













A TYPICAL BREEDING-PLACE FOR THE BULLFROG, BEEBE LAKE.



HYPOTHETICAL POND, SHOWING FORM, DISTRIBUTION, AND ARRANGEMENT OF ANURAN EGG COMPLEMENTS.

- A. Green-frog.
- B. American toad.
- C. Pickerel-frog.

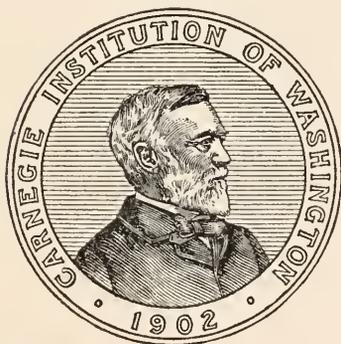
- D. Tree-toad.
- E. Bullfrog.
- F. Meadow-frog.

- G. Peeper.
- H. Wood-frog.
- I. Swamp Cricket-frog.

# NORTH AMERICAN ANURA

## LIFE-HISTORIES OF THE ANURA OF ITHACA, NEW YORK

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- |   |  |
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| B. <i>Rana clamata</i> .     | E. <i>Hyla versicolor</i> . | H. <i>Bufo lentiginosus americanus</i> . |
| C. <i>Rana palustris</i> .   | F. <i>Rana sylvatica</i> .  |  |

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- |  |                            |                              |
|--|----------------------------|------------------------------|
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| 2. <i>Hyla pickeringii</i> .             | 5. <i>Rana palustris</i> . | 8. <i>Rana catesbeiana</i> . |
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2. An adult wood-frog.
3. A series of wood-frogs from tadpole to transformed wood-frog. Dorsal aspect.  $\times 1$ .

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- |  |                              |                              |
|--|------------------------------|------------------------------|
| A. <i>Bufo lentiginosus americanus</i> . | C. <i>Hyla pickeringii</i> . | F. <i>Rana catesbeiana</i> . |
| B. <i>Rana palustris</i> .               | D. <i>Rana clamata</i> .     | G. <i>Rana pipiens</i> .     |
|  | E. <i>Hyla versicolor</i> .  | H. <i>Rana sylvatica</i> .   |



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NORTH AMERICAN ANURA

LIFE-HISTORIES OF THE ANURA OF ITHACA,  
NEW YORK

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By ALBERT HAZEN WRIGHT



## INTRODUCTION.

Notwithstanding the extensive use of our American Anura for anatomical and embryological purposes, comparatively little attention has been given to the collection of definite data bearing upon the breeding habits and larvæ of this group. In this connection, Boulenger (1897), in the preface to his work upon "The Tailless Batrachians of Europe," observes:

"I would also express a hope that a little book of this kind \* \* \* may have the effect of stimulating interest in a subject that has been too much neglected, and in the cultivation of which new workers will find much to repay their efforts, especially if applied in other regions of the globe, which, though richer in Batrachians, have as yet yielded little or nothing to our knowledge of the life-histories."

Dr. Gill (1898), in his review of the work just mentioned, remarks that he hopes this monograph\* "may serve as a model for other lands, and not least for the United States. \* \* \* Every sojourner in the country must have noticed the masses of transparent jelly-like spheres in the water, but none in the United States could refer such masses with certainty to the parent species." To a local study of these very phases of Anuran life, my investigations for the past seven or eight years have been directed.

The notes here brought together are largely the outcome of eight years' continuous and personal study in this region. In addition, the records of the Department of Zoology of Cornell University, from 1900 to 1904, have been added, and acknowledgments for these as well as for encouragement, assistance, and criticisms are gratefully extended to Professors Burt G. Wilder, H. D. Reed and J. G. Needham. To Dr. A. A. Allen, I am indebted for notes, for the use of several pertinent photographs and assistance in taking other photographs, particularly the flash-lights of croaking males. To Dr. Theodore N. Gill is due my gratitude for his interest in this work from its inception to its completion, and in Boulenger's "Tailless Batrachians of Europe" and Dr. Gill's review of it lie the model and original impetus of this study. Especial thanks are due Professors S. H. Gage, T. L. Hankinson, C. O. Houghton, C. R. Crosby and G. C. Embury. My greatest indebtedness is due my wife, Anna Allen Wright, who has contributed most of the illustrations and given this subject sufficient interest, work, and criticism to be its junior author. Finally, the Carnegie Institution of Washington assumed the publication of the book and has cooperated with me in endeavoring to present it in a suitable form.

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\* Science, N. S., vol. VIII, No. 209, pp. 933, 937.

## THE REGION STUDIED AND THE METHODS PURSUED.

The region of this study is at the southern end of Cayuga Lake and most of our observations were made in the immediate vicinity of Ithaca, New York. In fact, it was found that on the University property alone all the eight local species occurred in sufficient numbers to make possible the study of their life-histories. Numerous trips beyond these confines were made, but the above area proved the center of the most careful attention.

Within a radius of 3 miles of the Cornell University Campus most varied localities and environments are found. The region is an area of considerable glaciation and presents many different types of land topography associated with such physiographic history. The city of Ithaca and the Renwick marshes between the city and the southern end of the lake represent a fine delta, to whose level numerous hanging valleys suddenly drop. When Cayuga Lake, a former river-bed, was deeply eroded, the preglacial tributary streams in the last mile or mile and a half of their courses had to cut new postglacial channels to the new level of the present Cayuga Lake and dropped 400 feet to accomplish this end. Two of these postglacial gorges, Cascadilla and Fall Creek ravines, serve roughly as the northern and southern boundaries of our campus and of the region of my immediate interest in this paper.

The northern part of the delta (Renwick marshes) was very rich in Anura and harbored the whole eight species, the forms occurring in the following order of abundance: meadow-frog, toad, green-frog, peeper, tree-toad, pickerel-frog, bullfrog, and wood-frog. In ravines proper, the pickerel-frog is the most plentiful. When the postglacial ravines crossed old preglacial buried courses, amphitheatres were often formed and in such places (Beebe Lake) dams were constructed. Hither the toads, bullfrogs, green-frogs, meadow-frogs, and pickerel-frogs resort. Along these water-courses, where they approach their upland, gentle-sloping, preglacial course, numerous isolated pools occur near the streams. To these pools (some in woods and others in the open) the green-frogs, wood-frogs, peepers, and tree-toads come for breeding. In the upland back-waters and widened mill-ponds near the sources of our streams, the pickerel-frogs appear much in evidence. In one of our highland pools seven species breed and the tree-toads are common.

Maps of the various places were made and on each map was entered every egg-cluster found on the daily visits. Each cluster was followed through hatching and in some cases farther. The purpose of this method was to arrive at the hatching periods. With daily visits to these ponds from March 25 to August 15, the transformations could be recorded, and the periods of larval life determined.

Coincident with this out-of-door method, a parallel study was attempted in the laboratory. In almost every species mated pairs captured afield were isolated. The eggs from these captive pairs were taken through hatching and in some cases almost to transformation.

Very good results were also obtained from night-collecting and study with an electric flash-lamp. With this apparatus the capture of mated pairs was facilitated and many interesting observations upon the breeding-season conduct were recorded. The water-photographs of the series of each species, egg-areas, tadpoles, etc., were taken from live specimens. The measurements and characters of the eggs, tadpoles, and transformed individuals were based upon a large series of specimens, both living and preserved.

### A CATALOGUE OF THE ITHACAN ANURA.\*

The Anura of Ithaca include 8 species, representing 3 genera. These are *Bufo*, *Hyla*, and *Rana*.

*Bufo lentiginosus americanus* (LeConte). The *Common Toad*.—This terrestrial species is abundant, being found in almost every locality where sufficient cover exists for hiding during the day. Only at the breeding season are they found in the water.

*Hyla pickeringii* Holbrook. The *Peeper*.—In the spring it is common in ponds and marshes; thereafter, it is seldom seen while in the woods and upon the trees.

*Hyla versicolor* LeConte. The *Tree-toad*.—This common species is general in its distribution, both at the breeding season and later, when in the woods and among the trees.

*Rana pipiens* Schreber. The *Leopard- or Meadow-frog*.—This very abundant and swamp-loving form, after the breeding season, is commonly found in the meadow-lands.

*Rana palustris* LeConte. The *Pickerel-frog*.—This common species is frequent in the spring in the upland ponds and streams, though not uncommon in the marshy lowlands. In summer it is found in the moist meadows.

*Rana clamata* Latreille. The *Green-frog*.—This aquatic frog is abundant, inhabiting many more diverse localities than its close relative, the bullfrog.

*Rana catesbeiana* Shaw. The *Bullfrog*.—This, our least common Anuran, is strictly aquatic, preferring swamps, large ponds, or marshy streams.

*Rana sylvatica* LeConte. The *Wood-frog*.—This species, common in the moist woods, generally seeks shaded woodland pools or ponds for breeding.

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\*For detailed descriptions of the adult forms, consult E. D. Cope, *Batrachia of North America* (1889), Bull. U. S. Nat. Museum No. 34; for illustrations compare the excellent photographs in "The Frog Book," by Miss M. C. Dickerson.

## GENERAL ACCOUNT OF THE ITHACAN ANURA.

## THE FIRST APPEARANCE.

When arranged according to their first appearance in the spring, the eight species fall into five easily defined sections: (1) The peeper, the meadow-frog, the wood-frog. (2) The toad, the pickerel-frog. (3) The green-frog. (4) The tree-toad. (5) The bullfrog.

The criteria of arrangement are: the earliest, latest, and average dates of first emergence; the lowest and average maximum temperatures\* of the air; and the prevailing water-temperatures at the time and place of appearance. This last factor can be applicable only to the four species which hibernate beneath the water, namely: the meadow-frog, the pickerel-frog, the green-frog, and the bullfrog. Some of the pertinent data are given in the accompanying table:

Species.	Average date of first appearance.	Range of dates of first appearance.	Lowest air-maxima.*	Average air-maxima.	Water-temperatures.
Peeper.....	Mar. 26	Mar. 13 to Apr. 12	41° to —	51° to 52°	
Meadow-frog.....	Mar. 28	Mar. 5 Apr. 11	41 45°	50 53	41° to 46°
Wood-frog.....	Mar. 31	Mar. 19 Apr. 14	41 45	51 53	
American toad ...	Apr. 1	Mar. 19 Apr. 27	53 57	57 64	
Pickerel-frog.....	Apr. 3	Mar. 19 Apr. 25	48 58	58 67	45 53
Green-frog.....	Apr. 7	Mar. 28 Apr. 20	54 61	61 69	46 58
Tree-toad.....	Apr. 28	Apr. 16 May 8	58 61	66 70	
Bullfrog.....	May 20	May 11 June 4	68 75	76 79	57 69

The first group of three (namely, the peeper, the meadow-frog, and the wood-frog) forms a very distinct association. On the average, they appear March 26 to 31. The intervals between the three successive appearances average two or three days and that between the first and third averages five days. In the course of twelve years, all three have first appeared on the same day but once; two of the three have appeared on the same day in five different years. In these three we can expect, in very early seasons, the appearance by March 19 or earlier (sometimes two weeks earlier than the second group), and, in very late seasons, the appearance at least by April 14. All three may emerge under maximum air-temperatures as low as 41 to 45 degrees or under average air-maxima from 50 to 53 degrees. In the meadow-frog the water-temperature is the more potent factor of emergence and the effective temperatures begin with 41 to 45 degrees and upward.

The toad and the pickerel-frog follow soon after the first group. They appear, on the average, from April 1 to 3, an interval of only two days separating them. In very early springs, they may appear

\*All temperatures given in this study are in Fahrenheit.

by March 19, and in very late seasons sometimes not until April 27 (two weeks beyond that of the first group). These two never emerge at lower air-maxima than 48 or 53 to 58 degrees, and usually at average air-maxima from 57 to 67 degrees. The pickerel-frog hibernates in the water and usually appears when the water is at least 45 to 53 degrees.

In early springs, the second and first groups occasionally appear at the same time, *e. g.*, in 1903, when the temperature reached 68 to 75 degrees, four of the first five appeared on the same day, March 19. Furthermore, the interval between the dates of appearance for the wood-frog (the last of the first group) and the toad (the first of the second group) is only one day. In four of twelve years the toad has appeared with the wood-frog or anticipated it by one day. In all these mergings of first and second group appearances, the lowest air-maxima never descended below 48 degrees, which is 7 degrees higher than the lowest of the first group.

The green-frog appears, on the average, about April 7, or four days later than the last of the second group. In very early seasons, it has emerged as early as March 28 (9 days later than the second group), and in very late springs as late as April 20. The lowest air-maxima of any of its appearances are from 54 to 61 degrees, and the average air-maxima from 61 to 69 degrees. It hibernates beneath the water and the effective water-temperatures begin at 46 to 58 degrees and upward. Its appearance in three years has been synchronous with that of the pickerel-frog, which may appear at air-maxima 6 degrees lower, or at water-temperatures 1 degree lower. In these three years, the air-maxima were from 58 to 72 degrees. In 1908, on March 28, when the air-maxima suddenly ascended to 72 degrees, this species, the toad, the pickerel-frog, and the wood-frog came out on the same day.

The tree-toad appears on the average about April 28 (21 days after the green-frog). In very early springs, it has appeared as early as April 16 (19 days after the green-frog), and, in backward seasons, as late as May 8 (18 days after that of the green-frog). The lowest air-maxima of its appearance are from 58 to 61 degrees and the average air-maxima of all appearances are 66 to 70 degrees.

The bullfrog is the last to appear. It comes, on the average, about May 20 (34 days after the tree-toad); its earliest appearance is May 11 (25 days after the tree-toad), and its latest appearance is June 4 (27 days after the tree-toad). The lowest air-maxima at appearance are 68 to 75 degrees; the average of all appearances is from 76 to 79 degrees. It is our most aquatic form and emerges when the water reaches 57 to 69 degrees.

In conclusion, we see that the average dates of appearance range from March 26 to May 20. In the first 12 of these 55 days, six of the eight species appear. The extreme range of first appearance extends over 101 days, or from March 5 to June 4, a period almost twice the

normal range. Four species are mainly influenced in their outcomings by air-temperatures. The lowest air-maxima for these four forms range from 41 to 58 degrees (17 degrees), and the average air-maxima reach from 51 to 66 degrees (15 degrees). Water-temperature is the important factor in the other four species, although air-temperature plays a part; in these four the range of water-temperatures extends from 41 to 57 degrees (16 degrees). Naturally enough, the range of the air-temperatures is greater because of the lesser role air plays. The lowest air-maxima prevailing at the first appearances of these forms may be from 41 to 68 degrees (27 degrees), and the average air-maxima from 50 to 76 degrees (26 degrees).

#### THE MATING.\*

It is commonly believed that the mating of Anura occurs only at night. This seems to be the general rule with the Ithaca representatives of the group; nevertheless, mating during the day has been observed in the field with five species (*Rana sylvatica*, *picipiens*, *clamata*, and *palustris*, and *Bufo lentiginosus americanus*), and in the laboratory with one more (*Hyla pickeringii*).

The mating eagerness of the common toad is well-known. It will grasp anything embraceable that moves or comes in its way. None of our Ranidæ or Hylidæ has displayed any such fervor in the field. In these, there is no such preponderance of males in any one place, though in both families, when several males are kept in an aquarium with only one or two females, instances have occurred where a female was embraced by two males—a condition occasionally found in the field. Usually such cases are of very short duration, no such tenacity being evident as in *Bufo*, where sometimes six or seven males continue in a mass about the female for several hours (Plate XIII, Fig. 6).

The degree of ardor in the males seems to be in proportion to the gregariousness of the species, or, in other words, the greater the competition for the females the more intense the clasping instinct of the males. The eight species seem to fall in the following order of mating strength, namely: the toad, the meadow-frog, the pickerel-frog, the wood-frog (the swamp cricket-frog), the peeper, the tree-toad, the green-frog, and the bullfrog. It will be observed that the first forms are our most abundant species, and the last are the least common. Furthermore, the first in the list are gregarious and the last two quite solitary.

It has been reported that males of the two genera, *Rana* and *Hyla*, endure mutilation, but not to the extent which has been recorded in the genus *Bufo*. The males of the Ranidæ are, however, sufficiently tenacious in their embrace to admit of killing in this position by the slow

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\*For flash-lights of croaking males see Dr. Frank Overton's forthcoming "Frogs and Toads of Long Island." Bull. Brooklyn Institute of Arts and Sciences.



1



2



3



4

NORMAL EMBRACES OF LOCAL SPECIES STUDIED.

- 1. Mated pair of *Bufo lentiginosus americanus*. Axillary amplexation. X1.
- 2. Mated pair of *Rana sylvatica*. Pectoral amplexation. X1.
- 3. Mated pair of *Rana palustris*. Pectoral amplexation. X1.
- 4. Mated pair of *Rana pipiens*. Pectoral amplexation. X1.



addition of chloral hydrate to the water. In this way, permanent preparations may be made. Furthermore, males of the Ranidæ and of the genus *Bufo* have continued in the embrace for several days after a female has died. Occasionally they seize a dead female and maintain the clasp for varying periods.

In the numerous laboratory-mated pairs, which proved unfruitful as a rule, the males often continued the embrace for long periods. On several occasions the females died or else showed ugly scars on their breasts from the long hold of the males (Plate IV, Fig. 3). In one instance, a pair of *Rana pipiens* so remained continuously for five weeks and doubtless would have continued longer had the aquarium water-supply been watched more carefully; the male, in this instance, died at the end of the period named. Several other periods closely approaching this have been noted for other species. In all the mated pairs captured afield, the males normally retained their holds, no matter how long the journey to the laboratory, however roughly handled, or however hot the glass jar became from sun exposure. If they broke on the trip, they soon resumed, and seldom released when transferred from aquaria to aquaria or to photographic stands.

This amorous disposition frequently persists with unpaired males long after the active pairing season in nature is over, occasionally for as long as one month. In one instance an emaciated male *Chorophilus triseriatus* mated two and a half months after its customary breeding season. Then, too, unmated or fresh males may often seize a spent female and retain her for considerable periods, sometimes until her death.

Even with males which have once mated, records have been noted where mated pairs continued in the embrace or else resumed the embrace after the eggs were laid. In six species, this has been observed; the exceptions are *Rana catesbeiana* and *Rana clamata*, in which it doubtless has been overlooked because of the difficulties of observation and of their solitary nature. In the tree-toad the male has continued in the embrace after ovulation; in the peeper, 2 days afterwards; wood-frog, 3 days; meadow-frog, 4 days; pickerel-frog, 7 days; and toad, 12 days. This phenomenon is more likely to be observed in laboratory-mated pairs or field-mated pairs confined in the laboratory. It is suggestive of the possibility of a male mating more than once.

The males of the genus *Rana* usually have the thumb much enlarged at the breeding season and the margins of the webs of the hind feet are different from those of the females. In some they may be convex (Plate III, Fig. 1a) instead of concave, or less concave than in the female. Almost invariably, the male of a mated pair of *Rana* proves smaller in size (Plate II, Figs. 2-4) and darker in color. The latter fact may be partially due to the male's great activity in searching for the more

quiet female and also to its more sun-exposed position when mated. In the toads which lay in the shallows, the difference in color is not so noticeable nor is it in the night-laying tree-toads. In the peeper and the swamp cricket-frog, however, which lay by day as well as at night, the males are usually darker. In these tree-frogs, as in the toad, the males are distinguished by a viscid subgular pouch which in some forms may help the male to retain his hold of the female. In addition, the male toad has the first two fingers with horny excrescences.

#### THE CUSTOMARY AMPLEXATION.

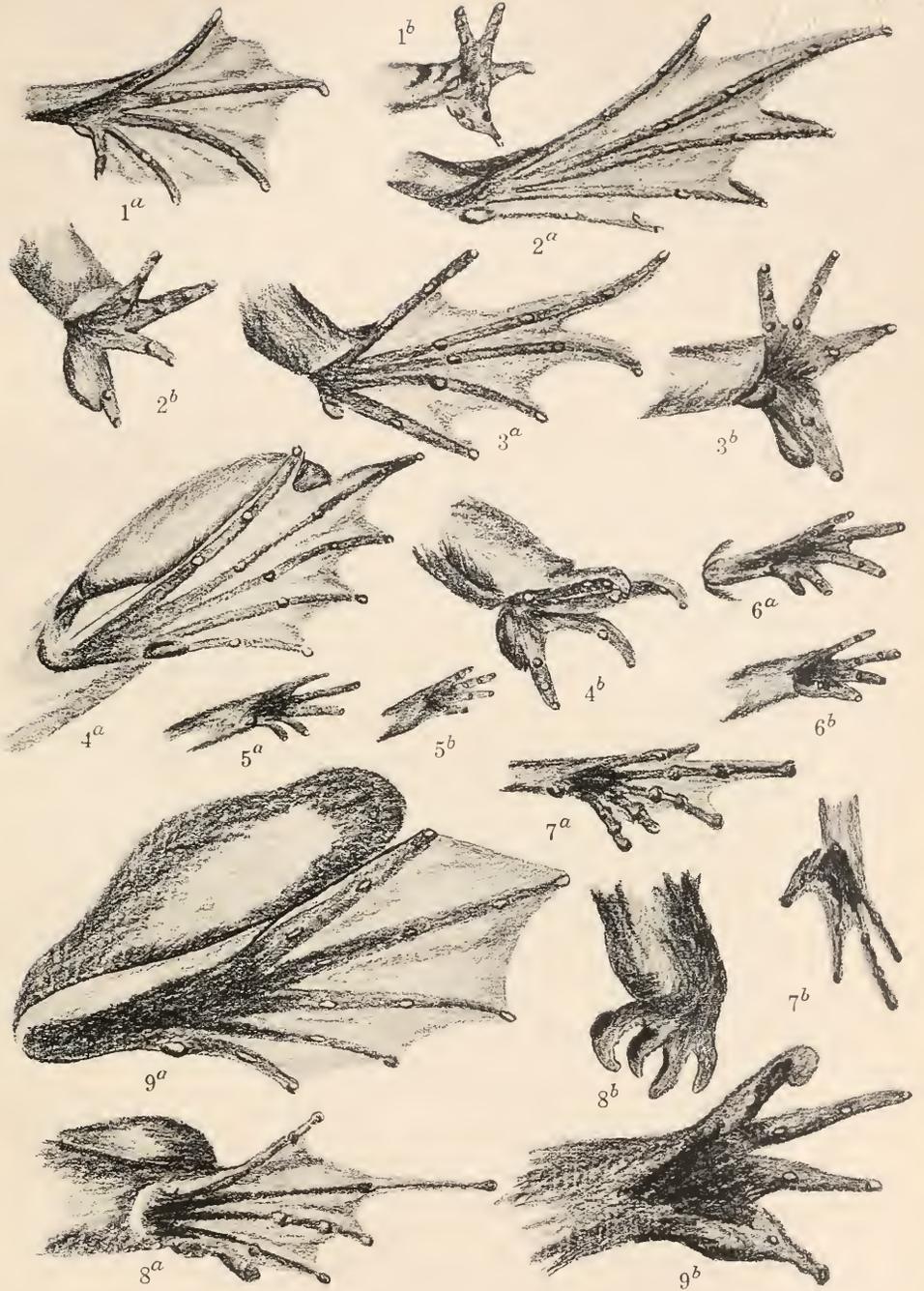
In all our eight Anura the embrace is behind or above the arms. In the five species of *Rana* it is usually pectoral, the hands appressed to the breast of the female; while in the two species of *Hyla* and in *Bufo* the hands of the male, with fingers folded back, are dug into the axils (axillary) or just above the axils (supra-axillary) of the female.

#### CROSS-EMBRACES.

The possibility of hybrids makes this phenomenon extremely interesting. Pairing between different species of Anura is quite frequently noted in captivity, though our usual isolation of each species did not give ample chance for it. Inasmuch as the mating occurred in captivity, no ovulation was expected, nor was it recorded in the instances which follow:

Males.	Females.	Males.	Females.
<i>Rana sylvatica</i>	× <i>Rana palustris</i> .	<i>Rana clamata</i>	× <i>Rana pipiens</i> .
<i>Rana sylvatica</i>	× <i>Rana clamata</i> .	<i>Rana clamata</i>	× <i>Rana palustris</i> .
<i>Rana pipiens</i>	× <i>Rana palustris</i> .	<i>Rana clamata</i>	× <i>Rana sylvatica</i> .
<i>Rana pipiens</i>	× <i>Rana clamata</i> .	<i>Bufo l. americanus</i>	× <i>Rana pipiens</i> .
<i>Rana pipiens</i>	× <i>Rana sylvatica</i> .	<i>Bufo l. americanus</i>	× <i>Rana clamata</i> .
<i>Rana pipiens</i>	× <i>Bufo l. americanus</i> .	<i>Bufo l. americanus</i>	× <i>Rana palustris</i> .
<i>Rana palustris</i>	× <i>Rana pipiens</i> .	<i>Hyla pickeringii</i>	× <i>Rana sylvatica</i> .
<i>Rana palustris</i>	× <i>Rana clamata</i> .	<i>Hyla pickeringii</i>	× <i>Chorophilus triseriatus</i> .
<i>Rana palustris</i>	× <i>Bufo l. americanus</i> .		

We have long suspected that when two species were vigorously mating and ovulating in the same area, embraces between the two might occur. In 1911 especial attention was given to this matter, and records of this sort were made in two different localities. On the same day (April 28, 1911) a male *Rana pipiens* mated with a female toad, and a male *Rana pipiens* with a female *Rana palustris* (Plate IV, Fig. 2). In each case, the individuals of the species concerned were very numerous and ovulating in the same space. In the solitary species there is not the strong inclination nor the chance for cross-embraces that there is in these abundant gregarious forms with overlapping or coincident breeding seasons and kindred places for ovulation.



HIND FEET (a) AND FORE FEET (b) OF BREEDING MALE ANURA.  $\times 1$ .

- |                            |                                     |  |
|----------------------------|-------------------------------------|--|
| 1. <i>Rana sylvatica</i> . | 4. <i>Rana clamata</i> .            | 7. <i>Hyla versicolor</i> .              |
| 2. <i>Rana pipiens</i> .   | 5. <i>Chorophilus triseriatus</i> . | 8. <i>Bufo lentiginosus americanus</i> . |
| 3. <i>Rana palustris</i> . | 6. <i>Hyla pickeringii</i> .        | 9. <i>Rana catesbeiana</i> .             |



## ABNORMAL EMBRACES.

Some of our Anura have embraced forms not of the same order or class. Occasionally, when placed in the same aquarium with a totally different sort of animal, they may seize it. Such records are:

<i>Hyla pickeringii</i>	×	<i>Ambystoma punctatum</i> .
<i>Chorophilus triseriatus</i>	×	<i>Ambystoma jeffersonianum</i> .
<i>Rana sylvatica</i>	×	<i>Ambystoma punctatum</i> .
<i>Rana pipiens</i>	×	<i>Amiatus calva</i> .

## DEPARTURES FROM THE CUSTOMARY EMBRACE AND THEIR SIGNIFICANCE.

Dr. Gill observes:

The "amplexation" or mode of approach of the males on the females, is characteristic, and in main features is common to the members of a genus, so far at least as the European species are concerned. So generally in conformity with structural features has it been regarded that the principal modifications have been used to differentiate and diagnose certain groups. \* \* \* Mr. Boulenger well remarks: "How exaggerated the importance attached to this correlation, which, besides, holds good only for the European forms, is now apparent to all." Nevertheless, within certain limits, the species of a genus agree in their mode of amplexation; only a too strict taxonomy can not be applied. For example, Mr. Heron Royer (Bull. Soc. Zool. France, 1890, p. 205) recognized 7 categories of amplexation—pectoral, axillary, supra-axillary, inguinal, axillo-inguinal, lumbo-pubic, and lumbar. \* \* \* In fact, such differences may be simple expressions of the relative size of the male and female and must vary as do the sexes. But there is a sharp contrast between amplexation round the waist and that behind or above the arms, and these two categories are the chief ones recognized by Mr. Boulenger.

I have seen the amplexation of the eight species under consideration, and feel with Dr. Gill that "differences may be simple expressions of the relative size of the male and female." In the eight species with normally three types (pectoral, axillary, and supra-axillary) of embrace, we have observed all the seven categories of Heron Royer but one (lumbo-pubic). Furthermore, we can hardly consider that there is a sharp differentiation between amplexation about the waist and that behind or above the arms. In addition to size, the beginning of sexual impulse, its height, its waning, or exhaustion after one mating, may bring departures from the normal mode of approach.

There are many chances for wrong conclusions regarding the taxonomic value of form of embrace, if based on few observations. At the beginning of pairing, often the male grasps a leg or some part and locks both arms together, keeping to the temporary hold until the normal embrace can be permanently secured. Occasionally, when not at the height of sexual impulse, or at the beginning of the breeding season, an embrace may be recorded not of the usual type for the species in question, *e. g.*, the first record of the embrace of *Rana clamata* was more of the *Hyla* type (Plate IV, Fig. 6); ever after, with one exception, how-

ever, it was *Rana*-like. Again, at the height of pairing, differences can readily be discovered in the same species; e. g., in *Hyla pickeringii* and *Bufo l. americanus* both axillary and supra-axillary types occur.

Male frogs embrace the head of a carp,\* bowfin, or any other fish because the normal pectoral and lumbar regions are too large; the head is the only region they can possibly span, and the eyes the only place into which they can dig the hands. The same was true of the peepers and swamp cricket-frogs when embracing *Ambystoma*. The head was a favorite region, as many as three being on it at once. When a female *Rana* or *Bufo* is in possession of a male embracing normally, the head region is the part most frequently seized by the supernumerary males. Sometimes, in such instances, a male will seize the head and hold the female from the ventral side, apposing his venter to that of the female, she then being in the possession of two males. Or a male may rest on the top of the male in possession, holding the female by the head.

There are a few records of lumbar embraces with four different species, typically axillary; apparently such records are explained by the weakening due partly to captivity and partly to previous fruitful mating and insemination. A male *Rana pipiens* so embraced for three hours and retained its hold, though roughly handled. In the field one record of lumbar amplexation was found with *Bufo l. americanus*. A weakened *Chorophilus* usually held to its axillary fashion, but often could not or did not maintain it; several times it slipped back to axillo-inguinal, inguinal, and lumbar modes, but never kept them permanently. In another instance three pairs of toads laid, broke, and then the males resumed the embraces; this they did for six days and the amplexation was lumbar or midway between lumbar and axillary.

It would seem that the lumbar form of approach is the least vigorous and the pectoral the hardest to break. Some examples of *Rana*, when weakened, slip to the lumbar embrace, although not so readily as species with the axillary form of embrace; and it is extremely difficult to transfer these lumbar *Rana* pairs to photographic stands or jars, an operation easily done for typical pectoral pairs and quite easily accomplished with typical axillary ones. When males of the genus *Rana* are brought into captivity before the normal breeding season for their species they sometimes feebly grasp a female in a lumbar fashion; e. g., a male *Rana clamata* so held a female May 15, 1913 (two weeks or more preceding the beginning of egg-laying in the field). Then, too, in the Pelobatidæ, where it is supposedly the normal rule (so recorded for European forms), the various species, when handled, break more easily than do those of the genus *Rana*, and this was our experience with a captive mating lumbar pair of *Scaphiopus holbrookii*, which so amplexated several times, but quickly released if receiving much attention.

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\*For a résumé of such phenomena see Dr. T. N. Gill's "The Family of Cyprinids and the Carp as its Type," Smithsonian Misc. Colls. vol. XLVIII, 1907, pp. 208, 209.



1. Cross-embrace of a male *Bufo lentiginosus americanus* with a dead female *Rana pipiens*. The amplexation is pectoral, not axillary.  $\times 0.5$ .
2. Cross-embrace of a male *Rana pipiens* with a female *Rana palustris*. The pair captured in the field in a mated condition.  $\times 0.5$ .
3. A female *Rana pipiens* showing the effects of 17 days' pectoral amplexation.  $\times 1$ .
4. A mated pair of *Rana pipiens* showing pectoral (*Rana*) type of amplexation.  $\times 0.75$ .
5. A pair of male *Hyla versicolor* showing the axillary type of amplexation, where fingers are folded back in the embracing male.  $\times 0.75$ .
6. A mated pair of *Rana clamata*, the small male holding axillary-like on the right side and partly pectoral-like on the left side.  $\times 0.5$ .



Cross and abnormal embraces give us our best clues to the role of size in the mode of approach. In three different instances a captive wood-frog held an *Ambystoma* in a lumbar embrace. It did not seek the head as did the smaller peeper and swamp cricket-frog. One cross-embrace of a male *Rana palustris* with a female of the larger species, *Rana clamata*, displayed several different methods. At first, the male held the female with the right hand dug into the axil, *Bufo* fashion, and with the left arm and hand reaching around to the middle of the breast, *Rana*-like. Once, it lost its hold and regained a lumbar amplexation. This it kept only a short time, and almost immediately began working slowly through inguinal and axillo-inguinal modes to the axillary type. Another cross-embrace between two other species, namely, between a male *Bufo* and a female *Rana pipiens*, proved equally interesting. At first, the toad held the frog with the right arm in front of that of the frog, and with the left arm behind. Later, both arms were behind and they met on the breast, as in males of the genus *Rana*.

Occasionally, in some cross-embraces, when the females proved large, the mating males would seize them from the venter. On April 10, 1908, a male *Bufo* thus seized a female green-frog. Its arms were behind those of the green-frog and went up on its back. A small male wood-frog with shorter span did the same, except that its arms were ahead of those of the female green-frog.

Thus, it may be seen that variations are not unusual, and that generalizations in this particular must be on numerous records. In the three genera we have observed six or seven modes when normally only three would be expected. Rarely a male displays a gamut of six or seven modes, especially when mating with a female of another species. All these mating phenomena came as an incident to the effort to secure mated pairs for ovulation in captivity. In this way, a positive check was established upon the identification of the eggs laid in nature.

#### THE OVULATION.

It is often asserted that the sexual embrace is continued for several days before ovulation. Such may be the case with individuals mated in captivity, but very few illustrations of it have been found among numerous mated pairs brought in from the field. At the outset the attempt to secure fruitful mating with captive specimens was given up. The few instances where successful show that the intervals between the beginning of the embrace and egg-laying are short. In one case, where a pair of wood-frogs were thus mated in laboratory, ova were deposited 90 minutes after the beginning of the embrace. With two similar pairs of *Chorophilus triseriatus*, 20 minutes and 90 minutes were respectively recorded. Another such mated pair of *Rana palustris* laid two days after the beginning of the embrace.

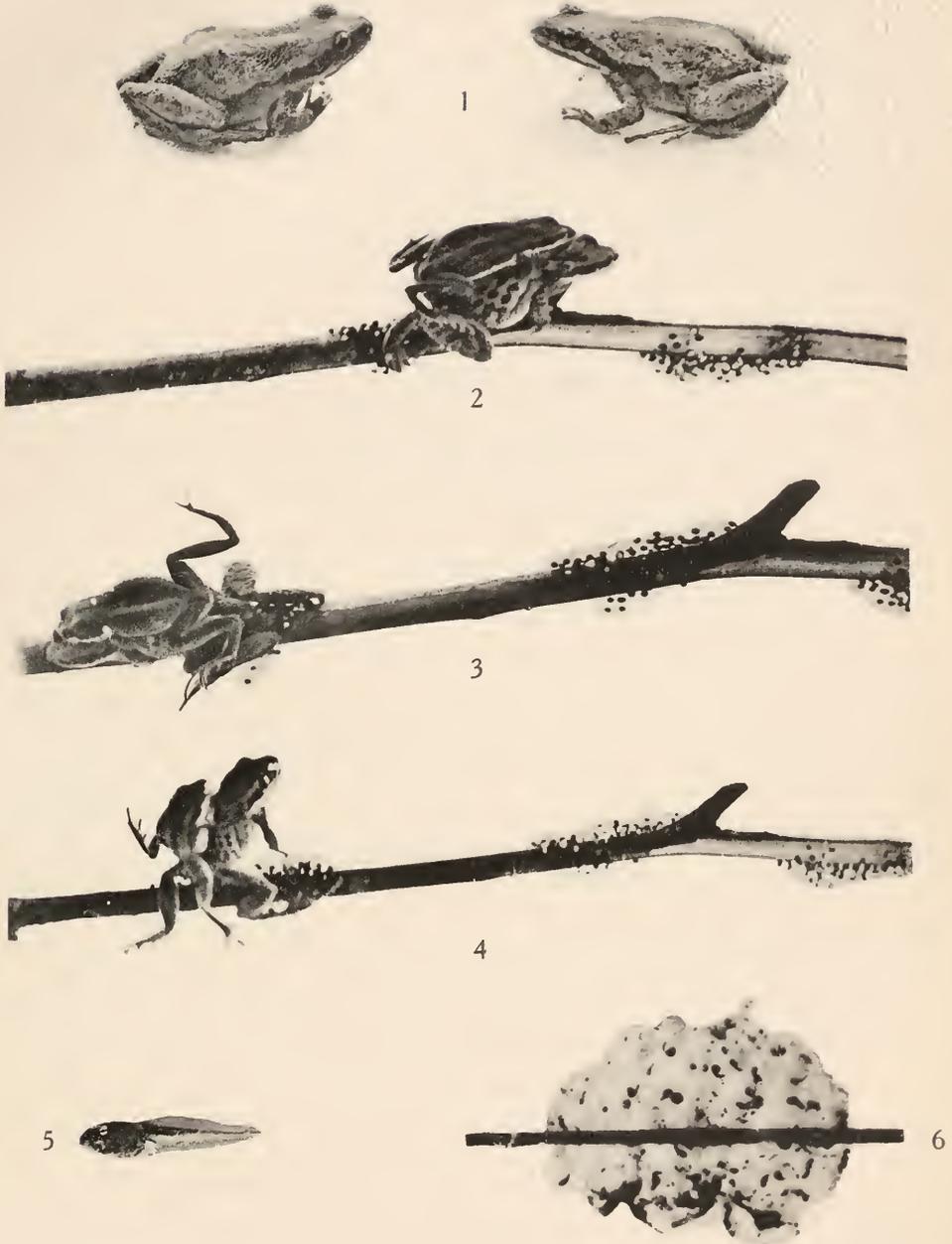
Whenever one or more mated pairs were secured on my night trips, I returned immediately to the laboratory, being reasonably certain of an egg-complement by the next morning. With 75 or more mated pairs (*Bufo* not counted) captured afield, this seemed the general rule. The two species which occasionally did not lay by the next morning were *Rana palustris* and *Rana pipiens*. In *Rana palustris*, as many as 14 days have transpired before ovulation. For six years, I have seen the mating of this species in areas where there were no eggs or very few. The next day after the record of such first matings in great numbers, countless bunches were recorded, implying a day or less in the embrace.

Ovulation without apparent mating has been recorded for three species. On April 28, 1906, an isolated female *Rana palustris* laid in an aquarium, no male being present; the same was recorded for *Bufo l. americanus* and *Rana clamata*. In each of these cases the whole complement was quickly laid and did not extend far beyond the period normally required for the species, as is often the rule with the delayed laying in captive pairs.

When mated, if the male be removed, the female often lays. With a member of the genus *Hyla*, an experiment was tried as follows: On the evening of June 17, 1907, two mated pairs of *Hyla versicolor* were captured. One pair was allowed to remain in the embrace; the other was separated. The next morning, both the attended and the unattended females had laid. Later, a mated pair was separated and the female was placed over night in a dry jar, but the next morning eggs were found, though no water was present. Three years later the same experiment was made with three pairs of *Bufo* with identical results. Even when the conditions are very untoward, the female often ovulates; *e. g.*, a pair of meadow-frogs escaped from a jar, traveled from a third floor to the first floor, and laid their egg-complement on the first floor staircase. Absence of mating, separation from mates, or presence in air (not water) can not prevent ovulation when once the process has reached an advanced stage. Apparently, the female must ovulate whether she would or not.

The spawning periods of the various species were considered from the following points of view: average date; range of spawning period; average interval and range of intervals between first appearance and first ovulation; the beginning and average maximum air-temperatures of ovulation; and the beginning and average water-temperatures of ovulation. The data will be found in the table at the top of the following page. In the spawning record there is a close approximation to the grouping of the first appearance. The same forms are associated, except that the last three species which appear in three distinct groups are here assembled in one.

The first three to appear, namely, the wood-frog, the peeper, and the meadow-frog, proceed at once to pair and ovulate. They appear, on



SWAMP CRICKET-FROG (*CHOROPHILUS TRISERIATUS*). PHOTOS BY A. A. ALLEN AND AUTHOR

1. A pair of swamp cricket-frogs.
2. A pair in position preparatory to ovulation.
3. A mated pair in act of ovulation.
4. The pair arising to surface for air after ovulation.
5. A mature tadpole.
6. An egg-mass.



Table showing spawning dates of the different species, the intervals between first appearance and ovulation, dates of first appearance, and temperatures of ovulation.

Species.	Spawning dates.		Intervals between first appearance and ovulation.	
	Average date.	Range of spawning period.	Average.	Range.
Rana sylvatica . . . . .	Apr. 4	Mar. 19 to Apr. 30	2	0 to 13
Hyla pickeringii . . . . .	Apr. 10	Mar. 30 May 10	6	5 15
Rana pipiens . . . . .	Apr. 11	Mar. 29 May 15	17	7 25
Bufo lentiginosus americanus . . . . .	Apr. 23	Apr. 5 July 25	21	7 34
Rana palustris . . . . .	Apr. 23	Apr. 6 May 18	23	10 32
Hyla versicolor . . . . .	June 2	May 10 June 17	32	24 43
Rana clamata . . . . .	June 7	May 23 Aug. 10	45	32 61
Rana catesbeiana . . . . .	June 28	June 16 July 10	44	31 54

Species.	First appearance.		Temperatures of ovulation.			
			Maximum air-temperatures.		Maximum water-temperatures.	
	Order.	Average date.	Lowest.	Average.	Lowest.	Average.
Rana sylvatica . . . . .	3	Mar. 31	41° to 43°	53° to 58°	41° to 48°	53° to 60.
Hyla pickeringii . . . . .	1	Mar. 26	43 51	52 58	43 48	53 53
Rana pipiens . . . . .	2	Mar. 28	43 44	51 55	43 48	53 55
Bufo l. americanus . . . . .	4	Apr. 1	50 51	65 67	51 66	63 65
Rana palustris . . . . .	5	Apr. 3	50 51	68 69	51 64	57 64
Hyla versicolor . . . . .	7	Apr. 28	61 72	72 79	67 75	67 71
Rana clamata . . . . .	6	Apr. 17	65 74	74 76	65 68	68 74
Rana catesbeiana . . . . .	8	May 20	71 72	80	66 71	70 71

the average, from March 26 to 31. They may begin to emerge from hibernation at low air-maxima of 41 degrees and upwards or at a water-temperature of 41 to 46 degrees. Usually, however, first appearances come on the average at air-maxima of 50 to 53 degrees. An advance of 0 to 2 degrees above the lowest air- and water-maxima may bring the beginning of ovulation, but ordinarily a rise of 1 to 3 degrees above the average air-maxima of appearance causes it. The minimum intervals between appearance and ovulation for the three species are 0, 5, 7 days; the average intervals, 2, 6, 17 days; the maximum intervals, 13, 15, 25 days. The wood-frog starts ovulation, on the average, about April 4, but has begun as early as March 19, or extended it to April 30. The peeper has begun, on the average, about April 10, but the earliest record is March 30, and the last extends well into May. Finally, the meadow-frog usually has begun April 11; the earliest record is March 29, and the last record is May 15.

The second group consists of the toad and the pickerel-frog, respectively fourth and fifth in first appearance as are they in ovulation.

In both respects they are almost coincident. Ovulation does not come so immediately after emergence as in the first group. They appear, on the average, from April 1 to 3. They may begin to appear at low air-maxima of 48 to 58 degrees, or on the average at air-maxima of 57 to 67 degrees. The water-temperatures of appearance are 45 to 53 degrees. The first ovulation may come at air-temperatures 2 to 3 degrees above the lowest air-maxima of appearance, or 6 degrees above the lowest water-temperature for the same event. On the average, the air advance is 8 to 11 degrees or the rise in water-temperature is 12 to 18 degrees. The minimum intervals between appearance and ovulation in the two forms are 7 and 10 days; the averages are 17 and 21 days; the maxima are 34 and 32 days. The toad begins spawning on the average about April 23; the earliest record is April 5; the latest is July 25. The pickerel-frog starts egg-laying usually on April 23; the earliest record is April 6; the last record of ovulation is May 18.

The last three to appear delay for considerable periods before ovulation.

The tree-toad appears, on the average, April 28. It may appear at low air-maxima of 58 to 61 degrees, or usually at an average of 66 to 70 degrees. The beginning of ovulation may start at 61 to 72 degrees (3 degrees higher than at appearance), or at a water-temperature 67 to 75 degrees. As a general rule, the air-maxima average 72 to 79 degrees (6 degrees higher than the average temperatures of appearance) for breeding, and the water-temperatures average 67 to 71 degrees. The minimum interval between first appearance and breeding is 24 days; the average is 32 days; the maximum is 43 days. The tree-toad begins spawning, on the average, about June 2; the earliest record is May 10; the last record is June 17.

The green-frog appears on or about April 7. It may appear at a low air-maxima of 54 to 61 degrees, or at water-temperatures of 46 to 58 degrees. As a general rule, 61 to 69 degrees is the average range of air-maxima at this time. Ovulation may begin at air-maxima of 65 to 74 degrees (11 or more degrees higher than that of appearance), or at a water-temperature from 67 to 71 degrees (21 degrees higher than that of appearance). On an average, it starts at 74 to 76 degrees (13 or more degrees above the average air-maxima of appearance), or at 68 to 74 degrees of water-temperatures (24 degrees above the water-temperature of appearance). The minimum interval between first appearance and first breeding is 32 days; the average is 45 days; the maximum is 61 days. The green-frog proceeds to spawn about June 7; the earliest record is May 23; the latest is August 10.

The bullfrog's average date of appearance is May 20. It may appear at air-maxima of 68 degrees, or at water-temperatures of 57 to 69 degrees. Usually, the average air-maxima of appearance are 76 to 79 degrees. It may begin ovulation at air-maxima of 71 to 72 degrees

(3 or more degrees above that of appearance), or at water-temperatures of 66 to 71 degrees (9 or more degrees above that of appearance). On the average, breeding comes at average air-maxima of 80 degrees (12 degrees higher than appearance data), or at water-temperatures from 70 to 71 degrees (13 degrees higher than that of appearance). The minimum interval between first appearance and ovulation is 31 days; the average is 44 days; the maximum interval is 54 days. Our records show that the average date for first eggs is June 28 (we suspect it may prove earlier with several years more of data); the earliest record is June 16, and the last is July 10.

The interval between the spawning season of the two extremes is so great that transformed examples of the first species (*Rana sylvatica*) are sometimes noted before the last species (*Rana catesbeiana*) begins laying. In some years, *e. g.*, 1907, transformed individuals of all the species have been found before *Rana clamata* finished spawning. In *Bufo lentiginosus americanus*, it occasionally happens that the progeny of the early-breeding toads may transform before the last stragglers of the species lay.

With six of the eight species, the spawning period usually covers four or five weeks, although the extreme record may be six weeks. Two species, *Rana clamata* and *Bufo l. americanus*, may require two and three months respectively for their breeding periods.

To summarize: The first frogs which appear breed almost immediately after emergence from hibernation, while those which appear last wait long periods before ovulation. In this series of eight species, the intervals between first appearance and first eggs are in an almost perfect ascending scale; and, in general, the order of first appearance is a fair but not absolute index of the order of egg-laying.

#### THE EGGS.

At the outset it was found that pairs mated in the laboratory seldom proved fruitful. A persistent effort was therefore made to secure field-mated pairs for ovulation in captivity. In this way, a certain check was established upon the determination of the eggs deposited in nature, where they were identified by the elimination method and by actual field observations. In the field, we witnessed the whole or a part of the process of ovulation of seven species and the other one species was recognized by the elimination method. In the laboratory, numerous pairs of six species laid in isolated jars.

The measurements used in the key were based on fresh eggs, none of which were beyond the fine morula stage. The color characters of the vitellus were taken at the time of ovulation with six species, and not later than six or eight hours after ovulation with the other two species. The results of the egg study appear in the table on the following page.

Table showing the data resulting from the egg study of the eight species of Anura under consideration.

Species.	No. of eggs each sexual period.	Egg-complement.		Shape.	Time required to lay a complement, and where laid.
Peeper.....	One....	800 to 1,000		Single.....	Several hours; among plants.
Tree-toad....	4 to 25..	1,500	2,000	Film.....	An hour or more; among plants or not.
Toad.....	Several.	4,000	7,000	Two spirals	2 or 3 hours or more; about plants, sticks, or free.
Wood-frog....	Several.	2,000	3,000	Sphere.....	3 to 15 minutes; attached to sticks, plants, or free.
Meadow-frog.	Several.	3,500	4,500	Plinth.....	Do.
Pickerel-frog.	Several.	2,000	3,000	Sphere.....	Do.
Green-frog....	Several.	3,500	4,000	Film.....	10 to 30 minutes; attached to plants, or free.
Bullfrog.....	Several.	12,000	20,000	Film.....	10 to 30 minutes; attached to brush.

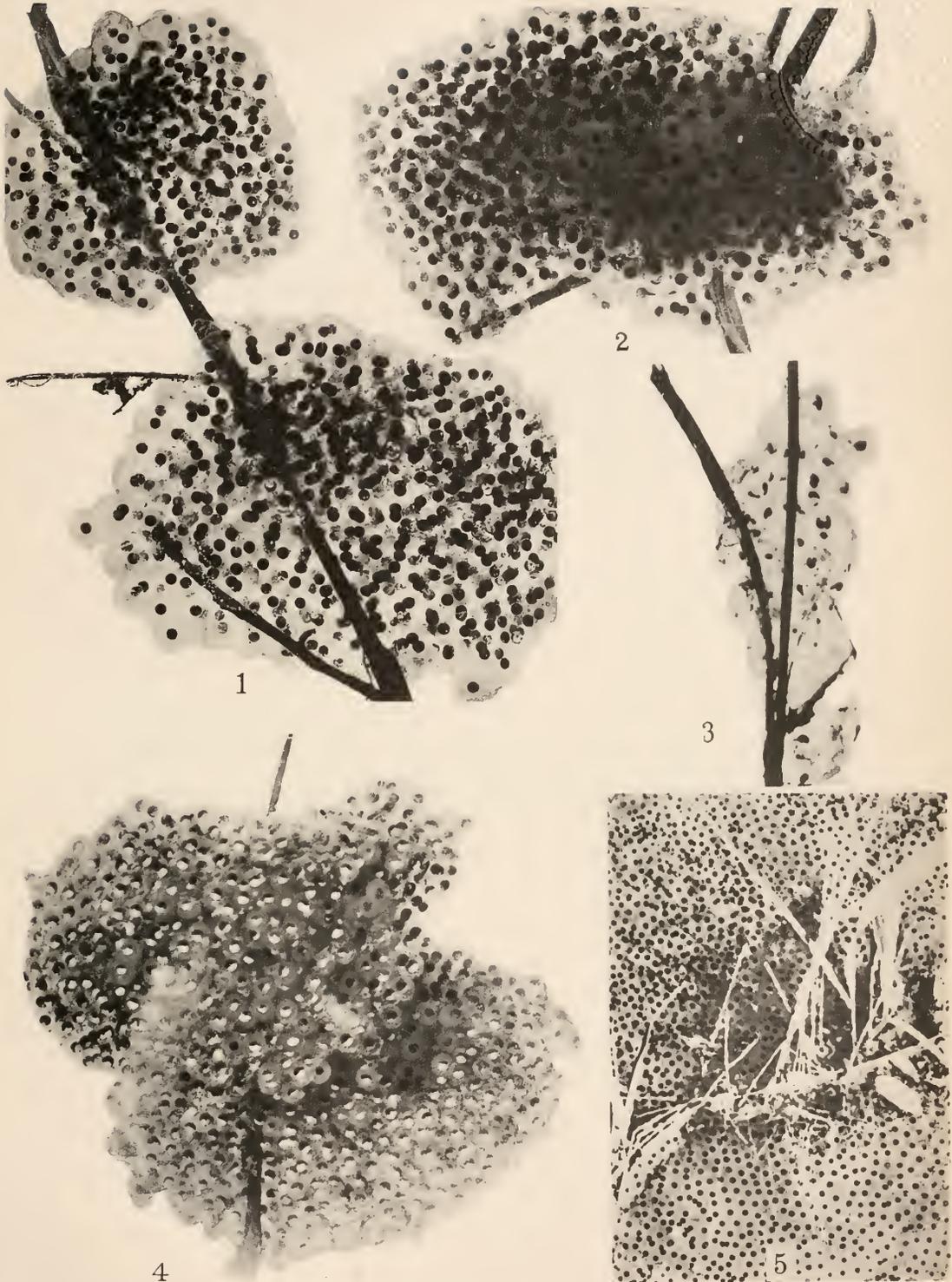
  

Species.	Specific gravity.	Jelly consistency.	Color of the eggs.	
			Vegetative pole.	Animal pole.
Peeper.....	Immersal (submerged).	Firm.....	Never yellow....	Black.
Tree-toad....	Buoyant (on surface)...	Loose.....	Yellow or cream.	Brown.
Toad.....	Immersal.....	Firm.....	White.....	Black.
Wood-frog....	Immersal.....	Firm.....	White.....	Black.
Meadow-frog.	Immersal.....	Firm.....	White.....	Black.
Pickerel-frog.	Immersal.....	Firm.....	Yellow.....	Brown.
Green-frog....	Buoyant.....	Loose.....	White.....	Black.
Bullfrog.....	Buoyant.....	Loose.....	White.....	Black.

The spherical eggs are closely surrounded by a vitelline membrane and one or two envelopes. In three species (the peeper, the swamp cricket-frog, and the bullfrog), only one jelly envelope is present; in the other six, there are two envelopes. Two forms, the pickerel-frog and the tree-toad, have the lower poles yellow or yellowish. In the others they are white or light cream. The black pigment of a wood-frog's egg often leaves only a small white spot on the lower pole, as in the European *Rana temporaria*.

Four species (the peeper, the swamp cricket-frog, the tree-toad, and the toad) have the vitelli from 0.9 to 1.4 mm. in diameter; the intermediate group (the green-frog and the bullfrog) have the vitelli 1.2 to 1.7 mm.; and the third group of three (the meadow-frog, the pickerel-frog, and the wood-frog) have the vitelli 1.6 to 2.4 mm.; the smallest of the five *Ranas*, the wood-frog, has the largest vitelli.

The eggs of three species (*Hyla versicolor*, *Rana clamata*, and *Rana catesbeiana*) float more or less upon the surface and have the jelly consistency very loose; these three with buoyant eggs usually breed after May 25. The eggs of the six remaining species are submerged and have



1. Egg-masses of *Rana sylvatica*, both masses globular; upper mass not fully expanded.  
 2. Egg-mass of *Rana pipiens*, plinth-like, not globular, as in Figs. 1 and 4.  
 3. Egg-mass of *Chorophilus triseriatus*. Several such bunches laid by one female.  
 4. Egg-masses of *Rana palustris*. Globular mass, frequently in tiers.  
 5. Egg-mass of *Rana clamata*. A surface film among vegetation.



firmer jelly envelopes. They are the first six to breed and are mainly through ovulation by the middle of May.

The egg-masses are spherical in the wood-frog and in the pickerel-frog; plinth-like in the meadow-frog; spiral in the toad; a surface film in the tree-toad, the green-frog, and the bullfrog; a submerged film or sphere in the swamp cricket-frog, and single eggs in the peeper. In all the nine species except the peeper, several eggs are laid at each sexual period (*i. e.*, at each emission and fertilization). Five species lay the whole complement in a few minutes. In the other four (the peeper, the toad, the swamp cricket-frog, and tree-toad) several hours may be consumed in completing the ovulation, and the females do not keep the same position throughout the whole process. The egg-complements range from 800 in *Hyla pickeringii* to 20,000 in *Rana catesbeiana*. A summary of the egg characters of each species follows in the accompanying key (page 18.)

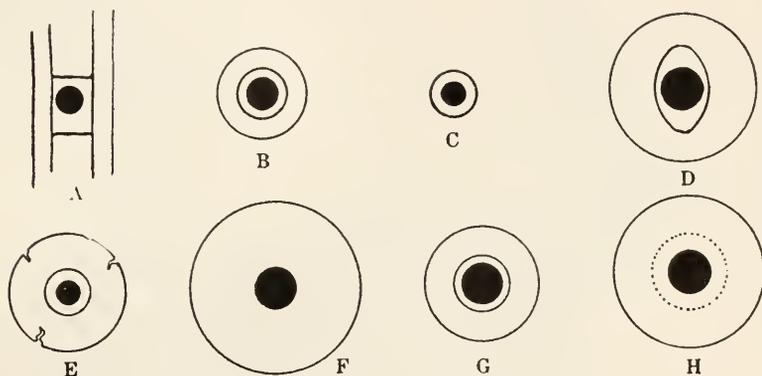


FIG. 1.—INDIVIDUAL EGGS.  $\times 4$ .

- A. Egg of *Bufo lentiginosus americanus* in two jelly-envelopes or tubes, the inner of which is divided by cross partitions.
- B. Egg of *Rana palustris*. Inner envelope and vitellus of same size as egg of *Rana pipiens* (G) but outer envelope smaller.
- C. Egg of *Hyla pickeringii*. The one envelope and the vitellus together appear the duplicate of the egg of *Hyla versicolor* (E) when it is stripped of its outer envelope.
- D. Egg of *Rana clamata*. Unlike the egg of *Rana catesbeiana* (F), it has an inner envelope and this is *elliptical*, not round as in most Anuran eggs.
- E. Egg of *Hyla versicolor*. The outer envelope often ragged in outline.
- F. Egg of *Rana catesbeiana*. Unlike the other four *Ranas*, it has no inner envelope.
- G. Egg of *Rana pipiens*. Compare B.
- H. Egg of *Rana sylvatica*. It has the largest vitellus of the eight species figured and larger envelopes than the confusing B and G.

## KEY TO THE EGGS OF ITHACAN ANURA.

- A. A single row of eggs within a long spiral string of jelly looped about plant stems, sticks, or resting upon the bottom; vitelline diameter, 1.0 to 1.4 mm.; inner envelope diameter, 1.6 to 2.0 mm.; outer envelope (outer spiral string of jelly) diameter, 3.4 to 4.0 mm. Egg-complement, 4,000 to 7,000. Season at Ithaca, April 5 to July 25; the average first date, April 23.....*Bufo lentiginosus americanus*
- AA. Deposited singly or in a mass.
- B. Deposited in a firm, consistent mass enveloping grass stems, twigs, etc., or free; submerged; often 15 to 20 bunches within an area of a few square feet.
- C. Small distinct middle envelope evident to the naked eye, 2.3 to 3.0 mm.
- D. Vegetative pole, yellow; animal pole, brown; mass globular; vitellus, 1.6 to 1.9 mm.; outer envelope, 3.6 to 5.0 mm. Egg-complement, 2,000 to 3,000. Season, April 6 to May 18; the average first date, April 23.....*Rana palustris*
- DD. Vegetative pole, white; animal pole, black; mass plinth-like; vitellus, 1.6 to 1.8 mm.; outer envelope, 4.2 to 6.0 mm. Egg-complement, 3,500 to 4,500. Season, March 29 to May 15; the average first date, April 11.....*Rana pipiens*
- CC. Large middle envelope apparently absent, slightly evident under the lens, 3.6 to 5.8 mm.; vitellus, 1.8 to 2.4 mm.; outer envelope, 5.2 to 9.4 mm.; mass globular; vegetative pole, white; animal pole, black. Egg-complement, 2,000 to 3,000. Season, March 19 to April 30; the average first date, April 4.....*Rana sylvatica*
- BB. Deposited not in a hard, consistent mass.
- C. In small bunches or attached singly; vitellus, 0.9 to 1.2 mm.
- D. Outer envelope loose, 4.0 to 7.8 mm.
- E. Middle envelope, 1.6 to 2.0 mm.; vegetative pole, yellowish or cream; in small bunches (4 to 25) usually floating on the surface of the water, either attached to vegetation or free; outer envelope, 4 to 6 mm.; vitellus, 1.1 to 1.2 mm. Egg-complement, 1,500 to 2,000. Season, May 10 to June 17; the average first date, June 2....*Hyla versicolor*
- EE. No middle envelope; vegetative pole, white; in bunches (20 to 100) usually attached beneath surface of water; outer envelope usually 5.0 to 7.8 mm., rarely 3.0 mm.; vitellus, 0.9 to 1.2 mm. Egg-complement, 500 to 800. Season, Mar. 20 to Apr. 15.....*Chorophilus triseriatus*
- DD. The one envelope firm, 1.4 to 2.0 mm.; vegetative pole, never yellow; single or in small bunches (4 to 12) attached to grass beneath the surface of the water; vitellus, 0.9 to 1.1 mm. Egg-complement, 800 to 1,000. Season March 30 to May 10; the average first date, April 10.....*Hyla pickeringii*
- CC. In large loose masses; vegetative pole, white; animal pole, black; vitellus, 1.2 to 1.7 mm.; at or near the surface of the water.
- D. Usually one continuous film, 1 to 2 eggs thick, on the surface of the water, the film's diameter being seldom one foot; middle envelope distinct, elliptical, 2.8 to 4.0 mm.; egg-mass usually attached to or amongst vegetation. Egg-complement, 3,500 to 4,000. Season, May 23 to August 10; the average first date, June 7.....*Rana clamata*
- DD. Either a film 1 to 2½ feet in diameter or a stringy frayed widespread mass; attached to twigs or sticks; almost invariably among brush, and at or near the surface of the water; no middle envelope. Egg-complement, 12,000 to 20,000. Season, June 16 to July 10; the average first date, June 28.....*Rana catesbeiana*



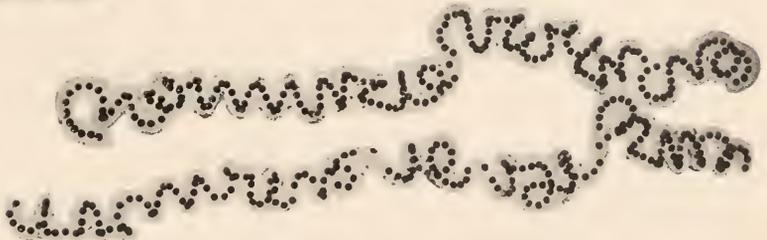
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1



4



2

1. Eggs of *Hyla pickeringii* laid in the aquarium.
2. Two egg-strings of *Bufo lentiginosus americanus*. A string from each oviduct.
3. Egg-mass of *Rana catesbeiana*. A surface film 18 inches in diameter laid among dead sticks and old boards.
4. A surface-packet of *Hyla versicolor* eggs attached to a *Potamogeton* leaf.



THE HATCHING PERIOD.

The hatching period depends mainly upon the season and its temperature. The wood-frog, meadow-frog, and peeper, which breed earliest, may require from 24 to 12 or 11 days. They have submerged eggs, and not infrequently the ponds freeze over after they are laid. The pickerel-frog, which breeds in the latter part of April, lays its eggs in deeper water than the toad. Usually its eggs require from 21 to 11 days for hatching, while the toad, which lays in the shallows (more influenced by air-temperatures), needs only 12 to 3 days. In these five forms, the eggs are submerged, though the position of the toad's eggs may at times approach the surface of the water. In the three forms which breed after May 25, the eggs are laid on the surface of the water, and are partially influenced by the higher air-temperatures. In this group (the green-frog, the tree-toad, and the bullfrog) the eggs hatch in 6 to 3 days. It was found that irrespective of species the eggs of all the eight forms would hatch in 4 or 5 days under the laboratory temperatures of 70 to 65 degrees. This explains the great differences in hatching period between the earliest and latest breeders and between immersal early eggs and buoyant late eggs. From a consideration of all the hatching data, the above table, which applies to all the eight species, is constructed.

Temperatures, in degrees.	Hatching periods, in days.
44 to 51	24 to 18 or 17
51 55	18 or 17 to 12 or 11
55 60	11 to 8 or 7
60 70	8 or 7 to 5 or 4
70 80	5 or 4 to 3

This explains the great differences in hatching period between the earliest and latest breeders and between immersal early eggs and buoyant late eggs. From a consideration of all the hatching data, the above table, which applies to all the eight species, is constructed.

THE LARVAL PERIOD.

According to the length of the larval period, the species of this region fall into two groups: those which transform during the season in which their eggs are laid and those which require one or more years for their development. The data are as follows:

Larval periods of the species.	Egg-season.	Average transformation size.	Vitelline diameter.	Egg to transformation period.	Larval period.
<i>Short larval period:</i>					
<i>Bufo l. americanus.</i>	Apr. 5 to July 25	mm. 9.6	mm. 1.0 to 1.4	days. 45 to 65	days. 40 to 60
<i>Hyla versicolor....</i>	May 10 June 17	16.0	1.1 1.2	46 65	40 60
<i>Rana sylvatica....</i>	Mar. 19 Apr. 30	16.0	1.8 2.4	61 115	44 85
<i>Rana pipiens.....</i>	Mar. 29 May 15	24.0	1.6 1.8	71 111	60 80
<i>Hyla pickeringii....</i>	Mar. 30 May 10	11.0	.9 1.1	90 100	75 90
<i>Rana palustris.....</i>	Apr. 6 May 18	24.0	1.6 1.9	90 100	75 90
<i>Long larval period:</i>					
<i>Rana clamata.....</i>	May 23 Aug. 10	33.0	1.2 1.7	1 year.	1 year.
<i>Rana catesbeiana..</i>	June 16 July 10	53.0	1.2 1.7	2 years.	2 years.

The forms with short larval periods generally complete egg-laying by July 1. Their tadpoles do not have to reach the transformation-size required of the two species with long larval periods. In the former group the average sizes of transformation range from 9.6 to 24 mm.;

in the latter group the average is from 33 to 53 mm. Besides, the vitelli of the former are larger in proportion to the size of the adults than in the two latter. In the three species of *Rana* with short larval periods the vitelline diameters extend from 1.6 to 2.4 mm., while those of the larger *Rana clamata* and *Rana catesbeiana*, with long larval periods, are only 1.2 to 1.7 mm., little more than the vitelli of the two species of *Hyla*. If *Chorophilus triseriatus* with a body-length of 1 inch and an egg-vitellus of 1 mm. be considered as the unit, the ratio of body-length to size of vitellus in our eight species will be as follows:

Chorophilus triseriatus.....	1.00	Bufo l. americanus.....	0.60
Rana sylvatica.....	1.00	Rana pipiens.....	.56
Hyla pickeringii.....	.80	Rana clamata.....	.48
Hyla versicolor.....	.75	Rana catesbeiana.....	.20
Rana palustris.....	.64		

Except for the wood-frog, the series begins with the smallest and proceeds nicely in order of adult size to the largest, namely, the bullfrog. The eggs of this species are proportionately only one-fourth or one-fifth of the size attained by the three members of the Hylidæ. The surprise in the comparison is that the wood-frog's egg is proportionately five times that of the bullfrog and almost twice that of its other three congeners.

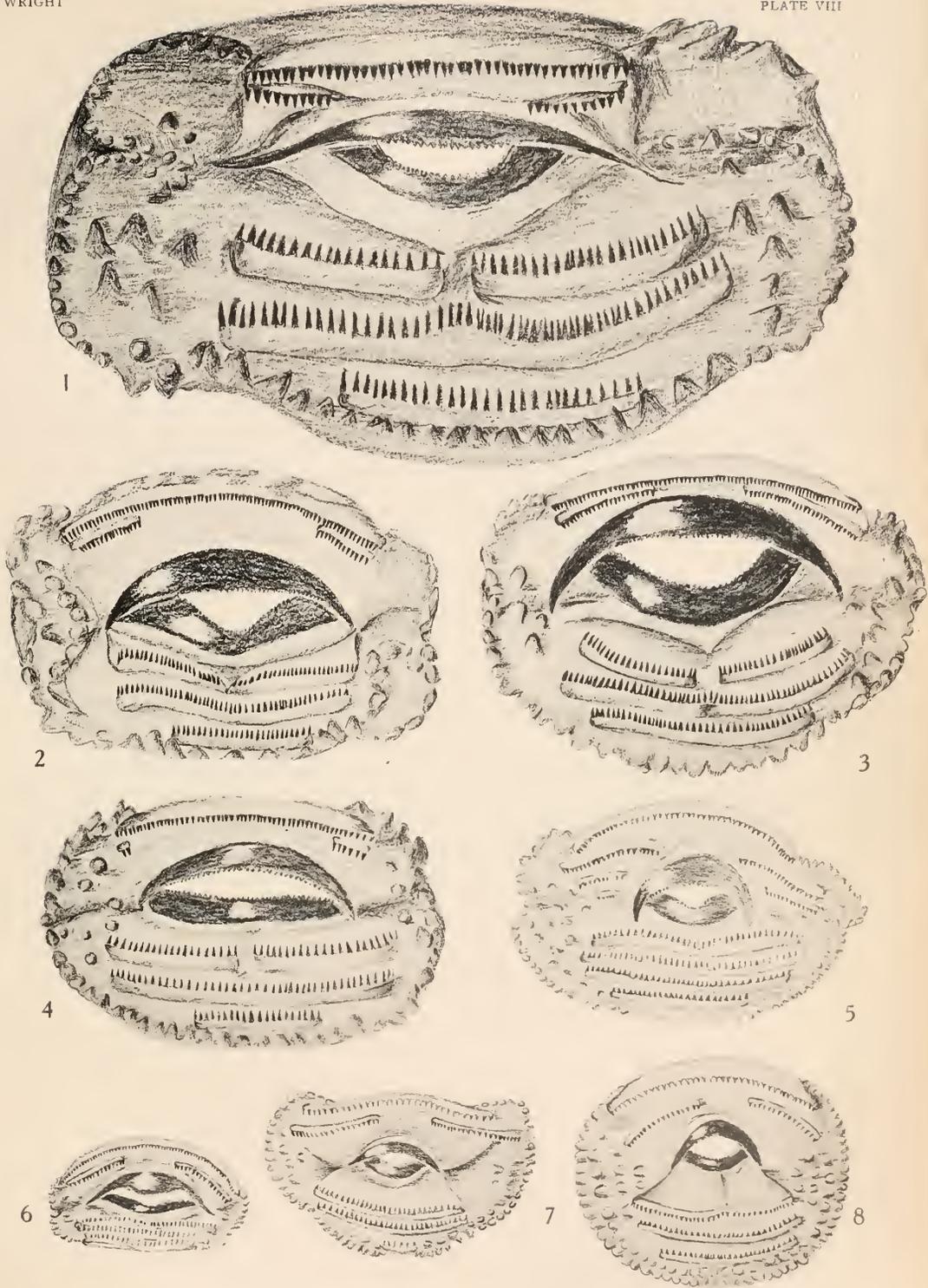
Thus, we see that the relative smallness of the eggs, the late deposition of the eggs, and the greater transformation-size required—all combine to make the green-frogs and the bullfrogs spend one or more winters in the larval stage.

Among the species with short larval periods there is considerable difference. The true larval periods of the toad, the tree-toad, and the wood-frog may be one-half that of the other three. The last species, namely *Rana sylvatica*, may at some seasons occupy just as long a period as the meadow-frog, the peeper, or the pickerel-frog.

#### THE MATURE TADPOLES.\*

As mature tadpoles, we have chosen specimens which correspond to the third period of Duges (beginning of the budding of the hind limbs). This makes our tadpoles comparable to Boulenger's descriptions of European forms. We have employed the same terms which he has well defined. In one particular we have departed from his plan. The upper labial teeth have been numbered from the outer edge of the lip to the inner row nearest the beak and the lower labial teeth from the row nearest the beak to the outer one next the papillose border. This is the vertical order in which they appear when the mouth is flattened out for examination. Furthermore, in our eight species, there is a tendency for reduction to take place in the upper labial row or rows nearest the beak and in the lower labial row or rows nearest the border.

\*Cf. Hinckley, Mary. On some Differences in the Mouth Structure of Tadpoles of Anurous Batrachians found in Milton, Massachusetts. Proc., Bost. Soc. Nat. Hist., vol. XXI, pp. 307-314.



MOUTH-PARTS OF MATURE TADPOLES. X15.

- |                              |  |
|------------------------------|--|
| 1. <i>Rana catesbeiana</i> . | 5. <i>Rana sylvatica</i> .               |
| 2. <i>Rana palustris</i> .   | 6. <i>Bufo lentiginosus americanus</i> . |
| 3. <i>Rana pipiens</i> .     | 7. <i>Hyla pickeringii</i> .             |
| 4. <i>Rana clamata</i> .     | 8. <i>Hyla versicolor</i> .              |



So, in both the upper and the lower labium, the last row will be the first to disappear or be reduced.

The following table, which presents the total length of the tadpoles, the length of their tails, the length and depth of their bodies, shows a curious correlation:

Species.	Greatest length.	Greatest length of tail.	Greatest length of body.	Greatest depth of body.
	<i>mm.</i>	<i>mm.</i>	<i>mm.</i>	<i>mm.</i>
Bufo l. americanus . . . . .	28.0	18	10.0	5
Hyla pickeringii . . . . .	33.5	22	11.5	7
Hyla versicolor . . . . .	46.0	32	16.0	13
Rana sylvatica . . . . .	47.2	33	17.2	13.8
Rana palustris . . . . .	74	49	26	16
Rana pipiens . . . . .	84	56	27.8	16.4
Rana clamata . . . . .	84.8	57	28	16.6
Rana catesbeiana . . . . .	145.0	100	45	38

Strangely enough, the ascending scale is the same for all four characters. For example, the toad tadpole is the smallest in all four particulars, as the bullfrog tadpole is the largest. In addition, the order of size for the tadpoles is identical with that for adults, if the toad be eliminated from the consideration.

Those who do not have dividers or lens at hand for relative measurements or for examination of mouth-parts, may wish some easily recognizable character for the determination of the forms. The coloration or markings on the tail or some equally striking character may furnish it. These have been italicized in the following synopsis of the tadpoles of our eight species.

## KEY TO THE TADPOLES.

*Spiracle sinistral.*

- A. Anus median. Tail *cloudy translucent, rounded at the end*, never twice the length of the body, but 2.9 to 5.0 its length. *Belly very dark, iridescent*. Nasal space in mouth, 1.4 to 2.2. Interorbital space not greater than the mouth. Labial series of teeth  $\frac{3}{3}$ . The lower margin of the labium always free of papillæ for a distance almost equal to the width of the mandible. Greatest length, 28 mm.....*Bufo l. americanus*
- B. Anus dextral. Lower lip bordered with papillæ. Interorbital space usually greater than mouth. Internasal space mainly 0.9 to 1.5 in mouth. Greatest length over 30 mm.
1. Upper caudal crests extending along the back, almost to between the eyes, which are lateral and visible from the ventral as well as the dorsal aspect of the body. Nostrils twice nearer the eye than the snout. Crests with dark blotches of color near the margins. Internasal space in mouth, 0.7 to 1.25.
    - a. Tail 2.2 to 3.5 times the length of the body, *scarlet or orange vermilion with black blotches more prominent near the margins of the crests*. *Belly conspicuously white or very light cream, slightly iridescent*. Tail 2.3 to 2.6 longer than deep. Spiracle 1.5 times nearer the base of the hind legs than the snout. Eye nearer the spiracle than the snout. Labial teeth  $\frac{3}{3}$ , the lateral upper row seldom extending beyond the upper fringe of teeth. The second row of labial papillæ extending across the lower margin of the labium. Internasal space 0.7 to 1.0 in mouth, never greater than it. Greatest length, 46 mm.....*Hyla versicolor*
    - b. Tail 1.4 to 2.1 times the length of the body, *heavily pigmented with purplish black blotches on the outer edges*. *Belly cream, iridescent*. Tail 1.4 to 2.1 longer than deep. Spiracle 2.0 to 2.6 nearer the base of the hind legs than the snout. Eye equidistant between the spiracle and the snout. Labial teeth  $\frac{2}{3 \text{ or } 2}$ , the lateral upper row always extending beyond the upper fringe, sometimes half of its own length; the lower third row, a little goatee which breaks the continuity of the papillose border on the lower jaw. Internasal space less or greater than the mouth, 0.8 to 1.25. Greatest length 33.5 mm.....*Hyla pickeringii*
  2. Upper crest not extending beyond the vertical of the spiracle. Eye dorsal. Nostrils nearer (but not twice nearer) the eye than the end of the snout. Mouth usually less than the interorbital distance. Tail, 1.3 to 2.2 times the length of the body. Labial teeth usually  $\frac{3}{3}$  or  $\frac{2}{3}$ , rarely  $\frac{1}{3}$  or  $\frac{1}{4}$ . Second row of papillæ seldom extending far inside the lower labium's margin.
    - a. Labial teeth  $\frac{3}{3}$  or  $\frac{4}{3}$ , at least one of the lateral upper row extending beyond the end of the upper fringe of teeth. Second row of papillæ distinct and extending a considerable distance inside the margin of the lower labium. Nostril equidistant between spiracle and snout. Internasal space less than the mouth, 1.1 to 1.9 in it. *A cream line along the upper jaw region*. *Belly with a decided pinkish bronzy iridescence*. Greatest length, 47.2 mm.....*Rana sylvatica*
    - b. Labial teeth  $\frac{3}{3}$ , rarely  $\frac{3}{3}$ , the lateral upper row not extending beyond the end of the upper fringe. The second row of papillæ not extending inside the margin of the lower labium. Dorsal tail crest not reaching the vertical of the spiracle. Extreme lengths, 84 to 145 mm.
      - (1) Eye nearer the snout than the spiracle. Labial teeth  $\frac{3}{3}$ , rarely  $\frac{1 \text{ or } 2}{3}$ . Muscular part of the tail, 1.35 to 1.95 (never more than 2) in depth of tail. Internasal space in mouth less or greater than it, 0.9 to 1.35. Belly not or very slightly iridescent.

## KEY TO THE TADPOLES—Continued.

*Spiracle sinistral*—Continued.

B. Anus dextral—Continued.

2. Upper crest not extending beyond the vertical of the spiracle—Continued.

b. Labial teeth  $\frac{2}{3}$ , rarely  $\frac{3}{3}$ , etc.—Continued.

(1) Eye nearer the snout than the spiracle—Continued.

(a) Nostril equidistant between eye and snout. Spiracle 1.08 to 1.44 nearer base of the hind legs than the snout. Labial teeth  $\frac{2}{3}$ , rarely  $\frac{3}{3}$ ; the upper lateral row of teeth at least one-fourth of the length of the upper marginal fringe of teeth. In ventral aspect, the sides of the body form a decided angle with the tail (except in one-year-old tadpole). *Tail with regular round black spots, some of which are dumb-bell-like in shape. Belly straw-color or maize-yellow, not iridescent. Internasal space in the interorbital space, 1.75 to 2.2. Greatest length, 145 mm. . . . . Rana calesbeiana*

(b) Nostril nearer the eye than the snout. Spiracle 1.35 to 1.8 nearer base of the hind legs than the snout. The upper lateral row of teeth never one-fourth of upper marginal fringe. *Tail greenish mottled with brown. Belly deep cream color without or with a very slight coppery iridescence. Labial teeth  $\frac{2}{3}$ , rarely  $\frac{1}{3}$ . In ventral aspect, the sides of the body gradually merge into the tail. Internasal space in the interorbital space 1.25 to 2.1. Greatest length, 84.8 mm. . . . . Rana clamata*

(2) Eye not nearer snout than spiracle. Labial teeth  $\frac{2}{3}$ . Width of muscular portion of the tail, 1.6 to 2.4 in depth of the tail. Internasal space 0.9 to 1.8 in the mouth. *Belly conspicuously iridescent.*

(a) Median space between the upper lateral rows at least twice the length of either one of them. *Crests very dark, opaque sometimes almost solid purplish black, and usually marked with aggregate spots or blotches somewhat like Rana clamata. Eye equidistant between the spiracle and the snout. Internasal space less or greater (0.9 to 1.8) than the mouth. Mouth in interorbital space 0.85 to 2.1. Greatest length, 74 mm. . . . Rana palustris*

(b) Median space between upper lateral rows equal to but not twice one of them. *Crests conspicuously lighter than the body, translucent, and marked with scattered fine spots and pencilings. Eye nearer the spiracle than the snout. Internasal space always less than the mouth in width (1.1 to 1.5 in the mouth). Belly deep cream with bronzy iridescence. Greatest length, 84 mm. . . . . Rana pipiens*

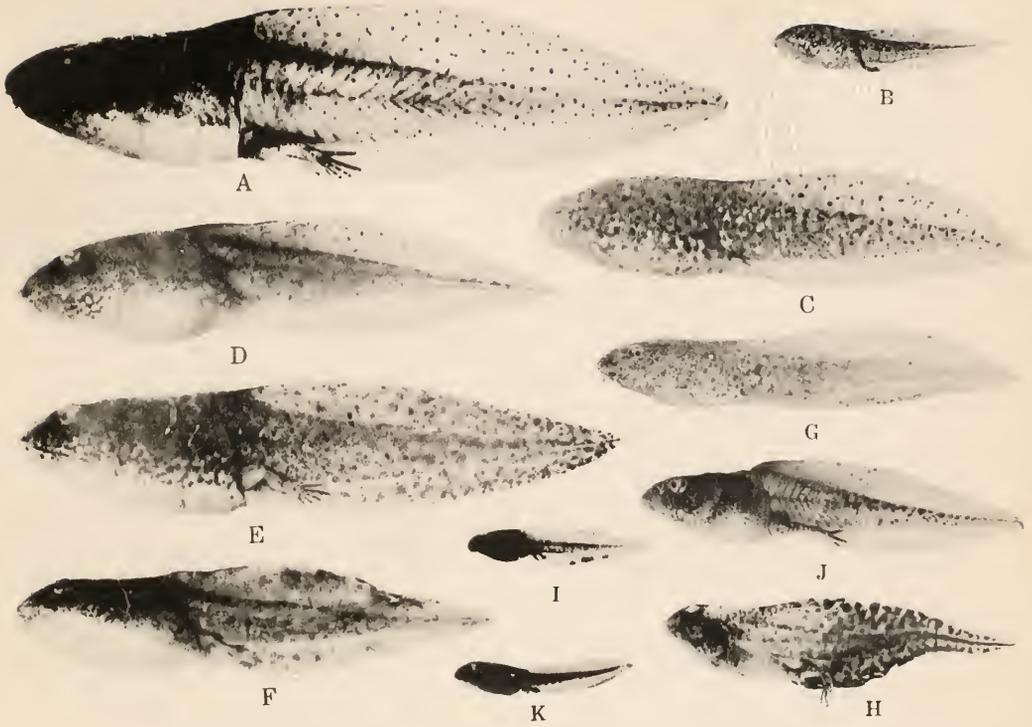
## THE TRANSFORMATION.

Transformation may begin in early June, but it occurs principally from the latter part of June to the first or middle of August, especially in July. Thereafter, until October or November, stragglers may transform. The approximate order of transformation is given in the following condensed table of data:

Species.	Transformation-size.		Transformation-dates.		
	Average.	Range.	Average.	Range.	
	<i>mm.</i>	<i>mm.</i>			
Toad.....	9.6	7 to 12	June 21	June 8 to August.	
Wood-frog.....	16.0	12 21	June 27	June 8	Aug. 1.
Green-frog.....	33.0	28 38	June 28	June 17	August.
Peeper.....	11.0	9 14	July 6	June 12	Aug. 1.
Meadow-frog....	24.0	18 31	July 12	June 30	Aug. 6.
Bullfrog.....	53.0	43 59	July 16	July 8	October.
Pickerel-frog....	24.0	19 27	July 23	July 14	October.
Tree-toad.....	16.0	14 20	July 25	July 18	Aug. 15.

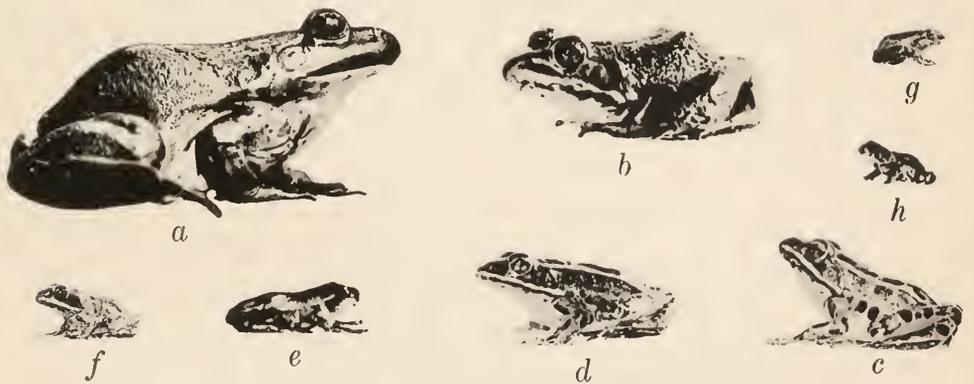
From the above, one might derive the following groups based on the period of transformation: The toad, the wood-frog, and the green-frog; the peeper and the meadow-frog; the bullfrog; the pickerel-frog and the tree-toad. The first three may vary in their order. Any one of them might be a possible first to transform. In the same way, the peeper and meadow-frog may change positions and occasionally the peeper tadpoles anticipate those of the green-frog. In such a case, however, neither is first or second in order of transformation. All our records of the bullfrog place it securely in the sixth position. The pickerel-frog and the tree-toad are very close in their order and interchange positions frequently.

If a composite curve were made of the eight curves of transformation-sizes, we would have a continuous record for seven forms from 7 to to 38 mm. A gap of 5 mm. separates the end of this composite curve from the beginning of that of the bullfrog, which transforms at sizes from 43 to 59 mm. An examination of the curve for the seven forms reveals three distinct modes and a suggestion of a fourth. These modes come at 10, 18, 22, and about 31 mm., respectively, and show clearly the groups of our Anura based upon transformation-size. They are: The toad and the peeper (ranges, 7 to 12 mm. and 9 to 14 mm., respectively; averages, 9.6 and 11 mm.; modes, 10 and 11 mm.). The tree-toad and wood-frog (ranges 14 to 20 mm. and 12 to 21 mm.; averages, 16 and 16 mm.; modes, 16 and 18 mm.). The pickerel-frog and the meadow-frog (ranges, 19 to 27 mm. and 18 to 30 mm.; averages, 24 and 24 mm.; modes, 22 and 22 mm.). The green-frog (range, 28 to 38 mm.; average, 33 mm.; mode, 31 mm.). The bullfrog (range, 43 to 59 mm.; average, 53 mm.; mode, 54 mm.). (Plate ix, Fig. 2; Plate x).



MATURE TADPOLES.  $\times 1$

- |  |  |
|--|--|
| A. <i>Rana catesbeiana</i> , third season (2 years old).       | F. <i>Rana palustris</i> .                                 |
| B. <i>Rana catesbeiana</i> , first season (3 to 5 months old). | G. <i>Rana clamata</i> , first season (3 to 6 months old). |
| C. <i>Rana catesbeiana</i> , second season (1 year old).       | H. <i>Hyla versicolor</i> .                                |
| D. <i>Rana pipiens</i> .                                       | I. <i>Hyla pickeringii</i> .                               |
| E. <i>Rana clamata</i> , second season (1 year old).           | J. <i>Rana sylvatica</i> .                                 |
|  | K. <i>Bufo lentiginosus americanus</i> .                   |



RELATIVE SIZES OF TRANSFORMED EXAMPLES.  $\times 1$ .

- |                              |  |
|------------------------------|--|
| a. <i>Rana catesbeiana</i> . | e. <i>Hyla versicolor</i> .              |
| b. <i>Rana clamata</i> .     | f. <i>Rana sylvatica</i> .               |
| c. <i>Rana palustris</i> .   | g. <i>Hyla pickeringii</i> .             |
| d. <i>Rana pipiens</i> .     | h. <i>Bufo lentiginosus americanus</i> . |





RANGE OF TRANSFORMATION-SIZE.

- |  |                              |
|--|------------------------------|
| 1. <i>Bufo lentiginosus americanus</i> . | 5. <i>Rana palustris</i> .   |
| 2. <i>Hyla pickeringii</i> .             | 6. <i>Rana pipiens</i> .     |
| 3. <i>Hyla versicolor</i> .              | 7. <i>Rana clamata</i> .     |
| 4. <i>Rana sylvatica</i> .               | 8. <i>Rana catesbeiana</i> . |





1



2



3



4

AMERICAN TOAD (*BUFO LENTIGINOSUS AMERICANUS*).

1. A female toad which was dug out of a sandy-loam bank, March 13, 1898. Wide awake when submitted to the temperature of a warm room.  $\times 0.75$ .
2. The same toad resuming the hibernating attitude when placed out-of-doors in a temperature almost freezing.  $\times 0.75$ . Figs. 1 and 2 by S. H. Gage.
3. A toad in its summer burrow. Photo by A. A. Allen.
4. A croaking male partly in the water. Flash-light.



degrees or more. To recapitulate: when the air reaches 53 to 57 degrees we have the lowest temperatures at which to expect toads emerging; as the air-temperature ascends from 57 to 64 degrees, we may predict them with a certainty.

THE VOICE.

The instant the toad fully awakens, its chief concern is to reach water. If it appears in March, frequently an interval of 18 to 35 days elapses before the first note; if, however, first emergence comes in April, the interval is negligible or from 1 to 4 days. An average interval for 12 years is 10 days. The note of the toad is long sustained, quite musical, rather high in pitch, and wholly unlike that of the other 7 forms herein considered. Their low variable trills or pipings in chorus are rather pleasing and do not especially annoy, even though continued day and night during the height of their breeding season. The first notes of the species for several years are:

Max. temp. day previous.	Date of first voice-records.	Max. temp. of date.
°F.		°F.
67	Apr. 19, 1900	62
60	Apr. 22, 1901	62
58	Apr. 21, 1902	72
44	Apr. 23, 1903	50
55	Apr. 23, 1904	60
67	Apr. 27, 1905	64
53	Apr. 13, 1906	64
60	Apr. 28, 1907	66
76	Apr. 23, 1908	81
65	Apr. 6, 1909	74
80	Mar. 30, 1910	79
56	Apr. 13, 1911	62

An average date of the beginning of singing is April 18; the earliest, March 30, 1910; the latest, April 27, 1905. It appears from the above that a maximum air-temperature of 60 degrees or more is the rule for the first trill of this species at Ithaca. For the day preceding the record, the maxima average 62 degrees; on the day of the record no maximum is beneath 60 degrees (one exception) and the average is 66; and each record with one exception is flanked on one or both sides by temperatures of 60 degrees or more. The first record of song in spring is almost invariably at night. The chorus-stage begins about 10 days after the first trill, or April 28, the extremes being April 23 and May 6. The chorus maxima do not descend below 60 degrees and average 69 to 71 degrees. A consideration of 44 voice-records shows 14 maxima between 50 and 60 degrees, 23 between 60 and 70 degrees, 33 between 70 and 80 degrees, 17 between 80 and 90 degrees, and 1 above 90 degrees, or averages of 68 degrees for the day previous to the record and 71 degrees for the day of the record. During the very last of April and through

most of May they may be heard by day even during its hottest portions. After May 20 their daily notes practically cease. At night their trills reach far into the summer, *e. g.*, in 1910 they were heard until June 26, in 1907 until July 15. Water-temperatures taken at the time of 16 voice-records in 1909–1911 show that the species begins piping when the water reaches 53 to 60 degrees.

The species, then, begins trilling usually at 60 degrees, though records as low as 50 degrees have been secured, the averages being from 62 to 66 degrees. They enter the chorus at 69 to 71 degrees. The effective water-temperatures seem to be from 53 degrees upward, their average being over 60 degrees.

#### THE MATING.

The males are noticeably smaller than the females (Plate II, Fig. 1), have dark throats, and at the breeding season possess dark-brown excrescences (Plate III, 8*b*), on the inner-upper side of the first two fingers (rarely on inner edge of third finger) and on the inner carpal tubercle. In color they average lighter, but as considerable mating takes place by day and in shallows, the females are often as light as their consorts. Both sexes repair to the water about the same time (the males slightly preceding), a condition that does not so generally obtain with the other *Anura* of Ithaca. At this migrating season, some of the paths, walks, and roads are almost completely covered with toads. The two sexes are commingled and frequently the male makes the journey on the back of the female, neither seeking cover during the daytime. Sometimes, in the early season, before the species has reached the crest of breeding, one can find hidden males at varying distances from a breeding spot. In little sunken pockets at the surface of the ground, they occasionally hide, not entirely under cover. The back is exposed to the sun and the skin is as dark as the dirt itself. The migrations begin early in April, but toads have been recorded migrating to breeding localities as late as June 14, by which date many of the early breeders are leaving or have left the ponds.

The males far outnumber the females, and the furious actions incident to the first meetings of the two sexes, or following the arrivals of other toads, are long-sustained and exhausting. Often five or more males are attached to one female, or else to each other in their attempt to reach the female. Not rarely do some of the females in such bunches die from suffocation and pressure.

Normally, the pair, if mated in water, lays at once. With every one of the numerous captive pairs we have secured ovulation on the day of capture or during the following night. Of course, where they meet on the migration, the male may be mated more than a day; but, when the water is reached, the embrace does not last long before eggs are laid. Rarely, after mating takes place, a sudden drop far below the normal

breeding temperature may cause them to become inactive, remain beneath the surface of the water, and delay ovulation. In one case I have circumstantial evidence to show a delay of 6 days.

The male embraces the female by digging its forearms into the axilla of the female, the forefingers of the male being folded up (Plate II, Fig. 1). In this way it is clearly seen how the dorsal horny excrescences of the first three fingers of the male come into use.

Sometimes the males resume the embrace after the females have laid their complements. The longest record is an embrace for 12 days after ovulation. In three instances, where pairs laid in water or in dry jars, the males resumed embraces soon after the completion of ovulation. Each had a lumbar amplexation or one midway between lumbar and axillary. They so remained for 6 days, and part of the time throughout this period they were in the lumbar amplexation. Only once (April 1, 1910) has a lumbar embrace been recorded in the field.

That cross-embraces are possible with this species, every naturalist knows. Cross-embraces between males of the genus *Bufo* and females of *Rana pipiens*, *palustris*, and *clamata* were noted. In one instance, March 31, 1910, a male *Bufo* seized a female *Rana pipiens* and held her with right arm in front of and the left arm behind the forearms of the female frog. The arms of the male toad almost met on the breast and there was no suggestion of the axillary or supra-axillary form of embrace. A little later, both forearms were placed behind the forearms of the frog, but they met on the breast, as in the fashion of the male *Rana*. In another case, a curious embrace was secured April 8, 1908, with a male *Bufo* and a female *Rana clamata*. The toad had his right hand dug into the axil *Bufo* fashion, but the left arm and hand went around on the breast *Rana* fashion. After a period it lost its grasp and regained a lumbar embrace, which it maintained only long enough to enable it to work slowly up to the customary axillary hold.

Furthermore, *Bufo* is the North American Anuran most easily led into abnormal embrace with dead animals, inanimate things, or live animals of other orders or classes; for example, on April 28, 1911, in the laboratory, a male toad was embracing a dead female *Rana pipiens* (Plate IV, Fig. 1). In the field, males have been found holding dead females. And almost every naturalist has tried out the amorous frenzy of the males with a finger, with sticks, stones, or a dozen other objects.

#### OVULATION.

At the spawning season, to find a thousand toads in one small pond is not a rare observation; hundreds of pairs may be recorded laying at one time; and in one instance 10 pairs were secured within an area  $1\frac{1}{2}$  feet square. Any water-hole, ditch, or transient pool may have one or more toads at this season. They prefer the shallows (Plate XII, Fig. 1) and are not particular whether it be grassy, weedy, or swampy,

whether the bottom be free or covered with fresh or dead vegetation. So long as water is at hand, their main desideratum is met. In choice of breeding spot, then, the toad is easily suited and will use a greater variety of localities than any other of our Anura. They begin ovulation about April 23, the extremes being April 5 and April 30. The first records are:

Max. temp. day previous.	Date of ovulation.	Max. temp. of date.
°F.		°F.
60	Apr. 22, 1901	62
58	Apr. 21, 1902	72
50	Apr. 24, 1903	56
55	Apr. 23, 1904	60
64	Apr. 28, 1905	76
68	Apr. 22, 1906	51
70	Apr. 30, 1907	67
82	Apr. 25, 1908	70
66	Apr. 5, 1910	81
76	Apr. 28, 1911	82

For the day preceding the record the maxima range from 50 to 82 degrees, and average 65 degrees; for the day of the record they range from 51 to 82 degrees and average 67 degrees. Every record is flanked on one side by 60 or more degrees, with one exception of 56 degrees. A consideration of the maxima for all (not just first) spawning records from 1906 to 1912 gives an average of 68 degrees for the day previous to the record, and 72 degrees for the day of the record. These temperatures, 68 to 72 degrees, indicate when the species enters the crest of spawning.

Water-temperatures taken at the place and time of spawning, yield averages of 63 degrees for water-surfaces and 65 degrees for water-bottoms, these seldom descending below 56 degrees (four exceptions from 46 to 51 degrees). Whenever low temperatures like the above occur, the mated pairs are inactive and probably begin under higher temperatures. None of the water-maxima descended below 63 degrees, and the minima were below 56 degrees but once (47 degrees); the maxima averaged 66 degrees, the minima 56 degrees. The effective and prevailing water-temperatures, then, seem to be from 56 to 66 degrees.

The crest of ovulation comes about April 30. Thereafter the number of spawning pairs diminishes. By May 15 or 20 laying in myriads is about completed and by May 20 or 25 nearly all the toads' eggs are hatched. In June there are a few stragglers, and our latest June records are June 18, 1902, June 17, 1906, and June 21, 1901. In rare instances, the species lays even in July, but we have only one definite date, *i. e.*, July 25, 1907. Professor S. H. Gage adds another late date (July 22, 1902) for Ithaca. So, spawning in this species occasionally extends far beyond the transformation-time of the first-hatched *Bufo* tadpoles of the season.

When spawning has begun or the female is almost at the ovulation process, it seems a difficult matter to arrest ovulation. On April 5, 1910, four pairs were captured, three of which were beginning laying and the fourth had not started. In the first jar we placed a female in water but isolated the male. The female finished her complement. In the second jar the pair were left in water and they completed ovulation. In the third case the pair were placed in a dry jar, but they laid their eggs. The fourth pair, which had not begun when captured, laid in a dry jar. In all cases, a male was present at the inception of spawning or during its entire process. We have one record (May 3, 1907) of a female laying with no male present. We tried only once to see if females would lay when placed with males of other species. A pair of mated toads and a pair of pickerel-frogs were taken. The males were taken off and transposed. The following morning the female toad had laid, but we have no certain evidence that the male pickerel-frog mated with her during the night.

#### THE EGG-LAYING PROCESS.

Egg-laying takes place both by day and by night. It has been noticed frequently, but the process was observed most minutely April 30, 1907, in a pond where hundreds of pairs were laying on introduced *Marsilea*. The male always seeks to get his vent as near that of the female as possible. Usually the male puts his hind legs, or his feet at least, between the hind limbs of the female. Great variations in this particular are observed. Rarely the outer metatarsal tubercle rests on the dorsum of the thigh of the female. Occasionally, instead of putting his legs between those of the female, a small male (though not exclusively so) draws his legs up after the usual fashion, except that they rest on the back of the female around her vent. In one case the soles of the male's hind feet were obliquely perpendicular and facing backward. Again, another male locked his hind legs under and at right angles to the thighs of the female. The females, at the beginning of fertilization, straighten their more or less bowed legs, which in turn hold the hind feet of the male. Each period of sperm- and egg-emission consumes about 5 seconds. Within this time a male makes from 4 to 12 emissions of sperm. At such a period, from each oviduct a string of eggs 2 to 7 inches long may be voided by a female at one effort. After this period of activity the male remains in the fertilization attitude from 1 to 3 minutes, *i. e.*, with his hind feet between those of the female. Instances have been recorded where they so remained 9 or 10 minutes. Often, however, when bothered by another male immediately after emission, he uses his hind legs to ward off the intruder.

Quite frequently the eggs after emission remain for some time about the vent. In some instances, the male holds them up temporarily by his hind feet, which are brought up under the vent of the female. In

every case they eventually drop to the level of all the eggs previously laid. After each period of emission the female moves, thus getting the eggs out of the way; and this doubtless facilitates the fertilization of the next mass of eggs. The period of rest is seldom less than 1 or 2 minutes, and often several minutes elapse between periods of sexual activity. When a pair lays from 4,000 to 7,000 eggs—two strings, each 20 or more feet long—it is easily seen that the egg-laying generally extends over 2 or 3 hours or more. An actual count of the eggs taken from one ovary of a mature female captured April 28, 1905, gave 2,356 ripe eggs.

#### THE EGGS.

The eggs are laid ordinarily in quiet water; it may be shallow, but not always so. The eggs are found in pools and ponds, artificial or natural, in marshes, back-waters, ditches, etc. The strings (Plate VII, Fig. 2; Plate I, Fig. 2B) rest merely on the bottom or are twined about vegetation or sticks which happen to be near at hand.

The eggs (Text-figure 1A) are laid in long spiral tubes of jelly. The vitellus varies from 1.0 to 1.4 mm. in diameter; 1.2 mm. is the modal diameter; the average is 1.1 mm. Each individual vitellus has a quadrangular envelope (Text-figure 1A), which has two of its sides parallel with and closely apposed to the inner tube of jelly. These individual envelopes abut and are inclosed within the inner tube, which varies in diameter from 1.6 to 2.2 mm. This inner tube is in turn incased in an outer tube of jelly. The latter may range from 3.4 to 4.0 mm. in diameter.

#### THE HATCHING PERIOD.

The hatching period is usually very short. In 1907 a few of the records are as follows: On May 14 and 15 myriads were laying in one place, and by May 18 all of the eggs were hatched; in another place, eggs laid May 14 at 10 a. m. were hatched by 10 a. m., May 17; some eggs laid earlier in the season (April 30) hatched in 5 days. In 1908 eggs laid April 25 hatched in 10 days when the maximum air-temperatures averaged 60 degrees. In 1910 the species began laying very early in April. On April 5 in one place it began when the air-temperature reached 81 degrees, but the eggs did not hatch until 10 days later, under an average of 57 degrees air-maxima. In another place, under quite different conditions, they hatched in 12 days. In 1911, in one locality they hatched in 5 days when the maximum water-temperatures averaged 71 degrees and when the maximum air-temperatures averaged 73 degrees. In another instance, they hatched in 9 days when the water averaged 62 degrees and the air averaged 65 degrees. The eggs are usually in shallow water which is quite responsive to air-temperatures.

In general, when the eggs are subjected to 70 degrees or more they hatch in 5 to 3 days; from 65 to 70 degrees, in 8 to 5 days; from 55 to 65 degrees in 12 to 8 days.



AMERICAN TOAD (*BUFO LENTIGINOSUS AMERICANUS*).

1. Myriads of transformed toads on the shore of Beebe Lake, Ithaca, N. Y.
2. Curled egg-strings.



THE MATURE TADPOLE.

Length of body 1.3 to 1.7 in the length of the tail, average 1.49. Width of body in its own length 1.25 to 1.7, average 1.52. Nostril nearer the eye than the snout. Eye usually nearer the snout, but occasionally equidistant between the snout and the spiracle. Distance between the nostrils contained in the interorbital space 1.2 to 1.8, average 1.6; in mouth 1.4 to 2.2, average 1.76. Spiracle sinistral, 1.3 to 1.8 nearer the base of the hind legs than the snout, average 1.54. Anus median. Depth of tail in its own length 1.25 to 2.7, average 1.97. Mouth contained in the interorbital distance 0.77 to 1.00, average 0.92. Greatest length, 28 mm. Greatest length of body, 10 mm. Greatest length of tail, 18 mm. Greatest depth of tail, 5 mm.

*Coloration of body* (Plate IX, Fig. 1κ): The ground color is a very dark brown or black overlaid with many fine gold and silvery spots, these aggregated in a few places. The venter is like the back, but the aggregates of bright spots are more silvery and more or less iridescent (coppery). The muscular portion of the tail is dark, like the back, with a few gold-spotted areas. The crests are *cloudy transparent*.

*Mouth-parts* (Plate VIII, Fig. 6): On the upper lip are two rows of teeth, a marginal row and a series of lateral teeth, the outer ends of which do not extend beyond the end of the marginal row. The median space between the lateral rows is almost equal to the length of a lateral row. Between the lateral series and the marginal series there is usually a dark line of color. Three straight non-wavy rows on the lower lip; the third row is long and forms the lip's margin, which has no papillæ along its median portion. In 90 specimens, there were few variations from the normal. In only two instances was the third lower absent, and in two others it was faint. Rarely, the second and sometimes the first lower rows are discontinuous in the middle or divided into several parts. In the upper labium the marginal fringe was broken but twice. In one instance the lateral row was almost absent on one side; and in another case the lateral series almost bridged the median gap.

THE LARVAL PERIOD.

This period ordinarily covers from 50 to 65 days. In 1907 eggs were first laid April 30 in one pond, where transformed individuals were first noted July 5, 66 days later; in another pond, 51 days were required for the species to reach transformation. In 1906 the first eggs were laid April 22, and the first larvæ transformed June 23, 62 days later. In 1908 a period of 64 days was secured. In 1911 the transformations came at periods ranging from 41 to 60 days.

THE TRANSFORMATION.

This is usually the first Anuran of the season to transform. When transformation is taking place, the shores of some ponds are black with myriads of little toads, their numbers being particularly notice-

able when they leave the shores and cross near-by roads and streets. Transformation begins the last of June and may continue into August. Our earliest record of transformation is June 8, 1911. In 1906, our first record is June 23; in 1907, July 4. An average date is about June 21.

The curve of 182 transformed individuals gives a range of 7 to 12 mm., an average of 9.6 mm., a mode of 10 mm. (Plate x, Fig. 1.)

#### THE AUTUMNAL DISAPPEARANCE.

The toad is observed quite commonly in September; but, as the colder days of October begin to appear, it goes, for varying periods, into its hiding-places, burrows, and covers, especially after the first hard frosts. Thereafter, occasionally during the warm spells (above the average for October days) it reappears. Most of our late records are in the month of October, the latest being November 4, 1907, the average, about October 20. The average maximum air-temperature for the day before the record is 66, as it is for the day of the record. For the day of the record and that preceding, the maxima are above 57, with the two following exceptions: In one instance, the temperature was as low as 48 on the day the specimen was found, but on the day previous it reached 67. The record of November 4, 1907, was flanked by 50 on either side. It therefore appears that the species may be observed in the fall, after it has retired one or more times, provided the temperatures ascend to 60 to 66 degrees. It has been recorded, however, under the temperatures of 48 to 57 degrees.



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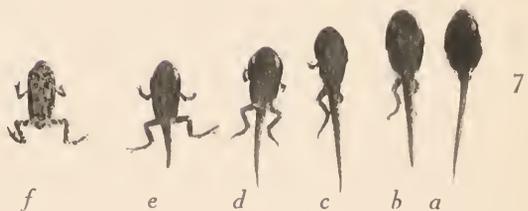
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PEEPER (*Hyla pickeringii*).

1. A croaking male. Note mosquito on his leg. Flash-light.
2. Same individual as in Fig. 1. Flash-light.
3. An adult peeper. Note cross on the back. Photo by C. R. Crosby.
4. Mated pair. Axillary amplexation.  $\times 1.5$ .
5. A series of peepers from tadpole to transformed peeper. Dorsal aspect.  $\times 1$ .

AMERICAN TOAD (*Bufo lentiginosus americanus*).

6. Mating mass of toads. Photo by A. A. Allen.
7. Series of toads from tadpole to transformed toad. Dorsal aspect.  $\times 1$ .



## AFFINITIES OF THE EIGHT SPECIES OF ANURA IN THE ITHACAN REGION.

The affinities of these forms have hitherto been based upon adult structural characters which we consider quite as important as the evidence herein adduced. But a supplementary consideration of the general habits, breeding phenomena, and tadpoles of our eight species reveals much of interest.

The wood-frog (*Rana sylvatica*) adult easily looks to be of the *R. temporaria* group, preferably *Rana agilis*. In adult habits they are close parallels. In both the active pairing is brief and the males have convex webbing on their hind feet. Among our eight species, the wood-frog has the vitelline sphere the largest, namely 1.8 to 2.4 mm., comparable to the relatively large vitelli of *R. agilis*. The envelopes about the vitelli of both species seem about the same size. In the wood-frog tadpole the upper caudal crest extends farther forward than in the other four species of *Rana*. In fact, it approaches the cephalic position of a *Hyla* tadpole and seems, from a comparison of figures, to be an exact duplicate of the tadpole of *Rana agilis*. The labial teeth formulas for both are  $\frac{3}{4}$ , rarely  $\frac{4}{4}$  in *R. sylvatica*. This condition of tadpole teeth sets the wood-frog apart from the other four frogs, which normally have  $\frac{2}{3}$ .

In two of the remaining four frogs (*Rana*), the second upper row of labial teeth is well developed, namely in *Rana pipiens* and *Rana palustris*. The mouth-parts look like those of *R. arvalis*, whose submerged egg-masses apparently resemble those of the above two forms. The vitelli of *Rana palustris* and *pipiens* are from 1.6 to 1.9 mm., while those of *Rana arvalis* are 1.5 to 2.0 mm.; the outer envelopes of the two American forms may reach 6 mm. in diameter, while those of *R. arvalis* often are 7 or 8 mm.

The other two species of *Rana*, namely *R. clamata* and *R. catesbeiana*,\* lay larger egg-complements, 3,500 to 20,000, more like *Rana esculenta* of Europe. As in the latter, in which the vitelli are 1.5 mm. in diameter, the eggs of these American forms are small, 1.2 to 1.7 mm. in diameter. The green-frog and the bull-frog begin breeding in May or later, as does the European "edible frog," and in all three there may be a very extended period of breeding. The adults, of these two species are the most aquatic forms in this country, as *Rana esculenta* is in Europe. With our species the larvæ regularly hibernate, while with *R. esculenta* it often happens but is not usual. In size of tadpole and labial mouth-parts, the larval characters are not unlike.

Of the relationships of the other three Anura, little need be said. On the structure of larval mouth-parts, *Bufo l. americanus* approaches *B. clamata*, while *Hyla versicolor* approaches *H. arborea*. *Hyla pickeringii* with its small goatee or third lower labial row suggests an approach to the type of *Bufo* mouth-parts.

\*Note the suggestive parallel in late spring appearance, vocal sacs, late egg-season, packet-film form of egg-complement, jelly consistency of eggs, etc., of *Hyla versicolor* and these two *Ranas*.

## LIFE-HISTORY OF THE AMERICAN TOAD.\*

The most familiar amphibian of our country is the common toad. It is easy of observation, and numerous are the good accounts of its habits, life-history, and structure. In appearance, it is stocky with short stubby limbs, has a conspicuously warty skin and decided head-crests (Plate XI, Figs. 1 and 2). It is more nocturnal than diurnal. When it first emerges in the spring it appears more frequently at night. Through the months of April and May it can be seen by day as well as at night, wending its way to shallow overflows, which may be clear, leaf-laden, grassy, weedy, or swampy. It seeks also transient or permanent ponds, ditches, and slow-moving portions of our streams. From the end of May to the first weeks of July they are leaving the breeding-places to resume a terrestrial existence until the same season comes again the next year. Their life from completion of breeding to hibernation is largely nocturnal, except in cloudy or rainy weather, or in favorable shady localities like gardens, etc. During the sunshiny hours they seek cover beneath piazzas, under board walks, flat stones, boards, logs, woodpiles or similar covers, in cellar entrances and countless other dark or moist situations. It is the most domestic of our Anura and presents an interesting sight when feeding in the streets or roads beneath our electric lights. When the cold severe weather of the autumn comes, then the toad digs backwards into its regular summer quarters (Plate XI, Fig. 3) or may choose another site for its hibernation.

## THE FIRST APPEARANCE.

This species appears about 6 or 7 days after the peeper, 4 days after the meadow-frog, and 1 day after the wood-frog. It emerges about the same time as *Rana palustris*, anticipating it by one or two days. Usually its first emergence each year comes in the evening or through the night. An average of first appearance from 1900 to 1912 yields April 9, but in the years of closer search (namely, 1906 to 1911) April 1 is the average and more likely date of emergence. The first records are shown in table herewith.

Usually its first emergence each year comes in the evening or through the night. An average of first appearance from 1900 to 1912 yields April 9, but in the years of closer search (namely, 1906 to 1911) April 1 is the average and more likely date of emergence. The first records are shown in table herewith.

The maximum air-temperatures for the day of the record range from 53 to 80 degrees or average 64 de-

grees; those for the day preceding range from 41 to 76 degrees or average 57 degrees. Each record is flanked on one side by a maximum of 53

Max. temp. day previous.	Date of first appearance.	Max. temp. of date.
°F.		°F.
47	Apr. 15, 1900	57
57	Apr. 22, 1901	62
55	Apr. 17, 1902	55
68	Mar. 19, 1903	75
55	Apr. 23, 1904	60
67	Apr. 27, 1905	64
41	Apr. 12, 1906	53
64	Mar. 27, 1907	70
63	Mar. 28, 1908	72
65	Apr. 6, 1909	74
76	Mar. 29, 1910	80
46	Mar. 26, 1911	56
42	Apr. 13, 1912	55

\*Cf. Prof. S. H. Gage's "Life-History of the Toad." Cornell Nature-Study Leaflets, 1904, pp. 185-206.

LIFE-HISTORY OF THE PEEPER.

This species is the smallest of our Anura; on the average it is about an inch long. Its best field-marks are its size and the oblique cross on its back. In the spring it seems to manifest no particular preference of habitat. It occurs in myriads in the open lowland marshes, and revels in the swamps at the sources of our streams, whether wooded or open, sphagnum or cat-tail. In fact, it seeks any pool, ditch, or pond, transient or permanent, grassy or muddy.

THE FIRST APPEARANCE.

It is our first frog to come out of hibernation. The first intimation of its presence in the spring is its call, and all our first records for the last ten years are of this nature. Its appearance is almost coincident with that of the spotted salamander (*Ambystoma punctatum*) and the wood-frog (*Rana sylvatica*). An average of the subsequent dates leads one to expect the peeper on or about March 26; the earliest spring record is March 13, 1911; the latest is April 12, 1901. The first appearance records are shown in table herewith.

Max. temp. day previous.	Date of first appearance.	Max. temp. of date.
°F.		°F.
44	Apr. 12, 1901	54
54	Mar. 28, 1902	56
57	Mar. 15, 1903	48
46	Apr. 3, 1904	30
76	Mar. 29, 1905	82
45	Apr. 6, 1906	41
54	Mar. 25, 1907	56
49	Mar. 25, 1908	37
40	Mar. 31, 1909	48
62	Mar. 22-23, 1910	60
42	Mar. 13, 1911	48

On the day previous to the record the maximum air-temperatures range, with two exceptions, from 44 to 57 degrees; on the days of the records the maxima are from 41 to 82 degrees, with two exceptions. In the case of March 25, 1908, we recorded a temperature of 41 degrees where the peeper was heard instead of the official 37 degrees. From the above official records one concludes that 41 degrees is requisite for first appearance. Viewed from another point, we find the record flanked on one or both sides by a maximum of at least 44 degrees. From temperatures taken personally at the time of the first record, we have 41 degrees on March 25, 1908, 54 degrees on March 22, 1910, and 50 degrees on March 13, 1911.

This form appears occasionally in midwinter. In 1906 from January 21 to 23, the air-temperatures ran up to 70, 66, and 68 degrees. In this period the peepers appeared in Renwick Marsh, at the base of West Hill, with its decided eastern exposure. In the same spot, January 24, 1909, a similar record occurred under a temperature of 62 degrees. All in all, we may consider, from first records and second appearances, that an air-temperature of 41 degrees or higher will bring the first appearance of the peeper. They are not dependent on water temperatures for first emergence. During the midwinter appearances

the marsh was frozen solid; on March 13, 1911, the record of appearance occurred in a marsh completely covered with ice. Air and ground temperatures are the controlling factors. Often, with favorable sun exposures, a side-hill where peepers are first heard may be several degrees higher than the air. For example, their first appearance on the university campus in 1911 (March 27) occurred on a side-hill with eastern exposure under air- and ground-temperatures of 54 degrees and 60 degrees respectively.

#### THE VOICE.

The peeper is most vociferous in the afternoon and evening, but numerous records have been made of full choruses under a hot noon-day sun. Nor is its note wanting in the early forenoon, for often the first mating records were secured by following the notes of the morning "peepers." In fact, when at the crest of the chorus stage (last of April or first week of May), their din may be heard incessantly day and night. Their notes are variable, but usually shrill, clear, and high-pitched, and can be heard at a distance of half a mile. Often an individual male calls 15 to 25 times a minute, each whistle being a second or less in duration. This species even more than its congener, the tree-toad, semi-inflates its vocal sac during its silent intervals. Often when we have suddenly captured them thus swollen, the collapse is accompanied with a curious squeak.

During the chorus-stage, the male in the pond has a very different note from one approaching it. The note of the latter lacks the strength and volume of the male already arrived and has a more querulous tremor in it. It is interesting to observe how suddenly a chorus will end at one's approach, only to be soon resumed if the intruder remain quiet. At this time, they may be among the grassy hummocks along the sides of the ponds, or in the shallow pools within the surface film of dead leaves or algae. Not infrequently when disturbed they may be seen leaping on this matted carpet before disappearance. In one instance we discovered one in the spathe of the skunk-cabbage. They may be taken at night with a flash-light without much effort, be they in grass, trees, or ponds, provided they "peep" occasionally. It is generally about 3 to 6 days after the first record, that the first chorus is noted; the extremes are 1 and 23 days. The records are given in the table on page 37.

In six of the ten records we observe, on both sides of the record, maximum temperatures of 60 degrees or more; in every case, 60 degrees or more on one side. Certainly the lone 54 degrees is a conservative temperature for the beginning of the chorus-stage. Of numerous air-temperatures taken at times of choruses, 52 degrees is the lowest secured. When the thermometer begins to ascend through 60, 70, and occasionally 80 degrees, as it does in the last two weeks of April, and from May 1 to 16, we have the crest of the chorus-stage; after the

middle of May the ear-splitting concert begins to abate, and by June 1 very few are to be heard; seldom after June 15 do we hear the peeper.

The question naturally arises, do not temperatures of water rather than of air influence the time of chorus? At this period the males are either on the bank or at the water's surface—in either case, more or less exposed to the air. Moreover, the peeper is more frequently found in shallow water, where, after the ice has gone the water quickly responds to air-temperatures. A consideration of 24 simultaneous air- and surface-temperatures, taken in chorus-season in years 1908 to 1911, shows that an average of the air-temperatures is 64 degrees, while the average of the surface-temperatures is only 3 degrees lower. In no case, with two exceptions, was a chorus recorded where the water surface descended below 57 degrees.

Interval.	Max. temp. day previous.	Date of first voice-record.	Max. temp. of day.
<i>Days.</i>	<i>°F.</i>		<i>°F.</i>
2	67	Apr. 21, 1900	70
1	54	Apr. 13, 1901	60
15	60	Apr. 12, 1902	50
4	68	Mar. 19, 1903	75
2	65	Mar. 31, 1905	64
6	41	Apr. 12, 1906	63
3	70	Mar. 28, 1907	69
3	63	Mar. 28, 1908	72
5	62	Mar. 27, 1910	76
23	37	Apr. 5, 1911	63

THE MATING.

We believe that the males are the first to appear in the ponds, though the retiring females may arrive at the same time. We consider that the males migrate day and night until arrival, more actively at night. Two of our ponds are situated at the bases of wooded embankments, 75 to 100 feet high, with eastern and southeastern exposures. Along these, from top to base, in early spring, we discover males migrating by day to the ponds. Or near other ponds rarely by day, more often by night, we occasionally capture the males on their way through the grass to the ponds. Never by day or at night, with the flash-light, have we so taken females. Rarely we do capture on the above embankments, in daytime, female peepers hiding under stones, some near the ponds, others at different distances up the embankment—all of which seems to indicate that the females are not so eager to hasten their migration or to enter the ponds until ready for ovulation. Our latest dates for males migrating downward from the crests of the embankments are April 18, 1910, and April 18, 1911, by which time most of the males have already arrived at their breeding-places. Once with the concourse, life is very strenuous and active for the males. They are

continually at the surface, and consequently are much darker in coloration than the less active females, which keep more to cover. At night both are much lighter and pop into view at once when light is flashed on them. The same result is frequently noted when mated pairs are captured at day. Whenever they arise to the surface the male only is exposed. He may be as dark as the darkest dead leaves in the pond, the female beneath being much lighter.

In the customary weather of spring, mating generally begins about April 1 and continues until May 1 or later. In one instance as late as June 4 (1902), at one of our best collecting-spots, Mr. T. L. Hankinson reported "two specimens were found clasped and hopping about the muddy grass-sheltered ground near a pond." The earliest record of mated pairs is March 30, 1907. Mating takes place largely at night, though in some cases pairs have been captured in forenoon, afternoon, or at midday. The embrace is axillary (Plate XIII, Fig. 4), and the smaller male holds the female behind and slightly above or on the plane of the shoulder, the hands with fingers folded back being in the axils of the female about half an inch back of the insertion of the arm. The gular sac in this species, as in the tree-toad (*Hyla versicolor*), seems to have also the secondary function of helping the male keep his hold of the female. In this species the sexual ardor is no less strong than in forms much larger. Often mated pairs when captured would break their holds, but if immediately put together they resumed their embraces before my return to the laboratory. All of the mated pairs captured afield lay by the following day, suggesting that they probably do not remain in the embrace for several days preceding ovulation.

A vigorous male which was accidentally placed in the *Rana sylvatica* jar embraced a male of this species March 31, 1907. When several males were placed with *Chorophilus triseriatus*, cross-embraces by males of both species ensued. On March 30, 1907, several eager males were placed in the common Amphibian jar and within a short time they began to embrace an *Ambystoma*. As many as three have been recorded clasping the head alone; and the same three presented a ludicrous sight arranged along the back of this salamander, which in this case was not disturbed, as in the case of the embrace of the male *Rana sylvatica*.

A few peculiar embraces within this species were noted. Once a female was in the possession of two males, the second above the first, and with a hold just ahead of the arms of the female. Sometimes a male will seize another male and have its fore limbs dug into the groin just ahead of the hind limbs of the male seized, with the face caudad.

#### OVULATION.

In the laboratory ovulation has usually begun at night, sometimes extending into the following day. In the field all our observations on spawning were made by day. Invariably we chanced upon them when it was already begun, never at the initiation of egg-laying. We believe

that every year when the species reaches the chorus-stage, spawning also begins or is already in progress. An examination of the following egg-laying records shows no maximum air-temperature below 51 degrees, and none for day of record below 50 degrees, a condition closely following the 54 and 52 degrees given for the chorus stage. On March 29, 1910, in the exact place at the bottom of the pond where ovulation was in progress, a temperature of 59 degrees was secured; at the surface, 60 degrees.

Max. temp. day previous.	Date of first egg-laying.	Max. temp. of date.
°F.		°F.
69	Apr. 25, 1904	58
64	Apr. 14, 1906	67
51	Apr. 25, 1906	50
79	Mar. 30, 1907	64
60	Apr. 28, 1907	66
69	Mar. 29, 1910	80

#### THE EGG-LAYING PROCESS.

As the time for egg-laying draws near, the female becomes very restless. No other Anuran of this region appears more nervous. If conditions are not just to her liking, she leaves at once. The first pair taken illustrated this very well. On April 25, 1904, we placed a pair in a large aquarium 1½ feet in diameter. It was 1½ feet high, had a wire-gauze screen over the top, and 2 inches of water in it. At 11 p. m., when I left the laboratory, they were still in the jar, but the next morning they were gone. The female with male attached, no doubt, had climbed the smooth perpendicular surface of 1½ feet, lifted the unweighted screen, and sought other quarters.

In the evening of April 28, 1907, three pairs were captured. At 8<sup>h</sup> 30<sup>m</sup> a. m., April 29, all three were ovulating. In every pair the fertilization took place when the pair was in a semi-horizontal or oblique position. At the moment of fertilization the male drew its vent down to meet the slightly upturned vent of the female. Immediately the female assumed an erect position, her hind limbs drawn up behind. The vent was then extended horizontally forward and the emission of a single egg followed.

The female, when egg-laying, hugs the stem or stick with the fore-arms. Both hind limbs are drawn up, so that the heels touch each other or one is a little cephalad or caudad of the other. None of the females just mentioned was seen lying lengthwise of a stem. Generally, a female came up from the side and faced at right angles to it. This position she kept for one or two, rarely four emissions. Usually she changed position after each emission, though it might only be to take the other side of the stem. Sometimes, when laying on the bottom

of an aquarium jar, with no stems to hold, the female may frequently bring the forearms together above and in front of the vent.

At each emission only a single egg is laid. A few bunches were recorded, but they were made up of singly deposited eggs, each of which was laid after a period of activity and movement in the jar. Instantly after the emission of sperm in the oblique position, the female swings to the erect position and voids a single egg. When laying at regular intervals she remains 5 to 10 seconds in this position. If the deposition be not at the crest of her egg-laying or if she be slightly disturbed, she may so remain 15 to 20 seconds. At the height of egg-laying an interval between fertilizations may be as small as 5 seconds.

One pair was watched very carefully and the following notes are the beginning of the record: Four emissions in one minute; pair went to surface for air; an interval of three quarters of a minute; five emissions in three-quarters of a minute; up again for air; one-half minute wait; five emissions in 50 seconds; up for air; etc.

Oviposition lasts for several hours. All three pairs had been laying for some time previous to 8<sup>h</sup> 30<sup>m</sup> a. m., when they were first noticed, yet one pair kept on until 3<sup>h</sup> 15<sup>m</sup> p. m. of the following day. Two of the pairs continued in the embrace 4 or 5 hours after egg-laying was apparently completed.

On March 29, 1910, an excellent opportunity came for observing the process in nature. At 10 a. m. I noticed a pair come to the surface and watched them return to the bottom. The periods of remaining in attitude for emission varied from 10 to 20 seconds. The female maintained a horizontal position, not upright as in previous pairs observed. She would lay an egg, then walk along or drag herself and mate along three or four steps, stop for another fertilization and emission, and so it went for some time through the weeds and matty vegetation without rising to the surface during my observations. Probably they come up occasionally, as when first seen. After a time they were captured, put in a wet handkerchief, and carried a mile to the laboratory. In an hour they were taken back to the pond in a glass jar with wire gauze over the top. In spite of this handling and the hot sun's rays through the glass they did not break until I placed the jar in the pond. They soon embraced again and continued laying as if nothing had happened. The process had begun and they could not stop it. Occasionally in laboratory, and more rarely in the field, we have recorded females dead after ovulation.

#### THE EGGS.

The eggs are submerged and laid singly. Both these conditions make them hard to find in the field. We have found them in water from an inch to 3 feet deep, among fine grasses and other plants, in matty vegetation and leaves of various sorts, but usually not far removed from the bottom, if not on it. Invariably in the field we have

recorded them arranged singly (Plate I, Fig. 2G), never in packets or masses, as often occurs in restricted captive quarters, where sometimes they are found in bunches of 4 to 12 eggs (Plate VII, Fig. 1). Neither have we seen eggs attached to sticks, yet in captivity such material has been used. Most of our field records of eggs were accidental. Seldom do we find them when especially bent upon it. The outer envelopes of peeper eggs (Text-figure 1c) range in diameter from 1.4 to 2.0 mm.; average 1.7 mm.; mode 1.8 mm. The vitellus diameter ranges from 0.9 to 1.1 mm.; the average 1.0 mm.; the mode 1.0 mm. The vegetative pole is white or creamy white, never yellowish; the animal pole is black or brownish. The egg of *Hyla versicolor* (Text-figure 1E) almost invariably has an inner envelope, while the reverse is the general rule for the egg of *Hyla pickeringii* (Text-figure 1c). But if one should find the latter egg with such an envelope, the two would not be difficult to distinguish. The inner envelope of the tree-toad egg would equal the diameter of the outer envelope of the peeper egg. Furthermore, the outer envelope of the tree-toad egg ranges from 4 to 6 mm. in diameter; that of the peeper egg, from 1.4 to 2 mm. The outer envelope of the tree-toad egg is loose in consistency and ragged on the outside; that of the peeper egg is firmer and smooth on the exterior. The egg-complement (1,500 to 2,000) of the tree-toad is laid in small packets at the water's surface from the last of May onward; each egg of the peeper's complement (800 to 1,000) is laid singly, submerged, and usually before the tree-toad has begun ovulation.

#### THE HATCHING PERIOD.

A mated pair captured on March 30, 1907, laid early on the morning of March 31. On the morning of the 4th of April, 5 days after deposition, the eggs were hatched. A month later another pair laid in laboratory and their eggs, under a higher temperature, hatched in 4 days. The eggs laid on the morning of April 29 began hatching on the morning of May 3 and half of them were hatched by 3 p. m. of the same day. Several attempts were made at placing egg-complements laid in laboratory in special hatching-trays in various ponds, but without success. Finally on March 29, 1910, a pair was placed in a glass jar and this was sunk in the pond of their capture, the wire-gauze top being on a level with the water's surface. They began laying in this receptacle at once. Fifteen days later came the first record of the eggs hatching. During this period, the minimum water-temperatures ranged from 50 to 66 degrees; the maxima from 67 to 79 degrees.

#### THE MATURE TADPOLE.

Length of the body 1.4 to 2.1 in the length of the tail, average 1.65. Width of the body in its own length 1.3 to 1.65, average 1.46. Nostrils twice nearer eye than the end of the snout. Eye lateral, equidistant from spiracle and snout. Distance between nostrils in interorbital

space 1.2 to 2.4, average 1.75; in mouth 0.8 to 1.25, average 0.923. Spiracle sinistral, 2.0 to 2.6 nearer the base of the hind legs than the snout, average 2.16. Anus dextral. Depth of the tail in its own length 2.4 to 3.15, average 2.72. Depth of the muscular part of the tail in its depth 1.75 to 2.6, average 2.15. The mouth is contained 1.2 to 2.6 in interorbital space, usually above 1.5. Greatest length 33 mm. Greatest length of body 11.5 mm. Greatest length of tail 22 mm. Greatest depth of tail 7 mm.

*Coloration of body* (Plate IX, Fig. 11): The background of the back is orange, heavily pigmented with dark (almost black) spots, the general tone being greenish; these dark spots are interspersed with very small shining gold-like ones. The venter is with a cream ground, pigmented with dark toward the sides and more decidedly from the gill region forward. The latter region is conspicuously marked with gold and silver. The whole is iridescent. The muscular part of the tail has an orange background at the base, becoming lighter and almost clean at the tip, the whole pigmented with small spots slightly coalesced. The crests are clear, heavily pigmented with purplish black blotches on the outer edge, particularly toward the tip; but occasionally these blotches are absent. Small gold spots are sparsely scattered over the whole surface.

*Mouth-parts* (Plate VIII, Fig. 7): Upper fringe not relatively as long as in *Hyla versicolor*. The second lateral row extends a considerable distance (sometimes half its own length) beyond end of upper fringe. On the lower lip there are always two rows of teeth, the second row being just inside the second row of papillæ. The rows of teeth are quite wavy in general appearance. In most specimens there is a little goatee of teeth on the lip's margin. In 28 tadpoles out of a series of 106 this little fringe of teeth is absent and in one case it was divided into two parts; often when it is absent the second row is discontinuous and one of the median ends of the second row dips toward the lip's margin. Furthermore, the second row when intact in its middle often bends decidedly toward this region. The upper fringe is rarely broken. In one specimen the lateral upper row of one side was missing.

#### THE LARVAL PERIOD.

This extends over a period of 90 to 100 days. In 1906 the first eggs were recorded on April 14. In the same pond the first transformed individuals were noted 93 days later (July 16). In 1907 eggs were recorded in a pond April 2. In the same place, 94 days later, on July 5, a few were found transformed. In another pond, where they began laying about the middle of April, transformed individuals were recorded 95 to 100 days later. In another case, where they began laying April 22, transformed examples were taken July 22, 91 days afterwards. In 1908 a period of 100 days was recorded, and in 1911 there was a record of 95 days. In every case cited the period given includes the entire

period from egg-deposition to transformation, not merely the true larval stage.

#### THE TRANSFORMATION.

Transformation usually begins as early as July 1, although the average date of transformation is July 6. The range of transformation is from June 12 to August 1. The first record for 1906 is July 17; for 1907, July 5; for 1908, July 21; for 1909, July 21. The earliest records of transformation are June 26, 1901; June 21, 1904; and June 12, 1911. In normal years the peeper tadpoles of the year have transformed by July 25. The latest transformation we have found is August 1, 1907.

The curve of 92 specimens from 17 different collections gives a range of 9 to 14 mm., an average of 11 mm., a mode of 11 mm. (Plate x, Fig. 2.)

#### THE AUTUMNAL DISAPPEARANCE.

In the autumn, about September 1, the peeper from the trees, bushes, and woods, from hillsides and lowlands, breaks its summer silence. In 1912 they began peeping August 26. Four-fifths of our fall records come in the month of October, particularly in the middle and latter part, the latest date before winter disappearance being November 26, 1908. In every instance the maximum air-temperature reached 60 degrees or higher.

## LIFE-HISTORY OF THE TREE-TOAD.

The tree-toad has little in common with its smaller relative, the peeper, and has a body twice as long, a warty skin, and no distinctive dorsal oblique cross. The tree-toad has considerable yellow or orange-yellow associated with the hind limbs, both on the posterior surface of the femur and along the side of either groin, where at times the closely applied hind legs conceal it. The peeper we associate with the ground more than its larger congener. The former may at certain seasons be a true tree-frog, yet it is only the tree-toad which we usually expect to observe or capture in trees, on vertical surfaces, etc. When the tree-toad repairs to the water, the peeper has left or is leaving. Finally, "the color and manner of distribution of its eggs" do not prove the same, as once supposed.

## THE FIRST APPEARANCE.

This is the seventh Anuran to appear from hibernation, and, like the bullfrog, it has no associate species coming out at the same time. When it awakens, the wood-frog has finished laying, the meadow-frog and the peeper have almost completed ovulation, and the toad and pickerel-frog have already started on their egg-laying period. The tree-toad appears the last of April or the first of May, the period when the largest bird-wave of the spring migration is reached; and, as the wave approaches its crest, the tree-toad enters its noisiest stage. The average first appearance, if it were derived from first voice-records, would be about May 4, but the first individuals (seen before they were heard) were recorded on the following dates:

Max. temp. day previous.	Date of first appearance.	Max. temp. of date.
°F. 52	Apr. 29, 1906	°F. 71
70	Apr. 30, 1907	67
48	Apr. 16, 1909	61

The first "heard records" are:

Max. temp. day previous.	Date of first voice-records.	Max. temp. of date.	Max. temp. day previous.	Date of first voice-records.	Max. temp. of date.
°F. 76	May 8, 1901	°F. 72	°F. 58	May 13, 1907	°F. 82
58	May 8, 1903	70	78	Apr. 27, 1908	76
83	May 7, 1904	76	70	Apr. 19, 1910	64
58	May 6, 1905	70	71	May 7, 1911	75
71	Apr. 30, 1906	64			

An average of our first intimations of their presence (in the springs from 1901 to 1912) gives May 1, and for the period of more careful attention (1906-1912), April 28. Our earliest records are April 16, 1909, and April 19, 1910.



1



4



A

B



E

F

5



2



3



D

C

TREE-TOAD (*Hyla versicolor*).

1. A typical place for the breeding of tree-toads.
2. A male tree-toad croaking. Flash-light.
3. A male tree-toad hit on the head by hot flash-light powder.
4. Egg-packet of tree-toad eggs attached to Potamogeton leaves.
5. A series of tree-toads from tadpole to transformed tree-toad. Dorsal aspect. X1.



From the nature of the places in which tree-toads are first found, air-temperature must be the influencing factor of first appearance. Sometimes, while scuffling along through the dead leaves of the woods, one happens upon them. We have found them on tombstones in a wooded cemetery; on a high hill some 50 to 75 feet above the pond they will finally reach; in large trees, and even on our back porch. The maximum air-temperatures for the first appearance of each year give an average of 70 degrees for the day of the record, and 66 degrees for the day previous. Every record with one exception is flanked on one side by a temperature of 70 degrees or more; and no record (one exception) descends below 58 degrees, which appears in four different instances.

#### THE VOICE.

The tree-toad so imitates its environment that it is best known by its voice. In fact, previous to 1906 our first appearances were based upon such records. In 1906 one day intervened between first appearance and the first note of the tree-toad, the ruling temperature being 71 degrees; in 1907 the interval was prolonged by cold weather (May 1 to 12, average maximum temperature 50 degrees; average minimum temperature 36 degrees), and the first warm day (May 13) immediately brought the males into voice; in 1909 two days passed at 10 and 8 degrees lower than 71 degrees, the temperature at which they finally began. An average of 20 air-temperatures taken at the moment of voice-record yields 69 degrees with no individual records below 61 degrees; an average of the Weather Bureau maxima for the days of first voice-records, from 1901 onward, gives 72 degrees with no individual record below 64 degrees. Hence, it is safe to conclude that 61 degrees is the minimum and 70 degrees the average effective heat. At the breeding season their loud resonant trills begin in late afternoon and continue sometimes long beyond midnight. Occasionally, a few trills will begin in midafternoon, the customary period being from 4 to 8 p. m. By the latter hour the chorus is well started. When at the height of their breeding and usually after a warm rain or during an overcast sky they may be heard at noon or before, the earliest in the day being 10 a. m. Rarely, stray individuals may be heard before noon or shortly after, even though no rain precedes or clouds are present.

About the middle of May, they are in the chorus stage. At Ithaca in the evening, all over the university hill and the hills nearby, along the wooded ravines, in the thickety edges and woods of our marshes, and on the campus itself at our very door, we may stumble upon the noisy tree-toads slowly approaching the nearest breeding-place. In one instance their resort is a pond at the end of a long hedge. Here, at the breeding season, every evening and sometimes after a thunder-shower by day, the males can be heard all along its length, slowly bound for the one objective pool, where some have already arrived.

The first tree-toads of any region may be heard in trees around their breeding-places for several days before they are recorded in the ponds; *e. g.*, June 3, 1907, males were recorded in trees about the college pond; but it was not until June 9 that they entered it. About a pond near the athletic field they were heard two days (June 8 to 10) before they reached the pond. In 1906 an interval of 4 days was recorded for the college pond (May 13 to May 17).

When the tree-toads are in chorus, their abundance is amazing, and the chorus is at times deafening when near at hand. In and about the ponds they may be taken in considerable numbers, *e. g.*, in one case, 20 in 15 minutes; in another, 9 in 20 minutes. In the grass and other areas about the ponds, one may find them migrating to the pond. At the breeding season, about the edges of the ponds and in the overhanging bushes, the collecting proves best. In the ponds, logs and flat vegetative surfaces prove the most likely perches. An experiment was tried on one croaking male perched with three others on a log. To show how tame he was, and at the same time to see how dazed he would be by a strong light, I stroked him with the lighted end of my flash-light. This was done 91 times without his stirring. He croaked just the same. When he stirred, it was only to change position to another place on the log, 2 inches away. The operation could readily have been repeated. Then, too, when captured between trills, the tree-toads sometimes have the sacs half-inflated, which in collapsing, produce a squeak, as in *Hyla pickeringii*. At times tree-toad males seem quite individualistic in their calls, and an individual tree-toad may give one or two voice-forms totally unlike the normal and better-known call.

In some ponds the species may be heard for a month or more after their first arrival; at the college pond we have the following records:

First arrival: May 17, 1906; June 9, 1907; June 5, 1911.

Last heard at pond: June 22, 1906; July 15, 1907; July 6, 1911.

Some, however, leave the breeding-places by the middle of June. In midsummer they resort to the trees again, and during the latter part of August and through most of September the males may be heard from time to time.

#### THE MATING.

The males are very fond of places full of lily-pads, *Potamogeton* leaves, algæ, or other large floating surfaces, suitable as resting-places or perches. In small ponds it is not uncommon, with one sweep of the flash-light, to see as many as 8 or 10 males thus perched.

The same kind of embrace obtains as in *Hyla pickeringii* (Plate IV, Fig. 5). In the aquarium it is often noticed that the male uses his viscid gular sac as a means of attachment, augmenting his discs. When mating, this sac often is partially inflated and doubtless helps the male to retain his hold. It is doubtful if the females repair to the breeding-ponds at the same time as the males. In 1906, from the beginning of

the chorus, I collected every evening for a week from 9 to 11 p. m., and each excursion yielded 6 or more males (and as many more were seen), but not a female. Furthermore, from careful searching in that time, no signs of eggs were found. The first eggs were taken 1½ weeks after the beginning of the chorus. In 1907 the males arrived two days previous to the females.

The duration of individual mating is not very long. In all the mated pairs captured, we recorded eggs the night of their capture, whether the males were left in the embrace with the females or removed. Mating is most active at night. By day, the tree-toad is less active, sometimes remaining in the water, or perching a few inches or feet above the water on grass, sedges, or ranker vegetation, ordinarily in green livery.

We have records of males mating with partly or fully spent females, with which they have or have not formerly mated. In captivity males will seize other males, but not retain them beyond a few minutes or hours at the most.

OVULATION.

The period of ovulation may last a month or more. Generally 20 to 35 days intervene between first appearance and first eggs, and 10 to 15 days between first arrival of species at a pond and first eggs. Ovulation normally begins the very last of May, reaching its crest in June. An average of all first dates gives May 25; or with the elimination of one very early date, June 2; and an average of crests comes June 7. The range of first breeding records extends from May 10 to June 17. The first egg-records and the crest-records are as follows:

Egg-records.			Crest-records.		
Max. temp. day previous.	Date.	Max. temp. of date.	Max. temp. day previous.	Date.	Max. temp. of date.
°F.		°F.	°F.		°F.
83	May 27, 1906	61	84	June 6, 1906	78
72	June 11, 1907	69	82	June 17, 1907	87
74	May 21, 1908	73	73	May 22, 1908	74
74	May 10-12, 1911	81, 89, 80	78	June 13, 1911	77
82	June 10, 1911	84			

In all instances the maximum air-temperatures for the day previous were from 72 to 83 degrees, averaging 77 degrees; for the day of the record, 61 to 89 degrees, averaging 77 degrees.

The crests follow soon after the initiation of ovulation. They come at maxima ranging from 73 to 84 degrees for the day previous, or with an average of 79 degrees; for the day of the record from 74 to 87 degrees, or with an average of 79 degrees. Then, from 61 to 87 degrees seems the range, with 72 to 79 degrees the common effective temperature.

The egg-laying may extend into July. In 1906 the last record for eggs was July 3; in 1907 it was June 21.

Inasmuch as this species lays at the surface of the water, the air-temperatures probably are as influential as the water-temperatures of the bottom or median plane of the water. The water-temperatures, however, range from 67 to 75 degrees with an average of 71 degrees, a result not much different from the effective air-temperatures already derived.

The female tree-toad will lay without attendant males. In one case a pair was allowed to remain in the embrace in water; another pair was separated, but the female remained in water; and a third pair was separated and the female left in a dry jar. All three females, two unattended and one attended, laid their egg-complements over night. In another case, a female which was brought into the laboratory began laying without an attendant male, nor was she previously mated so far as we know. After 200 eggs were deposited, a male was placed with her. Later in the day, the mated pair completed the complement.

#### THE EGG-LAYING PROCESS.

For a long time the manner of deposition in this form was unknown. Usually, in the field, the mated pairs were taken at the edge of the ponds, the hind parts just touching the surface of the water or the lower third or half of the body submerged. Another favorite attitude with single individuals, when away from the edge of the pond, was to rest the fore limbs on a *Potamogeton* leaf or similar floating surface, keeping just the dorsum of the head out of the water. It was known that a female in laboratory might lay as many as a thousand or more eggs, yet in nature we always found them floating on the surface in groups of 4 to 25, either attached or free. This meant either that the pair laid them in packets or else that soon after laying these packets floated away from one original mass. The second alternative is no longer tenable from actual observations of a pair which was depositing at 8<sup>h</sup> 30<sup>m</sup> p. m., June 15, 1907:

Number of sexual periods.	Intervals between periods of sexual activity.		Fertilizations and emissions.	Intervals between emissions.
	<i>min.</i>	<i>sec.</i>		
1.....	2	..	3	10, 10
2.....	3	..	3	16, 16
3.....	2	7	2	2
4.....	2	14	2	1
5.....	3	46	3	1, 1
6.....	..	35	2	1
7.....	2	29	1	....
8.....	2	41	2	1
9.....	..	..	2	3

The table is to be read somewhat as follows: At the first sexual period there were three distinct fertilizations and three emissions, a fertilization and an emission being simultaneous. Between the first fertilization and emission and the second one there was an interval of

10 seconds, as there was between the second and the third. When the third was completed, the pair rested for 2 minutes. The egg-laying might last an hour or more.

The female would become restless just before each sexual period. The fertilization took place beneath the surface of the water, when the female's body was at an acute angle to the surface and the dorsum of her head was above the water. After each fertilization the female would raise her vent above the water and lay 18 to 25 eggs. There would be three or four slight movements of the hind legs with each emission. In certain instances, after egg-laying had been completed, the pair remained in the embrace several hours.

#### THE EGGS.

In the field (Plate I, Fig. 2D) the first eggs found were secured May 27, 1906. Around a *Potamogeton* plant were three isolated patches of eggs numbering 6, 10, 14 respectively. Shortly after, they became common among the tall grasses and plants in the marshes, in mid-pond, or in the open around the edges of the ponds. They float and may often be seen at a distance of several feet because of the excessive number of air-bubbles interspersed with each small bunch of eggs.

During 1906 and 1907 eight different females laid in the laboratory. An estimate of one egg-complement (after a count of 400) was 1,800 to 2,000 eggs. A conservative estimate could not put the normal number below 1,000.

The egg-packets (4 to 25) may be 6 to 12 inches apart, or only an inch or less. (Plate VII, Fig. 4; XIV, Fig. 4). Sometimes these groups are arranged at more or less definite intervals, by means of which the approximate path of the pair can be traced. They are more frequently found attached, but often become free later. Occasionally the eggs are not found at the very surface. Such are attached eggs, and in these cases they were doubtless laid at the surface, but were later submerged, due to a change in level of water after rain-storms.

The egg-mass is loose in consistency. Each individual egg has a yellowish vegetative pole and a brown animal pole; the outer envelope is ragged around its edges and has a diameter of 4 to 6 mm., the average 5.2 mm., the mode 5.0 mm. The vitelline envelope is from 1.6 to 2 mm. in diameter, average 1.7 mm., mode 1.7 mm. The vitellus diameter is 1.1 to 1.2 mm., the average and mode both being 1.2 mm. (Text-figure 1 E.)

#### THE HATCHING PERIOD.

Eggs laid in the laboratory and kept under a temperature of 66 to 70 degrees hatched in 5 days. In May 1911 some eggs hatched in 4 days where the water-surface averaged 70 degrees or more for the period. On June 13, 1911, some eggs were found which were in the yolk-plug stage; they were probably laid June 11 or 12; on the 14th they approached hatching; on the 15th they hatched, giving 4 or 5 days

as the period of development to hatching. The water-surface averaged about 72 degrees.

#### THE MATURE TADPOLE.

Length of body contained 2.2 to 3.5 times in the tail, average 2.8. Width of the body in its own length 1.3 to 1.7, average 1.47. Nostrils nearer the eyes than the end of the snout. Eye lateral, visible from the venter, and nearer the spiracle than the snout. Distance between the nostrils 1.2 to 2.0 in interorbital space, average 1.63; in mouth 0.7 to 1.0, becoming equal about the time the arms are ready to push out, average 0.878. Spiracle sinistral, its distance from the base of the hind legs 1.5 times in its distance from the snout. Anus dextral. Depth of the tail in its own length 1.6 to 2.6, average 2.1, seldom under 2.0 unless the tip be broken or partially regenerated. Depth of the muscular portion of the tail at its base 2.3 to 3.6 in the depth of the tail. Mouth is contained 1.4 to 2.34 times in the interorbital distance. Greatest length 50 mm. Greatest length of body 16 mm. Greatest length of tail 32 mm. Greatest depth of tail 13 mm.

*Coloration of body* (Plate IX, Fig. 1 H): General color of back olive-green. Background of back yellowish, covered with many fine hair-like black markings and golden and black spots, becoming orange in the head region and sometimes almost vermilion about the eye; the golden and black spots are more pronounced toward the tail; on the sides is a decided iridescence. The eye is slightly bronzy. The venter in general is conspicuously white or light cream and slightly iridescent. The belly is covered with fine golden spots. From the gill-region forward the venter is greenish, a coloration produced by black and golden spots. The background of all the tail except the base is scarlet or orange-vermilion. The base of the tail is like the body. The tail is covered with black blotches, more prominent around the edges of the crests. These blotches become much more numerous as the hind legs develop.

*Mouth-parts* (Plate VIII, Fig. 8): Upper labium with two series of teeth, the boundary fringe of teeth and a second lateral row on either side. The median space between this lateral series is half of or less than the length of one of the lateral rows. There are three continuous rows on the lower labium; at times they are quite wavy. Papillæ and labium are sometimes more or less punctulate with black dots. The second row of papillæ extends across the lower labium beneath the third row of teeth, not terminating at its ends as in the five species of *Rana*. The upper fringe is rarely broken, although it occasionally is separated at the middle or resolved into three parts. The lateral series of teeth almost bridges the normal median space in some specimens. In 63 tadpoles the lateral upper row of one side was missing in but two specimens. In one tadpole the lower first row was absent; in two or three the second lower was in several parts or with one side gone; and in one specimen the lower third row was almost gone.

THE LARVAL PERIOD.

This period extends 50 to 60 days after egg-deposition. In 1906 the first eggs were laid May 27, and the first larvæ were transformed July 31, giving a total of 65 days for the egg and larval period. In 1907 the first eggs were laid June 11 in one pond, and the first transformed individuals from the same place were recorded July 31, a total of 50 days. In 1908 the first eggs were laid May 21 in the college pond; on July 6, 46 days later, some approached transformation, while on July 22 several were recorded in adult form (62 days from the egg deposition). In another pond, ovulation was begun on May 22, and on July 7, 46 days later, transformation was completed. In 1911 in one place eggs were deposited May 10; by July 18 all the tree-toad tadpoles were transformed (59 days later).

THE TRANSFORMATION.

This takes place largely during the last of July and the first of August. For 1906 and 1907 it began July 31. In 1907 the period of transformation was nearly completed by August 15. In 1908 and 1909 the species began this stage July 21 to 25. The first transformations were found July 30, 1910, and July 18, 1911. The range appears to be from July 18 to August 15, with the average of the first transformations on July 25, the mode on July 31. In the late autumn of 1911 the tadpoles were still recorded in one pond in which the authorities had placed copper sulphate to keep out the algæ; this possibly retarded the transformation of the tree-toad tadpoles so that they passed two or three months beyond the normal transformation period. The transforming individuals can best be secured along the edges of the pond or on floating lilies and vegetation. At other times they may be taken in the vegetation around the ponds or on the grass, sedges, and water plants at distances of 2 or 3 feet above the level of the water's surface. The size at transformation of 87 specimens varies from 13.6 to 20 mm.; the average is 16 mm.; the mode, 16 mm. (Plate x, Fig. 3.)

THE AUTUMNAL DISAPPEARANCE.

In midsummer, or before, they betake themselves to the trees again and by July 15 become infrequent. From this date to the latter part of August they are usually silent, but may trill sometimes during the sultry evenings of July, before or after a rain. Frequently they remain until August 1, not far from the pond or breeding-spot to which they repaired in early May. From August onward they often wander to localities quite remote from the water. During the latter part of August, through most of September, and rarely in the first days of October, the males may be heard from time to time. Our latest autumn records of tree toads are: October 24, 1905; September 18, 1907; and October 9, 1909.

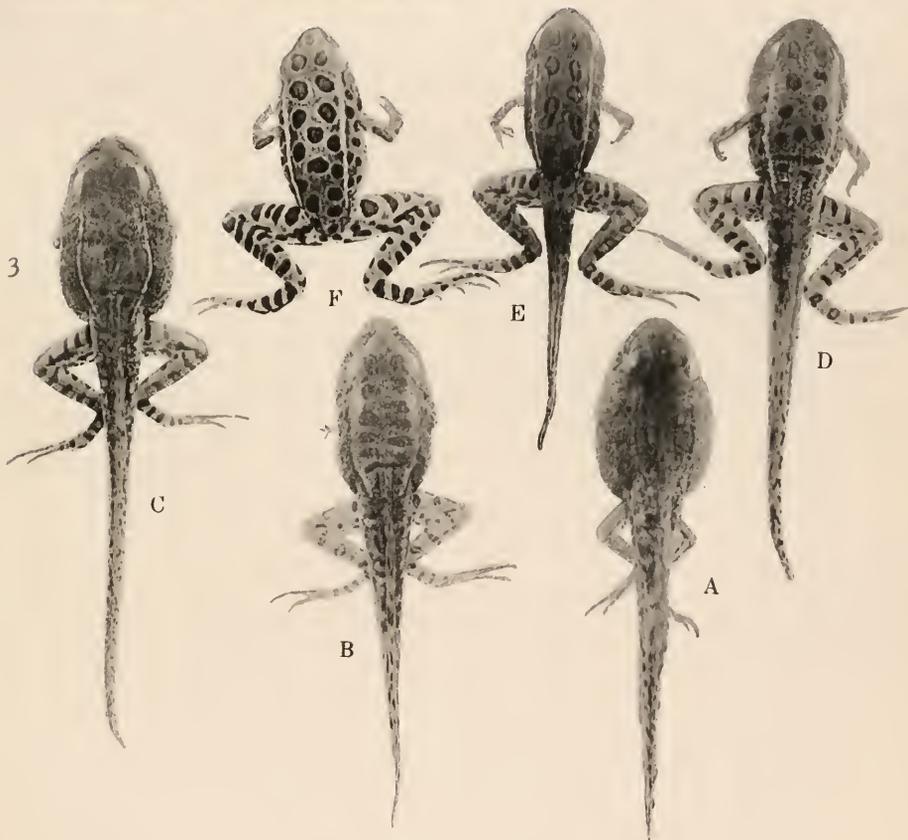
## LIFE-HISTORY OF THE LEOPARD-FROG OR MEADOW-FROG.

This is our most abundant and best-known frog. It is widespread and is common in its distribution. As the season advances it presents several color variations which need no description here. In fact, not many who go afield could mistake it, unless it be to confuse it with the pickerel-frog. The latter has, on the posterior underparts, orange or orange-yellow, which the leopard-frog lacks. The pickerel-frog has a more regular arrangement of the spots on the back and always has a distinctive brown coloring, while the meadow-frog is usually green (though it may at times appear brownish). In the early spring, until May, we find them in the water of the swampy marshlands, upland back-waters, overflows, and ponds. By the middle of May they begin to be found a short distance from the water. In early summer they leave the vicinity of the water and journey about over marshland, or leave the lowlands entirely and ascend the hills through the grassy woodlands, or through hay or grain fields of our cultivated districts. One of my most vivid recollections as a boy was following the mower in haying-time to collect the meadow-frogs which leaped out of the way or got caught in the knives. In midsummer and early fall they may still be found feeding away from the water. But with the oncoming of the distinctly autumnal temperatures, they return to the water to spend the winter.

## THE FIRST APPEARANCE.

In the early spring, when the maple-sugar camps are beginning to finish their work, when the streams are freeing themselves of ice and are overflowing the lowlands and swamps, the first meadow-frogs begin to appear in the dark settings of our marshes. They come down the ravines of our hills to the lowland marshes or emerge from the mud of the swamp itself, or from beneath stones in our streams. Along some of our watercourses in early spring, particularly where the west banks have good sun exposures, one frightens a succession of them as he proceeds along the banks. In fact, from the countless low croakings in the wide marshes before vegetation has started, one wonders whence such a frog population came. The average date of awakening is March 28, two days after the peeper and three days before the outcoming of the wood-frog. The first records from 1900 to 1912 follow:

Max. temp. day previous	Date of first appearance.	Max. temp. of date.	Max. temp. day previous.	Date of first appearance.	Max. temp. of date.
°F.		°F.	°F.		°F.
52	Apr. 7, 1900	52	54	Mar. 25, 1907	56
54	Apr. 13, 1901	60	40	Mar. 22-23, 1908	47
52	Mar. 23, 1902	52	35	Mar. 27, 1909	45
68	Mar. 19, 1903	75	50	Mar. 5, 1910	59
64	Mar. 27, 1905	58	46	Mar. 26, 1911	56
45	Apr. 6, 1906	41	43	Apr. 11, 1912	46



LEOPARD- OR MEADOW-FROG (*RANA PAPIENS*).

1. An area of egg-masses. Fourteen masses in the illustration.
2. A stick with three egg-masses; the two upper globular masses being of *Rana palustris* the lower plinth-like mass, *Rana pipiens*.
3. A series of meadow-frogs from tadpole to transformed meadow-frog. Dorsal aspect.  $\times 1$ .



The range of dates is from March 5, 1910, to April 11, 1901 and 1912; only four of the 12 records are in April, the others are in March.

The air-temperatures in this instance may not be directly influential in bringing the first appearance, yet they approximate the effective temperatures and serve as a convenient index of appearance to workers who might wish to know about its probable emergence from hibernation. The maxima for the day of the record show a range from 41 to 60 degrees; for the day previous, 42 to 68 degrees (the record 35 degrees for March 27 occurring when frogs were taken beneath stones). The average for the day of the record is 53 degrees; for the day previous, 50 degrees.

Numerous water-bottom and water-surface records taken at the time and in the place of appearance show averages of 43 and 46 degrees, or range from 41 to 50 degrees, a surprisingly close parallel with results secured with maximum air-temperatures. When the air-temperatures begin to approach 41 to 45 degrees, we may expect the appearance in spring; and when it mounts to 50 to 53 degrees, they ought to appear in numbers. When the water reaches 41 to 50 degrees, or an average of 43 to 46 degrees, they may be confidently expected.

THE VOICE.

In early spring the leopard-frogs form the second swamp-chorus to arrest attention. Individually, not possessing a loud voice, these concourses in our swamps, when most vociferous, can not well pass unnoticed. The croak may be a long low guttural note, 3 or more seconds long, followed by 3 to 6 short notes, each a second or less in length. At other times the short notes may precede, or the long and short be interspersed in innumerable ways, or the song may be composed entirely of either short or long notes. (See "Voice" under wood-frog.) In the early stages of the season, the croak may at times be subdued. This form begins croaking from 3 to 18 days, or on the average 7 days after first appearance, the range of dates

Interval.	Date of first voice-record.	Date of first chorus-record.
6 days	Apr. 12	Apr. 15
3	Mar. 28	Apr. 4
6	Mar. 28	Mar. 28
3	Mar. 30	Mar. 31
18	Mar. 23	Mar. 27
10	Apr. 5	Apr. 5

being March 23 to April 12, or the average March 31. In 1906 to 1911 the records are shown in table herewith.

From maximum air-temperatures it appears that the species begins to croak at 50 degrees or lower. Somewhere between this temperature and 60 to 63 degrees, we may expect the chorus to begin or may find it at its height. Water-temperatures taken at croaking reveal records as low as 41 to 48 degrees. Doubtless both air and water influence them, for at such times they may be on the banks or on water's surface which responds more or less to the air-temperatures. About the middle

of April their notes begin to become common, and from that date to May 1, or later, their calls are very common, even during the day. By the middle of May, they are beginning to be heard only during the evening. Sometimes in summer, during showers or on cloudy days, they resume croaking; for example, July 4, 1906, followed a rainy evening, was cloudy most of the time, and *Rana pipiens* was heard throughout the day. In the autumn they are rarely heard in the swamps, *e. g.*, September 14, 1912.

#### THE MATING.

The mating habits of this species are doubtless more familiar than those of any other North American frog. The males at the breeding season have the thumb much enlarged, but the webs of the hind feet are not quite so convex as those of the male wood-frog. At the mating period they are much darker than in early midsummer, the males usually darker than the females. For example, on April 1, 1910, I captured a mated pair in which both were very dark. The male was a very clouded green—in fact, as dark as any *Rana pipiens* just coming out of hibernation, and the female a dark brown, but much lighter than the male. These were exposed to the direct rays of the sun for an hour in a glass jar. At the end of this period, the male was a typical grass green of the summer coloration and the female a very light brownish green. As evening came on, they became darker again.

The period of mating begins April 1, or before; but the bulk of it does not come until the middle of April, and it continues for about three weeks, extending to the first or middle of May.

This species is not restricted to night courtship, although most of it occurs at this time. One can frequently observe the mating antics of this species in the day, if he can discover a spot where the species has already begun ovulation. In such localities we have taken most of our mated pairs. Before they are mated, here at the surface, the males are croaking. Occasionally, when wading through such an egg area, one hears croaks which at first puzzle; they come from the mated and mating frogs beneath the water and often reveal the game on the bottom. At such times one finds several males and gravid females about and under sticks. More rarely the pairs appear at the surface.

In the field the embrace probably does not last over a day or so. In many instances egg-laying followed immediately, the night after the capture; in several cases it came after 2 or 3 days. In pairs mated in captivity (usually unfruitful), we have recorded long periods of mating. One pair continued five weeks in the embrace, the male dying because the water was not changed. In another case a male so held a female 17 days, and upon her breast, where the two hands had been placed, were round scars (Plate IV, Fig. 3), the flesh being exposed. Not as frequently as with the toads, does the female die because of the vigor

or duration of the male's embrace. On April 25, 1911, I found a live male embracing a dead female which must have died several days previous. Did she die in the embrace? Two days later, when I returned, the pair was in the same spot.

The normal embrace is pectoral (Plates II, Fig. 4; IV, Fig. 4). The males while amplexating often half inflate the vocal sacs for short or long periods (75 times in one male) before croaking. These inflations may be rapid, as many as 60 per minute being noted. Sometimes for short periods a male will embrace another male. Once we recorded a male which in captivity resumed the embrace after its mate had laid its egg-complement. On April 1 they were captured; two days later the female laid; thereafter, for varying periods, the male broke and resumed embraces until April 5. More curious still, at 1 p. m., May 3, 1907, a male *Rana pipiens* was found embracing a female with a perfect lumbar amplexation. He kept it for 3 hours. He was handled roughly without making him relax his hold. Later, upon transference to the photographic stand, he broke his hold.

Cross-embraces with other species are not unusual in captivity. The matings with other species are: males of *Rana pipiens* with females of *Rana clamata*, *Rana palustris*, *Rana sylvatica*, and *Bufo lentiginosus americanus*. In this last instance, on May 6, 1907, a male embraced a female *Bufo* with a typical amplexation, *i. e.*, pectoral with hands appressed to the breast, and continued thus one day. In this species we have recorded two cross-embraces in the field. On April 28, 1911, we found toads and meadow-frogs mating in a certain area, and one pair proved to be a male meadow-frog mated with a toad. On the same day, in another area, pickerel-frogs and meadow-frogs were mating and laying in great numbers, the two species sometimes using the same twigs. It seemed probable that there should be cross-embraces. Later in the day, at this same place, there was found a male *Rana pipiens* mated with a female *Rana palustris* (Plate IV, Fig. 2). All hopes of fertile eggs vanished, however, because the female waited four or five days before laying her eggs, which were spoiled before ovulation. Another interesting incident happened in one of the aquaria several years ago, when males of this species were put with some bowfins (*Amiatus*); at several different times, a male embraced an *Amiatus* and rode around on its back for some time.

#### THE OVULATION.

Leopard-frogs prefer cat-tail swamps, marshy expanses of other types, grassy overflows, and shallow dead streams. In other situations than these, they breed sparingly. In austral localities they may begin ovulation before April 1. At Ithaca the ovulation rarely precedes April 10. The records from 1907 to 1912 are shown in the table on page 56.

The maximum air-temperatures for the day previous to the record (one exception) range from 43 to 76 degrees, or for the day of record (one exception) from 44 to 61 degrees, the averages being 51 and 55 degrees respectively. These are also borne out by second and third records.

Max. temp. day previous.	Date of first ovulation.	Max. temp. of date.
°F.		°F.
32	Apr. 11, 1907	44
55	Apr. 16, 1908	35
48	Apr. 16, 1909	61
76	Mar. 29, 1910	80
43	Apr. 10, 1911	52
50	Apr. 18, 1912	61

An average date of spawning is about April 11; our earliest record is March 29, 1910; our latest first record, April 18, 1912. The intervals between first appearance and first spawning range from 7 to 25 days, averaging 19 days.

In 1908, the species began laying at water-temperatures of 43 to 46 degrees, and reached the crest at 60 to 64 degrees. In 1909 it began at 45 degrees and started the crest at 52 degrees. In 1910 the water-surface records range from 55 to 64 degrees, the water-bottoms 52 to 64 degrees; the two averages were 59 and 57 degrees. In 1911 the species began at 43 degrees (water-surface and water-bottom) and entered the crest at 48 to 58 degrees. An average of water-surfaces is 53 degrees, their range 43 to 65 degrees; an average of water-bottoms is 51 degrees; their range 43 to 64 degrees; the average of maximum water-temperatures is 59 degrees; their range 54 to 63 degrees; the average of minimum water-records is 51 degrees, their range 45 to 58 degrees. An average of all the water-surface records taken gives 55 degrees, and of the water-bottoms 53 degrees, or an average of all water records secured from 1908 to 1912 gives 54 degrees. In general, when the maximum air-temperatures indicate 43 to 48 degrees, and certainly when they average 51 to 55 degrees, the meadow-frog begins spawning. The more important and effective temperatures, namely, those of the water, vary from 43 to 46 degrees at the first of the ovulation, and range from 52 to 65 degrees at the crest, the average of the totals for the whole breeding season for 4 years being 54 degrees.

We have a few unusual records of spawning. Dr. A. A. Allen succeeded in getting mated pairs to lay in a wet handkerchief. At 10<sup>h</sup> 20<sup>m</sup> a. m., April 23, 1907, a mated pair was captured and brought to the laboratory on the third floor; the next morning the cover of the jar was found knocked off and the pair had escaped. In an hour we found the trail of the pair. Halfway down the staircase between the second and first floors was a bunch of eggs 1½ inches in diameter, no expansion of the mass being possible.

#### THE EGG-LAYING PROCESS.

The meadow-frog may lay at any time of the day, even at noon (at which time, April 27, 1911, we saw a pair leaving its mass), but more frequently they spawn at night. They have a tendency to congregate in large numbers and often 40 or more bunches of eggs are recorded within small circumscribed areas. At such times, when an area is approached the mated pairs often seek cover under the bunches which have already been laid. From our first fragmentary observations, we concluded that a pair did not remain in position more than 25 minutes for the deposition of an egg-bunch, *i. e.*, after the egg-laying had really begun. Then, only the very end of the egg-laying had been observed. From a captive pair taken May 4, 1907, the following notes were secured: 3 fertilizations,  $1\frac{1}{2}$  minutes interval; 2 fertilizations,  $1\frac{1}{2}$  minutes interval; 4 fertilizations,  $1\frac{1}{2}$  minutes interval; etc. Several eggs were laid at an emission. A stick was in the jar and it was between the hind legs of the female. Neither she nor the male held anything. Doubtless this was in part due to the cramped quarters, which made them take a semi-vertical position. The male embraced with his hind limbs drawn up on the back of the female. Evidently the mated pair keeps the on position throughout egg deposition. Since this first observation, we find that egg-laying may be completed in 5 minutes. When on a horizontal branch the pair became very much flattened when spawning.

#### THE EGGS.

The egg-masses may be attached to submerged cat-tails (Plate I, Fig. 2F), twigs, sticks, grass, etc., or as often may rest on the bottom unattached. Several times the water's surface has been so low (4 to 8 inches) that the tops of the bunches appeared at the surface. They occur in the open, unprotected, marshy expanses, or in overflows where the edges and bottoms have plenty of grass. One will often find the egg-masses interspersed with algæ and dead leaves, which so fill the shallows that the bottom can not be seen. In this species, as in the wood-frog, the egg-masses may be clustered in special areas (Plate xv, Fig. 1). The meadow-frog, however, tends to seek shallower water and more swampy localities than the wood-frog.

Some of the dangers to meadow-frog eggs are newts, rapid drying of the shallows, and high-water currents. Many of the egg-masses are laid in very shallow water and it does not require very much evaporation to leave them high and dry. Sometimes this species lays in back-waters or slow-moving streams. With high-waters or sudden currents, the free masses of eggs, and some of the attached masses, are carried some distance from the original site. In this process the masses come to the surface; some separate into smaller ones, or even into the single constituent eggs, which float free on the water's surface, something that occasionally happens with *Rana clamata*.

The egg-mass at ovulation is 1 to 2 inches in diameter. After it has expanded, it is plinth-like (Plate VI, Fig. 2), the greater diameter varying from 3 to 6 inches, the smaller from 2 to 3 inches. The differences between the eggs of *Rana pipiens* and *Rana sylvatica* are summarized under the latter. The two egg-masses can easily be separated in the field by inverting the mass, thus revealing the vegetative pole of each egg. In the meadow-frog the whiteness of the egg-mass becomes very apparent, but in *Rana sylvatica* the general effect is not decidedly white because of the evident encroachment of the black of the animal pole on to the vegetative side.

In *Rana pipiens* the outer envelope ranges from 4.2 to 6 mm. in diameter, the usual range being 4.6 to 5.6 mm., the average 5.1 mm., the mode 5.0 mm.; the middle envelope is from 2.3 to 3 mm., the average is 2.4 mm., the mode 2.4 mm.; the vitellus is 1.6 to 2 mm. in diameter, the average is 1.7 mm., the mode 1.6 mm.; the vegetative pole is white, the animal pole black or brown (Text-fig. 1G).

#### THE HATCHING PERIOD.

In the field 13 to 20 days are required for hatching. In 1907, four different bunches, laid at different places April 10 and 11, hatched April 27, May 1 and 2, *i. e.*, 16, 21, 21, and 20 days respectively. Later in the season the periods for 16 different bunches laid April 22 to May 1 were: 14 days for 6 bunches; 16 days for 2 bunches; 17 days for 5 bunches; and 18 days for 3 bunches. In 1908 two different areas gave 18 and 19 days at average temperatures of 51 degrees and 50 degrees. In 1910 one area hatched in 17 days under an average of 53 degrees, and another in 14 days with an average of 55 degrees. In 1911, two different areas hatched in 20 days under averages of 48 to 50 degrees. In the laboratory four different bunches of freshly deposited eggs hatched in 6 days. Several bunches laid in the laboratory by mated pairs hatched in 5 or 6 days. It would appear that at 48 to 51 degrees they hatch in 20 to 18 days, at 53 to 55 degrees in 17 to 14 days, at 55 to 65 degrees in 14 to 7 days, at 65 to 75 degrees in 7 to 4 or 5 days.

#### THE MATURE TADPOLE.

Length of the body 1.3 to 2.2 in the length of the tail, average 1.7. Width of the body in its own length 1.4 to 1.7, average 1.5. Nostril 1.1 to 1.5 (average 1.3) nearer the eye than the end of the snout. Eye is 1.1 to 1.3 nearer the spiracle than the snout. Distance between nostrils in the interorbital space 1.5 to 2.2, average 1.8, seldom over 2.0; in mouth, 1.1 to 1.5, average 1.25. Spiracle sinistral, 1.25 to 1.7 nearer the base of the hind legs than the end of the snout, average 1.5, rarely reaching 1.7 or under 1.35. Anus dextral. Depth of tail in its own length 2.7 to 3.4, average 3.0. Depth of muscular portion of tail in depth of tail 1.6 to 2.4, average 1.9. Mouth contained in interorbital

distance 1.2 to 1.8, average 1.48. Greatest length, 84 mm. Greatest length of tail, 56 mm. Greatest length of body, 28 mm. Greatest depth of tail, 16.4 mm.

*Coloration of body* (Plate IX, Fig. 1D): Background of back, a dark brown covered with fine gold spots and many aggregate ones on sides, the general appearance somewhat similar to that of the green-frog, but darker. Background on front of head rather orange. The belly is deep cream covered with bronze-like iridescence. The gill region is pigmented with dark toward the sides, is covered all over with gold spots, and is iridescent. The throat-area is translucent and more extensive than in the pickerel-frog. Tail: Unlike the pickerel-frog tadpole, the tail is conspicuously lighter than the body, the crests being translucent and *marked with scattered fine spots and pencilings*. Gold spots occur toward the base of the tail. The eye is bronze.

*Mouth-parts* (Plate VIII, Fig. 3): Labial papillæ with black punctulations; upper fringe continuous. The space between the discontinuous second upper series is equal to and never twice one of the lateral rows of either side. The lower lip is as in the green-frog, bullfrog, and pickerel-frog. The second lower row is seldom discontinuous. In 45 specimens no decided departures from the normal were noted. The second upper row was not absent in any case, though in a very few examples it was faint or somewhat abbreviated. Occasionally the first lower row may be in three or four parts.

#### THE LARVAL PERIOD.

In 1906 eggs were recorded in one place April 25; in the same place larvæ transformed July 19, 85 days later. In 1907, in different localities, periods of 99, 103, 109, and 111 days respectively were recorded. In 1908 we have two records of 75 and 83 days; in 1911 we have two records of 94 days, or 77 and 71 days of the true larval period. The period from the egg to transformation may be from 71 to 111 days, or a true larval period of 60 to 80 days.

#### THE TRANSFORMATION.

The majority of the larvæ transform in July, although occasional records can be found far into August. The first records were July 12, 1900; July 14, 1901; July 21, 1903; July 25, 1905; July 8, 1906; July 18, 1907; July 7, 1908; July 16, 1910; June 30, 1911. The average is July 12; the range is June 30 to July 25. A consideration of all our transformation records from 1906 to 1911 shows that more than half of the transformations come between July 14 and 24. An average of all the records indicates July 17. The transformation-period for any one year consumes at least a month, sometimes running into August; our latest record at Ithaca is August 6, 1907. At the transformation season the young come out into the shallows; and if the year has been very

rainy, and the mortality consequently low, a region may have almost a plague of small meadow-frogs.

The size at transformation of 175 specimens varies from 18 to 31 mm., the usual range being 21 to 30 mm.; the average is 24 mm.; the mode 23 mm. (Plate x, Fig. 6.)

#### THE AUTUMNAL DISAPPEARANCE.

About the middle of autumn the meadow-frogs begin to take to their places of hibernation, usually in the first of October, when the light frosts come. In the middle of October, with the approach of heavy frosts, they are rarely seen. The greater part of our late records extend from October 3 to November 26, the latest being: November 18, 1899; October 31, 1902; November 5, 1907; November 26, 1908. So, when November 1 comes, we may expect most of the meadow-frogs to be under cover. An average of the very latest records gives November 12. A consideration of all the late appearances (1899-1912) which we have, gives maximum air-temperatures from 48 to 77 degrees, or an average of 66 degrees for the day of the record, and gives minima from 34 to 61 degrees, or an average of 45 degrees; for the day previous, maxima from 49 to 83 degrees, or an average of 64 degrees, and minima with an average of 41 degrees. Apparently then, after they have first entered their hibernation-quarters, they may emerge when the air of late October or early November reaches 61 to 64 degrees. They enter the mud of our marshes in great numbers and in such places the frog-catchers secure them in abundance in early spring, rarely in winter. In small ponds they seek the mud in the same fashion, but not in great hordes. They spend the winter under stones in our ravines and rocky streams, or beneath the flat stones on the riffles of our lowland streams, in the same situations where the young of basses and other fish may be taken, or beneath old logs under water. Whenever they seek very cold streams or springs which remain open all winter, they are occasionally recorded in the dead of winter, but are always more or less torpid.



PICKEREL-FROG (*RANA PALUSTRIS*).

1. An egg-area and one mated pair.
2. A croaking male showing vocal sac on either side of the head. Flash-light.
3. A series of pickerel-frogs from tadpole to transformed pickerel-frog. Dorsal aspect. X1.



LIFE-HISTORY OF THE PICKEREL-FROG.

The paucity of literature on the habits of the pickerel-frog is very evident. It has long masqueraded under the cloak of "like *Rana pipiens* in many respects." I have found that many a student has difficulty in distinguishing the two forms, but in life the brown of the pickerel-frog is wholly unlike the green of the meadow-frog; the spots are more regular and square; the rear ventral parts are a bright orange, the color so frequently associated with poisonous properties in Anura. A dog or any animal which has had experiences with the secretions of the pickerel-frog would no sooner try to eat one than it would a toad. Frequently we have made the mistake of putting live pickerel-frogs in jars with other forms, and have found the jar extremely frothy by the time the laboratory was reached, and not infrequently some of the other species were dead, apparently as a result.

In habitat they are not exactly similar to *Rana pipiens*. The meadow-frog is essentially a frog (in its greatest abundance) of the cat-tail and sedgy marshes, while the pickerel-frog is more often found in sphagnum bogs, marl ponds, cold streams, in the shallows of mill-ponds, or in the quiet waters of bayous away from the currents of our clear streams. It is the most abundant frog in our rock-bottomed and rock-walled ravines, where it quite frequently breeds in the deep holes at the bases of waterfalls and in the sources of our clear trout streams. It is not solely restricted to streams or their tributaries, but does occasionally seek swampy localities similar to the habitat of *Rana pipiens*, or quiet clear ponds for ovulation. Like *Rana pipiens*, soon after ovulation it leaves its breeding-grounds for meadow-lands. Some of the individuals which breed in the ravines keep more or less to them during the whole summer.

THE FIRST APPEARANCE.

In times of appearance and breeding we find an interesting parallel between this species and the common toad. To record one is an almost certain criterion that the other is at the same stage in its life-history. But in some years the toad precedes the pickerel-frog by a day or more, so that the latter comes fifth in the order of first Anuran emergence from hibernation. The records of first appearance are:

Max. temp. day previous.	Date of first appearance.	Max. temp. of date.	Max. temp. day previous.	Date of first appearance.	Max. temp. of date.
°F.		°F.	°F.		°F.
68	Mar. 19, 1903	75	70	Mar. 28, 1907	69
69	Apr. 25, 1904	58	63	Mar. 28, 1908	72
59	Apr. 10, 1905	68	79	Mar. 31, 1910	63
67	Apr. 15, 1906	58	63	Apr. 6, 1911	70

For the day preceding or for the day of the record no maximum goes below 58 degrees, the average being 67 degrees in either case. For a series

of second appearances, the maxima ranged from 48 to 62 degrees, averaging 53 degrees. The water-temperatures of first appearance range from 45 to 50 degrees. An average of all the first appearances is April 5, but a consideration of those from 1906 to 1911 gives April 3 as the more accurate date. The range of records is from March 19 to April 25.

#### THE VOICE.

Of our Anura, this and the rather silent wood-frog make the least audible disturbance at the breeding season. Its grating croak has little carrying power and is pitched low; higher than in *Rana pipiens*, but not so high as in *Rana sylvatica*, and it is more prolonged than that of the wood-frog. It is so characterless that the tendency will be to link it with a subdued *Rana pipiens*, but the latter has not so short a note. The pickerel-frog note is not always given "while floating at the surface of the water." I have heard it more often during the actual mating than at any other season. The males of this species, like those of *Rana clamata* and *Rana pipiens*, are much given to croaking beneath the surface of the water while in the embrace. Quite frequently the unmated males croak beneath the surface and occasionally the males at night appear to answer each other with a croak totally different from the normal one. After the breeding season, it is seldom if ever heard.

#### THE MATING.

Usually the male is the smaller, but sometimes mated pairs have been recorded where there was no appreciable difference in size. The male is darker than the female; as in other members of the genus *Rana*, it has the thumb enlarged at the breeding time; the webs of the hind feet of the male are a little less concave at the margins than in the female, though the difference is very slight. In mating areas some of the unmated males may be darker than the mated ones, possibly due to greater activity and greater exposure. Furthermore, the mated males are sometimes lighter than their females, though not often so.

Between first appearances and first matings, lengthy intervals elapse, the least being 7 days, the longest period 32 days, the average 20 days. The beginning of mating usually comes the last week in April, the earliest record being April 5, 1910, the average April 23. This species mates by day or by night. I have seen very vigorous matings at all times of day. At this season it is one of our most gregarious frogs, and is locally very much in evidence. It seems endowed with as much nuptial ardor as any of our 5 species of *Rana*, and it is about the easiest subject of the five to kill in the embrace—all of which is in keeping with its gregariousness. No other *Rana* while breeding is quite so oblivious of intruders or so easy to observe as the pickerel frog. Often, within a small area 6 feet square or less, one can find 12 to 15 pickerel-frogs mating or pairs in egg-laying positions. Any sudden movement

may send them into the mud, but the sexual impulse is so strong that within a very short time they come from their slight cover and resume mating. The mating-places are often but not always in shallows. Along the shores, within a short stretch, I have counted 20 or more frogs, actively mating, to say nothing of those in the water. In one instance, in a space 3 feet square, were 21 unmated males, 5 mated pairs, and 8 fresh egg-masses (representing 16 more frogs). In this species, when mating is at its crest, we have observed mated pairs on the banks, a phenomenon rarely if ever recorded for the others of the genus *Rana*. We have found them on sandy shores in the hot sun, in shady stony places, or in grassy edges of breeding-places—all, however, near a mating area; and no doubt they were mated in the water, and not on land as they approached the breeding-grounds.

Usually, with most of the Anuran species, mated pairs captured in the field generally laid the night of the same day of their capture, but the rule did not always hold true with *R. palustris*; in fact, it seemed the exception. To find pairs mated in the laboratory waiting two or three days before ovulation was not surprising, but frequently pairs from the field waited from 2 to 5 days before laying. In two instances, in different years (one in an early season, the other in a late season), each laid after remaining in the embrace a week. In 1912 a pair continued in the embrace 2 weeks before ovulation.

The embrace is pectoral (Plate II, Fig. 3), the usual *Rana* type. Often it is maintained after the eggs are laid. Particularly is this true of pairs mated in laboratory. On May 2, 1907, such a pair laid, but the male continued his hold; this I broke, but he resumed a few minutes later and so remained a week. Another pair brought from the field waited a week before the female began to lay and she occupied several days in laying her complement; thereafter they remained in the embrace 2 days. Similar periods from 2 to 5 days have been observed with several other pairs.

A few cross-embraces were noticed. On April 7, 1908, a male *Rana palustris* grasped a female *Rana clamata*; on the following day it was found that he had the right hand dug into the axil, *Bufo* fashion, while the left arm and hand reached around to the middle of the breast, *Rana* mode. Once he lost his hold and regained a lumbar amplexation. This he kept only a short time, working slowly up to the axillary embrace. Several times males have mated with females of *R. pipiens*, and once a male embraced a *Bufo lentiginosus americanus*. Similarly males of the above three species have been recorded mating with females of *R. palustris*.

One peculiar amplexation of *R. palustris* was noted. On April 23, 1908, a vigorous male was placed with a pair which had laid, but had continued in the embrace. The extra male seized the spent female while still clasped by her former mate; he apposed his venter to hers and held her back of her arms. We have no records of abnormal embraces with other than Anuran forms, as no opportunity was afforded for it.

## THE OVULATION.

In all the situations where eggs were recorded, clear water obtained. The best places for the observation of spawning were a pond heavily laden with dead leaves and a quiet back-water of one of our streams. In both instances they were connected with a stream in the spring, and then had their own currents; the first became absolutely cut off and quite remote from the stream, while the other ceased as a meandering subsidiary and merely kept its connection with the main channel. We have frequently found their eggs in the shallows of mill-ponds, and occasionally along the rocky shores of lakes. They also have laid in the deep holes of our ravines, particularly below waterfalls, also in lowland pools of the wide valleys of wandering streams. More rarely, did they breed in marshy stretches or in upland ponds disassociated with some creek or watercourse.

Ovulation usually begins the last week in April. The beginning of spawning for several years is as follows:

Max. temp. day previous.	Date of first spawning.	Max. temp. of date.
°F. 51	Apr. 25, 1906	°F. 50
66	Apr. 29, 1907	70
76	Apr. 23, 1908	81
81	Apr. 6, 1910	68
76	Apr. 28, 1911	82
61	Apr. 26, 1912	62

Thus, we see that the maximum air-temperatures range from 51 to 81 degrees, and that they average 68 degrees for the day before the record; for the day of the record, they range from 50 to 82 degrees and average 69 degrees. Every record is flanked on both sides by a temperature of 50 degrees or more, usually above 61 degrees. A consideration of 21 different breeding records (not first ovulations) gives an average of 67 degrees for the day of the record and only one record below 53 degrees; for the day before the record the average is 65 degrees, with only one individual case below 50 degrees. Every one of these records is flanked on one or both sides by at least 50 degrees. Water-temperatures taken at the time and place of breeding yield averages from 57 to 60 degrees; the maxima average 64 degrees, the minima 51 degrees. These temperatures, 51 to 64 degrees, well represent the prevailing warmth of the water at breeding.

The average date of ovulation is April 23; no record precedes this date except one, April 6, 1910. The bulk of the ovulation takes place the last week of April and the first week of May. The species seldom lays beyond May 15. The latest date for eggs was May 16 in 1906; May 18 in 1907; May 12 in 1909. The extreme period of breeding is

April 6 (1910) to May 18 (1907), or 6 weeks. In any single year, however, the period is about 3 weeks. The length of the breeding time was 21 days in 1906; 20 days in 1907; 19 days in 1910. The following summary of the 1907 spawning story for three ponds is representative of a normal year: 8 bunches on April 29; 15 bunches on April 30; 12 bunches on May 1; 30 bunches on May 2; 3 bunches on May 3; 2 bunches on May 14; 1 bunch on May 18.

We have noted more spoiled bunches of eggs in nature in *R. palustris* than in any other species of Anura. Sometimes all the bunches of a pond may be in such a condition. We have already alluded to the tendency of captive females not to lay for some time after being mated, and then a few eggs at a time for a week or more. Almost invariably these delayed complements are infertile. Again, we have an instance of a female's laying without an attendant male (April 28, 1906). Unlike some of our records of similar phenomena, she was not separated from a mating male, but was unattended when captured. As a result we may suspect that the spoiled condition may possibly be due partly to unattended and partly to delayed laying.

In conclusion, one may expect that the species will begin laying when the air reaches 50 to 61 degrees, and most certainly when 65 to 69 degrees are recorded, provided the water is 51 to 64 degrees.

#### THE EGG-LAYING PROCESS.

We have watched none of our species more carefully, both in the laboratory and afield, yet previous to 1911 we had not seen the complete egg-laying process, in all the 50 or more pairs of *R. palustris* observed. It does not last long; for example, May 3, 1907, one of our mated pairs in the laboratory had not laid at 3 p. m., but between 3 and 3<sup>h</sup>20<sup>m</sup> p. m. a fresh bunch of eggs was deposited. One of the best places to hunt for mated pairs is underneath egg-masses already laid or at the base of a suitable stick.

Some observations in 1907 will serve to show the nervousness of the mated females. At least four pairs were observed perched on a twig in what appeared to be an egg-laying position; after a time one pair left and until their capture hid for 20 minutes underneath the twigs upon which they formerly were; the second pair remained for 20 minutes on a twig which already had 2 bunches of eggs. In both instances the female merely rested on the twig, holding with neither her fore nor hind limbs. A third pair was discovered at 11<sup>h</sup>40<sup>m</sup> a. m. (May 3, 1907) the female sitting astride a horizontal stem. She was semi-erect, her fore limbs on a level with the stem; her hind limbs were not locked and her feet did not hold the stem. At 11<sup>h</sup>45<sup>m</sup>, she brought both heels up so that they touched under the twig; then she dropped one leg and remained with one heel touching the stem; at 12<sup>h</sup>05<sup>m</sup> her hind limbs were both brought up and her feet came in touch with each other; at

12<sup>h</sup>06<sup>m</sup> they put up for air, but saw me and put down immediately; at 12<sup>h</sup>15<sup>m</sup>, when I was obliged to leave for an afternoon class, they were resting on the bottom of the pond 1½ feet from the stick. The fourth pair (1906) previously mentioned was merely resting upon another bunch already laid. When we captured them 50 or 60 fresh, sticky eggs were found on the top of the old bunch.

Another description of a pickerel-frog congress April 28, 1911, will supplement that of May 1907. In a 9-foot square some 31 frogs were mating and laying in a shallow spot. The mated pairs were numerous and the females backed around aimlessly until a stick or stem was found. This a female kept a very short period, changing position or backing to another stem, a process she kept performing in rapid changes. As she moved about, other males interfered and endeavored to secure a hold; when other males troubled her, she helped her consort to kick them away. Usually an unmated male would grasp the male in possession by a leg or other parts and let go as quickly. Occasionally the seizure was long sustained, as with the toads. In one instance a male seized the mated male in front of his hind limbs, lumbar fashion; another male grasped him by the head and maintained his hold. When finally a pair actually were about to lay, the female grasped a stick or stem with her hind limbs and became perfectly horizontal and flattened, her hind limbs drawn up with the heels together. The male's hind legs were parallel to those of the female and slightly within them. The male would draw up his hind legs and thrust them back as if helping to push the eggs out. The frogs were very flat and the female's front feet were brought together. The egg-laying occupied about 3 minutes in all. There were 10 to 12 fertilizations. The male released his grasp almost immediately after the complement was laid, and put up for air, but the female remained in position about 2 minutes more. I left the area at 10<sup>h</sup>50<sup>m</sup> and returned at 11 o'clock to find another mass had been laid in the 10-minute interval.

#### THE EGGS.

The eggs of *R. palustris* are almost invariably submerged and attached to sticks (Plate I, Fig. 2c), twigs, or tufts of grass stems. The species seeks the shallows for egg-laying, although not exclusively. Almost every year we find some egg-masses in the middle of ponds where the water is 1 to 3 feet deep. They tend to lay in special areas (Plate XVI, Fig. 1), as *Rana sylvatica* and *Rana pipiens* often do. In 1907, in an area 3 by 3 feet, 18 bunches were deposited; in another area, 4 by 3 feet, 12 bunches were recorded. In 1911, in another spot, 3 by 3 feet, 31 bunches were found. All of these areas gave excellent illustrations of the building of bunches, one upon another. In 1907 at least one case of 4 successive bunches upon one twig was recorded, 10

instances of 3 successive bunches upon one twig, and 7 instances of 2 bunches (Plate xv, Fig. 2). The greatest number of bunches on one support was secured May 5, 1909, when 7 were noted. Quite frequently, on one tuft of grass or stick, one finds a bunch or more of *Ambystoma punctatum* or *Rana pipiens* eggs with as many as two *Rana palustris* complements immediately above them—seldom below, because laid later. At the time of deposition a bunch may be 1 to 2 inches in diameter, but it soon becomes  $3\frac{1}{2}$  to 4 inches. It is usually firm and globular (Plate vi, Fig. 4). Frequently it has been observed that some of the older egg-masses were quite frayed in appearance or scattered into several smaller masses. By observing the frogs it became apparent that this condition resulted from the nervous threshing of the females in their successive attempts at taking a satisfactory position. Then, too, *Notophthalmus viridescens* (the newt) often seizes an individual egg for food and pulls until it disentangles it. The egg-complement of *Rana palustris* may be from 2,000 to 3,000.

The bright yellow vegetative and brown animal poles make the eggs of *R. palustris* the most distinctive of all our *Rana* eggs. The outer envelope ranges from 3.6 to 5 mm.; the average is 4.0 mm., the mode 4.0 mm. The middle envelope ranges from 2.4 to 2.8 mm.; the average is 2.6 mm., the mode 2.8 mm. The vitellus diameter is from 1.6 to 1.9 mm.; the average is 1.7 mm., the mode 1.6 mm. (Text-fig. 1B.)

#### THE HATCHING PERIOD.

In nature the hatching may extend from 11 to 21 days. In 1906, when the average maximum air-temperatures were 60 degrees, 21 days were recorded for several bunches. In 1910 the same result was secured when eggs laid early (April 6) hatched 21 days later (April 27) under an average of 60 degrees maximum air-temperature. In 1907, of 69 bunches charted in 3 different ponds, 32 hatched in 14 days, 18 in 15 days, 19 in 16 days. In 1912 and 1911, several different bunches hatched in 11 days, the maximum air-averages being from 63 to 67 degrees.

In the case of fresh eggs brought into the laboratory, 6 to 7 days were required for hatching. About the same period was required for eggs laid in laboratory by mated pairs. Of the water-temperatures, we have too few to generalize with any degree of certainty.

#### THE MATURE TADPOLE.

Length of the body contained 1.4 to 1.9 times in the tail, average 1.6. Width of the body in its own length 1.4 to 1.85, average 1.6. Nostrils nearer the eyes than the end of snout. Eye about equidistant (sometimes nearer the snout) between spiracle and end of the snout. Distance between nostrils 1.5 to 2.1 in interorbital space, average 1.8; in mouth 0.9 to 1.8, average 1.2. Spiracle sinistral 1.2 to 1.9 times

nearer the base of the hind legs than the end of the snout, average 1.6. Anus dextral. Depth of the tail in its own length 2.3 to 3.2, average 2.7. Depth of the muscular part of the tail 1.8 to 2.2 in the depth of the tail. Mouth is contained 0.85 to 2.1 times in interorbital distance, average 1.45. Greatest length, 74 mm. Greatest length of body, 26 mm. Greatest length of tail, 49 mm. Greatest depth of tail, 16 mm.

*Coloration of body* (Plate IX, Fig. 1F): Background of back olive-green shading through yellowish on the sides and front of head to cream on the venter, the back being marked with fine black and yellow spots. The yellow is more marked at the base of the tail and in the region of the mouth. Blotches of white pigment occur on the belly. From the gill region forward, black as well as white pigment is prominent. The whole venter is conspicuously iridescent. The tail is very dark, particularly toward the tip; the whole marked with fine black and golden-yellow punctulations, the yellow ones usually aggregate; these groups of yellow spots are more numerous toward the base of the tail. In some specimens the dark punctulations are so numerous as to make the tail *purplish black*, a condition (when present) making these tadpoles almost as distinctive as the vermilion-tailed tadpoles of *Hyla versicolor*.

*Mouth-parts* (Plate VIII, Fig. 2): Labium and papillæ without black punctulations, as in the green-frog and the bullfrog. Upper rows of teeth in two series; the first is the upper continuous fringe bounding the lip's margin; the second is a row on either side, the median space between them being at least twice the length of either lateral row of this series. The lower 3 rows are after the green-frog plan. The first lower row is frequently broken in the middle. The upper fringe is seldom discontinuous unless injured; the second upper row of either side is almost invariably present, sometimes absent on one side, very rarely on both sides or faint on both sides. In 67 tadpoles examined, only four had this row missing. The lower second is occasionally discontinuous in the middle, but not so frequently as in *R. catesbeiana*. More rarely the third row may be discontinuous. In three specimens the lower teeth rows were in decided disorder.

#### THE LARVAL PERIOD.

The developmental period consumes about 90 to 100 days. In 1906 the first eggs recorded were April 25 and the first transformed example appeared July 24, an interval of 90 days. In 1907, in two different places (one a pond, the other a backwater) the first eggs were laid April 30, and 95 days later (August 3) the first transformed pickerel-frogs were observed in the same places. These eggs hatched in 14 or 15 days, thus giving a true larval period of about 80 days. In 1909 we have one record of 91 days. In 1911 the period from egg to transformation was 87 days, or 76 days of true larval life, for the eggs hatched in 11 days.

THE TRANSFORMATION.

This may begin the last week in July, but by far the greater number of larvæ transform in August. In 1906 our first record was July 24; in 1907, July 14 and 30; in 1908, July 25; in 1909, July 22; in 1910, July 26; and in 1911, July 25. An average of the first records is July 23. In 1907 a large proportion of the larvæ transformed the first week in August, though the stragglers continued to transform until September 1. In 1912, stages from the mature tadpoles with small hind legs to transformation were secured on September 1, and surely some of the material could not have transformed before September 15 or October 1.

The size at transformation of 61 specimens varies from 19 to 27 mm.; the average is 24 mm., the mode 23 mm. (Plate x, Fig. 5.)

THE AUTUMNAL DISAPPEARANCE.

Our latest records for this species extend from October 6 to 24. The maximum air-temperatures for the day previous to the record and for the day of the record show averages of 71 and 72 degrees, respectively, or temperatures from 63 to 83 degrees. When the frosty weather begins they betake themselves to cover. Quite frequently, after such periods, they can be found in our ravines under stones near the water's edge or in the water. Occasionally they are more or less active the whole year, provided they happen to be in a spring which remains open throughout the winter. We had long suspected that this species hibernated in the ravines more than any other Anuran at Ithaca. To determine this question we placed a trap at the mouth of a ravine to catch the Anura which might migrate to the swamp below for spring breeding purposes. For a week we secured plenty of *Rana palustris*, and frequently more of them than of all the other species combined.

## LIFE-HISTORY OF THE GREEN-FROG.

The green-frog and the bullfrog are our most solitary species. The structural differences which differentiate the two are emphasized in the account of the latter. In habitat the green-frog is not so restricted as the bullfrog. Both occur in swamps, and in our deeper, larger ponds and reservoirs. In the smaller ponds and pools only the green-frog is present. In fact, along our watercourses, there is hardly a small pond which can not claim a green-frog. In the swamps only *Rana pipiens* exceeds it in abundance. The latter, like the toad and peeper, often inhabits the less permanent situations; the green-frog usually chooses deeper, more permanent bodies of water.

## THE FIRST APPEARANCE.

The green-frog is our fourth *Rana* and sixth Anuran to appear in the spring. It usually appears about two weeks after the peeper, and 3 days after the pickerel-frog, the fifth Anuran to emerge. Our records of first appearance are:

Max. temp. day previous.	Date of first appearance.	Max. temp. of date.
°F.		°F.
38	Apr. 10, 1905	32
67	Apr. 15, 1906	58
50	Apr. 13, 1907	64
63	Mar. 28, 1908	72
80	Mar. 30, 1910	79
66	Apr. 20, 1911	56

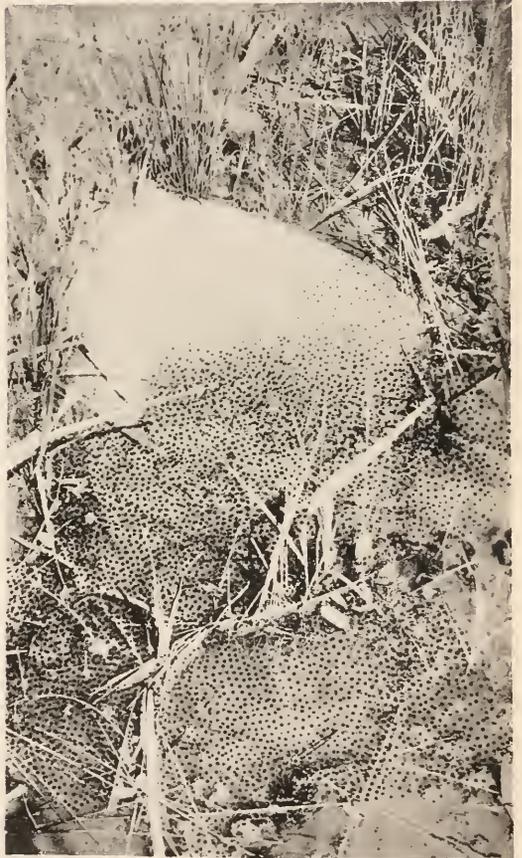
Of these six records, two were of individuals not out of hibernation of their own accord. The first record of 1905 was of two torpid individuals under a large stone for cover. The third record (1907) was of a specimen raked out of the mud of one of our ponds. An average date of appearance is April 7, the range being from March 28 to April 20. An average of the maximum air-temperatures for the day of the record is 66 degrees, or 61 degrees if the 1905 and 1907 records be included; for the day before the record, 66 or 61 degrees. In the pertinent records, no maximum goes below 56 degrees. Generally a week intervenes between these first records and their second appearance, which comes about April 14. Air-temperatures taken the day before and on the day of the second record yield averages of 54 and 69 degrees respectively. It seems that air-temperatures from 54 to 61 degrees usually find the species out of hibernation; and when at 61 to 69 degrees, the species begins to come out more commonly. The water temperatures of first and second appearances range from 46 to 58 degrees or higher. Inasmuch as the species hibernates in water, these water-records are the important factors of emergence.



1



2



3

GREEN-FROG (*RANA CLAMATA*).

1. Mated pair. Pectoral amplexation.
2. Two detached portions of an egg-film. Wind or current often separates the one film into several.
3. An egg-film (at surface) near the shore among grass.



## THE VOICE.

About a month after the first appearance, the green-frog just begins its croaking. Usually the males take their stand at the shallow edges of the ponds and pools, though we have seen them in mid-pond on the matted vegetation. The note is a low-pitched, short croak, with more carrying power than that of *Rana sylvatica* or *palustris*. Its character is as distinctive as that of the bullfrog, the other *Rana* which is in voice at the same time. It is, however, never so powerful or prolonged as in its larger congener.

Croaking begins by the second or third week in May, the average being May 10, the earliest April 26. The earliest records are:

Max. temp. day previous.	Date of first croaking	Max. temp. of date.
°F.		°F.
77	May 18, 1906	89
42	May 12, 1907	58
72	May 18, 1908	79
58	May 18, 1909	59
68	Apr. 26, 1910	62
82	Apr. 29, 1911	80

The air-records are at least as important as those of the water. None of the air-maxima for the day of the croaking descend below 58 degrees and they average 71 degrees. The day previous to the record, they are all (one exception) above 58 degrees and average 66 degrees. If the water-temperature enters into the matter at all, it is solely the surface-records. The surface-temperatures range from 64 to 72 degrees or higher when the species begins croaking in real earnest. About the first of June the voice of *R. clamata* is heard more frequently than that of any other *Rana*. It continues quite commonly until the middle of July or later. Thereafter, until the middle of August, their croaks become much scarcer. After August, they are seldom if ever heard.

## THE MATING.

In the males of the green-frog a development of the thumbs and webs occurs similar to that in the other species of *Rana*. The male has a yellow throat and a larger tympanum than the female. If the sexes differ in size, it is the male which is the smaller. Mating is more active at night than by day. It does not begin before the latter part of May. With captive individuals it has been noted as early as May 22. The interval between first croaking and actual mating may be considerable. In our night collecting, we not infrequently come to locate special places where a male may be found croaking several nights in succession. Egg-masses have subsequently been recorded in such spots so often that it has been found a good plan to keep such localities in mind when searching for eggs by day or night. About such masses the original

or other males are afterwards frequently found for varying periods. In fact, many have been captured in this way. The pectoral type of embrace (Plate XVII, Fig. 1), common to the genus, obtains. This amplexation, on May 22, 1906, appeared to be of the *Hyla* type (Plate IV, Fig. 6). Such an embrace might occur again with a small male, or if the species mate before the regular breeding period. In the above instance, however, the embrace was broken, and the next time the male mated in the manner of *Rana*. The males of this solitary species are less given to seizing females of other species than the other forms of *Rana* (bullfrog excluded). Cross-embraces between green-frog males and females of *Rana pipiens*, *palustris*, and *sylvatica* have been recorded. Males at the height of their breeding season will embrace each other for short periods.

#### THE OVULATION.

The green-frog begins ovulation in late spring or early summer. Our first records are:

Max. temp. day previous.	Date of first ovulation.	Max. temp. of date.
°F.		°F.
64	May 31, 1906	73
66	June 13, 1907	65
88	June 10, 1908	73
77	June 3, 1909	80
71	June 9, 1910	74
89	May 12, 1911	80

It appears, then, that air-maxima for the day of the record range from 65 to 83 degrees or average 74 degrees; for the day before the record they range from 64 to 89 degrees or average 76 degrees. No record is flanked on either side by a temperature less than 64 degrees. An average date of first egg-laying would be June 2, or June 7 if we consider the 1911 record abnormal. May 1911 was remarkably warm, the average being nearly 65 degrees, which was higher than that for any other May since 1880, and only one degree below the June normal; hence the record of May 12, almost a month earlier than the average date. The eggs first became common on the following dates:

Max. temp. day previous.	Date when eggs first became common.	Max. temp. of date.
°F.		°F.
84	June 6, 1906	78
82	June 21, 1907	88
80	June 3, 1909	83
96	May 23, 1911	93

It would seem that when the air-maxima approach 80 the species breeds commonly. During June and the first part of July the eggs of this form are very common; thereafter they diminish in numbers until the last of July or the first of August, when a few stragglers deposit the last eggs of the Anuran breeding season. Our latest records for eggs are: July 29, 1904; July 24, 1906; August 10, 1907; July 24, 1908; July 22, 1909; July 25, 1911.

Surface temperatures are probably very influential because of the position of the eggs. The average of 28 breeding records gives a range of coincident surface-temperatures from 65 to 88 degrees or an average of 76 degrees, only two records being below 68 degrees. In conclusion, we hold that when the air-maxima reach 65 to 74 degrees or the water-surfaces 68 to 76 degrees, *Rana clamata* ought to begin its breeding.

#### THE EGG-LAYING PROCESS.

This species lays almost entirely at night. Its solitary habit makes it difficult to capture mated pairs in the field. Evidently, from the form of the egg-mass, it keeps in one position or within a very small circumscribed area. The observations on the other species of *Rana* would lead one to expect that the female voided her whole egg-complement at one sitting. Furthermore, from experiences with other forms which lay their whole complement in one mass, it has been noted that any tendency to change of position conduced to frayed masses or subdivisions of the original mass—this condition of egg-mass being rarely if ever observed with a fresh green-frog mass. Recently (last of June 1914) Dr. G. C. Embury saw at 10 a. m., in one of his private ponds, a mated pair of green-frogs. At 1<sup>h</sup>30<sup>m</sup> p. m., in another pond, 3 feet away, he saw them jumping around and one chasing the other. At 3 p. m. he found the pair mated among burr-reed, water-cress, *Elodea*, and grass, where one-half of their egg-complement was already laid before discovery. The uncompleted film looked as if made up of half a dozen or more component masses which later merged into one. The pair were under observation for 10 minutes and during this period they laid two of the packets of eggs. The packet is laid  $\frac{1}{2}$  to 1 inch beneath the surface of the water and rises to form a part of the film. As the eggs came out, a slight wiggling or change of position was noticed.

#### THE EGGS.

The mass of eggs floats on the surface of the water (Plate XVII, Fig. 3). The typical form is a disc-like film (Plate VI, Fig. 5) of a single layer of eggs, loosely attached or free. They may be in the middle (Plate I, Fig. 2A) of the pond, where it is filled with a cover of algæ at the surface, or with *Nitella*, *Chara*, *Myriophyllum*, *Ceratophyllum*, or similar water-plants, which make a mat of vegetation from the bottom to the surface, or where isolated patches of grass, *Alisma*, etc., grow in the middle of a pond. Usually, without such conditions the masses are about the edges (Plate

xvii, Fig. 3) of the pond attached to grass, smartweed, etc., either growing in or extending into the water; in 100 or more cases hardly an exception has been noted to the surface deposition, but a few apparent exceptions have occurred. One egg-complement was in a somewhat scattered mass (1 foot in diameter) on leaves and twigs partially submerged. In another instance some of the complement was at the surface and the rest in water 4 to 6 inches deep. Inasmuch as such masses were found some time after their deposition, a rise in level of the pond could easily have made this anomalous condition. Another variation in egg-mass is occasionally recorded. The mass may be attached to grass stems, the point of attachment being some 4 or 5 inches below the surface of the water. This attachment serves as the apex of an inverted cone, and the base of the cone spreads out on the surface of the water. This also may be due to a rise in level of water.

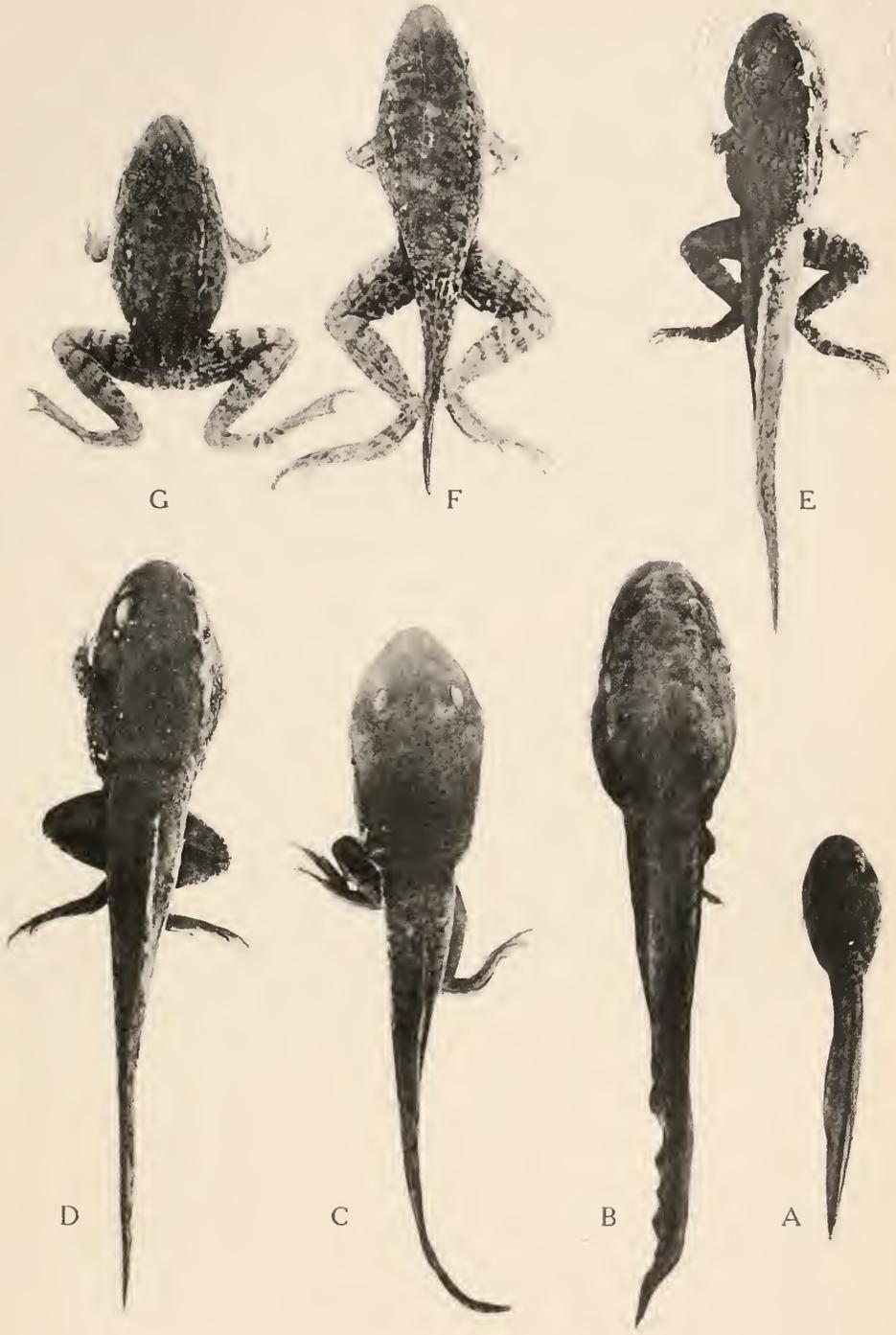
The lowering of the water-levels and the drying up of ponds prove the most serious dangers to eggs of this species. The eggs are laid in summer, the season when such phenomena occur with frequency. The short hatching period is one of the factors which saves many a mass from destruction. About the edges of ponds, spoiled egg-masses of this species are found every year. They are whitish in appearance when in a bad condition. Sometimes they are hung up high and dry, the entire mass being destroyed; at other times a portion hatches before the whole complement is doomed.

Rarely, a mass more than a foot square is recorded. Some of these may be composite. On June 15, 1910, in a certain pond where numerous pairs had laid, two bunches had been placed so close together as to make one film 15 by 10 inches. In another case, a mass just as large was secured, but here the evidences of its double nature were more evident.

For several years, we found small isolated packets (Plate xvii, Fig. 2) of eggs on the water's surface, distributed as tree-toad's eggs but without their individual characters. They could not be those of *Chorophilus*, for this species is not in this region. At last we found that, as egg-development went on, the egg-masses of the green-frog often lost their circular form, assumed irregular shapes, and separated into small masses of 25 or more eggs. In this case, it was a natural process due to the jelly becoming loose as hatching approached. But the egg-packets were of fresh eggs. In these instances, the wind or strong currents or both caused them to float away from the original mass.\*

The eggs have white vegetative and black animal poles. The outer envelopes range from 5.6 to 6.0 mm. in diameter, 5.7 mm. being the average, 6.0 mm. the mode. The middle envelope may be other than spherical and often has an elliptical form; it varies from 2.8 to 4.0 mm. in diameter; the average is 3.3 mm., the mode 3.0 mm. The vitellus ranges from 1.2 to 1.7 mm., the average 1.4 mm., the mode 1.2 mm. (Text-figure 1D.)

\*Recent observations explain this phenomenon nicely. The eggs are laid in separate packets which later merge in one filmy mass. The same condition obtains in *Rana catesbeiana*.



GREEN-FROG (*RANA CLAMATA*).  
A series from first season's tadpole to transformed green-frog. Dorsal aspect.  $\times 1$ .



## THE HATCHING PERIOD.

Inasmuch as the eggs to *Rana clamata* are generally laid in the summer and deposited on the surface of the water, the air-temperatures play a prominent role in determining the hatching period. This requires 3 to 6 days. We have numerous records of eggs hatching in 3 days when the air-maxima averaged from 80 to 88; in 4 or 5 days when they averaged 80 to 70 degrees. The earliest hatching record for the species is May 16, 1911. Seldom have we seen eggs hatched before June 1.

## THE MATURE TADPOLE.

Length of the body contained 1.5 to 2.1 times in the tail, average 1.75. Width of the body in its own length, 1.25 to 1.7, average 1.47. Nostrils decidedly nearer the eyes than the end of the snout. Eye distinctly nearer the end of the snout than the spiracle. Distance between nostrils 1.25 to 2.05 in interorbital space, average 1.6; in mouth 0.9 to 1.35, average 1.06. Spiracle sinistral, 1.35 to 1.8 times nearer the base of the hind legs than the end of the snout. Anus dextral. Depth of tail in its own length 2.5 to 3.7, average 3.1. Depth of the muscular portion at the base of the tail 1.35 to 1.95 in the depth of the tail. Mouth is contained 1.3 to 1.8 times in interorbital distance, average 1.5. Greatest length, 84.8 mm. Greatest length of body, 27.8 mm. Greatest length of tail, 57 mm. Greatest depth of tail, 16.6 mm.

*Coloration of body* (Plate IX, Figs. 1E, G): Background of back very dark and covered with very fine yellow spots, the whole consequently having an olive-green color with numerous distinct dark spots. Belly deep cream color without decided iridescence. The throat and sides are mottled with dark green. A slight coppery iridescence on the venter is more decided on the sides and on the tail. The tail appears green, mottled with brown; it is covered with fine yellow spots like the back.

*Mouth-parts* (Plate VIII, Fig. 4): Labium and its papillæ are strongly and finely dotted with black, this being more pronounced than in *Rana catesbeiana*. The labial mouth-parts of the latter when *in situ* are narrower than those of the green-frog. The labial mouth-parts of the bullfrog are contained in their width at least 2 times, while in the green-frog the depth is never more than  $1\frac{1}{2}$  in the width of the mouth-parts. The second upper row of each side is very short, never one-quarter of the upper fringe, as is frequent in *Rana catesbeiana*. There is never a third upper row. The lower labial rows are as in the bullfrog. In the lower rows of labial teeth *R. clamata* shows much less variation than occurs in the more delicate similar rows of *Rana catesbeiana*. Seldom do they depart from the normal arrangement. The greatest variation occurred in the second upper row of either side. About half of the specimens have the row on both sides; many have the upper row missing on one side; and rarely they are absent on both sides, thus giving the upper labium only one series of teeth.

## THE LARVAL PERIOD.

In 1906, transformed examples were recorded June 28. If in 1905 the species first began laying in June, as it usually does, we get a period of one year from egg deposition to transformation. In another pond the larvæ of 1906 began to transform June 28, 1907, and new eggs were recorded June 21, 1907. If in the previous year egg-laying occurred about the 21st of June, we have about a year for the interval between egg-deposition and transformation. In a small pond where the species first laid June 6, 1906 (this bunch being the only eggs laid in the pond during the season), the first records of transformation in 1907 were July 13, thus giving 372 days before transformation. In 1908 tadpoles were transformed July 21, or 400 days after the eggs were deposited. In 1910 eggs were laid in a certain pond June 9; and on June 29 of the succeeding year (1911) the tadpoles began to transform, 385 days later. The period, then, appears to be from 370 to 400 days.

## THE TRANSFORMATION.

Most of our records would bring transformation in the latter part of June and through July. Our first dates are: June 17, 1902; June 28, 1906; June 28, 1907; July 21, 1908; July 10, 1909; and June 29, 1911. The average of all is July 3, though June 28 is the more correct date. This makes the green-frog third in the order of transformation, the toad and wood-frog preceding it. Usually, by the first of August, transformation for the species is largely but not wholly completed. In a species which lays from the last of May to the middle of August or later, it is evident some transformations may range within the same limits. The size at transformation of 41 specimens varies from 28 to 38 mm.; the average is 32 mm.; the mode is 31 mm.

## THE AUTUMNAL DISAPPEARANCE.

During the most of October and early November, one often sees the green-frogs around the edges of ponds with *Rana pipiens*. These two very often hibernate in the same pond and in the same manner. Most of our records of late appearances come in the very last of October or the first week of November. An average of the latest dates of appearance is about November 3, our latest record being November 11, 1899. The average air-maxima for the day before and for the day of the record are 67 and 69 degrees and the minima 38 and 42 degrees. When the temperatures of late October or early November reach the above maxima, the green-frogs often come out, though they may have previously sought cover. They hibernate in the mud of our marshes and ponds. In the ravines they often seek winter-quarters underneath a submerged stone or kindred cover, occasionally under dead wet leaves of our stream beds. Not infrequently do we record them in the middle of the winter, provided they chose a spring for hibernation.



BULLFROG (*RANA CATESBEIANA*).

A series from the first season's tadpole (three months' old) to transformed bullfrog.  
Dorsal aspect.  $\times 1$ .



### LIFE-HISTORY OF THE BULLFROG.

Because of its size, appetite, vocal accomplishments, and supposed shyness, this species has received more attention than any other American member of the genus *Rana*. In the northeastern United States, it can be confused only with the green-frog. In common, they have the tympanic disc as large as (in females) or larger than (in males) the diameter of the eye; and the throat is yellow in the males. Unlike the green-frog, the lateral folds are absent, and the web of the fourth toe extends to its tip.

One commonly associates the bullfrog with marshy bayous, button-bush swamps, mill-ponds, or lakes. They are not, however, so restricted in habitat as some texts might lead the reader to infer. I have found them along both upland and lowland streams, in clear brooks which fed cold, marly, sphagnum ponds, and along water-courses laden with such marshy vegetation as lizard's-tail, marsh-cress, arrow-head, pickerel-weed, and swamp-loosestrife. Rarely they have appeared in small numbers in temporary or very small ponds—a more logical home for the green-frog. Such distribution can ordinarily be explained by the loss or draining of a former mill-pond or reservoir habitat nearby, and such records are more accidental than normal. Occasionally one finds them assembled in large numbers in very small circumscribed areas, due usually to some catastrophe or drought. In one instance, on June 16, 1913, we discovered that the water-space in a cat-tail swamp had shrunk to a hole 10 by 10 feet and therein were gathered the whole swamp's colony of bullfrogs, some 25 or 30 adults. They seem to prefer mill-ponds, hydraulic lakes, reservoirs, and kindred bodies of water. Our best collecting-grounds were a clear glacial lake in a kettle-hole with a slight suggestion of the sphagnum flora about it; a pond in a clear trout-brook; a large reservoir for a hydraulic laboratory; a disused mill-pond; and a wooded lake whose shifting water-level had made a fringe of overhanging dead trees, floating logs, and submerged roots and limbs. In every case the shores are more or less wooded, but more important are two other factors: shallows where the species can transform; and brush, stumps whose roots are at the edge of the pond or overturned, and driftwood along the banks.

#### THE FIRST APPEARANCE.

*Rana catesbeiana* is our last Anuran to emerge from hibernation, following three weeks after the tree-toad, which is then beginning the chorus-stage. When the bullfrog comes out, the first five species to appear in the spring are entirely or almost finished with their spawning. The bullfrog is such a wary form that in some years its presence is not suspected until June, when croaking begins. Our first records are shown in the table at top of page 78. From this, either for the day previous

or for the date of the record, we obtain no maxima below 68 degrees. The average of the maxima for the day previous is 79 degrees, the range 68 to 88 degrees; for the day of the record, the average is 76 degrees, the range 68 to 93 degrees. An average of the first records is May 20, but as those for 1908 and for 1911 are voice-records, we suspect the bullfrog first comes out by May 15.

Of all the frogs this species is most influenced by water-temperatures. The temperatures taken on the water's bottom range from 57 to 72 degrees on the day of the record, or average 69 degrees; on the day previous they range from 58 to 73 degrees or average 64 degrees.

When the air reaches 68 to 75 degrees (certainly at 76 to 79 degrees), we may expect the appearance of the bullfrogs, provided the water-bottoms are 57 to 64 degrees or average 64 to 69 degrees.

#### THE VOICE.

This phase of the bullfrog's life is best known. Its sonorous bass notes have received countless characterizations, among which are the familiar "blood 'n' 'ouns," "br-wum," "be drowned," "more rum," "jug-o-rum," "knee deep," and "bottle-o-rum." These notes have wonderful carrying power and are commonly heard in the evenings of early summer. They begin about two or three weeks after the frog emerges from hibernation; *e. g.*, in 1906 an interval of 19 days was noted, in 1907 the interval was 33 days. Between the first and second voice-records a week or more may pass: 6 days in 1908; 15 days in 1911. The range of first records extends from May 11 to June 19, the average being May 31. We have a few records in May; the vocal records become frequent in June and reach far into July, usually to its middle. The chorus-stage usually occupies the last of June and first two weeks of July. In 1906 and 1907 the bullfrog was last heard July 15; in 1909 on July 18; in 1911 on July 14; and in 1912 as late as August 26. When it approaches the silent period the croaking is not so loud or full. Our first voice-records are shown in the above table.

The maxima range from 68 to 93 degrees before the record, averaging 81 degrees. At the time of the record, they range from 74 to 93 degrees, averaging 82 degrees. The bottom-temperatures of the water for the

Max. temp. day previous.	Date of first appearance.	Max. temp. of date.
°F.		°F.
68	May 11, 1901	74
83	May 17, 1906	77
70	May 17, 1907	69
77	June 4, 1908	81
88	May 21, 1911	93
88	June 10, 1908	73
78	June 5, 1911	68

Max. temp. day previous.	Date of first voice-records.	Max. temp. of date.
°F.		°F.
68	May 11, 1901	74
80	June 5, 1906	84
93	June 19, 1907	77
77	June 8, 1908	81
88	May 21, 1911	93

day of the voice-records given in the table were from 62 to 70 degrees, or an average of 67 degrees; for the day previous they ranged from 62 to 69 degrees, an average of 66 degrees.

When croaking begins, the males often take certain perches in which they keep a proprietary interest. About one pond (Plate I, Fig. 1) I located seven such places, each with its possessor, only once finding two in one place. The characteristics of the stands can best be told from a list for one pond: the first was on a board in water filled with brush; another was perched on a log among brush beneath a float of a boat-house; the third was on the bank among some limbs extending into the water; the fourth was by an overturned stump whose roots were partly out of the water and partly submerged; the fifth was among some drift-wood along the shore; the sixth was on a stationary float; and the last was at the base of a tree fallen into the pond. At these stands one could have had good success in capturing the frogs by night. This rule of perches obtains more particularly when the species is not especially numerous in a pond or lake. When, however, the numbers of males about a lake are numerous enough to make their night croaking seem a real chorus, and when they are abundant among the fallen logs and brush of the swampy borders of lakes, it is not likely that any one individual holds a favorite site to the exclusion of the others. In such places one can easily take, in an hour or so, 30 or 40 adults with either flash-light or acetylene light.

If one wishes to secure them by day he may adopt the familiar red flannel on a hook. At the breeding season one occasionally finds them in grassy situations. Here they lie on the surface. One has only to wade amongst them to capture them by hand. At first they may become frightened, but soon they reappear. Whenever bullfrogs are hard to find or scarce in certain bad seasons let the collector search out a former mill-pond whose dam is gone, and in the temporary small ponds remaining he can frequently find the frogs in their circumscribed quarters.

The males croak mainly at night. In a shady place or while the sky is overcast and the air most oppressive, one will occasionally hear them croaking by day in May or June. In July, however, particularly in the middle of the month, several voice-records of single individuals have been made through the four hottest hours of mid-day.

#### THE MATING.

As with the other *Rana* males, the first finger of males of this species becomes enlarged. The embrace is in the customary *Rana* fashion. Of it, we have only one observation—two captives, a male and a female, on June 13, 1906. The amplexation was axillary and came after the pair were together two days in a large tank kept dark. About an hour after the beginning of the embrace I attempted to transfer them to the photographic jar and they broke their hold. Evidently the species

at this date was not at the height of the sexual impulse, even though mated in the laboratory with water-temperatures higher than in the ponds—all of which is confirmed by the first record of eggs laid in the field in 1906. These were deposited at least a week and a half later. The males begin croaking 15 or 30 days before actual spawning takes place. In 1906 an interval of 19 days came before spawning; in 1907 it was 21 days; and in 1908 it was 30 days. About small lakes, mill-ponds, or in swampy creeks, the males may take special croaking stands almost invariably near where there is brush in the water or limbs extending into it. I have known males to keep about one particular spot for 20 days in succession. Whether this same habit obtains for those inhabitants in our deeper swamps remains to be ascertained. Certainly when the species is numerous it may be otherwise. On the 16th of June, 1913, when the bullfrogs were laying freely in one lake, we found as many as 10 males within a space of 8 feet. Here among the dead branches of overhanging elderberry bushes they were hidden because of the dense mat the shrubs made. At this time in mid-day we had no difficulty in capturing, by hand, in half an hour, some 25 males, while of females we saw only 3 or 4. Later in the season the females appear more in evidence. Doubtless these easy captures were naturally due to the fact that it was their breeding season. I am, however, coming to believe that this species is as easy of capture as any other *Rana*. Even after a bullfrog has left the water's surface, one may capture it while it is swimming beneath the water, for they are very slow as compared with some of the other forms.

#### THE OVULATION.

This species lays the last of June or in July. The egg-records for the past few years are shown in the accompanying table.

The maximum air-temperatures prevailing the day before the record range from 71 to 89 degrees, and average 81 degrees; for the day of the record, they vary from 72 to 92 degrees or average 83 degrees. Each record is flanked on both sides by maxima of 71 degrees or higher. The water-bottom temperatures for these dates range from 66 to 74

Max. temp. day previous.	Date of first ovulation.	Max. temp. of date.
°F. 71	June 24, 1906	°F. 72
79	July 8, 1906	81
80	July 10, 1907	83
88	July 4, 1908 } (Dis. July 7)	85
89	June 16, 1913	92

degrees or average 70 degrees; for the day previous they range from 67 to 74 degrees or average 71 degrees. If, then, we assert that a water-temperature of 66 to 70 degrees must obtain for first ovulation and that more often 70 to 74 degrees proves the prevailing temperature, it is a conservative determination, for this species lays on the surface of the water where the temperature might be higher than the above temperatures of the water's bottom.

The breeding record extends from June 16 to July 10. Doubtless it begins earlier some years or extends beyond July 10 in belated seasons. On July 25, 1913, females were taken with ripe ova. An average of breeding records gives June 28.

#### THE EGG-LAYING PROCESS.

The egg-laying process usually occurs at night, when the species is most active. The bullfrog is a solitary form; yet at the height of breeding a mill-pond may have a dozen or more pairs in it. Or some lakes may be well enough supplied with them to furnish the famed bullfrog choruses of June and July. Probably, as with other species of *Rana*, when the process has really begun it takes but a very few minutes. At first we thought this species did not always keep the same position. Sometimes from the glutinous mass at or near the surface narrow string-like pillars extended down a foot or more to lower submerged branches. Then the strings were continued along the lower branches for various distances. A string-like deposition also occurs sometimes when the eggs are found on the finer roots of an overturned stump in the water. These two sorts of observations led us to the inference that the female did sometimes move during the deposition. The pancake-like film (Plate I, Fig. 2E) has, however, been recorded 5 or 6 times as frequently as the string-like deposition. Furthermore, it is our belief that the film is the usual method of ovulation, as it is in the bullfrog's nearest relative, the green-frog; and that the string-like depositions are secondary conditions. In the case of one film the water fell 4 or 5 inches and thin transparent strands and films of jelly extended from the original mass or disc on the water's surface to branches suspended above the water, thus showing the original attachment of the film. The jelly of this disc could be lifted 4 or 5 inches above the water, and yet keep the connection with the main mass. In another instance a disc was laid, and in one day's time the water rose 8 inches, but the mass retained its attachment to the twigs 8 inches beneath the new water-level, and the former discoidal form changed to the string-like form.

On June 16, 1913, when we discovered some 7 or 8 egg-complements, considerably more light on the egg-laying was revealed. More than ever are we of the opinion that in the expulsion of the eggs the two forms, green-frog and bullfrog, agree. In several of the complements, the egg-masses were in brush (Plate XX, Fig. 1) near the bank's edge, and all of these were of the film type or originally were. In one case the eggs had the spoiled appearance which green-frog eggs sometimes have when they have been stranded high and dry. The fresh films,  $1\frac{1}{2}$  feet or more in diameter, we could easily detect because of the great amount of air-bubbles in the mass.

Along the east edge of this particular lake occurs the deepest water and here for many years the tadpoles have often transformed. We

It is not a distinct marbling, as in the green-frog. Tail considerably lighter than the back and quite regularly covered with small *black spots* (almost entirely lacking on the lower crescent, some of which are dumb-bell-shaped). The fine yellow dots are assembled in small groups.

*Mouth-parts* (Plate VIII, Fig. 1): Edge of upper lip about equal to length of the horny beak and fringed with a continuous row of teeth. In either corner, beneath this fringe, is a short row of teeth about one-fourth of length of upper fringe. On the lower lip are three rows of teeth, the first (the longest) often discontinuous; the second is almost as long as the first; the third is much shorter. The dark-pigmented papillae do not extend along the edge of the upper lip beyond the vertical through the lateral tips of the horny beak. Along the sides of the lower labium are two series of papillae, the inner row of which usually terminates at the end of the lowest row of teeth. The middle portion of the lower labium's margin, then, is with a single row of papillae. Hinckley (1882) gives a third small row of teeth in the lower corner of each upper lip; in 50 or more first-season, second-season, and mature tadpoles, this occurred but once as he figures it. In two other cases such a row was present, but it was at right or obtuse angles to the first or second rows and might have been a part of one or both of them. Sometimes the upper fringe is entirely absent, present on one side, or the teeth of it may occasionally leave the mouth and be carried back over the forehead. The second row may be missing or present on only one side. In the lower labial teeth great variations obtain. Sometimes all three rows may be discontinuous in the middle; occasionally the second or third row may be missing, seldom the first. Rarely, when the outline, shape, and character of the papillae and margin of the lips are uninjured and normal, the labial teeth of the lower labium may be in considerable disorder with no suggestion of the three-rowed condition. In some cases 18 or 19 short, abrupt rows extending in all directions have been recorded.

#### THE TADPOLE OF THE SECOND SEASON.

The one year old tadpole (Plate IX, Fig. 1c) is generally like the mature tadpole. Seldom, however, do they show the hind legs developing. Instead of the venter being almost one continuous sheet of straw or maize yellow, it is, except for the belly, mottled or marbled with straw or maize yellow and the dark olive-green of the sides and back.

#### THE TADPOLE OF THE FIRST SEASON.

At the age of three to five months (Plate IX, Fig. 1b) the back of the tadpole is greenish brown, the background covered with very fine dark specks which show best on the sides, where the *finely sprinkled yellow or gilt spots* are fewer. These are gathered in closely set groups very near to each other. Some of the groups in their formation remind one of snow crystals. All over the back are the characteristic *black circular spots*,

which are both wely separated and distinct. Occasionally they have white or light centers and some of these, as in the one and two year old tadpoles, are *dumb-bell-shaped* or *linear*. The throat and chin are translucent with few black specks. The belly is one *uniform bronzy iridescent coat* (lik the wood-frog tadpole's venter). This iridescence continues on to the gill region of either side, breaking into *irregular patches* which are deeper seated than the large groups of *gill spots* which extend across the gill region from one eye to the other. The eye is black with bronzy peckings. Tail: Translucent. The very fine and dark pigmentation of the body background extends on the tail. The yellow-grouped spots are scarce and mainly at the base of the muscular part of the tail. The black circular spots are also few and show a greater tendency to the dumb-bell-shaped form than those on the body.

The smaller size, fine-speckled (salt-and-pepper effect) bodies, and lack of the striking light olive-green of tadpoles one and two years old, together with a venter wholly unlike these, make the tadpoles of the first season easy of identification. In 1912 some tadpoles of the first season, second season, and maturity were collected at the same time and place. The first-season forms measured in length 30 to 35 mm.; the second season specimens, 75 to 90 mm.; the mature forms, 100 to 145 mm.

#### THE LARVAL PERIOD.

The species spends two winters in the larval stage. Inasmuch as the eggs are small and deposited late in the season (usually last of June or in July), the tadpoles are small when winter arrives. The whole of the next season is consumed in growth, and it is not until another winter is passed that the larvae begin to approach transformation, which usually comes in July, *i. e.*, two years after egg-deposition. More rarely does the tadpole spend a third winter before transformation. Along one mill-pond (shores abrupt, 2 to 5 feet deep), on August 20, 1912, we secured, from the fine-matted rootlets of old weeping-willow trees, 100 two year old tadpoles, transformed, transforming, and some which clearly could not transform within two months if at all before winter came. In the same situation we took only 4 of the one year old forms, and some 20 to 30 of the first-season tadpoles (1½ to 2½ months).

#### THE TRANSFORMATION.

All our data of transformation comes in July or later. In 1906 the species was recorded as transforming July 16 and 24; in 1907 it was during the last of July; in 1909 transformation was at its height July 16 to 18; in 1910 on July 30; in 1911 it was July 8 to 14 and later, and in 1913 it reached from July 3 far into August. An average of the first dates places the beginning of transformation at July 15. The species evidently does not begin transformation before July 1, often extending to August 15. In 1910, when first recorded July 30, there

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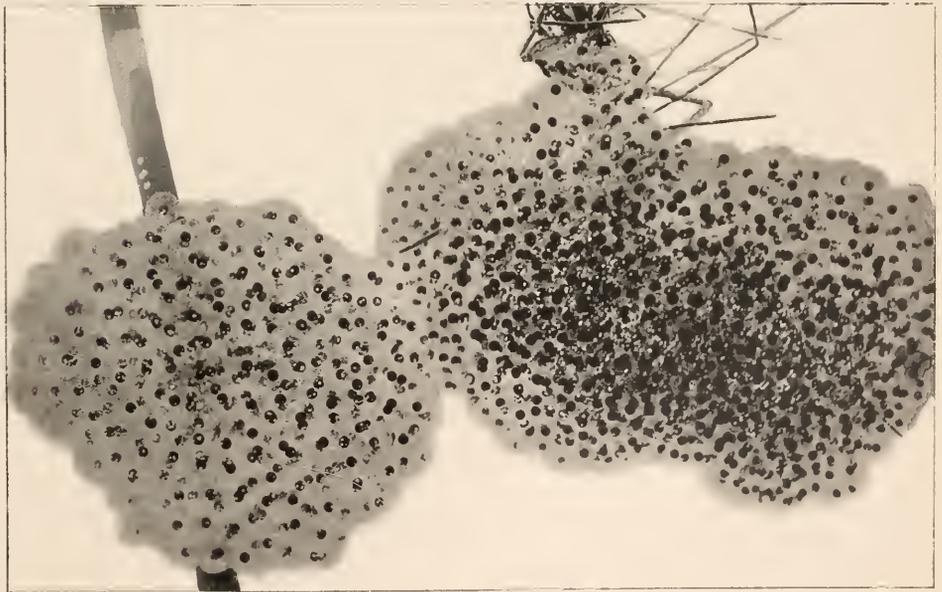
were tadpoles which would require two weeks more before transformation. In 1912, we found several transforming August 26, and a few tadpoles looked as if they might transform in October, November, or the next season.

The mature tadpoles in early summer begin to come out in the shallow water. Here they hide in the *Chara*, *Nitella*, *Myriophyllum*, *Ceratophyllum*, etc., or they rest beneath the lily-pads (*Castalia* and *Nuphar*), pond-weeds (*Potamogeton*), and other surface plants. Another favorite place of transformation is among pickerel-weed (*Pontederia*), arrow-head (*Sagittaria*), and water-plantain (*Alisma*), which afford an overhead cover. Occasionally, around ponds where shallows are absent, stumps—of trees and fallen logs—and trees fringe the edge and their roots extend out into the water. Thereon, we find a favorite transformation-site for the species. At this period they appear to be in hundreds or even thousands. The transformed individuals present a spirited sight as one approaches. They are shy and, long before one gets within range, they start skipping over the vegetation, giving the alarm note so characteristic of the species when surprised. Equally interesting is it when they occupy perches along the stumpy edges of deep ponds. It seems as if a wave of little bullfrogs keeps going before one as he skirts the pond.

Inasmuch as this species requires two years to mature, we might naturally expect that with varying conditions the tadpoles would be of diverse sizes at transformation, due to inequalities of growth. In none of the eight species under consideration is there such a range of size at transformation as in *Rana catesbeiana*, varying from 43 to 59 mm., a range of 16 mm., the average size of transformed *Hyla versicolor*, or  $1\frac{1}{2}$  times as much as the average size of transformed *Hyla pickeringii* or *Bufo lentiginosus americanus*, or twice as great as the range in any of the other seven species. A curve of 124 specimens gives 53 mm. as the average, or a mode of 54 mm. (Plate x, Fig. 8.)

#### THE AUTUMNAL DISAPPEARANCE.

This is truly an aquatic form, rarely leaving the water or its vicinity to take long migrations, except when catastrophes befall their ponds (breakings of dams) or breeding sites, when, to adapt themselves to new conditions, they may seek another equally attractive place or occasionally be found in spots not exactly typical for the species. Their active life from egg onward is spent in the water, and there its dormant period is passed. The latest autumnal records we have, are September 22, 1900, and October 14, 1899. In the latter case Mr. T. L. Hankinson found several torpid specimens under stones in our college hydraulic reservoir.



1. Bullfrog (*Rana catesbeiana*). An egg-film,  $1\frac{1}{2}$  feet in diameter.
2. Wood-frog (*Rana sylvatica*). The egg-mass of the wood-frog compared with that of the leopard-frog (at right).



LIFE-HISTORY OF THE WOOD-FROG.

This, our smallest *Rana*, awakens, spawns, and disappears into the woods, in such quick succession that it generally escapes notice. Often our first intimation of its presence is the eggs. In fact, at Ithaca, were it not for a street railway in the path of amphibian migration, this frog would seldom be seen before its eggs were recorded. Even with this excellent check, the two records often appear coincident, the frog coming rarely more than a day previous to egg-laying.

THE FIRST APPEARANCE.

*R. sylvatica* appears almost simultaneously with the meadow-frog and spring-peeper. It may appear 1 to 7 days after *Hyla pickerinii*, but averages 3 days later, and usually emerges after *Rana pipiens*, and among our early spring records there are several instances of its being seen or taken from beneath the ice of small ponds. An average of all our first spring records is about April 2; the average for the years when most intensive work was done gives March 31; or an average of the first appearances of the frogs themselves (exclusive of first egg-records) yields March 31. The first records are:

Max. temp. day previous.	Date of first appearance.	Max. temp. of date.
°F.		°F.
43	Apr. 14, 1900 (eggs).....	47
60	Apr. 13, 1901 (frog and eggs)...	57
34	Apr. 4, 1902 (frog).....	40
68	Mar. 19, 1903 (eggs).....	75
45	Apr. 5, 1904 (frog).....	54
48	Mar. 26, 1905 (frog).....	53
45	Apr. 6, 1906 (frog).....	44
70	Mar. 28, 1907 (frog and eggs)...	69
72	Mar. 29, 1908 (frog).....	41
44	Apr. 12, 1909 (eggs).....	59
51	Mar. 27, 1910 (eggs).....	62
56	Mar. 26-27, 1911 (frog).....	62

The appearance of *Rana sylvatica* is mainly influenced by air-temperatures. From records based upon the first appearances of the frogs alone, the maximum air-temperatures for the day previous range from 45 to 72 degrees, the average 53 degrees; for the day of the record, from 41 to 62 degrees, the average 51 degrees. In this computation the record of April 4, 1902, is eliminated, for it was of a frog observed beneath the ice of a pond. Inasmuch as they hibernate in logs, stumps, possibly beneath stones and among leaves, not in water, this individual must have appeared when the pond was free of ice. A cursory glance at the temperatures shows the records flanked on either side by maxima of at least 41 degrees. An average of all the first appearances (both frog and egg records) gives 55 degrees for the day previous, and 56 degrees for the day of the record. The data seem to point to an effective temperature between 51 and 56 degrees, although 41 to 45 degrees occasionally brings the species out.

## THE VOICE.

The croak of *Rana sylvatica* is higher-pitched than that of *Rana clamata* and not so strong in volume or carrying quality. It can be heard only a short distance from the pond whence it comes. In chorus it is more of a rattle than in any of the other frogs. When held in the hand and squeezed, the male can make a very grating noise. The croak would be confused only with that of *Rana pipiens*, for at this season no other *Rana* would make itself heard. The wood-frog's note is shorter, less sustained, and not as loud or as deep as that of *Rana pipiens*. The meadow-frog's note may be several short croaks followed by two or more longer ones, or vice versa, or the shorts and longs may be interspersed in other fashions—a prolonged croak; while the wood-frog's note is very short, not always a succession of croaks—a sharp and snappy clack. At times, however, 2 to 4 or 6 notes may be given in rapid succession; and when close at hand they sound high and grating in character. The croak of the meadow-frog may take 6 seconds if the succession be given, or less than one second if only one croak be sounded; but that of the wood-frog never extends over a second. The croaking begins the latter part of March and may reach to April 15. The records for several years show an average date of April 9, the mode April 6. The latest dates for several years are: April 16, 1900; April 13, 1901; April 14, 1909; April 13, 1911.

When croaking, they are at the surface or in shallow water, where the air-temperatures may play an influencing role. A consideration of 16 records of the species at croaking periods shows a range of maximum air-temperatures from 52 to 80 degrees, averaging 62 degrees. In 1910 and 1911 surface-temperatures of the water were taken whenever the species was heard; the range was from 47 to 60 degrees, with an average of 53 degrees. Between the lowest air-temperature (52 degrees) and the lowest water-surface temperature we have only 5 degrees, and no doubt the two are the respective limiting temperatures for this shy species. At all seasons, except the breeding time, the wood-frog is silent and retiring. In water at the spring congress they are difficult to approach. At ordinary approach the best one can hope for is only a series of surface ripples. We have observed several concourses at noon-day with opera-glasses. Such assemblies may not last more than a day or so each year and careful watching is necessary to secure the opportunity. Usually, by approaching flat on ground, using elbows to move along, and stopping from time to time to look with bird-glasses, one can reach the very edge of the pond where the croakers are. Anywhere from 50 to 200 males have thus been observed floating at the surface. The scene resembles a small toad assembly in which there is the same scrabbling and zeal of mating. They disappear simultaneously, on seeing anyone and, going through the pond a minute later, one would wonder where the 200 males could be, to say nothing of the females.

THE MATING.

At the approach of the breeding season, the males have the thumb much swollen and the webbing in the hind feet with margin convex, not concave as in the females at all seasons and in males at other seasons of the year. In fact, this web character is sufficient to distinguish the males at a glance. The males are also usually with a darker coloration than the quiet, less active females. At times, even in the daylight, the females may be as light as any *Hyla pickeringii* of the night.

The period of mating has begun in some years as early as the middle of March and may rarely extend to May 1. The species is customarily at the height of sexual ardor the last week of March or the first week in April. They mate by day or more frequently during the night. Some of the most vigorous of matings have taken place at noonday with full sunshine, in early morning, midforenoon, or midafternoon.

The customary *Rana* embrace (Plate II, Fig. 2) has been recorded in every pair observed. The early eggs laid soon after ice has left the ponds, the apparent coincidence of appearance from hibernation and first egg-records, and actual records of the beginning of embrace and ovulation substantiate the conclusion that this species does not usually remain in the embrace several days before spawning. In the case of most of the mated pairs captured in the field, the egg-laying came the evening following the capture; in one case of a pair mated in the laboratory, ovulation came 1½ hours after the beginning of embrace; in four field-mated pairs, they laid not on the evening of capture, but in the forenoon of the following day; in one case, a pair waited until the second evening after the capture; another pair, 48 hours; and finally, the longest period recorded was of a pair which waited 4 days.

Wood-frog pairs separate after ovulation, as is common with all *Anura*. Occasionally it happens that a male which has once mated will resume an embrace with a spent female, a condition suggesting the possibility of such males mating in nature the second time. In laboratory, 3 such instances have been observed, one pair continuing for three days in the second embrace. Such embrace, however, because of the weakened condition of the male, may not at first be normal. Once a male grasped a female wrong end to, the forearms being about the loins. Later it resumed the customary embrace. Rarely these males will croak beneath the water from two to six times at a period. Sometimes a fresh male will embrace a spent female apparently without discerning the condition of its mate.

The tenacity of the embrace may be very pronounced. Mated pairs captured afield have seldom broken, however handled. They have withstood journeys of 2 or 3 miles without separation. They can be fixed *in copula* by the slow addition of chloral hydrate. Once, in its absence, with NaCl and chloroform such a preparation was made, though the male relaxed slightly. Because of the short period of

embrace, the mortality of females is low. Only once have we recorded a mated pair dead in the embrace.

For the first few years of our investigation the wood-frog males were regularly isolated or kept with females of the same species, thus precluding any chance of cross-embraces with other species. For the last two years more opportunity was given for this phenomenon. A male placed in the common frog and salamander jar seized a female *Rana palustris* and would not release until its hold was forcibly broken. Another embraced a male *Rana pipiens*, but not with much vigor. A wood-frog embraced a female *R. clamata* normally and abnormally. In the latter instance it seized the female with venters apposed and with his forearms in front of those of the female. In another instance, another male of *R. sylvatica* embraced normally a half-grown green-frog. Cross-embraces would ensue with females of other species of *Rana* if an opportunity were afforded. Of abnormal embraces, we have one peculiar record noted March 30, 1907. A male had accidentally been put in the *Ambystoma* jar and soon had one of the salamanders in his embrace. The salamander repeatedly swam around and around in the jar, but the embrace was too tenacious for it to disengage the frog. This embrace was continued for an hour or more and was just in front of the hind limbs. To make doubly certain, another vigorous male was placed in the jar, and in the evening of the same day (March 30) a second record of the same phenomenon was recorded. On April 21, 1913, another male in the laboratory was observed embracing an *Ambystoma* just back of the fore legs.

#### THE OVULATION.

For spawning, this species usually chooses still water, rarely the backwaters or bayous of streams. It prefers the leaf-laden ponds and transient pools of wooded districts, though not wholly restricted to such localities. Occasionally we have seen the frogs migrating to swampy cat-tail stretches for spawning and have both observed and heard them in such situations. Two of our best collecting-spots were a grassy pool and a high upland pond, both of which were out in the open and ordinarily dried up in midsummer. In wooded districts we have found them even using pools no more than  $1\frac{1}{2}$  by 4 feet. Our first records of wood-frog spawning have been as shown in the above table.

Max. temp. day previous.	Date of first ovulation.	Max. temp. of date.
°F.		°F.
43	Apr. 14, 1900	47
54	Apr. 13, 1901	60
49	Apr. 6, 1902	54
68	Mar. 19, 1903	75
45	Apr. 5, 1904	54
56	Apr. 4, 1905	70
45	Apr. 6, 1906	41
70	Mar. 28, 1907	69
43	Apr. 1, 1908	48
59	Apr. 12, 1909	69
51	Mar. 27, 1910	62
58	Apr. 8, 1911	47

For the day previous to the record, we find no maximum air-temperatures below 43 degrees and an average of 53 degrees; for the day of the record, a low temperature of 41 degrees and an average of 58 degrees. Each record is flanked on one side by 45 or more. It appears that when the air-temperatures begin to approach 43 to 45 degrees, we may expect the frogs to lay eggs. An average date of spawning would be about April 4; our earliest record is March 19, 1903; our latest first record, April 14, 1900. In general, wood-frogs spawn most in the first half of April, though occasionally earlier or later in some years.

In some early springs, usually the last of March, the spawning begins with a rush and the species may be practically through laying within 4 to 6 days after the beginning of ovulation. In 1907 and 1910, we had good illustrations of this condition in the eight or nine localities under observation. A summary of the egg-complements for these years follows:

Date.	No. of bunches.	Date.	No. of bunches.
1907.		1910.	
Mar. 28	3	Mar. 26	1
Mar. 29	30	Mar. 27	2
Mar. 30	32	Mar. 28	12
Apr. 2	1	Mar. 29	29
Apr. 25	1	Mar. 30	13
		Mar. 31	13
		Apr. 1	1
		Apr. 30	1

In these instances, as in many others of early spawning, the bulk of egg-laying may be completed by April 1 and then 3 to 4 weeks may intervene before a stragglng record appears the latter part of April. Our latest records for spawning are: April 27, 1906, when no eggs were laid for two weeks previous; April 25, 1907, 23 days interval; April 24, 1908, no interval; April 30, 1910, 29 days; April 20, 1911, no interval. It will be observed that in 1908 and 1911 no intervals are recorded; in each of these the spawning began later in April. In 1908 it began April 1 and continued to April 24; in 1911 it started April 6 and ran continuously to April 20. In each, inasmuch as the spawning begins later, it bridges the mid-April gap, which appears in the earlier spawning seasons of this species. Furthermore, when the species begins late the continuous spawning record is stretched over two or three weeks instead of one, as in the earlier seasons.

In 1908, we began taking water-temperatures to determine the effective warmth necessary to start and to bring to a crest the spawning. In four different ponds, the species gingerly began at 41 degrees. When the water ascended to 48 degrees several records came, but it reached the crest in three different localities at temperatures of 53, 54, and 58

degrees. Thereafter, the temperatures were below 52 degrees, with one exception. An average of 22 water-temperatures for this year gives 48 degrees. In 1910 the species began at a water-surface temperature of 57 degrees or water-bottom record of 50 degrees. When the spawning reached the crest, these were respectively 60 and 59 degrees. From the crest onward to end of spawning the water-surfaces ranged from 55 to 68 degrees; the water bottoms, from 53 to 60 degrees; the averages for the whole season were water-surfaces 60 degrees, water-bottoms 56 degrees.

In 1911, the water-surfaces averaged 53 degrees, the water-bottoms 51 degrees; the crests in three ponds came at 50, 51, 70 (water-surfaces) and 48, 51, 67 degrees (water-bottoms) respectively. In this year maximum and minimum records were kept, and no minimum below 42 degrees was recorded, the maxima ranging from 44 to 62 degrees, the average being 54 degrees. A grand total of all our water-surface and water-bottom records show averages of 56 and 53 degrees respectively.

To recapitulate: When the maximum air-temperatures reach 41 to 43 degrees, or average 53 to 58 degrees, we may go out with some expectation of finding the wood-frogs spawning, provided the water-temperatures are at least 41 to 48 degrees. At the latter temperature the spawning reaches its height usually at about 53 to 60 degrees.

#### THE EGG-LAYING PROCESS.

Most of the egg-complements are laid at night, yet we have frequent instances of day-laying, both in the laboratory and in the field. In the former they have laid throughout the day; in the field we have numerous indications of it. According to our record, day-laying in the field seems to occur in the early morning or late in the afternoon. On April 10, 1911, between 12<sup>h</sup> 30<sup>m</sup> and 8 p. m., a fully expanded bunch was found which must have been laid before 7 p. m.; on March 28, 1907, a pair was observed leaving an egg-mass at 8 a. m.; and on April 6, 1908, a female was beginning laying at 11<sup>h</sup> 30<sup>m</sup> a. m.

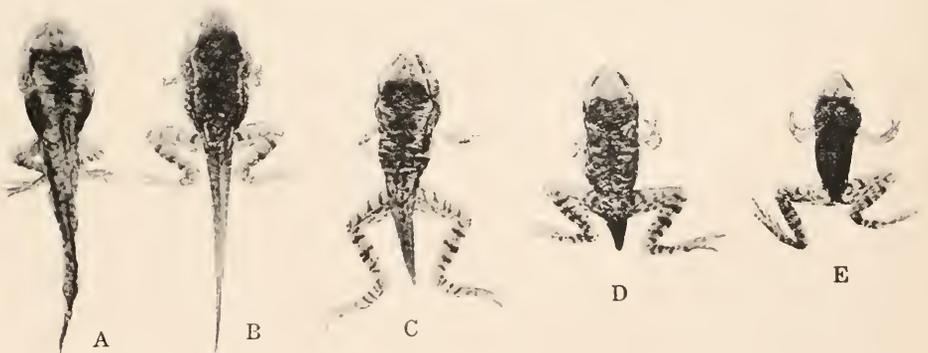
This species is gregarious at this season. Where the first bunch of eggs is laid, one is quite certain to find others depositing their complements later. In this way the whole egg-content of a large pond may frequently be massed in a small limited area (Plate XXI, Fig. 1). In 1906 one area of 6 bunches was recorded. In 1907 (March 29) there were 10 bunches in an area 8 by 8 inches; about a foot north was another area of the same dimensions with 8 bunches; on the subsequent day the interval was filled with 10 more, thus making 28 bunches in an area 28 by 8 inches. In one instance, one bunch of eggs was found and a stake was driven near it as a marker; the next morning it was hardly to be seen, for 9 new masses had been laid about it. In 1908, on April 8, an area 18 by 10 inches possessed 37 bunches. In another pond, on April 13, one small *Alisma* plant, not yet above the water's surface,



1



2



3

WOOD-FROG (*RANA SYLVATICA*).

1. An egg-area in a pond filled with dead sticks and leaves.
2. An adult wood-frog.
3. A series of wood-frogs from tadpole to the transformed wood-frog. Dorsal aspect.  $\times 1$ .



had 16 bunches attached to it. In 1910, in still another locality, 22 bunches were recorded in one small area.

We have found that to capture mated pairs it is best to watch the area about the first bunch of eggs deposited in a pond. Most of the numerous pairs taken were thus secured. They are often under cover near the egg-area or at times directly beneath the masses. Our best record of captures may serve to show how fruitful such search can be. On April 6, 1908, under and above the sedge area which two days later had 37 bunches, six pairs of mated frogs were captured.

The time consumed in the laying is quite short. On April 27, 1906, a gravid female was taken and at 11<sup>h</sup>30<sup>m</sup> a. m. was placed with two males. By 1<sup>h</sup>30<sup>m</sup> p. m. it was mated. At 2<sup>h</sup>30<sup>m</sup>, when I left the laboratory, there were no eggs. At 3 o'clock, upon return, a whole bunch was found, thus taking 30 minutes or less in the laying. Since this record (our first evidence) we have found that 5 to 10 minutes suffice for the process.

Of the egg-laying position and process, we have three observations. At 7<sup>h</sup>35<sup>m</sup> a. m., March 28, 1907, I found a horizontal tuft of grass with a bunch of wood-frog's eggs. Upon closer examination a mated pair was discovered near the attachment of the blade, evidently in the egg-laying act. After a minute or so, they became uneasy and suddenly attempted to escape. The blade was perfectly horizontal and the female was resting on it, not holding it. The bunch they laid was the second on the stem. At 7<sup>h</sup>45<sup>m</sup> I left and returned again at 10<sup>h</sup>30<sup>m</sup> a. m. When about to take this second bunch, another mated pair was detected directly beneath the blade. On the following day, in another pond, another favorite position was noticed. A mated pair was lying on top of the bunches of one of the egg-areas already described, and from the restless movements of their legs they were evidently ready to begin laying; this process is not rapid at first. Probably, as with some of the other frogs, a few eggs may be extruded and then a short interval may pass before the rapid ovulation of the bulk of the complement comes. For example, on April 6, 1908, when a rapid rush was made on an area containing 17 bunches, it was observed that a mated pair had been frightened from the top of the egg-area. About the vent of the mated female were 15 fresh eggs, the beginning of ovulation to which reference has already been made.

We have long suspected that the female *R. sylvatica*, as with other species of *Rana*, might lay without attendant males. At 8<sup>h</sup>45<sup>m</sup> p. m., March 30, 1910, a female was captured near the edge of a pond. It was on its way to the water. In the laboratory it was placed with a spent female. Three days later it laid a whole complement, with no males near it, much less mating with it. Evidently, when captured, the female was on the eve of laying, as we believe is true of all the females of this species the minute they reach the ponds.

## THE EGGS.

The eggs may be deposited near or a few feet from the edges of our ponds, or in the middle of the pond (Plate 1, Fig. 2H). They are usually attached to grass stems, weed stalks, twigs, brush, or rarely resting free on the bottom. In this species the egg-bunches tend to be attached more than in *Rana pipiens*. Sometimes, but rarely, we secure wood-frog and meadow-frog masses on the same twig, yet they may be breeding simultaneously and in the same pond. The egg-mass at the time of laying may be an inch in diameter. In the case of the mated pairs of April 27, 1906, and March 28, 1907, the egg-bunches measured an inch in diameter just after laying. Within 2 or 3 hours the bunches had assumed their normal diameters. Freshly laid masses are always very bluish in tinge. The egg-bunch is globose,  $2\frac{1}{2}$  to 4 inches in diameter. In many hundreds of wood-frog bunches, only once (April 12, 1911) have I recorded the plinth form of egg-mass, as in *Rana pipiens*.

The eggs are usually found in shallow water, 6 inches to 2 or 3 feet deep, though occasionally egg-records have been made in greater depths. Furthermore, I have found quite a pronounced tendency on the part of this species to lay near the edge of the pond. As a consequence, not infrequently in larger ponds, when very warm weather follows the greater bulk of ovulation, many egg-masses are left high and dry; such a condition is also not unusual in some of the smaller pools in the wooded districts. A far more serious source of danger is freezing. Most of the bunches are laid from  $\frac{1}{2}$  to 2 inches beneath the water's surface. In many instances, long before the hatching period approaches, the tops of these complements appear at the surface because of the reduction of water-level by rapid evaporation. In 1907 (April 11) the tops of exposed masses in two ponds were frozen in a crust of ice and spoiled. The following year, on April 17, in another pond, a thin, transparent crust formed, which was sufficient to kill the upper part of several bunches. In all the cases observed, however, the lower portions not caught within the sheet of ice have progressed nicely in development.

The eggs of *Rana sylvatica* are to be confused only with those of *R. pipiens* (Plate xx, Fig. 2). In the former the egg-mass is globose; in the latter it is plinth-like. In *R. pipiens* the middle envelope is evident to the naked eye, but not in *R. sylvatica*. The eggs of *R. sylvatica* are freer and the outer envelope of each egg keeps its spherical form better than in *R. pipiens*, where the eggs are closer together and have smaller outer envelopes as well as vitelli.

The outer envelope ranges from 5.2 to 9.2 mm. in diameter, rarely below 5.4 mm. or above 8.0 mm.; the usual range is 5.8 to 7.0 mm.; the average is 6.4 mm. The indistinct middle envelope is 3.6 to 5.8 mm.; the usual range is 3.6 to 4.4 mm.; the average is 3.8 mm.; the mode is 3.6 mm. The vitellus is 1.8 to 2.4 mm., rarely exceeding 2.2 mm.; the average is 1.9 mm.; the mode is 2.0 mm. The vegetative pole is white, the animal pole black or deep brownish (Text-fig. 1n).

## THE HATCHING PERIOD.

On March 29, 1907, eggs were laid in three ponds; the first, a shallow exposed pond which dried up June 28; the second, deeper, also exposed, which dried up the last of August; the third, a deep, heavily-shaded, permanent pond. A bunch laid in one of these ponds March 29 was brought into the laboratory April 1, and in a temperature of 66 to 70 degrees hatched within  $4\frac{1}{2}$  or 5 days from first deposition. At the same time (March 29) a mated pair laid a bunch of eggs in the laboratory. These hatched under the above temperatures in  $4\frac{1}{2}$  days. On April 10 the eggs of the three ponds had the tops of the bunches frozen and thus killed. From April 6 to 21 the average maximum air-temperature was 39 degrees, the average minimum was 28 degrees, at no time above 46 degrees. On April 22, 24 days after deposition, the eggs in the two exposed ponds were hatched, while those in the shaded pond did not hatch until several days later.

In 1908 *R. sylvatica* began laying first in the second and third ponds above mentioned. Often, however, the species lays first in the third pond, which is spring-fed, opens earliest, and is least responsive to air-temperatures. In the third pond, the species began laying on the 2d of April at a water-temperature of 41 degrees. From April 3 to 5 the pond was covered with ice. April 6, ovulation became more brisk. From April 6 to 22 the water averaged 44 degrees. On the 23d the water-temperature jumped to 64 degrees, and by the 25th the eggs were hatching, 23 days after extrusion. In the second pond, egg-laying began April 1, at a water-temperature of 41 degrees. Then came ice, as in the third pond, until April 6, when the bulk of ovulation occurred. Thence onward, to April 23, the water averaged 47 degrees, 3 degrees higher than in the third pond, and the eggs hatched on this date, 22 days after deposition. In the first pond the species began April 6 under 58 degrees, the water averaged 50 degrees until April 23, the day of hatching, which came 17 days after extrusion. In the laboratory, from April 6 to 8, several pairs laid, and these under temperatures from 65 to 72 degrees hatched in 6 or 7 days.

In 1909, in the second pond, the eggs hatched in 23 days. In 1910, in the third (spring-fed) pond the eggs hatched in 17 days under water-surface temperatures from 50 to 67 degrees, the average was 58 degrees; temperature of water-bottoms 46 to 61 degrees, average 53 degrees. In the first pond they hatched in 14 or 15 days, the maximum air-temperatures ranging from 43 to 81 degrees, average 61 degrees. The water-surface records were 52 to 73 degrees, average 63 degrees; the water-bottom temperature was 49 to 63 degrees, average 54 degrees. In the second pond one bunch, laid March 27, hatched April 3, only 7 days after deposition. The weather was very uniform and the temperatures were: maximum air-temperatures 62 to 80 degrees, average 70 degrees; surface-temperatures 56 to 68 degrees, average 61 degrees; water-bottoms 56 to 64 degrees, average 59 degrees. The bulk of the

oviposition, however, came March 28 and 29, and all these hatched in 11 or 12 days, April 9. The range of maximum air-temperatures was 43 to 80 degrees, average 66 degrees; water-surfaces 52 to 68 degrees, average 61 degrees; water-bottoms 48 to 64 degrees, average 59 degrees; range of maximum water-temperatures 67 to 80 degrees, average 73; minimum water-temperatures 50 to 71 degrees, average 61.

In 1911 the eggs hatched in 17 days in the spring-fed pond, where the maximum water-temperatures averaged 54 degrees, the minimum 44 degrees, the surface 50 degrees, and water-bottom 48 degrees. In another pond (under an average maximum of 57 degrees, minimum 44 degrees, water-surface 53 degrees, water-bottom 51 degrees) they hatched in 13 days. Finally, in the second pond above, a maximum average of 63 degrees, minimum of 51 degrees, water-surface of 55 degrees, water-bottom of 54 degrees, brought the ova to hatching in 13 days. In the first pond (under a minimum of 48 degrees, the surface 54 degrees, bottom 50 degrees) the eggs hatched in 14 days.

It would appear that with average water-temperatures of 44 to 50 degrees the eggs usually hatch in 24 to 17 days; with temperature of 50 to 60, in 17 to 7 days; with temperatures of 60 to 70, in 7 to 4½ days.

#### THE MATURE TADPOLE.

Length of body 1.5 to 2.2 in length of tail, average 1.8. Width of body in its own length 1.3 to 1.58, average 1.41. Nostril equidistant from eye and end of snout. Eye equidistant (sometimes nearer the snout) from spiracle and from snout. Distance between nostrils in interorbital space 1.7 to 2.9, average 2.5, seldom under 2.0; in mouth 1.1 to 1.9, average 1.72. Spiracle sinistral, 1.5 to 2.0 nearer base of hind legs than snout, average 1.73, rarely reaching 2.0 or under 1.7. Anus dextral. Depth of tail in its own length 1.9 to 3.1, average 2.5. Depth of muscular part of tail in depth of tail 1.75 to 2.8, average 2.47, rarely below 2. Mouth contained 1.36 to 2 times in interorbital space, average 1.62. Greatest length 47.2 mm. Greatest length of body 17.2 mm. Greatest length of tail 33 mm. Greatest depth of tail 13.8 mm.

*Coloration of body* (Plate IX, Fig. 1J.): Background of back and sides greenish black marked with fine gold and with a few orange spots; also with iridescent areas, particularly on the sides, giving the whole a dark greenish-brown appearance. *A cream line extends along the upper jaw.* The venter has a cream ground; belly slightly pigmented at the sides; gill region quite heavily pigmented, but overlaid with silver spots; throat region a lavender gray with fine dark and silver spots; the whole venter iridescent, giving the belly a distinct pinkish bronze appearance. Iris of eye bronze. Tail somewhat lighter than body, the pigment graded evenly over the muscular portion and crests, but as a whole darker above; small gold spots are scattered over the surface, some of which become iridescent.

*Mouth-parts* (Plate VIII, Fig. 5.): The upper lip has the customary fringe of teeth on the boundary. Beneath this, on either side, are two rows, the first being more lateral to the mandible than in the other four species of *Rana*. The lower lip contains four labial rows, which are more wavy than in the other four species of *Rana*. In 44 specimens, eight were found with 3 lateral rows on each side of the upper lip, *i. e.*, three besides the upper lip fringe; in three or four instances there were three lateral rows on one side, and in one instance one of these was subdivided. In the lower lip the fourth row is rarely absent; the second is sometimes discontinuous in the middle, the first discontinuous in one-half of the specimens.

#### THE LARVAL PERIOD.

The development period lasts about 90 days. In 1906 the first eggs were laid April 16; 93 days later (July 8) our first transformed examples were noted. Eggs laid March 29, 1907, in three different ponds, developed and larvæ transformed in 91 days in a shallow transient pond (dried up June 28); in 97 days in another exposed pond (dried up the last of August); in 115 days in a deep, heavily-shaded, spring-fed, permanent pond. The true larval periods were, in these three instances, 67, 73, and 85 days respectively. In 1908 the periods from eggs to transformation were 96 days (73 days of larval life) and 95 days (74 days of larval life). In 1911, in one pond, only 61 days intervened between eggs and transformation, 44 days of larval life; in a second pond, the interval was 75 days or 62 days as larvæ; in a third, 78 days or 62 larval days. As larvæ, the periods range from 44 to 85 days with an average of 67 days; from eggs to transformation the periods are 61 to 115 days, the average being 89.

#### THE TRANSFORMATION.

Transformation begins about the first day of July. In 1906 the first record was July 8; in 1907, June 28. The first record for 1906 (July 8) was for a spring-fed, permanent, deep pond, where this species in 1907 did not begin to transform until July 22, and this lasted until August 1. In 1907, in another pond, transformation began June 28 and the species was recorded as transforming there for a period of 11 days. In 1908 the species began to transform July 6 in two ponds, and so continued until July 21. In 1911 we have our earliest record of transformation, namely, June 8. An interval of 19 days elapsed before the species began transformation in the other ponds. Thus we see that transformation may begin as early as June 8 or extend to August 1. An average of first dates for several years gives June 27, or approximately July 1.

The size at transformation of 139 specimens varies from 12 to 21 mm., rarely over 19 mm.; the average is 16 mm., the mode is 18 mm. (Plate X, Fig. 4.)

## THE AUTUMNAL DISAPPEARANCE.

This silent species is not often recorded in autumn. Our late records are mostly in the month of October, the latest being October 30, 1905. Through midsummer (including first weeks of September) one occasionally comes upon this form in the woods in much lighter livery than in the early spring. Thereafter, it begins to think of its winter quarters, and by the last of September or first of October it seeks cover. We have found it in wooded ravines under stones, beneath boards in a wooded sphagnum area, under boards in the vicinity of a sawdust pile near the woods, in stumps and kindred places—never, so far as our experience goes, in water.





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