A STUDY OF THE LIFE HISTORY OF PSEUDACRIS BRACHYPHONA (COPE) IN WEST VIRGINIA WITH SPECIAL REFERENCE TO BEHAVIOR AND GROWTH OF MARKED INDIVIDUALS

Dissertation

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By

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INTRODUCTION

The Upland Chorus Frog, *Pseudacris brachyphona*, was described by Cope (1889) as *Chorophilus feriarum brachyphonus*, on the basis of a single specimen from "west Pennsylvania near the Kiskiminitas River." No further reference to it appeared in the literature until Walker (1932) established it as a valid species. Wright and Wright (1934) discuss the known range and give some notes on its life history. Netting (1933) lists it from four Pennsylvania counties while Green (1936, 1937 and 1938) discusses its distribution and breeding behavior in central West Virginia. Barbour and Walters (1941) present data on the relation of temperature to breeding activity in eastern Kentucky while Walker (1946) summarizes the known facts of its life history in a discussion of its occurrences in Ohio.

When I moved to Huntington, in the southwestern part of West Virginia, in 1938, I found the species to be one of the most abundant frogs in that area. The scarcity of available information on its life history and the opportunity to study the species under almost ideal conditions stimulated me to continue the studies that I had begun at my former residence. This dissertation embodies the results of this study that was begun at Elkins, West Virginia, in 1936 with the gathering of small amounts of data until 1942 when an intensive study was begun that was
carried through the spring of 1949 at Huntington, West Virginia.
THE PROBLEM

The literature of North American herpetology contains numerous references to the life histories of our toads and frogs. At first these observations were associated with the descriptions of new species but gradually they became identified as a part of a new phase of herpetology.

The first effort to bring together the findings of the many workers in this field was the contribution by Mary Dickerson entitled "The Frog Book" published in 1906. This was followed by a study of the Anura of Ithaca, New York, by A. H. Wright (1914). Dr. Wright's numerous contributions to the life histories of our Salientia also include a study of the frogs of the Okefenokee Swamp (1932) and his three editions of the Handbook of Frogs and Toads of the United States and Canada (1934, 1942 and 1949).

With the publication of the Third Edition of Wright's Handbook, many of the essential facts regarding our Salientia were recorded. Such data as the time and extent of the breeding season, the number of eggs laid and their description, the hatching time and the length of larval period, voice, type of breeding habitat and the description of the tadpole have been worked out for most of our species.

In addition to these contributions there has been
an increased emphasis on certain phases of salientian behavior. The studies of Bragg on the ecology and breeding behavior of Oklahoma Anura, Noble and Aronson's work on sex recognition and the releasing mechanism, Moore's investigations of speciation in Rana, Blair's studies on isolating mechanisms in Bufo, and Goin's work on the genetics of Eleutherodactylus have inaugurated a new approach to the life history studies of our frogs and toads.

It would appear from the literature that satisfactory strides were being made in rounding out the life histories of our frogs and toads. In 1946, Dr. Charles F. Walker raised several points in need of further investigation. In his Frogs and Toads of Ohio (p. 18) he states, "Much remains to be learned about the commonest species. For only a few species are any data available concerning the rate of growth and the length of time necessary to attain maturity. Many pertinent subjects remain almost entirely unexplored. To mention some of the more obvious, it may be pointed out that almost nothing is known as to the length of life of the individual, the extent of the mating activities of the individual male in the course of a season, the relative number of males and females and of different age groups in the populations."

It was with many of these unsolved problems in mind that the life history of Pseudacris brachyphona was selected as a problem for study. Many of the essential facts
of the animal's life history, that were known about other frogs, were unknown for this species. In addition to the investigation of these points, the study of its natural history provided an opportunity to investigate some of the unsolved problems that were suggested by Dr. Walker.

In undertaking a study of the life history of the Upland Chorus Frog, *Pseudacris brachyphona*, certain specific problems were organized as follows:

1. What characteristics in the development, transformation, and growth of the individual through maturity to death are distinctive?

In this phase of the study, the essential facts about larval development, hatching, length of larval period, size at transformation and size at sexual maturity, time required to attain sexual maturity, rate of growth and length of life are presented.

2. What are the relations of the members of a breeding population to one another and to their environment.

This phase of the study covers the effects of environmental factors upon the emergence of the adults from hibernation, the coming together of the sexes, sex recognition, amplexus, movement into and within the breeding area, and composition of the population in age groups.

3. What are the relations of the members of the colony to those of closely related species?
This phase of the study deals with those mechanisms which isolate this species from closely related forms, with which the Upland Chorus Frog is, nevertheless, able to breed and produce hybrids.
THE AREA

The study was conducted in a small valley lying one mile southeast of Huntington, West Virginia, in the southwestern portion of the state, along the Ohio River. The valley, formed by the first two of the foothills that rise beyond the old river terraces, is about one mile long. The mean elevation of the valley floor is 620 feet. The hills that rise above the valley reach an elevation of 900 feet with an average slope of 12 per cent. A narrow black-top road passes through the valley to communicate with U.S. Highway 52 at the lower (western) end. The valley for years sheltered only three frame houses but several modern dwellings have been erected recently in the lower end.

A small stream that flows almost due west through the valley provides a flood plain on which are located many small ponds that contain water until late spring or early summer. Both the north and the south slope of the valley have pools located on their terraces. From eight to ten of these pools within an area of one third square mile are utilized each year by breeding frogs. Figure 1 shows a map of the area traced from an enlarged contour map and on this the pools are shown. Figure 2 is a reproduction of an aerial photograph of the area.

The valley slopes are covered with open hardwood
forest. The white oak, Quercus alba, post oak, Q. stellata, black oak, Q. velutina, pignut hickory, Carya glabra, kingnut hickory, C. laciniosa, and shagbark hickory, C. ovata, predominate on the south-facing slope while beech, Fagus grandifolia, buckeye, Aesculus octandra, basswood, Tilia americana, tulip poplar, Liriodendron tulipifera, and sugar maple, Acer saccharum, predominate on the north-facing slope. Sycamore, Platanus occidentalis, black willow, Salix nigra, and blue beech, Carpinus caroliniana are found in the valley along the stream.

The understory of the south slope is composed principally of buckberry, Vaccinium stamineum, pussytoes, Antennaria plantaginifolia, dittany, Cunila origanoides, and coreopsis, Coreopsis major, while on the north slope are to be found nettle, Urtica sp., jewelweed, Impatiens biflora, trillium, Trillium grandiflorum, Solomon's Seal, Polygonatum biflorum, blue cohosh, Caulophyllum thalictroides, water leaf, Hydrophyllum macrophyllum, and black cohosh, Actea brachypoda.

The amphibian population is confined to Plethodon richmondi and P. g. glutinosus along the slopes with Eurycea b. bislineata and Eurycea l. longicauda, Desmognathus f. fuscus, Pseudotriton montanus diastictus and Gyrinophilus porphyriticus duryi along the stream in the valley. Breeding frogs offer little competition to the
Pseudacris population. *Hyla c. crucifer* is absent except for an occasional individual. *Hyla v. versicolor* breeds regularly in small numbers. *Bufo terrestris americanus* and *Bufo woodhousii fowleri* call in the valley but move further down in the valley to spawn as do *Rana p. pipiens*, and *Rana clamitans*. There are no *Triturus* nor *Ambystomas* in the valley.

Reptiles are uncommon except for an occasional specimen of *Natrix s. sipedon* that invades the breeding ponds. On the wooded slopes are sometimes found *Terrapene c. carolina*, *Eumecea fasciatus* and *Lampropeltis getulus nigra*.

Both the north and the south slopes of the valley have large outcroppings of coarse sandstone of the Morgantown series. Toward the tops of the hills these attain the dimensions of fair-sized cliffs of thirty feet or more in height. The floor of the valley is underlain with Birmingham shale and this also forms the bed of the stream toward the lower end of the valley. The deposits of this valley are all identified as belonging to the Conemaugh division of the Pennsylvanian.
MATERIALS AND METHODS

The area was visited nightly during the breeding season to observe the behavior of the frogs and to collect them for marking. On these trips standard equipment included notebooks, headlamp, collecting bags, dip net, sling psychrometer, thermometers, steel measuring tape, stop watch and jars for the eggs and tadpoles. During the course of each trip notes were made of weather conditions, temperature at several places in the pool, humidity and time of day at which the observations were made. Each pool in the area was numbered and collections and observations at the pools were kept separate. Calling males, egg clusters, mated pairs and unmated females were studied on each trip and indicated on a sketch of each pool. The activities of mated pairs, as well as unmated females, were sometimes observed for hours with notes being taken throughout the period of observation. On cloudy days the activity of the frogs at the pools were sometimes observed at a distance with 8x binoculars so as not to disturb the frogs.

On each visit to the pools an effort was made to collect every frog. The collection from each pool was kept in a separate bag. Moreover, each mated pair was kept apart from other mated, as well as unmated individuals. The frogs were then taken into the laboratory where the marked
frogs were checked and the unmarked frogs were marked. When the pools were visited the following evening, they were first cleared of as many of the new arrivals as possible before the frogs caught during the previous evening were released back into the pool.

In the laboratory the frogs were marked, sexed, measured, and notes taken on the dorsal pattern, the pool in which each frog was collected, the place in which each frog was to be released and the date of release. These data were recorded in 5" x 7" notebooks, a page being devoted to each frog. Figure 3 shows two specimen pages from a notebook. The frogs were not always released in the same pool from which they had been taken but were sometimes introduced into other pools, as well as between pools to study their movements.

The body length of each frog was measured with vernier calipers from tip of snout to tip of the urostyle. Measurements were read to the nearest tenth of a millimeter. In order to measure the living frogs as uniformly as possible, each frog was grasped by the hind legs and pulled across a moist glass plate. In this position the frog was relaxed and it was possible to secure a measurement with a minimum of error. Additional measurements made on preserved frogs may be defined as follows: head length is the distance from the posterior margin of the tympanum to the tip of the snout; head width is the
greatest width measured at the level of the articulation of the upper and lower jaw; hind leg is the longest distance from the inner junction of the hind leg with the body to the tip of the fourth toe, with leg extended. Measurements of eggs and small larvae were made with an ocular micrometer set in a binocular dissecting scope. Tadpoles were measured from tip of snout to the posterior margin of the hind limb bud for body length and from tip of snout to tip of tail for total length. Volumes of tadpoles and eggs were obtained by measuring the displacement of water.

A method of marking that would last for more than one season and still be suitable to such a small frog had to be devised. The method of fastening a tag to the waist of the frog, as suggested by Breder, Breder and Redmond (1927) was not considered suitable because of its temporary nature. The jaw tag, as used by Raney (1940) was not considered advisable on such a small frog. Earlier studies by Hamilton (1934) and George (1940) had shown that the toe-clipping method was useful in marking frogs for future recognition. Since the foot of Pseudacris was different from that of Bufo or Rana, it required different treatment, so a new system was devised in which a large number of toes could be clipped in many combinations.

The toes of one foot were removed singly or in combinations as 2, 3, 4, 2-3, 2-4, etc. By marking the
other foot in the same manner, twenty-two frogs were marked. The next series began with that of each of the eleven combinations of the right foot with all eleven combinations of the left foot. For example, eleven combinations of the left foot were clipped with the second toe of the right, another set of the left foot with the third of the right and so on. This gave a total of 143 marked frogs. By excising the second, third or fourth digit of the forefoot with the combinations of the hind feet, 858 frogs were marked. By using combinations involving two fingers with the above, it was possible to mark several thousand frogs. The present combinations result in the maximum loss of five digits and these to only a few frogs (seventy-two out of 509 marked in 1945 and 1946 or 14 per cent of those marked). If frogs with three or more digits excised were handicapped, we would expect fewer frogs with those toes clipped to show up in the returns. Of the frogs marked in 1945 and 1946, 85 per cent had three or more toes clipped. When frogs of these two year classes were recovered in 1946 and 1947, it was found that 86 per cent of them had three or more toes clipped. Observations on toe-clipped and non-mutilated frogs in the laboratory, as well as in the field, indicated that the injury did not hinder their jumping or swimming activity.

The toes were clipped by holding the frog on the
stage of a dissecting microscope with a lamp under the stage. It was possible to see the tips of cartilage between the joints and so remove the digit with a sharp scalpel without any injury to the cartilage. Figure 4 shows the technique employed in marking the frogs while Figures 5 to 8 show frogs with the toes clipped. A study of the skeletons of toe-clipped frogs stained with alizarin revealed no regeneration when the toes had been severed at the joint. Occasionally a toe that had been clipped would develop a bulbous expansion at the tip as though the injured tissue had been stimulated to rapid growth.

Although field work on this species had been carried on since 1936, the toe clipping, and certain other methods of study were not begun until the spring of 1945. The entire season of 1946 from March 15 to June 15 was devoted to the study in the field with the time divided between Huntington, West Virginia, and an area in Hocking County, Ohio, where Pseudacris brachyphona occurred with Pseudacris nigrita triseriata. Since then the field work has been carried on throughout the year at Huntington, with most of the work being done on week ends except during the frog breeding season when an effort was made to get into the field each night.
DESCRIPTION OF PSEUDACRIS BRACHYPHONA

**Pseudacris brachyphona** agrees with other members of its genus in its small size (average length less than 40 mm), toes webbed only at the base, fourth toe of hind foot extremely long, toe disks not conspicuously wider than the toes, and the skin of the belly finely pebbled or granular.

It differs from other members of its genus in its exact size, dorsal pattern, and the relation of hind leg to body length. It is one of the largest of its genus, attaining a length of 42 mm. in the female. The body lengths of 800 adult males ranged from 23.5 to 35.0 mm. with a mean of 27.14, while the body lengths of 200 females ranged from 29.6 to 43 mm. with a mean of 34.9 mm. Figure 9 shows the measurements of these 800 males and 200 females from the population under observation at Huntington, based on the percentage of each size group in the population. The heel of the hind legs, when extended forward along the sides, reaches a point anterior to the eye in most specimens. The head is broad and the snout blunt.

The dorsal coloration is of various shades of brown, varying from a light tan or cream color to a dark grayish or greenish brown. A dark stripe extends from the nostril through the eye and caudal along the side of the body.
There is a prominent triangle between the eyes. The upper surface of the limbs is colored like the back, though marked with darker blotches. The belly is white or cream color with a trace of yellow in the groin.

The pattern of the back is variable but distinctive. It usually consists of a pair of broad, dark stripes that curve inward toward the midline. In about 40 per cent of the specimens studied these two stripes meet in the midline to form a crude "H"-shaped design. Occasionally the dorsal pattern is broken into many small irregular spots while a few specimens were collected in which the dorsal pattern consisted of three parallel stripes as in Pseudacris nigrita triseriata. Specimens with this latter type of marking have been noted in populations from Hocking county, Ohio, where P. n. triseriata is found, as well as Huntington, West Virginia, where the latter species does not occur.

The design of the dorsal pattern is a permanent feature, and individuals were identified and distinguished from one another from year to year by slight differences in this pattern. At the time each frog was marked, a sketch was made of the dorsal pattern with any peculiarities being noted. When a recovered frog was identified by its toe formula, the design of the back was noted and found to conform to the original design even in frogs that had been marked four or five years before. The dorsal pattern is
apparent at the time of transformation.

The dorsal coloration of the female during the breeding season is usually a rich brown with a reddish cast while that of the male is more variable and lacks the reddish tones. The vocal sac of the males, which is of the sub-gular type, is dusky or greenish brown while the throat of the female is white or cream colored and this color corresponds with that of her entire ventral surface. Even in sub-adult males, before the vocal sac takes on any pigment, the wrinkled skin of the throat is distinctive. Small brown spots are frequent on the skin of the female's belly. Although the dorsal pattern appears at transformation no relation between the pattern types and the sexes has been found.
Pseudacris brachyphona ranges from western Pennsylvania southward through Maryland, Virginia, southeastern Ohio, Kentucky, West Virginia and Tennessee to central Alabama. Figure 10 shows its distribution as plotted from the records of specimens examined in the University of Michigan Museum of Zoology, the Carnegie Museum and the West Virginia Biological Survey. All of these localities fall within what is known as the Appalachian Plateau, an area to which this species appears to be confined.

Throughout the northern part of its range, it is the dominant species of its genus, being replaced in dominance to the east by a form of uncertain status known as Pseudacris nigrita feriarum and to the west by the wide-ranging Pseudacris nigrita triseriata. To the south it is replaced by Pseudacris nigrita nigrita.
HABITAT AND GENERAL BEHAVIOR

*Pseudacris brachyphona* is typically a woodland frog; it may be found in woodlands during late spring and throughout the summer and fall. In this habitat it frequents shady ravines and wooded slopes where it is seldom observed because of its somber colors, its small size and its inability to climb above the forest floor. Wright and Wright (1949) list the habitat as, "springy hillsides, grassy pools, ditches, sources and along upper courses of upland rivulets - more hilly than lowland habitats." Netting (1933b) writes of finding "specimens wandering about on wooded mountain slopes in Pocahontas county, West Virginia." Walker (1946) states that, "Scattered individuals may be encountered during the summer months on wooded slopes and hilltops, and a few have been found in marshy openings below springs and along brooks, seldom far removed from forest cover."

On land, *P. brachyphona* is an active, agile species that moves within and over the forest litter. Occasionally a specimen will be found a foot or so above the ground in vegetation. Their inability to climb is offset by their agility in leaping, but their presence off the ground is more accidental than habitual. On one occasion several were found calling from a bush into which they had leaped from a bank above.
Various investigators have endeavored to correlate weather conditions with the emergence from hibernation and stimulus to breeding among the amphibia. Blanchard (1930) demonstrated that the Spotted Salamander, *Ambystoma maculatum*, arrives at the breeding ponds on the first night on which there is rain after the winter frost disappears. Wright (1914) indicated that maximum temperatures for several days prior to emergence play a part in the emergence of *Hyla c. crucifer*, as well as other species of frogs, in a study at Ithaca, New York, Savage (1935) demonstrated that the mean spawn date of *Rana t. temporaria* in England was influenced by the weather of a long period preceeding it. Rain was most important, but temperature played a part in their breeding activity according to this investigator. Numerous other papers point to the influence of rainfall or milder weather as the stimulus for emergence but fail to offer any substantial data to support their contention.

*Pseudacris brachyphona* emerges from hibernation during late February or early March. Table I lists the earliest date for its appearance at Huntington for ten seasons as extending from February 22 to March 23. This range of dates over a period of a month indicates that some external factor may bear some influence upon their emergence. Consequently the factors of temperature and
rainfall were analyzed to determine their relation to emergence.

Table II shows the amount of rainfall in relation to their initial appearance. In only two instances out of the ten, rain occurred within a twenty-four hour period before their emergence. In three of the years no rain fell within a forty-eight hour period. From these data the conclusion can be drawn that immediate rainfall is not necessary for their appearance since their emergence was not always accompanied by rainfall. Bragg (1946) points out that those frogs which are limited to woodland, breed within a definite season and may be influenced by rainfall but not controlled by it.

The temperature column under Table II indicates that the lowest maximum temperatures for a forty-eight hour period prior to their emergence was 54° while minimum temperatures ranged from 29° to 53°. No correlation could be found between these temperatures and emergence. From this it is evident that maximum and minimum temperatures for the period immediately before their emergence had no influence on them. Since P. brachyphona is a land hibernator it is doubtful if the temperature a day or two prior to emergence would influence their activity.

An extended period during which the temperature might be above or below normal might influence their emergence. The data were examined and it was discovered
that in those years that were characterized by an early emergence the temperature for a month or more prior to their emergence had been above normal. Figure 11 shows the dates of emergence plotted against the deviation in rainfall and temperature above and below the norm for the years of their emergence. In every instance there is a close correlation between the temperature and the frog's emergence. In those years when the emergence was early, i.e., February, the temperature for the previous thirty days ranged from 11° to 7.8° above the norm for that period. In those years when the emergence was late, i.e., 1940, 1941, 1943, 1946 and 1947 the temperature ranged from 2.5 below normal to normal. In three of the years, 1944, 1948 and 1949, the rainfall curve shows no relation to their emergence. This supports an earlier contention that rainfall is not necessarily concerned with their emergence. The data do, however, support the conclusion that the temperature over an extended period prior to emergence affects the activity of the frogs.
BREEDING BEHAVIOR

The breeding season in *Pseudacris brachyphona* extends over a period of several months. These observations support the statement by Noble and Noble (1923) that members of this genus are "protracted breeders." The extreme dates for which data are available are February 22, 1949, and June 29, 1939, at Huntington, West Virginia. The maximum length of a breeding season was 121 days (1939). At higher elevations the season is later in getting underway and consequently later in closing. At Camp Woodbine, Nicholas County, West Virginia (elevation 2000 feet), the season has been recorded from April 1 to July 2 (Green 1938). Viosca (1938) records the frogs in voice in Alabama on January 21 and 22. Evidence of breeding activity was based upon pairs in amplexus and the presence of freshly laid eggs in the pools. Vocal activity is not in itself an evidence of breeding activity. Vocally active males have been recorded for every month in the year at Huntington.

The date of their emergence and movement toward the breeding pools coincides with the date on which they begin to call. In this respect they differ from many species of frogs that emerge from hibernation weeks before exhibiting any vocal activity. A pool which may display no signs of amphibian activity on a night in early March may contain dozens of calling males a few hours later with others joining the chorus in a mass movement from the hillsides.
The number of males builds up rapidly at the pools at the beginning of the season. Late emerging individuals supplement this breeding population and balance the numbers lost by movement to other pools or those leaving the area. Figure 12 shows the number of males and females collected in the study area during a typical season such as 1947. The figure indicates that the breeding season may be divided into three phases. The first period, or period of maximum activity, starts with the first night of the breeding season, rapidly builds up to a peak in numbers of frogs and remains relatively stable throughout the length of the period. The numbers of frogs fluctuate little during this period. There are some new additions and occasional departures. Females arrive at the ponds, mate and depart. Throughout this period the volume of the chorus remains about the same. The males call every night (weather conditions permitting), as well as throughout the day when the sky is overcast. During the day the males may be found hiding under the debris around the margin of the pool or in the water near the edge. The first period covers about three weeks.

The first period merges gradually into the second phase which is characterized by a decline in activity. During this period the males call less frequently. The intervals between choruses lengthen. Females are not common at the pools during this stage. The period of decline
comes to an end when the males are no longer regularly found at the breeding pools.

The third period, or the period of sporadic breeding, now begins. Small numbers of frogs may remain near the pools to call after a shower but only a heavy downpour or a prolonged rain will bring back large numbers of males and some females to breed. This period finds the pools with shrinking water levels and with a heavy growth of vegetation. The frogs' visits become less frequent until late June when most of them have left the vicinity and retired to the wooded hillsides. There, under the low vegetation, they will be found during the summer foraging for food.

The breeding season of Pseudacris brachyphona closely parallels that of other members of the genus within areas where their ranges overlap. In southeastern Ohio, where the Upland Chorus Frog occurs with Pseudacris nigrita triseriata, it was found that it emerges later in the season, deposits its eggs later, and leaves the area later than does the other species. Results of the study in this area as reported by Walker (op. cit.) are shown below:

<table>
<thead>
<tr>
<th></th>
<th>P. n. triseriata</th>
<th>P. brachyphona</th>
</tr>
</thead>
<tbody>
<tr>
<td>First emergence</td>
<td>Feb. 20</td>
<td>March 10</td>
</tr>
<tr>
<td>First eggs</td>
<td>Feb. 21</td>
<td>March 18</td>
</tr>
<tr>
<td>First transformation</td>
<td>May 23</td>
<td>June 17</td>
</tr>
<tr>
<td>Latest chorus</td>
<td>Early May</td>
<td>June</td>
</tr>
</tbody>
</table>
In 1946, Pseudacris n. triseriata was at the height of its breeding season when observations were begun at the Ohio locality. Large numbers of egg masses were seen and many pairs in amplexus were observed. Although Upland Chorus Frogs were calling over the area no eggs were found, nor were any seen until April 4 and these appeared to have been freshly laid. The Pseudacris n. triseriata chorus continued until April 14, after which an occasional male called intermittently. Choruses of the Upland Chorus frog were heard over the area until May 24, and occasional males were heard calling after that date.

A period of maximum breeding activity was also found in the case of Pseudacris n. triseriata. In this species the breeding activity reached an even greater intensity with large choruses throughout the hottest part of the sunny days. After the peak of breeding activity was reached, the activity declined rapidly and the frogs deserted the breeding area much earlier than did P. brachyphona.

Breeding Site

During the breeding season the frogs select small, quiet bodies of water not far removed from their woodland habitat. Table III gives data on the pools utilized in the study area at Huntington, West Virginia. These are usually woodland pools and roadside ditches. The frogs
avoid running water although they have been found breeding in the current of a swollen roadside drain. Among the situations where calling males and pairs in amplexus have been taken are in shallow swamps, backwater of a flooded stream, water-filled furrows of a plowed field, water-filled tracks of a car wheel, cow tracks, a rock garden pool, basement excavation, pool formed at the base of an uprooted tree, water-filled depressions around rotted stumps, pool at the base of a cliff, seepage along the top of a cliff, ditches along railroad tracks, blasted depressions in a rock quarry and seepage below a hillside spring. Figures 13 and 14 show two typical P. brachyphona pools (Pools 2 and 4).

All of these habitats were within three hundred yards of a woodland area, and most of them were much closer than that. The breeding pools contained quiet, shallow water. In many of the pools the water was muddy. Leaves and other remains of plant material were usually present, although there were some instances where eggs were deposited in pools that were devoid of plant material. Water depths ranged from three inches to three feet with pools less than twelve inches in depth being more common and consequently more frequently selected.

Other amphibians utilize these pools for breeding at the same time. Those species observed breeding at the same time and in the same pools as Pseudacris brachyphona
were *Hyla c. crucifer*, *Hyla v. versicolor* and *Bufo terrestris americanus*. Walker (*op. cit.*) lists eight species of amphibians whose eggs have been found in pools where Upland Chorus frogs were laying. There are a few isolated instances where *P. brachyphona* and *P. n. triseriata* were observed breeding in the same pool.

In those areas where both species occur the ecological segregation is usually well defined. In southeastern Ohio, the two species seek out their separately favored niches, the Swamp Chorus frog selecting the wide valleys and the Upland Chorus frog the hillsides of the narrower ravines. Within these habitats the first species utilizes swamps that are exposed and filled with clumps of vegetation while the second is more partial to roadside ditches and shaded woodland pools.

On Droop Mountain, Pocahontas County, West Virginia, where *P. brachyphona* occurs with *P. nigrita feriarum*, the latter utilized the swampy areas of an open meadow while the former was found in pools and ditches along a woodland path. In no instance were the two species found breeding in the same pools although they were in the area at the same time.

The Upland Chorus frogs are most easily collected during the breeding season. At that time the males congregate in large numbers at the pools and call vigorously from exposed situations. During the height of a chorus
they remain oblivious to any disturbance and it is easy to walk among them and collect them under the beam of a headlamp. During the day they are secretive but may be found under vegetation and debris around the edge of the pond.

In contrast to the active, vociferous males that frequent the shallow water along the margin of the pool, the females remain quietly under water in the deeper parts of the pool until ready for mating. The females enter the water, usually before midnight, where they remain until the eggs have passed down the oviducts to accumulate in the expanded uterus that empties into the cloaca. When this condition is attained the female leaves the deeper region of the pool, where she may rest unchallenged, to seek out a male for mating. Females were observed to approach the pond, jump into the water and swim to the middle of the pool where they remained submerged, supporting themselves on some vegetation, until ready for amplexus. Dissection of females collected immediately after amplexus were compared with dissection of those taken upon entering the pool and the observations made supplied the basis for this view.

Females arrive at the pools at approximately the same time the males do. Barbour and Walters (op. cit) state that, "apparently the males preceeded the females to the ponds by about eight days." Observations within
the study area fail to support this statement. Table I shows that in those years for which records of females are available, in every instance, females appeared in the pools on the same night that the males started calling. Since the females are inconspicuous at the first of the season, and usually enter the water late at night or early in the morning, and may not mate the first night, it is conceivable that they might have been overlooked by Barbour and Walters. The same table referred to above shows that although females appeared at the pools on the same night as the males, eggs were not laid from one to eleven days after the female's first appearance.

Voice

Vocal expression in *Pseudacris brachyphona* is confined to the male. This is the situation that prevails in all the known hylids (Noble and Noble (op. cit.). The male's distinctive sound, uttered to inform females that he is ready to breed, and referred to as his "call," is one of the most characteristic features of the breeding season. It has been described variously as follows: "a rasping, rather drawn-out monosyllable, similar to that of the Striped Chorus Frog, but it is uttered more rapidly, has a higher pitch and a more nasal quality" (Walker (op. cit.;) "an ungreased wagon wheel complaining at each revolution" (Netting, 1946); and a "qurack" (Viosca (op. cit.).
The call consists of a series of "icks" which are uttered rapidly as one drawn-out rasping sound that rises from a lower to a higher pitch. These notes are uttered at the rate of about forty to seventy times a minute, varying with changes of air temperature and other factors. At times the frogs will call so slowly at a low temperature that it is possible to distinguish the individual notes.

The call possesses a unique quality that distinguishes it from any other frog. It is similar to that of _P. n. triseriata_ and _P. n. feriarum_ except that it is uttered more rapidly and lacks the metallic "clicks" of these species. Even when temperature conditions are such that _P. brachyphona_ is uttering its call slowly or the other species are calling rapidly there is a distinctive quality in the pitch and tone so that they can be distinguished.

The frogs begin calling shortly after emergence from hibernation as they work their way downhill toward the breeding pools. Male frogs were observed at distances of twenty to sixty feet above the pools and were watched as they moved downhill into the pools. Noble (1931) states that the voice of the Salientian males serves to orient other males toward the pools. Choruses could be built up in pools from which no males called merely by introducing ten to fifteen males into the pool. This was discovered by marking the males, and by collecting marked frogs from the pool on successive nights.
Attempts to find a correlation between the rate of call and environmental conditions were not too successful. Harper (1937) found a close correlation between the rate of call and the air temperature in *Pseudacris ornata*. Bragg (1942), working with *Pseudacris streckeri*, concluded that, "higher temperatures of either water or air might stimulate a higher rate of calling but there are other unknown factors which complicate matters."

Since the frog usually calls with the body partly submerged, both air and water temperatures were studied in relation to the frog's vocal activity. Table IV shows the relation of these two factors to the volume of vocal activity.

High temperatures of water and air are conducive to greater vocal activity, i.e., there are many frogs then calling, while lowering temperatures retard calling, i.e., there are fewer frogs calling at low temperatures. On March 21, with the air temperature remaining at 34° no frogs called in a pool with a water temperature of 44°, while a few called in another pool where the water temperature was 48°. On the other hand a water temperature of 48° and an air temperature of 57° produced a large chorus. From these data it is evident that low air temperatures (34° to 37° F.) check the calling. Since a high air temperature is usually correlated with a high water temperature in the shallow water of the pools where
the males call, high water or air temperatures bring about widespread vocal activity.

A sudden change in air temperature may affect calling, as on March 13 when the temperature dropped from 56° to 44° within an hour, and the calling dropped during this period from a large chorus to the calls of a few isolated individuals.

In addition to the volume of the chorus, the rate of call is also influenced by the temperature. Figure 15 shows the rate of call plotted against air and water temperatures. In both instances the rate of call increases rapidly as the temperature rises. At higher temperatures the rate of call bears a closer relation to the water temperature since individuals call as rapidly in water at 60° as they do when the air temperature is 65°. Since the average rate of call is derived from a number of calls that showed a wide variation, it is concluded that other factors affect the rate of call besides the air and water temperatures. Among these could be cited individual differences which may be determined by age, size, and physiological condition.

The individuals of a colony may start out calling slowly and increase their rate of call as the chorus gains volume. Individuals may likewise slow down and vary their rate of call from that of the rest of the chorus. For this reason it is believed that the frog's rate of call is
influenced by his physiological condition, as well as by the external conditions of his environment.

The lowest air temperature at which the frogs were observed to call was 36° F., while the lowest water temperature was also 36° F. The maximum air temperature was 67° while the maximum water temperature was 60°.

The chorus usually begins with a few scattered individuals starting out slowly; others join in and the chorus grows until it is in full swing. It may stop abruptly, but it usually tapers off as a few tardy individuals terminate the chorus. In the late phase of the breeding season, when the chorus is short and very rapid, it starts with an explosive eruption and ceases as suddenly as it starts.

Choruses have been observed to start with the passing of an automobile along the highway, the discharge of a shotgun, the tapping of pebbles together and the call of an isolated frog in the collecting bag.

Males also utter a single sound that varies in pitch from a low gutteral note to a high pitched squeak. This is frequently given in the collecting bag or when securing a calling station during the excitement of a large chorus.

Sex Recognition

The bringing of the sexes together in order to accomplish amplexus, and ultimately the fertilization of the eggs, involves a chain of events that varies in
different members of the Salientia. Banta (1914) showed that in the case of Wood Frogs, _Rana sylvatica sylvatica_, the males clasped any kind of moving objects but retained the mating grip only on female Wood Frogs. Noble and Ferris (1929) demonstrated that the great girth of the female Wood Frog enabled the male to retain his hold on her plumper body. Cummins (1920) proved that sight played no part in sex recognition in the Wood Frog. Miller (1909) found that in toads, _Bufo terrestris americanus_, "males cannot distinguish at sight males from females."

Prior to amplexus the male Upland Chorus frog calls from a variety of situations. Almost any available object in or close to the breeding pool may serve as a support. Occasionally, males were observed calling with legs outstretched in the water but the most frequent postures were the squatting position at the edge of the pool or the hanging position while balancing themselves partially submerged on some support with their forelegs.

Males were observed calling from the same spot throughout an entire night and marked frogs were often observed using the same station night after night. This was particularly true when only one or two frogs called from an isolated area. While the frogs are in chorus, there is a minimum of movement among the calling frogs. Occasionally one member of the chorus shifts position to a different station or one swims across a small area to take up his
station on the opposite side of the pool.

During the excitement of a large chorus, the erratic movements of some individuals, together with the arrival of other males in the chorus, bring some males in contact with other males. Under these conditions clasping of males by males was observed. Clasped males struggle violently and secure their release. Calling males that are clasped by other males are released because of the difficulty of holding to the bodies that alternately inflate and deflate. In one ditch a dead male, its body swollen by decomposition, was observed to be clasped by the same male on two successive nights.

The stimulus to retain a hold on the female must be provided by one of two conditions or both: the quiet, receptive condition of the female or/and the differential in girth between male and female. A female was seldom observed in the region of a chorus unless she was mated at the time or shortly thereafter. Her presence in an unmated condition in the vicinity of a male in chorus indicated her readiness for mating. The stimulus to clasp the female had to be provoked by either the male or female and since males were seldom clasped it appeared that the female must initiate this reflex. Subsequent observations supported this conclusion.

The males appeared to be unaware of the female's presence until the proper releaser was employed. The
following excerpts from field notes taken March 30, 1945, indicate this: "A swimming female came in contact with a swimming male at the edge of the pond. He supported himself by holding to her with his forelegs but made no effort to clasp her." Again on March 15, 1945: "I saw another female approach a male that was calling from a clump of grass. As he called he moved around and in his movements touched her. He seemed unaware of her presence. She swam away." And again on March 23, 1946: "she is near enough to touch him, in fact her snout is touching his left arm. The female turns and swims away from the male that now starts to call. He had made no attempt to clasp her."

The stimulus to clasp was provided the male by a characteristic approach of the female that was observed many times. The following notes of May 16, 1945, describe this behavior: "At Pond 7 two males were calling. I watched a female approach them. She moved toward one of the calling males and as she came up to him she turned around and backed between his forelegs. As she pushed herself under him he clasped her." On April 1, 1946, a calling male was located about twenty inches from the female. She did not move directly to the calling male but to one side of him and as she got opposite him, about eight inches away, she made a right angle turn and moved toward him. As she backed under him in the characteristic fashion, he clasped her.
At no time during the years of observation was a male seen to approach a female and clasp her. Nor did males clasp other males except when the clasped male had "accidentally" assumed the position the female assumes prior to her being clasped.

Observations indicate that the female exercises some choice in the selection of a mate. On several occasions a female was observed floating near several calling males. She would pass by calling males to mate with another one beyond. On April 2, 1945, a female was observed to approach three calling males that were stationed in a triangle about a foot apart. She passed within five inches of one male, then within four inches of another, then leaped toward the third but instead of mating swam away from the chorus.

These movements on the part of the female which stimulate the male to clasp may be interpreted as a courtship preliminary to amplexus. A similar procedure has been observed in *Pseudacris nigrita triseriata*. On March 28, 1946, near Rockbridge, Hocking County, Ohio, breeding activity was observed from 9:30 A.M. until 2:10 P.M. During the period of observation there was a bright sun, the edge of the swamp under observation was not shaded and the water temperature was 74 °F. Many male Swamp Chorus frogs were calling over the area. On several occasions females were observed to approach calling males and back up to them whereupon they would be clasped.
Sometimes the female would approach the male from the side and after a preliminary nudging with her snout, he would turn and clasp her.

Similar movements have been observed in *Hyla crucifer crucifer* in which the female assumed the initiative and performed the introductory courtship that initiated the clasping. Noble and Noble (1923), in their study of *Hyla andersonii*, observed females leaping on the backs of males, prior to their being clasped. These authors also noted a selectivity on the part of the female, in which she was observed to pass by calling males on her way to other males.

**Amplexus and Oviposition**

Clasping occurs on land or in shallow water where the calling males are concentrated. Amplexus is "axillary," with the thumbs of the male thrust in the axillae of the female. When clasped the female swims to the deeper part of the pool and remains submerged for a varying amount of time, coming to the surface at intervals for air and returning to the deeper water. While submerged she holds to some object such as a branch, weed stalk or grass blade for support. During this time the clasping male remains securely fastened to the female with his thumbs thrust into her armpits and his small body drawn up into a compact mass upon her back.
Oviposition usually begins within a few hours after clasping although frogs have remained clasped forty-eight hours in the laboratory before laying eggs.

Observations of oviposition in the field and in the laboratory indicate that a regular sequence of behavior is followed for each emission. The female crawls or swims slowly among the vegetation on the bottom of the pool until she selects a suitable object for the attachment of the eggs. Clinging to the object with her hands she arches her back, points her head upward, and extends her hind legs. Simultaneously the male shifts position backward and extends his legs. This brings his cloaca in a position immediately above hers. As the forepart of the body and head of the female are extended to their maximum, the eggs are deposited. As the male reaches the backward extent of his movement and emission of sperm from his cloaca covers the eggs emerging from her cloaca. The female flexes her legs and the male returns to his original position. During the process there is no contact between male and female other than the attachment to the axillary region. The female crawls along the stem and deposits another emission of eggs while the male repeats his movements. This continues until several egg clusters have been deposited, and the pair then rises to the surface for air. The eggs deposited in the several clusters during the sexual period now become merged into one homogenous mass and the eggs of
the individual emissions cannot be distinguished.

The female initiates the process with the arching of the back and head. This compels the male to shift his position. Observation of clasped pairs failed to reveal any movement on the part of the male until the backward movement was started in response to the female's movement.

Variations of the above process were observed. In one case the female grasped a slender weed stalk that bent with her weight so that she hung upside down. Oviposition was carried out in the regular manner despite the inverted position and the movements of the male did not vary from those described above. In several cases the female extended only one hind leg while the other was bent and grasped the stem. On several occasions the feet of the female twitched spasmodically as the eggs were extruded.

Observations on amplexus and oviposition in *Pseudacris nigrita triseriata* indicate that the breeding habits of the two species are quite similar. The females of both species clasped the stem with their forefeet, and both flex the head, and this is followed in both cases by the shifting of the male posteriorad. One slight difference was noted: the female Upland Chorus frog holds to the stem with her hind legs flexed while the Swamp Chorus frog usually holds with her hind legs extended and occasionally clasps the stem with one hind foot.
The process of oviposition in the Spring Peeper was quite different from that of *Pseudacris brachyphona*. There is no flexing of the head in the Spring Peeper. The cloaca is first bent upward toward that of the male and then downward as the egg is deposited. This process is repeated eight to ten times as the female advances along the stem and deposits one egg at a time which sinks to the bottom of the pool where it adheres to the algae or debris on the bottom. Although the literature contains numerous references to the female's habit of attaching her eggs to stems or twigs, this behavior was observed only when the female was confined to a small receptacle in the laboratory.

The entire process of oviposition of the Upland Chorus frog occupies a period of two to three hours. From sixteen to twenty sexual periods are employed, each one taking from two to six minutes. Each sexual period consists of from one to fifteen emissions and fertilizations. The number of eggs voided at each emission varies from one to nine and the time between emissions ranges from fifteen to thirty seconds. The pair rises to the surface after each period of egg laying and rests for as long as fifteen minutes before continuing the process.

The number of eggs laid by the females ranges from 318 to 1,479 with an average of 828 eggs. Dissections of females with no eggs in their oviducts revealed a range of 607 to 1,121 with an average of 758 eggs. Barbour and
Walters (op. cit.) obtained a range of 983 to 1,202 with an average of 1,092 from dissections of ten average sized females.

Egg laying usually takes place between the hours of 10:00 P.M. and 2:00 A.M. The female usually enters the water early in the evening, mates and leaves the pool before morning. A few instances of late afternoon oviposition were observed, presumably by females that had entered the water the evening before. The height of the sexual activity is reached shortly after midnight since more pairs were observed in amplexus at that time than at any other time throughout the twenty-four hour period.

Many of the male frogs mate during the season following their transformation. Evidence for this was obtained by marking a series of recently transformed individuals and releasing them at the breeding pools and recovering them the following year in breeding condition. On June 2, 1946, eighty-five recently transformed frogs were released with the fourth finger of each hand excised. Of these, five were recovered the following year. On June 16, 1946, thirty-three were released with the third finger on each hand excised. One of these was recovered the following year. The data on the recovered frogs are shown in Table V.

Of these 118 frogs marked, two were recovered in 1948 and two in 1949. Because of their small size it was difficult to clip the fingers at the exact joint so it is possible
that the digits of many of the frogs regenerated. This accounts, in part, for the low percentage of recovery. Added to this factor is the high mortality which a recently transformed frog meets because of predation and other factors.

None of the recently transformed frogs that were recovered the following year were females. Dissections of several frogs taken in July, ranging from 16.0 to 20.0 mm., showed that there are about the same number of females as males in the juvenile population. Since this is true we should expect about half of the marked frogs to be females. Females within the 16 mm. class collected in July show distinct ova within the ovaries. The smallest breeding males collected were in the 22 mm. class while the smallest breeding females were in the 30 mm. class. This size differential between the sexes within the breeding population may be explained in two ways: either the females grow faster and attain sexual maturity their first year at a larger size, or the females do not breed until their second year.

Two females, UMMZ 105143 and 105144 collected by W. E. Duellman in Hocking County and Ross County, Ohio, respectively, on May 18, 1947, are 18.2 and 21 mm. body length. The unusually small size of these females at this time of the year may indicate a longer period of growth necessary for the female to attain sexual maturity, or they
indicate the result of a late summer or fall breeding in which case their development was interrupted by winter. Walker (op. cit.) suggests the possibility of fall spawning in referring to a collection of tadpoles from Hocking County, Ohio, on November 18, 1942. The usual absence of immature females from spring collections suggests that the latter explanation may prove to be correct.

The males may remain within the vicinity of the breeding pools throughout the breeding season, calling from the pools regularly during the early part of the season and returning sporadically throughout the later phases of the season, following periods of rainfall. During the seasons of 1945 through 1949, 273 male frogs were captured more than once during the season. The interval between captures ranged from five to seventy-nine days. Many of these frogs were recaptured several times during the season, two being taken at least four times. Of the 273 frogs recovered, seventy were observed to mate with females, either in the field or in the laboratory. Eleven of these seventy that were observed mating were subsequently recovered the same season calling at the pools. Although none of these eleven was observed to mate more than once during the season, their presence at the pools in a reproductive condition indicates that males of this species may mate more than once during the season.
Only two females were recovered more than once during the same season. Female No. 600 was taken in Pool 4 on March 23, 1947. She was released after marking, and she was recovered in the same pool on April 3rd. During the interim there was a cold snap during which breeding activity was suspended. Female No. 719, marked in 1947, was collected on March 16, 1948, in Pool 1, and she was released in the same pool. She was recaptured on March 23rd in Pool 4, about 150 yards from Pool 1. There is no explanation for this extended period at the pools. All evidence to indicate that a female breeds more than once during the season is negative.

Dissection of females collected after the completion of oviposition indicates that the female deposits her total number, or complement of eggs during one nocturnal visit to the pond. Exceptions to this occur when the process is interrupted by temperature fluctuations or by disturbance of the mated pair.
THE EGGS

The eggs are attached to the various objects in the pools. Partially submerged weed stems, twigs, grass, margins and petioles of leaves provide the principal points of attachment. Masses are not found floating on top nor resting on the bottom of the pools.

The mass is a loose, irregular cluster that slips easily through the fingers. Its size varies, depending upon the number of eggs it contains. A count of forty-five egg masses showed a range from four to 133 eggs with a mean of forty eggs per mass.

In appearance, each egg is marked by possession of a dark brown animal pole and a creamy white vegetal pole, and the latter forms from one third to one half the egg. Twenty eggs measured with an ocular micrometer showed a range in diameter of 1.34 to 1.71 mm. with a mean of 1.48 mm. The single gelatinous envelope ranged from 6.0 to 8.5 mm. in diameter with a mean of 7.0 mm. The mass of each egg is 0.26 cc.

Each mass is originally composed of the eggs extruded during several separate emissions that comprise one period of sexual activity. As the female sometimes deposits several separate lots of eggs with little or no movement between emissions, these individual clusters may coalesce to form a single mass. This occurs within a period of two
hours as the gelatin of the envelope absorbs water and swells.

The eggs of *Pseudacris brachyphona* may be identified through a combination of several characters: they are found in small, quiet pools, attached to vegetation or other debris in small, loose clusters of five to one hundred eggs; the eggs are small (6.0 to 8.5 mm. in diameter); pigmented and with only one envelope.

Differences between the eggs of *Pseudacris brachyphona* and *Pseudacris nigrita triseriata* are summarized in Table VI.
DEVELOPMENT OF THE EGG

Detailed data on early development are not available because of the lack of suitable equipment for maintaining a constant water temperature. Green (1938) states that at room temperature, hatching occurs 110 hours after laying. Barbour and Walters (op. cit.) state that hatching occurred indoors from seventy-two to ninety-six hours when kept at a temperature ranging from 18° to 22° C. (64° to 71.6° F), while in the pools hatching occurred from seven to ten days within a temperature range of 35.5° to 55.4° F.

The following notes on development were taken in the laboratory from observations on a mass of twenty-five eggs that were laid at 10:30 A.M., March 20, 1945. The water temperature during this period was kept at 74° F (variation ± 3°)

12:45 P.M. First cleavage furrow appears.
1:00 First cleavage furrow has extended half-way around egg.
1:20 First cleavage furrow completely encircles egg and the second furrow has begun.
2:00 Second cleavage furrow has extended half-way around egg.
2:20 Third cleavage furrow (latitudinal) complete.
3:00 Fourth cleavage.
3:30 Early blastula.

March 21: 9:00 A.M. Yolk plug stage.
   1:30 P.M. Formation of neural folds.

March 22: 9:00 A.M. Development of tail bud. Embryo rotating.

March 23: 9:00 A.M. Muscular movements noticeable.

March 24: 12:00 noon. Three embryos hatched.
   2:00 P.M. Six more embryos hatched.

Total hatching time for the nine embryos varied from 97.5 to 99 hours.

The time required for development of the egg in the pools was much longer since temperatures early in the season were much lower than 74°F. Freshly laid eggs were placed in jars of pond water and kept on the bottom of the pond while observations were made on their development. Although no effort was made to determine the average temperature during their development, it was found that time required for development of the egg varied from ten days to two weeks. Freshly laid eggs kept in a refrigerator at a temperature of 40°F required four days to reach the early blastula.
HATCHING

Hatching was observed several times in the laboratory, under the dissecting scope, and numerous times in the field with the naked eye. The following account, taken from notes of April 15, 1945, describes the complete process:

"Prior to hatching the larva lies coiled within the capsule. There is a slight bulge within the membrane where the head presses against it. The circulation within the gills can be plainly seen. Ciliary movement is quite strong. The bulge in the membrane becomes larger. The head is pressing against the chorion. There are striations in this membrane that run toward the head parallel to the body showing that the pressure of the head against the membrane is producing a tension. The egg becomes more and more elongate. It looks as though this is caused by the straightening of the embryo. Whereas the larva has been rotating slowly and evenly up to this time it now slows to almost a stop. All this has taken place within one and a half hours. The particles within the egg membrane continue to rotate, showing that there is still some ciliary motion. The nose is definitely out of the capsule but there is no movement of the larva as yet. The membrane seems to part without any force of the larva. The secretions of the glands of the head are supposed to play a part in dissolving this membrane (Noble, 1926). The head completely fills
what opening there is. Exit from the egg is gradual, the membranes clinging to the embryo as it moves outward. As the body emerges the larva gives a violent lashing with its tail that frees it from the membranes.

At hatching the embryo measures 4.5 to 5.0 mm.

The above process is similar, in its essential points, to the hatching process described for *Pseudacris nigrita triseriata* by Bragg (1948) in a paper in which he points out the differences of hatching of the above species with *P. clarkii*, *P. streckeri*, as well as *Hyla versicolor* subsp.
LARVAL DEVELOPMENT

The recently hatched tadpole drifts to the bottom of the pool where it lies on its side for some time. At this stage the mouth is not yet open although the anus has opened, the tail tip is rounded, myotomes are clearly visible, eyes are nonfunctional and the gills are small knobs. The tadpoles movements are spasmodic and jerky and it remains quiescent for long periods of time unless artificially stimulated. The adhesive organ is poorly developed and at this stage it is not used for support.

After four days the external gills are replaced by internal gills, the eyes are well-developed and are moved by their muscles, the mouth has acquired its jaws and the labia are forming, the rows being incomplete. Within the next few days the tadpoles feed on the algae that cover the vegetation in the pool. Their bodies become more rounded, the tail crests become developed and their movements are less spasmodic and better controlled.

Transformation takes place from fifty to sixty-four days after hatching at a length of approximately 30 mm.
THE TADPOLE

The tadpole of *Pseudacris brachyphona* was described by Green (1938) on the basis of specimens collected in Tucker and Randolph Counties, West Virginia, at an elevation of 2,000 feet. The material on which the description was based has been reviewed. The maximum size of the tadpoles in this material was 25.0 mm. Since collections from Cabell County contain individuals that are 32 mm. long it has been necessary to use the larger measurements along with additional data in supplementing the original description.

GENERAL APPEARANCE: Tadpole small, deep bodied; maximum total length before metamorphosis 32 mm.; tail tip obtuse, rounded; dorsal crest full, extended to about the vertical of the spiracle; spiracle not prominent, sinistral, below lateral axis, directed backward and slightly upward; eye slightly dorsal to lateral axis; anus dextral, opening about on the level of the ventral crest. Body black-brown above, uniformly and closely stippled with bronze; body transparent, dorsal and ventral tail crests with finely scattered pigment areas; musculature of tail with finely scattered pigment dots, more numerous on dorsal surface.

MOUTH PARTS: Labial teeth 2/3. Entire mouth, except a median dorsal space, about 1/2 the length of the upper row of teeth, surrounded by a continuous papillary fringe, with extra papillae inside fringe at the angles of the mouth; inner row of upper labial teeth divided medially, the two
halves separated from each other by about one half the length of either half row; inner row of lower labial teeth slightly indented medially and about the same length as second row; outer row about one half length of second row; upper mandible broadly U-shaped, slightly denticulated along external edge; length almost that of upper row of teeth; lower mandible V-shaped.

MEASUREMENTS OF A TADPOLE:

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<table>
<thead>
<tr>
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<tbody>
<tr>
<td>Total length</td>
<td>31.3 mm.</td>
<td>Spiracle to vent</td>
<td>7.5 mm.</td>
</tr>
<tr>
<td>Body length</td>
<td>11.8</td>
<td>Spiracle to eye</td>
<td>4.9</td>
</tr>
<tr>
<td>Body depth (max)</td>
<td>6.4</td>
<td>Eye to snout</td>
<td>3.2</td>
</tr>
<tr>
<td>Body width (max)</td>
<td>7.7</td>
<td>Eye to nostril</td>
<td>1.3</td>
</tr>
<tr>
<td>Tail length</td>
<td>18.5</td>
<td>Nostril to snout</td>
<td>1.7</td>
</tr>
<tr>
<td>Tail depth (max)</td>
<td>6.2</td>
<td>Mouth width</td>
<td>3.0</td>
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<tr>
<td>Musculature of tail (max)</td>
<td>2.2</td>
<td>Internasal distance</td>
<td>1.4</td>
</tr>
<tr>
<td>Spiracle to snout</td>
<td>7.5</td>
<td>Interorbital distance</td>
<td>3.4</td>
</tr>
</tbody>
</table>

Comparisons of the tadpole with that of *Pseudacris nigrita triseriata* failed to reveal any significant differences between those of the two species. Minor details in measurements were encountered but these were so variable as to have no value in the determination of differences. Color differences were not constant with the two species hence were of no use in distinguishing the two. In those areas where the two species were known to occur together, the habitat in which the tadpoles were found might offer
some clue as to their identification but this would not be absolute.
ACTIVITY OF TADPOLES

When the recently hatched tadpole frees itself from its egg membranes it sinks to the bottom where it lies on its side. For the next several days its activity consists of a swimming movement for short distances that begin spontaneously and terminate as suddenly with the larva sinking to the bottom where it rests on its side. The mouth is not yet functional at this stage.

The tadpoles are not active swimmers. Their time is divided between resting quietly on the bottom of the pool or floating idly on the surface. There is no evidence of schooling in their behavior. They are usually distributed at random throughout the pool and do not show a preference for any particular spot. In those pools that are exposed to sunlight there is a noticeable increase in the activity and more individuals may be found swimming back and forth, nipping at the algal mats or working the algae from a plant stem. As transformation time approaches they spend more time at the surface or rise to the surface more often.

They are particularly wary and any disturbance sends them scurrying to the bottom where they seek shelter among the plants and debris that is usually present. Their nocturnal activity closely parallels that of the daytime although there are fewer to be found on the surface and more on the bottom.
FOOD OF ADULTS

The digestive tract of forty-two specimens of adult Pseudacris brachyphona were examined to obtain information on the type of food eaten. The entire alimentary canal from the lower esophagus to the posterior rectum was removed and the contents placed in a watch glass with some water for examination under a binocular dissecting microscope. Eleven of the tracts were empty or contained unidentifiable material. The summarized results of the examination are shown in Table VII.

All of the animals that were eaten were those that lived on or near the ground or could have been obtained a few inches above the ground. No evidence was obtained from the food study that the frogs climb to secure their food at any height above the ground. The finding of small stones and sand grains in eleven (35 per cent) of the stomachs indicate the habit of feeding close to the ground.

The average size of the food items is very small. The beetles were less than one millimeter in length and consisted of two species. The largest single item was a fat lepidopterous larva that was 4 mm. long and was rolled into a compact ball in the lower region of the stomach. With respect to bulk, this one larva was larger than the total volume of the twenty-one beetles.
All of the animals eaten could have been caught during the day in sheltered, shady situations, although they may have been eaten at night. The frogs have never been observed to feed at night while in chorus. Since all the food items are terrestrial animals it appears that feeding is done on land and not while in the water.

Five of the stomachs contained plant material in the form of portions of grass blades and small seeds.

Most of the stomachs (sixteen) contained just one item of food, nine of them contained two items, five contained three items and one contained four identifiable items.
MOVEMENT

Studies of frog movement were begun in the spring of 1945 and carried through 1949. Data were obtained from the records that were kept of the recoveries of marked frogs within the study area. A total of 1,189 adult *Pseudacris brachyphona* were marked by the toe clipping method during the five seasons. Data on these recoveries are summarized in Tables VIII and IX.

The study area, described in an earlier part of this paper, comprised a strip of land about 0.2 miles wide and one mile long along both sides of the Right Fork of Four Pole creek. This area contained ten pools that were used each year for breeding by the frogs. The concentration of the frogs at the breeding pools during the early parts of the season and the ease with which they could be captured at night, facilitated the accumulation of records. Of the 1,189 frogs marked, 406 or 34.1 per cent were recovered at least once. The percentages of recoveries shown in Table VIII are considered high for so small a frog, especially since some of the recoveries extended over a period of four and five years and the effects of predation, adverse weather conditions and other factors must have reduced their numbers considerably. Raney (1940), working with the Bullfrog, *Rana catesbeiana*, obtained 65 per cent recoveries of his marked frogs throughout one season of study.
Of the ten pools involved in the study, three (1, 3 and 4) are located on the flood plain of the stream in the valley, four (6, 7, 8 and 10) are located in roadside ditches above the valley floor while three (2, 5, and 9) are located on the hillside some distance above the valley floor. The direction of movement of the frogs into and out of the breeding area was determined from data covering the recoveries of the frogs at these pools throughout the season.

A mass movement of the frogs occurs at the beginning of the season toward the pools. A study of the number of frogs to be found at three of the most widely used pools reveals some interesting fluctuations in numbers. Table X shows the number of frogs taken at three of the pools throughout the season of 1947. The figures for 1947 were selected because more time was spent in the field on this phase of the work in 1947 than any other year and also because the recoveries were greater for that season.

Pool 1 is the largest of the pools in the valley and it contains more frogs during the early parts of the season. It is exposed to the sun and warms up rapidly later in the season. Pool 4 is located under the same conditions as pool 1 but the water is shallower and is unsuitable for breeding later in the season. Both pool 1 and pool 4 are about two feet above the stream bed. Pool 2 is located on a hillside 110 yards above the stream bed and is shaded the
latter part of the season.

As the frogs emerge from hibernation they move down the slope toward the pools. Many stop at pool 2 temporarily but move on down to pool 1 or 4 in the valley. Later in the season when they leave the pools in the valley they move uphill. Their return to the pools following a rain late in the season is for a short stay only and the pools on the slopes receive most of these frogs.

The number shown in Table X include sixty-seven frogs that were subsequently recovered, either at the same pool where first captured (40) or at a different pool (27). Of the twenty-seven that moved between pools, nine moved from pool 1 to pool 2; fifteen from 4 to 2; two from 1 to 9; and one from 4 to 1.

Most of the recoveries were of frogs that moved uphill from pool to pool. Seventy-two recoveries from 1945 to 1949 were of frogs that moved in this direction. The following data show the number of frogs (numeral inside the parenthesis) that moved from pool to pool (numeral outside the parenthesis) in an uphill direction: 4-2(32): 1-2(8): 4-9(6): 4-5(6): 7-2(5): 1-7(4): 1-6(3): 1-9(3): 4-6(1): 4-7(2): 5-2(1): and 5-7(1). These movements are shown graphically in Figure 16.

With the exception of frog No. 65 there was recovered in pool 2 five days after it had been released in pool 4 on March 24, all of the frogs moving uphill were
recovered after April 11. This indicates that the return to the hillsides from the valley pools does not occur until the first phase of the breeding season has ended.

These recoveries represent extremes of five and seventy day intervals from the first capture to the last recovery within the season, with a mean of thirty-eight days. It is entirely possible that the frogs may have moved between pools or out of the breeding area in the interval between captures, but this was not observed in any of the seventy-two frogs.

The greatest distance covered by a frog in one of these uphill movements was from pool 4 to 9 (six frogs), a horizontal distance of almost 2,000 ft. Two of these frogs were recovered thirty-two days after their first capture. The others ranged from forty-three to sixty-six days. Pool 9 is a shallow ditch along a woodland road. All of these frogs were calling from the ditch when recovered in late May.

The following records were taken from several examples that illustrate this movement:

Example 1. In 1945, No. 51 collected in pool 1 on March 15 was recovered in pool 4 on April 2. It was released in pool 4 and was recovered in pool 2 on June 12.

Example 2. In 1947, No. 225 collected in pool 4 on March 23 was later recovered in pool 2 on April 14. It was released in pool 4 the next day and was taken in pool 2 again on May 26.
Example 3. In 1947, No. 256 collected in pool 4 on March 26 was recovered in pool 1 on March 30. Released in pool 4 it was recovered in pool 2 on April 15.

There were eleven recoveries of frogs in their movement downhill. In these cases the movement was from 2-7(3): 2-4(2): 7-4(2): 4-10(2): 2-1(1): and 2-10(1). Six of these eleven movements occurred within the first three weeks of the breeding season. Two of the frogs were captured in pool 2 late in April and recovered in pool 4 a short time later. They may have been late arrivals at the pool or they may have been frogs that had been overlooked earlier in the season. The other three recoveries are treated in the next paragraph.

Three frogs, marked in 1945 (Nos. 98, 233 and 249) were recovered at the lower end of the valley along the highway at the beginning of the 1946 season. This was almost 4,000 ft. from where they were last seen in 1945, a figure which represents the greatest distance travelled by any of the marked frogs. Although the movements of these three occurred the same year, there was no heavy rainfall during this period that would have raised the streams to flood stage to account for passive movement. In 1947, roadwork in the lower end of the valley destroyed the pools where these frogs had been recovered and no observations were made at this place in later years. It is possible that many of the frogs that were not recovered migrated over a
wider radius and utilized other breeding pools outside the study area.

In their movements from pool to pool, the frogs often crossed a well-travelled hard-surfaced road. It was also necessary to cross a stream to move from the north-facing slope to any of the pools in the valley. In the early spring this stream averages six feet in width. Yet many recoveries indicate that the frogs crossed and recrossed the stream to move toward or away from the pools during the breeding season.

The problem of downhill migration to the breeding ponds has received considerable attention in the literature. Many species of Amphibia, upon emerging from hibernation, move downhill toward the breeding area. In such a frog as *Pseudacris brachyphona*, where temporary pools are utilized, suitable breeding pools are frequently reached before arriving at the bottom of the hill. In fact, streams are usually encountered in valleys and these are not utilized by breeding *P. brachyphona*. Most streams have flood plains and the occurrence of temporary pools on these flood plains may, in part, explain the advantage of a downhill migration.

One explanation for the movement of frogs downhill is that of geotaxis (Cummings, 1912). Savage (1935), in a study of the migrations of *Rana temporaria* toward the breeding pools to determine the stimulus to migration, took exception to this view on the ground that frogs not only
move downhill toward the ponds but also horizontally. He concluded that the frogs are directed to the breeding pools by the sense of smell that responds to pond odors due to a particular algal flora of the breeding pond. It has been observed in _P. brachyphona_ that their movements are directed toward the ponds at the foot of the hill although they encounter numerous obstacles in their downward journey that defy the theory of a positive response to gravity. The fact that so many of the frogs pause temporarily in the hillside pools before proceeding on their movement downhill while so few utilize these pools for breeding early in the season indicates that the urge to get to the foot of the hill must be stronger than the urge to breed even when an apparently suitable habitat is reached. Whether it is this urge to move downhill that is stronger or whether there is some physical factor that distinguishes the hillside pools from those in the valley has not been determined. The temperature of the valley pools is 2° to 4° higher than those on the hillside at the beginning of the season. Because of drainage and other factors they are usually larger. They contain less vegetation, decayed leaves and other trash. None of the pools can be characterized by their algal flora during the early phase of the breeding cycle.

The selection of a valley pool during the early stages of the breeding cycle and the return to the hillside pools for late season breeding might be considered an economy
from the standpoint of survival of the species. The valley pools warm up more quickly and transformation is reached earlier than on the hillsides. Hillside pools are most often located in the woods and do not dry out as quickly as the valley pools. Table X shows that the two larger pools, No's 1 and 4 in the valley, are utilized at the beginning of the season while pool 2 attracts a larger number of frogs toward the end of the season.

Many of the frogs were collected at the same pool more than once during the season and were not collected at any of the other pools. The number of frogs taken at one pool only, as compared with the number recovered at more than one pool, is shown in Table XI.

Although 181 of the 513 recoveries were taken at the same pool throughout the season, this is not sufficient evidence that the frogs do not move from pool to pool during the breeding season. Of these 181 recoveries, 144 represent only one recovery. During the interval between capture and recapture the frogs could have appeared at any of the other pools and escaped detection. Since the frogs do not remain at the pools during the entire breeding season, considerable wandering could have taken place between captures. Their recovery at the same pool indicates that either they were in the vicinity so that their return to the same pool is more convenient than to any of the other pools or else it demonstrates a homing instinct that brings them back to
the same pool more than once.

Male frogs may be found calling at the pools for an extended period. The following data for *P. brachyphona*, recaptured after being marked in the breeding pond give the number of days (numeral outside parenthesis) after being marked that the frog was retaken, and the number of frogs (numeral inside the parenthesis) retaken after a given number of days at the same pool where released:

1(1), 3(10), 4(2), 5(7), 6(7), 7(11), 8(1), 9(5), 10(8), 11(1), 12(6), 13(8), 14(6), 15(3), 16(5), 17(1), 20(1), 21(1), 22(6), 23(2), 24(3), 29(2), 36(1), 38(1), 39(1), 41(2), 46(3), 51(2), 54(1), 58(2), 65(5), 70(1), 71(3), 72(1), and 77(1).

Considerable movement of the frogs between pools occurs as is shown in Table XI. Horizontal movements from pool to pool within the breeding area accounted for about 12 per cent of the recoveries. All of the records were between pools 1 and 4, about 700 feet apart, and involved eleven frogs, one of which was a female. The numbers of days between release and recapture were as follows: (number of frogs for each day interval one except where number is shown in parenthesis): 1, 5 (2), 7, 15, 18 (2), 19, 53, and 65 (2). The following data are taken from field notes and illustrate this movement: In 1946, No. 91 was released in pool 4 on March 18 and was recovered in pool 1 on March 23, a distance of 600 feet. Another, No. 576, released in
pool 4 on March 26, 1947, was recovered in pool 1 on March 30. This frog was released in pool 4 on April 6 and recovered in pool 2 on April 15. On March 23, 1948, No. 661 was released in pool 1 and was retaken in pool 4 the following evening, while No. 719 moved from pool 1 to pool 4 from March 18 to March 23.

Blair (1943) states that male toads do not always remain at the same pond until mated but may move to other breeding areas. Piatt (1941) concluded that male toads do not move to other breeding sites but remain at the same one until mated. Although the behavior of *P. brachyphona* demonstrates that they do move from breeding pool to other breeding pools it would be difficult to demonstrate that frogs moving to other pools had not mated.

On the other hand, eleven of the male frogs that were recovered at the pools were known to have mated previously during that season. In 1945, No. 35 was taken into the laboratory where it mated with ♀ No. 34 to produce fertile eggs. It was released in pool 1 on March 17 and was taken four more times that season, the last date being June 13 at pool 2. Other frogs had similar histories while many were observed during amplexus and later recovered.
HOMING

The movement between pools during the breeding season suggested that the frogs might be trying to return to a pool with which they were familiar. Either the frogs remained in the first pool they encountered that offered the necessary environmental factors for breeding or some directing influence was responsible for guiding them to the same pool from one year to the next. In order to test this theory the data for returns from one year to the next were analyzed to see how many of the frogs returned to the same pool to breed in that they had bred in the previous year. The results are shown in Table XII.

Of thirty-four frogs that were marked in pool 1 in 1945, twenty-one or 61 per cent of them were recovered in that same pool the following year. At the same time, of nineteen frogs marked in pool 4, fourteen were recovered in pool 4 the following year. In 1946, thirty-one frogs were marked in pool 1 that were subsequently recovered and 87 per cent of these were recovered in the same pool the following year.

The results of 1948 are significant. All of the frogs marked in 1947 were released in pool 4. Yet of the sixty-seven frogs that had been taken in pool 1, fifty-nine of them returned to the same pool where they had been captured the year before despite the fact that all of them had been left in pool 4.
From the proximity of the breeding pools in this study area to one another and the apparent ease which a frog travelling downhill from the hibernating area could reach one pool as well as another in the valley, we would expect to find the frogs selecting the first pool they reached rather than return to the same pool on successive years. Noble (op. cit.) has suggested that the first frogs to arrive at the breeding ponds start calling and thus their voices serve to attract other males to the ponds. Although the voices of the first frogs to arrive at the ponds may serve to orient the frogs in the general direction of the ponds, there is evidence that the frogs exercise selectivity in their choice of a pool and do not necessarily remain at the first one they come to. During the breeding season in the valley where this study was made, the din of frog voices from the pools is so great that a frog could be directed to a number of pools. The fact that the greater percentage select the same pool for more than one year indicates an ability to find the way back to that particular pool.

Although Raney (op. cit.) found no evidence to support a homing tendency in *Rana catesbeiana*, Breder, Breder and Redmond (op. cit.) found some evidence of homing in the Green frog, *Rana clamitans*. Bogert (1947) in a study of homing in the Carolina toad, *Bufo terrestris terrestris*, found that many of the toads were familiar with an area of
more than a mile wide. He concluded that while topo-
ographical knowledge plays no role in homing behavior,
auditory cues offer the best explanation for the homing
ability of toads released beyond territory familiar to them.

Although sufficient data to establish definite proof
is lacking, the evidence seems to indicate that a frog
returns to the same pool to breed from which it has trans-
formed. Of eighty-five recently transformed frogs marked
on June 2, 1946, and released, two were retaken the following
year at pool 4. The eighty-five frogs had been collected
from pool 4 and another pool several miles from the study
area so it could not be definitely said that the two frogs
that returned to pool 4 had transformed there, but there is
that possibility.

In a frog with breeding habits like those of \textit{P.}
\textit{brachyphona}, which makes use of temporary pools, the return
to pools previously used from which they had transformed
would eliminate pools that would dry up before transformation
had taken place. Such a tendency to return to previously
used pools would establish a pattern for survival of the
species in an area where indiscriminate use of unsuitable
pools might mean extinction of the species.
GROWTH AND LONGEVITY

Data on growth were obtained through comparisons of body measurements of 291 adult male frogs recovered within a year after marking, nine female frogs recovered within a year after marking, fifty-four male frogs recovered within two years after marking and six females recovered two years after marking. Some data on growth within a season was obtained by measurements of recaptured frogs within that season, while measurements were available on six frogs that were recovered a year after the known date of their transformation.

Measurements of the frogs were obtained during the breeding season. As the breeding season covers a period of approximately three months, the measurements from one season to the next might fall within a period that would range from ten to fourteen months. In late season this period might account for the entire year's increase. Data on several frogs that were measured near the beginning of the breeding season and again toward the end of that same season indicate little or no growth for that period.

The length frequencies of the frogs marked from 1945 through 1949 are shown in Table XIII. Recoveries of frogs for the year 1946 through 1949 supplied data on growth increments which are shown in Tables XIV, XV and XVI. The distribution of the growth increments into size groups as
shown in Table XIV are plotted in Figure 17.

Considerable variation in annual increments is shown. The mean annual increment obtained, 2.8 mm, is considered high for such a small frog. Raney and Lachner (1947) obtained a mean annual increment of 3.0 in a study of the growth of 124 male toads, *Bufo terrestris americanus*, that ranged in size from 63 to 94 mm.

The growth increment was greatest for the smallest frogs; specimens ranging in size from 22.6 to 23.5 mm. grew from three to nine millimeters in one season with an average increment of 6.0 mm. Forty-five of the frogs showed no increment or some decrease. Raney and Lachner (op. cit.) found that 20 per cent of their toads showed no growth or some decrease.

The loss in length of some individuals may be attributed to one of two factors, either an error was made in one of the measurements or an actual decrease in length occurred. If an error had been made in the measurements, other errors must also have been made in the other size groups so that the errors would equalize each other in a large number of measurements. Since the smaller frogs show a much greater increase in length, an error of two millimeters would be hidden, while a larger frog showing a slight increase might show a loss because of an error in measuring.

Raney and Lachner (op. cit.) suggested that one of
the possible explanations for the measured loss of their toads was due to the jaw tag which interfered with normal feeding. This suggestion must be eliminated in the case of *P. brachyphona* since the jaw tag was not used and the frogs did not seem to suffer any inconvenience from having their toes clipped.

The other possible explanation is that the largest frogs actually shrink in length after a year or so. The large *P. brachyphona* are not necessarily the oldest, since data are available to show that a frog may attain a body length of 27 to 28 mm. one year after transformation and that frog could attain maximum size within another year by an increment of six or seven millimeters, which was done by some of the frogs in Table XVI. Of the fifty-four frogs for which data are available for the second year of growth, forty-two (78 per cent) showed an increase in length the second year, while the other twelve showed no increase or decrease. If the frogs continue to grow, even more slowly, as they approach maximum size, then we must consider the apparent loss in length as due to an error in measurement.

Of the fifteen females for which data are available, six or 40 per cent showed no growth or a decrease in length over the previous year. In this group, as with the males, the smaller frogs showed the greater increment. One frog 42 mm. long showed a decrease of 5 mm. in length from the
previous year's measurement. This loss is difficult to explain as it seems unlikely that such an error would be overlooked at the time of measuring. Only two other females showed a decrease and each of these of only 1.0 mm.

The amount of growth attained during the period from transformation to the breeding season the following year appears remarkably uniform, varying from 15.4 to 18.0 mm. in the six frogs for which data are available as shown in Table V. This variation is not as great as that between four frogs of the year that were collected on October 6, 1946, and measured 15.9, 16.1, 17.8, and 19.4 mm. respectively.

The range in measurements of these frogs might be attributed to differences in the date of transformation, some metamorphosing earlier than others, or it may have been a difference due to sex, their external sexual characteristics not being apparent at that time. Of the six recently transformed frogs, five were released on the same date and the other one released two weeks later. All six were collected over a period from March 23 to April 3, 1947, with the last frog to be released showing the greatest growth increment.

There is considerable variation in growth during the first season which can be attributed to the difference in time the frog is active from transformation to hibernation; those frogs emerging early could have a two month start over the late broods. The six frogs recovered one year after
transformation fell within the 28 to 30 mm. size group. Of the male frogs in breeding condition taken at the ponds, forty-three were in the 22 to 24 mm. size group while 374 were within the 25 to 27 mm. group. There is no evidence that these frogs were one year old when first marked but undoubtedly many of them were. Furthermore, considerable growth must take place in late fall since the largest of the frogs collected on October 6 was at least 2.5 mm. shorter than any collected at the ponds the following spring.

Figure 18 shows the growth of the 291 male frogs whose growth increment was plotted in Figure 17. The vertical line at 33 mm. represents the average maximum growth toward which these frogs were progressing. This line was obtained by plotting the mean growth increment for the 291 frogs. The average growth increment line crossed the line of no growth, or zero, at a point on the 33 mm. line. Theoretically this is the maximum growth attained by most of the frogs. If the growth for these same frogs could be plotted for successive years it would come closer and closer to this vertical line. A few would cross as they have done in Figure 20. For most of them this line would never be reached. Although cold blooded animals may continue to grow as long as they live, there is a figure toward which their growth progresses each year, as is shown here.
LONGEVITY

The natural age attained by any amphibian in its native habitat is unknown. There are records available for some species which have been kept in captivity but the conditions of a laboratory existence are quite different from the unprotected environs of an animal's native home.

The data from the returns of the marked Pseudacris brachyphona indicate that two of the frogs had attained an age of at least five years, if we assume that they were at least one year old when marked. Eleven of them were recovered three years after marking so that their age was at least four years. Senning (1940) was able to determine the age of Necturus by an examination of lines on the parasphenoid bone. This method was applied to P. brachyphona but no satisfactory results were obtained. Force (1933) estimated growth in the Leopard Frog in Northern Michigan on the basis of comparisons of size groups taken from three collections in July. Bishop (1926) used size groups in estimating growth and age in Necturus. Blanchard (1931) separated fall collections of Hemidactylium scutatum into three size groups, based on size characteristics. The first group consisted of juveniles in their first season, the second group consisted of those a year older and the third group consisted of adults. The overlap between the sizes of the second year juveniles and the adults led Blanchard to conclude that some
individuals may become mature a season earlier than their class, and some may be delayed a season longer. The conclusions reached by Force, Blanchard, Bishop and others are based on the assumption that members of a size group are all of the same year or age class. The range in increment of the various size groups of _P. brachyphona_ suggests that such a method would have no value because of the overlapping of sizes for the different ages. In Table XIV there are eleven male _Pseudacris brachyphona_ that were marked at the body length of 23 mm. Yet the following year the measurements of these eleven frogs that were now one year older varied from 32 to 26 mm. Table XIII shows that out of 996 male frogs that were marked, only one attained a length in excess of the 31 to 33 size group. According to this a frog might approach its maximum size in just one year of growth. On the other hand its growth may be so slow that it would be "passed" by a frog of the next year class. The technique of grouping amphibians in year classes according to their sizes appears to have no justification on the basis of the findings of the growth of _Pseudacris brachyphona._
ESTIMATED POPULATION

A variety of techniques have been developed to determine the total number of a certain species within an area. These techniques are of three distinct types: (a) by counting the number over the whole area or a sample of it, (b) by ratios based on banding or marking and later recapture of sample individuals and (c) by indirect observation through the use of indices.

The technique of estimating populations based on the ratio of individuals banded to those present in the returns was used by Lincoln (1930) in estimating waterfowl populations and has since been referred to as the "Lincoln Index" although a similar method was used much earlier (Stickel, 1950). Jackson (1939) revised the Lincoln Index to estimate populations, taking both death, birth and migration into account, in estimating numbers of tsetse flies. Krumholtz (1943) estimated fish populations by checking fin-clipped fish over a period of twenty-two days netting and calculating the population over a modified Lincoln formula.

Table XVII shows that the greatest number of frogs obtained in one season was 438. This figure represented newly marked individuals as well as recoveries of those marked in the preceding two years. Since no intensive effort was made to obtain every individual frog within the area,
this figure of 438 frogs has no significance in relation to the total population of the area. The very fact that some frogs "skipped" years in being recovered is evidence that not every frog within the area was seen.

Stickle (1950) points out that if the principle of the equation used in the Lincoln Index is to be applied in making the estimates, it must be assumed that (a) all animals in the population have equal chances of being collected, (b) certain areas do not receive particular attention to the neglect of other areas and (c) the balance between marked and unmarked animals is assumed to remain undisturbed between the two sampling periods.

Various modifications of the Lincoln Index have been devised to take into consideration differences in behavior of the sexes, and other factors which would alter the estimate.

During the first phase of the breeding season of *Pseudacris brachyphona* the males are concentrated at the breeding pools. Although the number of females fluctuates greatly from night to night, the number of males remains relatively constant. Collections made over the breeding area provided figures that were used as a basis in estimating the number of males in the area.

An intensive effort was made at the beginning of each season to clean out the pools of marked and unmarked males in order to obtain some idea of the number within the breeding area at that time. Within the first week of
emergence when the breeding season was at its height, the pools were worked over several times during a single night with the assistance of several student collectors. The frogs were carefully checked for marked individuals. These data were used to compute the estimated population by Lincoln's formula. The one used was as follows:

\[
\text{Estimated no. in the population} = \frac{\text{total taken} \times \text{total marked}}{\text{marked recovered}}
\]

Table XVIII shows the results of these computations based on the data for the years 1946, 1947 and 1948.

The range of the frogs within the area was computed as a circle with the center at the breeding pools and the radius the greatest distance known to have been travelled by a frog in moving away from the breeding pools. This gave an area of 5.5 acres over which the frogs ranged outside of the breeding season if we consider that all parts of the range were favorable habitat.

The figures obtained indicate that the population of Pseudacris males in the area was much greater than the number of individuals obtained by field collections. They indicate that the population of males is between 100 and 150 per acre in this valley.
POPULATION TURNOVER

To determine what per cent of the population was composed of the various age groups, the yearly returns of marked individuals were studied. The number of frogs marked each year with the number recovered for each subsequent year of the study is shown in Table XIX.

The number of years required for a year class to shrink to zero is termed the population turnover, while the rate of shrinkage of any year class is termed the turnover rate.

The findings are based on the data obtained from 1,702 frogs caught, of which 1,189 were original markings, 328 were returns, i.e., caught any subsequent year after marking, and 185 were repeats, i.e., caught again the same year as marked.

The first year catch consisted entirely of unmarked frogs, plus repeats of these. During subsequent years the catch consisted of new unmarked frogs plus returns of previous years and repeats of both. The results of these years, exclusive of repeats, are shown in Table XIX.

The make-up of the captures is read horizontally. Thus the season of 1946 yielded 260 new frogs plus fifty-six of the previous years catch of 253. The season of 1947 yielded 331 new frogs plus seventy-nine of the 260 marked in 1946 plus twenty-eight of the 253 marked in 1945.
The history of a year class is read diagonally downward; thus the 1945 year class is represented by the series 253 - 56 - 28 - 6 - 2.

Although Table XIX indicates that the turnover period is six years, since all of the frogs were at least one year old (plus or minus two months) when marked and none were recovered the sixth season, it does not give a true picture of the rate of turnover. No provision has been made for this error but obviously one exists, even though slight. The number of frogs recovered in subsequent years after marking represents only those that were captured and does not include those survivors in the population that were not recovered. That this condition prevails is borne out by the recovery of marked frogs that had not been recovered the previous year.

Another source of error is suggested because of a difference in the breeding behavior of the two sexes. It has been shown that the males remain at the pools for extended periods and even return after leaving the area when breeding conditions are suitable. The females appear at the ponds once during the season and leave after spawning. This differential in behavior accounts for an unbalanced population at the ponds at any one time and also accounts for a high percentage of males in the year's catch.

Since the figures in Table XIX are for both males and females, with the latter far in the minority, it might
be inferred that the unbalanced ratio of the sexes might account for an error. When the data for the males were arranged in a table similar to that for the two sexes, it was found that the results were almost identical. Since no evidence was found that females live longer than males, it was concluded that the population turnover in females was similar to that of males.

The age composition of the frog population may be computed from the survival series corrected on a scale of 100:

<table>
<thead>
<tr>
<th>Frogs</th>
<th>Numbers (Table XIV)</th>
<th>Percentages of the population</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 year after marking</td>
<td>100</td>
<td>71.0</td>
</tr>
<tr>
<td>2 &quot; &quot; &quot;</td>
<td>28.1</td>
<td>20.0</td>
</tr>
<tr>
<td>3 &quot; &quot; &quot;</td>
<td>9.2</td>
<td>6.8</td>
</tr>
<tr>
<td>4 &quot; &quot; &quot;</td>
<td>2.3</td>
<td>1.8</td>
</tr>
<tr>
<td>5 &quot; &quot; &quot;</td>
<td>0.4</td>
<td>0.4</td>
</tr>
<tr>
<td>6 &quot; &quot; &quot;</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>140.0</strong></td>
<td><strong>100.0</strong></td>
</tr>
</tbody>
</table>

Figure 19 shows graphically the composition of the Pseudacris population in the study area at Huntington based on the above figures.

The population declined at the rate of 71 per cent from the first to the second year, 67 per cent from the second to the third year, 75 per cent from the third to the
fourth year and 82 per cent from the fourth to the fifth year.

The rate of shrinkage appears rather uniform at first but climbs rapidly between the fourth and fifth year, a figure one might expect since so few frogs were available to compute this figure.
AVERAGE AGE

The average age of a species in nature would be computed by averaging the age at death of each member of the population. In an amphibian the term average age might include mortality during the larval period or it might be taken to mean the average age after transformation had been reached. The literature contains no references to average age in frogs. Consequently it was necessary to approach the problem by using techniques that had been applied to other groups of animals.

Burkitt (1926) computed the average age of birds by using the yearly death rate. He reasoned that the number of surviving young must equal the number of adults that die yearly if the population is to remain constant. If a frog lives \( n \) years, there would be \( \frac{1}{n} \) frog die yearly. If an individual Pseudacris brachyphona lives for five years then in order to maintain a status quo in the population, \( \frac{1}{5} \) frogs would die yearly. The yearly death rate of \( P. \) brachyphona has been figured at a figure close to 70 per cent. Therefore if 70 per cent of the population die yearly, the average age may be computed as follows:

\[
\frac{.70}{n} = \frac{1}{n} \quad \text{and} \quad n = 1.4 \quad \text{the average age.}
\]

Nice (1937) in Table XXVII shows that a bird with a 30 per cent survival will attain the age of five years.
and an average length of life of 1.4 years. These figures agree closely with those computed for *P. brachyphona* in this study.
CROSSES WITH OTHER SPECIES

Within the area studied there were four small species of Hylidae. No more than three of these occurred in any one area. In the mountains of Pocahontas County, West Virginia, there occurred in the same area *Hyla c. crucifer*, *Pseudacris brachyphona* and *Pseudacris nigrita feriarum*. In southeastern Ohio there occurs *Hyla c. crucifer*, *Pseudacris brachyphona* and *Pseudacris nigrita triseriata*. At Huntington, West Virginia, *Hyla c. crucifer* has been observed breeding in the same pools that were used by *Pseudacris brachyphona*. In Hocking County and Jackson County, Ohio, *Hyla c. crucifer* has been observed using the same breeding pools as *Pseudacris brachyphona*. Although *Pseudacris brachyphona* and *Pseudacris n. triseriata* have been observed calling from the same pools, there are no observations on their breeding in the same pools at the same time.

Since these different species occupy somewhat similar habitats during the breeding season there was the possibility that interspecific, or even intergeneric, crosses might occur in nature.

Several differences between the eggs and breeding behavior have been observed between the species of *Pseudacris* and *Hyla c. crucifer*. The eggs of *Hyla c. crucifer* are laid singly and have a thin, well-defined envelope. The
breeding call of *Hyla c. crucifer* is a high-pitched whistle; quite distinct from that of the three species of *Pseudacris*. During amplexus and oviposition there is no flexing of the head as in *Pseudacris*; the cloaca is first bent upward toward that of the male and then downward as the egg is deposited on the object or in the water. Although no cross embraces were observed in the field it was not difficult to effect them in the laboratory. Table XX shows the results of the cross embraces between the various species available.

Tadpoles were obtained in each case except those hybrid crosses involving female *Hyla c. crucifer*. In these crosses the development appeared to be abnormal and the larva died before reaching the hatching stage. Blair (1941) obtained similar results in crosses involving *Hyla c. crucifer* and *Pseudacris n. triseriata*. He suggested that the lack of cleavage might be attributed to a lack of penetration of the *P. n. triseriata* sperm. The differences in the behavior of the two species during oviposition might also explain the low percentage of cleavage. A cross involving a female *P. brachyphona* and a male *Hyla c. crucifer* resulted in 43 per cent cleavage with 132 tadpoles.

Non-hybrid crosses developed normally and hatching occurred within the expected time. Both hybrid crosses involving *Pseudacris brachyphona* and *Pseudacris n.*
triseriata resulted in large, healthy tadpoles. Failure to carry them through metamorphosis was due to an unfortunate accident that occurred during my absence from the laboratory where an assistant was feeding them. Blair (1941) obtained forty-three metamorphosed young, three of which lived 195, 259 and 272 days respectively beyond metamorphosis as a result of crossing female Pseudacris n. triseriata with male Hyla c. crucifer.

Despite the ease with which these different species were able to hybridize in the laboratory there was no evidence that hybridization occurred in nature. No observations were made of cross matings in the pools and no individuals were collected that appeared intermediate in characters between any two of the species. If such matings did occur, what happened to the offspring? If they did not occur, what prevented them from occurring?

Among the species of Pseudacris some ecological factor appeared to be most important as an isolating mechanism. The two species of Pseudacris found in any of the habitats studied were found in breeding condition at the same season of the year, their breeding behavior was quite similar although their call was sufficiently distinct to separate them. But it was rare to find them breeding in the same body of water and then not at the same time.

The female Pseudacris brachyphona has been observed
to show selectivity in picking a mate from a group of calling males. The degree to which voice serves as an isolating mechanism has not been worked out. But there is no doubt that voice serves as an isolating mechanism.

In *Hyla c. crucifer* there is an ecological mechanism which frequently serves as an isolation factor. Male *Hyla crucifer* often call from a station above the water to which they have climbed and to which the female must climb in order to secure the male. Such a location would serve to isolate male *Hyla crucifer* from female *Pseudacris*.

One other factor which should be considered as an isolating mechanism is that of physiological rhythm. The breeding tempo of *Pseudacris n. triseriata* is much faster, the season starts earlier and ceases sooner than that of *Pseudacris brachyphona*. This separates the two species except for those few individuals that appear in the middle of the breeding season of each species.

The isolating mechanisms that prevent cross matings between *Hyla crucifer* and the three species of *Pseudacris* in this study might be summarized as those of ecological, voice response and physiological rhythm.
MORTALITY FACTORS

The factors that affect the size of a population of a small frog such as Pseudacris brachyphona may be grouped under the headings of predation, environmental changes and competition with its own and closely related species.

Those factors which affect the larvae are different from those which affect the adults. Drying up of pools before transformation and the scouring out of pools by heavy rains and floods affect the survival of large numbers of larvae. Silt and muddy water seem to have little or no effect upon the hatching of the eggs or the development of the larvae. Predation of larvae by Ambystoma and Triturus have been noted and these might be an important factor in some parts of its range.

Predation by bull frogs, water snakes, turtles, herons, and other well-known enemies of frogs are not so likely to be an important factor because of the location of the pools and the habitat of the frogs. The small, isolated woodland pools and roadside ditches are not frequently visited by these predators as are the larger bodies of water.

Land use practices affect entire populations of these frogs. The encroachment of suburban dwellings frequently destroy their breeding places and render the entire
area unfit for the survival of the species. Within the past ten years numerous examples of this practice have been noted within the Huntington area with their disastrous effect upon the frogs. Within the last two years the entire series of pools in the study area was levelled by a bull­dozer. In 1950 the frogs made futile efforts to breed in the shallow water of what had once been their breeding pools. By 1951 the population had dropped to a small fraction, with none of the one year class present in the area.

Forest fires, diversion of streams, cultivation of farm lands destroy breeding areas of this species while destruction of forest cover removes the habitat that is occupied for eight to nine months of the year.
CONCLUSIONS AND SUMMARY

The present study embodies the results of seven years' investigation on the natural history of *Pseudacris brachyphona* in which special attention has been given to the movements and behavior of marked individuals.

The life history, as worked out near Huntington, West Virginia, through observations of breeding colonies in the field and experiments and analysis in the laboratory of detailed data accumulated during these observations may be summarized as follows:

1. *Pseudacris brachyphona* may be distinguished from members of its genus by its characteristic dorsal pattern and longer legs in relation to body length. There is pronounced sexual dimorphism. The dorsal pattern displays an individualism which is retained throughout life.

2. It inhabits the Appalachian Plateau with most of the records occurring in western Pennsylvania, West Virginia, southeastern Ohio and eastern Kentucky.

3. Throughout its range it is a woodland species.

4. At Huntington, West Virginia, it emerges from hibernation in late February or early March.

5. The temperature for several weeks prior to its emergence influence the date of initial activity, the warmer year being accompanied by an earlier emergence. Immediate rainfall bears no relation to emergence.

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6. Upon emergence from hibernation the males congregate in pools of quiet water within or not far removed from the woodland habitat and call lustily.

7. There is evidence that the rate of call is influenced by the temperature of the air and the water as well as the physiological state of the animal.

8. Calling males remain in the vicinity of the pools throughout the length of the breeding season, while the females visit the pools for one night during the season.

9. Sex recognition is preceded by a form of courtship initiated by the female. Clasping of the male occurs when the female presents herself by backing between the male's forelegs.

10. Clasped females swim to deeper water where the pair remains submerged for some time before oviposition.

11. During oviposition the female clings to some slender vegetation, initiates the egg laying process by a characteristic flexure of her back and a rigid extension of her hind legs that is accompanied by a shifting of the male backward while he discharges sperms over her packet of eggs. The eggs are fastened to the supporting vegetation.

12. Oviposition may occupy two or three hours, with the total complement of 300 to 1,500 eggs being laid.

13. The eggs are deposited in a loose cluster that contains from four to 133 eggs with a mean of forty.

14. The eggs range from 1.34 to 1.71 mm. in diameter
with a single gelatinous envelope that averages 7.0 mm. in diameter.

15. Hatching occurs after about ninety-eight hours at a temperature of 74°F. It is a gradual process that occupies two hours.

16. The embryo measures 4.5 to 5.0 mm. at hatching.

17. A description of the tadpole is given.

18. Transformation occurs fifty to sixty-four days after hatching, depending upon the temperature.

19. The breeding season may be divided into: (a) a period of maximum activity, (b) a period of decline in activity, and (c) a period of sporadic activity.

20. The food of the adult consists of small insects, larvae and worms that were obtained on or close to the surface of the ground.

21. A study of the growth and movements of 1,189 marked individuals, marked by toe clipping, was made. Of this number, 406 or 34.1 per cent, were recovered at least once. Males exceeded the females, not only in number marked but in percentage of recoveries. Recoveries of individual frogs ranged from once to five times in one season.

Movements between the hibernating area and breeding pools showed that the pre-breeding movement is downhill toward the valley pools, the frogs pausing temporarily at hillside pools before moving on toward lower pools. During the breeding season there is some movement of the males
between pools. The post-breeding migration is uphill, away from the pools. Late season breeding activity was confined largely to hillside pools close to the summer range and away from the more exposed valley pools. Maximum distances travelled were 2,000 feet within the same season by six frogs and 4,000 feet from one season to the next by three frogs. In their movements the frogs crossed highways and a stream six feet wide.

The data show that the frogs tend to return to the same pool which they had used the previous seasons for breeding. The data point to the supposition that the frogs return to the same pools to breed from which they had transformed.

22. Data based on the recoveries of 360 male and female frogs from one and two years after marking over a period of four years were used to study growth. The mean annual increment was 2.8 mm. for the males for the year after they were first marked. Growth was greatest in the smaller frogs. A number of frogs showed a loss in length from one year to the next, a phenomenon observed by other workers with other species of Salientia. The growth increment is most rapid during the first year after transformation and decreases as the frogs get older.

Data from the returns indicate that *Pseudacris brachyphona* attains a maximum age of five years. It was concluded that age determination based on size groups in a frog were valueless because of the overlap of the individual
growth increment.

23. The number of years required for a year class to shrink to zero was found to be six years.

The composition of a population of the frogs within an area was found to consist of 71 per cent one-year old frogs, 20 per cent two year-olds, 6.8 per cent three year-olds, 1.8 four year-olds, and 0.4 per cent five-year-olds. The population declines at the rate of 71.9 per cent the first year, 67 per cent the second year, 75 per cent the third year, and 82 per cent the fourth year. The average age was computed to be 1.4 years.

24. The breeding behavior of Pseudacris brachyphona was compared with that of P. n. triseriata. Differences were found in habitat, extent of breeding season, diurnal activity, call and the eggs. Similarities were observed in amplexus and oviposition. Crosses and reciprocal crosses between the two species resulted in tadpoles in each case.

The breeding behavior of Pseudacris brachyphona was also compared with Hyla c. crucifer since these two were known to breed in the same pools. Differences between these two species were noted in the eggs, call and oviposition. Crosses between female Hyla crucifer and male Pseudacris brachyphona were unsuccessful in producing tadpoles while the reciprocal cross resulted in 43 per cent cleavage and 132 tadpoles.

Although there is no evidence that hybridization occurs in nature, it was concluded that because of the
differences in the breeding behavior the occasional hybridization that might result would have little effect on altering the character of the species.
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<table>
<thead>
<tr>
<th>Earliest date of call</th>
<th>Earliest date for female</th>
<th>Earliest date for eggs</th>
<th>Transformed individuals first seen</th>
<th>Latest date of call</th>
<th>Latest date for eggs</th>
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<td>June 29</td>
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* Station at Huntington, West Virginia.  ** No data available.
**TABLE II**

TEMPERATURE AND RAINFALL CONDITIONS PRIOR TO EMERGENCE AND ON DAY OF EMERGENCE
FOR PSEUDACRIS BRACHYPHONA*

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<th>Date of first appearance</th>
<th>Maximum temperature day heard calling</th>
<th>Minimum temperature day heard calling</th>
<th>Maximum temperature day previous</th>
<th>Minimum temperature day previous</th>
<th>Precipitation 24 hours before emergence</th>
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<td>.10</td>
</tr>
<tr>
<td>1948 Feb. 27</td>
<td>58</td>
<td>32</td>
<td>61</td>
<td>51</td>
<td>.40</td>
<td>.41</td>
</tr>
<tr>
<td>1949 Feb. 22</td>
<td>66</td>
<td>42</td>
<td>56</td>
<td>40</td>
<td>.00</td>
<td>.09</td>
</tr>
</tbody>
</table>

* Weather data collected by U. S. Engineer's Office at Huntington, West Virginia, one mile from study area.

** No data.
<table>
<thead>
<tr>
<th>Pool</th>
<th>Length</th>
<th>Width</th>
<th>Surface area</th>
<th>Average depth</th>
<th>Maximum depth</th>
<th>Distance to woods</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>60 ft.</td>
<td>15 ft.</td>
<td>450 sq. ft.</td>
<td>18 in.</td>
<td>30 in.</td>
<td>50 yds.</td>
</tr>
<tr>
<td>2</td>
<td>30</td>
<td>20</td>
<td>400</td>
<td>4</td>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td>3 **</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>30</td>
<td>8</td>
<td>240</td>
<td>8</td>
<td>30</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>30</td>
<td>30</td>
<td>700</td>
<td>10</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>10</td>
<td>0.66</td>
<td>6</td>
<td>3</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>7</td>
<td>40</td>
<td>3</td>
<td>100</td>
<td>8</td>
<td>18</td>
<td>30</td>
</tr>
<tr>
<td>8</td>
<td>50</td>
<td>0.75</td>
<td>42</td>
<td>3</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>9</td>
<td>30</td>
<td>.50</td>
<td>15</td>
<td>2</td>
<td>3</td>
<td>0</td>
</tr>
</tbody>
</table>

* Huntington, West Virginia.

**Included in Pool 1.
TABLE IV

RELATION OF AIR AND WATER TEMPERATURES TO VOCAL ACTIVITY OF PSEUDACRIS BRACHYPHONA

<table>
<thead>
<tr>
<th>Date</th>
<th>Air temperature</th>
<th>Water temperature</th>
<th>Vocal activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>March 8</td>
<td>37°F</td>
<td>40°F</td>
<td>few calling</td>
</tr>
<tr>
<td>&quot; 9</td>
<td>43</td>
<td>46</td>
<td>few calling</td>
</tr>
<tr>
<td>&quot; 12</td>
<td>57</td>
<td>48</td>
<td>large chorus</td>
</tr>
<tr>
<td>&quot; 13</td>
<td>56-44</td>
<td>54</td>
<td>few calling</td>
</tr>
<tr>
<td>&quot; 15</td>
<td>60</td>
<td>56</td>
<td>large chorus</td>
</tr>
<tr>
<td>&quot; 21</td>
<td>34</td>
<td>44</td>
<td>none calling</td>
</tr>
<tr>
<td>&quot; 21</td>
<td>34</td>
<td>48</td>
<td>few calling</td>
</tr>
<tr>
<td>&quot; 22</td>
<td>37</td>
<td>46</td>
<td>few calling</td>
</tr>
<tr>
<td>&quot; 23</td>
<td>52</td>
<td>54</td>
<td>large chorus</td>
</tr>
<tr>
<td>&quot; 24</td>
<td>42</td>
<td>50</td>
<td>large chorus</td>
</tr>
</tbody>
</table>

* Season of 1945 at Huntington, West Virginia
TABLE V

RECOVERY OF PSEUDACRIS BRACHYPHONA MARKED THE
PREVIOUS YEAR AT TRANSFORMATION*

<table>
<thead>
<tr>
<th>Frog no.</th>
<th>Released</th>
<th>Size when released</th>
<th>Recovered</th>
<th>Size when recovered</th>
</tr>
</thead>
<tbody>
<tr>
<td>565</td>
<td>June 16, 1946</td>
<td>11.6 mm.</td>
<td>Mar. 23, 1947</td>
<td>29.6 mm.</td>
</tr>
<tr>
<td>569</td>
<td>June 2, 1946</td>
<td>11.6</td>
<td>Mar. 23, 1947</td>
<td>29.4</td>
</tr>
<tr>
<td>578</td>
<td>June 2, 1946</td>
<td>11.6</td>
<td>Mar. 23, 1947</td>
<td>28.1</td>
</tr>
<tr>
<td>666</td>
<td>June 2, 1946</td>
<td>11.6</td>
<td>Mar. 24, 1947</td>
<td>27.3</td>
</tr>
<tr>
<td>712</td>
<td>June 2, 1946</td>
<td>11.6</td>
<td>Apr. 3, 1947</td>
<td>28.4</td>
</tr>
<tr>
<td>764</td>
<td>June 2, 1946</td>
<td>11.6</td>
<td>Mar. 31, 1947</td>
<td>27.0</td>
</tr>
</tbody>
</table>

* Huntington, West Virginia.
<table>
<thead>
<tr>
<th></th>
<th>P. brachyphona</th>
<th>P.n. triseriata</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diameter of egg</td>
<td>1.34-1.71 mm.</td>
<td>0.9-1.2 mm.</td>
</tr>
<tr>
<td>Diameter including envelope</td>
<td>6.0 -8.5 mm.</td>
<td>5.0-7.8 mm.</td>
</tr>
<tr>
<td>Number of envelopes</td>
<td>one</td>
<td>one or two**</td>
</tr>
<tr>
<td>Size of largest egg mass</td>
<td>133 eggs</td>
<td>300 eggs</td>
</tr>
<tr>
<td>Size of average egg mass</td>
<td>40 eggs</td>
<td>74 eggs</td>
</tr>
<tr>
<td>Largest complement of eggs</td>
<td>1,479</td>
<td>1,500</td>
</tr>
</tbody>
</table>

*Smith (1934) reports Kansas specimens of Pseudacris nigrita triseriata with two egg envelopes whereas Livezey and Wright (1947), and Bragg (1948) report but one. Ohio specimens had but one.*
TABLE VII

AN ANALYSIS OF THE FOOD OF THIRTY-ONE SPECIMENS OF *PSEUDACRIS BRACHYPHONA*

<table>
<thead>
<tr>
<th>Food item</th>
<th>Number of stomachs containing item</th>
<th>Percentage of stomachs containing item</th>
<th>Total number of item in all stomachs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coleoptera</td>
<td>14</td>
<td>45</td>
<td>21</td>
</tr>
<tr>
<td>Spiders</td>
<td>8</td>
<td>25</td>
<td>8</td>
</tr>
<tr>
<td>Hemiptera</td>
<td>4</td>
<td>13</td>
<td>4</td>
</tr>
<tr>
<td>Ants</td>
<td>3</td>
<td>9</td>
<td>3</td>
</tr>
<tr>
<td>Aphids, leaf hoppers</td>
<td>3</td>
<td>9</td>
<td>3</td>
</tr>
<tr>
<td>Insect remains</td>
<td>3</td>
<td>9</td>
<td>3</td>
</tr>
<tr>
<td>Diptera</td>
<td>1</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Centipede</td>
<td>1</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Pill bug</td>
<td>1</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Earthworm</td>
<td>1</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Lepidopterous larva</td>
<td>1</td>
<td>3</td>
<td>1</td>
</tr>
</tbody>
</table>
### TABLE VIII

**NUMBER OF *PSEUDACRIS BRACHYPHONA* RECOVERED FROM THOSE MARKED FROM 1945 THROUGH 1949**

<table>
<thead>
<tr>
<th>Year marked</th>
<th>Number marked</th>
<th>Number recovered</th>
<th>Per cent recovered</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
<td>Male</td>
</tr>
<tr>
<td>1945</td>
<td>192</td>
<td>61</td>
<td>108</td>
</tr>
<tr>
<td>1946</td>
<td>237</td>
<td>23</td>
<td>110</td>
</tr>
<tr>
<td>1947</td>
<td>286</td>
<td>45</td>
<td>106</td>
</tr>
<tr>
<td>1948</td>
<td>160</td>
<td>28</td>
<td>56</td>
</tr>
<tr>
<td>1949</td>
<td>143</td>
<td>14</td>
<td>6</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>1,018</strong></td>
<td><strong>171</strong></td>
<td><strong>386</strong></td>
</tr>
<tr>
<td><strong>Grand Total</strong></td>
<td><strong>1,189</strong></td>
<td></td>
<td><strong>406</strong></td>
</tr>
</tbody>
</table>
TABLE IX

RECOVERIES OF ALL FROGS MARKED FOR EACH YEAR CLASS FOR PSEUDACRIS BRACHYPHONA

<table>
<thead>
<tr>
<th>Year marked</th>
<th>Number of times recovered</th>
<th>Year recovered</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1945 1946 1947 1948 1949</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>42 34 19 5 2</td>
<td>102</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>17 12 8 1 0</td>
<td>38</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>6 9 1 0 0</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>5 0 0 0 0</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>0 1 0 0 0</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>33 56 20 5</td>
<td>114</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>5 19 3 0</td>
<td>27</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>1 4 1 0</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>37 60 14</td>
<td>111</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>2 19 0</td>
<td>21</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>1 4 0</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>0 1 0</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>24 25</td>
<td>49</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>4 5</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>0 0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>8</td>
<td>8</td>
<td></td>
</tr>
</tbody>
</table>

Total 70 95 147 142 59 513

115
# TABLE X

**DISTRIBUTION OF *PSEUDACRIS BRACHYPHONA* AT BREEDING POOLS**

<table>
<thead>
<tr>
<th>Date</th>
<th>Pool 1 Male</th>
<th>Pool 1 Female</th>
<th>Pool 2 Male</th>
<th>Pool 2 Female</th>
<th>Pool 4 Male</th>
<th>Pool 4 Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>March 23</td>
<td>43</td>
<td>3</td>
<td>36</td>
<td>4</td>
<td>33</td>
<td>2</td>
</tr>
<tr>
<td>24</td>
<td>52</td>
<td>21</td>
<td>7</td>
<td>2</td>
<td>33</td>
<td>6</td>
</tr>
<tr>
<td>31</td>
<td>36</td>
<td>8</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>April 4</td>
<td>48</td>
<td>8</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>10</td>
<td>59</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>14</td>
<td>5</td>
<td>0</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>19</td>
<td>0</td>
<td>0</td>
<td>6</td>
<td>0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>May 21</td>
<td>0</td>
<td>0</td>
<td>26</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>26</td>
<td>0</td>
<td>0</td>
<td>18</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

*Season of 1947 at Huntington, West Virginia.*
<table>
<thead>
<tr>
<th>Year marked</th>
<th>Recovered at one pool</th>
<th>Recovered at more than one pool</th>
<th>GRAND TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number of times recovered</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>1945</td>
<td>37</td>
<td>12</td>
<td>6</td>
</tr>
<tr>
<td>1946</td>
<td>20</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>1947</td>
<td>41</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1948</td>
<td>38</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>1949</td>
<td>8</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>144</td>
<td>24</td>
<td>11</td>
</tr>
<tr>
<td>Marked in pool</td>
<td>1946 pool</td>
<td>1947 pool</td>
<td>1948 pool</td>
</tr>
<tr>
<td>---------------</td>
<td>----------</td>
<td>----------</td>
<td>----------</td>
</tr>
<tr>
<td></td>
<td>1 2 4</td>
<td>1 2 4</td>
<td>1 2 4</td>
</tr>
<tr>
<td>1</td>
<td>21 5 8</td>
<td>27 0 4</td>
<td>59 2 6</td>
</tr>
<tr>
<td>2</td>
<td>0 4 1</td>
<td>1 14 1</td>
<td>3 2 0</td>
</tr>
<tr>
<td>4</td>
<td>4 1 14</td>
<td>1 3 14</td>
<td>6 0 9</td>
</tr>
</tbody>
</table>
### TABLE XIII

**SIZE GROUPS OF *Pseudacris brachyphona* MARKED FROM 1945 THROUGH 1949**

<table>
<thead>
<tr>
<th>Year marked</th>
<th>Length in millimeters</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1945 ♂</td>
<td>18</td>
<td>80</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>22</td>
</tr>
<tr>
<td>1946 ♂</td>
<td>14</td>
<td>84</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>5</td>
</tr>
<tr>
<td>1947 ♂</td>
<td>7</td>
<td>113</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>24</td>
</tr>
<tr>
<td>1948 ♂</td>
<td>1</td>
<td>47</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>20</td>
</tr>
<tr>
<td>1949 ♂</td>
<td>3</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>43</td>
<td>374</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>54</td>
</tr>
</tbody>
</table>

* Huntington, West Virginia.

** 1,189 frogs marked by end of 1949 season. No measurements taken on twenty-six of these frogs.
## TABLE XIV

LENGTH AND ANNUAL GROWTH INCREMENT OF 291 MARKED MALE PSEUDACRIS BRACHYPHONA

<table>
<thead>
<tr>
<th>Length in millimeters when first marked</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>23 24 25 26 27 28 29 30 31 32 33</td>
<td></td>
</tr>
<tr>
<td>----------------------------------------</td>
<td>-------</td>
</tr>
<tr>
<td>9 1</td>
<td>1</td>
</tr>
<tr>
<td>8 2</td>
<td>2</td>
</tr>
<tr>
<td>7 4 1 3 1</td>
<td>10</td>
</tr>
<tr>
<td>6 4 8 3 1</td>
<td>16</td>
</tr>
<tr>
<td>5 4 5 13 10 3 1</td>
<td>36</td>
</tr>
<tr>
<td>4 2 2 9 9 16 9 2 1</td>
<td>50</td>
</tr>
<tr>
<td>3 2 5 6 14 11 5 1 1</td>
<td>45</td>
</tr>
<tr>
<td>2 2 3 2 9 10 10 7 4 1</td>
<td>48</td>
</tr>
<tr>
<td>1 3 9 10 7 7 2</td>
<td>38</td>
</tr>
<tr>
<td>0 1 2 8 7 7 2</td>
<td>27</td>
</tr>
<tr>
<td>-1 1 1 6 4 2</td>
<td>14</td>
</tr>
<tr>
<td>-2</td>
<td>4</td>
</tr>
<tr>
<td>Total</td>
<td>11    13    33    35    52    47    35    24    27    11    3  291</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Mean Annual Increment</th>
</tr>
</thead>
<tbody>
<tr>
<td>6.0 4.8 4.5 4.2 3.4 2.4 1.5 1.1 0.5 -.36 -1.3 2.8</td>
</tr>
</tbody>
</table>

Numbers in thousands.
**TABLE XV**

**LENGTH AND ANNUAL GROWTH INCREMENT OF NINE MARKED FEMALE *PSEUDACRIS BRACHYPHONA***

<table>
<thead>
<tr>
<th>Annual increment in millimeters</th>
<th>Length in millimeters when first marked</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>31</td>
<td>32</td>
</tr>
<tr>
<td>--------------------------------</td>
<td>----</td>
<td>----</td>
</tr>
<tr>
<td>4</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>-1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Growth increment in millimeters</td>
<td>Length in millimeters when first marked</td>
<td>Total</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>-----------------------------------------</td>
<td>-------</td>
</tr>
<tr>
<td></td>
<td>23</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td></td>
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<tr>
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<tr>
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TABLE XVII

RETURNS FROM *Pseudacris Brachyphona* MARKED FROM 1945 THROUGH 1949

<table>
<thead>
<tr>
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<tbody>
<tr>
<td>oo</td>
<td>192</td>
<td>55</td>
<td>24</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>oo</td>
<td>61</td>
<td>1</td>
<td>4</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Marked 1946</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>oo</td>
<td></td>
<td>237</td>
<td>76</td>
<td>24</td>
<td>4</td>
</tr>
<tr>
<td>oo</td>
<td></td>
<td>23</td>
<td>3</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Marked 1947</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>oo</td>
<td></td>
<td>286</td>
<td>78</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>oo</td>
<td></td>
<td>45</td>
<td>6</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Marked 1948</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>oo</td>
<td></td>
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<td>160</td>
<td>29</td>
<td></td>
</tr>
<tr>
<td>oo</td>
<td></td>
<td></td>
<td>28</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Totals</td>
<td>253</td>
<td>316</td>
<td>438</td>
<td>302</td>
<td>51</td>
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</table>
TABLE XVIII

ESTIMATED POPULATION OF MALE PSEUDACRIS BRACHYPHONA
BASED ON RECOVERIES OF MARKED AND UNMARKED INDIVIDUALS*

<table>
<thead>
<tr>
<th>Year</th>
<th>Number marked previously</th>
<th>Date recovered</th>
<th>Number recovered marked</th>
<th>Number recovered unmarked</th>
<th>Estimated population</th>
</tr>
</thead>
<tbody>
<tr>
<td>1946</td>
<td>192</td>
<td>March 17</td>
<td>14</td>
<td>64</td>
<td>1,069</td>
</tr>
<tr>
<td>1947</td>
<td>429</td>
<td>March 23</td>
<td>33</td>
<td>79</td>
<td>1,456</td>
</tr>
<tr>
<td>1947</td>
<td>429</td>
<td>March 24</td>
<td>24</td>
<td>69</td>
<td>1,662</td>
</tr>
<tr>
<td>1948</td>
<td>715</td>
<td>March 16</td>
<td>33</td>
<td>43</td>
<td>1,646</td>
</tr>
<tr>
<td>1948</td>
<td>715</td>
<td>March 23</td>
<td>39</td>
<td>60</td>
<td>1,815</td>
</tr>
</tbody>
</table>

* For seasons of 1946, 1947 and 1948 at Huntington, West Virginia.
### TABLE XIX

**COMPOSITION OF PSEUDACRIS BRACHYPHONA CAPTURES**

<table>
<thead>
<tr>
<th>Year</th>
<th>Newly marked</th>
<th>Returns</th>
<th>Total catch</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1 yr.</td>
<td>2 yr.</td>
</tr>
<tr>
<td>1945</td>
<td>253</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1946</td>
<td>260</td>
<td>56</td>
<td></td>
</tr>
<tr>
<td>1947</td>
<td>331</td>
<td>79</td>
<td>28</td>
</tr>
<tr>
<td>1948</td>
<td>188</td>
<td>84</td>
<td>24</td>
</tr>
<tr>
<td>1949</td>
<td>157</td>
<td>30</td>
<td>14</td>
</tr>
<tr>
<td>Totals</td>
<td>1,189</td>
<td>269</td>
<td>66</td>
</tr>
<tr>
<td>Averages</td>
<td>238</td>
<td>67</td>
<td>22</td>
</tr>
<tr>
<td>Scale of 100</td>
<td>100</td>
<td>28.1</td>
<td>9.2</td>
</tr>
</tbody>
</table>
TABLE XX
RESULTS OF MATINGS AND CROSS MATINGS OF THREE SPECIES OF HYLIDAE

<table>
<thead>
<tr>
<th>Cross</th>
<th>Number of crosses producing eggs</th>
<th>Average number of eggs laid</th>
<th>Average per cent of cleavage</th>
<th>Number of tadpoles</th>
<th>Number of crosses with cleavage</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. brachyphona x ♂ P. brachyphona</td>
<td>14</td>
<td>285</td>
<td>68</td>
<td>1,263</td>
<td>11</td>
</tr>
<tr>
<td>P. brachyphona x ♂ P. n. triseriata</td>
<td>3</td>
<td>480</td>
<td>59</td>
<td>328</td>
<td>2</td>
</tr>
<tr>
<td>P. brachyphona x ♂ Hyla crucifer</td>
<td>1</td>
<td>578</td>
<td>43</td>
<td>132</td>
<td>1</td>
</tr>
<tr>
<td>P. n. triseriata x ♂ P. n. triseriata</td>
<td>3</td>
<td>401</td>
<td>81</td>
<td>600</td>
<td>3</td>
</tr>
<tr>
<td>P. n. triseriata x ♂ P. brachyphona</td>
<td>4</td>
<td>299</td>
<td>87</td>
<td>462</td>
<td>4</td>
</tr>
<tr>
<td>Hyla crucifer x ♂ Hyla c. crucifer</td>
<td>2</td>
<td>171</td>
<td>71</td>
<td>107</td>
<td>2</td>
</tr>
<tr>
<td>Hyla c. crucifer x ♂ P. n. triseriata</td>
<td>1</td>
<td>150</td>
<td>34</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Hyla c. crucifer x ♂ P. brachyphona</td>
<td>1</td>
<td>73</td>
<td>20</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>
Figure 1
Map of the area in which the study was done at Huntington, West Virginia, traced from a contour map of the Guyandotte Quadrangle.
Figure 1.
Figure 2

Reproduction of an aerial photograph of the area.
Figure 3

Two specimen pages from field notebook. The number at the top of the page represents the number of the frog. The sex and length in millimeters are given to the left below the number. The formula for the toes clipped are shown at the right. The diagram represents the extent of pattern on the dorsal surface. The data below these figures represent the captures of the frog.
Figure 3.
Figure 4

This photograph shows the technique of clipping the toes. A microscope lamp is mounted under the stage of a binocular dissecting microscope. The light shining through the delicate membranes of the toes enabled the digits to be clipped with less damage to the cartilages.
Figure 5.

Figure 6.
Figure 7


1946

March 23. Calling in Pool 2.
March 24. Released in Pool 2.

1947

March 23. Calling in Pool 2.
March 24. Anesthetized in laboratory with chloretone, photographed for this figure and on
April 3. Calling in Pool 4.
April 4. Released in Pool 4.
May 30. Died in the laboratory.

Figure 8


1946


1947

March 26. Anesthetized with chloretone in laboratory, photographed for this figure and on
May 21. Calling at Pool 5.

1948

March 2. Calling at Pool 2.
March 4. Released in Pool 2.
March 15. Calling in Pool 2.
March 16. Released in Pool 2.
March 23. Calling in Pool 1.
March 24. Released in Pool 1.
Figure 7

1946
March 23. Calling in Pool 2.
March 24. Released in Pool 2.

1947
March 23. Calling in Pool 2.
March 24. Anesthetized in laboratory with chloretone, photographed for this figure and on
April 3. Calling in Pool 4.
April 4. Released in Pool 4.
May 30. Died in the laboratory.

Figure 8

1946

1947
March 26. Anesthetized with chloretone in laboratory, photographed for this figure and on
May 21. Calling at Pool 5.

1948
March 2. Calling at Pool 2.
March 4. Released in Pool 2.
March 15. Calling in Pool 2.
March 16. Released in Pool 2.
March 23. Calling in Pool 1.
March 24. Released in Pool 1.
Figure 9

Body length frequency curve for *Pseudacris brachyphona*
Figure 9.
Figure 10

Distribution of *Pseudacris brachyphona*
Figure 10.
Figure 11

Temperature and rainfall relations to the emergence of *Pseudacris brachyphona*. The deviation from normal in inches and degrees is shown against the earliest date of appearance.
Fig 11. Temperature and rainfall relations to the emergence of Pseudacris brachyphona. The deviation from normal in inches and degrees for a 30 day period prior to emergence is shown against the earliest date of appearance.

Figure 11.
Figure 12

The number of male and female *Pseudacris brachyphona* at the pools during the breeding season.
Figure 12.
Figure 13

Pool No. 2 looking from the east. The highway that runs through the valley is to the left and downhill about fifty yards.
Figure 14

Pool No. 4 as seen from the west. The highway that runs through the valley is to the left and above the pool.
Figure 15

Relation between the rate of call and the air and water temperature in *Pseudacris brachyphona*.
Figure 15.
Figure 16

Late season movement in *Pseudacris brachyphona.*
The pools are represented by Roman numerals. The direction of the movement is shown by arrows, with the number of frogs moving in that direction shown by the arabic numeral. The elevation of the pools above the valley floor is shown in the upper left hand corner.
VERTICAL DISTRIBUTION OF POOLS

900 FT.

V, II
VI, VII, VIII
I, IV

600 FT. VALLEY FLOOR

0.5 MILE

Figure 16.
Growth of 291 male *Pseudacris brachyphona* for a one year period.
ANNUAL GROWTH INCREMENT

<table>
<thead>
<tr>
<th>Length when marked (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.3 2.4 2.5 2.6 2.7 2.8</td>
</tr>
</tbody>
</table>

Diagram showing data points.
Figure 18

Growth of 291 adult male *Pseudacris brachyphona* for one year period plotted against the growth of the same frogs the second year. The vertical line at the right represents the mean maximum growth of these male frogs.
Figure 18

NUMBER OF FROGS

FIRST YEAR

SECOND YEAR

20 40 60 80

35 mm.
Figure 19

Composition of a population of *Pseudacris brachyphona* in year classes. The 1945 year class can be traced through to extinction.
Figure 20

Survivorship curve for *Pseudacris brachyphona*. The population declines approximately 70 per cent each year from that of the previous year.
Figure 20.
I, Norman Bayard Green, was born in Bloomington, Garrett County, Maryland, November 15, 1905. I received my secondary school education in the public schools of Elkins, West Virginia. My undergraduate training was obtained at Davis and Elkins College where I received the degree of Bachelor of Science in 1926. I accepted a position as teacher in Elkins High School in 1926. My graduate studies were continued during the summer at West Virginia University from which school I received the degree of Master of Science in 1931. In September, 1938, I was appointed a critic teacher in the campus Laboratory School of Marshall College. In 1945 I was appointed Assistant Professor of Zoology at Marshall College and Head of the Department of Zoology. I was promoted to Associate Professor in 1947, a position which I hold at this time. I enrolled at Stone Institute of Hydrobiology in June, 1942, where I continued my studies during the summer months, with the year 1946 being spent in residence. My time during the following years was divided between my teaching duties at Marshall College and the completion of the requirements for the degree of Doctor of Philosophy.