (*Liquidambar styraciflua*), pignut hickory (*Carya glabra megacarpa*), and Florida maple (*Acer Floridanum*). Underneath, especially near the ecotone, are many smaller trees most of which are less than 40 feet tall. This stratum is composed of American holly, sweet gum, laurel oak (*Quercus laurifolia*), Florida elm (*Ulmus floridana*), and black gum (*Nyssa sylvatica*). The shrub vegetation near lines L-O is sparse and composed of a few French mulberry (*Callicarpa americana*), young laurel oak, sweet gum, and American holly plants. Between lines K and L the shrubs are more dense, with laurel oak, American holly, dwarf sumac (*Rhus copallinum*), and French mulberry most abundant. A hawthorn (*Crataegus sp.*), toothache tree (*Zanthoxylum clava-herculis*), and black haw (*Viburnum obovatum*) are of less importance in this stratum. In the ecotone between lines H and K, young sweet gum, laurel oak saplings and St. Andrew's cross (*Ascyrum hypericoides*) form the sparse shrub vetegation.

Vines recorded in the plot are poison ivy (*Rhus toxicodendron*), Virginia creeper (*Parthenocissus quinquefolia*), pepper vine (*Ampelopsis*

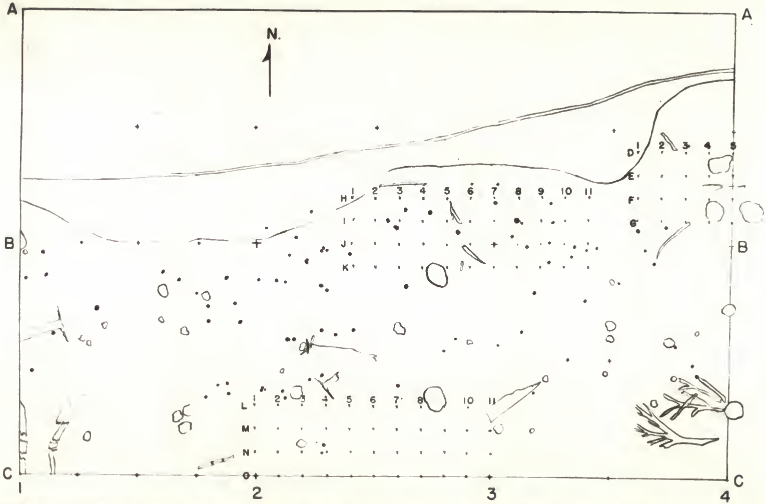


Figure 3. The crosses show position of grid stakes; live oak trees are indicated by open circles, smaller trees by dots. The letters and numbers designate the grid lines, and the location of fallen logs is also given.

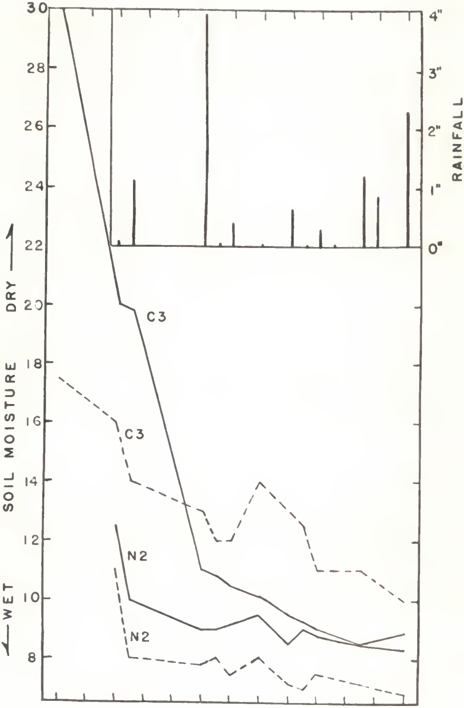
arborea), trumpet vine (*Bignonia radicans*), and muscadine grape (*Vitis sp.*).

The highest elevations of the plot are along the south border. In this area the dense mat of herbaceous vegetation and vines is dominated by ironweed (*Vernonia gigantea*), yellow jessamine (*Gelsemium sempervirens*), partridge berry (*Mitchella repens*), and violets (*Viola sp.*). Of common occurrence here are two species of panic grass (*Panicum spp.*), elephant's foot (*Elephantopus tomentosus*), bedstraw (*Galium sp.*), creeping cucumber (*Melothria crassifolia*), *Ruellia sp.*, *Smilax sp.*, spurge nettle (*Jatropha stimulosa*), and woods grass (*Oplismenus setarius*). The herbs in the shaded ecotone are very sparse with *Smilax sp.*, pepper vine, and panic grass comprising most of the plants. In the ecotonal areas where sunlight reaches the lower stratum, a dense growth of tea weed (*Sida sp.*), wood sages (*Teucrium nashii*), and dogfennel (*Eupatorium sp.*) is found.

In the prairie a dense stand of dog fennel, groundsel tree (*Baccharis halimifolia*) and bagpod (*Glottidium vesicarium*) are dominant. In the low herbaceous level a mat of plants includes sensitive plants (*Leptoglottis microphyla*), Florida betony (*Stachys floridana*), sun rose (*Crocanthemum corymbosum*), frog fruits (*Lippia nodiflora*), a fleabane (*Erigeron sp.*), a rush (*Juncus sp.*), sedges (*Rhynchospora spp.* and *Carex sp.*) and grasses (*Panicum spp.* and *Paspalum spp*). Most of this vegetation was killed in August, 1953, when the entire prairie was inundated for several weeks.

The soils of the higher elevations to the south of the plot have

Figure 4. The change in soil moisture as correlated with amount of rainfall given in the inset. The smooth line gives moisture at three inches depth, the dashes at one inch below the soil surface. C3 is located in the Xeric hammock, and the measurement in the ecotone is near N_2 in the trap system.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C3
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been classified as Kanapaha fine sands. They are generally loose, friable, and well drained. Moving north in the plot, the elevation decreases rapidly about 15 feet to the prairie where Plummer fine sands occur. Outcrops of bedrock indicate the margin of the lower prairie which results from solution of the Ocala limestone. The soils of the ecotone are intermediate between the above two types. The soils of the entire area are thin, nowhere being more than 36 inches thick over the underlying bedrock.

Slight water seepage from the higher elevations to the ecotone and prairie habitats produces the generally more moist soils of the latter. Tests of soil moisture were made with a Wheatstone bridge circuit and gypsum conductivity blocks placed in the soil at one and three inches depth at the highest elevation (C 3 in Figure 3) and in the ecotone (N 2 in Figure 5). The relationship between the soil moisture and rainfall recorded in the plot during late July and August, 1953, is given in Figure 4.

This plot was surveyed with the idea that it would all be utilized in study and that a comparison of the toads in the prairie, in the hammock, and in the ecotone would be made. It was soon apparent that collecting toads in the dense prairie grasses was impracticable. Therefore the work done in the plot was confined to the ecotone and hammock areas. When it was later decided that more precise locations of toad captures were needed, collection of data was mainly directed to the three areas surveyed in a 10-foot grid system. However, throughout the study, data were taken from toads in any part of the plot where they were seen,

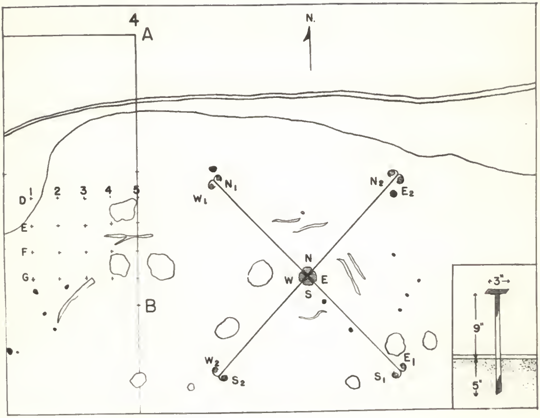


Figure 5. The trap system east of Plot 1, with inset showing cross section view of fence.

although the most effort was spent in the small grid systems.

In the late spring, 1953, a trap system was built on the east end of this plot. The trap, constructed as shown in Figure 5, had its nearest ends placed 30 feet from the east border of the plot. This distance was selected to avoid trapping toads resident in the plot during their normal daily activities. The main object of the trap was to determine the presence of, absence of, and rate of dispersal by toads resident in the plot.

Plot 2. Drug Gardens. Plot 2 is located in the College of Pharmacy drug gardens on the campus of the University of Florida. Much of these gardens has a park-like appearance with the herbaceous and shrub vegetation removed, and replaced by a lawn and cultivated shrubs. However, in the northwest corner the leaves are allowed to remain on the ground, and the herbaceous vegetation is not lawn-like even though it is occasionally clipped by a power mower. This northwest portion of the gardens was surveyed into a grid system of lines 10 feet apart, which were designated as shown in Figure 6.

The elevation of this plot is lowest in the southwest corner (N-1) and increases about 5 feet to the north, northeast, and east. In the area between lines 3-13 and B-H, cultivated plants are growing and the arborescent vegetation is scant. Leaf litter is not abundant in this area and it appears that soil temperatures and soil moisture would vary more in this open unprotected portion than in the remainder of the plot. The soils here are loose, friable Kanapaha Fine Sands. These blend into the more

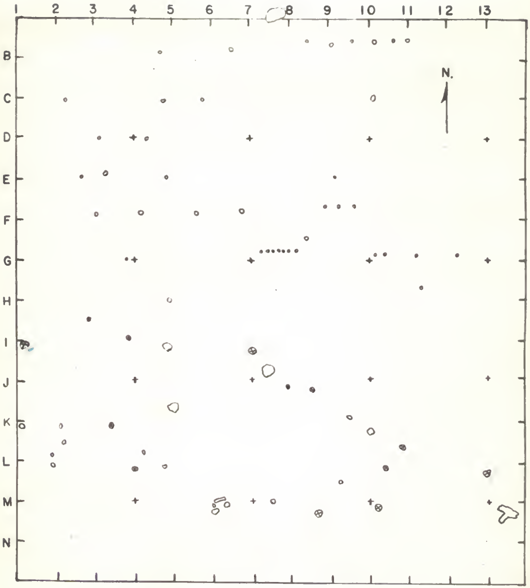


Figure 6. A map of the northwest corner of the Drug Gardens on the campus of the University of Florida. Open circles denote oak trees, solid dots other trees, and crosses grid markers.

compact and more moist Plummer Fine Sands of the lower portions in the plot. In the remaining part of the surveyed plot a thick arboreal vegetation is dominated by hickory, sweetgum, and live oak. Loblolly pine (Pinus taeda), cedar (Juniperus silicicola), black gum, and American plum (Prunus Angustifolia) are present.

Shrub vegetation is absent. The rather sparse herbaceous component comprises primarily panic grasses (Panicum spp.), partridge berry, violets, and elephant's foot. Other herbs are a bedstraw (Galium pilosum), wild potato (Ipomea pandurata), Virginia creeper, poison ivy, and Ruellia sp.

Research was begun in this small plot in August, 1951, and was continued through September, 1953. From December 1, 1951, through March 23, 1953, an effort was made to visit the plot about five nights weekly. The visits were made under all types of weather even though on many occasions, it seemed obvious that no toads would be active. The time of the visits was scattered at random between the hours of six and eleven p.m.

The purpose of the nightly field work was to obtain data on the factors influencing the activity rates of spadefoot toads and to gather data on their burrow habits and home range. The nightly work was limited to fifteen minutes duration, which was the length of time needed to cover the plot adequately. If, in this length of time, no toads were observed, it was assumed that no toad activity existed for that particular set of conditions.

Plot 3. Carr Ranch. In the spring of 1952, a semi-controlled population density experiment in fenced areas was established. The location of such an experiment not only needed to be relatively permanent and within easy travelling distance, but it needed to be one where the equipment was safe and where cattle would not trample the fence. An area with these attributes and with a plant community similar to that of plots 1 and 2 was not easy to find. A tract at the Carr's ranch west of Micanopy, Alachua County, Florida (R 20 E, T 11 S, S 34) at an elevation of 110 feet satisfied most of these needs.

Preliminary experiments showed that a hardware cloth fence of 3/8 inch mesh would retain the toads if it were buried 12 inches below and reached 10 inches above the soil surface. On top of the vertical fence a horizontal strip five inches wide was secured as is shown in the inset of Figure 7. Five circular enclosures were made with such a fence; each pen having a perimeter of 100 feet, a radius of about 15 feet, and enclosing a forest floor of 696 square feet. All of the toads resident in the pens were removed in late May and early June and the toads of a particular size group were introduced in late June, 1952. Three levels of population density were established: ten toads were put in each of two pens (#3 and #5 of Figure 7), twenty toads were introduced into each of two pens (#2 and #4), and in the fifth pen, forty toads were placed (#1).

In the experimental areas the toads were usually found just inside the fence. This fence also served to collect arthropods (Arachnida, Diplopoda, Insecta), Amphibia (*Bufo terrestris*, *Rana sphenocephala*, *Rana*

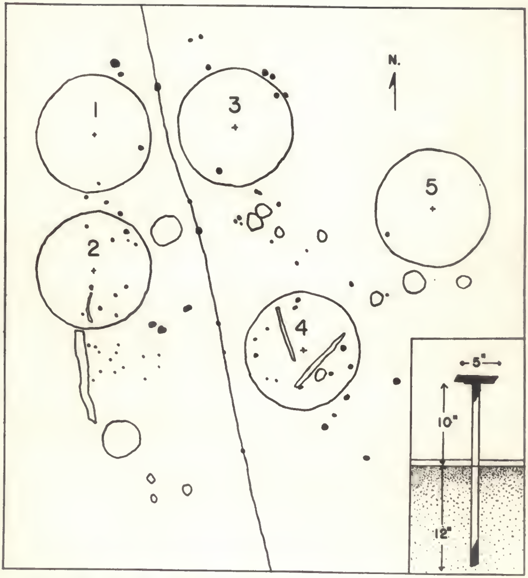


Figure 7. A map of the five fenced enclosures located on the Carr Ranch near Micanopy. Open circles designate oak trees while solid dots represent other trees.

catesbeiana, Reptilia (*Sceloporus undulatus*, *Thamnophis sirtalis*) and Mammalia (*Reithrodontomys humulis*, *Peromyscus gossypinus* and *P. Nuttalli*). This fence acted as a barrier for organisms and the area along the fence was optimum for predation.

The arborescent vegetation around these plots is dominated by large live oaks, sweetgum, and loblolly pine, while a dense lower layer of smaller trees is dominated by ironwood (*Carpinus caroliniana*), American holly, pignut hickory, black gum, water oak (*Quercus nigra*) and hercules club (*Aralia spinosa*).

The shrub vegetation varies from one pen to another. In pens 2 and 4 no shrub vegetation is present, while in the other three, French mulberry and saplings of laurel oak, sweetgum, and pignut hickory are present in very limited amount. The plots are located in areas of sparse shrub stratum vegetation that are surrounded by dense vegetation composed mostly of wax myrtle (*Myrica cerifera*), laurel oak, live oak, water oak, dwarf sumac, French mulberry, and pignut hickory.

The herbaceous vegetation is scant in pens 3 and 4, in the eastern two thirds of pen 2, and in the eastern third of pen 1. The amount of herbaceous vegetation varies directly with the amount of light; therefore, with the very dense cover of small trees in pen 3 and in pen 4 the herbs are most sparse. The herbs in this pen are elephant's foot, partridge berry, Virginia creeper, pepper vine, *Ruellia sp.*, *Panicum sp.*, a sedge (*Scleria triglomerata*), bedstraw (*Galium pilosum*), and woods grass.

In pen 4, the west third of pen 2, and the west two-thirds of pen 1, more light reaches the floor and a dense carpet of herbs is present. In these areas a ragweed (Ambrosia sp.) woods grass, yellow jessamine, bedstraw, wild potato, fireweed (Erechtites hieracifolia), a spiderwort (Tradescantia sp.) and a smartweed (Polygonum sp.) were recorded.

The highest elevations of the area are on the north of pens 1, 3, and 5 with decreases to the south. Pen 4 is at the lowest elevation. The soil of pens 1, 2, and 3 is a Kanapaha Fine Sand, while in pen 4 and 5 Blichten fine sand is found. In this area the Kanapaha sands are better drained and generally drier than the Blichten sands.

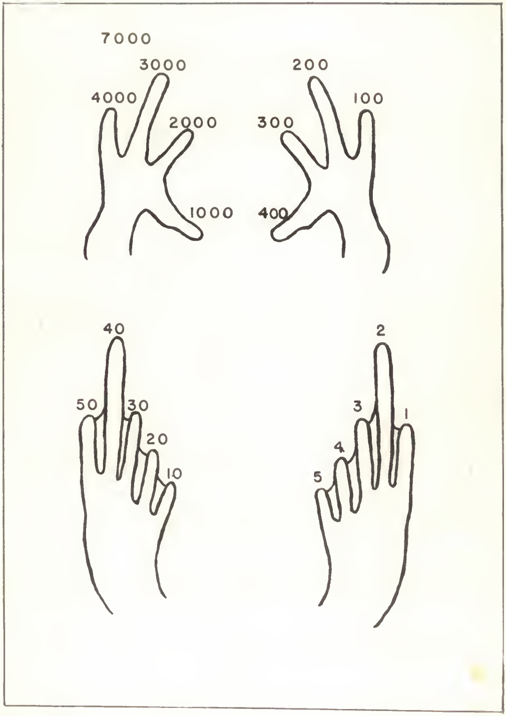
METHODS OF STUDY

Spadefoot toads do not move rapidly and are easily captured when they are above the soil surface. They are readily seen during their nocturnal feeding activities by the beam of a six volt headlight at distances of 30 to 50 feet. The eyes of the spadefoot reflect a characteristically constant, dull, red color.

Each toad was marked by removing toes with scissors at the joint between the second and third phalanx. The toes were numbered as indicated in Figure 8 and in most cases only one toe on each foot needed to be removed.

The greatest head width of the toads was measured with vernier callipers to the nearest tenth of a mm. The total length was recorded to the nearest millimeter by holding the snout firmly on a mm. ruler, fastened to a clip board, and by applying steady, gentle pressure to flatten the toad. The sex of the adult male was determined by the

Figure 8. The system of numbering toes for a four digit specimen number. Removal of the distal two phalanges of the right toe on each foot gives the animal number 1111.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presence of dark epidermal pads on the front medial digit whereas most adult females were identified by easily observable eggs seen through the body wall. The sex of young individuals was not determined. The location of the toad capture and any data concerning the toad's burrow were recorded relative to the particular grid system. All of the above data and any other general observations at capture time were written on a McBee KeySort card (type Ks371N) that measured 3 1/4 x 7 1/2 inches.

The exact time of capture was not reported, but only the hour of capture. For example, if observation began at eight p.m. and continued through nine p.m., all captures made in that hour were grouped together and recorded as eight p.m. captures. If field work continued beyond nine p.m., all of the subsequent hours' captures were designated as nine p.m. captures.

Measurement of the climatic environment was made at the beginning of the night's work, and at each hour on the hour afterward. The climatic data, such as temperature, relative humidity, vapor-pressure deficit, wind movement, and cloud cover, were added in the laboratory to each of the KeySort cards representing toad captures for the particular unit of time.

Observations of the temperature and humidity were made as nearly as possible in the three inches above the soil surface. Several instruments were utilized for this and it is believed that each was an improvement over the earlier ones used by me for measuring the microclimate. In July and August, 1951, wet and dry bulb temperatures were taken with an "egg beater" type psychrometer. This instrument has two thermometers mounted on an egg beater mechanism. From September, 1951 through January, 1952, these data were taken with a standard aspiration psychrometer manufactured by the Friez Instrument Division of the Bendix Aviation Corporation. This instrument was modified by replacing the slower acting standard thermometers supplied with the instrument with quick reading rectal thermometers. The modified instrument was used from February, 1952, through October, 1952. Then an instrument using two Western Electric thermistors and a Wheatstone bridge circuit to measure changes in electrical resistance of the thermistors as the temperature changes was used. This gave sensitive and satisfactory recordings of the microclimate. It is described by Platt (1950).

No suitable instrument was available to measure small wind velocities under the forest canopy and only general observations concerning wind movements were made. Observations were taken concerning the general cloud cover, rainfall, airmass characteristics, and soil moisture.

TOAD ACTIVITIES

Underground activities. The spadefoot toad spends much of its lifetime in a burrow measuring from 3/4 to 1 1/4 inches in diameter and from two to twelve or more inches in depth. The majority of toads were found at depths of less than eight inches. The depth of burrows was given for S. holbrooki by Holbrook (1842) as about six inches, while Ball (1936) found individuals as deep as 2.1 meters. Bragg (1944) gave evidence that S. bambifrons exhibits a direct correlation between depth of burrow and soil moisture. The burrow is usually filled with loose soil and sometimes it can be distinguished only as a tube of loose sand, contrasted to the harder packed earth surrounding it. When leaving the burrow, the animal turns spirally and gradually moves to the surface. Occasionally toads are observed in their burrows below the ground level with a small aperture extending through the soil to the atmosphere. When spadefoots are out of their burrow, a distinct opening can be observed. Upon return, the toad backs into the burrow orfice and disappears from sight by digging with the hind legs and by turning in a circular direction.

Each individual toad had a particular burrow or burrows that it used for considerable periods of time, emerging nocturnally to feed. The duration of time that spadefoots spent underground without leaving the burrow was checked in plot 2. Finely ground chalk dust was spread on the surface over the burrow entrance and surrounding soil, with the toad in its burrow, so that subsequent emergence could be detected.

Burrows of 18 individuals in plot 2 were treated in this manner. The duration of time individual burrows were studied varied from five nights for one, to 332 nights for another toad. For this study, a toad-night was defined as the record for one individual per night during the duration of study. When three nights elapsed between field trips and an individual's burrow indicated that he had emerged, one toad-night of activity and two of uncertainty were recorded, since emergence on two of the nights was unknown. A total of 2,264 toad-nights was recorded on which activity was unknown or uncertain on 947. Of the remaining 1,317 toad-nights, 1,124 were those when toads definitely did not emerge, while they were recorded active on 193. The toads were active 8 per cent and definitely underground on 58 per cent, and conditions were unknown on 34 per cent of the toad-nights. It is believed that most of this 34 per cent would fall in the inactive category if complete data had been obtained.

If a toad was active on 8 per cent of nights it would emerge from its burrow 29 nights annually. In Table 1 are given records of individuals whose burrows were studied for more than 150 nights. These indicate that emergence on 8 per cent of the nights on a long-term basis is probably the correct order of magnitude.

The length of time individuals remained definitely underground averaged 9.45 days while the median observation was 4.85 days. The extreme record was of 104 days duration. After activity on June 6, 1951, a female was inactive for 96 days. She emerged one night and was inactive for 11 days, active one night, inactive for 16 days, active the night of October 13, 1951, and was then inactive for 104 days until emergence on February 20, 1952.

TABLE 1

OBSERVATION DATA ON BURROWS OF SEVERAL INDIVIDUAL TOADS IN PLOT 2

Duration of Observation	No. Nights Active	No. Nights per Annum	No. Nights not Active	No. Nights per Annum
162	16	36	26	59
247	21	31	174	257
278	9	15	26	34
306	23	27	139	166
321	19	22	153	174
332	28	31	278	306

Presence or Absence of Activity: When dates of toad emergence were plotted, the greater number of toad emergences occurred in the spring and fall seasons, and less in the other seasons. The association between toad-nights of emergence and spring and fall seasons was tested using the four-fold chi square test shown in Table 2. A significant association existed between emergence and the months of March, April, May, and September, October and November with a probability of less than 0.01 that the association could be attributed to chance factors alone. For statistical techniques employed throughout this research reference should be made to standard texts such as Simpson and Roe (1939) and Snedecor (1946).

Air temperatures may have contributed to this association since they were less extreme during spring and fall seasons. An association

TABLE 2

TESTS FOR INDEPENDENCE BETWEEN FREQUENCY OF NIGHTS OF EMERGENCE AND NON-EMERGENCE, AND CLIMATIC FACTORS

Rainfall

	Not Active	Active	Total
+ Avg. Month Rain	471	128	599
- Avg. Month Rain	653	65	718
Total	1124	193	1317

$X^2 = 39.6 \quad P < 0.01$

Rainfall

	Not Active	Active	Total
.1" less week	254	51	305
.1" more week	870	142	1012
Total	1124	193	1317

$X^2 = 50 \quad P < 0.01$

Seasons

	Not Active	Active	Total
Summer Winter	546	38	584
Spring Fall	578	155	733
Total	1124	193	1317

$X^2 = 55.7 \quad P < 0.01$

Temperature

	Not Active	Active	Total
90°+ 50°-	539	68	607
50° 90°F.	585	125	710
Total	1124	193	1317

$X^2 = 10.7 \quad P < 0.01$

between toad-nights of emergence and maximum-minimum daily temperatures that were between 50° and 90° F. was disclosed by a chi square test in Table 2. This means that toads were more apt to be active on nights when the daily maximum-minimum temperature was within this temperature range.

Rainfall was apparently another factor of importance in determining emergence. Independence was tested between the number of toad-nights of emergence and weeks when total rainfall was greater than 0.1 inches, and a strong association was indicated in Table 2. Also in Table 2 toad-nights were tallied by months and the frequency of emergence from burrows was positively correlated with months when more than the monthly average precipitation fell.

Factors affecting the emergence of the toads from their burrows were also examined by measuring environmental factors and comparing these with presence or absence of nocturnal toad activity. This was done in plot 2 from December, 1951, through March, 1953, and it was calculated that the temperature of nights showing mean toad activity was 69.01° F.; three standard deviations of toad activity each side of the mean gave the theoretical range of from 48.67 to 89.35° F. Temperatures were recorded on the ground surface and the observed temperature range of activity was 50° to 84° F. as shown in Figure 9.

It was illustrated that rainfall affected the activity of toads when the number of nights of toad activity (and no activity) were tallied by weeks and tested for independence with weeks of some recorded rainfall as contrasted with those of no rainfall. A definite association is seen

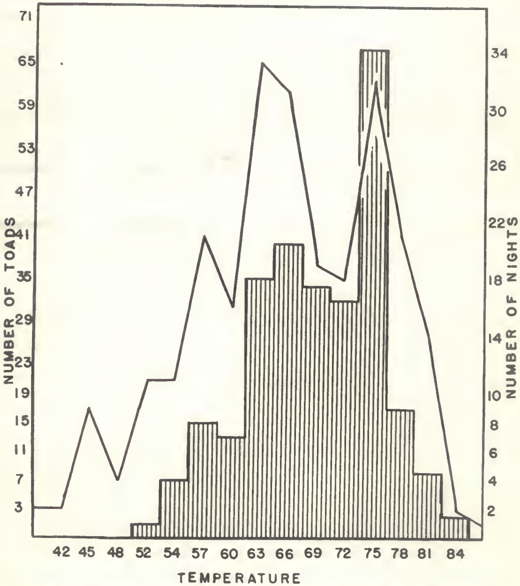

Figure 9. The histogram illustrates the number of toads caught in Plot 2 for each of the temperature categories; the line represents the number of nights of field work at the various temperatures.

(in Table 3) between number of nights of toad activity and weeks with recorded rainfall.

Since the spadefoot toad has a moist pervious skin it would be more apt to be active on nights when atmospheric moisture is high, than the contrary. It is usual to compare rates of activity with atmospheric moisture recorded as per cent relative humidity. The rate of drying that an animal encounters can be closely approximated by use of vapor pressure deficit, as Kucera (1953) showed the correlation of evaporation rate to the vapor pressure deficit exceeded 70 per cent. This deficit in the present study expresses in inches of mercury the difference between saturation vapor pressure and the actual vapor pressure at a given temperature.

Relative humidity and vapor pressure deficit were determined during each nightly visit. The nights were divided into two categories, those with relative humidities 79 per cent and lower and those 80 per cent and higher, and a chi square test showed an association existed between nights of observable activity and nights with 80+ per cent humidity as shown in Table 3. This same procedure was followed using categories of nights with a vapor pressure deficit 0.159 inches mercury and less, and 0.160 inches and greater. In Table 3, independence was shown between the lower deficits and nights of activity.

Many of the factors thus far examined were combined and studied for association with activity by testing general weather types. It was noted earlier that polar air masses reaching Gainesville bring either cold-dry, or cold-wet weather depending on their location and the

TABLE 3

CHI SQUARE TESTS FOR ASSOCIATION BETWEEN NIGHTS OF ACTIVITY AND SOME CLIMATE FACTORS

Relative Humidity

	Not Active	Active	Total
Less than 79%	68	22	90
More than 80%	61	103	164
Total	129	125	254

$X^2 = 34$ $P. < 0.01$

Weekly Rainfall

	Not Active	Active	Total
Rain	30	58	88
No Rain	94	58	152
Total	124	116	240

$X^2 = 17$ $P. < 0.01$

Vapor Pressure Deficit

	Not Active	Active	Total
.159-	37	27	64
.160+	92	98	190
Total	129	125	254

$X^2 = 1.7$ $P = 0.20$

resulting Gainesville wind direction. It is also remembered that maritime tropical weather is usually warm and moist, and that frontal and cyclonic weather is connected with much of the rainfall from October through May of each year. The air mass category to which the weather of any particular night belonged was determined by the author from general observations and by use of the daily weather maps published in the Tampa Tribune.

An association was found to exist between nights of toad activity and cold-wet as contrasted to cold-dry types of weather, as seen in Table 4. Since both were cold, significance was attached to the moisture difference. When extremes of both temperature and air moisture were studied using warm-moist contrasted with cold-dry polar weather, a very significant connection was shown (Table 4) between nights of recorded activity and the warm-moist weather. Since the factors of temperature and air moisture were involved, a chi square test of activity contrasting all warm weather masses and all polar air masses was made to test association between the warm ones and nights of activity. It is seen in Table 4 that there is dependence between these factors. Finally comparing all moist air masses and all dry types in this table, it appears that nights of toad activity are associated with nights of high air moisture.

Rates of Activity. In the foregoing analyses all field trips were classified into categories of nights when toads were or were not active with no mention of rates. Rate of activity as used here is simply the number of toads captured per 15-minute nightly field trips in plot 2, or number of toads captured per hour in plot 1.

TABLE 4

TESTS FOR ASSOCIATION BETWEEN NIGHTS OF RECORDED ACTIVITY AND VARIOUS GENERAL WEATHER TYPES

Air Mass

	Not Active	Active	Total
Cold Wet	30	10	40
Cold Dry	38	0	38
Total	68	10	78

$X^2 = 8.8$ $P. < 0.01$

	Not Active	Active	Total
Warm Wet	17	62	79
Cold Dry	38	0	38
Total	55	62	117

$X^2 = 56$ $P. < 0.01$

	Not Active	Active	Total
All Cold	68	10	78
All Warm	17	62	79
Total	85	72	158

$X^2 = 65.9$ $P. < 0.01$

	Not Active	Active	Total
All Wet	52	94	146
All Dry	38	0	38
Total	90	94	184

$X^2 = 47$ $P. < 0.01$

Data are given in Figure 10 on time of activity in plot 1. It will be noted that both of the all-night records for number of captures reached a peak after sundown. A smaller peak occurred immediately before sunrise with an intervening low in activity in the early hours of the a.m. The two nights differ as a result of the difference in length of summer and winter days. It is notable that in the graph representing average activity rate for the entire study during all seasons, the largest number of captures occurred very early in the evening with a decline in early morning that preceded the second peak before sunrise.

Correlation between activity rate and temperature is shown in Figure 9 with a peak rate near the mean of 69° F. and minimal activity near the extremes of 50° F. and 84° F. The data presented above that illustrated an association between non-emergence from burrows and the winter season might indicate (1) that the toads respond to a cyclic, seasonal phenomenon and in that sense hibernate during the winter, or (2) there are more days of sub-minimal temperature in the winter, and the toads might be as active on warm days in winter as in any other season. It was shown in Figure 1 that the maximum-minimum temperatures fluctuated between high temperatures during moist, tropical weather and low temperatures during polar weather from October through April. It will be shown below that toad captures were significantly less during the polar air mass domination. If the rate of activity on the warm, winter nights compared with that on days of similar temperature range in the summer, it could be concluded that spadefoots in the Gainesville region did not hibernate in the cyclic, seasonal sense, but rather

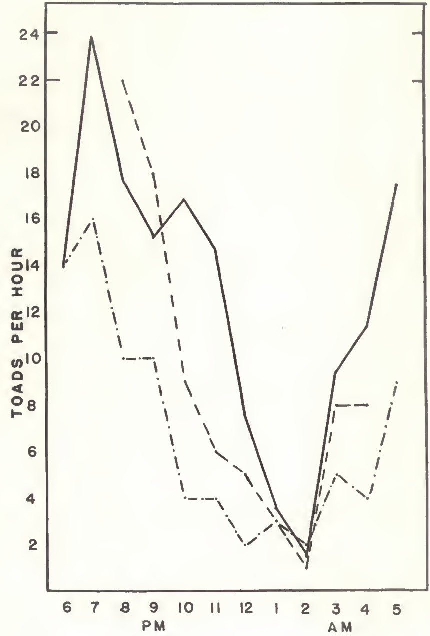

Figure 10. Plot 1 data on time of activity given here are (1) dots and dashes illustrate night of December 30, 1951, (2) dashes equal night of June 14, 1952, and (3) the solid line represents the average for all data.

became inactive during sub-minimal temperatures and resumed activity during favorable temperatures. If this were true, then the lower activity during the winter season would be directly correlated with the number of sub-minimal temperature days. A test was made by choosing one category such as the days on which the maximum temperature was greater than 70° F. during the months from October through April, and designating these as warm, winter days. The second category, known as the cool, summer days, occurred when the maximum temperature did not exceed 90° F. between May and September. The temperature definitions were arbitrarily chosen after studying Figure 1 and with the normal temperature range of activity in mind.

When the activity for the cool, summer nights was compared with that on warm, winter nights by chi square test of the frequency distribution shown in Table 5, to determine whether they could have been drawn from a homogeneous population, a X^2 of 2.21 with a P. value of 0.80 led to the conclusion that the rate of activity on warm, winter nights was not significantly different from that of cool, summer nights.

TABLE 5

FREQUENCY DISTRIBUTION OF TOADS CAPTURED PER 15 MINUTES IN PLOT 2

Number Toads per 15 Minutes	Warm, winter nights	Cool, summer nights
0	29	31
1	16	10
2	18	17
3	12	9
4	6	2
5+	4	4

A correlation (r) value was sought between toads caught per unit time and relative humidity and vapor pressure deficit in plot 2. No statistically significant r. values were obtained from plot 2 data. All data from plot 1 were tested for correlations and these data were then considered in several temperature ranges, and the results are given in Table 6.

TABLE 6

CORRELATION COEFFICIENT VALUES FROM PLOT 1

Relative Humidity			Vapor Pressure Deficit		
All °F.	r = 0.08	P = Not Sign.	All °F.	r = 0.18	P = 0.02
53-64°F.	r = 0.46	P = 0.01	53-64°F.	r = 0.05	P = Not Sign.
65-73°F.	r = 0.10	P = Not Sign.	65-73°F.	r = 0.13	P = Not Sign.
74-82°F.	r = 0.12	P = Not Sign.	74-82°F.	r = 0.15	P = Not Sign.

It was noted that a fair correlation did exist between activity rate and vapor pressure deficit in general. However, when these data were considered in the three temperature categories no significant correlation was found. It was observed in the field that humidity played a greater role in activity rate at the lower temperatures and the author's impression was that the lower the temperature, the higher the relative humidities that would be required for activity. This was partly substantiated by the statistically significant correlation existing between relative humidity and activity rate in the low temperature range of 53-64°F. although other r. values for relative humidity were not significant.

The low correlation values probably resulted from additional factors such as rainfall, soil moisture, seasonal effects, and amount of previous favorable weather, so that significant correlation between activity rate and small units of air moisture measurement was obscured. The problem became complex since all these factors did not necessarily vary directly with air moisture to produce higher activity rate.

The relationship of temperature and humidity with activity can be illustrated in another fashion, as shown in Table 7. The values given are the mean activity rates for the particular temperature and humidity ranges in plot 1. Under each of the three temperature ranges with an increase in humidity, there followed an increase in mean activity rate, and except under high humidities, the middle temperature range had higher mean rates. Data on vapor pressure deficits are also given, and the same conclusions can in general be made, except that in the middle temperature range, an exceptionally high mean rate occurred in the high deficit category. This might be attributed to a small sample size.

To test the effect of air moisture on spadefoot activity the relative humidity and pressure-deficit data were divided into two categories of (1) relative humidity 79 per cent and less, and 80 per cent and greater, and (2) vapor pressure deficit of 0.159 and less, and 0.160 inches mercury and greater, as seen in Table 8. A statistically significant difference existed between mean rates under contrasted high and low humidities in plots 1 and 2, as shown by the high t. values. Differences between mean activity under the two groups of pressure deficit

TABLE 7

MEAN ACTIVITY RATES, EXPRESSED AS NUMBER OF TOADS PER HOUR, FOR THE VARIOUS ENVIRONMENTS IN PLOT 1

		Temperature °F.		
		53-64	65-73	74-82
Relative Humidity	89-99%	20.8	20.0	17.7
	77-88%	13.4	18.2	14.8
	Less than 77%	5.5	16.0	9.4
Vapor Pressure Deficit	0-.079	19.5	18.8	17.3
	.08-.159	14.3	18.8	16.7
	.16-.239	4.0	7.0	14.2
	.240+	0.0	16.0	8.5

TABLE 8

TESTS FOR STATISTICAL SIGNIFICANCE OF DIFFERENCE BETWEEN MEAN ACTIVITY OF AIR MOISTURE CATEGORIES

Relative Humidity	Mean and Two Standard Errors	Standard Deviation	N	Significance
Plot 1				
79%-	11.43 ± 3.3	7.56	21	t. = 2.88
80%+	18.10 ± 1.47	10.31	198	P. = 0.01
Plot 2				
79%-	0.467 ± 0.20	0.945	90	t. = 5.77
80%	1.494 ± 0.24	1.54	164	P. = 0.01
Vapor Pressure Deficit				
Plot 1				
0.160+	16.02 ± 1.59	8.66	119	t. = 2.00
0.159-	18.87 ± 2.52	12.33	96	P. = 0.05
Plot 1				
53-64°F.				
0.160+	12.75 ± 5.12	8.88	12	t. = 1.87
0.159-	20.76 ± 5.96	12.27	17	P. = not sign.
65-73°F.				
0.160+	17.91 ± 2.34	7.76	44	t. = 0.76
0.159-	13.92 ± 4.58	13.92	37	P. = not sign.
74-82°F.				
0.160+	15.46 ± 1.96	7.98	66	t. = 1.02
0.159-	17.38 ± 3.60	11.55	41	P. = not sign.
Plot 2				
0.160+	0.75 ± 0.26	1.04	64	t. = 2.44
0.159-	1.26 ± 0.22	1.54	190	P. = 0.05

were not significant when data were divided into temperature ranges, but were significant at the 5 per cent level when temperature was not considered. Even though highly significant differences were not shown between means of the two pressure categories, a reliable difference did exist between the ranges of activity rates in the two categories. A test for real differences between the standard deviations under high and low vapor pressure deficit yielded a t. value of 3.6 ($P. < 0.01$). The maximum number of toads per hour under low deficits in plot 1 was 55 while it was 37 under high deficits. Under low vapor pressure deficits there was greater variation in the number of captures per unit time than under the drier conditions.

The same two relative humidity categories were used and plot 2 data were divided into the nights when one or less as compared with two or more toads were caught. This point of separation was used because it was half-way between mean activity rates of the two humidity classes. A four-fold chi square table using the two categories of humidity and two classes of activity gave a chi square value of 23.5; association existed between high humidity and high activity. ($P. < 0.01$). A similar test was made using categories of vapor pressure deficit of 0.159 and less and 0.160 and more, and a somewhat significant association existed between high deficits and low activity rates. ($X^2 = 4.2$, $P. < 0.05$).

A direct correlation was indicated between activity rate and amount of daily rainfall. In this calculation only those field trips were considered when rainfall was recorded for the day and when toads were active. A significant positive correlation coefficient of 0.31 existed for plot 1 data (t. = 3.2, P. < 0.01), and of 0.37 for those from plot 2 (t. = 3.2, P. < 0.01). Thus it is concluded that on days of recorded rainfall and recorded activity, the greater the amount of rainfall the higher the activity rate.

The highest rate of activity in plot 1 occurred during Front weather, with the rate decreasing respectively under warm-moist (MT), cold-wet (Polar, with northeast winds), and cold-dry (Polar with northwesterly winds) climate. In Table 9 the MT weather is subdivided into MT-wet and MT-dry categories according to the presence or absence of rainfall and moist or dry soils. Even though the atmospheric humidity may have been high, if the soils were quite dry and little rainfall had been recorded, the toad activity was restricted.

TABLE 9

A SUMMARY OF ACTIVITY RATE PARAMETERS FOR SEVERAL TYPES OF WEATHER EXPERIENCED IN NORTH FLORIDA

Weather Type	Mean Activity and Two Standard Errors	Standard Deviation	N.
Plot 1			
Front	20.1 ± 2.93	6.72	21
MT	15.87 ± 2.02	8.37	69
MT-wet	17.8 ± 2.2	8.0	53
MT-dry	9.44 ± 3.05	6.1	16
P-wet	14.75 ± 4.88	8.43	12
P-dry	--	--	2
Plot 2			
Front	2.62 ± 0.69	1.59	21
MT	2.31 ± 0.29	1.12	61
P-wet	1.50 ± 0.51	0.81	10
P-dry	--	--	38

When means of activity for the different weather types were tested for significant differences, it was found that a highly significant difference ($P. < 0.01$) existed between means of Front and MT-dry ($t. = 5.0$) and between MT-dry and MT-wet weather ($t. = 3.9$). A fairly significant ($P. = 0.05$) difference was calculated for the means of wet Polar and Front weather ($t. = 2.0$), and between Front and MT air ($t. = 2.1$). All other comparisons of means failed to show statistical significance.

Feeding Activities. A major function of the toad's surface activities is the capture of food. Starting about two hours after sundown and following heavy rainfall, a series of four collections of 26, 25, 22 and 26 toads was made in habitats near but no closer than 1000 feet to plot 1. The toads were taken on January 19, June 8, August 18, and October 1, 1953, in an attempt to sample their food in each of the four seasons.

Stomach contents were comprised by groups of the insects, the Arachnida, and the Myriopoda. The number of recognizable individuals was tallied, and the animal remains were then dried and weighed. These data are presented in Tables 10 and 11. Note that by frequency of occurrence, Coleoptera were most abundant with Hymenoptera, Orthoptera, and Arachnida of decreasing importance in the order given. When the dried weight of all collections was pooled, the Coleoptera composed the greatest weight with Orthoptera, Hymenoptera, and Myriapoda decreasing in that order. The increased percentage composition of Coleoptera when weight was considered resulted from the relatively heavier chitinous elytra, whereas the small bodies of the ants reduced their relative importance.

Considerable variation existed from one collection to the other. From the standpoint of frequency of occurrence, a taxonomic group may have been most abundant during one month whereas the group may have had the least representation during this same month if total dried weight was considered. For example, in Table 10 for the Orthoptera, the month of least percentage is October, whereas in Table 11 the month of greatest percentage composition is also October. The explanation may be that earlier in the year there were many individuals of small size, but that by October although the body size was much larger, the population density had been considerably reduced. A great deal of variation existed in these small samples, and no general conclusions as to seasonal variation were drawn from these data.

TABLE 10

PERCENTAGE FREQUENCY OF OCCURRENCE IN STOMACHS OF THE SPADEFOOT TOAD

	January	June	August	October	Total
Orthoptera	11	16	12	8	12
Hemiptera	4	--	3	2	2
Homoptera	--	4	--	1	1
Lepidoptera	3	4	10	2	4
Coleoptera	38	33	37	44	39
Hymenoptera	25	21	23	34	27
Arachnida	12	19	5	4	9
Myriapoda	7	3	10	5	6

TABLE 11

PERCENTAGE OF TOTAL DRIED WEIGHT FOR EACH COLLECTION OF STOMACH CONTENTS OF THE SPADEFOOT TOAD

	January	June	August	October	Total
Orthoptera	4	12	7	14	11
Hemiptera	11	--	4	Trace	1
Homoptera	--	14	--	1	4
Lepidoptera	2	1	17	2	4
Coleoptera	46	33	37	71	54
Hymenoptera	8	21	10	6	10
Arachnida	23	11	10	1	7
Myriapoda	6	12	19	6	10
Total Weight	.362	.910	.786	2.141	4.239
Weight of Trash and unknowns	.278	.094	.031	.122	.525

The capture of prey occurred on the ground surface and generally with the toad out of its burrow. However, toads were observed sitting in the burrow mouth and not protruding above the level of the leaf cover. These observations were made when the environment was near the minimum for toad activity. One such observation in plot 2 on December 5, 1951, was at a temperature of 59°F. and a relative humidity of 89 per cent. It seemed reasonable to think that the more favorable the environmental conditions, the further from the burrow an individual toad might move in search of food. Also, the further a toad moves from the burrow, the greater the likelihood of mortality. It seemed important, therefore, to study the relationships of various environmental factors with the distances of movement from a burrow.

TABLE 12

DISTANCES OF MOVEMENT DURING FEEDING ACTIVITIES MEASURED IN FEET FROM A BURROW THAT THE GIVEN INDIVIDUAL WAS KNOWN TO OCCUPY

Distance Movement	Plot 1	Plot 2	Plot 3		
			Pen 1	Pens 2,4	Pens 3,5
0-2	520	99	65	99	47
3-5	167	25	31	45	23
6-8	99	21	13	10	25
9-11	54	23	9	18	8
12-14	16	9	5	1	2
15-17	15	10	1	-	3
18-20	11	8	1	2	-
21-23	3	4		1	1
24-26	2	4		1	
27-29	1	1		2	
30-32	1	3			
33-35		-			
36+		2			
Total	889	209	125	179	109
Mean	3.66	6.64	2.76	2.82	3.50

It is seen in Table 12 that by far the major part of the recorded movements were within several feet of the burrow. The frequency distribution did not follow a normal curve, and there was strong evidence ($P < 0.01$) that these arrays did not conform to a poisson distribution, although they were more nearly poisson than normal. Since the tools for testing significance of difference between populations are based on normal or poisson distributions, and could not be used, a chi-square test for independence was applied in the study. The difference observed between recorded movements in plots 1 and 2 was real. Although significance of difference in means could not be calculated, the data were divided into cohorts of five or less and six or more feet and tested by chi square for association with the two plots. A significant association was shown between the greater distances and plot 2 ($P. < 0.01$). Since the toad density in plot 1 was higher, this difference between plots may be a density effect. The influence of several factors was tested for their relationship to distance of movement. They were:

A. Sex. The data from plots 1 and 2 were inspected to learn if individuals of one sex tended to move further than the other. The average movement in plot 1 for males was 3.69 feet and for females 3.64 feet. The data for the two sexes were placed in categories of (1) two feet and less, (2) three to five feet, (3) six to 14 feet, and (4) 15 feet and greater, and a X^2 test for independence was made that gave a non-significant value of 0.9. No association existed between movement and sex.

B. Head Width. Using data from plot 1 where both head width and distance of movement were recorded, an association was shown to exist between the two factors. A X^2 test was designed (Table 13) that revealed a tendency for the smaller toads to be taken at greater distances than would be expected if no correlation existed between body size and movement.

TABLE 13

A CHI SQUARE ANALYSIS OF RELATIONSHIP BETWEEN TOAD SIZE AND DISTANCE MOVEMENT*

Movement Distance		16 mm. and less	17 to 19 mm.	20 mm. and more	Total
0-2'	Expected	(118.1)	(321.1)	(74.9)	
	Observed	98	330	86	514
3-5'	Expected	(37.7)	(102.4)	(23.9)	
	Observed	42	105	17	164
6+	Expected	(46.4)	(126.1)	(29.4)	
	Observed	62	114	25	201
Total		202	549	128	875

$X^2 = 14.95 \quad P. = .01$

*Expected values are given in parentheses.

C. Habitat. The data from plot 1 were separated into those from the ecotone and those from the hammock. The average distance moved in the hammock, 3.07 feet, was less than that in the ecotone, 4.11 feet. Testing the distributions for independence between habitat and distance moved, a significant ($P. = 0.01$) association was shown between the ecotone and distances greater than three feet.

D. Population Density. An opportunity to compare the distance movement from a known burrow under different population densities occurred in plot 3. In Table 12 are given data from pen 1 with 40 toads per unit area, pens 2 and 4 with 20 toads per unit area, and pens 3 and 5 with ten toads per unit. The pen with the highest density had the lowest mean movement distance while it increased as the density decreased in the other two levels. The distance data were separated into categories of less than five and six feet or more, and independence was tested between them and the three population levels. Independence was shown between distances and the high and middle densities. However, when the middle and low population levels were tested a correlation was found between the low density and greater movement distances ($X^2 = 4.37$, $P. = 0.05$), and the same general relationship held when the highest and lowest levels were compared ($X^2 = 4.5$, $P. < 0.05$). Hence, population density was one factor affecting the amount of toad movement from a known burrow.

E. Seasonal Influence. It was pointed out earlier that field work was conducted in plot 2 almost daily without respect to favorable or unfavorable toad-environments. The data obtained on feeding movements from this study then could be used to examine the effect of seasonal weather. The average movement was nearly the same for three seasons (Table 14), with the winter average being considerably less. Using the

TABLE 14

FREQUENCY DISTRIBUTIONS OF DISTANCE MOVEMENT FROM A KNOWN BURROW PLOT 2, ACCORDING TO SEASONS

Distance in feet	December-February	March-May	June-August	September-November
0-2	28	43	14	14
3-5	2	11	2	10
6-8	3	10	5	3
9-11	3	9	2	9
12-14	1	3	1	4
15-17	1	6	1	2
18-20	1	3	1	3
21-23	-	2		2
24-26	1	1	2	
27-29	1	-		
30-32		2	1	
33-35		-		
36+		2		
Total	41	92	29	47
Average	4.59	7.00	7.10	7.45

X^2 test for independence between the four seasons and distance groups of two feet and less, and three feet and more, a value of 13.1 ($P. < 0.01$) was calculated. Deviations from expected values in the winter and fall seasons contribute most to the chi square value.

F. Temperature and Vapor Pressure Deficit. A more elaborate chi square test was designed that not only checked association of temperature and vapor pressure deficit with distance of movements, but also examined the type of variation with temperature while pressure deficits were held constant and checked deficit effects while temperatures were held constant. The data were first divided into four temperature categories, and then within each of these groups a test was made for an association between distance of movement and vapor pressure deficit. The test under only one temperature range, for all temperatures, and a summary of chi square values from all tests are given in Table 15. The X^2 values indicate no significant association under categories of 54-64°F. and 77-82°F. between movement and vapor pressure deficits. In the ranges from 65-70°F. and 71-76°F. a significant association was shown between greater distances and lower deficits. When these data from all temperatures were totaled, a real connection was illustrated between greater distances and lower pressure deficits, i.e., the toads moved farther with lower pressure deficits.

To test whether frequency distributions of movement plotted with pressure deficits had homogeneous variation under the four temperature ranges, the X^2 values and degrees of freedom were added for the four temperature groups. From this total was subtracted the X^2, and degrees of freedom calculated for the data when temperatures were disregarded (Table 15), giving $X^2 = 9.33$ with nine degrees of freedom in the test for heterogeneity. This was not statistically significant, hence the indications are that the direction of frequency variation of distances travelled plotted against vapor pressure deficit was homogeneous for the four temperature groups.

In Table 16 a similar analysis was made where the data were first separated into four pressure deficit categories and then, under each of these, associations were tested between movement and temperature. It is seen from this table that under pressure deficits less than 0.019 and from 0.06 to 0.119" Hg. no significant association was found between temperature and movement distance. In the pressure deficit group from 0.02 to 0.059" and for those greater than 0.12" Hg. distance of movement was dependent on temperature. The data were totaled so that a test for independence was made between movement and temperature for all deficits, and a real connection was revealed between distance of movement and temperature. A test for heterogeneity of distributions under the four deficit categories was conducted in a manner like that above, and the chi square value was 13.6 with nine degrees of freedom. This was not statistically significant and thus the frequency distribution of distances against temperature is homogeneous under the four deficit categories.

TABLE 15

A SIMULTANEOUS ANALYSIS OF ASSOCIATION BETWEEN DISTANCE OF FEEDING MOVEMENT FROM A KNOWN BURROW AND TEMPERATURE AND VAPOR PRESSURE DEFICIT*

	Temperature 54-64°F.					All Temperatures				
Vapor Pressure Deficit						Vapor Pressure Deficit				
Distance	.00-.019	.02-.059	.06-.119	.12+	Total	.00-.019	.02-.059	.06-.119	.12+	Total
0 to	(12.1)	(10.7)	(8.2)	(.97)		(117.7)	(128.7)	(156.5)	(106.1)	
2 feet	8	11	11	2	32	83	134	169	123	509
3+	(12.9)	(11.3)	(8.8)	(1.0)		(85.3)	(93.3)	(113.5)	(76.9)	
feet	17	11	6	-	34	120	88	101	60	369
Total	25	22	17	2	66	203	222	270	183	878

SUMMARY OF CHI SQUARE VALUES

Source	X^2	d.f.	P.
Temp. 54-64	6.474	3	<0.10
Temp. 65-70	10.819	3	<0.02
Temp. 71-76	24.957	3	<0.01
Temp. 77-82	1.945	3	0.70
Total	44.195	12	
X^2 Sub-Total	35.87	3	<0.01
X^2 Heterogeneity	8.325	9	0.50

*Values in parenthesis are expected frequencies, while the others were observed.

TABLE 16

A SIMULTANEOUS ANALYSIS OF ASSOCIATION BETWEEN DISTANCE OF FEEDING MOVEMENT FROM A KNOWN BURROW AND TEMPERATURE AND VAPOR PRESSURE DEFICIT*

	Vapor Pressure Deficit .00-.019					All Pressure Deficits				
	Temperature (Degrees F.)					Temperature (Degrees F.)				
Distance	54-64	65-70	71-76	77-82	Total	54-64	65-70	71-76	77-82	Total
0 to	(10.3)	(16.6)	(48.5)	(7.4)		(38.3)	(85.3)	(201.4)	(184.0)	
2 ft	8	17	47	11	83	32	77	195	205	509
3+	(14.7)	(24.1)	(69.5)	(10.6)		(27.7)	(61.7)	(145.6)	(133.0)	
feet	17	24	71	7	119	34	70	152	112	368
Total	25	41	118	18	202	66	147	347	317	877

SUMMARY OF CHI SQUARE VALUES

Source	X^2	d.f.	P.
V.P. Deficit .00-.019	3.923	3	0.30
V.P. Deficit .02-.059	9.580	3	0.02
V.P. Deficit .06-.119	2.181	3	0.70
V.P. Deficit .12+	8.370	3	<0.05
Total	24.054	12	
X^2 Sub-Total	10.428	3	<0.02
X^2 Heterogeneity	13.626	9	<0.20

*Expected frequencies are enclosed in parenthesis while observed values lack them.

Data from plot 2 were investigated and an association was also denoted between distance of movement from a known burrow and the level of pressure deficit and temperature. There was a greater frequency in the higher distance category at the low deficits and there were more movements that exceeded three feet for the higher temperatures than would be expected on a chance basis.

SPATIAL RELATIONSHIPS

Spatial Distribution. The distribution of Scaphiopus in major habitats of Florida was discussed earlier. A more detailed examination of the spatial distribution of toads in plot 1 was undertaken when it was observed that the concentration of toads was uneven in the plot. General observations indicated that there was a tendency towards aggregation in the ecotonal areas, especially where the low shrub and herbaceous vegetation was sparse. There were almost no captures of toads in areas where the shrubs were dense, as, for example, between lines L and K extending through the western two-thirds of the plot (Figure 5). In the more open areas of the hammock, as between lines L and O, the density seemed to be between that of the ecotone and the area of dense vegetation. Following procedures outlined by Dice (1952), a test of the spatial distribution in plot 1 was made for data collected between July 26 and December 30, 1951. This selection of material was made because after December, 1951, observation was not concentrated uniformly over the plot. The area was divided into quadrats 25 feet square and for each night's data the number of quadrats in which 0, 1, 2, 3 . . . n individuals were caught was recorded. The results of the study are given in Table 17. A chi square test yielding a value of 399 gave strong evidence ($P. < 0.01$) that the distribution did not follow a poisson type. Dice (ibid.) stated that if the distribution was not random and the variance was greater than the mean, an aggregational phenomenon was denoted. In this problem, the variance was 4.68 and

TABLE 17

AN ANALYSIS OF SPATIAL DISTRIBUTION OF TOADS IN PLOT 1*

No. Individuals per Quadrat	25' Units	10 Square Foot Quadrats			
		Total Burrows	Burrows, Sum. '53	Captures, Ecotone	Captures, Hammock
0	78	1,517	51	6,006	2,864
1	53	173	30	998	262
2	37	15	7	104	8
3	30		2	18	
4	19				
5	11				
6	11				
7	6				
8+	8				
Total	253	1,707	90	7,126	3,134
Mean	2.11	0.119	0.556	0.1768	0.0859
Variance	4.68	0.135	0.536	0.1899	0.0887

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*The frequencies listed are the number of quadrats per field trip totaled for the study period.

the mean 2.05; thus aggregation within this plot was statistically shown.

A test for aggregation within a homogeneous habitat was made utilizing the techniques above, except that quadrats ten feet square were utilized in the surveyed ecotonal and hammock areas. The locations of known burrows in the ecotone were plotted for each month of study, and when the monthly totals were added, they formed a distribution not different from a poisson type ($X^2 = 1.74$). The burrows of the active population were studied most intensively and were best known during the summer 1953 and when these were plotted, the distribution was not significantly different from a random type. ($X^2 = 0.20$). However, there was a slight indication that these burrow locations were more evenly spaced than in a random distribution.

The capture sites in the hammock were located on the ten foot grid system for night trips and a test for deviation of the distribution gave evidence that it was of the poisson type ($X^2 = 1.4$). Therefore the surface activities of toads in the hammock were such that individuals were randomly distributed in space.

However, a similar test of the spatial distribution of capture sites in the ecotone, when data were treated as above, indicated a statistically significant deviation from the poisson distribution. ($X^2 = 33.03$). Factors involved in this aggregation in surface movements are unknown, but there appeared to be more captures just inside the ecotone and near a fallen mass of twigs, leaves, and other debris near 1-9 in Figure 3. Possibly the tendency towards aggregation in the ecotone resulted from movements to optimal feeding locations, and the habitat was not homogeneous with respect to food supply. If a shortage of food existed in the higher density of this ecotone, the toads might be forced to gather in the more favorable feeding locations.

Home Range. A home range can be defined as "the area over which an individual animal habitually travels while engaged in his usual daily activities." This statement by Dice (ibid.) is applicable to the following discussion, except that in the present work movements associated with breeding were excluded from consideration of home range. He gives a good general discussion of the home range concept and methods of its study; he also says that, "Relatively little is known about the home ranges or territories of amphibians and reptiles."

The method of determination of home range size in the present study was the "minimum-home-range" method that produces more consistant and reliable results than other variations of the technique, according to Mohr (1947). It involves plotting the capture locations and connecting the outside points to form an irregular polygon. The area of this was calculated, providing an estimate of home range size. This method was especially applicable since captures of individuals were not restricted to traps in a grid system, but were spatially at random; thus a more accurate picture of the utilization of space was given. A standard for conversion of paper weight to area in square feet was established by weighing 25 pieces of paper cut to scale to 0.0001 gram. Care was taken to use paper with a low coefficient of variation. Paper representing the home range was weighed and the conversion to area made.

The average home range of 88 individuals in plot 1 that had been captured more than six times was 108.4 square feet with a range from 7.1 to 892. The average for males, 91.2, was smaller than that for females, 111.5, but the difference between means was not statistically significant.

One or more capture sites of most individuals were considerably apart from the others, which tended to be clustered. Apparently if the home range represents the average utilized areas, a more accurate picture of the amount of space used would be obtained, if the ten per cent of total captures that represented extreme wanderings were eliminated. Using only the remaining 90 per cent of capture locations, the mean range area was 67.7 ± 6.9, the variation being from 2.6 to 356 square feet. The average home area of 39 males was 60.8 ± 9.9 while that for 49 females was 73.5 ± 9.3; that for the males being smaller; but again the difference lacked statistical significance. The method of utilizing only 90 per cent of captures was continued in the following studies.

The distance of movement for food was greater in the ecotone than in the hammock; therefore it was not surprising that the average of 68 ecotone home ranges, 70.3 ± 8.8, appeared to be greater than that for 20 hammock ranges, 53.0 ± 7.2. The difference lacked significance. This comparison involved not only different habitats, but also population levels. The density in the ecotone was greater than that in the hammock, indicating that the ecotone was more favorable as a toad environment.

Several statistical analyses of the connection between the length of time that individuals were under observation and their home range size, indicated no statistically significant correlations or associations. Examination was made of the relationship between size of range and the number of captures for toads, and a significant (P. = 0.01) correlation coefficient of 0.34 was determined for the relationship. Then, the data were placed in categories of seven to 12, 13 to 18, and 19 and more captures; while the ranges were grouped into less than 50, 50 to 100, and greater than 100 square feet, and a significant association was revealed between size of area and number of captures ($X^2 = 23.7$, P. = 0.01). The number of captures, and indirectly the time factor, must be considered in statements of home range size. A trend line, fitted by the method of least squares, illustrating the relationship between number of captures and size of average range is given in Figure 11.

Many toads moved their burrows one or more times within their home range. The average area of the 37 toads for which only one burrow was known was 51.0 ± 10.1. This was significantly less than that for ones with more than one recorded hole, 81.3 ± 9.4. In the analysis of home range the observer then should consider data on the shift of burrow locations.

Records are available on 89 shifts of burrow location made by 39 spadefoots. The average distance the site was moved was 10.8 ± 0.77 feet with a recorded range from two to 38 feet. The times of movement were not associated with any particular climatic or seasonal phenomena. The average time that burrows of these 39 toads were used was 115 days.

This had little biological significance, however, since 29 of them were used only one night, while ten were occupied more than one year, and one was recorded in use for 713 days. No evidence was obtained that more than one toad uses the same burrow.

Thirty-one individuals moved their burrows to one or more new locations within the home range, but did not return to the original ones. Eight of the toads alternated their utilization of from two to five burrows. For one period they would emerge from burrow A, then for a second interval use burrow B, then C, and finally return to use A or B. Illustrations of this are as follows: Figure 12, #1045--two burrows, #1155--four burrows; Figure 13, #120--five burrows; Figure 14, #1305--two, and #3241--two burrows. As further illustration data on #1045, #1155, and #120 are given in Table 18. Careful study of these records, especially for the 1953 summer period, when almost daily visits were made, will show that these toads did not use any one burrow for any extended time. The records of #120 and #1155 indicate that there was fairly equal use made of the several holes involved.

Examination of home range shapes formed by connecting the outside points of captures allowed the following breakdown: circular or square, i.e., #443 in Figure 14, 11 ranges; rectangular or rectilinear, i.e., #1305 in Figure 14, 39 ranges; essentially linear, i.e., #1004 in Figure 14, 34 individuals, and triangular, four ranges. A summary of burrow locations within the 88 ranges studied in plot 1 showed that 20 had a central location, while 109 were located peripherally.

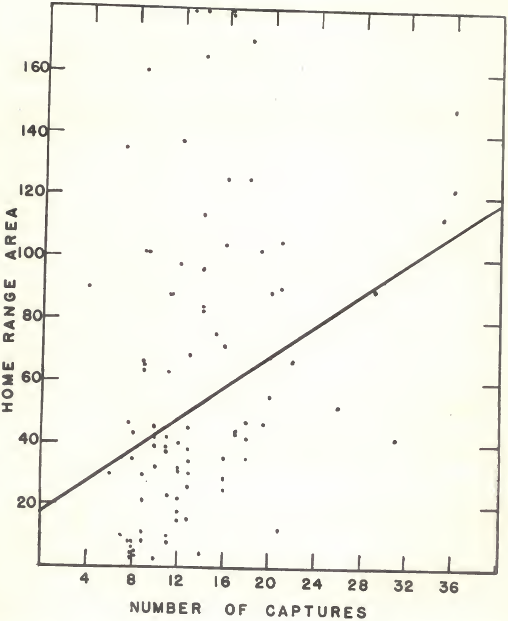


Figure 11. A trend line, fitted by method of least squares, expressing the average relationship between the number of captures and the area of an individual's home range measured in square feet.

Figure 12. Ranges in the ecotone of plot 1. O = burrow; _____ connects capture sites with knownburrow; - - - burrow use assumed; - . - movement of burrow site; number over latter indicates times burrow use laternated. North is toward the bottom, west to the right.

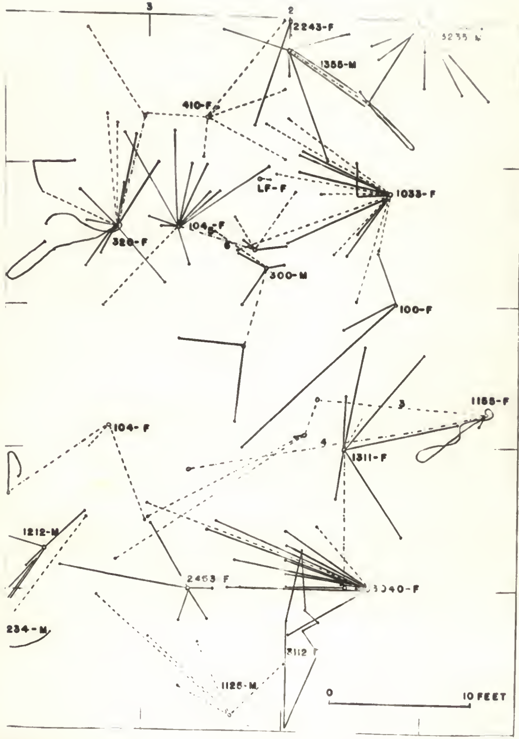
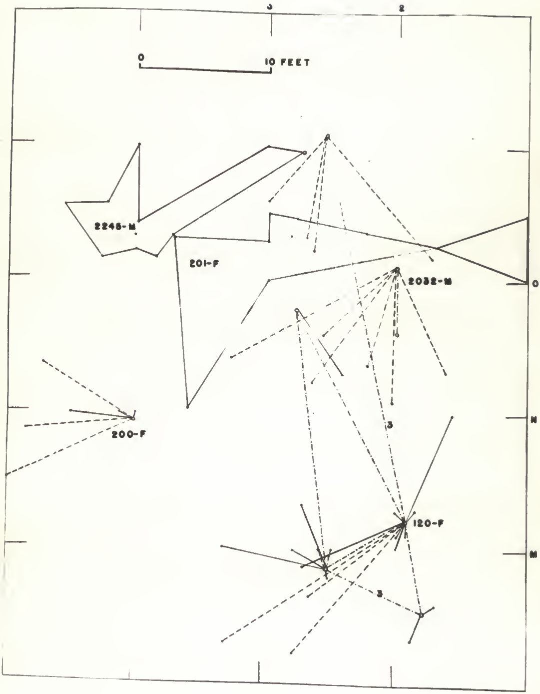

3
2
2243-F
3235 M
1355-M
410-F
6
LF-F
1033-F
1045-F
6
320-F
300-M
F
100-F
3
1155-F
104-F
4
1311-F
E
1212-M
234-M
2463 F
3040-F
D
2112 F
1125-M
0
10 FEET

Figure 13. The home ranges of individuals in the most crowded part of the hammock in plot 1. The symbols are the same as in Figure 12. The capture sites of #2245 and #201 are connected with lines since the burrow location was not found.


3
2
0
10 FEET
2245-M
201-F
2032-M
0
N
3
200-F
120-F
M
3

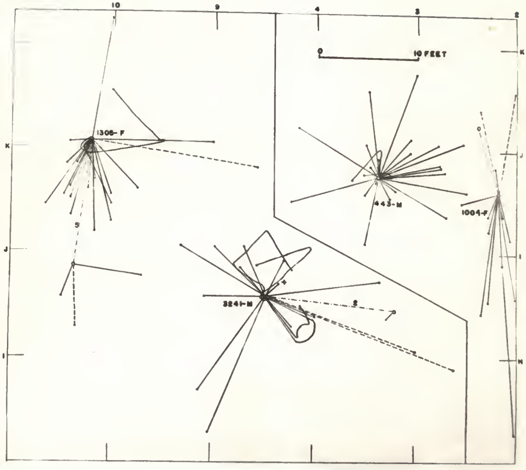


Figure 14. Home ranges of selected individuals from the ecotone in plot 1. The symbols are similar to those in Figure 12.

TABLE 18

RECORDS OF BURROW SHIFTING AND ALTERNATION FOR THREE INDIVIDUALS FROM PLOT 1

Animal Number	Burrow Number	Location	Dates Used	Captures	Days
1045-♀	I	5 NNW G-3	3-13-52 to 6-29-53	17	473
	II	4 SSE F-2	7-2-53	1	1
	I	5 NNW G-3	7-10-53	1	1
	II	4 SSE F-2	7-16-53	1	1
	I	5 NNW G-3	7-21-53 to 8-11-53	6	21
	II	4 SSE F-2	8-17 to 8-18-53	2	2
	I	5 NNW G-3	8-19 to 8-27-53	4	8
120-♀	I	12 SSE 0-2	12-30-51 to 6-3-52	4 (+3?)	155
	II	2 S 0-2	8-28 to 9-2-52	2	5
	I	12 SSE 0-2	9-12 to 10-8-52	2 (+2?)	26
	II	2 S 0-2	4-26 to 6-24-53	8	59
	III	3 NW 0-3	7-6 to 7-7-53	2	2
	IV	5 E M-2	7-10 to 7-14-53	2	4
	V	4 N M-2	7-18 to 7-21-53	2	3
	IV	5 E M-2	7-25 to 7-26-53	2	2
	II	2 S M-2	8-10 to 8-12-53	3	3
	V	4 N M-2	8-16 to 8-18-53	3	3
	IV	5 E M-2	8-21 to 8-22-53	2	2
1155-♀	I	1 1/2 WSW E-2	10-14-52 to 6-6-53	7	235
	II	4 SSW E-2	6-24-53	1	1
	III	5 WSW E-1	7-8 to 7-14-53	2	6
	II	4 SSW E-2	7-16-53	1	1
	III	5 WSW E-1	7-23-53	1	1
	IV	3 WNW E-3	7-26 to 7-27-53	2	2
	III	5 WSW E-1	7-31-53	1	1
	IV	3 WNW E-3	8-10-53	1	1
	III	5 WSW E-1	8-16 to 8-18-53	2	2

Examination for overlapping of ranges for toads of the same sex in the most crowded portion of the hammock (Figure 13), indicates that there is no functional overlap. A similar study for areas of highest density, i.e. the ecotone in Figure 12, shows that there is only a slight overlap between several of the individuals. The overlap that does exist is only apparent as the ranges did not overlap in the same time period.

From the ranges shown in Figures 12 and 13 possible avoidance reactions were noted. Observe in the former that in movement of its burrow, #1155 crossed the range of #1311 on two separate occasions. In Figure 13 notice that #120, when it twice moved its burrow southward, apparently avoided the ranges of #2032 and #201.

The existence of a homing reaction in which individuals returned long distances from breeding grounds to exact locations of departure was demonstrated for Scaphiopus by the capture of seven individuals before, during and after the breeding on April 7, 1953 (see Table 19). The toads were caught and positively identified (1) in the plot, (2) either in the breeding areas or between them and the plot, and (3) again in the home area; this definitely indicated a homing movement.

A more circumstantial type of evidence gathered during the reproductive period concerning homing behavior was obtained by observation of females. The records showed that #1045, #1155, and #1030 (Table 19) had ovarian eggs when they were caught before breeding, and they were later captured at or near the same home location with no eggs. The assumption was made that they travelled at least several hundred feet to

TABLE 19

DATA ON CAPTURES INDICATING A HOMING REACTION

Number	Date	Capture Location	Observations
4	3-21-53	1 SW I-9	
	4-7-53	300 SW C-1	Calling in pond, 700' from above
	4-12-53	3 NE K-7	25' from departure point
300	3-11-53	4 NE F-2	At burrow
	4-7-53	1/4 mile SW plot	Calling in pond
	4-12-53	4 NE F-2	At burrow
1104	3-11-53	5 S O-1	
	4-7-53	200 SW C-1	350' from home area
	6-9-53	12 W O-1	In burrow
1125	11-13-51	10 NNW D-2	In burrow
	4-7-53	300 SW C-1	Swimming in pond
	6-29-53	2 S H-9	
	7-2-53	6 NW D-3	Near probable departure point
1304	3-31-53	8 SWS B-4	In burrow
	4-7-53	150 SW C-1	About 600' movement
	5-5-53	7 SSW B-4	
2215	6-27-52	30 W C-4	About 900' from probable departure
	4-8-53	500 NW B-1	♀ spent, eggs gone
	6-8-53	45 W C-4	
2313	3-21-53	1 E H-7	
	4-7-53	200 SW C-1	
	7-26-53	10 NNE H-7	
1045	3-11-53	1 E G-2	Eggs in body cavity
	4-26-53	5 NNW G-2	Very few eggs
1155	3-11-53	1 SW E-2	Many eggs in body cavity
	4-26-53	2 SW E-2	No eggs
1030	9-2-51	C-1	Eggs in body cavity
	4-12-53	15 W C-1	No visible eggs
2245	8-14-53	7 SW O-5	
	8-25-53	Trap W	Released east of trap system
	8-26-53	Trap E-1	

TABLE 19 (Continued)

Number	Date	Capture Location	Observations
100	8-21-53	2 E F-1	In burrow
	8-24-53	3 SE E-3	Moving away from plot?
	8-25-53	Trap W	Trap adjacent home range area
	8-26-53	Trap E	Returning direction to home site
3224	4-9-53	15 S K-3	
	8-25-53	Trap E	Returning towards plot?
	8-27-53	2 NW E-2	Movement to plot continued

the nearest pool, deposited their eggs, and then returned to their home area.

A few records were obtained (#2245, #100, #3244 in Table 19) during the breeding period of August 24, 1953, from the trap system located east of plot 1. They indicated that the animals were trapped as they were leaving the plot, and after their release, they were subsequently caught in another trap, denoting that their movement was towards the plot.

Light can be shed on the relationship between movement within the home range and the type of micro-habitat. In Figure 12 between lines 1-4 and from line D to south of line G, the habitat was homogeneous with almost no herbaceous or shrub vegetation. West of line 1 and north of line D the ecotone was composed of a dense growth of herbs and shrubs. The movements from burrows of #1033, #3040, and #1125, were all in the direction of the open areas and away from the dense vegetation. The radiation from burrows of #320 and #1045 was much more nearly symetrical and was located entirely in one phase of the habitat. There was a lower toad occupancy in the portions of densely vegetated ecotone than in open habitat.

In Figure 14 the movements of #1305 were nearly all clustered in one area north of the burrow. This area coincides with a mass of dead leaves, twigs, and rotten wood. The correlating factor between sites of capture and debris probably was food. The movements from the burrow by #1004 were mostly towards the ecotonal break between hammock and prairie, and they produced a linear shaped range.

The curved lines connecting capture points with burrows of some individuals in Figures 12 and 14 were the paths followed by toads on their return to the burrow after capture. It was normal for toads to move in a direction away from the burrow, to turn sharply one or more times, and then to proceed to the burrow. The approach was seldom direct. It was usual for the animal to circle the burrow from 270 to 360 degrees before entering, when about two to four inches from the aperture.

Observation of many approaches by toads to their burrows showed that they were spatially well orientated when near them, and there was little or no apparent hesitation in moving into the hole. On several occasions individuals backed from several inches distance into an aperture that was hidden beneath a large, fallen leaf or a mat of leaves.

Dispersal. One method of analysis for the rates of movement or dispersal of the adult population was the study of the percentage of new animals taken each field trip. Theoretically after a preliminary period all of the animals in the population would be marked, and the retake percentage or the proportion of the catch that had been previously marked should approach 100. Actually some new toads were taken even at the end of the study representing immigration into the area. Since for consecutive census periods the population density remained approximately the same, it follows that nearly the same number of animals had emigrated.

Retake percentage plotted against the cumulative number of hours in the field is given in Figure 15. The curve rose rather rapidly beginning in July and extending through August, 1951, before it dropped suddenly during the heavy rains and breeding of September,1951. It rose again in October and remained nearly constant until February, 1952, when it dropped considerably during a period of heavy rains and another slight breeding season. The curve reached a peak of 100 per cent in April and a low of 50 per cent in May, 1952. The higher retakes between 80 and 90 hours represented work done in the hot dry summer of 1952. Lower percentages came during the wet fall, 1953, with slightly higher values for the winter period. Heavy rains and an extensive breeding in early April were correlated with the drop to below 50 per

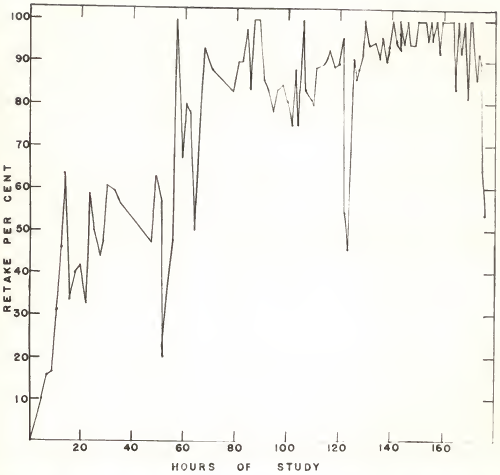


Figure 15. Changes in percentage retakes in plot 1 in relation to the cumulative number of study hours.

cent retakes after about 120 hours' work. Following this shift in the population, the retake percentage climbed and remained high during the intensive field work of the summer of 1953, until it fell during breeding in August, 1953. Four of the five major declines in retake per cent occurred during breeding seasons and times of extensive rainfall.

New toads were recorded much less frequently during the hot, dry summer of 1952 and the cold, dry winter periods than during the wetter spring and fall seasons. In the summer of 1953, the amount of rainfall was measured and work carried on 44 nights from June through August. A X^2 test using categories of rainless as compared with days of some rainfall and days of 100 per cent retake contrasted with less than 100 per cent retakes denoted an association between the immigration of new toads and days of some recorded rainfall (Table 20).

TABLE 20

A CHI SQUARE TEST FOR INDEPENDENCE BETWEEN RAINY DAYS AND RETAKE PERCENTAGE

	Nights		
	100% Retakes	Less than 100%	Total
Rainfall Days	11	20	31
Rainless Days	10	3	13
Total	21	23	44

$X^2 = 4.71$ P. < 0.05

During this summer period between June and August, 1953, the trap system (Figure 5) was in operation at the east end of plot 1 to test amounts of dispersal. Twenty captures were made in this trap between June 1 and August 22, only one of which represented an animal previously marked in the plot. These 20 captures occurred in connection with wet, rainy days. From August 23 through 27 results indicated that the major dispersal occurred during breeding periods (Table 21).

Heavy rains connected with a stationary weather front fell on August 21, 22, 23, 1953, and in mid-afternoon of the latter day breeding choruses of the spadefoots began. Successful breeding in the ponds 300 feet SW C-1 and one-half mile southwest of the plot was denoted by neural-groove stage tadpoles the following afternoon. Toads trapped during the movement towards the breeding area were checked at two p.m. August 24. Since it was assumed that if toads were trapped in the south quadrant of the system, they they were heading in a northerly direction, the results reflected a major movement from the south towards ponds in the prairie. Toads trapped in a quadrant were released in the opposite one, midway between the open arms of the trap fences.

Heavy rains continued the night of August 24, but only non-breeding males were seen in the ponds southwest of the plot. Many toads were heading through the plot from the direction of the prairie towards the southwest. Many were slimy and they seemed to be moving away from the breeding areas. The migrations were checked this night by trap inspection the next morning. The relationships of the trap with the prairie were such that captures in the north and east quarters seemed to represent movements from the prairie whereas for the other half of the system the opposite was true. It appeared that a great deal of travelling in all directions occurred this night, and the majority of toads were head-

TABLE 21

NUMBERS OF TOADS TRAPPED EAST OF PLOT 1 DURING AUGUST 1953 BREEDING*

Trap	2 P.M. 8-24-53	9 A.M. 8-25-53	9 A.M. 8-26-53	8 P.M. 8-27-53
W	-	16	10(1)	-
W_1	-	9	3	-
W_2	-	-	1	-
N	-	10	7(4)	-
N_1	1	4	1	1(1)
N_2	-	-	-	-
E	3	70	7(3)	-
E_1	-	-	1(1)	-
E_2	-	2	1	-
S	-	25**	4	-
S_1	-	-	-	1(1)
S_2	6	17***	1	1

*Numbers in parenthesis are of toads marked the first two days in opposite quadrants.

**Plus one dead.

***Plus seven dead.

ing away from breeding areas in the prairie.

The trap results for the nights of August 25 and 26 were such that no conclusions could be made concerning the major direction of movement. However, 11 captures giving data on directional movements of toads trapped in opposite quadrants on August 23 and 24 are enclosed by parenthesis in Table 21. It is seen that there was a greater percentage of toads returning in a southerly and westerly direction than otherwise. These were probably trapped the first two days as they moved towards the prairie to breed, and then on the latter two days after the breeding was finished they were moving back to the south and west toward their home areas.

Ten of the toads trapped on August 24 had been marked in the plot earlier. Taken in Trap E, on the side opposite the plot, were: #1043, last taken October 8, 1952, at 3 SW N-5; #1440, last observed December 3, 1951, at 20 S K-11; and #3223, captured April 9, 1953, at 15 S K-3. Another toad last seen April 9, 1953, was trapped in S_2. Six toads, marked in the plot and seen there during the summer, were trapped in the western quadrant that faced the plot. The location of last capture for each of these six and the corresponding date of observation was: 3 E J-10, 6-30-53; 7 SW O-5, 8-14-53; 10 SWS G-1, 8-19-53; 2 S D-5, 8-24-53; 3 SE E-3, 8-24-53; and 3E H-9, 8-22-53. Two of these were seen in or near their home range the same night that they were later trapped when moving out of the plot.

In Table 22 data from plot 1 on dispersal as measured by the greatest distance between captures for particular time units are listed.

TABLE 22

RESULTS OF AN ANALYSIS OF MAXIMUM DISTANCES BETWEEN CAPTURE-SITES IN PLOT 1

Distance Feet	Entire Study	Seasons				Months			
		Winter	Spring	Summer	Fall	Dec.-Feb.	Mar.-May	June-Aug.	Sept.-Nov.
1	30	20	17	28	14	7	9	45	9
4	33	17	20	18	19	8	13	27	8
7	25	14	19	26	11	9	10	24	6
10	39	7	15	28	16	2	9	44	10
13	32	4	10	14	6	2	7	19	-
16	38	-	12	20	7	1	5	23	2
19	32	3	5	14	7	1	2	13	2
22	24	2	1	8	2	1	-	8	1
25	17	-	2	5	5		3	3	-
28	11	-	1	5	1		-	3	1
31	16	1	1	5	1		1	3	-
34	9	-	1	-	1			-	2
37	1	-	1	2	2			2	1
40	3	-	-	1	1			-	-
43	3	-	-	-	-			-	-
46	5								
49	3								
52	2	4	5	8	9			4	1
55	6								
58	2								
61	6								
64	4								
67	2								
70	3								
73	1								
76	-								
79	2								
82	1								
85	1								
88	-								
91	2								
94	1								
97	2								
100	2								
103	5								
106	1								
107+	31								

Greatest distances for monthly units were totaled in the four groups given in the table. When the greatest known dispersal distances for the study were plotted, it was seen that the bulk of toads did not move more than 32 feet. A breakdown of time intervals for movements that were not known to be directly correlated with breeding is given in Table 23. One 200-foot movement took place in nine days or less; 123, 125, and 250 foot movements took place in approximately one month's time, and all of the others had long periods between captures.

TABLE 23

TIME INTERVALS FOR THE LONGER DISTANCES BETWEEN CAPTURE SITES OF PLOT 1 TOADS

Distance	Dates	Distance	Dates
123	11-13-51 to 12-3-51	189	11-12-51 to 6-3-52
125	9-12-52 to 10-8-52	193	10-5-51 to 9-12-51
130	3-21-52 to 6-27-52	200	6-6-53 to 6-18-53
130	7-31-51 to 3-13-52	203	12-30-51 to 8-15-52
135	9-14-51 to 1-23-53	217	3-21-52 to 6-14-52
142	12-30-51 to 12-10-52	220	8-28-51 to 2-20-53
146	10-5-51 to 6-14-52	220	5-22-52 to 3-21-53
175	4-12-53 to 6-9-53	250	4-24-52 to 6-8-52
183	3-12-52 to 3-11-53	250	8-14-51 to 6-27-52
184	6-14-52 to 3-11-53	250	12-30-51 to 3-11-53
		300	7-26-51 to 6-14-52

Data in Table 22 lead to the conclusion that most of the dispersals were of relatively short distance, and they accounted for the gradual addition of new toads in the study area. Shifting of the population components occurred in greater amounts during the fall and spring seasons, and was probably most directly correlated with rainfall.

The greatest measured amount of population shift occurred a day or so before, during, and shortly after breeding activities.

POPULATION DENSITY

Techniques of Analysis. One major problem in this part of the investigation was estimating population density under field conditions. An excellent opportunity to study various estimation techniques was available in plot 3 where there was a known beginning-population density.

The most obvious method of density determination is to count the number of individuals per unit area. A reference to an earlier section on the length of time toads remain underground (p. 29) will illustrate the difficulty of this simple count. In pen 1 of plot 3, 40 individuals were introduced. Cumulative data on the number of these that were observed and known to be present after a given number of observation periods were, respectively, 19, 3; 21, 5; 23, 8; 27, 14; and 29, 17. That meant that even after the pen had been searched 17 times only 72.5 per cent of the population had been captured. After this length of time emigration and immigration would have changed the original population if it had not been enclosed by fence, and mortality would in any case have changed its size.

One modification of this method was to add to the number actually counted those toads that were taken in periods both before and after the one under consideration. The animals could not leave the fenced areas of plot 3, so that if a toad was taken late in the study, the assumption was made that it was present continuously from the beginning. In plot 3 this estimate for a particular period improved as later work reported the presence of individuals. Even the adjusted count was probably lower than the actual population size for the latter part of the study. Using this method in the natural populations required the assumption that if a toad was taken before and after, but not during a particular period, it had been present in the area but had remained unobserved during the interval.

Using records of capture of marked and released individuals several statistical methods are available to estimate the population. The method known as the Lincoln Index, discussed by Dice (op. cit.), utilized results of two successive field trip records. The formula may be written:

$$P = \frac{X}{Y}$$

where P is the population size at the time of the first trip, X is the number of toads marked the first night, and Y is the proportion of the second night's catch that was marked on the first trip.

A revision of this method was proposed by Hayne (1949b), that provided a way of averaging all estimates for sets of paired field trips. This suggestion was based on the idea that the percentage of retakes for any particular observation varies directly with the number of animals previously marked in the population. The formula is:

$$Y = \frac{X}{P}$$

where P is the population size, X is the number of animals previously marked and released, and Y is the proportion of the population marked. To obtain an estimate, one must find the trend line that best fits this relationship for the results of the census period. The trend line shown in Figures 16 and 17 that passes through the origin on the X and Y axis, can be drawn by eye or obtained by statistical means. Hayne (ibid.) gave the following formula to obtain an estimate of population size directly:

$$P = \frac{WX^2}{WXY}$$

where the repeated variables are as defined immediately above and where W is the number of captures per field trip and, as usual,   calls for summation.

Assumptions inherent in this method, as well as the simpler one, were discussed by Hayne (ibid.), Dice (op. cit.) and others. To use these methods one must assume that no significant additions have been made to the population during the census period either by reproduction or by immigration. Marking must not cause differential mortality, and/or emigration. Finally there must exist an equal probability of capture for every animal in the population, whether previously handled or not.

This last point is of special importance since some species become "trap shy" while others may get the "trap habit." Emlen, Stokes, and Davis (1949) found that the brown rat becomes trap wary after first capture, and the probability of capture of unmarked animals became so much higher than that of marked, that the index method was quite unreliable. Contrariwise, Chitty and Kempson (1949) found that field voles had a new object reaction before first capture, but later tended to return to traps more and more and developed the "trap habit."

Recently Tanaka (1951, 1952, 1953) proposed a method using a mark-and-release index, B. With this method the assumption of an equal probability of capture for marked and unmarked animals need not be made. The equation used by Tanaka is:

$$Y = \left(\frac{X}{P}\right)^B$$

where X, Y, and P are defined as above and B is the mark-and-release index. If B = 1, the equation is rectilinear; the probability of capture is equal for marked and unmarked, and it is the same equation as that used by Hayne. If B is greater than 1, the probability of capture is greater for unmarked animals; while if B is less than 1, the probability is less for unmarked than for marked individuals. When B is greater than 1, the resulting curve and its relationship to the rectilinear 1 is given for plot 1 data in Figure 16, whereas the relationship to the trend line when B is less than 1, is illustrated in Figure 17. It is noted that when B is different from 1, the equation becomes curvilinear. Factors that regulate the probability of capture for marked and new animals will influence this index. In the present study, the test was whether marked or unmarked individuals were more liable to observation and capture. This could be affected by a tendency for the observer to see animals of known home range or burrow location more than unfamiliar ones. It could also be influenced by emigration and immigration of animals.

The data from plots 1 and 3 were placed in census periods and analyzed with the above methods. It was desirable not only to have a sufficient number of field observations in a census period so that the

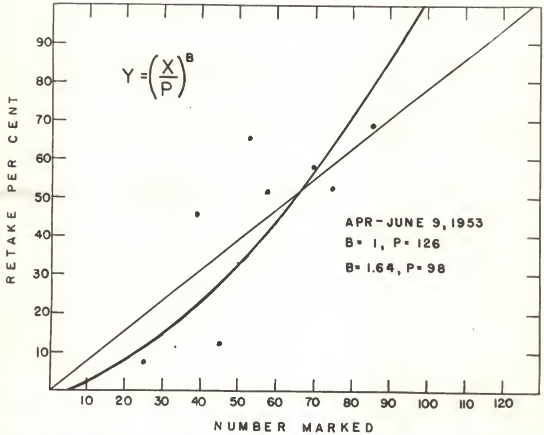


Figure 16. The relationship between the rectilinear and curvilinear methods of population estimation, when B is greater than 1.

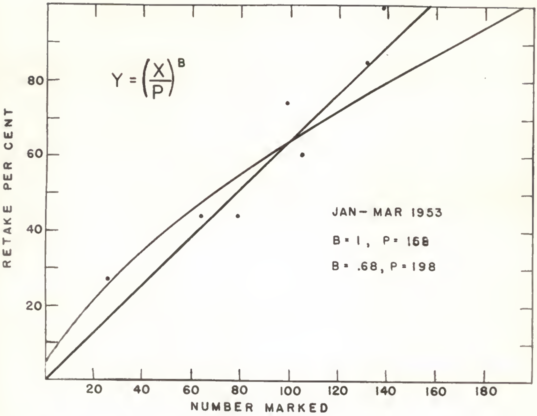


Figure 17. The relationship between rectilinear and curvilinear methods of estimation when B is less than 1.

TABLE 24

A SUMMARY OF FIELD CENSUS DATA FROM PLOT 3

Period	Date	Number of Captures			Proportion Previously Handled (Y)	Number Previously Handled (X)
		New	Previously Marked	Total (W)		
1	July 23, 1952	30		30		
	July 24	10	13	23	.57	30
	July 25	4	12	16	.75	40
	Aug. 11	4	17	21	.81	44
	Aug. 12	2	11	13	.85	48
	Aug. 29	-	2	2	1.00	50
	Aug. 31	1	8	9	.89	50
2	Sept. 8, 1952	9		9		
	Sept. 17	9	2	11	.18	9
	Sept. 22	3	1	4	.25	18
	Sept. 23	10	4	14	.29	21
	Oct. 7	8	6	14	.43	31
	Oct. 17	9	12	21	.57	39
	Oct. 18	3	10	13	.77	48
	Nov. 10	3	13	16	.81	51
	Dec. 10	-	3	3	1.00	54
	Dec. 20	3	18	21	.86	54
3	Jan. 8, 1953	4		4		
	Jan. 20	18	1	19	.05	4
	Feb. 3	17	12	29	.41	22
	Feb. 11	2	5	7	.71	39
	Feb. 25	7	14	21	.67	41
	Mar. 3	4	12	16	.75	48
	Mar. 10	-	6	6	1.00	52
	Mar. 12	8	32	40	.80	52
	Mar. 18	7	18	25	.72	60
	Mar. 23	2	39	41	.95	67
4	Apr. 1, 1953	10		10		
	Apr. 10	25	6	31	.19	10
	Apr. 24	6	8	14	.57	35
	May 1	9	15	24	.625	41
	May 6	2	7	9	.78	50
	June 3	8	13	21	.62	52
	June 10	3	16	19	.84	60
	June 15	1	19	20	.95	63

TABLE 24 (Continued)

Period	Date	Number of Captures New	Number of Captures Previously Marked	Number of Captures Total (W)	Proportion Previously Handled (Y)	Number Previously Handled (X)
5	July 1, 1953	3		3		
	July 9	1	-	1	.00	3
	July 15	2	1	3	.33	4
	July 18	3	1	4	.25	6
	July 20	3	8	11	.73	9
	July 29	-	2	2	1.00	12
	Aug. 6	4	7	11	.64	12
	Aug. 11	-	1	1	1.00	16
	Aug. 20	3	7	10	.70	16
	Aug. 23	7	13	20	.65	19
	Aug. 26	1	5	6	.83	26

TABLE 25

A SUMMARY OF CAPTURE DATA FROM PLOT 1

	Number of Captures			Proportion	Number
Period Date	New	Previously Marked	Total (W)	Previously Handled (Y)	Previously Handled (X)
1 July 26, 1951	17		17		
July 31	17	2	19	.105	17
Aug. 2	20	1	21	.048	34
Aug. 14	19	5	24	.21	54
Aug. 22	9	8	17	.47	73
Aug. 28	1	2	3	.67	82
Sept. 7	20	5	25	.20	83
Sept. 14	5	5	10	.50	103
Sept. 21	15	10	25	.40	108
Sept. 28	11	7	18	.389	123
2 Oct. 5, 1951	19		19		
Oct. 6	14	1	15	.067	19
Oct. 17	4	-	4	.00	33
Oct. 25	17	4	21	.19	37
Oct. 30	20	4	24	.167	54
Nov. 13	22	10	32	.31	74
Dec. 3	14	15	29	.52	96
Dec. 30	24	12	36	.33	110
Jan. 4, 1952	5	6	11	.545	134
Jan. 16	3	3	6	.50	139
3 Mar. 13, 1952	38		38		
Mar. 21	21	3	24	.125	38
Apr. 9	1	3	4	.75	59
Apr. 24	24	8	32	.25	60
Apr. 30	7	4	11	.364	84
May 9	4	1	5	.20	91
May 16	2	1	3	.33	95
May 22	6	3	9	.33	97
May 29	13	14	27	.52	103
4 June 3, 1952	25		25		
June 14	33	12	45	.267	25
June 21	8	9	17	.53	58
June 27	13	20	33	.61	66
July 1	4	17	21	.81	79
July 15	-	2	2	1.00	83
July 29	-	3	3	1.00	83

TABLE 25 (Continued)

	Number of Captures			Proportion	Number
Period-Date	New	Previously Marked	Total (W)	Previously Handled (Y)	Previously Handled (X)
Aug. 7	-	2	2	1.00	83
Aug. 15	1	1	2	.50	83
Aug. 28	7	8	15	.53	84
5 Sept. 2, 1952	40		40		
Sept. 12	11	3	14	.21	40
Sept. 19	22	5	27	.185	51
Oct. 8	16	6	22	.273	73
Oct. 14	21	16	37	.43	89
Oct. 28	1	4	5	.80	110
Nov. 11	9	11	20	.55	111
Dec. 10	12	18	30	.60	120
6 Jan. 2, 1953	3		3		
Jan. 19	23	-	23	.00	3
Jan. 23	38	14	52	.27	26
Feb. 7	15	12	27	.44	64
Feb. 20	20	16	36	.44	79
Mar. 2	6	17	23	.74	99
Mar. 11	26	39	65	.60	105
Mar. 21	7	39	46	.85	131
Mar. 31	0	2	2	1.00	138
7 Apr. 12, 1953	25		25		
Apr. 26	14	1	15	.07	25
Apr. 30	7	6	13	.46	39
May 5	7	1	8	.125	46
May 20	4	8	12	.67	53
June 5	13	12	25	.48	57
June 6	5	7	12	.58	70
June 8	11	12	23	.52	75
June 9	5	10	15	.67	86
8 June 13, 1953	5		5		
June 14	22	1	23	.043	5
June 16	22	2	24	.083	27
June 18	4	10	14	.71	49
June 19	4	10	14	.71	53
June 23	27	19	46	.41	57
June 24	6	21	27	.79	84
June 29	6	25	31	.81	90
June 30	3	8	11	.73	96

TABLE 25 (Continued)

Period-Date	Number of Captures			Proportion Previously Handled (Y)	Number Previously Handled (X)
	New	Previously Marked	Total		
9 July 2, 1953	14		14		
July 3	1	1	2	.50	14
July 6	10	5	15	.33	15
July 7	4	5	9	.55	25
July 8	2	4	6	.67	29
July 10	10	11	21	.52	31
July 14	0	7	7	1.00	41
July 16	10	12	22	.55	41
July 18	-	6	6	1.00	51
July 21	1	9	10	.90	51
July 23	-	5	5	1.00	52
July 25	-	1	1	1.00	52
July 26	1	11	12	.92	52
July 27	2	9	11	.82	53
July 30	-	7	7	1.00	55
July 31	-	2	2	1.00	55
10 Aug. 4, 1953	5		5		
Aug. 5	9	2	11	.18	5
Aug. 10	13	6	19	.32	14
Aug. 11	13	10	23	.44	27
Aug. 12	3	9	12	.75	40
Aug. 14	5	7	12	.58	43
Aug. 16	3	11	14	.79	48
Aug. 17	3	18	21	.85	51
Aug. 18	9	15	24	.63	54
Aug. 19	4	10	14	.71	63
Aug. 21	2	22	24	.92	67
Aug. 22	9	17	26	.65	69

data could be better studied statistically, but also these periods should group results as nearly homogeneous to seasonal, climatic, and biological factors as possible. Within a census period a toad was considered an "unmarked" or "new" animal if it had not been observed, and "marked" if it had been taken earlier during the particular census period.

Census Results. Data from plot 3 are given in Table 24 with the exception of results of work done after August, 1953, and of dates on which no toads were observed. These data were used to obtain the estimates of population size given in Table 26. It appears that the adjusted count was the most reliable measure for plot 3 populations and that the greatest error in this count was during the last census period. The simple count of the number of toads was considerably below that of the adjusted count in three of the five census periods, and was especially low during the two summer periods. These two counts of the population were nearly the same for the periods from January through June, 1953, when the amount of activity was high.

The statistical method proposed by Hayne (1949b)produced results that tended to underestimate the population size. This was specially noted during the two summer periods where this index estimate of population size was lower than the adjusted count by 26 and 20 (Table 26). The method of population measurement given by Tanaka (1952) produced estimates that were not greatly different from the former ones except during the last period of the summer of 1953. During that summer, the mark-and-release index was much less than one, indicating that the

TABLE 26

A SUMMARY OF POPULATION ESTIMATES FOR PLOTS 1 AND 3

Period	Simple Count	Adjusted Count Number	Adjusted Count Toads per Acre	Hayne Estimate	Tanaka Estimate	B	Adjusted Estimate
Plot 3							
7/52-8/52	51	89	1,114.0	53	56	.908	
9/52-12/52	57	76	951.3	62	67	.95	
1/53-3/53	69	74	926.3	68	66	1.02	
4/53-6/53	64	66	826.1	70	72	.865	
7/53-8/53	27	45	563.3	25	38	.427	
Plot 1							
7/51-9/51	134	133	379.8	313	289	.989	
10/51-1/52	142	178	508.4	255	264	.96	
3/52-5/52	116	167	477.0	224	271	.92	
6/52-8/52	91	158	451.2	109	105	1.00	167
9/52-12/52	132	179	511.2	205	187	1.11	212
1/53-3/53	138	168	479.8	158	198	.68	222
4/53-6/9/53	91	128	365.6	126	98	1.64	90
6/13-6/30/53	99	124	354.1	112	117	1.09	107
7/53	55	83	237.	56	64	.76	76
8/53	78	105	299.9	88	98	.577	116

probability of capturing previously marked animals was greater than for new ones.

Associated with the low estimates of the population attained by the index methods during the summers of 1952 and 1953 was an especially low amount of toad activity. If the probability of capture is the same for all individuals in a population during a particular census period, the population estimates should not vary with the amount of total toad activity. It was recognized that rates of toad emergence varied from season to season and from one type of weather to another. It was assumed, however, that the probability of emergence for any individual toad in a census period would be proportional to the rate of activity for the entire population. If this were true, the marked toads would mix at random in the captured population and amount of activity would not seriously influence the index estimates.

The assumption that an individual emerges during a census period in proportion to the total group emergences was not valid. General observations during these summer periods indicated that toad captures were of a small segment of the total population, and the remainder of the total did not appear in the sample at all. Similar information was obtained by study of emergence and non-emergence from burrows in plot 2 from June through August, 1952. The burrows of ten toads were observed and from these only five animals were active during the summer period. Of these five, one emerged ten times in a period of 33 nights; another came out four out of eight nights; a third emerged four in a span of 25 nights; another was recorded twice in ten nights; while the last was active only one night during the summer. The activity of these toads was condensed into relatively short periods.

A further test was employed for some data from plot 3 using records of 26 animals caught in pen 1 and known to be present from July, 1952, through June, 1953. First, in this test it was assumed that each individual would be captured in proportion to the number of field trips in each period of: (1) July-August, (2) September-December, 1952, (3) January-March, and (4) April-June, 1953. For example, if an individual was captured a total of ten times during the year, and if 20 per cent of the total field work was done in the first period, it was expected that the toad should have been caught twice during that first period. A chi square value was calculated, then, for this individual for this first period using the formula:

$$\frac{(\text{Observed} - \text{Expected})^2}{\text{Expected}} = X^2$$

and the total value for each of the periods for all 26 animals was added. The X^2 value was 121.66 with 75 degrees of freedom. $(P. < 0.01)$. In other words, there was good evidence that spadefoots were not observed at random with regard to the four periods studied. The number of toads not observed in each period and the weighted average number of times the active toads appeared are, respectively: July-August, 14, 3.10; September-December, 13, 2.08; January-March, 2, 2.96; April-June, 5, 2.32. In the summer, over half of the cohort was not observed, but those toads that were active were seen a greater number of times, on the average, than for any other season.

The B index figures shown in Table 26 are for the most part very near one. Only one index, that for April to June, 1953 in plot 1, greatly exceeded one. This period followed the breeding of April 7, and the high chance of capture for new animals reflected the immigration associated with breeding migrations.

Of the indices lower than one in both plots, the majority occurred during the summer time, especially the summer of 1953. These resulted from (1) less immigration and emigration of the population, (2) smaller numbers of active toads than tended to emerge more times, thus increasing the captures of animals previously handled, and (3) the smaller active population increased the chance for toad locations and habits to be learned by the observer. The second item was probably not the least important.

An adjusted estimate of the plot 1 population was calculated, using a simple proportion between the Tanaka estimate for plots 1 and 3, and the adjusted count for plot 3. The assumption required was that toads in plot 3 would react to environmental factors essentially in the same manner as those in the wholly natural situation. Since the proportion and direction of error in the Tanaka estimate for plot 3 was known, the theoretical population of the natural site could be estimated. The major source of error comes from the incidence of immigration-emigration that affected the B in plot 1. This error can be detected in Table 26 for the April-June, 1953 period, where high population dispersal caused a very high B value (1.64) in plot 1, while the same figure for plot 3 was less than 1.

TABLE 27

POPULATION ESTIMATES FOR TWO HABITATS IN PLOT 1

Census Periods	HAMMOCK Hayne Estimate	 Adjusted Count Total	 Toads per Acre	ECOTONE Hayne Estimate	 Adjusted Count Total	 Toads per Acre
7/51-9/51	67.6	36	261.4	192.2	97	456.8
10/51-1/52	74.2	46	334.0	187.9	132	621.6
3/52-5/52	44.6	40	290.4	178.2	127	598.0
6/52-8/52	26.2	38	275.9	84.4	120	565.1
9/52-12/52	55.7	49	355.7	148.4	130	612.2
1/53-3/53	49.2	38	275.9	129.5	130	612.2
4/53-6/9/53	25.6	31	225.1	93.4	97	456.8
6/13-30/53	28.3	32	232.3	85.4	92	433.2
7/53	13.7	36	261.4	49.7	47	221.3
8/53	17.8	27	196.0	58.4	78	357.3

A breakdown of population estimates for the hammock and ecotone habitats in plot 1 is given in Table 27. These data, like those in Table 26, were probably underestimated for the summer census periods, using the Hayne index method, and were low for the first and last periods, using the adjusted count technique. Examination of the conversion to toads per acre indicated that the density of the ecotone was about double that of the hammock except during July and August, 1953. During July, 1953 the apparent density in the hammock exceeded that in the ecotone; the explanation for this exception is probably that it results from poor sampling. It has already been noted that the greatest error in the adjusted count method came during the last periods of the study. The apparently higher density in the hammock may result from lower activity rates for ecotone toads, which in turn would decrease the number of toads known to be present in the ecotone during this latter period. The density of plot 3 was about twice that of the total census area of plot 1. It should be mentioned that the three density levels of plot 1 in toads per acre were 2,503, 1,252, and 625.9 at the beginning of the experiment. Therefore, the lowest beginning density level in plot 3 was higher than any density estimate for plot 1.

Data from plot 1, in Tables 26 and 27, show that in general there was a gradual decrease in density from the beginning to the end of the study. This continued decrease reflected the lack of any really successful reproduction during the research.

REPRODUCTION, GROWTH, AND AGE GROUP DISTRIBUTION

Reproduction. Spadefoot toads do not have a particular breeding season in the cyclic, seasonal sense, but rather breed only during or after very heavy rainfall. They reproduce in temporary water, and their loud, harsh voices elicit movements to the breeding areas (Carr, 1934). Bragg (1945) cited the above observations as characteristic of the xeric amphibian breeding pattern. He further pointed out that spadefoots fall into two general groups with respect to breeding response. One group responds to violent rainstorms while S. hurteri and S. holbrooki are greatly stimulated by large amounts, but not violence, of rainstorms.

Dr. C. J. and Mrs. Olive Goin have recorded the dates of spadefoot reproduction in a temporary pond in their backyard near Gainesville on: September 24, 1947, a large chorus after a storm; March 9, 1948, breeding chorus; April 5, 1949, a large chorus after rainstorms; August 22, 1949, a heavy rain and another chorus; September 5, 1950, very heavy breeding chorus after hurricane rains; and October 18, 1950, a chorus at some distance from Goin's residence after another hurricane.

The first chorus recorded during this study was associated with a passing cold front that brought 2.18 inches of rain during the night of September 17, 1951. Not many more than a half dozen pairs bred in Goin's backyard and none were recorded near the Drug Gardens, nor near plot 1. A small chorus after a heavy thunderstorm near Micanopy was reported by Dr. Archie Carr on September 22, 1951, but no spadefoot breeding was reported around Gainesville. The production of young from the former chorus was negligible.

A stationary cold front brought steady, heavy rainfall beginning on February 15, 1952; 3.14 inches were recorded on the University campus the morning of February 16, and 0.84 inches the next morning. Spadefoot toads bred the night of February 15, in the Goin's backyard, and near plot 2. Cold weather followed with minimum-maximum temperatures (F.) reported as February 16) 55°-70°, 17) 37°-62°, 18) 41°-68°, 19) 47°-75°, 20) 57°-74°, 21) 48°-72°. The water temperature at noon on February 19, in the breeding pond at Goin's, was 55°F. The eggs began to hatch on February 21; the incubation time was six days. No young produced in this chorus were observed in the plots.

Large breeding congresses the early morning of April 7, 1953, were again associated with a cold front that gave Gainesville 4.58 inches of rainfall for the day. Toads were not calling at ten p.m. the night before, but Mrs. Goin heard them calling at 3:30 a.m., and they were still breeding at seven a.m. They also bred north of Gainesville and in plot 1. Eggs were found in seven shallow (less than 18" deep) puddles in the grass prairie between plot 1 and Hogtown Creek to the north; the closest to the plot being: 1) 50' northeast A-1, 2) 65' north-northeast A-1, and 3) 200' north D-1. A number of breeding ponds in the hammock south of plot 1 contained eggs with the closest being 300' southwest C-1.

A barometric recording begun at two p.m. on April 7 showed a low of 29.6 inches at that time with a steady rise to 29.84 at noon the following day. Some toads were calling the night of April 7, but in the ponds only several pairs in amplexis were discovered. Many males but no unpaired females were observed. The eggs had hatched by eight p.m. on April 8, an incubation period of less than a day and a half.

None of these ponds around plot 1 retained water long enough for the tadpoles to metamorphose. The puddles in the prairie were dry by April 25, and the pond 300 feet southwest of C-1 was reduced to a puddle one inch deep and several feet in diameter by April 30. Some rain gave respite, but by May 3, the pond was dry and the tadpoles had not yet emerged. Very few young were produced from this reproductive period.

Another stationary cold front brought heavy, continued rains that stimulated large choruses in the Gainesville region on August 23, 1953. Toads began calling in mid-afternoon and continued in breeding choruses all night. Recorded daily rainfall beginning August 21 was 0.21, 1.66, .74, 2.60, .41, and 1.25 inches. The eggs laid in this period were hatching by mid-afternoon, August 24; the hatching period being about 24 hours or less. This chorus was large and a considerable population of young toads emerged after the present study was concluded in this plot.

All four records of breeding were associated with long, heavy rainfall during the time of cold fronts. Time required for eggs to hatch varied from about one day in August 1953, to six days during colder weather in February, 1952. For a detailed description of larval stages, reference should be made to the works of Trowbridge (1941, 1942) and Richmond (1947). Unfortunately no observations were obtained on the behavior, mortality, or other factors during the time of movements of the young away from the ponds. Young toads were seen the afternoon of September 27, 1953, apparently heading in all directions from several ponds. Records kept by the Goins in their backyard studies indicate that about six weeks elapse between emergence from the pond and initiation of burrow life. Recently emerged young were observed on June 2, 1949, and most of them had disappeared and had probably burrowed by the end of July, 1949. Many small young appeared from the ponds September 18, 1949, and most had utilized burrows by the last of October. Then from another chorus, young emerged on October 1, 1950, and began to burrow by October 29, with nearly the entire group disappearing by November 16, 1950.

Growth. Measurements of growth taken during the study were limited to determining the greatest head width, interorbital distance, and snout-vent length. Weights of toads were not observed since they could not be efficiently taken in the field and since the amount of stomach contents would produce great variation. The interorbital distance was measured with vernier calipers, but since difficulty was met in establishing definite landmarks for reference, this was discontinued after October, 1951. Total body length was at first measured with vernier calipers and later by placing the toad on a ruler fastened to a clipboard. The taking of body length was not easy since the toad could contract or relax, and thus change its size. Head width provided the most constant, least variable, and most used measurement of body size. Data for October, 1951, from plot 1 were examined to illustrate the relationships between these three body sizes. Total body length was correlated with head width where r. = 0.93, and their relationship was expressed by $Y = 3.63 + 0.269 X$, where X equalled body length and Y was head width. The r. value was 0.83 between head width and interorbital distance, and $Y = 15.28 + 0.293 X$, where Y was head width and X was interorbital distance. Finally the correlation coefficient between body length and interorbital distance was 0.85 and the regression was $Y = 0.923 + 0.0917 X$, with Y the body length and X the interorbital span.

The age of only a few individuals was definitely obtained in the study of growth rate. These toads were produced in the September, 1951, breeding and the records of their growth are given through the first 18 months in Table 28. To examine rate of body growth in plot 1, individuals captured for the first time between July and September, 1951, and later retaken at least once, were placed in categories according to their first observed head width. Only one measurement per individual per month was utilized in this work.

The type of growth illustrated by the young from the September, 1951, reproduction was that of very rapid growth in the first few months with the rate of change decreasing as head width increased. These early data were better fitted by the curvilinear equation $Y = 8.4 + X^{.21}$, than by the three first degree equations in Table 28. Likewise for the group beginning at 14-15 mm. the equation $Y = 13.91 + X^{.065}$ more nearly fitted the observed data. In the larger toads a rectilinear equation expressed

TABLE 28

A SUMMARY OF HEAD WIDTH GROWTH DATA FROM PLOT 1 WITH THE APPROPRIATE VALUES TO BE SUBSTITUTED IN THE EQUATION Y = Ay + bX WHERE Y IS HEAD WIDTH IN MILIMETERS AND X IS TIME MEASURED IN MONTHS

Source of Data	Number Toads	Number Records	Ay	b.	F.	
0-6 mo.'s	11	11	6.40	1.212	39.9	**
7-12 mo.'s	8	14	8.76	0.474	11.4	**
13-18 mo.'s	8	17	12.23	0.165	1.44	--
14-15 mm.	31	158	14.7	0.101	145.00	**
16 mm.	23	158	16.07	0.056	63.78	**
17 mm.	61	252	17.02	0.049	89.18	**
18-19 mm.	41	192	18.48	0.023	12.38	**
20 + mm.	8	42	20.21	0.017	0.95	--
14-15 mm.	10	59	14.40	0.124	93.10	**
14-15 mm.	13	80	15.16	0.077	42.10	**
16-17 mm.	19	132	16.42	0.107	561.00	**
16-17 mm.	41	275	16.54	0.041	60.10	**
18-19 mm.	26	103	18.35	0.047	28.53	**
18-19 mm.	15	89	18.17	0.040	22.40	**

the records satisfactorily. It is noticed in Table 28 that as the toads get older (or their size larger) the rate of growth, b., decreased rapidly. The F. values with a double asterisk are at, or below, the 1 per cent level of statistical significance, a single asterisk indicates the 5 per cent level, and no asterisk denotes lack of statistical significance.

An examination of records of toads first reported as juveniles showed that on the average they attained sexual maturity during their second year after metamorphosis. The average head width of 47 female toads when their sex was first detected by the presence of ovarian eggs was 15.36 mm. The average head width of 32 males at the time when the dark epidermal pads on the fore feet were first observed was 15.70 mm. No doubt the actual size of adult attainment was smaller than these averages, since time probably elapsed between development of the sex characteristic and its observation by the author. It will be shown below that head widths such as these were reached on the average at 19 and 15 months respectively.

An analysis of sexual divergence in growth rate was made for toads that had an initial head width of less than 13.0 mm., that were first observed between July through September, 1951, and that reached sexual maturity during the period of study. Forty-one records involving seven males were fitted by the equation $Y = 11.81 + X^{.125}$, and the average growth two years later was 17.55 mm. Eight females were recorded 47 times and the equation $Y = 11.74 + X^{.103}$ produced the average Y value 16.22 mm. when X was 24 months.

For a comparison of male and female growth rates in the larger size groups rectilinear equations were used and the data are presented in Table 28. A test (t.) was made for the significance of difference between the rates of growth, b., for the sexes. In the category 14-15 mm. the males grew at a faster rate than the females and the difference was significant at the 1 per cent level (t. = 2.67). Although the rate of increase for the 16-17 mm. group was less than that of the 14-15 mm. one, the males still grew faster than the females (t. = 9.47, P. $<$ 0.01). In the largest size group, the rate for both sexes was still less than for smaller toads, but in these older ones the rate of growth for the males was only slightly larger than that of the females and the difference lacked statistical significance (t. = 0.4).

To represent growth data on the 494 individuals from plot 1 that were retaken one or more times is not feasible because of the space that would be required. However, two males and two females were chosen for each of the beginning head width categories on the basis of those with the largest number of captures over the longest period of time. The records of these individuals are given in Figure 18.

One of the objectives of work in plot 3 was to determine the effect of density on rate of growth. When records were plotted there seemed to be three major sources of variation that could be statistically analyzed. These were: (1) effect of differing initial body sizes, (2) a seasonal or temporal effect, and (3) population density. Even though an attempt had been made to select small toads of nearly the same size, the records indicated that three natural categories of beginning head-widths could be constructed. They were (1) 12 and less, (2) 13-14, and (3) greater than 14 mm. The study continued from June, 1952, through November, 1953, and the following three time periods of six months duration were chosen: (1) June through November, 1952, (2) December, 1952 through May, 1953, and (3) June through November, 1953. The three density levels in this plot were discussed in an earlier section. The data were tabulated so that, if necessary, the results for a particular time, under one density, and in a certain beginning size group could be investigated.

Data from the density and size categories were lumped and subjected to an analysis of covariance for the three time units. The F. value was 5.87 with two and 574 degrees of freedom, indicating that the significance was below the 1 per cent level and that greater variations in growth existed between time categories than within them. The rates of growth for the three categories were 0.2130 ± 0.0283, 0.0827 ± 0.039 and 0.0661 ± 0.0435. It would seem that if season and growth rate had a direct relationship, then the rate during the June through November periods of both years should be more alike than they actually were. The explanation of the differences found among the three periods was probably related to a decrease in rate as body size of the population increased. The toads were small when they were introduced; as time passed, they grew in size, and their rate of body increment decreased.

An analysis of covariance for the three size categories over all periods and with the density levels ignored, gave a high F. of 60.2. There was significantly greater variation between size categories than

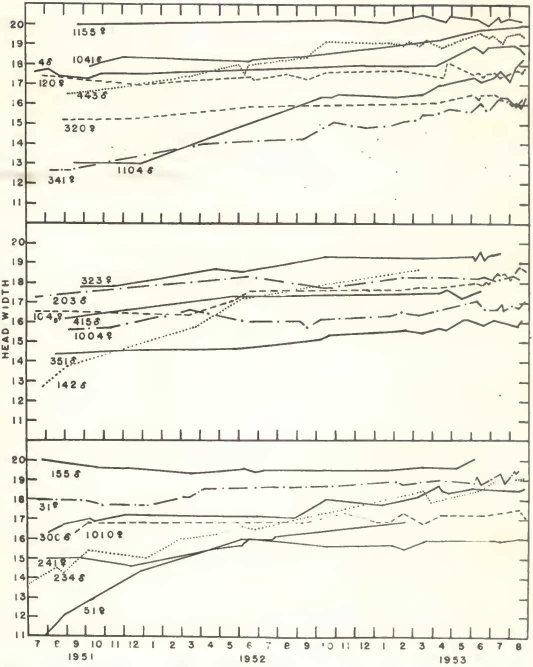


Figure 18. Records of head width growth for 11 males and 11 female individuals.

within them. The regression slopes for the three size groups listed above were respectively 0.2940 ± 0.0500, 0.1221 ± 0.0374, and 0.1151 ± 0.0233. Differences between the first two rates were significant at the 1 per cent level, but no real difference existed between the second and third.

Growth data for the three size groups were then studied for each of the three time units separately. During the first six months differences between the three sizes were statistically true, since the F. value attained was 12.1 with two and 227 degrees of freedom. The regression slopes for them were 0.5558 ± 0.1005, 0.1793 ± 0.0595, and 0.1538 ± 0.0314 with a significant difference between the first two but not between the last two values. During the second and third six-month periods, an analysis of covariance failed to show that a significant difference existed between the size groups, and the rates of growth likewise did not differ greatly. In summary, the differences in growth were found between the smallest and middle-size toads during the first six months as well as for the average of all time units, but differences were never illustrated in any analysis between the middle and largest size categories. The smallest group of toads grew much faster during the first six months, but by the end of the period they had reached a size nearer the other toads and their rate of growth was slowed so that it did not differ from them.

Time and size were ignored and an analysis of covariance disclosed that a statistically significant variation existed between the three densities ($F. = 37.6$, $P. < 0.01$). The millimeter increase per month under the high, medium and low populations were respectively, 0.0901 ± 0.0311, 0.1614 ± 0.0290, and 0.2233 ± 0.0460. The highest density had the lowest rate of growth, but the difference between it and the middle one was at the 10 per cent level of significance (t. = 1.7), whereas the difference between the middle and low levels had still less significance (t. = 1.1). A comparison between the rates in the high and low density denoted a P. value at the 2 per cent level (t. = 2.4).

The first six months of study were chosen for another test of density effects with the data further subdivided into size groups. An analysis of covariance disclosed a significant variation between density levels in growth rate for the smallest toads (F. = 6.9, d.f. = 36, 2, P. <0.01). The slopes for the high, middle, and low densities were 0.1959 ± 0.1950, 0.8323 ± 0.0995, and 0.9002 ± 0.225. The probability values for the difference between slopes were 0.005 for the first two, more than 0.05 for the second two, and 0.02 for the first and last.

Similar tests were made on the size group 13-14 mm. head width and the F. value was 3.69, which is at the 5 per cent probability level. The rates of growth for the three densities were respectively 0.0907 ± 0.0707, 0.1317 ± 0.0690, and 0.4094 ± 0.1390. The same pattern of variation was found here but a statistical significance was determined only for the difference between rates of growth of the extreme density levels (P. = 0.05). Finally, the same series of checks were made on the size group with greater than 14 mm. head width where the F. value was significant at the 5 per cent value (F. = 4.36). The regression slopes were 0.0729 ± 0.387, 0.2183 ± 0.0539, and 0.3235 ± 0.0307. The significance of difference in growth rates was at the 5 per cent degree for the first two and at 0.025 when the highest and lowest densities are compared; however, no real difference was found between the low and middle density growth values.

To summarize, when compared with each other, the middle and low densities had no different effect on rate of body increase. In all of the tests a significant difference in rate of growth was shown between the highest and lowest population levels, and this was also true between the highest and middle levels for the sizes 12 and less and greater than 14 mm. during the first six months. In all of the calculations, the rate varied indirectly with the population size.

The construction of a theoretical average growth curve for most of the toad's life was of value in age group distribution studies. Data from toads known to have been produced during the September, 1951, and April, 1954 breeding periods in plot 1 were combined to calculate the average head width for the first 24 months after metamorphosis. Concerning all of the data following this first period, an assumption was necessary for the age of the toads.

It was assumed for the purpose of these studies that if it took, for example, 5.2 months for these toads of known age to reach a mean head width of 11.81 mm., it would also on the average have taken the same time for toads from any other reproductive chorus. This assumption postulates equally favorable growth conditions. Therefore, for the males of the beginning category of 13 mm. or less, the equation given above would fit a curve that joined the curve of the toads of known age and would extend to 31.2 months age. Using this assumption, curves for the categories 16-17 and 18-19 mm. head width were added and the curve is given in Figure 19.

The same assumption was also made for female growth data. Categories of head width 13 and less, 16-17, and 18-19 mm. were used to estimate the mean growth rate for females through eight years. These data are also illustrated in Figure 19.

Age Group Distribution. The frequency distributions of head widths in plot 1 were tallied for males, females, and for those of undetermined sex and these data are presented in Tables 29 and 30. If an individual was captured more than once in a month it was represented in the tally by only one measurement expressing the average for the month. The monthly frequencies were then lumped to form nine time categories.

The age group distribution of the population in plot 1 was estimated by making use of the calculated average growth curve in Figure 19. It was recognized that any attempt to assign age to head width cohorts based on the average growth of the population was subjected to error caused by individuals attaining size ahead or behind the average. In this study, it was assumed that males were less than two, between two and five, from six to eight, or nine or more years old if their head width was 17 and less, 18-19, 20-21, or 22 mm. and greater, respectively.

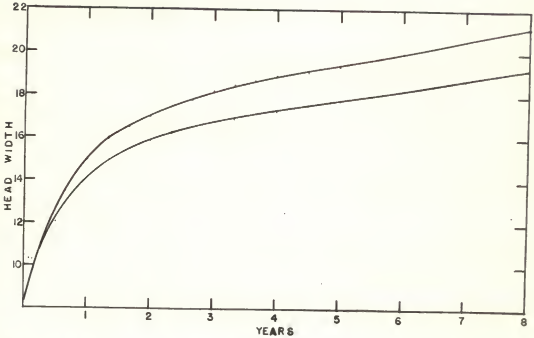


Figure 19. A theoretical growth curve extrapolated statistically and combining growth rates for several groups of toads. The upper curve is for males and the lower represents female growth.

Likewise it was assumed that females and those of underdetermined sex were, respectively, less than two years, three to five, six to eight, or nine or more years old if the head width was 15 and less, 16-17, 18-19, and 20 mm. and larger. Using these arbitrary categories, the percentage age distribution was as given in Table 31.

It is seen in Table 31 and from careful study of head width frequencies that the relative number of young toads constantly decreased during the two years. Likewise it will be noted that the number of individuals in the six to eight year old class increased considerably through the period of observation. The offspring produced in connection with the breeding choruses of September, 1951, scarcely affected the total picture of age distribution and there was no evidence of young individuals from reproduction in February, 1952. The very small toads that appeared resulted from the preceeding April breeding and represented only 6.72 per cent of the population caught during August, 1953. This small addition to the population after a reproduction as heavy as that of April, 1953, reflected the very high mortality of larvae resulting when most of the ponds dried before larval metamorphosis.

TABLE 29

FREQUENCY DISTRIBUTIONS OF HEAD WIDTHS GIVEN FOR MALES*

Head Width	7-8 1951	9-11 1951	12/51-2/1952	3-5 1952	6-8 1952	9-11 1952	12/52-2/1953	3-5 1953	6-8 1953
11	2								
12	1								
13	3	3	2	3	1				
14	3	4	3	7	2	2		1	
15	4	14	7	7	5	4	4	1	1
16	5	9	8	10	16	5	8	8	6
17	17	21	13	16	23	27	21	22	36
18	18	26	13	19	24	31	27	35	31
19	11	20	10	12	11	18	25	48	34
20	5	12	2	7	13	15	5	6	29
21		2		5	5	4		3	11
22		1		1	1	4	3	4	
23	1								
24								1	1
25								1	1
	70	112	58	87	101	110	93	30	150

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*Head widths are given in mm. and the months are lumped into groups of three. The lines divide estimated age classes as discussed in text.

TABLE 30

FREQUENCY DISTRIBUTIONS OF HEAD WIDTHS GIVEN FOR FEMALES AND THOSE OF UNDETERMINED SEX IN ()*

Head Width	7-8 1951	9-11 1951	12/51-2/52	3-5 1952	6-8 1952	9-11 1952	12/52-2/53	3-5 1953	6-8 1953
8									(4)
9									(1)
10	(1)		(1)						(1)
11	1(3)	1(1)	(1)						
12	6(5)	(1)		(1)	(3)				(2)
13	7(8)	4(8)	(3)	1(1)	(1)	1			
14	4(8)	8(12)	2(9)	7(3)	7(7)	6	4(5)	2(2)	(4)
15	6(2)	5(11)	12(7)	4(6)	9(1)	10(3)	13(3)	8(1)	15(1)
16	8(1)	28(6)	11(3)	27(5)	16(2)	21(2)	28(5)	29(2)	31(1)
17	22(2)	34(3)	14(2)	45(3)	27	29(1)	34	38	36
18	11	33	14	25	24	26(1)	26	37	44
19	6	15	4	10	8	13(2)	12	22(1)	29(1)
20	3	5		2	4	6	5	4	10
21		1	1		2	1	1	2	1
22				1	3	3	1	4	
23						1	1	2	1
	74(30)	134(42)	58(26)	122(19)	100(14)	117(9)	125(13)	148(6)	167(15)

*Head widths are given in mm. and the months are lumped into groups. The lines divide estimated age classes as discussed in text.

TABLE 31

ESTIMATED PERCENTAGE DISTRIBUTION OF AGE GROUPS IN PLOT 1*

Age Class	7-9 1951	9-11 1951	12/51-2/52	3-5 1952	6-8 1952	9-11 1952	12/52-2/53	3-5 1953	6-8 1953
0 to 2 yr.	50.0	37.5	50.0	31.1	35.8	25.4	27.3	16.6	21.8
3 to 5 yr.	35.1	38.5	35.2	46.5	36.3	42.8	48.9	52.8	39.8
6 to 8 yr.	12.6	21.5	14.4	20.6	23.3	25.4	18.6	24.3	34.3
9 yr. +	2.3	2.4	0.7	1.8	4.7	6.4	5.2	6.3	4.2
Total Number	174	288	142	228	215	236	231	284	332

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* Age separations determined by use of data in Tables 29 and 30 based on average growth rate in Figure 19.

SURVIVAL AND DISAPPEARANCE RATES

Data on survival and rate of disappearance for toads from plot 1 were selected by using only those individuals that were first observed between July and September, 1951, and only those that were resident in parts of the plots surveyed in ten-foot quadrats. This selection provided records on a cohort that was under greatest field observation for the longest time. There were 153 toads recorded during these first three months.

Two major reasons for disappearance, other than death, were known. First of all, the toads could have simply moved from the area under consideration, and secondly their periods of surface activity could have been such that the author would not have seen them. With regard to the first point, a number of toads first captured in the limited area under consideration were later retaken in adjacent habitats, so that possibly a large number of the cases of loss resulting from dispersal was prevented by the examination of these adjacent areas in plot 1. A part of the apparent departure in the later part of the study was unreal, actually resulting from a lack of observation of these toads. If field work had continued, the number of toads surviving during the spring and summer of 1953 would have been recorded as much higher than that given in Table 32.

No records of actual death were obtained, but injuries were observed. Five toads had one entire front arm missing and two had most of one rear foot gone. Of these, all the wounds had healed except one; this one had a mangled and partly infected front leg stump on April 12, 1953 and was not observed later. Death from fire is a possibility. In plot 1 a campfire at D-5 (Figure 3) between October 25 and 28, 1951, apparently caused burns over most of the venter and one forearm of toad #104, for on November 13, 1951, the healing wounds were seen when it was caught at 4 NE F-3. The burns eventually healed and the toad survived throughout the study.

The records of percentage apparent survival in the plot 1 cohort as well as data on these toads grouped into three size categories are given in Table 32. For the reasons already mentioned, the data for periods after March, 1953, were probably quite inaccurate. It was noticed that a large drop in survival percentage occurred during the first several periods. Disappearance was high during the September, 1951, and February, 1952, breeding seasons. The rate of loss between April, 1952, and March, 1953, averaged six toads per 100 for each three months.

With regard to survival in the three size groups it is seen in Table 32 that the lowest rate was for the smallest toads, and the largest toads also had a low survival value; on the average, the 15-17 mm. category had the highest rate of survival. The average rate of loss for the 14 and less, 15-17, and 18 mm. and greater head width groups through March, 1953, were 11.84, 7.69, and 9.70.

No significant difference in apparent survival existed between the sexes, for the percentage survival of 53 males was 62.3, while that for 68 females was 63.2 through March, 1953. The average disappearance

TABLE 32

A SUMMARY OF SURVIVAL AND DISAPPEARANCE RATES FOR A SELECTED COHORT FROM PLOT 1

Time Unit	Totals		14 mm. and Less		15 to 17 mm.		18 mm. and Greater	
	% Survival	Rate of Loss	% Survival	Rate of Loss	% Survival	Rate of Loss	% Survival	Rate of Loss
10-12/1951	79.7	25.4	75.0	25.0	79.2	20.8	82.1	17.9
1-3/1952	71.2	10.7	64.6	13.9	75.3	4.9	71.4	13.0
4-6	67.3	5.5	54.2	16.1	72.7	3.5	71.4	0.0
7-9	62.8	6.8	50.0	7.7	68.8	5.4	67.9	5.0
10-12	58.8	6.3	45.8	8.3	66.2	3.8	60.7	10.5
1-3/1953	55.6	5.6	45.8	0.0	61.0	7.8	53.6	11.8
4-6	40.5	27.1	31.3	31.8	45.5	25.5	42.9	20.0
7-8	27.5	32.3	22.9	26.7	27.3	40.0	35.7	16.7
Average through 3/53		10.0		11.8		7.7		9.7

rate through this period was 7.54 per 100 for males and 7.21 for females per three months.

The density effect on survival was studied in plot 3, for which the density conditions have already been discussed. Since the fences prevented emigration-immigration of toads, the disappearance in this plot more certainly reflects actual death than in the unfenced plots. The highest survival values were in the medium densities, while much lower values were shown in the high and low levels. Likewise the highest average rates of loss, 6.30 and 5.83, were found in the high and low levels, while the average, 4.11, in the medium populations was the lowest (Table 33). The rates were based on monthly time units. When the data are recorded in three-month periods for plot 3, the average disappearance rates were 24.7, 12.7, and 17.6 per 100 for the high, medium, and low density levels, respectively. The average rate for all data from plot 3 through March, 1953, was 15.14 whereas that for plot 1 was 10.03.

A seasonal variation in disappearance rate was observed in plot 3 and is recorded in Table 33. The highest average values from July, 1952, through August, 1953, were for July and August, 1952, and next highest for June through August, 1953; the three-month average values being respectively 10.3 and 9.9 losses per 100 toads per month. The average of monthly rates were 2.1, 0.4, and 4.8 for September-November, 1952; December-February, 1953; and March-May, respectively. For these periods, highest apparent survival rates occurred when the activity rate

TABLE 33

A SUMMARY OF SURVIVAL AND DISAPPEARANCE DATA FROM PLOT 3

Time Unit	High Density % Survival	High Density Rate of Loss	Medium Density % Survival	Medium Density Rate of Loss	Low Density % Survival	Low Density Rate of Loss	Totals % Survival	Totals Rate of Loss
1952								
7	92.5	7.5	92.5	7.5	75.0	25.0	89.0	11.0
8	77.5	16.2	87.5	5.4	75.0	0.0	81.0	9.0
9	70.0	9.7	82.5	5.7	75.0	0.0	76.0	6.2
10	70.0	0.0	82.5	0.0	75.0	0.0	76.0	0.0
11	70.0	0.0	80.0	3.0	75.0	0.0	75.0	1.3
12	67.5	0.0	80.0	0.0	75.0	0.0	74.0	1.3
1953								
1	67.5	0.0	80.0	0.0	75.0	0.0	74.0	0.0
2	67.5	0.0	77.5	3.1	75.0	0.0	73.0	1.4
3	65.0	3.6	75.0	3.2	75.0	0.0	71.0	2.7
4	57.5	11.5	72.5	3.3	65.0	13.3	65.0	8.5
5	52.5	8.7	70.0	3.5	60.0	7.7	61.0	0.0
6	45.0	14.3	62.5	10.7	55.0	8.3	54.0	11.5
7	37.5	16.7	55.0	12.0	40.0	27.3	45.0	16.7
8	37.5	0.0	55.0	0.0	40.0	0.0	45.0	0.0
9	20.0	46.7	50.0	9.1	35.0	12.5	35.0	22.2
10	20.0	0.0	42.5	15.0	35.0	0.0	32.0	8.6
11	20.0	0.0	35.0	17.7	25.0	28.6	27.0	15.6
Average Thru 8/53		6.3		4.1		5.8		15.1

was low during the winter months of 1952-1953. The rates of loss were high during the fall of 1953, but since this was the end of the study, many of the toads not recorded would probably have been caught if work had continued.

DISCUSSION

The common name of hermit or solitary spadefoot toad for _S. holbrooki_ probably arose from the many reports of its secretive underground life. A number of writers have shown interest in this seclusive behavior, and Wright (1932) summarizes the most important of these. The author gets the feeling, in reading some of these descriptions, that the early observers viewed with a mystical awe the sudden deluge of breeding toads after a heavy rainfall; especially when they were considered very rare between choruses.

Bragg (1944) refuted the idea that spadefoots seldom emerge from underground burrows. The present study substantiates and documents the conclusion of Bragg, since toads emerged from their burrows about 8 per cent of nights on a long-term basis and remained definitely underground at least 58 per cent of the time, and probably much more. The number of days spent underground without emergence varied from one to 104, and averaged a little under ten days. Time underground was definitely related to the seasons, the greater time underground being associated with the winter and summer months. A seasonal, cyclical type of hibernation-aestivation was not illustrated. The number of emergences from marked burrows during the spring and fall seasons was significantly greater than that of the other seasons; the increased emergence was especially apparent during March and April and September and October. This increase in these seasons may be associated with (1) a greater amount of optimal activity weather than occurs in winter or summer, or (2) a greater food supply available during the spring and fall than in the other seasons. Given suitable climates, the toads may be just as active one part of the year as during another. Seasonal factors likewise affected the distance of movement from a known burrow in feeding operations.

Phylogenetic interpretations based on habits (Bragg, 1945) and on morphology (Tanner, 1939) have indicated that the center of origin of Scaphiopodidae was near northern Mexico. It was concluded by these authors that this xeric form divided into two lines, one of which was the sub-genus Scaphiopus including S. holbrooki, that moved into mesic conditions of eastern North America. Bragg (ibid.) observed many habits, especially those related to breeding patterns, that indicated a phylogenetic link with forms having xeric adaptations. He further concluded that the sub-genus that moved east has adapted to a mesic environment in many respects. The toads inhabited forested areas in this study and the statistical analyses indicated that they are active during moist mild weather. Rainfall and atmospheric moisture are major factors influencing spadefoot activity; the highest coefficients of correlation were obtained between the number of toads observed per unit time and the amount of daily rainfall. Significant correlations were also obtained between activity and air moisture, but for other factors the data had to be lumped to show only a general association between weather and activity. Rainfall is more effective in this regard than atmospheric moisture, which, in turn, is more effective than temperature. These data substantiate for S. holbrooki a conclusion of Bragg (1944) for S. bombifrons that they tended to leave their burrows in greater numbers during and after rainfall than at drier periods, and that decreased activity during hot, dry summers was usual.

Concerning the time of nocturnal activity, Carr (1940) said: "On winter nights they emerge from their holes about eight-thirty or nine o'clock; even in an area thickly populated with spadefoots it is very unusual to find one in the open before eight p.m." Data from the present study indicated that a peak activity occurs immediately after sundown with a smaller peak just before sunrise; whereas the lowest activity occurs about two a.m. The time of these peaks varies with the time of sunrise and sunset. During nights when work was done at sunset, before dawn, or through the entire night, it was seen that the increase in toad activity coincided with quickening of other life. The calls and movements of birds were noted, but the nuisance of mosquitoes was most striking about the time toads became more active before dawn. Park (1940) discussed the general problem of nocturnal activity and cited literature illustrating that the community is divided into species characteristically nocturnal and those normally diurnal. Park, Barden, William s (1940) gave a figure representing activity of nocturnal and diurnal species at sunset, from which it was concluded that in a general way the total number of species active may be greater in the period of gradual overlap of day and night.

Spadefoot activity may be correlated with physical factors since temperature and vapor pressure deficit decrease relatively fast during the early evening and toads may well be stimulated by this. However, temperature and humidity vary only slightly, and for practical purposes none, in the hour before sunrise. This would seem to eliminate correlation with these factors for the pre-dawn increase in activity. No time was available for investigation of the numbers of insects and other possible prey of toads during the hours of the night. However, it is proposed in further studies to test the hypothesis that the change from darkness to light, and vice versa, brings a mixture of prey that are normally nocturnal or normally diurnal. Analogy to the interdigitation of species in the ecotone between two communities can be made, i.e., this is a kind of temporal ecotone.

The type of behavior, with regard to emergence from burrows, offered a serious drawback to the estimation of population densities by index methods. The data presented in this study indicate that there is a rotation of utilization of toad-habitat by segments of the total population. One part appeared night after night for awhile and then remained inactive for a second unit of time. One group, then, would appear for a time and feed and then remain underground for a considerably longer period. The active and inactive cohorts were not discrete, but rather the individuals composing the groups changed continuously; in fact, during optimal weather all or nearly all of the group may be emerging. It is possible that this behavior was related from a phylogenetic standpoint to the adaptations of desert forms to longer periods of sub-minimal environment and only brief intervals of optimal weather. This type of response might be necessary in a xeric community, but would not necessarily be detrimental in a mesic one.

If the situation described above is true, the index methods of population estimation proposed by Lincoln (1930), Hayne (1949 b), and Tanaka (1952), would not measure total toad population size, but rather estimate the segment that was active. In the study, the index methods did underestimate the population, especially during minimal toad weather, i.e., the summer periods. The explanation probably lies in the necessary assumption for the index methods that the marked animals mix at random with the total population. This was negated for Scaphiopus since there was evidence that toads did not emerge from their burrows at random with regard to time, and a larger population percentage appeared to be inactive during some seasons than at others.

Travels for the possible collection of food away from a known burrow were significantly greater in the ecotone than in the hammock habitat of plot 1. Likewise, and as a direct result of the greater movements, the home ranges of toads in the ecotone were greater than those in the hammock. The spatial distribution of capture sites in the hammock was random. However, in the ecotone while the burrows were spatially at random, there was good evidence that the toads aggregated in their feeding operations. This grouping from spatially random burrows would require greater movements than, for example, in the hammock where the burrows and capture sites were distributed alike. The areas of aggregation in the ecotone were in the open habitat near the junction with herbaceous growths of the prairie grasses. Another area of toad concentration was around large piles of leaves, twigs, and rotting plant materials. Probably the movements of toads were in response to optimal food conditions.

These data were analyzed using ten foot quadrats. When data from the same area were tested, using 25 foot sample plots, a contagious distribution was illustrated (Cole, 1946). In this case the toad distribution seemed to be correlated with the type of micro-habitat. Cole (ibid.) hypothesized that contagious distributions may be made up of intermingled random distributions of groups of different sizes. Data from the present study may substantiate this, since when the contagious distributions of the larger sample plots were restudied using smaller quadrats, random distributions were indicated in all except the ecotonal capture-site records.

The analysis of food habits by studying four collections of stomachs in each of the seasons produced results that do not differ greatly from those that Carr (1940) obtained from 100 stomachs collected on January 12, 1932. The percentage composition of total bulk was: Gastropoda, 2.3; Myriapoda, 25.6; Lepidoptera, 11.6; Orthoptera, 27.9; Arachnida, 9.3; Coleoptera, 18.6; vegetable, 2.3; unidentified and sand, 2.3. Bragg (1944) reported that he had no record of the Scaphiopus eating vertebrates, but he did have record of their eating spiders, flies, hymenoptera, moths, beetles, and bugs.

Smaller toads had a significant tendency to move greater distances than larger toads from known burrows in feeding. There is probably an obvious connection between this and the calculated higher rate of loss for small toads than for larger ones. The greater the distance a toad moves from his burrow, the greater the probable chance of capture. In addition to these hazards connected with distance the toad is likely to be less well orientated with regard to escape.

An examination of burrow and capture sites for toads living in the area, where the forest micro-habitat with little or no vegetation in the lower strata meets the prairie habitat with its densely vegetated cover, indicated that they almost always moved from their burrows to the more open habitat. Their holes were so situated that movement in one direction would have carried them into dense, low plant growth and in the other into open forest areas. The observed behavior may possibly reflect the phylogenetic connections this species holds with desert forms illustrating a similar functional response to prairie or open habitats through adaptation of preadaptation; or it may lack this type of evolutionary significance.

The variability in home range size was tremendous. The large variation produced parameters that made reaching statistically significant conclusions very difficult. Differences were shown, however, between range-size for toads having only one burrow as contrasted with those having more. Significant correlations were also shown between range-size and number of captures per individual.

Data suggested that spadefoot toads have several burrows within their home range that are occupied alternately. Nest movement within a home range was reported for mammals by Nicholson (1941), and for birds by Erickson (1938). This was the first record of burrow or home-site movement within a home range for amphibians, and also the first record of an alternating use of nest sites within a home range. In estimating home range size, one must consider not only the length of time involved in the study, but also the relationship of burrows or nests to the range. If a study was of such short duration that only wanderings around one of several burrows were recorded, the size of the true range would be considerably underestimated by the observer.

A statistical treatment of capture data was devised by Hayne (1949 a) to locate the geographic center of activity, that he used in a method of home range size estimation. Such a center of activity was calculated for the toad in this study, #3241, indicated by a + in Figure 14, to show its relationship with the biological center of activity, the burrow. If certain individuals had been chosen, i.e. #1305 in Figure 14, or #3040 or 1033 in Figure 12, the statistical center would have been further distant from the burrow. This adds evidence to Hayne's statement that the center of activity does not necessarily have any biological significance apart from being an average of capture points.

In a review of the literature on methods of range analysis, Hayne (ibid.) discussed one method where it was assumed that the greatest distance between points of capture constitutes the diameter of a circle, or major axis of an ellipse, which is the animal's home range. For this method then it is assumed that home range shape is that of an ellipse or a circle. Enumeration of home range shape frequencies for S. holbrooki illustrated that the majority were not circular or elliptical in outline, and the assumption of such a shape would not be correct. Data from the home range studies further substantiated Dice's (1952) conclusion that in many cases, the location of the burrow is not central to the home range.

The relationship between the concept of home range and territoriality needs consideration. Any animal consistantly occurring in a particular area might be said to have a home range. If other members of the same species, and more specifically members of the same sex, are excluded from the area, the concept of territoriality is illustrated. The difference in the concept used depends on the definition used by the observer for territoriality and his skill in observation.

Territoriality has been reported for many species of birds and mammals. One definition often used, especially for birds, is that territoriality involves the defense of a specific area either by physical contact and/or by threat display. No threat, combat, or any kind of aggressive display was observed in this study. If may be that only those species with more obtrusive behavior are known to conform to this definition while the phenomenon might actually exist in some species in which the defensive fighting or display is too subtle for the observer to discern.

Recently, one type of territoriality in breeding amphibians was shown by Martoff (1953), using statistical means to illustrate that breeding Rana clamitans maintained relative positions. Dice (op. cit.) uses a similar idea in stating that if individuals of the same sex have ranges that do not overlap, it is generally assumed that territoriality exists. In the study of Scaphiopus ranges, when only 90 per cent of captures for any given animal were utilized, the overlap was not great, and when the ranges were plotted separately for males and females, there was only slight overlap. In the most crowded part of the plot, the overlap was only slight when plotted for the 26 months, and overlap did not exist between individuals when small time units were used. According to this definition, the spadefoots exhibit a territorial behavior.

Another definition is as follows: "Territoriality includes homing or the defense of a given area, or both. Homing reactions are concerned with an animal's becoming so adjusted to a specific area that returns are made, perhaps to the precise spot, when activities or environmental accidents cause removal," given by Allee Emerson, Park and Schmidt (1949, p. 412). Under this definition Breder (1927) would have documented the existence of territoriality in amphibians. He reported that Rana clamitans returned considerable distances to its home area, and he recorded homing movements as great as one-quarter mile in Bufo fowleri. Likewise, territoriality in amphibians would again be substantiated since the homing reaction was shown for spadefoots; some individuals returned over long distances from breeding choruses to their original site of departure. Griffin (1953) gave a general discussion of various types of orientation and mechanisms employed in homing behavior, some of which might be useful in a needed study of spadefoot orientation in homing migrations.

The combination of low rates of dispersal, the homing behavior, and territoriality may be quite important in the evolution of this species. Reproduction takes place in localized temporary ponds to which toads from the immediate vicinity migrate. In general, each pond has a limited area of influence in the breeding migrations. Field evidence was not obtained for this idea, but it seems logical since toads would most likely move from home areas to the nearest chorus. One exception was observed, when a toad moved from the plot, passed a nearby pond, and joined a chorus one-quarter mile from the home area.

The territorial behavior tends to stabilize the population, and if the toad habitat were already occupied by individuals with established territories, new toads would be discouraged in immigration attempts. This behavior would reduce dispersal and mixture of the groups using different breeding ponds. Another isolating mechanism is the homing reaction that insures that a large proportion of toads leaving their home area and migrating to the pond would return to their home site. All seven of the plot 1 residents that were observed during breeding movements were later seen back in the plot.

Dispersal from one group to another occurs when some toads fail to return home from reproductive migrations. It also occurs when individuals move small, cumulative distances in one direction, taking them from one population to another. The dispersal of young in all directions from the breeding pond continues until the young have found suitable habitats. If there is available space for addition of new members to the group, it seems reasonable to suspect that the young would establish themselves in areas nearest the pond. They would continue to move from the pond area if there were no available niches or if the habitat were unfavorable.

Population movements were observed during only two breeding periods in this research. Little evidence was obtained for the ideas that follow; they are proposed more as pure speculation in areas needing intensive field research. It seems possible that spadefoots, in general, occur in small population units associated with spheres of influence of respective breeding ponds. Territoriality and homing help to stabilize and isolate these groups. Dispersal occurs when homing behavior fails, to a slight extent by normal non-breeding movements, and through long continued movements of young out of the immediate region of larval development. If these ideas are correct, the spadefoot population pattern serves as an example of a theoretical model proposed by Sewall Wright (1945), and discussed later by Allee (op. cit.). In what is now generally known as the Sewall Wright effect, Wright concludes that the type of population that would exhibit the most rapid rate of evolutionary change is a large one that is broken into a number of small populations that are interconnected by some dispersal and gene exchange.

By the end of the study, the density of plot 1 was reduced to one-third of that beginning in July, 1951. The study of survival values indicated that the percentage remaining under observation was in this same order of magnitude. This cut in number resulted from poor reproductive success in the 26 months during which observations were made. Under some conditions this lack of successful reproduction could have continued, and since mortality continues, the population would become quite small. As the number decreased, the toads around particular breeding sites might become more isolated, and the inter-connected "island" population model more pronounced. In such small "island" populations, the Sewall Wright effect would become more potent.

Population density in the ecotone was about double that in the hammock. The soils were wetter in the ecotone than in the hammock, and thus might provide more nearly optimal conditions. Probably the major factor was that in the ecotone there was a mixture of animal species characteristic of both the prairie and the hammock and the food supply would then be greater than in the hammock.

The explanation for three observed phenomena in this study may well be related to the greater food supply found in the tension zones or spatial or temporal ecotones. The observations are (1) that the density of the spatial ecotone was about double that of the homogeneous hammock habitat, (2) that the observable surface activity during the early evening and pre-dawn hours greatly exceeds that of the other nocturnal hours, and (3) that the number of emergences from marked burrows during the spring and fall seasons is significantly greater than that of the other seasons. Concerning the latter, Mrs. Olive Goin, in unpublished data, records a quickening of activity for cold-blooded vertebrates during these fall and spring seasons. Further research may illustrate that typically winter and normally summer active species may overlap in their activity and provide a greater food supply for carnivorous species.

During the first months of study the population density was high, and only about half of the toads were functionally adult. After 26 months of poor breeding success, the density was cut to one-third its original level, but the percentage of the population of reproductive age was very high. The age group distribution had changed during the study from one with a large percentage of young to one in which only about 22 per cent was less than two years old. This may be a type of self-regulating mechanism, whereby, as the density decreases, the percentage of functional adults increases.

Speaking of growth in the higher animals, Thompson (1948) said that "in all cases growth begins slowly; it attains maximum velocity somewhat early in its course, and afterward slows down towards a point where growth ceases altogether. But in cold-blooded animals, as fish or tortoises, the slowing down is greatly protracted, the size of the creature would seem never to reach, but only to approach asymptotically to a maximal limit." The growth curve illustrated for toads in this study did not follow the typical S shape, but rather began immediately with a very rapid rate of increase. The earlier unmeasured stages of newly emerged spadefoot growth may have illustrated the slow beginning rate. The measured rate decreased as growth continued, and the oldest individuals still had a slight but perceptible increment.

The dampening effect of overcrowded individuals on growth rate has been shown many times (Allee, 1951); the present study adds to the evidence for amphibians under natural situations. These data illustrated that there was an inverse relationship between increased density and a decreased growth. The difference between growth under the highest and lowest levels tested was statistically significant as it also was in several tests between the highest and medium density levels. In none of these tests between growth in the lowest and medium levels was a real difference found. The reason for the decreased growth probably lies in the lesser food supply per individual. Also, with a larger group there is more mutual stimulation, thus increasing the amount of activity and amount of energy expended for functions other than growth (Ludwig and Boost, 1939).

One big gap in the knowledge of Scaphiopus concerns its predators. The underground daylight existence and the nocturnal feeding operations reduce danger of capture as well as make it difficult to obtain predation data. Goin (1947) observed a hog-nosed snake (Heterodon simus) removing a toad from its burrow while Carr (1940) reported the predation of toads in breeding chorus by several species of gulls in the streets of Tarpon Springs, Florida. McAtee (1932) did not list Scaphiopus as preyed on by Nearctic birds. During breeding periods of April and August, 1953, a sizeable quantity of eggs failed to develop, and leeches (Hirudinea) were seen in the egg masses. McAtee (ibid.) said: "Leeches prey upon eggs and young amphibians and there are numerous insects which destroy tadpoles, such as the giant water bug, backswimmers, water scorpions, predaceous diving beetles and their larvae, and the nymphs of dragonflies." In the larval stages it is probable that a large number are killed by predators and many die when ponds go dry. Childs (1953) reported nearly 75 per cent loss of spadefoot tadpoles, possibly from predation by the Raccoon (Procyon lotor) after 19 days of larval development. Only 50 individuals survived from a beginning population of 200 larvae in this experiment. When the young toads emerge and disperse, until satisfactory habitat conditions are found, it is believed that a large loss occurs as a result of predation and unfavorable physical environment.

In this study, the precise relationship is unknown between disappearance and death rate. In the non-experimental field plot, death, dispersal, or the failure to observe resident toads combined together to produce an effect equal to the disappearance rate. Since habitats around the selected area of mortality study were searched for toads, the fraction of losses resulting from dispersal was considerably reduced. A number of toads originally recorded in the area under consideration were later observed in adjacent areas. The disappearance data through March, 1953, probably does not include many individuals that were living in the area but were not seen, since nearly a third of the total field hours of observation in this plot were made after March. This should have been sufficient field time to reduce greatly the number of resident toads that were present but not captured. It is believed that the rate of loss of toads in plot 1 through March, 1953 closely approaches the actual death rates.

The approximation of death rates by disappearance rates in plot 3 was even closer, since the fences prevented dispersal of the population. Although toads were examined when found outside enclosures, none was ever caught that had escaped from a pen. There was evidence during the latter part of the study that toads were immigrating into pen 3, but the reverse was not true. If loss data are restricted to those through August, 1953, so that ample observation hours followed, to record the presence of toads inactive during previous months, they would represent death rates quite accurately.

In these experimental areas it was shown that loss was lowest in the middle density and higher as the density either increased or decreased. The rate of disappearance of toads illustrated, then, both an inverse and a direct density-dependant relationship. This might be interpreted in the light of discussions by Allee (op. cit.) as an illustration under field conditions of the undercrowding effect on mortality. This possible conclusion is clouded by the fact that the density of plot 1 was lower than the lowest in the pens, yet it had a lower apparent death rate instead of higher, as would be expected. The average rate of loss for all toads in plot 3 is greater, 15.14, compared with 10.03 for plot 1. The greater death rates in the experimental plot may be partially explained by (1) as noted in the description of plot 3, the fences acted as an exceptionally good collector of organisms and the predators might have concentrated their efforts here, and thus at the same time taken more toads, or (2) the fact that the density of plot 3 was double that of plot 1, gave another example of the direct density-dependent mortality relationship. At any rate, direct comparisons between toad-loss in plot 1 and plot 3 were not conclusive because of the fences that collected the toads and other animals.

The micro-environmental conditions of the five fenced pens were as nearly the same as could be obtained and since pens with different initial population sizes were scattered at random in the area, the habitat factor could probably be dismissed. This may provide an unverified and experimentally unanalyzed example of relatively adverse effects on survival of both undercrowding and of overcrowding; however, conditions of this experiment make it doubtful that the undercrowding factor is responsible for the higher disappearance rate in the lowest experimental population density.

SUMMARY

A. The activity of S. holbrooki was studied statistically and the limits and variability of response to environmental factors were defined. An adaptation to mesic conditions was observed. It was shown that:

1) toads emerged from their burrows in the order of 29 nights annually, while the number of known consecutive days underground averaged 9.45, with a range from one to 104.

2) burrow emergence and nights of activity were associated with:

   (a) temperatures between 50 and 90°F.

   (b) weeks with rainfall greater than 0.1 inches.

   (c) relative humidities of 80 per cent and higher.

   (d) the months of March-May, and September-November.

   (e) warm-moist weather as contrasted to cold-dry; cold-moist against cold-dry; all moist versus all dry; and all warm contrasted to all cold types.

3) the rate of nocturnal activity expressed as number of toads observed per unit time:

   (a) was highest just after sundown and just before dawn, with least activity around two a.m. The peaks in activity were possibly related to periods of greatest food supply in a temporal tension zone.

   (b) was greatest in this study at 69°, with a decrease to the minimal and maximal activity temperatures of

50 and 84°F.

(c) illustrated no hibernation of spadefoots, in the seasonal, cyclical sense in the Gainesville region.

(d) was not significantly correlated (r. value) with relative humidity except in the restricted temperature range 54-64°F.

(e) was correlated at the 2 per cent level of significance with vapor pressure deficit.

(f) on the average increased within restricted temperature ranges as relative humidity increased and as vapor pressure deficit decreased.

(g) divided into categories of high and low was shown to be directly associated with certain categories of relative humidity and pressure deficit.

(h) was different under contrasted categories of high and low relative humidities and pressure deficit, as illustrated by t. tests for significance of difference in group means.

(i) was significantly correlated with amount of daily rainfall.

(j) was on the average significantly greater under frontal than all maritime, dry maritime, and wet polar types of weather. It was also greater for wet maritime than for dry maritime types.

4) the emergence of toads from burrows was not at random with

regard to time. Nights of activity for individuals tended to be concentrated in short periods of time with much longer times when no surface activity was apparent. Possibly, this behavior was evolved as an adaptation to desert, xeric conditions in the early evolution of the family.

B. The food of spadefoots as illustrated by stomach contents was mostly comprised by beetles, Orthoptera, ants, lepidopterous larvae, and spiders living on the forest floor.

C. The distance toads moved from a known burrow to feed averaged 3.66 feet and the modal class was two and less feet. The distance of feeding movements from a known burrow:

1) was not different for males and females.
2) was significantly greater for small toads than for those of larger sizes.
3) was greater on the average in the ecotone than in the hammock, which relationship may have resulted from climatic differences or also from difference in food distribution.
4) was greatest in the low density level in experimental areas and lowest in the high population levels. A real association was found in comparisons of low and middle and also in low and high density levels.
5) was associated with seasonal phenomena. Greater distance frequencies were strongly associated with spring and fall seasons.
6) was dependent on the vapor pressure deficit. Movements

were also associated with deficits in restricted temperatures from 65-76°, but not from 54-64 and 77-82°F.

7) was associated with temperature. From 0.06 to 0.119 and less than 0.019" pressure deficit there was no connection between temperature and distance. Movement was dependent on temperature in limited deficit ranges between 0.02 and 0.059 and greater than 0.12" Hg.

D. Spadefoot toads aggregate in certain major communities, especially in forests without considerable leaf detritus. There is a strong tendency towards aggregation within a non-homogeneous major habitat; the greater frequencies associated with sparse shrub vegetation. The location of burrows within an homogeneous habitat was at random and showed no aggregational trends. Records of capture sites in uniform hammock illustrated the same relationship, but in the ecotone there was evidence that although the burrows were spatially at random, the capture sites denoted a contagious distribution. Here the mechanism of aggregation was that of movement from burrows to optimal food capture locations, and with regard to the food supply the habitat was not uniform.

E. Observations on aspects of home range behavior included the following points:

1) the size of the home range was estimated using the "minimum home range" method proposed by Mohr (1947). The size of spadefoot home range based on individuals caught more than six times in plot 1

(a) averaged 108.4 sq. feet, extremes being 7.1 to 892 feet. If only 90 per cent of the captures, those nearest the center of the range, were plotted, the range mean was 67.7 with a variation from 2.6 to 356 sq. ft. Only 90 per cent captures were utilized in the following analyses.

(b) was greater on the average for females, 73.5, than for males, 60.8; the difference was not statistically significant.

(c) was greater, but not significantly, for ecotonal habitat toads, 70.3, than for those living in the hammock, 53.0.

(d) was not correlated with the length of time the home area was studied.

(e) was strongly associated with the number of captures of individuals.

(f) was significantly greater for those with more than one recorded burrow than the opposite.

2) records of 89 burrow shifts made by 39 individuals indicated that the average distance of movement was 10.8 feet and the average length of time these were used was 106 days with a range from 1 to 713. Thirty-one toads moved their burrow but never returned to former ones, while eight alternated their utilization of from two to five burrows. There was apparently equal utilization of these in their shift of home sites.

3) the assumption of a circular or elliptical home range for statistical purposes would be inaccurate for Scaphiopus in this study, since the majority illustrated a linear or rectilinear shaped range.

4) the ranges of members of the same sex did not overlap in the most populated hammock area, and in the heavier densities of the ecotone there was only very slight, if any overlap. Avoidance behavior was interpreted in the relationships between several toads in movements of their home range. These data led to the conclusion that territoriality was exhibited by these toads.

5) homing behavior, over extended round-trip distances, was observed in this study. Seven toads were caught in the home plot before breeding, at distances between the plot and breeding ponds as great as one-fourth mile, and then back at their point of departure later. Three females with eggs, were handled in the plot before breeding and then observed at the same site with no ovarian eggs later; which led to the conclusion that they had returned from a breeding pond. Trapping evidence during the August, 1953, reproduction also denoted the homing instinct.

6) it was shown that the micro-habitat influenced the direction of movement from the burrow. When it was located near the junction of dense shrub vegetation with open areas, the toads almost always moved towards the open habitat. This behavior

may be an adaptation inherited from more primitive desert and grassland forms; or it may only be a function behavior with no evolutionary significance.

7) observation of toad behavior in relation to the burrow indicated that they were spatially well orientated within the home range area.

F. The dispersal of the adult spadefoot population:

1) was shown by an analysis of influx of new toads and its influence on retake percentage to be directly connected with the occurrence of rainfall. The greatest population changes as illustrated by retake percentage took place during the four breeding seasons.

2) was found to be negligible during the summer 1953, with the exception of movements associated with the August, 1953, reproduction.

3) was examined by study of greatest distances between capture points for the whole study, seasonal, and monthly periods. This illustrated that by far the majority of dispersal records were of short distance, and those records of long movements generally covered a considerable length of time.

4) over longer distances was probably accomplished by several short movements in the same general direction.

G. Density estimation in plot 1 and/or plot 3:

1) was very inaccurate using the method of simply counting the number of individuals observed; the reason being that the

toads were not active on the ground surface enough to be observed in short field studies.

2) was accomplished by counting individuals seen in a census period and adding those handled before and after the period under consideration. This adjusted count produced quite good records for plot 3. In plot 1 it involved the assumption that the toads had not been absent from the area. These estimates were low for periods near the end of the study.

3) was accomplished using a rectilinear index method and a curvilinear one, and the results were compared. The difference between these two procedures was not great for this study, but if anything, the curvilinear approached the estimate made by adjusted count more closely.

4) using the index techniques was not too reliable since it was shown that the marked population did not mix equally with the total population as a result of the non-random activity-time relationship discussed above. To use these indices one had to assume that the marked toads do mix at random with the total. The failure of this assumption was apparently related to the underestimation of the population size using these methods.

5) using the curvilinear equation produced mark-and-release indices very close to one. This meant that the probability of observing marked toads equaled that of finding new animals.

The indices less than one denoted greater probability of capture for marked animals, and were reported mostly during the summer periods, where

(a) less dispersal movements decreased the chance of new animals being introduced.

(b) there were smaller numbers of active toads, that tended to emerge more times, thus increasing the chance of capture for marked animals.

(c) the smaller active population increased the chance for toad locations and habits to be learned by the observer.

The indices greater than one, where there was greater probability of capture for new animals, occurred, as during the spring, 1953, when breeding movements increased dispersal.

6) indicated that the density of toads in the ecotone was about double that of the hammock. The density in the natural situation was less than half that of the experimental areas.

7) illustrated that the lowest beginning population density of plot 3 was considerably greater than that of plot 1; the former being 625.9 and the latter between 400-500 toads per acre.

8) reflected the lack of effective reproduction during the study, since the density continuously decreased from the beginning to the end. This decrease during longer periods of low breeding success would cause very low populations.

H. During the course of this study, four breeding choruses were recorded, on September 18, 1951, February 15, 1952, April 7, and August 23, 1953, in conjunction with heavy rains of stationary frontal weather. There was evidence that breeding was connected with large amounts of rainfall, as Bragg (1945) reported.

I. The production of young toads in the 1951 reproduction was very small, none at all for 1952, slight (i.e., 6.7 per cent of total population) for April, 1953, and considerable for the August, 1953, period.

J. For the study of body growth, the head width was utilized since it was a more reliable and consistent measurement. The relationship between head width and interorbital span and total body length was expressed by rectilinear equations. Concerning development and growth of head width:

1) the age from metamorphosis was known only for a few toads produced in September, 1951, and April, 1953. Other data were extrapolated as described in the text.
2) it was pointed out that the rate of increase in body size continually declined as the individual grew older and larger.
3) definite physical set characteristics were observed at 15.36 and 15.70 mm. head width on the average for females and males. This size was attained, on the average, at 19 and 15 months respectively after leaving the pond.
4) significant sexual divergence in rate of growth was illustrated for all but the largest size groups, with the males growing at a faster rate and attaining a larger size.

5) field records of head width growth for 11 males and 11 females were presented.

6) analyses were made on the effect of time, beginning size, and density level in the experimental pens with initial population of known size.

7) the level of density was shown to hold an inversely proportional relationship with rate of growth. A significant difference was illustrated between growth in the highest and lowest densities. There seemed to be no real difference between growth in the lowest and middle levels. A statistically significant difference was denoted for growths between high and middle densities in the smallest and largest body size categories studied during the first six months.

8) a theoretical growth curve through eight years of life was extrapolated to express statistically the average rate of increase.

K. To examine the age of the population throughout the study, the frequency distributions of head width were plotted for males, females, and those of undetermined sex or juveniles. This led to the conclusion that the relative number of young decreased and the older group frequencies increased as a result of poor breeding success. In the first period, about half of the group was less than two years old, while in the summer of 1953, about 20 per cent were that old. Likewise, the per cent of toads with age estimated greater than six years was about 15 per cent at the beginning and 39 at the end of study. This population showed signs of aging.

L. Disappearance rate was studied in plot 1 and plot 3. Concerning loss of spadefoots:

1) no evidence of predation on adults was secured in this research and published records are few. Causes of death are predation from one species of hog nosed snake and several species of sea gulls, and possibly from fire.
2) the rate of loss seemed to be highest for toads beginning with head width 14 mm. and less, lowest for toads 15-17 mm. and high again for older toads with head width 18 mm. and greater.
3) in plot 1, there was some evidence that disappearance rate was higher during breeding periods in 1951 and 1952.
4) there was no significant difference in rates for males and females.
5) average rates of loss were lowest in middle densities, highest in the largest populations of plot 3, and also nearly as high in the lowest density. From this standpoint, it appeared that the middle density was optimum for survival with lower and higher density having lower values. This may be an illustration of undercrowded, overcrowded, and optimal population effects on mortality. However, the lowest density was considerably higher than that found in the natural situation that had a low rate of loss.

6) the average departure rate for plot 1 was 10.0 toads per 100 per three months and 15.14 toads per three months in plot 3. The higher rates of disappearance in the experimental area was probably related to the aggregation of animals by the fences, thus making better hunting grounds for predators. A wide variety of animals was observed along these fences. The density of the experimental area was about double that of plot 1, so the increased rate of loss of the former could also be a result of the higher population size.

7) there seemed to be a seasonal variation in losses with highest rates during June-August, and March-May, September-November, and December-February decreasing in that order. The winter periods of least activity rate exhibit the lowest losses. The explanation may be that the less activity results in less probability of capture by predator.

M. The percentage survival curve for <u>Scaphiopus</u> from egg to old age can be roughly inferred. There was some evidence that survival percentage drops suddenly and sharply during egg, larval stages, and through burrow establishment. The rate of survival then decreases only slowly with young terrestrial individuals having a lower rate of survival than those, say from 15-17 mm. head width. As the toad reaches ages where the head width is 18 mm. and greater, the survival values decrease again, possibly being associated with attainment of the physiological life span. This type of survival curve would possibly be described as a positive skew curve, as given by Allee, Emerson, Park, Park, and Schmidt (1949), for which good examples have been lacking.

LITERATURE CITED

Allee, W. C. 1951. Cooperation among animals. New York: Schuman. 233 pp.

Allee, W. C., A. E. Emerson, O. Park, T. Park, and Karl Schmidt. 1949. Principles of animal ecology. Philadelphia: W. B. Saunders. 837 pp.

Ball, S. R. 1936. The distribution and behavior of the spadefoot toad in Connecticut. Trans. Conn. Acad. of Arts and Sci. 32: 351-379.

Bragg, A. N. 1944. The spadefoot toads in Oklahoma with a summary of our knowledge of the group, I. Amer. Naturalist. 78: 517-533.

________ 1945. The spadefoot toads in Oklahoma with a summary of our knowledge of the group, II. Amer. Naturalist. 79: 52-72.

Breder, C. M., Jr. 1927. Frog tagging: A method of studying Anuran life habits. Zoologica. 9(3): 201-229.

Carpenter, C. R. 1952. Comparative ecology of the common garter snake (Thamnophis s. sauritus) and Butler's garter snake (T. butleri) in mixed populations. Ecol. Monographs. 22(4): 235-258.

Carr, Archie F. 1934. A key to the breeding songs of the Florida frogs. Fla. Naturalist. 1(2): 19-23.

________ 1940. A contribution to the herpetology of Florida. Univ. of Florida. Biol. Sci. Series. 3(1): 1-118.

Childs, H. E. 1953. A selection experiment in nature using albino and normal spadefoot toads. Bul. Ecol. Soc. America. 34(2): 48-49.

Chitty, D. and D. A. Kempson. 1949. Prebaiting small mammals and a new design of live trap. Ecol. 30: 536-542.

Cole, L. C. 1946. A theory for analyzing contagiously distributed populations. Ecol. 27(4): 329-341.

Cooke, C. Wythe. 1939. The scenery of Florida as interpreted by a geologist. Tallahassee: Fla. Geol. Surv. Bul. 17: 1-118.

________ 1945. Geology of Florida. Tallahassee: Fla. Geol. Surv. Bul. 29: 1-339.

Dice, L. R. 1952. Natural Communities. Ann Arbor: Univ. of Michigan Press. 547 pp.

Emlen, J. T., A. W. Stokes, and D. E. Davis. 1949. Methods for estimating populations of brown rats in urban habitats. Ecol. 30: 430-442.

Erickson, M. M. 1938. Territory, annual cycle, and numbers in a population of wren-tits (Chamaea fasciata). Univ. of California Publ. Zool. 42: 247-334.

Goin, Coleman J. 1947. A note on the food of Heterodon simus. Copeia 1947 (4): 275.

Griffin, Donald R. 1953. Sensory physiology and the orientation of animals. Amer. Scientist. 41(2): 209-244.

Hayne, Don. W. 1949 a. Calculation of size and home range. Jour. Mamm. 30(1): 1-18.

_______ 1949 b. Two methods for estimating population from trapping records. Jour. Mamm. 30(4): 399-411.

Holbrook, J. E. 1842. North American Herpetology, 2nd Ed. Vol. IV.

Kucera, C. L. 1954. Some relationships of evaporation rate, vapor pressure deficit, and low wind velocity. Ecol. 35(1): 71-75.

Laessle, Albert M. 1942. The plant communities of the Welaka area. Univ. of Florida Biol. Sci. Ser. 4(1): 1-143.

Lincoln, F. C. 1930. Calculating waterfowl abundance on the basis of banding returns. U. S. D. A. Circ. 118: 1-4.

Ludwig, W. and Charlotte Boost. 1939. Uber das Wachstum von Protisten Populationen und den allelokatalytischen Effekt. Archiv. Protistenkunde 92: 453-484.

Martoff, B. S. 1953. Territoriality in the green frog, Rana clamitans. Ecol. 34(1): 165-174.

McAtee, W. L. 1932. Effectiveness in nature of the so called protective adaptation in the animal kingdom, chiefly as illustrated by the food habits of Nearctic birds. Smithsonian Misc. Coll. 85(7): 1-201.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. Amer. Midl. Nat. 37: 223-249.

Nicholson, A. J. 1941. The homes and social habits of the woodmouse (Peromyscus leucopus noveborecensis) in southern Michigan. Amer. Midl. Nat. 25: 196-223.

Park, Orlando. 1940. Nocturnalism. The development of a problem. Ecol. Monog. 10(3): 486-536.

Park, Orlando, A. Barden, and E. Williams. 1940. Studies in nocturnal ecology, IX. Further analyses of activity of Panama rain forest animals. Ecol. 21 (2): 122-134.

Platt, R. B. and J. N. Wolf. 1950. General uses and methods of thermistors in temperature investigations, with special reference to a technique for high sensitivity contact temperature measurement. Plant Physiology. 25(3): 507-512.

Richmond, N. D. 1947. Life history of Scaphiopus h. holbrooki (Harlan). Part 1: Larval Development and behavior. Ecol. 28: 53-67.

Rogers, J. S. 1933. The ecological distribution of crane-flies of northern Florida. Ecol. Monog. 3(1): 1-74.

Simpson, George G. and Anna Roe. 1939. Quantitative zoology. New York: McGraw-Hill.

Snedecor, George W. 1946. Statistical methods. Ames, Iowa: Iowa State College Press. 485 pp.

Stickel, L. F. 1950. Populations and home range relationships of the box turtle, Terrapene C. carolina (Linnaeus). Ecol. Monog. 20(4): 352-378.

Tanaka, Ryo. 1951. Estimation of vole and mouse populations on Mt. Ishizuchi and on the uplands of southern Skikoku. Jour. Mamm. 32(4): 450-458.

_______. 1952. Theoretical justification of the mark-and-release index for small mammals. Kochi Women's College. 1: 38-47.

_______ and Seiyu Teramura. 1953. A population of the Japanese field vole infested with Tsutsugamuchi disease. Jour. Mamm. 34(3): 345-352.

Tanner, V. M. 1939. A study of the genus Scaphiopus. Great Basin Nat. 1(1): 3-26.

Thompson, D'arcy W. 1948. Growth and form. New York: MacMillan Company. 1116 pp.

Trowbridge, A. H. and M. S. Trowbridge. 1937. Notes on the cleavage rate of Scaphiopus bombifrons Cope with additional remarks on certain aspects of its life history. Amer. Nat. 71: 460-480.

Trowbridge, M. S. 1941. Studies on the normal development of Scaphiopus bombifrons Cope, I. The cleavage period. Trans. Amer. Micro. Soc. 60: 508-526.

________ 1942. Studies of the normal development of Scaphiopus bombifrons Cope, II. The later embryonic and larval periods. Trans. Amer. Micros. Soc. 61: 66-83.

Wright, A. H. 1931. Life histories of the frogs in Okefinokee Swamp, Ga. New York: The MacMillan Company. 497 pp.

Wright, Sewall. 1945. Tempo and mode in evolution. A critical review. Ecol. 26(4): 415-419.

BIOGRAPHICAL SKETCH

Paul Guy Pearson, born December 5, 1926, in Lake Worth, Florida, attended Lake Worth High School and after graduation in 1944, he served in the United States Naval Reserve until July of 1946 . He attended Palm Beach Junior College and graduated from the University of Florida with a Bachelor of Science degree with Honors in June, 1949. Graduate studies were begun in June, 1949, and he received a Master of Science degree in February, 1951. While at the University of Florida, he was employed as an undergraduate assistant and as a graduate assistant until August, 1952. Then he was employed as a Teaching Assistant until June, 1954.

He was awarded the Phi Sigma award for 1953 for outstanding graduate biological studies at the University of Florida. He holds membership in the American Society of Mammalogists, American Society of Ichthyologists and Herpetologists, Ecological Society of America, Phi Sigma, Phi Theta Kappa, Phi Kappa Phi, Phi Beta Kappa, and Sigma Xi.

This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of the committee. It was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

June 7, 1954

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