Ontogenetic Changes in Phototactic Behavior of *Ambystoma tigrinum tigrinum* (Amphibia: Urodela)

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Abstract

Phototactic behavior was studied for five different developmental stages of the tiger salamander, *Ambystoma t. tigrinum* (Green). Specimens from a vernal pond in Indiana were given the choice between a light or dark chamber. Chi squares were significant ($P < .01$–$.005$) for positive phototaxis for three stages of the aquatic larvae. The two terrestrial stages of specimens collected immediately after metamorphosis and adults were significantly photonegative ($P < .005$). The difference in phototactic behavior between aquatic and terrestrial stages is probably related to environmental factors influencing development and survival of *A. t. tigrinum* in these habitats. The photopositive orientation of the larvae may be an adaptation for increasing developmental rate by orienting the larvae to the warmest parts of the pond. The photonegative newly metamorphosed individuals and adults are fossorial and nocturnal.

Introduction

Phototactic orientation has been noted in various species of *Ambystoma*. Photopositive orientation was observed in the larvae of *A. maculatum* (15) and in the larvae (6) and adults (11) of *A. ordinarium*. Negative phototaxis was observed in the older larvae of *A. opacum* (9) and in the young larvae and adults of *A. macrodactylum croceum* (1, 3).

Reversal of phototaxis has been found during ontogeny of two species of *Ambystoma*. Anderson (3) found *A. macrodactylum sigillatum* to be photopositive in the larval stage reversing to negative phototaxis at metamorphosis. Marangio (11) found *A. opacum* to be photopositive in early larval stages reversing to photonegative orientation with the development of hindlimbs.

The phototactic behavior of *A. tigrinum* (Green), the widest ranging species in the genus, has never been studied. There are seven subspecies in North America, and the subspecies in Indiana, *A. t. tigrinum*, occurs throughout most of the eastern United States exclusive of the Appalachian highlands (10). Many authors have noted that adult *A. t. tigrinum* are nocturnal and fossorial (7, 12, 13, 16), and field studies by Dineen (8) and Anderson and Graham (5) indicate that the larvae are active at night. It was the purpose of this study to conduct laboratory tests on the phototactic behavior of larval, newly metamorphosed and adult individuals of *A. t. tigrinum* from a temporary pond in Indiana.

Materials and Methods

Eggs, larvae, newly metamorphosed individuals and adults of *A. t. tigrinum* were collected in 1976 from a vernal pond in St. Joseph County, Indiana. Eggs were kept at 12 C until Harrison stages 44-45 (14). The temperature was then raised to 16 C and larvae hatched within four days. These newly hatched larvae and all other salamanders collected were kept in aquaria in an incubator with a constant temperature approximating the temperature of the pond at the time of collection.

Chambers used for testing all salamanders except newly hatched larvae were modified from three 26 X 50 X 30 cm aquaria. Two of the aquaria were control chambers, and the remaining aquarium was the test chamber. In the center of each aquarium was a 15 X 18 cm open ended can with a 5 X 8 cm opening cut into the base on either side. Glass dividers, 6 X 17 cm, extended from the can to the sides of the aquarium. These pieces were secured with aquarium sealer, and the entire apparatus was painted opaque black.

The aquaria were supplied with pond water and placed beneath two 40 W fluorescent lights with approximately 125 FC of light reaching the water surface. One side of the test chamber was covered with a heavy cardboard lid for the dark condition while the other side was left exposed to the light source. One of the control chambers was covered entirely and the other left completely exposed.

The newly hatched larvae were tested in three smaller aquaria, 27 X 19 X 10 cm. Each aquarium was divided in half by a 19 X 10 cm piece of glass raised 1.5 cm from the bottom to allow a space beneath the divider for placing the specimen to be tested. These aquaria were painted and set up in the same manner as the larger chambers.

Specimens tested were classed according to their developmental stage. Adults (83-114 mm snout-vent length) were collected and tested during the breeding season in early March. Newly hatched larvae (14-17 mm SVL) were tested within one week after hatching in mid-April. Intermediate larvae (18-38 mm SVL), characterized by developed forelimbs, were collected and tested in mid-May. Large larvae (36-62 mm SVL), *i.e.*, those possessing developed hindlimbs, were collected and tested in early July. In mid-July the pond began drying and larvae were metamorphosing and emigrating from the pond. Newly metamorphosed specimens (55-64 mm SVL) were collected from pit traps as they left the pond.

Adults, newly hatched and intermediate larvae were tested between 1700-2200 hours. Large larvae and newly metamorphosed individuals were tested between 700-1200 hours. For each trial, the aquaria were supplied with a depth of 3.5 cm of fresh pond water. One animal was placed in each chamber at a time, either within the can or, for the newly hatched larvae, beneath the glass divider. After 18 minutes, the position of the salamander was recorded as either being in the dark or light side of the chamber. The few animals that remained within the can or beneath the divider were disregarded in the computations. At least 20 individuals were tested in all experimental and control situations for each developmental stage. Results were subjected to chi square analysis.

Results

Chi squares were significant for positive phototaxis for the three larval stages and negative phototaxis for newly metamorphosed and adult *A. t. tigrinum* (Table 1). The values of chi-square computed were highly significant when compared with critical values in standard chi-square tables. $P < 0.005$ for all tests except for large larvae in which $P < 0.01$. The controls at all stages were randomly distributed between the two sides ($P < 0.05$-0.001) indicating that the orientation found was not due to factors other than the light variable being tested. Two of the newly hatched larvae and two of the large larvae in experimental chambers did not move to either side and were disregarded in the analyses.

TABLE 1. *Results of light-dark choice tests for* Ambystoma t. tigrinum. X^2 *is the computed chi-square value.* $P < 0.005$ *in all tests except for large larvae in which* $P < 0.01$.

Developmental stage	N	Light	Dark	X^2
Newly hatched larvae	48	36	12	12.0
Intermediate larvae	20	17	3	9.8
Large larvae	28	21	7	7.0
Newly metamorphosed	30	4	26	16.1
Adults	20	1	19	16.2

Discussion

During the year of this study, eggs were laid throughout March and hatched in April. The pond dried completely by the end of July, and a considerable number of large larvae desiccated before completing metamorphosis. In this pond, selection favors larvae possessing adaptations enabling them to develop fast enough to metamorphose during the short period of the pond's existence.

Anderson (2) found that photopositive behavior in larval *A. macrodactylum sigillatum* oriented them to the warmest parts of ponds. *A. t. tigrinum* larvae collected in the daytime for the present study were associated with the warmer, shallower areas of the pond. Anderson (4) found that an increase in ambient water temperature increases developmental rate of *Ambystoma* larvae which experience short growing seasons. Thus, the photopositive orientation we found in *A. t. tigrinum* larvae may be an adaptation for increasing developmental rate by orienting the larvae to the warmest parts of the pond.

Various reports (7, 12, 13, 16) indicate that the terrestrial stages of *A. t. tigrinum* are nocturnal and fossorial. This is consistent with the results that adult and newly metamorphosed individuals in this study were photonegative.

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