NOVEL ASPECTS OF THE LIFE HISTORY OF TWO AMBYSTOMAS[1]

W. Leslie Burger
University of Illinois, Urbana, Illinois

Certain phases of the life history of *Ambystoma tigrinum nebulosum* Hallowell and *Ambystoma texanum* (Matthes) that have come to my attention seem to be worthy of note. This opportunity is taken to report on both species though observations concerning the former were made on the west slope of the Rocky Mountains during the summer of 1946 and those concerning the latter were made in east central Illinois in the spring of 1948.

I am indebted to Dr. A. O. Weese and Dr. J. C. Johnson, president and director, respectively, of the Rocky Mountain Biological Laboratory, for assistance in the study of the first species. Thanks are also due to Robert Haas, Max Hensley, Arthur Flechsig and Robert Reese, graduate students in the Department of Zoology of the University of Illinois, for companionship and assistance in the field while I was observing the second species. Dr. Hobart M. Smith first called the alga-egg relationship in *Ambystoma texanum* to my attention. For his assistance throughout the preparation of this paper I owe him a special note of thanks.

Ambystoma Tigrinum nebulosum Hallowell

During the six week session (July 10-August 20, 1946) of the Rocky Mountain Biological Laboratory, specimens of *Ambystoma tigrinum nebulosum* were found in abundance in the vicinity of Gothic, a ghost mining camp seven miles north of Crested Butte, Gunnison County, Colorado. A general ecological survey revealed that the major aquatic habitats of the area fall logically into seven types: (1) flowing water, (2) glacial kettle ponds, (3) beaver ponds, (4) cattle "tanks," (5) oxbow ponds, (6) natural lakes, (7) artificial lakes. Of the 75 bodies of water searched, *A. t. nebulosum* was found in 17 which included only three of the habitats: glacial kettle ponds, beaver ponds, and natural lakes. The specimens found fall into three age groups: young larvae, advanced larvae, and adults. Examination of the distribution of the different combinations of age groups in the aquatic habitats suggests an interesting situation.

A total of three natural lakes, 16 glacial kettle ponds, and approximately 50 beaver ponds were examined for salamanders. The frequencies of occurrence in these habitats (*i.e.* the number of instances of a habitat in which *A. t. nebulosum* was found divided by the total number of examples of that type of habitat examined) seem to have some significance. Glacial kettle ponds with a frequency of .63 seem to be the favorite present habitat, at least of larvae. The five glacial kettle ponds in which larvae were not found were practically filled

[1]Contribution from the Rocky Mountain Biological Laboratory and the University of Illinois Museum of Natural History.

by vegetation. Beaver ponds (frequency .10) seem usually to be too cold for salamanders because of the steady flow of water. Natural lakes (frequency .33) may have once furnished many suitable habitats for *A. t. nebulosum,* but most of the natural lakes in the Gothic area have been stocked with trout, which cause the extinction of the salamander.

The variation of altitude (8,000-10,000 feet) of the habitats in which *A. t. nebulosum* was found seemed to have little effect. However, nearby Emerald Lake with an altitude of approximately 11,500 feet is said to have contained only neotenic salamanders of this species, before it was stocked with trout in 1928. Whether or not the neotenic condition was caused by factors related to the higher altitude can only be surmised.

TABLE 1. *Age composition of A. t. nebulosum populations in the aquatic habitats investigated**

Groups in Pond	Glacial Kettle Ponds	Beaver Ponds	Natural Lakes	Total
Young larvae	5	2	0	7
Young and advanced larvae	0	0	0	0
Young larvae and adults	2	1	0	3
Young, advanced larvae, and adults	0	0	0	0
Advanced larvae	3	2†	0	5
Advanced larvae and adults	1	0	0	1
Adults	0	0	1	1
Total	11	5	1	17

*The figures refer to numbers of each kind of pond or lake in which the different combinations of larvae and adults were found, not to numbers of specimens. Large samples were collected in all cases indicated.

†In one beaver pond containing advanced larvae, a single young larvae was found.

The fact that there were two distinct size groups of larvae suggests that larval development requires two years and that the two groups represent first-and second-year larvae. This hypothesis is based primarily on the supposition that only a prolonged period of winter dormancy would bring about such a cleavage into age groups. The short growing season is less than two months, making the hypothesis quite credible.

In the laboratory, second-year larvae fed readily on first-year larvae while cannibalism was not noted within either age group. Furthermore, first-year larvae were found in the stomachs of a number of second-year larvae shortly after they were collected, but only one first-year larvae was collected alive in a pond containing second-year larvae (see footnote, Table 1). The exclusiveness shown in the distribution of the two age groups (Table 1) coupled with the cannibalistic tendency of second-year larvae suggests that each pond produces a crop of emerging larvae (subadults) on alternate years in spite of the fact that presumably adults breed every year in suitable ponds. The larvae of alternate years seem to serve as food for those remaining in the pond from the preceding year. The course of events in a specific pond would be as follows: (1) adults breed in a pond; (2) the resulting brood of larvae develop partially the first season and pass the winter, probably in the mud at the bottom of the ponds; (3) adults breed in the pond the following spring, but (4) the second-year larvae feed on the young larvae apparently eliminating the young brood completely; (5) the second-year larvae, apparently developing much more rapidly the second season than the first, emerge in late summer. The next spring when adults breed in the pond there are no larvae from the preceding year, so the cycle is repeated. Second-year larvae collected after July 28 showed signs of losing their gills, and after August 10 none could be found in the ponds. At this time the smaller first-year larvae were still to be found in their ponds.

This cannibalism is perhaps similar to the phenomenon described in the tadpoles of several species of *Scaphiopus* by Ball (1936) and Bragg (1946). Cannibalism seems to arise in these forms under a special combination of conditions including warm water, inadequate food, and crowding, in which case it is presumed to favor survival.[2] It will be of great interest to see whether further data comfirm the present inferences and, if so, how general and how varied is this special sequence of larval development of *A. t. nebulosum* under different conditions of altitude and latitude.

The stomachs of second-year larvae contained dragonfly nymphs, leeches, *Dytiscus* (diving beetles), and tadpoles of *Rana pipiens* and *Bufo boreas,* in addition to first-year larvae of *A. t. nebulosum*. The principal item in the stomachs of adults was the pond snail, *Lymnaea stagnalis*.

AMBYSTOMA TEXANUM (MATTHES)

During the spring of 1948, I had an opportunity to observe the breeding of *Ambystoma texanum* in an area known as Busey's Pasture on the northern edge of Urbana, Champaign County, Illinois. Busey's Pasture is an open mesic forest through which wind several long oxbow ponds, remnants of the former course of the west branch of the Salt Fork of the Vermillion River (Wabash River drainage). The ponds are shallow, seldom exceeding a yard in depth, with

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[2]A somewhat similar cycle of effective broods due to cannibalism has been reported by Thompson (1941, p. 209) for crappie.

debris from the trees that line the water's edge covering the bottom in most places. A large amount of plant and animal life is supported by the ponds in spite of the fact that the surrounding area is very much disturbed and that the ponds are not permanent. Portions of the area serve as a junk yard and trash is dumped into the ponds at several places.

When Busey's Pasture was visited for the first time in the spring, on March 4, during a short warm spell, ice was still present in the center of the ponds and the ground was frozen except on the very surface. Several hours search at night by gasoline lantern revealed only one adult *Ambystoma texanum,* under a log at the water's edge. Soon after this visit there was a heavy snow and the weather turned severely cold.

The weather began to warm up again about March 14. After a brief shower (from 10:00 to 11:00 P. M.) on March 18 another visit was made to the area, and breeding was found to be well under way. Individuals of both sexes of *Ambystoma texanum* were abundant in the ponds. Spermatophores were found here and there in groups on leaves, twigs and branches in water from six to 18 inches deep and within a distance of approximately three feet of the shore. Around logs, submerged branches, and other cover were large concentrations of spermatophores. Beside a large log several feet from the shore of one of the ponds there was an aggregation of approximately 20 adult salamanders milling about in an area of less than two feet square. When disturbed by our light, they scattered, and the side of the log and leaves and twigs in the vicinity were seen to be covered by spermatophores. Apparently breeding was in its early stages for, while spermatophores were very abundant, only three masses of eggs could be found. When the ponds were visited again the next night, which was clear, spermatophores were still in evidence, but the communal activity observed the night before had apparently ceased. Active egg laying had not begun.

The ponds were not revisited until March 30 when a trip was made during the day. Eggs had been deposited in the same situations as the spermatophores, with concentrations in the same places. There were a large number of egg masses on the side of the log where the breeding aggregation had been observed on March 18. A few masses of freshly laid eggs remained.

In a portion of one of the ponds, which had not been previously visited, there was a great concentration of egg masses around the base of a clump of willows about 10 feet from the edge of the pond. The egg masses formed almost a solid mass around the base of the willows to which they were attached like clusters of small grapes. In this area of less than one square yard it was estimated that there were at least two solid cubic feet of *Ambystoma texanum* eggs. The number of eggs in 35 egg masses averaged 11.9 eggs per cluster with a range from 6 to 29. The larger egg masses, perhaps those with more than nine or ten eggs, may have really consisted of several egg masses in close adherence though careful examination gave no indication of this. At the first visit to the ponds in Busey's Pasture on March 10 a few individuals of *Pseudacris nigrita triseriata* were calling. The next night the species was in full chorus. When the ponds were again visited on March 30, masses of *Pseudacris* eggs were scattered among the masses of *Ambystoma* eggs in much smaller numbers.

The egg capsules of *Ambystoma texanum* are composed of two layers of gelatinous material which are perfectly clear for a time after the eggs are laid, but the egg envelopes soon take on a greenish tinge. By the time of hatching, the egg capsule was usually so clouded with green that the enclosed embryo was scarcely visible. The green color was caused by a unicellular green alga which seems to be the same as that described by Gilbert (1942) in the egg envelope of *Ambystoma maculatum.* Gilbert (1944) described experiments in which the alga-egg relationship was proved to be symbiotic, benefiting both the algae and salamander embryo. It was demonstrated that the embryo has a more rapid rate of development in the presence of the algae, presumably because of the increased oxygen supply. Furthermore, the algae were found to grow vigorously in the egg sheath in the presence of an embryo, presumably because of the carbon dioxide and nitrogenous wastes, but grew poorly when the embryo was removed. Gilbert (1942) also reports algae as regularly present in the eggs of *Ambystoma jeffersonianum.*

There is some evidence that the alga-egg relationship observed in *Ambystoma texanum* is also symbiotic. This evidence may be summarized as follows:

1. Egg masses in shady parts of the ponds did not develop the typical algal growth and had a high percentage of mortality caused by an unidentified water mold. There is a possibility that the absence of algae contributed to the susceptibility of the eggs to infection with water mold.
2. Egg masses were brought into the laboratory and divided into two portions, one of which was kept in the dark and the other in sunlight. There was no significant difference in the rates of development, but failure to control the temperature makes the results of this experiment inconclusive. In egg masses kept in the dark there was the same high mortality from water mold as had been observed in shady portions of the ponds in Busey's Pasture.
3. Another experiment demonstrated that algae failed to develop within egg capsules from which the embryo had been removed. The algal growth on such egg masses was on the external surface only.
4. The great similarity of the structure of both egg and spermatophore and the breeding habits of *Ambystoma texanum* to those of *Ambystoma jeffersonianum,* as described by Smith (1907, 1911), and to those of *Ambystoma maculatum,* as described by Breder (1927), suggests similarity in other aspects.

The egg-alga relationship has thus far been conclusively demonstrated to be symbiotic only in *Ambystoma maculatum.* The above evidence does not conclusively indicate that the relationship is symbiotic in *Ambystoma texanum,* though such is strongly indicated to be the case.

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NEWS OF TENNESSEE SCIENCE

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the Biology Division on "Experimental Radiation-Induced Hormone-Secreting Ovarian Tumors; Adenocarcinoma with Hypervolemia."

On July 5, Dr. Max Delbruck, a former Tennessee resident, and Professor of Biology at the California Institute of Technology, presented a special seminar in Oak Ridge on the subject "Problems in Bacterial Viruses."

Recent Publications by Tennessee Authors

Aebersold, P. C. (AEC, Oak Ridge). 1949. Isotopes: Their distribution and use. *Sci. Monthly*, 69 (6) : 349-359.

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